This Week's Citation Classic™ CC/NUMBER 50 DECEMBER 10, 1984

Briggs D E. Biochemistry of barley germination: action of gibberellic acid on barley endosperm. *J. Inst. Brew.* **69**:13-19, 1963.
[Brewing Industry Research Foundation, Nutfield, Surrey, England]

In gibberellic acid solution, decorticated and degermed barley grains produced many hydrolytic enzymes. The starchy endosperm frequently dissolved, and soluble substances appeared in the liquid. In response to gibberellic acid, α-amylase appeared to be synthesised *de novo*, and endosperm breakdown spread from the aleurone layer. [Cited in over 120 publications, this is the most-cited article published in this journal to date.]

Dennis E. Briggs
Sub-Department of Malting and Brewing
Department of Biochemistry
University of Birmingham
Birmingham B15 2TT
England

September 14, 1984

"This publication was one of a series concerned with enzyme formation in barley grains.[1-3] Earlier, there had been conflicting views on whether or not the aleurone layer of the endosperm, like the embryonic scutellum, had a role to play.[4] The work was intended to assist the malting industry, since a key part of malting is the controlled germination of grains.[5,6] The work was carried out in laboratories in a converted stable block at the Brewing Industry Research Foundation, with technical resources that, even then, were primitive and that dictated the experimental approaches used. I had been studying enzyme production by isolated barley embryos supplied with various nutrients. However well they were 'fed,' they produced less α-amylase than appeared in germinating whole grains. Maltsters were using gibberellic acid to accelerate germination, gibberellins had been detected in malt,[7,8] and a weak gibberellin-like organic acid originating in the barley embryo stimulated the production of α-amylase and other enzymes in degermed grains.[8,9] These facts, combined with observations on the effects of gibberellic acid on degermed grains,[8-10] redirected my work.

"The first experiments confirmed that living embryos produced a water-soluble material that induced α-amylase formation in *living* degermed grains—an observation arguing against zymogen activation or the release of a bound, preformed enzyme, as was known to occur with β-amylase. When degermed, decorticated grains were next incubated in liquid with gibberellic acid, it was staggering to see the greater parts of the starchy endosperms dissolve, over several days, demonstrating the gibberellin-induced appearance of enzymes capable of degrading the cell walls, the structural proteins, and the starch. Breakdown products accumulated in the liquid and included sugars, amino acids, peptides, enzymes, and inorganic phosphate. Breakdown spread inward from the aleurone layer, indicating this was the source of at least many of the enzymes, a fact later confirmed using isolated aleurone tissue.[3,4,8] This tissue is also the major source of the inorganic phosphate, and some sucrose.[6,8] Hydrolytic enzymes appeared that could degrade synthetic glycosides, disaccharides, oligosaccharides, polysaccharides, proteins, and dipeptides. Later DNA, RNA, and phosphates were added to the list.[4-6,8] In addition, peroxidase appeared.

"Nutrients had little effect on the production of α-amylase, but respiratory inhibitors and agents blocking protein synthesis were inhibiting, and [C^{14}]-amino acids were incorporated into soluble proteins. Thus it appeared that α-amylase was at least being synthesised *de novo* and was not being released from a zymogen, as had been proposed.

"The reason for the frequent citation of this paper is presumably because it was the first to describe a range of characteristics of the aleurone response to gibberellic acid and appeared just before a massive increase in research on this topic occurred. Although the experiments reported have been criticized, both with and without justification, nearly all the suggestions and conclusions made have withstood further examinations.[4,6,8] Indeed, the fascination of the 'aleurone system' has caused the vital functions of the embryo to be seriously neglected."[5]

1. **Briggs D E.** A modification of the Sandstedt, Kneen and Blish assay of α-amylase. *J. Inst. Brew.* 67:427-31, 1961. (Cited 75 times.)
2. ----------. Development of enzymes by barley embryos *in vitro*. *J. Inst. Brew.* **68**:470-5, 1962.
3. ----------. Origin and distribution of α-amylase in malt. *J. Inst. Brew.* 70:14-24, 1964.
4. ----------. Hormones and carbohydrate metabolism in germinating cereal grains. (Milborrow B V, ed.) *Biosynthesis and its control in plants*. London: Academic Press, 1973. p. 219-77.
5. ----------. Endosperm breakdown and its regulation in germinating barley. (Pollock J R A, ed.) *Brewing science*. London: Academic Press. Vol. 3. In press.
6. **Briggs D E, Hough J S, Stevens R & Young T W.** *Malting and brewing science. Volume 1. Malt and sweet wort.* London: Chapman and Hall, 1981. 389 p.
7. **Radley M.** The occurrence of gibberellin-like substances in barley and malt. *Chem. Ind.—London* **1959**:877-8.
8. **Briggs D E.** *Barley*. London: Chapman and Hall, 1978. 612 p.
9. **Yomo H.** Sterilisation of barley seeds and the formation of amylase by separated embryos and endosperms. *Hakkō Kyōkaishi* **16**:444-8, 1958.
10. **Paleg L G.** Physiological effects of gibberellic acid: I. On carbohydrate metabolism and amylase activity of barley endosperm. *Plant Physiol.* 35:293-9, 1960. [See also: **Paleg L G.** Citation Classic. *Current Contents/Agriculture, Biology & Environmental Sciences* **10**(13):26, 26 March 1979.]

