DIFFUSION OF GENE PRODUCTS

By Karl Sax
Arnold Arboretum, Harvard University
Communicated June 24, 1942

The phenotypic expression of a gene may depend upon its relation to neighboring genes in the chromosome, the transmission of gene products from the nucleus to the cytoplasm and the diffusion of gene products from cell to cell. Although examples of position effect are rather limited, it is clear that the effect of a gene may be conditioned by neighboring genes. This action might be attributed either to the effect of adjacent genes in the production of gene products, or to the early interaction of products of adjacent or neighboring genes. There is abundant evidence that gene products may pass through the nuclear membrane. Even during the “resting stage” of a cell the genes are active in controlling cellular development, as shown by the variation in growth of microspores in triploid Tradescantias. The diffusion of gene products from cell to cell or even to relatively remote tissues is shown by the transplant experiments of Beadle, Ephrussi and Caspari in Drosophila and Ephestia. Larval eye discs transplanted to abdomens of other larvae may be autonomous in pigment development or may be controlled by the host, depending on the genetic constitution of the implant and of the host. A remarkable case of a similar nature has been found in Habrobracon by Mrs. Whiting. Eye mosaics may have a sharp line of cleavage between the colored segments, or the colors may merge and interact at the boundary of the mosaic areas, depending on the genetic composition of the mosaic males. It is evident that certain gene products are diffusible while others are not.

The development of the microspores in certain plants provides further evidence on the diffusion of gene products. In nearly all basic diploid plants the microspores rarely develop into pollen grains if a chromosome or even part of a chromosome is missing. Due to “non-disjunction” of bivalent chromosomes at the first meiotic division the daughter nuclei are either deficient or carry an extra chromosome. The deficient nuclei undergo the second meiotic division, because the cells have been condi-
tioned for one more division cycle, but the resulting deficient microspores fail to develop. The rare occurrence of N-1 microspores which reach the stage of nuclear division has been attributed to non-disjunction at the second meiotic division. In *Uvularia* the deficient microspores die if they become separated from their complementary hyperploid sister cells, but heat treatment during meiosis often causes the microspores from a pollen mother cell to remain attached. Barber found that the deficient microspores in such attached cells undergo nuclear division and that the nuclear divisions in both the hypoploid and hyperploid microspores are synchronized. Apparently substances essential for growth and development are able to pass from hyperploid to deficient microspores only when the cells are attached. Barber has described similar cases in certain orchids.

In the normal development of *Tradescantia* microspores there are conspicuous granules in the cytoplasm during early development. These granules gradually disintegrate and begin to disappear before the initiation of prophase of the nuclear division. In sterile microspores the granules persist and are present when nuclear division occurs in the neighboring normal cells. The sterile microspores fail to develop and are much smaller than normal microspores. According to Schmitt and Johnson the granules in *Tradescantia* microspores are composed primarily of protein.

Occasionally *Tradescantia* microspores are found in which the chromosomes are separated by complete or partial cell wall formation. These dumb-bell shaped microspores have three chromosomes in each lobe and the lobes are separated by cell walls or by deeply constricted regions (figure 1). The aberrant microspores are about as large as normal cells, but the protein granules persist until metaphase. The granules had disintegrated more than those found in adjacent sterile microspores, but were very conspicuous when compared with the condition in normal microspores (figure 1). The origin of these aberrant microspores is obscure. They may be produced by non-disjunction at the first meiotic division, followed by incomplete separation of the two daughter cells of the deficient dyad, or they may be produced by the failure of the chromosomes to unite in a single nucleus at the telophase of a normal second meiotic division.

The development of attached half-microspores with only three chromosomes in each cell is not unexpected since deficient cells are conditioned for the following nuclear division. The persistence of the protein granules does suggest that the action of all chromosomes must occur to effect disintegration of the granules. Apparently gene products from the isolated groups of chromosomes cannot diffuse fast enough, especially when separated by a cell wall, to effect the complete disintegration of the granules. The growth of the cell is nearly or quite normal, however, as one would expect in view of Barber's results with attached microspores. Evidently the growth-promoting substances can pass through the thin walls of
attached microspores, but the products responsible for granule disintegration are inhibited by cell walls or perhaps even by cytoplasmic isolation. These results with plant microspores are in complete accord with the variation in diffusion of gene products found in Drosophila and Habrobrachon.

One of the most interesting cases of diffusion of gene products has been described in Neurospora by Dodge.8 Two races when grown together produce a heterocaryotic mycelium containing nuclei from each parental race. The resulting mycelium shows a great increase in growth although no nuclear fusion occurs. Dodge suggests that the growth substances produced by the nuclei of the two races supplement each other to produce the increased growth—a situation comparable to the hypothesis suggested by Robbins to account for heterosis in tomatoes. The results with Neurospora show that gene products necessary for growth need not be produced in the same nucleus in order to be effective, but can diffuse into the cytoplasm from different nuclei and unite in promoting increased vigor.
Summary.—Gene products essential for growth are able to diffuse between attached cells, but not between isolated microspores. The gene products necessary for disintegration of protein granules are unable to diffuse freely through a cell wall in aberrant Tradescantia microspores. This variation in the diffusion of gene products is in accord with the results found in insects.


---

**THE EFFECT OF X-RAY STIMULATION ON THE BIOELECTRIC POTENTIALS OF THE AVIAN EGG**

BY ALEXIS L. ROMANOFF AND ARTHUR A. BLESS

AGRICULTURAL EXPERIMENT STATION, CORNELL UNIVERSITY, AND DEPARTMENT OF PHYSICS, UNIVERSITY OF FLORIDA

Communicated June 12, 1942

Introduction.—The electrical activity of living systems has recently received a great deal of attention from a number of investigators. It is recognized that bioelectrical potentials are not merely an accidental by-product of the activity of the living organisms, but are probably conditioned by the organism and, according to some observers, profoundly influence its living processes. The electrical potentials and the electrical fields are created by ions and their spacings which are “the irreducible relatedness of the components of living things,” as Northrop and Burr¹ expressed it.

The vital activity of the blastoderm of the hen’s egg has been investigated recently by Romanoff and Cottrell.² The results have shown that the potential difference between the blastoderm and the albumen of fresh fertile eggs is much larger than the potential of infertile eggs. The electrical activity of the blastoderm is therefore an indication of the vital activity of the organism. In view of the importance of this criterion of vital activity it seemed interesting to determine the physical factors that affect the potential, and the bearing these factors have on the later life of the embryo. This paper deals in particular with the effects of x-rays on the bioelectric potential.

Experimental Methods.—About 1200 fresh White Leghorn eggs³ were