

RESEARCH IN BIOLOGY.

Conducted by Homer C. Sampson.

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It is the object of this department to present to teachers of physics the results of recent research. In so far as is possible, the articles and items will be nontechnical, and it is hoped that they will furnish material that will be of value in the classroom. Suggestions and contributions should be sent to Dr. Homer C. Sampson, Department of Zoology, Ohio State University, Columbus, Ohio.

XENIA.¹

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If a garden with sweet corn happens to be growing near a field where the ordinary starchy corn of the "dent" or "flint" types are planted, and the pollen from the field blows into the garden, the mature ears of the sweet corn will show a sprinkling of starchy grains. Likewise, if a cross is made between corn with blue endosperm and white endosperm strain, if blue is used for the pollen parent, the seed will be blue, or mottled blue and white. These are examples of xenia. Xenia refers to the immediate influence of pollen in producing changes in the color or chemical composition of endosperm tissue. Whenever xenia occurs, the endosperm resembles that of the staminate parent and not the carpellate parent.

The striking feature of xenia is that the change is apparent in the seeds the same year that the cross pollination occurs, and before the embryo produced as the result of the cross pollination is grown. Fifty years ago this was regarded as phenomenal, or at least extremely puzzling to people of an age in which interest was often allowed to be captured by the merely curious things of nature. Coupled with this pseudo-scientific diversion was a widespread belief in telegony. By this is meant an alleged influence of a male parent upon offspring subsequent to his own. If a mare, for instance, which had borne progeny from matings with a zebra produced striped colts on subsequent matings with a horse, the stripes in these colts were thought to be a result of some far-reaching influence of the zebra mating. Notions of this sort are entertaining as myths, not unlike the willow wand method by which Jacob increased the number of his sheep at the expense of Laban's flock. However, such stories have no place in scientific literature. Yet at the time when xenia was first observed, belief in telegony was by no means limited exclusively to popular fancy. Xenia as a demonstrable fact had to be sifted out from such creatures of the imagination as just mentioned.

¹Botanical Publications. No. 103.

That xenia should seem puzzling at first to plant growers and botanists is readily understandable. Did they not plant seeds that they could reasonably believe to be pure? Yet the seeds they harvested were often mottled or spotted in appearance. Further, from these spotted seeds, when planted, came a mixed population with all sorts of variations. As long, however, as such cases were regarded as being simply monstrosities or more popularly "freaks," there was little chance of discovering the processes in plants preceding the appearance of xenia.

First of all it was necessary to show that xenia is an actual fact and not a chance freakish occurrence. In some of the early observations of xenia not enough was known of the history of the seed used to make sure that cross pollination had not previously taken place. When, however, De Vries in 1899 published the result of some of his work, the fact of xenia was completely established. He used strains of corn in which it was known that there had been no previous cross pollinations—a sweet corn and a starchy corn. He found that sweet corn with starchy corn for the pollen parent always produced starchy grains. Here was an indisputable example of xenia producing a definite chemical change in endosperm composition. De Vries showed further that the kernels exhibiting xenia produced, when planted, true hybrids between starchy and sugary corn. We now know that such hybrids, if self pollinated, will in the second generation show the segregation of starchy and sugary endosperm in the usual Mendelian fashion.

About the same time that De Vries experiments were published, Correns concluded from some similar experimental work that the effects of foreign pollen cross pollinations were limited to the endosperm, and that the pericarp and other parts of seeds exhibiting xenia showed no changes. These two sets of experiments are referred to because they make clear the point that xenia is a definite occurrence, and second that it is limited in its effect to a particular portion of the seed, namely, the endosperm in which only the color or the chemical composition is altered.

The explanation of the mechanism by means of which xenia effects are produced came, however, from an altogether different source. August 24, 1898, is the date when Nawaschin announced before the Russian Society of Naturalists his observations on "double fertilization" in *Lilium martagon* and *Frittilaria tenella*. This is one of the greatest of botanical discoveries, and one which

has been so widely discussed that it only needs to be mentioned here. In brief, Nawaschin and the host of scientists who followed him established the fact that the endosperm of our higher plants is as much a product of fusion as is the embryo. The pollen tube discharge contains, at the time of fertilization, two male nuclei. The first fuses with the egg cell of the female gametophyte and forms the embryo. The second unites with a definitive nucleus or "endosperm nucleus" as it is called and forms the endosperm. This endosperm nucleus is usually itself a product of the fusion of two or in many cases several nuclei from the female gametophyte. A typical case is the one in which two polar nuclei from the opposite ends of the female gametophyte unite, and to this fusion is later added the second male nucleus of the pollen tube discharge. On account of the union, then, of three nuclei the term triple fusion is more appropriate than the somewhat ambiguous "double fertilization."

