HERITABLE CHARACTERS OF MAIZE

VII. SHRUNKEN ENDOSPERM[1]

C. B. HUTCHISON
New York State College of Agriculture, Cornell University, Ithaca, N. Y.

IN 1914 Professor R. A. Emerson received from Dr. M. R. Gilmore of the Nebraska Historical Society several small packages of maize seeds which the latter had collected the previous year from gardens of the Ponka Indians on the Niobrara reservation in Nebraska. Among these packages was one containing starchy and sugary, white, red, and purple, and self-colored and speckled kernels, all of which had been taken from a single ear. These seeds were planted at the Nebraska Experiment Station by Dr. Emerson and a number of the resulting plants self-pollinated. On one such self-pollinated ear in this pedigree there appeared among the starchy kernels certain ones with an unusual type of indentation. The kernels of flour corn ordinarily are not indented at all but are smooth and rounded in shape like flint corn. The starchy kernels on this ear were floury in texture and most of them smooth and rounded. Some, however, were deeply indented at the top with a smooth crease or, in the case of broad and thick kernels, with a deep dimple. Others were indented not at the top but on the sides, as if in drying the endosperm had shrunken and the sides of the kernel had fallen in. Still others were indented at both the top and sides which gave them a shrunken and pinched appearance. When these unusually shaped seeds were planted and the resulting plants selfed, they were found to breed true for this character and subsequent tests have shown it to be inherited as a simple recessive to the normal or full endosperm. It has been called "shrunken" and is designated by the genetic symbol *sh*, the dominant allelomorph of which is *Sh*.

In 1918 shrunken was crossed with a number of other types of maize to determine its relation with other known genetic factors. Subsequently, thru the kindness of Dr. Emerson, all of this material came into possession of the writer.

