

Photosynthesis research on yellowtops: Macroevolution in progress

U. Kutschera^{a,*}, K.J. Niklas^b

^a*Institut für Biologie, Universität Kassel, Heinrich-Plett-Str. 40, 34109 Kassel, Germany*

^b*Department of Plant Biology, Cornell University, Ithaca, NY 14853, USA*

Received 15 May 2006; accepted 1 June 2006

Abstract

The vast majority of angiosperms, including most of the agronomically important crop plants (wheat, etc.), assimilate CO₂ through the inefficient C₃ pathway of photosynthesis. Under ambient conditions these organisms lose about 1/3 of fixed carbon via photorespiration, an energetically wasteful process. Plants with C₄ photosynthesis (such as maize) eliminate photorespiration via a biochemical CO₂-pump and thus have a larger rate of carbon gain. The genus *Flaveria* (yellowtops, Asteraceae) contains not only C₃ and C₄ species, but also many C₃–C₄ intermediates, which have been interpreted as evolving from C₃ to fully expressed C₄ metabolism. However, the evolutionary significance of C₃–C₄ *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 C₃ to C₄ photosynthesis, which is arguably a macroevolutionary event. We conclude with comments relevant to the current Intelligent Design debate.

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

*Corresponding author.

E-mail addresses: kut@uni-kassel.de (U. Kutschera), kjn@cornell.edu (K.J. Niklas).

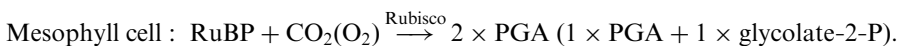
Introduction

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 (CO₂) 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 CO₂-assimilation was discovered in the 1960s, only a few years after Melvin Calvin (1911–1997) and his colleagues had resolved the details of photosynthetic CO₂-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 CO₂-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 CO₂-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 CO₂ via the one-step C₃ “*Chlorella*-type” pathway of photosynthesis. In these green organisms, the five-carbon sugar RuBP is the primary CO₂-acceptor and the first product of photosynthetic CO₂-fixation is the three-carbon (C₃) molecule 3-phosphoglycerate (PGA). However, Rubisco, the enzyme catalyzing the fixation of CO₂, is bifunctional. Both CO₂ and atmospheric oxygen (O₂) compete with one another at the active site of Rubisco. Carboxylation results in the formation of 2 × PGA, whereas oxygenation of RuBP leads to the production of 1 × PGA and 1 × glycolate-2-P (oxygenase reaction). Thus, the primary reaction of one-step C₃-photosynthesis occurring in chloroplasts can be summarized as follows:



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

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