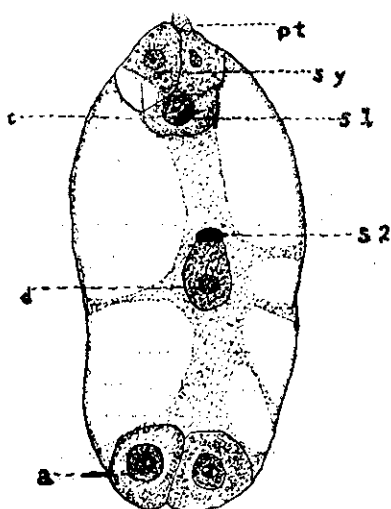


FIG. 1.

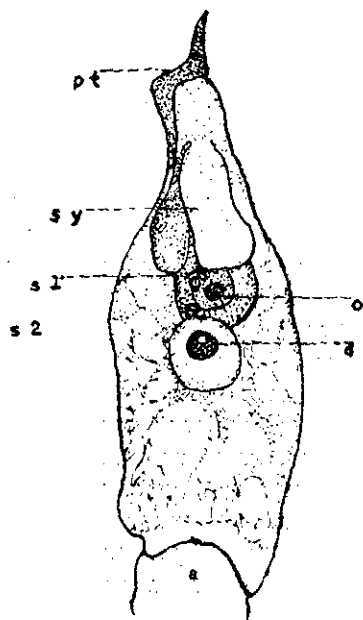


FIG. 2.

FIGURES 1 AND 2. DOUBLE FERTILIZATION.

FIGURE 1. *Ranunculus cymbalaria* (buttercup), entire embryo sac, showing two male nuclei, s1 and s2, fusing with the egg nucleus, o, and with the endosperm nucleus, d. The pollen tube, pt, and the two synergids, sy, are seen above and the antipodals, a, below; x360; after Guignard.

FIGURE 2. *Helianthus annuus* (sunflower), showing coiled male nuclei. The letters refer to the same structural parts indicated in FIGURE 1. After Nawaschin.

The figures reproduced here serve as a general illustration of the two types of fusion preliminary to seed formation. In the first figure, *Ranunculus cymbalaria*, the entire embryo sac is shown, the synergids at the top and the antipodals below. Just underneath the synergids the egg cell is seen fusing with the small dark nucleus of the first male cell of the pollen tube discharge, while in the center of the embryo sac is the second male nucleus in fusion with the endosperm nucleus. The second figure, *Helianthus annuus*, is quite similar, only the antipodals are not shown. In the buttercup the male nuclei are oval, while in the sunflower they are coiled.

After Nawaschin, Guignard in a great number of instances, Land, Strasburger, Miss Thomas and many other botanists have seen and described triple fusion. So great was the activity of these investigators that as early as 1903 the list of observations covered more than sixty species distributed among some forty genera and sixteen families. Since that time a number more have been added and are being added. The occurrence of triple fusion is now regarded as so general that it attracts interest only as further confirmatory evidence, and because there are irregularities and departures from the generalizations in the number of nuclei entering into the fusion. This need not be discussed here.

With the establishment as a fact of the fusion for endosperm formation as well as for embryo formation, the whole mystery of xenia was dispelled. Since the pollen tube discharge has two male nuclei, both originating from the same pollen grain, they may be considered potentially equal bearers of hereditary characters. In the female gametophyte, too, we find that the hereditary characters are of the same kind in the endosperm nucleus and the egg nucleus. Since the endosperm or definitive nucleus is formed from the fusion of nuclei that had divided from sister nuclei of the egg cell, the definitive nucleus must contain, qualitatively, the same hereditary characters as the egg. In point of quantity, however, there is a difference in the endosperm nucleus; for in the fusion of the two polar nuclei preliminary to endosperm formation, each polar nucleus brings a single set of chromosomes into the fusion or endosperm nucleus. But since each set has the same hereditary characters, and since a male nucleus like the one which united with egg fuses with the endosperm nucleus, it is to be expected that an endosperm will be formed partaking of all of the characters present in the fertilized egg.

