The Mystery Behind Flowering

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Flowering, phytochrome, MADS box genes.

The concepts of photoperiodic induction, hormonal regulation and florigens used to form the basis of our knowledge of flowering. Consequent upon the advancement of technology, our present day understanding suggests that a number of events like switching on of a cascade of genes, and the subsequent activation of MADS box genes, result in the activation of the the genes responsible for flowering in angiosperms.

Flowers, like stars and the moon have long been a staple of poets around the world. A poetic mind may be thrilled and inspired with the beauty of flowers, but a scientific mind also looks for an explanation of the process of flowering. A number of questions need to be answered to understand the complex process of flowering in angiosperms. How does a plant receive the signal for shifting from a vegetative to a reproductive stage? What is the nature of the stimulus received by a plant to initiate blossoming, as well as the termination of the reproductive stage in perennials, are a couple of such basic questions.

Early Concept of Flowering

Day length is well-known to be involved as a stimulus in the process of flowering. This photoperiodic induction of flowering was first reported in the early half of the 19th century. It is now well established that the photoperiodic stimulus is perceived by a pigment in the leaves, called phytochrome, which acts as a photoreceptor. The phytochrome can be inter-converted between two forms, Pfr and Pr. Pr absorbs red light (660 nm) and is converted to Pfr, which is, in turn, converted back to Pr in the presence of far-red light (730 nm). Though Pfr is unstable, it is the more active form of the pigment and it mediates most light responses. This active form of phytochrome induces the produc-

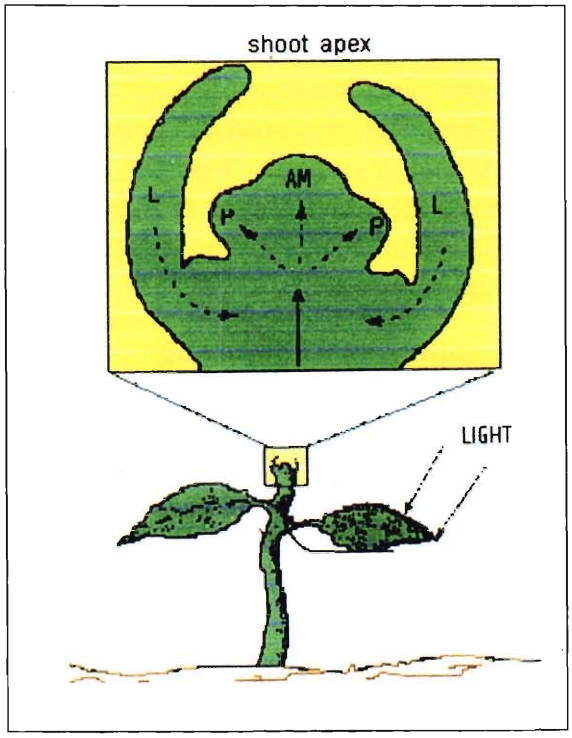
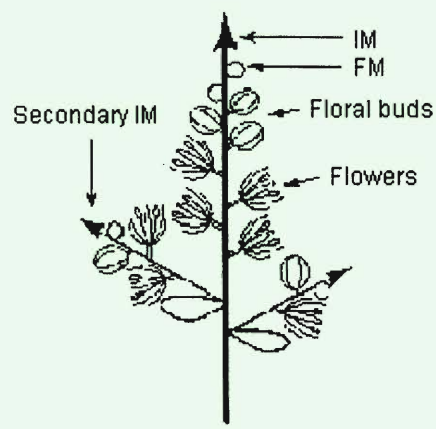


Figure 1. The pathway through which the photoperiodic signal is translocated from the receptor leaves (L) to the shoot apical meristem (SAM) and the leaf primordia (P).

tion of florigen (flowering hormone) in the leaves, and the florigen is thus translocated to the apical meristem and helps in its conversion into a floral meristem (*Figure* 1, *Box* 1). The chemical nature of florigen is yet to be established, but it is suspected to be an isoprenoid or a steroid.

Box 1. The Inflorescence and Floral Meristems

During early shoot development, leaves are produced from the shoot apical meristem (SAM). Meristems are plant tissues containing relatively undifferentiated cells undergoing frequent mitotic cell division. As the plant matures under appropriate environmental conditions, it switches from vegetative to reproductive developmental phase. During this transition, apical and lateral meristems are converted to inflorescence meristems (IM). The inflorescence meristem produces a series of reproductive lateral meristems called floral meristems (FM). Each floral meristem ultimately gives rise to a single flower.



Besides phytochrome and florigen, gibberellin too has a role in inducing flowering, although the details of its action are yet to be understood. According to a recent hypothesis, there are two factors involved in the flowering process. The first one is gibberellin, and the second is anthesin. Together, gibberellin and anthesin constitute the true florigen. It is postulated that a critical balance between Pfr and Pr is the genesis of the stimulus for the production of florigen.

