

Lyons J M. Chilling injury in plants. *Annu. Rev. Plant Physiol.* 24:445-66, 1973.
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This review article summarized the horticultural and physiological manifestations of chilling injury—a descriptive term for the physiological damage that occurs to many tropical and subtropical plants when exposed to low, but non-freezing temperatures in the chilling range (generally 15°C down to 0°C). Additionally, a proposed mechanism to describe how these low, but non-freezing temperatures, could lead to this physiological damage was articulated, which proposed as the common event that of a temperature-induced phase transition in the cellular membranes as the primary response to chilling injury. [The SCF® indicates that this paper has been cited in more than 515 publications.]

On Comparing Apples and Oranges: Chilling Injury Revisited

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In an earlier *Citation Classic*®,¹ I described the genesis of the hypothesis that a temperature-induced change in membrane structure provided a mechanism to explain how low temperature brought about the physiological changes leading to chilling injury in sensitive plants; and how John Raison, scientific officer in the Plant Physiology Unit, Commonwealth Scientific and Industrial Research Organisation, at Sydney University, Australia, and I collaborated on a series of experiments which led to articulation of the hypothesis described in this 1973 review. This original research measured the respiration rates in vitro of mitochondria derived from plants sensitive and insensitive to chilling injury as a function of temperature. Differences between the two suggested that a physical transition or phase change occurs in cellular membranes of chilling-sensitive plants when exposed to low temperatures in the 10°C to 12°C range which did not occur in chilling-insensitive species.

In that *Citation Classic*,¹ I described that the thermotropic membrane lipid-phase-transition hypothesis developed by John and me was

seriously questioned, and yet it was widely used to explain the alterations in metabolic activity in chilling-sensitive plants at low but nonfreezing temperatures (the reason I professed for our many citations). Two aspects of this scientific controversy are worth revisiting some 20 years later. One is that there was considerable discussion at scientific meetings on our work, and occasional mention in literature, that by comparing responses of chilling-sensitive and chilling-insensitive plants very little of value could be derived because we were in fact trying to compare "apples and oranges." That is, these comparisons were of species from evolutionarily distant taxa, and hence the studies would preclude any genetic analysis of differential low-temperature response.² In some recent studies, R.S. Criddle et al.³ have reported on experiments with plant calorimetry demonstrating that calorimetric measurements, in conjunction with measurement of other input-output parameters, provide a quantitative understanding of metabolism which demonstrates in a most elegant fashion the value in comparing "apples and oranges."

The second noteworthy aspect of this controversy was that John and I often talked about the definitive experiment to establish the validity of our hypothesis. That experiment was to transfer through microinjection technology, which was developing at the time, the "membranes" from chilling-sensitive to chilling-insensitive species (and the reciprocal) to ascertain whether we could reverse the temperature response in each case. While we never initiated these experiments, it appears that Norio Murata and his laboratory⁴ have conducted "the definitive experiment." That is, they have demonstrated that they can influence the degree of chilling-sensitivity of *Nicotiana tabacum* by transformation with complementary DNAs for glycerol-3-phosphate acyltransferases from highly chilling-sensitive squash and from chilling-insensitive *Arabidopsis*, and by doing so, alter the sensitivity of the derived transgenic plants.

In a letter to me shortly before his death in March 1991, John wrote and reflected on the science that we had done together, and about the controversies involved in that work, and said, "Whether it will be judged successful research is immaterial. It was satisfying to me." I feel it will be judged successful as well.

1. Lyons J M & Raison J K. Oxidative activity of mitochondria isolated from plant tissues sensitive and resistant to chilling injury. *Plant Physiol.* 45:385-9, 1970. (Cited 255 times.) [See also: Lyons J M. Citation Classic. (Barrett J T, comp.) *Contemporary classics in plant, animal, and environmental sciences*. Philadelphia: ISI Press, 1986. p. 98.]
2. Vallejos C E, Lyons J M, Breidenbach R W & Miller V F. Characterization of a differential low-temperature growth response in two species of *Lycopersicon*: the plastichron as a tool. *Planta* 159:487-96, 1983.
3. Criddle R S, Breidenbach R W & Hansen L D. Plant calorimetry: how to quantitatively compare apples and oranges. *Thermochim. Acta* '93:67-90, 1991.
4. Murata N, Ishizaki-NUhizawa O, Higashi S, Hayashi H, Tasaka Y & Nishida I. Genetically engineered alteration in the chilling sensitivity of plants. *Nature* 236:710-3, 1992.

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