That this is actually the case is shown by such experiments as those of De Vries referred to above, and which can be repeated by anyone.

If, for example, we cross starchy and sugary corn using starchy corn for the pollen parent, the mature ear at the end of the season, i. e., the generation in which the cross is made, will have starchy grains wherever the silk received the pollen bearing determiners for starchiness. Both the endosperm and the embryo are hybrids, but the condition of hybridity is evident only in the endosperm. If some pollen from the sweet corn was received by other silks on the same ear, we will have sugary grains scattered among the starchy grains. The wrinkled, sugary grains are, of course, pure. The embryo of the starchy grains like the endosperm are true hybrids between sugary and starchy corn. If these embryos are allowed to germinate and reproduce by self pollination, the first generation after the cross will have only starchy grains. But if the grains of this generation are allowed to germinate and produce a second generation by self pollination, the progeny show the usual Mendelian hybrid segregation of three starchy grains to one sugary grain. Xenia, then, can be regarded as an indicator of the hybridity of the embryo under certain conditions. We have only to know the history and nature of the seeds in order to understand what these conditions are. For this reason it will be interesting to consider for a moment the seed of corn. It has been selected as offering instructive evidence in illustrating the parts of a seed in their genetic relation to one another.

A botanist or a geneticist is not willing to answer the question "What is a seed?" by saying "What you plant." He thinks of the parts of the seed from the standpoints of their origin and from what later becomes of them if the seed really be planted. A seed is made up of three essential parts, the embryo, the reserve food materials and the seed coats. The embryo is a young plant and contains the sporophyte, or diploid number of chromosomes. This is usually designated as $2x$. The seed coats or pericarp are remnant tissues of the sporophyte plant which bore the ear. In corn, the pericarp consists of the ovulary wall, the inner and outer integuments of the ovule and the remains of the nucellus. These have coalesced into a single rather tough membrane in the mature seed. It might be mentioned in passing that since the ovulary wall is included in this membrane, a grain of corn is botanically a fruit, but this fact does not concern the present discussion. The seed coat contains

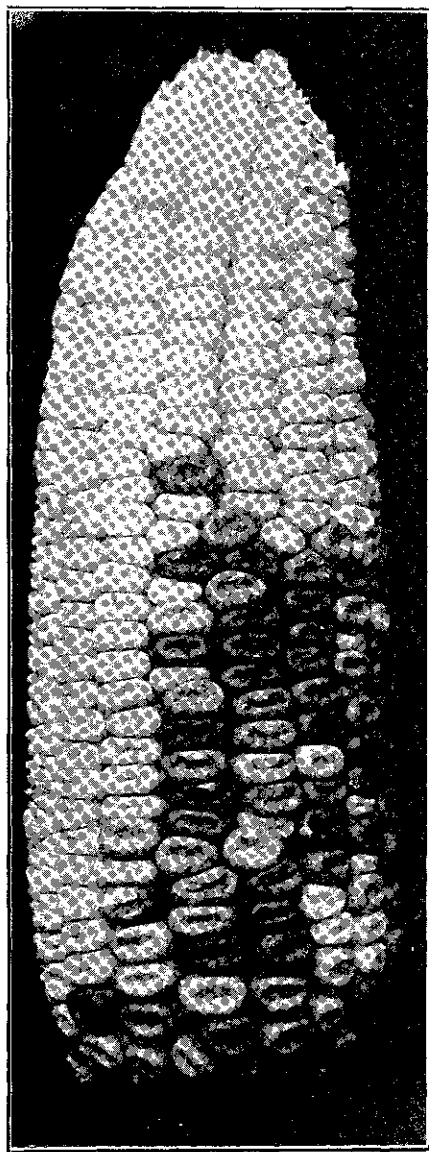
the sporophytic chromosome number since it is all tissue of the old sporophyte which bore the ear. If there were any remnant of the female gametophyte which had not been used up as food material by the developing endosperm and embryo, it would have the genetic constitution of x number of chromosomes, or the haploid number. The endosperm has a constitution of $3x$, or if several polars have joined in with the usual fusion in a multiple fusion, an " n " x chromosome number.

