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This Week's Citation Classic®

Spanswick R M. Electrogenic ion pumps. *Annu. Rev. Plant Physiol.* 32:267-89, 1981.
[Section of Plant Biology, Division of Biological Sciences, Cornell University, Ithaca, NY]

The evidence for electrogenic ion pumps in plant cells was reviewed. A case was presented for the existence of an electrogenic, ATP-dependent H^+ pump, and the theoretical and experimental basis for a relationship between pump activity and membrane conductance was restated. [The *SCI®* indicates that this paper has been cited in more than 280 publications.]

Creating Plant Proticity

Roger M. Spanswick
Section of Plant Biology
Division of Biological Sciences
Cornell University
Ithaca, NY 14853-5908

This review article was published at the transition between two phases of investigation of ion transport in plants. It was preceded by two decades of electrophysiological work that had established the importance of electrogenic ion pumps in controlling the resting electrical properties of plant cell membranes, and it marked the beginning of subsequent work[1] providing a direct demonstration of H^+ transport in isolated membrane vesicles.

The electrophysiological approach was important because of the inherent problems involved in measuring unidirectional or even net H^+ fluxes in intact cells and tissues. Particularly in Characean cells, in which it was possible to make accurate measurements of membrane conductance, there was a clear discrepancy between measured values of both membrane potential and conductance compared to those based on estimates using fluxes of the major ions and the constant field equations, as had been advocated as an initial hypothesis by Jack Dainty in his review[2] 19 years earlier. As a graduate student in the Biophysics Department in Edinburgh, I helped Dainty proof his review by reading aloud every word and punctuation mark. Upon reading the proofs of my own review, I was reminded that an apparent difference between American and British usage was evident in both cases in the replacement of each instance of "due to" by "because," or was it simply that the same person was still copy editor for *Annual Reviews*? In any case, my own work was heavily influenced by Dainty, including my first paper[3] with my PhD advisor Elwyn Williams, which laid the basis for much of my later work in this area and was itself an earlier *Citation Classic®*.

The idea of a "conducting pump," while not original, was somewhat at odds with most contemporary treatments which assumed that electrogenic pumps acted as constant current sources. The attribution of conductance to the electrogenic pump in the Characeae has stood the test of time and fits well with the recent work on the effect of orthovanadate on the electrical properties of *Nitella*.[4] Whether the electrogenic pumps of higher plants exhibit high conductance at the resting potential is still not well established because it is difficult to measure the conductance accurately when plasmodesmata provide significant leakage of current to neighboring cells. In principle, it should be possible to approach this problem by using whole-cell patch clamp techniques, but there are quantitative problems relating to access and seal resistances that still have to be resolved.

While the electrophysiological evidence for the presence of an H^+ pump in the plasma membrane of plant cells was indirect, it did coincide with attempts to apply the chemiosmotic approach to transport of ions and organic molecules across plant cell membranes, and complemented work on proton cotransport systems. It also attracted the attention of developmental plant physiologists interested in the "acid growth" hypothesis for auxin action. Thus it gained more attention than if it had been of interest only to the relatively small community of plant electrophysiologists.

The review also mentioned unpublished work, from my own and other laboratories, on direct demonstrations of ATP-dependent H^+ transport in isolated membrane vesicles. It took us three attempts to publish our own work,[5] but that gave us time to identify the membranes as being of tonoplast rather than plasma-membrane origin. It was, in fact, one of the few cases in which work on plants presaged work on animal systems, which have a very similar ATPase (now known as the V-type ATPase) associated with acidic organelles such as the lysosome.

1. **Sze H.** H^+-translocating ATPases: advances using membrane vesicles. *Annu. Rev. Plant Physiol.* 36:175-208, 1985. (Cited 470 times.) [See also **Sze H.** Life and H^+ pumps. Citation Classic. *Current Contents/Agriculture, Biology & Environmental Sciences* 24(18):8, 3 May 1993.]
2. **Dainty J.** Ion transport and electrical potentials in plant cells. *Annu. Rev. Plant Physiol.* 13:379-402, 1962. (Cited 185 times.)
3. **Spanswick R M & Williams E J.** Electrical potentials and Na, K, and Cl concentrations in the vacuole and cytoplasm of *Nitella translucens*. *J. Exp. Bot.* 15:193-200, 1964. (Cited 135 times.) [See also: **Spanswick R M.** Citation Classic. (Barrett J T, comp.) *Contemporary classics in plant, animal, and environmental sciences.* Philadelphia: ISI Press, 1986. p. 77.]
4. **Cruz-Mireles R M & Ortega-Blake I.** Effect of Na_3VO_4 on the P state of *Nitella translucens*. *Plant Physiol.* 96:91-7, 1991.
5. **DuPont F M, Bennett A B & Spanswick R M.** Proton transport in microsomal vesicles from corn roots. (Marmé D, Marrè E & Hertel R, eds.) *Plasmalemma and tonoplast: their functions in the plant cell: report of a workshop held September 8-11, 1981. Strasbourg, France.* Amsterdam, The Netherlands: Elsevier, 1982. p. 409-16.

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