

Flowers T J, Troke P F & Yeo A R. The mechanism of salt tolerance in halophytes. *Annu. Rev. Plant Physiol.* 28:89-121, 1977. [School of Biological Sciences. University of Sussex, Falmer, Brighton, Sussex. England]

This review defined halophytes as plants able to complete their life cycle at high external salinities with high internal ion concentrations. High rates of ion uptake were judged important in osmotic adjustment. Evidence from metabolic studies together with direct measurements suggested a distinct compartmentation of ions within cells. Simple organic substances were surmised to act as compatible solutes in balancing cytoplasmic and vacuolar water potentials. [The SC[®] indicates that this paper has been cited in more than 505 publications.]

Sun, Salt, and Halophytes

Tim J. Flowers School of
Biological Sciences
University of Sussex
Sussex BN1 9QG, England

The summer of 1976 was exceptionally hot and dry in Britain, and I clearly remember driving Jack Hanson across the Sussex Downs, uncharacteristically brown from the drought. It was a talk with Jack that started me on the study of halophytes, and the publication of this review and my subsequent work owe much to him.

Having completed my doctoral work with Fred Milthorpe in Sutton Bonington during 1967, Doyle Peters, a visitor at the School of Agriculture, arranged for me to spend a year at the University of Illinois: I was to work in Jack's laboratory on mitochondria from soybean. At some time towards the end of my year in Urbana, Jack and I were discussing the effects of solutes on enzymes—since I had been exposing mitochondria and mitochondrial enzymes to various osmotica—and the question of whether halophytes might have "salt-tolerant" enzymes arose. It was this discussion (I am not sure exactly when it happened) that set me on the path that has dominated my research to date.

I moved to the University of Sussex in the late summer of 1968 and began collecting

shoots of halophytes from the coast nearby and assaying their enzymes. In 1971 I was joined by my first graduate student, Tony Yeo: Tony investigated the physiology of what must now be my favourite plant, *Suaeda maritima*. We were later joined by Peter Troke, whose thesis on "Salt Tolerance in Fungi" was completed in 1976. It was the combination of Tony's and Peter's literature searches—a somewhat more tedious process in the early 1970s than at present—and the dearth of then-current reviews (the previous *Annual Review* looking at salt tolerance in plants as a whole had been published 19 years earlier¹) that pointed to a clear niche for a new analysis. A letter was sent to Jack, who was on an *Annual Review* editorial committee, and our article was "commissioned." In rereading our review I can clearly see Tony's contribution on ion transport and Peter's on compatible solutes: I suppose I filled in the gaps.

I never noticed that the review had a dramatic influence on my research or that of others, but studies of the effects of salinity on plants have continued to grow steadily over the years, presumably reflecting the ever-growing need for irrigation and the use of marginal saline land in agriculture. There were nearly 200 papers on higher plants in which the title or keywords referred to salinity published in 1992: In 1981 only about 50 such papers contained the word salinity in the title. In spite of the research efforts involved, however, we are still struggling to raise productivity on these lands. Halophytes could play an important role if they can be suitably domesticated, and this may be a reason for the "success" of the review. Recently the distribution of halophytes among the flowering plants has been extensively mapped.² We have continued to improve the methodology for the use of ion localisation in plants³ and to try to understand the physiological and biochemical basis of salt tolerance in *Suaeda maritima*.^{4,5} We⁶ and others⁷ have continued to review progress in the field.

1. Bernstein L & Hayward H E. Physiology of salt tolerance. *Annu. Rev. Plant Physiol.* 9:25-46. 1958. (Cited 265 times.)
2. Aronson J A. *Haloph: a data base of salt tolerant plants of the world*. Tucson, AZ: Office of Arid Land Studies. University of Arizona, 1989. 77 p.
3. Hajibagheri M A & Flowers T J. Ion localization in plant cells using the combined techniques of freeze-substitution and X-ray microanalysis. *X-ray microanalysis in biology: experimental techniques and applications*. (Sigeo D C, Morgan A J, Sumner A T & Warley A, eds.) Cambridge, England: Cambridge University Press, 1993. p. 217-30.
4. Leach R P, Wheeler K P, Flowers T J & Yeo A R. Molecular markers for ion compartmentation in cells of higher plants. [I. Lipid composition of the tonoplast of the halophyte *Suaeda maritima* (L.) Dum. *J. Exp. Bot.* 41:1089-94. 1990.
5. Flowers T J & Dalmond D. Protein synthesis in halophytes: the influence of potassium, sodium and magnesium in vitro. *Plant Soil* 146:153-61. 1992.
6. Flowers T J, Hajibagheri M A & Clipson N J W. Halophytes. *Quart. Rev. Bot.* 61:313-37. 1986.
7. Rozema J. Growth, water and ion relationships of halophytic monocotyledonae and dicotyledonae: a united concept. *Aquat. Bot.* 39:17-33. 1991.

Received October 15, 1993