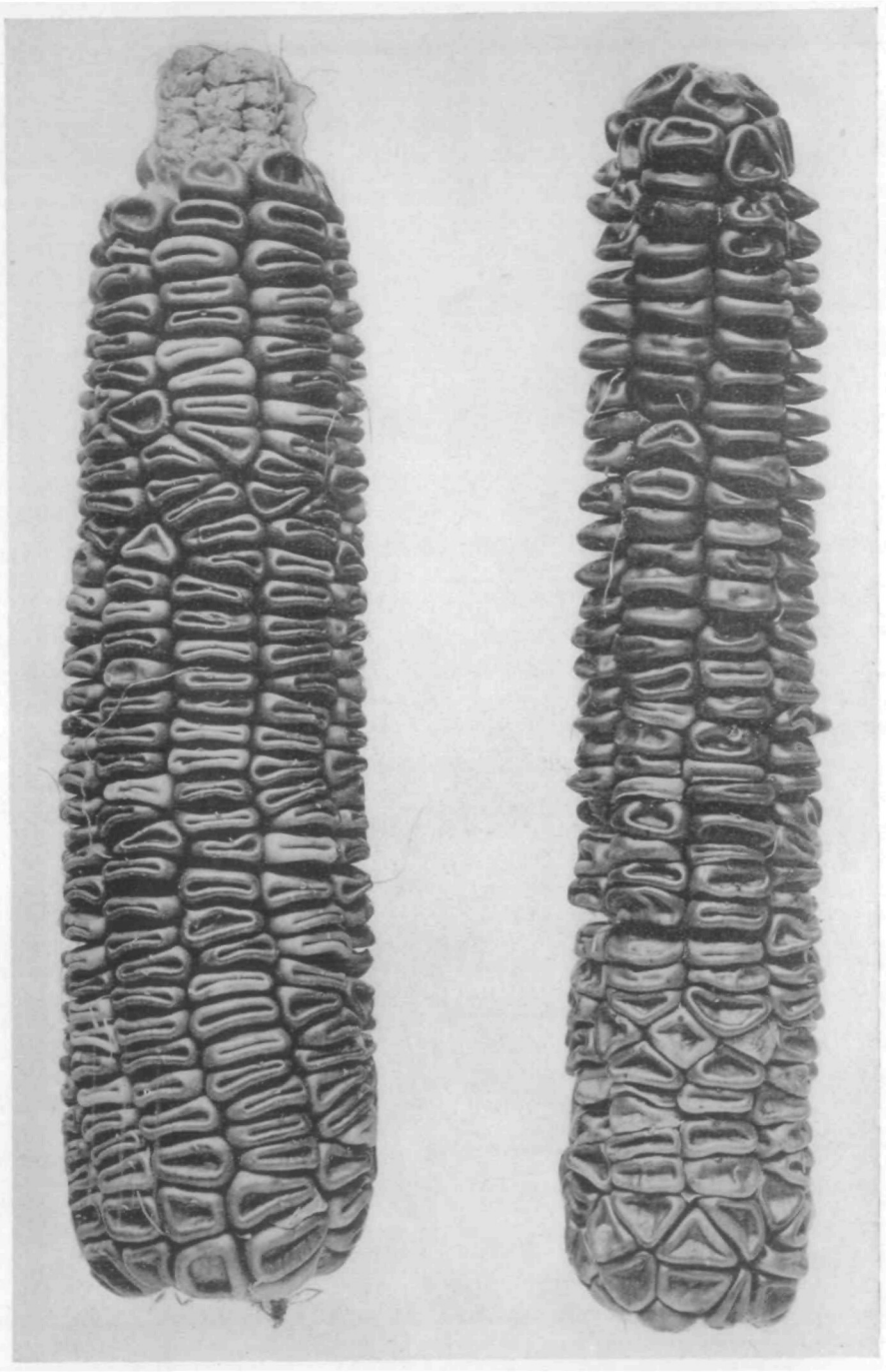
DESCRIPTION OF SHRUNKEN ENDOSPERM

An adequate conception of the nature and general appearance of shrunken kernels may best be had from examination of the accompanying illustrations. In Figure 20 two selfed ears from homozygous shrunken plants are shown and in Figures 21 and 22 ears containing both shrunken and non-shrunken kernels in approximately equal numbers. The latter ears are the result of pollinating plants heterozygous for the factor for shrunken with pollen from homozygous shrunken plants. Figures 23 and 24 show different views of shrunken and non-shrunken kernels taken from the same ear.

It will be noted from Figures 21 and 22 that where the rows are straight and the kernels fairly uniform, especially in the middle portion of the ear, shrunken kernels are usually more flat, somewhat broader, and frequently shallower than non-shrunken ones. In such kernels the top is usually folded in to form a deep and smooth crease altho at times the indentation is from the sides of the kernel giving them a pinched appearance and leaving considerable space between the kernels at the top. On the butt or tip of the ear where the kernels normally are irregular in shape, or where adjoining kernels fail to develop, shrunken kernels are characterized by a deep, broad and rounded dimple.

