

Ridge I & Osborne D J. Hydroxyproline and peroxidases in cell walls of *Pisum sativum*: regulation by ethylene. *J. Exp. Bot.* 21:843-56, 1970.  
[Agricultural Research Council, Unit of Experimental Agronomy, Dept. Agricultural Science, Univ. Oxford, England]

This paper implicated two covalently bound wall proteins in the control of plant cell expansion. It showed that ethylene gas increases the levels of wall-bound peroxidases and hydroxyproline-rich glycoproteins in peas, where the gas is a natural regulator that slows down cell expansion. [The SC1® indicates that this paper has been cited in over 130 publications since 1970.]

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"By 1968, when I completed my doctorate, ethylene had become (just about) acceptable to plant physiologists as a true growth regulator rather than as a metabolite with strange effects on growth. I had worked on both ethylene and peroxidases for my dissertation, supervised by Daphne Osborne, and welcomed the offer to remain with her during the last two years of the Agricultural Research Council Unit's existence in Oxford. We were interested in cell growth and wanted to know how a simple hydrocarbon gas acted so powerfully to slow down and reorient expansion in pea stems, producing short, broad cells. Looking for ethylene-induced changes in cell walls seemed to offer the best hope of solving the problems.

"Early in 1969, I began to follow up a chance observation made with fresh sections of pea stems stained for peroxidase activity that there seemed to be a lot more activity associated with cell walls after ethylene treatment. Ethylene did, it turned out, increase markedly the levels of both ionically and covalently bound isozymes of peroxidase associated with cell walls, especially in young cells. But since no one knew then (or now) what is the function of wall-bound peroxidases, this did not seem to help in ex-

plaining ethylene's action on cell growth. Two things now combined to trigger a more fruitful line of enquiry: the knowledge that horseradish peroxidases contain hydroxyproline and Lampport's paper<sup>1</sup> about the proteins of cell walls, especially the hydroxyproline-rich glycoprotein fraction, which seemed a possible candidate as a cross-linking agent that determined the capacity of walls to be loosened and stretched. The idea occurred that ethylene might slow down cell expansion by increasing the levels of hydroxyproline-rich protein in cell walls and that covalently bound wall peroxidases might be one of these proteins.

"All techniques were to hand, except the assay for hydroxyproline and, having mastered this, it took only a week to show that ethylene does indeed increase the levels of hydroxyproline in wall proteins. The eventual outcome was this paper linking together the unlikely bedfellows of ethylene, peroxidases, and hydroxyproline-rich proteins and making several speculative suggestions, one of which (that wall peroxidases may hydroxylate proline in wall proteins) we later showed to be quite wrong<sup>2</sup> while another (that covalently bound wall peroxidases were hydroxyproline-rich) was given some support.<sup>2</sup>

"It would be gratifying, but untrue, to say that this paper has become a *Citation Classic* because it was right. More realistically, it was interestingly wrong and may have stimulated others to prove it so: present evidence suggests that ethylene inhibition occurs too rapidly to be accounted for by deposition of hydroxyproline-rich proteins. Even more realistically, it has probably been cited by workers in quite separate fields for quite different reasons: by 'peroxidase-ologists' because it was one of the first papers to draw attention to wall-bound peroxidases and describe an assay for them; by people working on ethylene, for the reasons given above; and by people interested in wall proteins, especially those with a physiological rather than purely biochemical bent.

"A recent review of ethylene action appeared in *Annual Review of Plant Physiology*<sup>3</sup> and of wall proteins in *The Biochemistry of Plants, Volume 3*.<sup>4</sup>

1. Lampport D T A. The protein component of primary cell walls. *Advan. Bot. Res.* 2:151-218, 1965.
2. Ridge I & Osborne D J. Role of peroxidase when hydroxyproline-rich protein in plant cell walls is increased by ethylene. *Nature-New Biol.* 229:205-8, 1971.
3. Lieberman M. Biosynthesis and action of ethylene. *Annu. Rev. Plant Physiol.* 30:533-91, 1979.
4. Lampport D T A. Structure and function of plant glycoproteins. (Preiss J, ed.) *The biochemistry of plants: a comprehensive treatise. Volume 3. Carbohydrates: structure and function.* New York: Academic Press, 1980. p. 501-41.