

A plant thermometer gene for measuring climate change

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In the past couple of years, there has been an unprecedented interest and documentation in the phenomenon of climate change and its possible impact on the environment. Larger implications of climate change are being discussed at national and global levels in different fora. Global temperature is the main indicator of climate change and an estimated global warming of 12°C in a century will result in widespread changes in the environment and biodiversity. For example, a recent increase in spring temperature in temperate zones has caused accelerated onset of flowering in many plants, despite an unchanged photoperiod environment^{1,2}. Thus, biodiversity and crop productivity are greatly affected leading to complications in food production. However, plants show a greater plasticity in development and response to a range of stresses. Unlike animals which can fight or flight when faced with adverse environments, plants are sessile and have therefore developed regulatory mechanisms to adapt to changing environments by continuously altering their growth, metabolism, reproduction, phenology and overall developmental mechanisms. How plants sense these changes and adapt quickly and accordingly is the subject of intense research worldwide.

Flowering is a major developmental switch in plants, controlled by many cues, including ambient temperature, season, photoperiodicity, light quality, stress and developmental history of a plant. Due to climate change, a number of adaptations have been observed in plants in terms of flowering as a major physiological determinant of evolution. Although many plants have shown a rapid acceleration in flowering time in response to climate change¹, species that do not are going locally extinct at a high rate³. This indicates that phenological responses to temperature change are of high adaptive value. Plants have developed delicate mechanisms to sense changes of even 1°C temperature. Ambient temperature drives the thermal clock which regulates flowering. A molecular understanding of the mechanism of temperature perception will enable us to understand how different species will

respond to further increases in temperature in terms of flowering and productivity, and will be a key step toward breeding crops resilient to climate change. At a molecular level too, flowering is a complex process involving numerous genes and gene interactions. Identification of key genes that regulate flowering in response to temperature changes is important to such breeding and crop improvement.

In *Arabidopsis*, many of the signal inputs from multiple pathways that sense and respond to various environmental and endogenous cues converge on the central floral repressor gene *FLOWERING LOCUS C (FLC)*. The terminal effectors of these pathways controlling *FLC* expression are now known to represent many types of chromatin-modifying factors, including histone acetyltransferases, histone deacetylases, histone methyltransferases, polycomb-type proteins and a putative histone demethylase⁴. Thus, *FLC* serves as a model for how chromatin remodelling and modification can regulate a critical developmental switch. The fundamental repeating unit of chromatin, the nucleosome, consists of ~150 bp of DNA wrapped around a protein particle composed of two copies of

each of the four core histones: H2A, H2B, H3 and H4, which in turn are encoded by multiple gene copies. Besides, eukaryotic genomes also encode variant histones that are deposited independently of DNA replication and serve to functionally specialize or differentiate specific chromatin regions. In yeast, fruit fly and humans, the histone variant H2A.Z is deposited into chromatin by a conserved protein complex known as SWR1, Tip60 and SRCAP respectively. H2A.Z is a key player of chromatin organization which performs many functions (Box 1). In *Arabidopsis*, loss-of-function mutations in two genes encoding putative homologues of components of the SWR1/SRCAP complex, ACTIN-RELATED PROTEIN6 (ARP6) and the Snf2 protein PHOTOPERIOD-INDEPENDENT EARLY FLOWERING (PIE1), lead to premature flowering as a result of reduced *FLC* expression. Repression of flowering requires activation of *FLC* expression by the histone variant H2A.Z (ref. 5).

Additionally, two autonomous flowering pathway genes, *FVE* (a retinoblastoma-associated component)⁶ and *FCA*, are necessary for mediating the ambient temperature response to flowering². *FVE*

Box 1. Role of H2A.Z

- Histone modification and chromatin architecture/reconfiguration.
- Creating unique higher-order chromatin domains poised for transcriptional activation and regulation of gene expression.
- Protection and maintenance of euchromatin.
- Heterochromatin formation.
- Facilitation of the intramolecular folding of nucleosomal arrays while simultaneously inhibiting the formation of highly condensed structures that result from intermolecular association (global chromosomal fibre decondensation).
- Alteration of nucleosomal positioning.
- Establishment of a buffer to *SIR-2*-dependent gene silencing caused by heterochromatin proteins.
- Repair of DNA breaks.
- Assembly of chromosome centromeres.
- Marking 5' and 3' ends of euchromatin.
- Stabilization of chromatin.
- *Caenorhabditis elegans* embryogenesis.
- Activation of promoter by *Htz1* (yeast H2A.Z).
- Serving as an epigenetic memory function by marking actively transcribed regions and providing competence for the reactivation of silenced genes.
- Establishment and maintenance of cell fate during development.

