

The complex world of flower

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In this world, there are numerous things to enjoy in life, whether they are natural or manmade. Among these is the presence of flower. “Angiosperm” translates to “covered seed”, in contrast to naked seed for gymnosperms; and most angiosperms are referred to as “flowering plants”. The term “angiosperm” derives from two Greek words: angeion (vessel), and sperma (seed). They are a much more recent evolutionary development having been reported to have originated in the early Cretaceous about 130 million years ago.

Angiosperms cover all continents on this earth ranging from the hottest, wettest tropics to the harshest deserts to the coldest arctic environments. Angiosperms are divided, according to morphological characters, into two large groups, dicotyledon (dicot) and monocotyledon (monocot). The dicot comprises approximately 165,000 to 180,000 species; the monocots are the smaller of the two groups, consisting of about 60,000 species (<http://www.biologyreference.com>).

To start, flower is a plant organ whose main function is to attract vectors bringing in pollens to initiate the sexual reproduction process. The event of fertilization (union of pollen or male organ to egg or female organ) usually leads to production of seed. This is so wonderful and crucial to our existence because food is one of four necessities in our struggling lives. Oil, carbohydrate, even protein are found abundantly in seed part of plants and this is why flower, the part who starts it all, is so important.

Many techniques have been used to study the flower development. Studies on the floral defective mutants of *Arabidopsis* and *Antirrhinum* (snapdragon) reveal many genes involved in the flower formation process. Flowering time of *Arabidopsis* and most plants is influenced by both environmental conditions, which include length of day, temperature, light quality, and nutrient deprivation, and developmental factors associated with the age of the plant (Martinez-Zapater *et al.*, 1994). This complexity is mediated by several genetic pathways that control responses to different environmental signals.

Specific signals act upon the different growth phases. The switch to flowering involves an integration of many signaling pathways, resulting in the up-regulation of the flowering genes. Key players like *FLOWERING LOCUS T (FT)* and *SUPPRESSOR OF CONSTANS1 (SOC1)* are responsible for the change in shoot meristem identity and the induction of flowering (Kardailsky *et al.*, 1999; Kobayashi *et al.*, 1999; Wigge *et al.*, 2005; Oliver *et al.*, 2009). Overexpression of *FT* results in dramatic early flowering in *Arabidopsis* while loss of function mutation in *FT* causes late flowering. *SOC1* was identified by a screening for suppressor mutations of early flowering phenotype in 35S overexpressed *CONSTANS (CO)* plants. The *soc1* mutation delays flowering under both long- and short-day conditions. This is a characteristic of mutations that affect the autonomous flowering pathway that are crucial to most plants (Onouchi *et al.*, 2000).

The transition between the two phases is a result of intricate interactions between yet another shoot meristem identity gene *TERMINAL FLOWER1* (*TFL1*) and floral-meristem identity genes. *TFL1* gene controls shoot meristem identity throughout the plant life cycle, affecting the number and identity of all above ground organs generated. *TFL1* acts throughout plant development to influence each phase of growth; *tfl1* mutants have a shorter vegetative phase, making less leaves, branches, and flowers than the wild type.

Two *Arabidopsis* genes, *LEAFY* (*LFY*) and *APETALA1* (*AP1*) are required to specify floral meristem identity and inhibit *TFL1* gene (Wiegand *et al.*, 1992, Pena *et al.*, 2001). Over expressing either *LFY* or *AP1* results in a phenotype similar to when the *TFL1* is mutated. The transcription factor *LFY* acts upstream of *AP1* in the floral developmental pathway. Expression of the *LFY* or *AP1* transcription factor in non-reproductive meristem can cause a conversion to a floral meristematic fate in a variety of species examined, demonstrating that they are master regulators of floral development and they act in partially redundant manner to specify floral meristem identity.

One dramatic difference between a floral and vegetative shoot apical meristem is that a floral meristem is determinate meaning that it produces

only a finite set of organs and then stop proliferating. This conversion to determinate fate implies that all cells in the floral meristem must have committed to a differentiation pathway. In *Arabidopsis*, this commitment is controlled by expression of a MADS domain-containing transcription factor called *AGAMOUS* (*AG*). Expression of *AG* is activated early in floral development at the apex of floral meristem (Drews *et al.*, 1991) by two transcription factors, *LFY* and *WUSCHEL* (*WUS*). In turn, the determinacy of floral meristem depends on negative feedback of *WUS* by *AG* (Lohmann *et al.*, 2001)

More is known on the genetics pathways controlling the specification of different organ identities. Homeotic mutation causing substitution of one organ type with another has been very useful in the identification of genes involved in this process. A model called “ABC” has been proposed to explain the floral development process (Bowman *et al.*, 1991a; Coen and Meyerowitz, 1991). This simple model proposed 3 classes of genes: A, B and C. These classes have overlapping expression in various whorls. Class A alone encodes sepals, while class B overlapping with class A encodes petals. On the other hand, when class B overlapping with class C stamens will be formed; while class C alone encodes the carpel (Fig. 1). A and C expression are confined to distinct whorls since these genes negatively regulate each other’s expression.