Today's Viewpoint About Flowering

With the availability of molecular biological techniques, the understanding of flowering has changed a lot during the last thirty years. Today, we can view the whole process as consisting of two steps. In the first step, the vegetative meristem is converted into reproductive (floral) meristem, and in the next step this reproductive meristem is differentiated into floral organs.

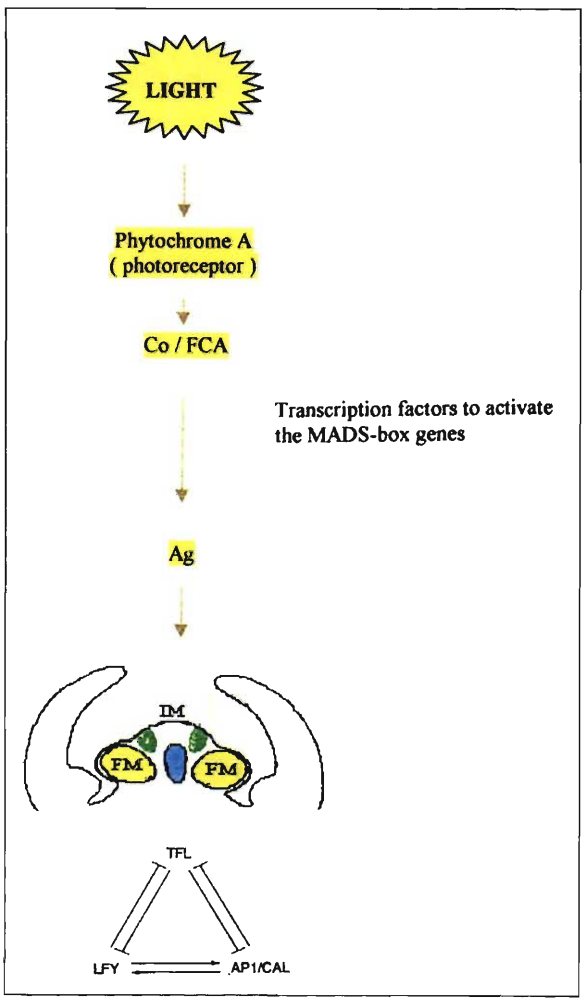


Figure 2. Genes controlling flower primordium specification in Arabidopsis.

Therefore, two key questions to be asked about flowering are: how the vegetative meristem is converted to a floral meristem, and how floral identity is determined.

1. How is the vegetative phase converted to reproductive phase?

A series of genes are involved in the conversion of the shoot apical meristem (SAM) to inflorescence meristem (IM) and floral meristem (FM). Most of the studies attempting to understand this complex mechanism were carried out using *Arabidopsis* as a model system (*Figure* 2).

Concomitant with the photoperiodic induction, two major genes CONSTANS (Co) and FCA are induced. The products

Box 2. MADS Box Genes

Most plant homeotic genes belong to a class of related genes known as MADS box genes. The acronym 'MADS' is derived from the first letter of the first discovered members of this class of genes.

1) MCM1 – a yeast gene which encodes a transcription factor necessary for mating type determination
2) AGAMOUS/DEFICIENS – floral organ identity genes.
3) Mammalian serum response factor is found to induce the transcription of proto-oncogenes.

Many of the genes that are known to determine floral organ identity are MADS box genes such as DEFICIENS gene of *Antirrhinum* (Snapdragon) and AGAMOUS, APETALA1 and APETALA3 of *Arabidopsis*. MADS box genes encode proteins that function as transcription factors but they differ among themselves in structure. The MADS box genes share a characteristic conserved nucleotide sequence known as the MADS box, which encodes a protein structure known as MADS domain. The MADS domain enables these transcription factors to bind to a region of DNA with a specific nucleotide sequence. Such binding causes the transcription of the gene in the immediate vicinity. Proteins that bind to specific DNA sequences and act as 'switches' to 'turn on' or induce the expression of genes are called transcription factors.

of these genes are transcription factors that activate the MADS box genes (*Box* 2). As a result, AGAMOUS (Ag), an important member of the MADS box genes family, and also a major decision point of the whole morphogenetic process, is switched on. This gene directly regulates the expression of LEAFY (LFY) and APETALA1 (AP1) genes that are actively involved in directing a meristem to develop into a flower.

2. How is floral organ identity determined?

For the quest of unveiling the mystery behind flowering, Elliot Meyerowitz and Enrico Coen proposed a model in 1991. The model proposed that the floral organization in each fold or whorl is determined by a unique combination of three organ identity genes. Activity of Type A gene alone specifies sepals, whereas formation of petals requires both A and B gene activity. Stamens are formed by a combination of the activity of both B and C genes, whereas the activity of C alone specifies carpels (*Figure* 3). The model also proposed that activity of A and C mutually represses each other. This famous model, named as ABC model, is the most widely accepted till date.