is a homologue of the mammalian retinoblastoma-associated protein, a component of a histone deacetylase complex^{6,7}. Both *FCA* and *FVE* promote flowering in response to, or independent of elevated growth temperatures. *FVE* not only regulates flowering time through the floral pathway integrator *FLC*, but is also involved in sensing cold temperature. *FVE* may exert its effects on temperature-dependent pathways by modulating H2A.Z, perhaps through acetylation, which affects nucleosome stability. Although *FLOWERING LOCUS T (FT)* gene mediates and promotes the thermosensory flowering pathway, *CONSTANS (CO)* is, in turn, the major regulator of *FT* expression, along with other phytochrome genes, in response to long photoperiods⁸.

Another temperature-dependent pathway that also affects flowering time in plants, vernalization (extensive period of cold treatment for induction of flowering), is also perturbed in the background of a genetic mutation in *ARP6* (refs 5, 9). Certain *Arabidopsis* genotypes require vernalization for flowering and this requirement is suppressed by *arp6* mutation. This effect is mediated through *FLC*, whose expression is dependent on the SWR1 complex. In a large field experiment, it was found that natural temperature fluctuations were likely to be sufficient for overcoming *FLC*-induced repression of flowering in *Arabidopsis*¹⁰. Temperature fluctuations of this type are likely to signal through H2A.Z dynamics, which is consistent with the observation that perturbation of H2A.Z in *arp6* is sufficient to overcome a vernalization requirement^{9,11,12}.

This shows that some master genes regulate numerous downstream genes in response to changes in ambient temperatures and affect important plant functions like flowering. Kumar and Wigge¹³ have recently studied the chromatin status at the *FT* locus which responds to temperature and is altered in the absence of the histone protein, H2A.Z. They have provided an explanation for how the thermal induction pathway may activate *FT* expression in response to higher temperature independently of the gene *CONSTANS*. The work of Kumar and Wigge¹³ has demonstrated some important molecular findings as to how the nucleosomes containing the alternative histone H2A.Z are essential to perceiving ambient temperature correctly. By a forward genetic screen of fast neutron

mutagenized population of *HSP70::LUC* reporter strain of *Arabidopsis*, they studied transcript profiling and complementation analysis with simultaneous revealing of *arp6* alleles and showing that Hsp70 is an output of the ambient temperature sensing pathway. It was also shown that ARP6 is in the ambient temperature sensing pathway that controls flowering and developmental responses to ambient temperature, by studying the response of *arp6-10* in short-day treatments by thermal induction.

Thermal time is a key measure for the rate of transition through the developmental phases and that phase transition is accelerated by a higher ambient temperature¹⁴. *Arp6-10* caused a specific upregulation of all the developmental decisions regulated by temperature and plants deficient in *ARP6* displayed a constitutive warm temperature developmental programme. In *Arabidopsis*, a functional *ARP6* allele accounts for almost half of the ambient temperature transcript responses and correspondingly, a mutation in this allele, *arp6* mutation, results in the global misregulation of the ambient temperature transcriptome. This suggests that *ARP6* is important and necessary to coordinate the transcriptome in response to ambient temperature. H2A.Z occupancy dynamics is independent of the transcriptional response and is a function of ambient temperature shifts (Figure 1). *ARP6* encodes a subunit of the SWR1 complex that is conserved among eukaryotes and is necessary for inserting the alternative histone H2A.Z into nucleosomes arrays *in vivo* in place of

H2A (ref. 15). The HSP70+1 nucleosome shows a constitutive temperature response in *arp6* mutation and chromatin architecture responds dynamically to changes in ambient temperature. H2A.Z nucleosomes wrap DNA more tightly, and the role of H2A.Z in controlling the temperature transcriptome is conserved. Also, it can be inferred that while nucleosomes are temperature-responsive regulators of transcription and act as a fulcrum between thermosensing and flowering pathways, the deposition machinery for incorporation of H2A.Z into chromatin controls multiple developmental processes upon sensing environmental signals like rise in temperature. H2A.Z can act as a kingpin and a key chromatin thermostat to potentiate the transcriptional activation of a large number of genes and bring about repression of the transition from vegetative to reproductive development through the promotion of *FLC* expression¹⁶.

