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This Week's Citation Classic®

El-Sharkawy M & Hesketh J. Photosynthesis among species in relation to characteristics of leaf anatomy and CO_2 diffusion resistances. *Crop Sci.* 5:517-21, 1965.
[Dept. Agronomy, Univ. California, Davis, CA; CSIRO, Canberra, Australia; and Dept. Plant Breeding, Univ. Arizona, Tucson, AZ]

This paper showed that C_4 tropical grass leaves with rapid photosynthetic CO_2 exchange rates had well-developed chlorophyll-containing bundle sheath cells and a large internal mesophyll surface exposed to air. A C_4 dicot, *Amaranthus* sp. (pigweed), had similar characteristics. C_4 leaves did not exhibit photorespiration and had higher photosynthesis:transpiration ratios and lower stomatal conductances than C_3 leaves. C_4 and C_3 leaves had similar CO_2 exchange rates in air containing 1,000 ppm CO_2. [The *SCI*® indicates that this paper has been cited in over 145 publications.]

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After obtaining a master's degree in genetics and plant breeding from Louisiana State University, Baton Rouge, I (ME-S) moved to the University of Arizona, where I had the good fortune to work under the supervision of John Hesketh, also a newcomer to Tucson. Our research formed a part of an extensive laboratory and field effort to elucidate factors limiting photosynthesis and dry matter production among species.[1] In the summer of 1964, while we were measuring CO_2 exchange rates of field-grown cottons at the Campbell Avenue Farm, a serendipitous observation was made. A leaf of weed amaranth that was growing in the cotton plots was inserted into the leaf chamber. Its photosynthetic CO_2 exchange rate was much higher than that of the many cotton leaves we had just measured. We immediately prepared leaf sections for microscopic observation and saw that this weed amaranth possessed "Kranz anatomy" (i.e., leaves with two types of chloroplast-containing cells: vascular bundle sheath and mesophyll cells).[2,3] This was the first dicotyledonous species found to possess the Kranz anatomy and photosynthetic rates similar to those of the efficient C_4 tropical grasses such as maize, sorghum, and sugarcane.

Later, when I moved to work with Bob Loomis and Bill Williams at the University of California, Davis, we found that another species, *Amaranthus edulis*, also had rapid photosynthetic CO_2 exchange rates and a zero CO_2 compensation point.[4] This amaranth had been cultivated for food by the Aztecs and Incas before the time of Cortez. This previously neglected yet efficient C_4 plant has recently received the attention of agricultural research and development agencies as a potential food crop.[5]

Although numerous papers and reviews concerning the photosynthetic C_4/C_3 phenomenon have been *Citation Classics*, I believe that this paper has been cited mostly because of: (1) the significance of the discovery of the many aspects of the C_4:C_3 phenomenon in plant science; (2) the comparison of transpiration and leaf conductances between C_4 and C_3 plants; and (3) the link between leaf Kranz anatomical features and C_4 photosynthetic behavior.

Currently, I am working with my colleagues at CIAT on another under-researched tropical crop, cassava (*Manihot esculenta*). Once again, leaf anatomy plays a significant role in the response of the plant to the environment.[6,7] Hesketh is contributing significantly to the new field of crop modeling.

1. **Muramoto H, Hesketh J & El-Sharkawy M.** Relationships among rate of leaf area development, photosynthetic rate, and rate of dry matter production among American cultivated cottons and other species. *Crop Sci.* 5:163-6, 1965.
2. **Haberlandt G.** "Kranztypus," vascular bundle sheath cells containing chloroplasts, along with mesophyll cells. *Physiologische Pflanzenanatomie.* Leipzig: Engelmann, 1904. p. 253.
3. **Laetsch W M.** The C_4 syndrome: a structural analysis. *Annu. Rev. Plant Physiol.* 25:27-52, 1974. (Cited 200 times.)
4. **El-Sharkawy M A, Loomis R S & Williams W A.** Photosynthetic and respiratory exchanges of carbon dioxide by leaves of the grain amaranth. *J. Appl. Ecol.* 5:243-51, 1968.
5. **National Research Council. Board on Science and Technology for International Development (BOSTID).** *Amaranth: modern prospects for an ancient crop.* Washington, DC: National Academy Press, 1984. 90 p.
6. **El-Sharkawy M A & Cock J H.** Water use efficiency of cassava. I. Effects of air humidity and water stress on stomatal conductance and gas exchange. *Crop Sci.* 24:497-502, 1984.
7. **El-Sharkawy M A, Cock J H & De Cadena G.** Influence of differences in leaf anatomy on net photosynthetic rates of some cultivars of cassava. *Photosynth. Res.* 5:235-42, 1984.

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