This Week's Citation Classic®

Evans L T & Dunstone R L. Some physiological aspects of evolution in wheat.
Aust. J. Biol. Sci. **23**:725-41, 1970.
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In order to gain a wider perspective on the physiological changes that have accompanied and contributed to wheat domestication and improvement, wild progenitors and cultivated wheats at the diploid, tetraploid, and hexaploid levels were compared for photosynthesis, respiration, translocation, growth, and other physiological attributes. [The *SCI*® indicates that this paper has been cited in over 135 publications.]

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November 10, 1986

Twenty years ago I was asked to review Hutchinson's book, *Essays on Crop Plant Evolution*,[1] and was struck by how much use cytogeneticists interested in crop domestication had made of wild relatives and presumed progenitors, compared with the almost total neglect of these plants by physiologists. The last sentence of my review, urging my colleagues to widen their physiological comparisons by including wild progenitors, was deleted by the editor. This stimulated me to begin the process myself, although most of my research until then had been in a different field (the physiology of flowering).

Wheat seemed the best prospect for such work because its wild progenitors were both known and available. (As it turned out, they were "known" with rather more confidence then than now.) So I began assembling a comprehensive set of genotypes and getting acquainted with them in preliminary experiments, in which I was enthusiastically joined by Bob Dunstone.

Our main experiments explored many aspects of the comparative physiology of wheat domestication and improvement. But the finding for which our paper is usually cited was the unexpected observation that the maximum photosynthetic rate per unit leaf area in wheat had *fallen*, not risen, in the course of domestication. Here was a striking paradox. Yield in wheat, as in many crops, is greater when crop photosynthesis is increased by raising irradiance or CO_2 levels, so how could improved yield potential be associated with a fall in maximum photosynthetic rate? There were many sceptics, some of whom misunderstood the nature of the paradox. However, our finding was confirmed sooner than we expected because, unknown to us, Khan and Tsunoda had been working with a comparable range of material in Japan,[2] and their paper was sent for publication only a month after ours.

Two clues to the subsequent resolution of the paradox were presented in our 1970 paper. First, although the flag leaves of wild progenitors reached higher photosynthetic rates, these declined more rapidly than those of the modern varieties, so that after several weeks the ranking for photosynthetic rate corresponded more closely with that for yield potential. Secondly, the higher rates of the wild progenitors were associated with smaller leaves; subsequent research suggests that selection for larger leaves is generally associated with a fall in photosynthetic rate per unit leaf area, but that crop photosynthesis and growth gain more from the former than they lose from the latter.

Dunstone and I went on to explore other aspects of wheat physiology, and the generality of our findings was checked in cowpeas by Mary Lush[3] and in rice by Mary Cook,[4] as well as in other crops elsewhere. As a result, the comparative physiology of crop domestication and improvement is now better understood.[5]

The paper has probably been cited by crop physiologists from so many countries because of the perspective gained from these experiments rather than for the individual findings. It would be nice to think that some of the fellowships and honours that have come my way derived from this and related papers,[6] but I gather that they were for my more "basic" work on the physiology of flowering, which would never reach *Classic* citation rates.

1. **Hutchinson J,** ed. *Essays on crop plant evolution.* Cambridge, England: Cambridge University Press, 1965. 204 p.
2. **Khan M A & Tsunoda S.** Evolutionary trends in leaf photosynthesis and related leaf characters among cultivated wheat species and its wild relatives. *Jpn. J. Breed.* **20**:133-40, 1970.
3. **Lush W M & Evans L T.** The domestication and improvement of cowpeas (*Vigna unguiculata* (L.) Walp.) *Euphytica* **30**:579-87, 1981.
4. **Cook M G & Evans L T.** Some physiological aspects of the domestication and improvement of rice (*Oryza* spp.). *Field Crop. Res.* 6:219-38, 1983.
5. **Evans L T.** Physiological aspects of varietal improvement. (Gustafson J P, ed.) *Gene manipulation in plant improvement: 16th Stadler Genetics Symposium.* New York: Plenum, 1984. p. 121-46.
6. **King R W, Wardlaw I F & Evans L T.** Effect of assimilate utilization on photosynthetic rate in wheat. *Planta* **77**:261-76, 1967. (See also commentary in: *Contemporary classics in plant, animal, and environmental sciences.* Philadelphia: ISI Press, 1986. p. 48.)