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This Week's Citation Classic®

Fischer R A & Hsiao T C. Stomatal opening in isolated epidermal strips of Vicia faba. II. Responses of KCl concentration and the role of potassium absorption. *Plant Physiol.* 43:1953-8, 1968.
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Stomatal opening in light in isolated epidermal strips was stimulated by floating them on KCl solutions. Opening was closely associated with net potassium uptake, which was sufficient to account for the increase in guard-cell osmotic pressure. A new mechanism of stomatal opening was proposed. [The *SCI*® indicates that this paper has been cited in over 110 publications since 1968.]

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The work arose as I was drawing to the close of a somewhat unadventurous PhD research project in the Department of Water Science and Engineering at the University of California (UC), Davis. Epidermal strips or peels of tobacco and broad-bean leaves were tested as part of a study on the aftereffect of water stress on stomata, which are located in the epidermis. The exciting result was that the stomata were able to open partially when the epidermal strips were replaced on top of exposed leaf mesophyll and illuminated. For a long time, the mechanism of stomatal opening had intrigued scientists. Although the classical starch-sugar hypothesis (internal generation of increased osmotic pressure through starch to sugar conversion) still held sway, there were several other competing hypotheses. The challenge that arose was to see if the stomata in isolated epidermal strips with no other living cells present could be made to function normally when kept away from leaf mesophyll.

It was in fact not very difficult to demonstrate stomatal opening in isolated epidermal strips of the broad bean. Floating the strips on 10 mM KCl was sufficient to permit opening in response to light plus CO_2-free air. In terms of aperture change, guard-cell osmotic pressure increase, and cytoplasmic streaming, the opening response matched that of nonisolated stomata. The response to potassium concentration and the measurement of potassium uptake with radioactive tracers, which confirmed that accumulated potassium plus an anion could account for the osmotic pressure increase, were reported in this paper. It was suggested that the observed starch breakdown, rather than low molecular weight sugars, might provide both energy and organic acid anions. We were lucky with our reporting of the results because, unknown to us, a Japanese worker, M. Fujino, had come close to the same conclusion regarding the role of potassium accumulation,[1] but initially had published in obscure Japanese bulletins.

Our paper and the ones surrounding it[2,3] caused considerable interest and some controversy,[4] because it was the first unequivocal proof for a mechanism by which guard-cell osmotic pressure increased. Also, the mechanism proposed contradicted the classical hypothesis. There was interest from both ion uptake physiologists, who were well represented at UC Davis and had stimulated our thinking, and from stomatal physiologists. Since 1970 there has been a great increase in stomatal research, with the development of very refined techniques for the study of guard-cell mechanisms[5] and renewed interest in the relationship of function to mechanisms of aperture control.[6]

It is gratifying that the basic tenets of our paper have not been overturned and that at least some of this renaissance of interest in stomata might have stemmed from the work. I was awarded first prize in the 4th International Potash Institute Competition for Young Research Workers in 1972. My research nowadays, however, is largely in crop physiology and agronomy. Ted Hsiao, my PhD thesis adviser and now a professor at UC Davis, continues to run an outstanding research and teaching facility in plant-water relations.

1. **Fujino M.** Adenosinetriphosphate and adenosinetriphosphatase in stomatal movement. *Sci. Bull. Fac. Educ. Nagasaki Univ.* 18:1-47, 1967. (Cited 125 times.)
2. **Fischer R A.** Stomatal opening in isolated epidermal strips of Vicia faba. I. Response to light and CO_2-free air. *Plant Physiol.* 43:1947-52, 1968. (Cited 65 times.)
3. ----------. Aspects of potassium accumulation by stomata of *Vicia faba*. *Aust. J. Biol. Sci.* 25:1107-23, 1972.
4. **Levitt J.** Stomatal opening: role of potassium uptake. *Science* 163:494, 1969.
5. **Zeiger E.** The biology of stomatal guard cells. *Annu. Rev. Plant Physiol.* 34:441-75, 1983.
6. **Zeiger E, Farquhar G D & Cowan I R, eds.** *Stomatal function*. Stanford, CA: Stanford University Press. In press, 1985.

