

**Epstein E & Hagan C E.** A kinetic study of the absorption of alkali cations by barley roots. *Plant Physiol.* 27:457-74, 1952.

Rates of absorption of rubidium ions by excised barley roots are interpreted in terms of enzyme kinetics. The ion corresponds to the substrate, and a 'carrier' to the enzyme. Instead of catalysis through formation of an enzyme-substrate complex, the effect is ion transport across the membrane via transitory formation of a carrierion complex. Potassium and rubidium were found to be mutually competitive; sodium did not effectively compete with them. [The SC<sup>®</sup> indicates that this paper has been cited over 145 times since 1961.]

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"This was, I believe, the first paper in which experimental results on biological ion transport were interpreted in terms of Michaelis-Menten formalism as applied by its originators to enzymic catalysis. Such analysis of transport is commonplace now. Let me trace its genesis in work with plant tissue.

"I did my Ph.D. work with P. R. Stout in D. R. Hoagland's famous Division of Plant Nutrition in Berkeley after World War II. Stout pioneered the use of radioisotopes in the study of mineral plant nutrition. From him I learned to handle this new and powerful tool. It made possible accurate determinations of absorption rates in short experimental periods, essential for what was to follow.

"Equally important was what I learned in class. Hoagland insisted that the permeability of plant cell membranes to inorganic ions was low. He and his collaborators had shown that ion transport was driven by active cell metabolism. And several investigators—Hoagland himself, W. J. V. Oster-

hout, L. Jacobson and R. Overstreet, among others—had conceived of what were variously called 'binding compounds' or 'carriers' or 'pumps' which effected the absorption of ions by plant cells from their medium. That idea had become central to my thinking when, in 1950, I joined the new Department of Agriculture radioisotope unit in Beltsville, Maryland.

"With the encouragement of S. B. Hendricks, I set out to investigate the mechanism by which plants preferentially absorb potassium in favor of sodium—only one instance, I knew, of a phenomenon common throughout the world of life. As Stout's research assistant, I had often analyzed plant tissues for potassium and sodium. (The determinations were done by gravimetric analysis!) Potassium predominated, whether there was much or little sodium in the soil.

"I discussed the matter with C. E. Hagen, another new arrival. Sodium either did not interfere with the entry of potassium, we reasoned, or did so feebly. Did competition kinetics prevail? But it soon dawned on us that even straightforward kinetic analyses were lacking. Then came one of those flashes of insight, so common in popular accounts of science, so rare in reality: if ion absorption rates followed Michaelis-Menten kinetics, the 'carrier' concept would receive a powerful boost—would become a rigorously testable hypothesis of ion transport.

"I taught myself the excised barley root technique which I had never even observed in Berkeley where it originated. I used rubidium labeled with <sup>86</sup>Rb as an analog of potassium in the experimental solutions, and thus a start was made in the enzyme-kinetic analysis of ion transport in plants. Later, at Davis, the story turned out to be much more complex than it seemed at first,<sup>1</sup> but the basic scheme has stood the test of time."

I. **Epstein E.** Kinetics of ion transport and the carrier concept. *Encyclopedia of plant physiology.* New Series. Vol. 2. Part B. (Lüttge U & Pitman M G. eds.) Berlin: Springer-Verlag! 1976. p. 70-94.