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IN BRIEF

Transcription Factors and Darwin's "Abominable Mystery": Positive Autoregulation in Floral Zygomorphy

The Cretaceous was a great time for angiosperms; so great that Darwin himself identified the dramatic increase in the number of angiosperm species as an "abominable mystery" (reviewed in Friedman, 2009). Trying to explain the astonishing explosion of angiosperm diversity gave Darwin such trouble that he even toyed with the idea of a lost continent where angiosperms had diversified off the (fossil) record. However, he also landed on another, more likely, explanation: the interaction between plants and insects. Indeed, one key evolutionary innovation that appeared in some major lineages at this time was a change in floral symmetry, from radially symmetrical actinomorphic flowers to bilaterally symmetrical zygomorphic flowers. The morphological diversity of zygomorphic flowers allows more specific interactions with pollinators with bilateral vision, such as insects; this interaction may drive speciation by facilitating reproductive isolation.

Zygomorphic and actinomorphic flowers of *P. heterotricha*. Typical flowers of *P. heterotricha*, left, show bilateral symmetry, with reduced dorsal petals (dp). Rare *peloric* flowers, right, show radial symmetry. (*Reprinted from Yang et al. [2012], Figures 3B and 3C.*)

Zygomorphy has arisen multiple times in independent angiosperm lineages and involves recruitment of *TEOSINTE BRANCHED1/CYCLOIDEA/PCF* (*TCP*) genes (reviewed in Preston and Hileman, 2009). These TCP transcription factors alter development along the dorso-ventral axis by increasing or decreasing dorsal growth. For example, in *Antirrhinum majus*, two dorsally expressed *TCP* genes regulate cell cycle genes and ventral identity genes to produce floral asymmetry by affecting cell number, shape, and fate. Differential gene expression along the dorso-ventral axis requires both establishment and maintenance. **Yang et al. (2012)** examine the maintenance of gene expression of two genes from the CYC2 TCP clade, *CYC1C* and *CYC1D,* in *Primulina heterotricha*. *P. heterotricha* has a zygomorphic flower with two reduced dorsal petals (see figure) and abortion of both the dorsal and lateral stamens. At the stage when *P. heterotricha* flowers become dorso-ventrally differentiated, *CYC1C* and *CYC1D* are strongly expressed in the dorsal petals and the dorsal/lateral stamens. However, in rare *peloric* flowers with radial symmetry (see figure), *CYC1C* and *CYC1D* are not expressed, indicating that these genes may regulate the dorsal reduction of petal size and the dorsal/lateral abortion of stamens. Indeed, transgenic *Arabidopsis thaliana* overexpressing *CYC1C* showed reduced petal area, with smaller petal cells, indicating an effect on cell expansion.

The promoters of *CYC1C* and *CYC1D* both have consensus CYC binding sites, and the authors next examined whether these transcription factors act in their own regulation. Electrophoretic mobility shift assays and chromatin immunoprecipitation showed that CYC1C and CYC1D bound to the promoters of both genes, indicating both auto- and cross-regulation. In transient gene expression assays, the CYC binding site was essential for reporter gene activation by CYC1C, showing positive regulation of gene expression. Phylogenetic analysis of *CYC*-like genes showed that the CYC binding site was present only in the promoters of zygomorphic lineages, not in actinomorphic lineages. Therefore, this autoregulatory positive feedback loop may play a role in the maintenance of gene expression and regulation of dorso-ventral differentiation in zygomorphic flowers in multiple lineages. Future research will uncover further interesting details, including mechanisms for establishment of gene expression and methods by which this autoregulatory feedback mechanism may be implemented in other lineages.

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