

## Energy-Linked Potassium Influx as Related to Cell Potential in Corn Roots—Commentary

**Cheeseman JM, Hanson JB (1979)** Energy-linked potassium influx as related to cell potential in corn roots. *Plant Physiol* **64**: 842–845

Jack Hanson was an early and vociferous proponent of the chemiosmotic hypothesis as an explanation for the transport of ions across plant membranes. Both in studies of plant mitochondria and of plant roots, during the 1960s and 1970s, his lab promoted the hypothesis with respect to coupled proton and ion transport. For roots in particular, Hanson strove to make the link between proton fluxes and nutrient acquisition, especially potassium (Hanson, 1978).

Leading up to this article, the Hanson lab had a vibrant mix of students working on membrane transport in mitochondria (David Day, Janice Kimpel, Samir Abou-Khalil, and Paul Birnberg), isolated plasma membranes (John Gronewald), and intact roots (Willy Lin, John Cheeseman, Chris Chastain, and Pete Lafayette). By 1977, it was possible to combine two of the cutting-edge techniques of the day, isotope transport and electrophysiology, with mathematical modeling based on biophysical principles. The result was this seminal study of the role of the plasmalemma  $H^+$ -ATPase in generating a nonequilibrium membrane potential and of potassium transporters, both “active” and “passive,” in dissipating it.

The first critical finding, based on inhibitor treatments, was that in the absence of the proton pump or at high  $K^o$  (the electrical chemical activity of  $K^+$  in the external medium),  $K^+$  fluxes were as predicted from a constant passive permeability. However, that permeability was itself dependent on the mechanism by which the pump was inactivated. The nature of “passive permeability,” however, was (and is) poorly understood. The passive model also failed at low  $K^o$ .

As  $K^o$  was increased from the “mechanism I” into the “mechanism II” range, this study demonstrated clearly not a definable break but a gradual substrate inhibition of carrier function. At the same time, there was a  $K^+$  stimulation of electrogenic plasma membrane ATPase activity. Thus,  $K^+$  transporters (at the time believed to be associated directly with the ATPase) were suppressed while the  $H^+$ -extruding function was increased, giving a substantial hyperpolarization of the pump component of the membrane potential.

Not long after publication of this article, interest in ion transport largely shifted to the molecular level (although H.J. Kronzucker’s lab is a noteworthy exception). Thus, we now know that the number of genes encoding putative transport proteins is much greater than the one or two we envisioned. The cost of this shift, however, may well have been a loss of appreciation of the connection between genes and physiology. As noted by Véry and Sentenac (2003), “There has been little progress from molecular studies in identifying active  $K^+$  transport systems and elucidating their mode of energization” (p. 593). As plant biology progresses from the -omic level to that of integrated systems biology and, finally, once again, to addressing organismal biology (Kronzucker et al., 2001), studies such as those of Hanson and his students will be appreciated for their prescience.

### LITERATURE CITED

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