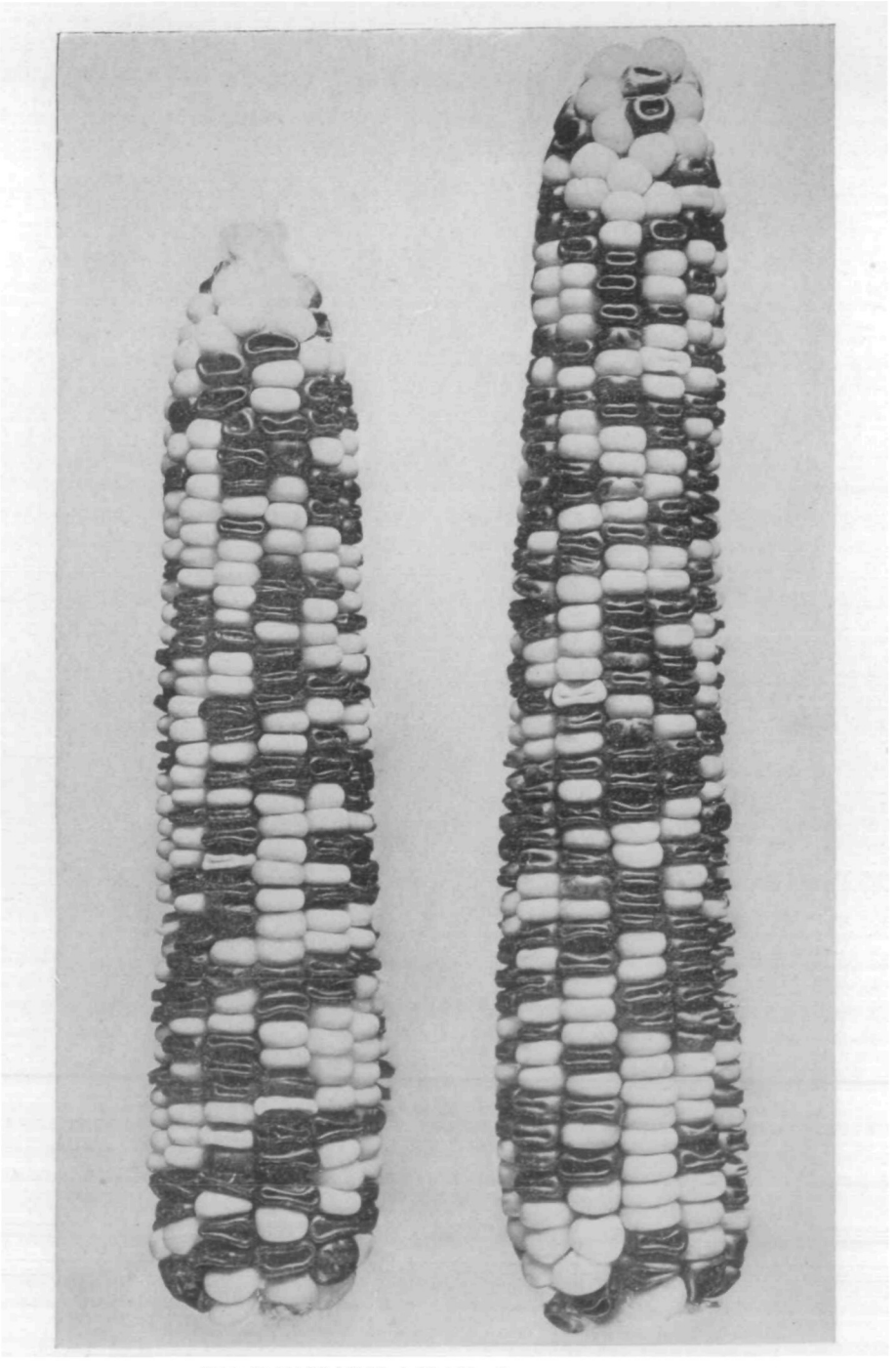
The shrunken indentation is sometimes not unlike the creased or rounded dimple found in ears of a flinty type of dent corn—particularly on the butt

[1] Paper No. 87, Department of Plant Breeding, Cornell University, Ithaca, New York. Photographs by W. I. Fisher.



