On the Origin of C₄ Species in Yellowtops

C₂ photosynthesis is the product of several biochemical and structural adaptations that concentrate CO₂ at the site of Rubisco (for ribulose-1,5-bis-phosphate carboxylase/oxygenase), thereby increasing photosynthetic efficiency in conditions that promote photorespiration. Having evolved independently up to 66 times in angiosperms, the C₂ pathway represents a striking example of convergent evolution (Sage et al., 2012). Typically, C₃ photosynthesis depends on the metabolic interaction between two cell types. CO₂ is initially fixed as a four-carbon compound in mesophyll cells and is then concentrated in bundle sheath cells, which contain Rubisco and other enzymes of the Calvin cycle (Hatch et al., 1975). The glycine decarboxylase complex (GDC), which catalyzes the release of CO₂ from the metabolites of photorespiration, is largely restricted to bundle sheath cells in C₃-C₄ intermediate and C₄ species, where it functions as a CO₂ pump that further concentrates CO₂ in the vicinity of Rubisco. Given that the GDC is expressed throughout photosynthetic tissues in C₃ plants and is restricted to bundle sheath cells in C₃-C₄ and C₄ species, this spatial confinement of GDC already in C₃-C₄ intermediates is thought to represent an important step in the evolution of C₄ photosynthesis (Sage, 2004; Sage et al., 2012).

The GDC consists of four proteins (P, L, T, and H), with the P protein (encoded by GLDP) constituting the decarboxylase (Oliver and Raman, 1995). Schulze et al. (pages 2522–2535) investigated how the bundle sheath–specific expression of GDC was established during the evolution of C₄ photosynthesis in the genus Flaveria (yellowtops), which includes C₃, C₄, and C₃-C₄ intermediate species. First, they demonstrated that the GLDP genes in Flaveria clustered into three groups (A, B, and C) and that only two of these (A and B) accumulated in leaves and were involved in photorespiration. Flaveria trinervia, a C₃ species, contained a functional A-cluster gene (GLDPA) and a B-cluster pseudogene (GLDPB*), whereas the C₃ species examined contained functional genes in both of these clusters. The authors then fused the 5'-flanking sequences of the GLDPA genes from two of the C₃ species to β-glucuronidase and expressed these fusions in Flaveria bidentis, a C₄ species. Both of these genes were strongly expressed in the bundle sheath cells but not in mesophyll cells (see figure). Thus, the last common ancestor of extant C₃ and C₄ Flaveria spp appears to have had a bundle sheath–specific GLDP gene. A similar analysis demonstrated that the group B GLDP gene of a C₃ Flaveria species was expressed in all photosynthetic tissues of a transgenic C₃ species.

Interestingly, RNA-seq analysis showed that C₃-C₄ intermediate species had lower levels of group B GLDP transcripts than did a C₃ reference, and that most C₄ species examined had none. In contrast, levels of group A GLDP transcripts were most abundant in C₃-C₄ intermediates and low in C₄ species.

Based on these results, the authors present a model that explains how GLDP expression gradually became specific to the bundle sheath cells in Flaveria. The C₃ species contain two versions of the GLDP gene, one of which is expressed exclusively in bundle sheath cells, and the other of which is expressed ubiquitously in leaves. During the evolution of C₄ species, the ubiquitously expressed version became a pseudogene, leaving only the bundle cell-specific version of GLDP.

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REFERENCES


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