Genetics of identity

Flower development

The story of the outmoded ABC model shows that even the most successful concepts must be continually re-evaluated.

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Flowers are complex structures. They typically consist of four types of organ arranged in four whorls: sepals, petals, stamens and carpels. No wonder that their development is complicated. Nevertheless, there seem to be simple rules that underlie this process, as was realized when it became possible to analyse 'floral homeotic mutants' — plants with flowers that have seemingly normal floral organs in places where organs of another type are normally found.

In the model plant thale cress (*Arabidopsis thaliana*), homeotic mutants are categorized as A, B and C. Ideal class A mutants have carpels in the first whorl instead of sepals, and stamens in the second whorl instead of petals. Class B mutants have sepals rather than petals in the second whorl and carpels rather than stamens in the third; and class C mutants have petals instead of stamens in the third whorl and sepals instead of carpels in the fourth.

The existence of defined classes of mutants suggested simple combinatorial models, such as the 'ABC' model of flower development. This proposes three different floral homeotic functions to explain how the different floral organs adopt their unique identities during development. These functions are termed A, B and C, with A specifying sepals in the first floral whorl; A + B, petals in the second; B + C, stamens in the third; and C, carpels in the fourth. Because they had been identified by mutant analysis, it was clear that the homeotic functions are provided by sets of floral homeotic genes. In *Arabidopsis* there are at least two A-function genes, two B-function genes and one C-function gene, all of which encode transcription factors — proteins that recognize specific DNA motifs and thereby regulate the expression of the genes that contain them.

Besides elegance, simplicity was certainly among the most attractive features of the ABC model, which found its way into modern textbooks and numerous reviews. However, it was soon realized that the model is incomplete. Expression of ABC genes throughout a plant does not transform leaves into floral organs. Thus the ABC functions, although necessary, are not sufficient to superimpose floral organ identity on a leaf development programme.

Another class of genes (*SEPALLATA*) is now known to be required and, together with the ABC genes, is sufficient for specification of petals, stamens and carpels. How do these *SEP* genes fit into the ABC model? Some have argued that they contribute to B and C functions, but they are more likely to have an additional function.

Indeed, despite these insights, I wonder whether floral homeotic functions are still a useful concept at all. Now that we know that there are at least as many floral homeotic functions as there are types of floral organ, the concept no longer provides a useful simplification. Wouldn't it suffice to refer to the four different states of floral organ identity on the one hand, and to the combinations of floral homeotic genes that specify these organ identities on the other? This seems to be a particularly useful way of thinking about the control of floral organ identity in the light of new evidence about how floral homeotic genes interact and exert their functions at the molecular level.

Proteins that are encoded by the floral homeotic genes of *Arabidopsis* are now known to bind to DNA as multimeric complexes that contain B-function and SEP proteins, as well as either an A-function or a C-function protein. These are exactly the combinations of proteins that are sufficient to specify petal or stamen identity, respectively. This finding immediately suggests future research goals: to define the exact structures of the transcription-factor complexes inside the living plant cell; to identify the target genes for which transcription is regulated by the binding of the complexes; to explain the gene specificity of that binding; and to study how target-gene function brings about floral organ identity. Neither the concept of floral homeotic functions nor the ABC model will offer any help in achieving these exciting ambitions.

Was the ABC model an intellectual detour, or even an obstacle to scientific progress? Not at all. It provided a working hypothesis with numerous implications that could be experimentally tested, so it was an incredibly useful concept for a while. But scientific terms and concepts should be continually evaluated with respect to their heuristic value. Now that we have a direct understanding of the molecular mechanisms involved, there may no longer be a need for the abstract concept of floral homeotic functions to be squeezed between floral homeotic genes and floral organ identity. ABC functions may now obscure, rather than enlighten, our understanding of the linkage between molecular genetic events and floral phenotype.

The ABC model undoubtedly attracted many enthusiastic researchers to study flower development, and as such formed the basis for rapid progress in the field. So it could be that, ultimately, the success of the ABC model contributed to its abolition. ■

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Floral combinations: the wildflower *Hepatica nobilis*

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FURTHER READING

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