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# This Week's Citation Classic

**Heber U.** Metabolite exchange between chloroplasts and cytoplasm. *Annu. Rev. Plant Physiol.* **25**:393-421, 1974. [Botanisches Institut, Universität Düsseldorf, Federal Republic of Germany]

**Chloroplasts are bounded by an envelope which is tight enough to retain even *in vitro* the components of the complex biochemical machinery necessary to perform photosynthesis. Yet it also permits efficient export not only of products but also of intermediates. The article attempts to describe how the dilemma of having to keep the vessel tight while allowing transfer is solved. [The *SCI*® indicates that this paper has been cited over 150 times since 1974.]**

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"My involvement with the material of this review dates back to 1957 when I worked at the University of Bonn on plant frost hardiness. It became of interest to know whether sucrose and other water-soluble sugars can act as cryoprotectants in leaves providing protection against freezing to sensitive chloroplast membranes. Behrens's method to isolate liver nuclei in a non-polar solvent from freeze-dried liver was adopted for chloroplasts. It permits rapid freeze-stopping and leaves water-soluble compounds where they are *in vivo.* Incidentally, non-aqueous methods of chloroplast isolation were developed simultaneously and independently by Stocking[1] and by Thalacker and Behrens.[2]

"It turned out that in chloroplasts of frost-hardy leaves there is enough cryoprotectant present to protect chloroplast membranes against freezing. Damage to photosynthetic membranes aroused interest in photosynthesis. The hope to alleviate ignorance led to stays in Berkeley and Stanford where photosynthesis research flourished. It soon became apparent that much work had been done on the flow of carbon and of electrons in photosynthesis, but little or none on the flow of photosynthetates in the cell. Non-aqueous chloroplasts offered themselves as research tools. The findings of the first years obtained in collaboration with J. Willenbrink,[3] K.A. Santarius, Margret Hudson and U. Hallier[4] of the University of Bonn and with W. Ullrich and W. Urbach[5] of the University of Wurzburg were disturbing; some of them were in conflict with published evidence. While everyone knew that isolated chloroplasts readily reduced added NADP in the light, chloroplast and cytoplasmic NADP pools appeared to be separated. 3-Phosphoglycerate which was supposed to be in separate respiratory and photosynthetic pools appeared to mix freely. Sucrose, a reputed end-product of photosynthesis, did not appear to be synthesized in the chloroplasts. Confusion and disbelief by others were disheartening. A scientific controversy flared up which helped to stiffen the back. Fortunately, by this time work on aqueously isolated chloroplasts had improved considerably and contributed to clarify the issue. H.W. Heldt in Munich identified specific translocators in the chloroplast envelope and published very elegant studies on their role in transport.[6] Shuttle transfer and its significance for energy metabolism was first demonstrated by C.R. Stocking[7] in Davis and later in my laboratory, now in Düsseldorf, in collaboration with C.H. Krause[8] and K.A. Santarius.[9] M. Kirk and H. Gimmler came to Düsseldorf and also provided valuable information. Slowly the pieces of the puzzle fell into place. When I received an invitation to write on the subject, D.A. Walker already had a much better review in press[10] than I ever hoped to produce. I first considered to decline the offer, but then some aspects seemed to merit broader coverage, and so another review came into existence. "I am supposed to express an opinion on why this publication is often cited but I find it difficult to explain a surprise without doing research."

1. **Stocking C R.** *Meth. Enzymol.* **23**:221-8, 1971.
2. **Thalacker R & Behrens M. Z.** *Naturforsch.* **14b:**443-6, 1959.
3. **Heber U & Willenbrink J.** *Biochim. Biophys. Acta* **82**:313-24, 1964.
4. **Heber U, Santarius K A, Hudson M A & Hallier U W.** *Z Naturforsch.* **22b:** 1189-99, 1967.
5. **Heber U, Santarius K A, Urbach W & Ullrich W.** *Z. Naturforsch.* **19b**:576-87, 1964.
6. **Heldt H W.** *Horiz. Biochem. Biophys.* **2**:199-229, 1976.
7. **Stocking C R & Larson S A.** *Biochem. Biophys. Res. Commun.* **37**:278-82, 1969.
8. **Heber U & Krause G H.** Transfer of carbon, phosphate energy and reducing equivalents across the chloroplast envelope. (Hatch M D, Osmond C B & Slatyer R O, eds.) *Photosynthesis and photorespiration.* New York: Wiley Interscience, 1971. p. 218-25.
9. **Heber U & Santarius K A.** Z. *Naturforsch.* **25b**:718-28, 1970.
10. **Walker D A.** Chloroplast and cell—the movement of certain key substances, etc. across the chloroplast envelope. (Northcote D H, ed.) *Plant biochemistry.* London: Butterworth. 1974. p. 1-49.