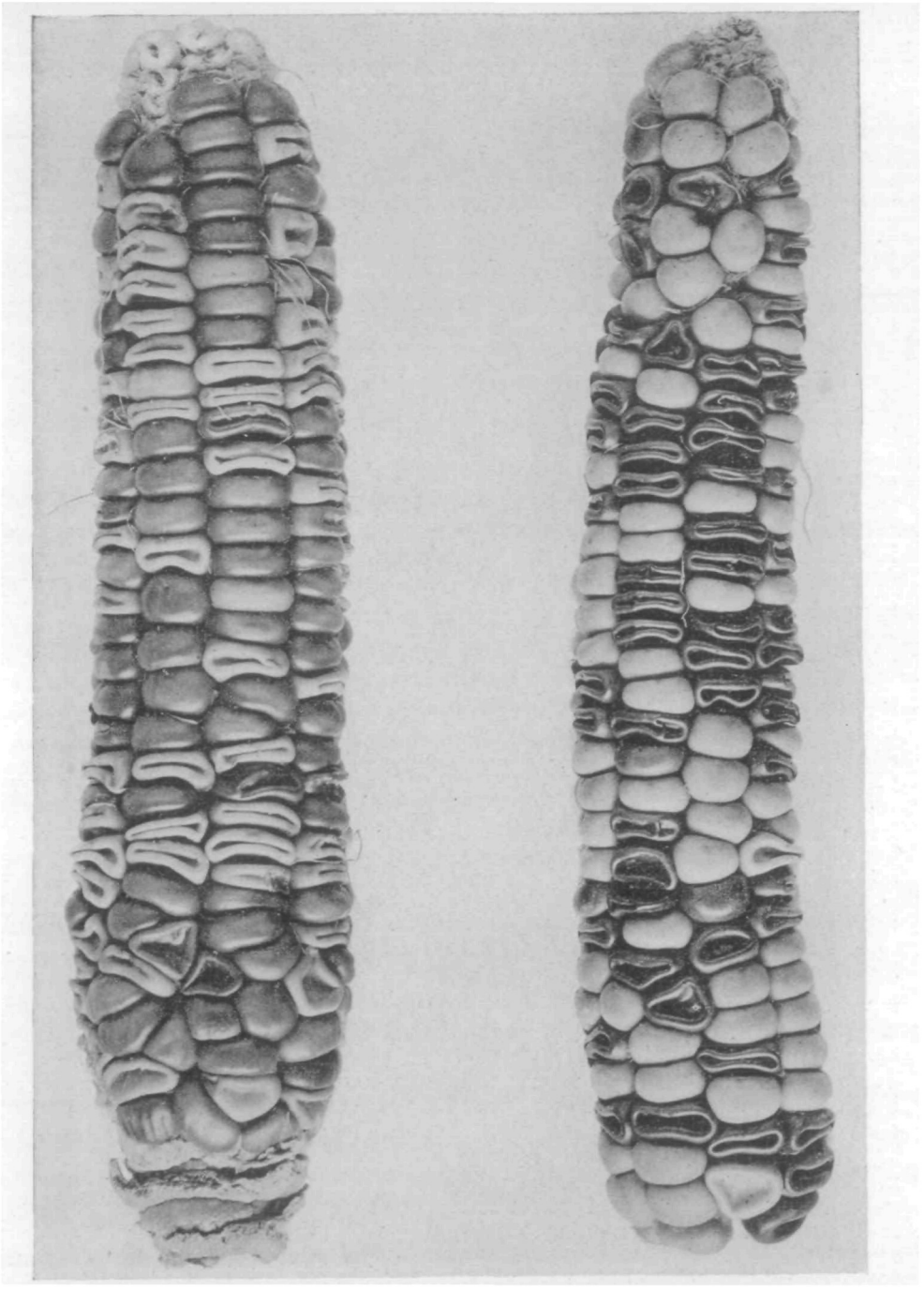
SHRUNKEN KERNEL MAIZE EARS BRED FROM PONKA INDIAN CORN

Among some maize seeds obtained from the Ponka Indians of Nebraska in 1914 were some that were deeply indented at the top and some indented on the sides, as though the endosperm had shrunken causing the sides to fall in. When these seeds were planted they were found to breed true, and subsequent tests have shown this condition to be inherited. (Fig. 20.)



EARS WITH BOTH SHRUNKEN AND NON-SHRUNKEN KERNELS

One of the parents of this hybrid had colored seeds with shrunken endosperm, and the other had white seeds which were not shrunken. These hybrid ears show that the parental combinations tend to reappear, that is most of the colored seeds are shrunken while the colorless ones are not. (Fig. 21.)



