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THE ARGUMENT FOR CHEMICAL MEDIATION OF NERVE IMPULSES[1]

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WHEN an impulse travels along a nerve it is attended by a quick rise of negative electrical potential, followed by a quick fall. The duration of this "spike potential" includes the absolutely refractory and the relatively refractory periods of nerve function. The fall is not immediately to zero, but is checked by a slower, negative after-potential. And that in turn is followed by a longer, positive after-potential. The changes are more rapid in fibers of large diameter than in small fibers; the spike lasts only 0.4 msec. in the fastest fibers (*e.g.,* those supplying skeletal muscles) and thereupon the nerve can be stimulated again.[2] As elsewhere in the body, such electrical phenomena are signs of physicochemical or chemical processes which accompany functional activity. In nerve there must be to a large extent a restoration of the resting state, when an impulse has passed, before another impulse can traverse the same course. Associated with the electrical phenomena of nervous activity is a use of oxygen, an output of carbon dioxide and a display of heat. Since a nerve soon ceases to transmit impulses in the absence of oxygen, it is reasonable to assume that the increased metabolism, demonstrable when a nerve functions, indicates that chemical work is involved. According to evi-

[1] The annual Alpha Omega Alpha address, given on October 13, 1939, at the celebration of the fiftieth anniversary of the founding of the Medical School of the University of Minnesota.

[2] H. S. Gasser, Harvey Lectures (Baltimore), 32: 169–174, 1937.

the nucellus, are found. Shortly after fertilization active cell division is initiated in the integuments as well as in the endosperm mother cell and the zygote. The cells of the inner integument divide longitudinally so that this tissue normally continues to have two layers of cells at the later stages of development. The cells adjacent to the endosperm are tapetal-like in appearance.

In material collected 48 to 72 hours after pollination in which the collapse of fertile ovules is frequent the cytoplasm of the cells immediately adjacent to the endosperm becomes finely vacuolate and densely staining, and the resemblance to tapetal cells is gradually lost. This condition, which makes its first appearance on the funicular side of the ovule in the region of the vascular bundle, is often seen before any impairment of the embryo sac becomes evident. Breakdown of the endosperm follows, beginning in the chalazal region and progressing toward the embryo. At this stage there is extensive meristematic activity in the chalazal portion of the inner integument. Through transverse division of the cells this tissue may come to be three to five layers in thickness. The ovule may continue to enlarge for several hours, even after the endosperm has broken down, but its growth soon ceases.

The frequency of collapse of fertile ovules in alfalfa is much higher following self-pollination than after outcrossing to unrelated plants. In a representative experiment involving seven individuals on which the two types of matings were made under strictly comparable conditions the average values were 34.4 per cent. and 7.1 per cent., respectively, in the interval up to 144 hours after pollination.[2] The relatively high survival of ovules containing hybrid, as compared with inbred, embryos and endosperms affords a clue to the cause of somatoplastic sterility.

Fertilization initiates development of the embryo and the endosperm and stimulates mitosis in the surrounding somatic tissue. The ovule, quiescent prior to gametic union, suddenly springs into active growth. Further development of these structures is largely dependent upon food moved in from other parts of the plant, the visible reserves immediately at hand in alfalfa being very limited in amount and quickly disappearing after fertilization. The critical factor for survival at this stage seems to be the manner in which the translocated food is shared between the endosperm, on the one hand, and the inner integument, on the other. The partition of nutrients appears to depend upon the rate of growth inside and outside the embryo sac. It may be assumed that the synthetic processes are essentially alike in the different tissues concerned, and hence, that the same raw materials are in concurrent demand. Under these conditions of parallel growth the available foods will be shared between the inner integument and the structures within the embryo sac in proportion to the velocity with which growth is occurring in the respective tissues. Continued development of the ovule following fertilization demands a balance in rate of growth between the endosperm, which is the dominant tissue within the embryo sac, and the adjacent maternal tissue which will insure the nourishment of both. If, during early development, the balance is upset by failure of the endosperm to keep pace with growth in the extensive surrounding tissue the endosperm starves and, eventually, the ovule collapses.

Following hybridization in alfalfa, the rate of growth of the endosperm, as measured by the number of nuclei, is found to be significantly higher than after selfing. The two classes of embryos, on the other hand, grow at only slightly different, and much lower, rates. As mentioned above, only about one fifth as many fertile ovules collapse after crossbreeding as after selfing. The initial conditions in the ovule outside the embryo sac being alike in the two cases, it seems clear that the higher survival following crossing is the result of the more active growth of the hybrid endosperm. Conversely, following self-fertilization, the rate of growth of the endosperm is frequently so low that the balance soon shifts in favor of the integument. The hyperplasia we have described then arises, causing collapse of the endosperm and, eventually, terminating development of the ovule.

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BOOKS RECEIVED

ADAMSTONE, F. B. and WALDO SHUMWAY. *A Laboratory Manual of Vertebrate Embryology; Anatomy of Selected Embryos of the Frog, Chick and Pig.* Pp. vii + 87. 38 figures. Wiley. $1.25.

American Geophysical Union. *Transactions of 1939. Part I, Reports and Papers, Regional Meetings, Los Angeles and Spokane, December, 1938. Part II, Twentieth Annual Meeting, Washington, D. C., April, 1939; Symposium on Floods. Part III, Twentieth Annual Meeting, Reports and Papers, General Assembly and Sections of Geodesy, Seismology, Meteorology, Terrestrial Magnetism and Electricity, Oceanography and Volcanology. Part IV, Twentieth Annual Meeting; Reports and Papers, Section of Hydrology.* National Research Council of the National Academy of Sciences, Washington.

CLARKSON, ROSETTA E. *Magic Gardens; a Modern Chronicle of Herbs and Savory Seeds.* Pp. xviii + 369. Illustrated. Macmillan. $3.00.

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MABY, J. CECIL and T. BEDFORD FRANKLIN. *The Physics of the Divining Rod.* Pp. xv + 452. 51 figures. Bell & Sons, London. 21s.