

This Week's Citation Classic

Downton W J S & Tregunna E B. Carbon dioxide compensation—its relation to photosynthetic carboxylation reactions, systematics of the Gramineae, and leaf anatomy. *Can. J. Bot.* **46**:207-15, 1968. [Botany Department, University of British Columbia, Vancouver, British Columbia]

Plants with low CO₂ compensation values are shown to possess the newly discovered C₄ pathway of photosynthesis¹ and a unique type of leaf anatomy in which chloroplasts are concentrated around vascular bundles. These correlations permit rapid screening of taxa for photosynthetic pathway. [The SCI[®] indicates that this paper has been cited over 120 times since 1968.]

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"Until Hatch and Slack¹ reported an alternative photosynthetic pathway to the Calvin cycle in sugarcane, the only suspected difference in photosynthetic physiology among higher plants was that corn and sugarcane lacked photorespiration. This difference was based primarily on the ability of these plants to completely remove CO₂ from a sealed system. At the time that the C₄ pathway of photosynthesis was proposed, I was a graduate student with the late E.B. Tregunna at the University of British Columbia and we had just found that certain grasses and some dicotyledons of the Amaranthaceae and Chenopodiaceae also possessed low CO₂ compensation values (Γ). When Hatch *et al.*² later reported that corn had the new photosynthetic pathway, we were tantalised by the possibility that low Γ and the C₄ pathway might be related.

"Working in a climate of considerable scepticism regarding the reality of the new pathway and even doubts

about the existence of photorespiration, we checked the species listed in Hatch *et al.*² for Γ and found low Γ and the new pathway to be invariably associated. ¹⁴CO₂ fixation by the low Γ dicots indicated that they also assimilated according to the C₄ scheme.

"We were particularly intrigued by the existence of both high and low Γ species in the genus *Atriplex*. An important clue came when during a sequence of Γ measurements we noticed that leaves from the low Γ plant *A. rosea* contained prominent green veins whereas the high Γ *A. hastata* did not. Microscopic examination of sectioned *A. rosea* leaves subsequently revealed a type of leaf anatomy resembling that in the low Γ grasses! This anatomical correlation immediately provided a simple and rapid means for identifying 'C₄' species.

"Our recognition of these and other relationships with the new pathway soon came to the attention of many botanists. As the C₄ pathway gained acceptance, researchers in physiology, biochemistry, anatomy, cytology, taxonomy, and ecology were quick to investigate aspects of the C₄ 'syndrome' related to their specialties. The resultant ground swell of research activity, which no doubt contributed significantly to the frequent citation of our article, has over the past decade provided considerable insight into the intricate structural and functional relationships which constitute the C₄ pathway and led to the identification of over 900 'C₄' species."

1. Hatch M D & Slack C R. Photosynthesis by sugarcane leaves. A new carboxylation reaction and the pathway of sugar formation. *Biochem. J.* **101**:103-11, 1966.
2. Hatch M D, Slack C R & Johnson H S. Further studies on a new pathway of photosynthetic carbon dioxide fixation in sugarcane and its occurrence in other plant species. *Biochem. J.* **102**:417-22, 1967.