SHOWING SHRUNKEN ENDOSPERM IN BOTH WHITE AND COLORED SEEDS

The kernels on these ears show linkage of the shrunken endosperm character with two different aleurone characters. (Aleurone is the thin external layer of the kernel containing the color character.) The ear at the left is the result of crossing a hybrid plant with one that was pure for colorless aleurone and non-shrunken endosperm. In this instance one of the parents of the hybrid was white and shrunken and the other was colored and not shrunken. Again the parental combinations reappear, most of the white seeds being shrunken and the colored ones not. In the ear at the right the parent of the hybrid with non-shrunken endosperm also had white aleurone. Note that very few of the white seeds are shrunken, showing that this aleurone factor also is linked with the new character, shrunken endosperm. (Fig. 22.)

and tip kernels. Usually, however, the dimple or crease is much more pronounced than in ordinary dent corn. The shrinking from the sides of the kernel presents a condition which the writer has never observed in dent corn, the indentation of which is usually rough and always at the top. The most striking difference in the two types of indentation aside from one of degree is the fact that in shrunken kernels a cavity is usually found within the upper part of the endosperm as if the cells in this region had not been filled with starch as the kernel matured (See Figure 24.) Previous to the hard dough stage shrunken kernels are smooth and rounded in outline. As they begin to dry the top or sides sink in to such an extent at times that the cavity is closed altho its outline may be distinctly seen. In other cases, particularly where there is a fairly thick layer of corneous starch at the top of the kernel the latter may be almost smooth in outline. In such kernels the cavity beneath the shell of corneous starch is very pronounced. On the other hand, in dent corn the endosperm is filled, the indentation being due to a greater shrinking of the soft starch at the top of the kernel than of the corneous starch on the sides.

By reason of this fact, little difficulty has been found in distinguishing shrunken from non-shrunken kernels with starchy endosperm. It is difficult, however, always to classify shrunken and non-shrunken kernels in sweet corn, particularly on ears of the Country Gentlemen type where the kernels are long, narrow and pointed and very irregular in shape. Such separations are much more readily made on eight or ten rowed ears of sweet corn where the kernels are broad and rounded and fairly regular in outline.

In examining shrunken and non-shrunken kernels one is apt to gain the impression that the former are lighter in weight than the latter since they are apparently not fully developed. This, however, is not the case. Data obtained by weighing the shrunken and non-shrunken kernels on the ears from six F_1 plants that had been backcrossed to shrunken show that while the non-shrunken kernels are slightly heavier the difference is not statistically significant. These data are given in the following table:

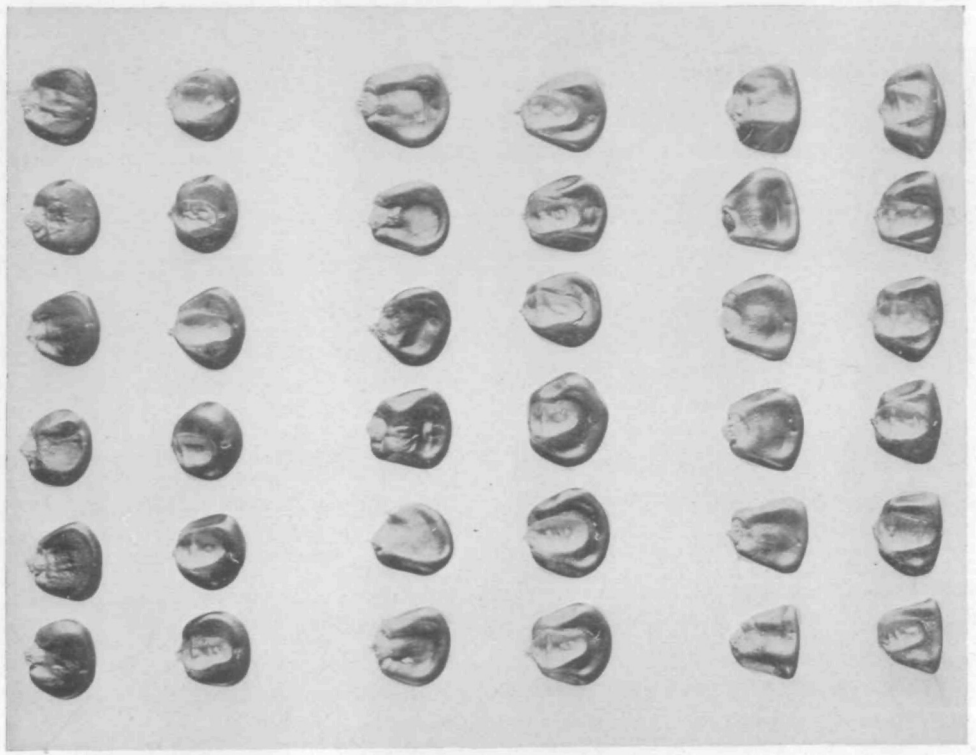
	Number of kernels weighed	*Average weight of kernels*
Non-shrunken	914	272 ± 8.42 mg.
Shrunken	874	259 ± 10.89 mg.
Difference		13 ± 13.76 mg.