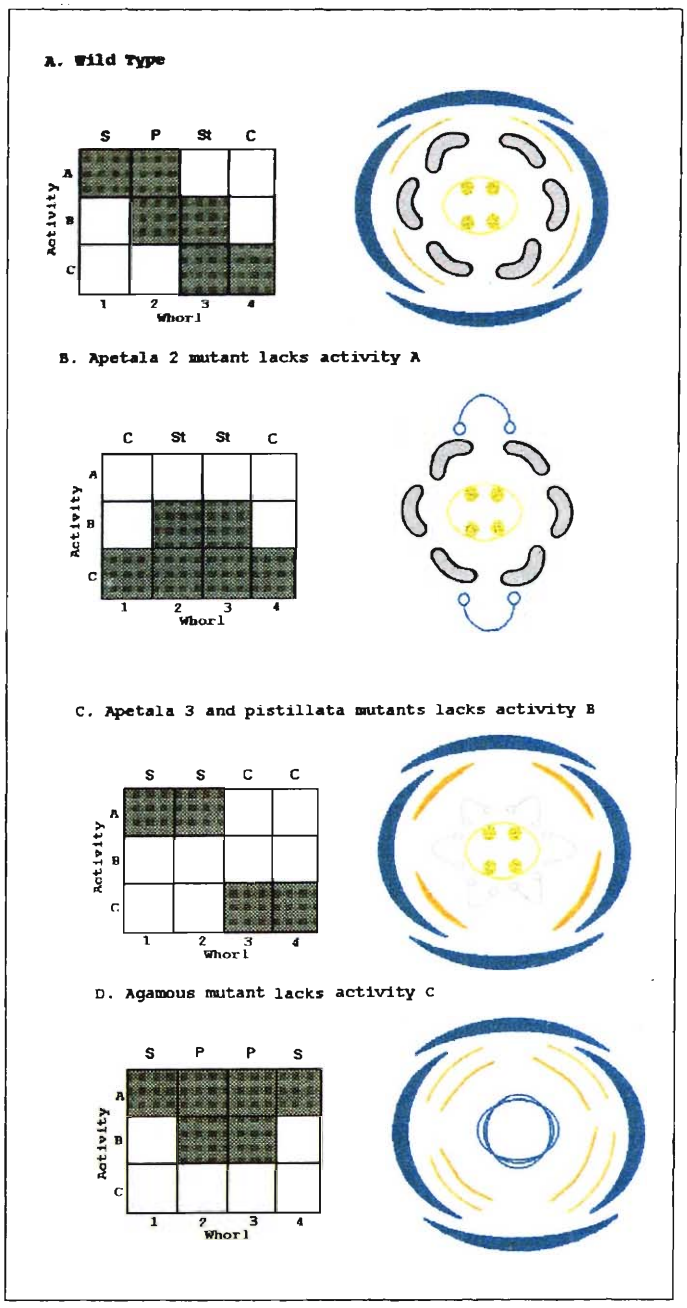


Figure 3. Expression pattern for three classes of floral organ identity genes in wild type Arabidopsis and their respective mutants. (S = Sepal, P = Petal, St = Stamen and C = Carpel)

Conclusion

Flowering is a unique biological phenomenon by which most plant species perpetuate themselves from one generation to another. The metamorphosis of vegetative meristem to a repro-

Suggested Reading

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ductive meristem has interested scientists for a long time. Considerable progress has been made in unveiling the mechanisms behind flowering. However, there are still gaps which need to be bridged for an in-depth understanding of the entire mechanism. Such understanding, in future, will not only open up new vistas of science but also provide us with a better ability to manipulate the process of flowering for improvement of crop plants.

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Speaking of Science and for Science

Conveying the essence of science and its excitement in an understandable way to a layman or a non-expert is an art that few scientists have mastered. This has its very important role and value in society; it is also an important duty of the science community, that is being neglected in modern times. KSK had this skill as it is clear from his many articles on science and related issues in Tamil and English as well as the talks that he has given in All India Rao. He was also an ardent spokesman for science.

KSK strongly believed that one can convey even very complicated scientific facts in his mother tongue – in this case, Tamil. His scholarship and appreciation of Tamil literature must have given him the gift to perform this task with ease. In one of his articles he speaks of his school science teacher Thirumalai Kozhunthu Pillai, who enthused the students by teaching science in an understandable way in chaste Tamil. Listening to him he got the conviction that difficult scientific concepts could be conveyed in Tamil.

Those of us whose spirit is strong but flesh is weak can gain strength to write science in our mother tongue by studying the works of people like KSK and modern scientists like Narlikar and others.

Through his own first rate scientific work and also through his scholarly personality he was a spokesman for Indian science. One hears that KSK was in many committees and held many responsible scientific administrative positions: he was President of the National Academy of Sciences and also Member of Atomic Energy Commission. It is said that whenever Pandit Jawaharlal Nehru found time (or wanted to get away from politics) he would rush to NPL to listen to KSK of the latest in science. Apparently he always enjoyed listening to KSK, but at the end never forgot to ask KSK 'how this is going to help my countrymen'. I really do not know what KSK's reply was.

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