From what has been said we are now in a position to understand why xenia occurs. If a cross pollination is made between a race with dominant characters expressible in the endosperm and a race with contrasting characters, we have xenia resulting. The reciprocal cross in which the dominant characters came from the carpellate parent and the recessive characters from the staminate parent would not show xenia. As a process then, xenia is simply a part of normal seed formation. It is only when the male nucleus introduces dominant characters visible in the endosperm (or xeniophyte) that we have a change which once was regarded as surprising.

There are also certain cases on record which bear out beautifully the cytological evidence of triple fusion. In some crosses between corn with flinty and with floury endosperm, it was seen that no matter which way the cross was made, the grains resembled the carpellate parent. This is explained by Hayes and East on the ground that since the recessive, floury endosperm entered into the endosperm in two doses when it was used for the carpellate parent, and the dominant flinty as the staminate parent brought in only one dose, the single dose was not sufficient to show xenia. This is a splendid example of cytological evidence furnishing a theory for which experimental genetic work was necessary in order to establish proof. To illustrate the above, let the dominant character, flinty, be represented by H , and the recessive character, floury, by h . Then in a cross with the flinty for the staminate parent the endosperm would be Hhh and no xenia would appear. The embryo would be Hh , however. In this connection it is worth remembering that dominance of flinty over floury is a postulate only, since the endosperm with three sets of chromosomes always must express either one or the other character. The embryo has only two sets of chromosomes but the expression of the condition is revealed in the endosperm.

The photograph shows the result of some experimental work which can be carried out easily. The silks of an ear of white corn were carefully divided at the time of extrusion. On one

portion of the silks pollen from a race of blue flint was placed. The rest of the ear received pollen from the plant which bore it. An attempt was made to divide the silks so carefully that all blue grains would appear in about one-



fourth of the ear and all white grains on the rest of the ear. The photograph shows how nearly successful this was. Only a few blue grains appear out of line and only one or two white ones in the blue area. Some grains that look almost white in the photograph were quite blue when seen on the ear. This simple experiment has a good deal of instructional value since it proves unquestionably that xenia as an outward demonstration of triple fusion can be secured as desired.

There are a number of variations of the experiment which could as easily be performed and which would serve as well. Instead of blue and white, starchy and sugary, or yellow and white, or flinty and sugary would serve as well for illustrating xenia. In the above pairs of characters the dominant is named first. It is only necessary to avoid pericarp colors, of which red is the most common example, in selecting material to demonstrate xenia. A character expressed in the pericarp

FIGURE 3. Photograph of an ear of white dent corn, a portion of which was pollinated by blue flint after carefully dividing the silks.

could not produce xenia, since the pericarp is old sporophyte tissue and is already completely formed before the endosperm fusion takes place. In the crosses between colored and colorless grains which show xenia, it is the color of the endosperm visible through a colorless pericarp.

This brings up another interesting point. Xenia occurs following endosperm fusion. Xenia cannot occur unless a fusion somewhat paralleling the fusion between egg and sperm has taken place. Physiological influences of a male nucleus on egg development or on the growth of tissues near the region of the egg cannot be called xenia. There are some not entirely confirmed cases on record of a change in the color of fowls' eggs and of canary eggs following hybridization. These have been styled "xenia." A geneticist, knowing the facts of xenia and xeniophyte, would quickly point out that such an influence, if genuine, cannot possibly correspond to our cases of double fertilization and xenia.

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THE UNIVERSITY OF CHICAGO.

Since 1892 more than 62,000 students have been in attendance at the University of Chicago for at least one quarter, according to the new *Annual Register* just issued by the University of Chicago Press. Degrees have been conferred, inclusive of these conferred at the Summer Convocation, June, 1918, upon 11,895 persons, including 1,106 who have received the degree of Doctor of Philosophy. Forty-seven honorary degrees have been conferred.

The members of the several Faculties now number: Professors 105, Associate Professors 46, Assistant Professors 53, Instructors 68, Associates 9, Assistants 95, Professorial Lecturers 11, besides library assistants, laboratory assistants, and readers. In all departments and in all grades of service the University employs about 1,300 persons.—[*University Press*.