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Photosynthesis research on yellowtops: Macroevolution in progress

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Abstract

The vast majority of angiosperms, including most of the agronomically important crop plants (wheat, etc.), assimilate CO_2 through the inefficient C_3 pathway of photosynthesis. Under ambient conditions these organisms loose about 1/3 of fixed carbon via photorespiration, an energetically wasteful process. Plants with C_4 photosynthesis (such as maize) eliminate photorespiration via a biochemical CO_2-pump and thus have a larger rate of carbon gain. The genus *Flaveria* (yellowtops, Asteraceae) contains not only C_3 and C_4 species, but also many C_3–C_4 intermediates, which have been interpreted as evolving from C_3 to fully expressed C_4 metabolism. However, the evolutionary significance of C_3–C_4 *Flaveria*-intermediates has long been a matter of debate. A well-resolved phylogeny of nearly all *Flaveria* species has recently been published. Here, we review pertinent background information and combine this novel phylogeny with physiological data. We conclude that the *Flaveria* species complex provides a robust model system for the study of the transition from C_3 to C_4 photosynthesis, which is arguably a macroevolutionary event. We conclude with comments relevant to the current Intelligent Design debate.

Keywords: Evolution; *Flaveria*; Intermediate forms; Macroevolution; Photosynthesis

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Introduction

Agronomists have long known that the average crop yield of maize (*Zea mays*) is much larger than that of many other domesticated grasses such as wheat (*Triticum aestivum*) or barley (*Hordeum vulgare*). According to *Agricultural Statistics* (USDA 1980), the average yields obtained for maize, wheat and barley are 3.06, 1.03 and 1.21 tons grain/acre, respectively. The reasons for these striking differences were debated when these data first became available 25 years ago. However, today we know that the approximately two-fold larger average crop yield of maize compared to wheat (and barley) is largely attributable to the more efficient photosynthetic mode of the maize plant (Sage and Monson, 1999; Sage, 2004). Like its relatives sugarcane and sorghum, *Z. mays* is characterized by a biochemical pump that concentrates the atmospheric carbon dioxide (CO_2) around the key enzyme of photosynthesis, ribulose-1,5-bisphosphate (RuBP) carboxylase/oxygenase (Rubisco, localized in the stroma of chloroplasts) after diffusion via the stomata into leaf cells. This sophisticated two-step mechanism of CO_2-assimilation was discovered in the 1960s, only a few years after Melvin Calvin (1911–1997) and his colleagues had resolved the details of photosynthetic CO_2-fixation in suspensions of the green alga *Chlorella* (Hatch, 1992; Kutschera, 2002).

In this contribution, we describe a model system that has been used to elucidate the phylogenetic development of the CO_2-pump in higher plants such as maize. This (and other) arguably macroevolutionary transition has been addressed in previous publications (Kutschera and Niklas, 2004, 2005), where background information on the topic discussed here is summarized.

Photorespiration and the CO_2-pump of the maize plant

Over the past decades, it has become very apparent that more than 90% of all land plants, including most crop species (wheat, barley, etc.) assimilate CO_2 via the one-step C_3 "*Chlorella*-type" pathway of photosynthesis. In these green organisms, the five-carbon sugar RuBP is the primary CO_2-acceptor and the first product of photosynthetic CO_2-fixation is the three-carbon (C_3) molecule 3-phosphoglycerate (PGA). However, Rubisco, the enzyme catalyzing the fixation of CO_2, is bifunctional. Both CO_2 and atmospheric oxygen (O_2) compete with one another at the active site of Rubisco. Carboxylation results in the formation of $2 \times$ PGA, whereas oxygenation of RuBP leads to the production of $1 \times$ PGA and $1 \times$ glycollate-2-P (oxygenase reaction). Thus, the primary reaction of one-step C_3-photosynthesis occurring in chloroplasts can be summarized as follows:

$$\text{Mesophyll cell: RuBP} + CO_2(O_2) \overset{\text{Rubisco}}{\longrightarrow} 2 \times \text{PGA } (1 \times \text{PGA} + 1 \times \text{glycolate-2-P}).$$

Importantly, only PGA can be converted in the stroma of chloroplasts into carbohydrates. The second product of the oxygenase reaction, glycolate-2-P, cannot