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This Week's Citation Classic®

Varner J E. Gibberellic acid controlled synthesis of α-amylase in barley endosperm. *Plant Physiol.* 39:413-5, 1964.
[RIAS, Martin-Marietta, Baltimore, MD]

The endosperm half of a barley seed produces several hydrolytic enzymes in response to added gibberellins, making it an attractive experimental system for studying the mechanism of action of gibberellic acid. This paper shows (by the use of a radioactive amino acid) that at least part of the α-amylase is produced in the aleurone layers by *de novo* synthesis. [The *SCI*® indicates that this paper has been cited in over 235 publications.]

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From 1957 to 1961 I studied the influence of the pea shoot-root axis on the cotyledons. Although it was clear that a factor from the axis had some control over metabolism in the cotyledons, I was not able to develop an experimental protocol suitable for purifying the factor or for studying its mode of action. In 1961 I moved to the Research Institute for Advanced Studies (RIAS), a division of the Martin-Marietta Company, in Baltimore, in order to devote my full time to basic research in plant biochemistry.

At RIAS I began to look at the barley endosperm system. In 1960 and 1961 Les Paleg[1] published three papers that showed that gibberellic acid added to the embryo-free barley endosperm caused large increases in α-amylase activity in the endosperm. According to Paleg's papers, this system was clean and convenient and a likely system for studying the biochemistry of hormone action. A search of *Chemical Abstracts* showed that Harugaro Yomo[2] published several short papers in Japanese between 1957 and 1960 on the barley endosperm system. One of these showed that isolated aleurone layers secreted amylase following treatment with gibberellins. Further examination of the literature revealed that G. Haberlandt[3] had published a paper in 1890 that made it clear that he understood the barley endosperm system, that he knew that the starch-modifying activity was secreted by the aleurone layer, and that starch modification did not occur in the absence of the embryo.

I spent the next few weeks doing "quick and dirty" experiments to make sure that I could repeat the main experiments of Haberlandt, Yomo, and Paleg. I used whatever barley line came to hand—it turned out to be Himalaya (Herman Wiebe identified it for me and told me that it could be obtained from R.A. Nilan of the Department of Agronomy at Washington State University). At a later time I tried about 20 different barley lines. None of these had as low a background in the absence of gibberellic acid nor as great a response to added gibberellic acid as the Himalaya variety. Through such serendipity, Himalaya barley seed became a much-used experimental material.

In my first experiments the amylase-catalyzed disappearance of starch-iodine color was estimated by eyeball colorimetry, volumes were quantified by drop counting, and the results were only recorded mentally. It soon became clear that this was a wonderful system, and I settled in to try to understand it. Ram Chandra and Maarten Chrispeels joined me in a deliberate effort to exploit a perfect system handed to us by colleagues we hadn't yet met.

In biology we are dependent on clean systems that behave reproducibly. If the system is also simple, inexpensive, and convenient, so much the better. The barley endosperm system is all of the above. We owe a great debt to the biologists—in this case Paleg, Yomo, and Haberlandt—who bring these systems to our attention.

For 30 years the barley endosperm has been used in studies of gibberellin action, abscisic acid action, biosynthesis of gibberellins, ethylene action, mechanism of secretion, membrane synthesis, control of gene expression, the role of isozymes, anaerobiosis, and, most recently, the role of heat-shock proteins.[4] It still has the attributes of a system that will be useful for years to come.

1. **Paleg L.** Physiological effects of gibberellic acid. III. Observations on its mode of action on barley endosperm. *Plant Physiol.* 36:829-37, 1961. (Cited 90 times.)
2. **Yomo H & Inuma H.** The modification of the ungerminated barley endosperm with gibberellin. *Agr. Biol. Chem. Tokyo* 26:201-2, 1962. (Cited 15 times.)
3. **Haberlandt G.** Die Kleberschicht des Gras-Endosperms als Diastase ausscheidendes Drüsengewebe (The so-called adhesive layer of Gramineae endosperm as diastase of excretory glandular tissue). *Ber. Deut. Bot. Ges.* 8:40-8, 1890. (Cited 25 times since 1955.)
4. **Belanger F C, Brodl M R & Ho T-H D.** Heat shock causes destabilization of specific mRNAs and destruction of endoplasmic reticulum in barley aleurone cells. *Proc. Nat. Acad. Sci. USA* 83:1354-8, 1986.