INHERITANCE OF SHRUNKEN ENDOSPERM

As stated above the character shrunken endosperm is inherited as a simple recessive to the normal or non-shrunken. Numerous crosses have been made between shrunken and non-shrunken plants and the F_1 seeds produced have been normal in all cases. A number of such hybrid kernels have been planted and the resulting plants selfed for F_2 progenies. Two such progenies consisted of 705 non-shrunken and 239 shrunken kernels. This is a deviation of only 3 ± 8.97 seeds from the 3: 1 relation expected when the parents differ in a single pair of factors. A number of F_1 plants also were backcrossed with the recessive shrunken in connection with some linkage studies to be described later. A total of 20,556 kernels resulting from such backcrosses have been examined, of which 10,295 were shrunken and 10,261 non-shrunken. This is a deviation of only 17 ± 48.3 seeds from the 1 : 1 ratio expected. Evidently shrunken endosperm is differentiated from the normal by the single factor pair *Sh sh*.

LINKAGE RELATIONS OF *Sh sh* AND *Wx wx*, AND *Sh sh* AND THE ALEURONE FACTORS *C c* AND *I i*

The fact that waxy endosperm and aleurone color in maize are linked was first established by Collins and Kempton (1911). Bregger (1918) was able to show that the particular aleurone color factor concerned is the *C c* pair. Among the crosses made by Dr. Emerson in 1918 with shrunken one involved