Unprecedented fluctuations in the mean global temperatures in the next 50–100 years can be disastrous to most wild and cultivated plant biodiversity, and subsequently to all the life dependent on plants³. Even though plants exhibit phenomenal developmental plasticity in terms of adaptation to extremes of climate change, such plasticity is limited. Crop productivity will be significantly affected even due to smaller changes in the mean global temperature. The challenge now is therefore to design climate-resilient crops by conscientious breeding. Knowledge about candidates that can act both as genetic markers of climate change and

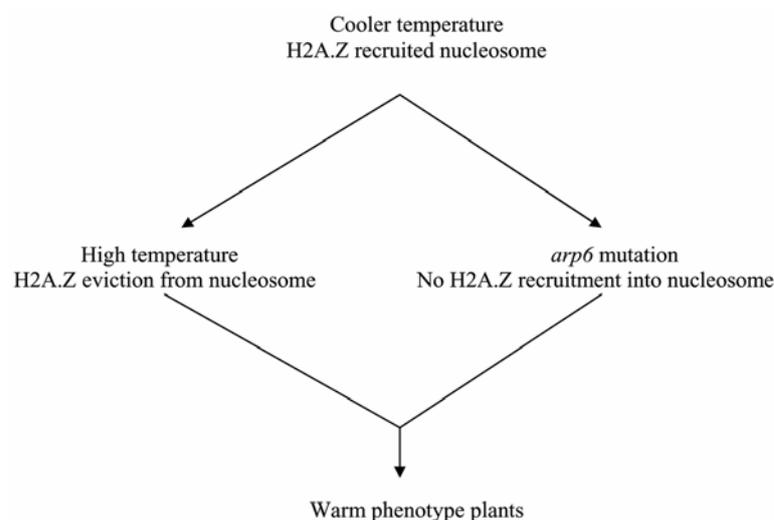


Figure 1. Mechanism of warm phenotype development in *Arabidopsis* either by high temperature or by *arp6* mutation vis-à-vis H2A.Z recruitment.

potential candidates for utilization in breeding needs to be improved. Several candidate genetic factors, including *H2A.Z*, *FVE*, *FLC*, *FLT*, *ARP6*, *PIE1* and many polycomb genes already show promise in this direction. Studies of Kumar and Wigge¹³ in the identification of the thermostatic role of H2A.Z histone in the *arp6* mutational background resulting in genotypes phenocopying warm-grown plants highlight H2A.Z as a typical marker for perceiving ambient temperatures like a thermometer, with far-reaching implications. Climate-change OMICS has become an important methodology in identifying such genomic markers for understanding plant molecular responses (albeit on a reductionist approach) and adaptations to climate change. Picturesque denouement of the works by Kumar and Wigge¹³ and others is indeed illuminative in genetically dissecting and understanding some of the basic plant phenomena such as temperature stress that can surely strengthen crop breeders and biotechnologists in the

fields of agriculture and horticulture in designing climate-resilient crops as well genetic tinkering of flowering and plant architecture.

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NEWS

IISc's plunge to train school teachers

The Indian Institute of Science (IISc), foremost among the science, engineering and technology institutes in the country, is creating its second campus at Kudapura in Karnataka with help from the State Government. The dream for a new IISc campus was realized when on 26 February 2011 its first activity, the Talent Development Centre (TDC), was formally inaugurated. TDC has been created with an aim to provide training to science teachers at all level beginning with high school teachers, and to conduct discussion meetings, seminars, and winter and summer schools. It also aims at providing academic and research facilities for high school, college and university students.

Though IISc has been conducting a High School Science Teachers Training Programme once every year, for the past 35 years in different districts of Karnataka, the need for a permanent place to conduct the courses has long been felt. The first training school at the new cam-

pus was thus conducted soon after the inauguration of the centre. The aim of the course is training teachers so that they convey the excitement of science and engineering to their students. The course trains teachers but eventually benefits a large number of students. The institute's talent is being used to develop talents elsewhere in the country.

The first course at the new campus was held during 27 February to 8 March 2011. About 95 government high school science teachers from Chitradurga district, Karnataka, were selected for training by the Education Department of Karnataka. The 10-day course touched upon all areas of science – physics, chemistry, biology, mathematics and computers. Each day of the course was divided into morning lecture session and afternoon practical session. Lectures were mainly fundamental in nature with some specialized ones, and laboratory experiments were designed to match the high school level. Apart from lectures in

particular subjects, talks on topics of general interest such as water, pollution, energy conservation and satellite communication were also delivered. About 40 lectures were delivered and 15 experiments in physics, chemistry and biology each, were conducted by the teacher trainees. The programme was planned by M. S. Hegde (IISc).

The vision of the High School Science Teachers Training Programme is to inculcate among the teachers a culture of learning. Over the next five years, the course aims at training about 5000 teachers. The next training course will be held in June–July 2011, after which the course is aimed at being conducted every month. Though the program is meant for Karnataka school teachers, there is undoubtedly a need to conduct such courses on a national level, said Hegde.

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