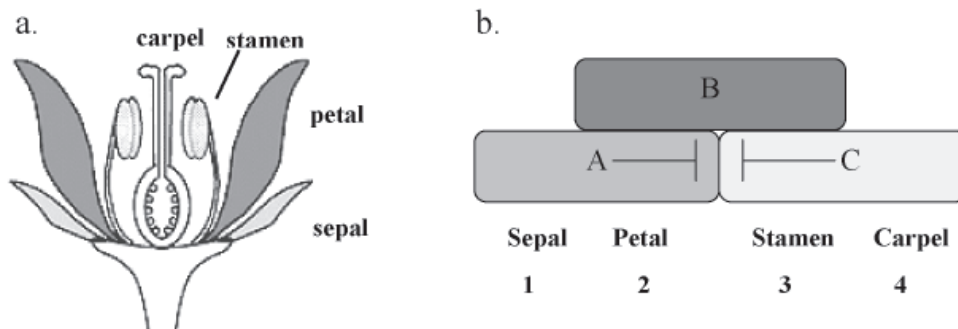


Figure 1 (a) Basic structure of a complete flower (from: <http://www.mm.helsinki.fi/mmsbl/english/research/Gerberalab/abc.html>); (b) ABC model.

After the formulation of the ABC model, *Arabidopsis* genes have been identified that correspond to class A, B and C. For class A, *APETALA1* (*AP1*) and *APETALA2* (*AP2*) have been reported. *AP1* is initially expressed throughout the floral meristem but later on its expression is restricted to the first and second whorl (sepal and petal) by action of *AG*. *AP2* transcripts are found throughout the flower but its function is delimited to the first and second whorls also by the action of *AG* (Mandel *et al.*, 1992; Jofuku *et al.*, 1994; Gustafson-Brown *et al.*, 1994). This implies that *AG* acts post-transcriptionally to specify area that *AP2* would act and vice versa, and *AP2* restricts the *AG* expression to the third and fourth whorl (Drews *et al.*, 1991). Thus *AG* is a gene in class C. Early in flower development *AG* RNA is evenly distributed through out third and fourth whorl, but later on *AG* RNA is restricted to specific cells in stamens and carpels (Bowman *et al.*, 1991b).

For class B, two genes have been identified in *Arabidopsis*. *APETALA3* (*AP3*) and *PISTILLATA* (*PI*). These two genes encode proteins containing MADS domain that bind to DNA as a heterodimer. Their expressions are throughout the petal and stamen primordial and are dependent on cross-regulatory interactions between the gene products. Many studies reported that *AP3* and *PI* are both necessary and sufficient to control the petal and stamen development anywhere in the flower (Zik and Irish, 2003).

This ABC model has been revised to include a fourth class of genes that is necessary for proper development of the inner three whorls of the flower. The three functionally redundant *SEPALLATA* genes: *SEP1*, *SEP2* and *SEP3*, specify the identity of petals, stamens and carpels. In *sep1 sep2 sep3* triple mutants, all floral organs are sepal-like and the flowers are indeterminate even when the B and C genes are still function normally, showing the roles of the SEP genes in organ identity as specifying petal,

stamen and carpel (Pelaz *et al.*, 2000). Interaction between SEP proteins and gene products from the ABC genes has been demonstrated using yeast two-hybrid and immunoprecipitation experiments. With this information, the ABC model has been updated to simple ABCE model that includes the E class gene in the model (Fig. 2).

In this ABCE model, one additional class of gene (E) has been added to the ABC model. These four classes of genes are working in combination to regulate the development of four distinct floral organ identities. In Figure 2, the floral primordial is represented as a dome shape with specific gene activities represented in various shades of gray. Class A is represented by the deepest shade of gray while class C is the second deepest shade. Class B is in white and class E is in the palest gray. With the addition of E class, new regulatory control has been explained. In the ABCE model, classes A+E specify sepal in the first whorl; classes A+B+E specify petal in the second whorl; classes B+C+E specify stamen in the third whorl and classes C+E specify carpel in the fourth whorl.

Predictions on expected phenotypes of various mutants have been made correctly based on this model. For example, in *pi ag* (or *ap3 ag*) double

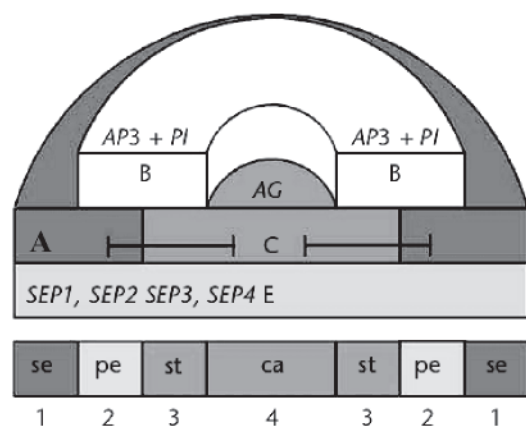


Figure 2 Simple ABCE model of flower development.



Figure 3 (a) *Arabidopsis* wildtype; (b) *pi ag* double mutant (Krizek, 2009).

mutants, A class activity is found in all floral whorls because of the lack of C class activity to restrict its expression. Then according to the ABCE model, the mutant plant would have sepal in all whorls because the only activities left are from classes A and E which together specify sepal (Fig. 3).

As for now, the ABCE model is the most up-to-date and widely accepted version of genetic regulation of flower development. More progress is being accomplished in understanding and uncovering yet more unidentified genes involving in floral development, their interactions, and their modes of expression, which eventually leading to a new or updated version of the old model. Consortium of researchers is diligently working on this mystery as complete knowledge on this matter is essential for future genetic manipulation whether to increase yield, change flowering time or even create designer flowers suited for each person's desire.

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