LATERAL VIEWS OF SHRUNKEN AND NON-SHRUNKEN KERNELS FROM A SINGLE EAR

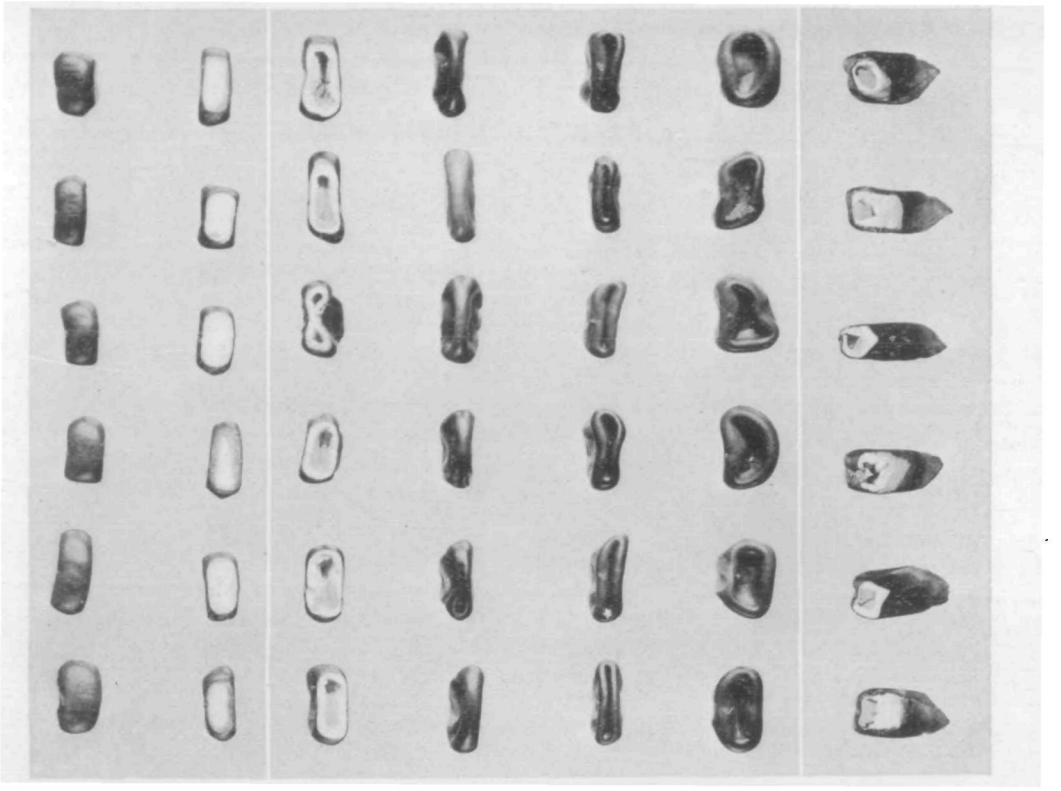
The two rows at the left are non-shrunken kernels; in the middle two rows the indentation is from the sides of the kernels, and in the two rows at the right the indentation has taken the form of a deep crease. The latter character is shown better in the kernels in the centre of Fig. 24. (Fig. 23.)

the *C c* and *Sh sh* factor pairs. A homozygous red aleurone shrunken plant of the genetic constitution *C C sh sh* was crossed with a colorless aleurone non-shrunken plant of the constitution *c c Sh Sh*. An F_1 plant of this cross, grown in the greenhouse during the winter of 1918–19, was selfed giving a small F_2 progeny. On this ear shrunken and non-shrunken kernels were found as well as colored and colorless but all of the shrunken kernels were also colored. This clearly indicated that the *Sh sh* and *C c* factor pairs are linked. To definitely establish the fact the writer in 1919 made a number of backcrosses between F_1 plants and the double recessive. Twenty-eight such backcrossed ears gave progenies totaling 8,326 kernels distributed as follows:

Colored non-shrunken	Colored shrunken	Colorless non-shrunken	Colorless shrunken
136	3,992	4,049	148

The parental combinations of the characters concerned in this cross are in great excess, there being 8,041 kernels of these combinations and only 284 of the other two. This is very far from equality which is expected with independent inheritance. It is evident that the factor pair *Sh sh* belongs to the same linkage group as *C c* and *Wx wx*, with a crossover percentage in this case of approximately 3.4 for *Sh sh* and *C c*. In Figure 21 two such backcrossed ears are illustrated. It will be noted that most of the colored kernels are shrunken and most of the colorless ones are smooth. A few kernels of the opposite combinations, however, are to be found on each of these ears.

The ear on the left in Figure 22 illustrates the coupling series of these two factor pairs. In this case the parental combinations were *C Sh* and *c sh*. This ear is the result of pollinating an F_1



CROWN AND EDGE VIEWS OF NORMAL AND ABNORMAL KERNELS

The first two rows at the left show kernels in which the endosperm is completely developed. Those in the third row are cut in cross-section to show the cavities which are often found in the upper part of shrunken kernels. The 4th, 5th and 6th rows show the variation in the size and shape of shrunken kernels. In the last row at the right the kernels are cut to expose the cavities in the upper part of the endosperm. (Fig. 24.)

plant of the genetic constitution $\frac{C\ Sh}{c\ sh}$ by the double recessive $\frac{c\ sh}{c\ sh}$. Again it will be noted that while most of the colored kernels are smooth and most of the colorless ones shrunken a few kernels show the opposite combinations of these characters.

To determine the linkage relation of shrunken and waxy a non-shrunken waxy plant of the genetic constitution *Sh Sh wx wx* was crossed with a shrunken starchy plant of the constitution *sh sh Wx Wx*. Several F_1 plants of this cross were backcrossed to double recessive shrunken waxy plants. Twelve ears were obtained from these pollinations containing a total of 2,105 kernels which were distributed among the four possible classes as follows:

Non-shrunken starchy	Non-shrunken waxy	Shrunken starchy	Shrunken waxy
229	813	833	230

Here the parental combinations of the two factor pairs concerned total 1,646 and the new combinations 459. The crossover percentage for *Sh sh* and *Wx wx* in these particular crosses is 21.8.

On the basis of these data the probable order of the three genes in this linkage group is

C	Sh	Wx
c	sh	wx
O	3.4	25.2

It must be remembered, however, that the percentage of crossing-over is variable and that the order of the genes can definitely be determined only in backcrosses where all three pairs of factors are involved at once. Material

is now available for making this three point test.

Shrunken has also been crossed with another aleurone factor *I i*, the existence of which was first established by East and Hayes (1911). The interaction of the recessive allelomorph *i* of this factor pair with the dominant allelomorphs of three other factor pairs *A a*, *C c* and *R r* is necessary for the development of aleurone color (Emerson, 1918). When the dominant allelomorph *I* is present no color develops. A homozygous red aleurone shrunken plant with the constitution *i i sh sh* was crossed with a homozygous non-shrunken plant which was also homozygous for *I* and, therefore, had colorless aleurone. Its genetic constitution for the factors in question was *I I Sh Sh*. The immediate kernels produced were colorless and non-shrunken. Several F_1 plants produced by these kernels were backcrossed to the double recessive. Twenty-eight backcrossed ears were obtained with a total of 7,294 kernels. All four combinations of the characters in question appeared among these kernels, the numbers in each class being as follows:

Colored non-shrunken	Colored shrunken	Colorless non-shrunken	Colorless shrunken
134	3,509	3,525	126

The parental combinations here total 7,034 while the other two total only 260. It is evident, therefore, that the factor pair *I i* also belongs with the *C c Sh sh Wx wx* linkage group. The crossover percentage for *I i* and *Sh sh* in this case is 3.6. One of these backcrossed ears is shown on the right in Figure 22.

The very close approximation of the *Sh sh—C c* linkage relation by that of *Sh sh—I i* suggests three interesting possibilities. *C c* and *I i* are (1) very closely linked, (2) they are on opposite sides of *Sh sh* and approximately equally distant, or (3) they are allelomorphic. It is impossible at present to determine which of these possibilities is correct but investigations are now in progress which are expected to throw some light upon the problem.

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Fellowship in Crop Breeding

There will be a fellowship in the study of crop improvement at the Michigan Experiment Station, East Lansing, Michigan, to be filled on or before September 1st, 1921. It is a half-time fellowship, open to graduates of our Universities with farm experience or graduates of Agricultural Colleges, who have had a good course in genetics, the more genetics the better.

The holder of the fellowship is expected to complete a master's degree in two years, majoring in plant breeding and taking his minor in some other department. Half of his time will be devoted to actual crop improvement work, connected with the Department of Farm Crops.

The breeding work during the coming year will include work on corn, oats, rye, wheat, beans, alfalfa, clover, fiber, flax, hemp, potatoes, sugar beets, timothy, and winter vetch.

The candidate would need to furnish a copy of his grades from the Registrar's records, and give references to those who know of his abilities. The fellowship offers $800 for half time during each of two years. Interested persons should communicate with the Department of Farm Crops, Michigan Agricultural College, East Lansing, Michigan.