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OBSERVATIONS ON THE MORPHOLOGY OF "REVERSED GERM" IN TWO LINES OF DENT CORN

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On the ears of most varieties of corn the germinal face of each kernel is oriented toward the tip of the ear. Occasional kernels may be found in which the orientation is toward the base of the ear; these are known in the literature as "reversed germ," "reversed" or "inverted" kernels. This character, which has been observed and described in various corn varieties, particularly in Country Gentleman sweet corn, so far has not been studied intensively in dent corn from a combined genetical and morphological viewpoint.

In connection with a genetic study of this character in a strain of field corn, the writer has had occasion to consider its morphological background and it seems of sufficient interest to present the morphological findings separately from the genetical study.

An ear with an unusually high percentage of reversed germ kernels has been detected in an inbred dent corn line in the breeding program of the Department of Agronomy and Plant Genetics of the University of Minnesota. In the progeny of that ear the percentage of reversed germ kernels per ear ranged from 4.4 to 63.0 per cent. Fig. 1 shows one of these ears on which the reversed germ kernels are marked with an (X). An inbred line of field corn derived from the Golden Glow variety was obtained from Canada; 60.6-97.8 per cent of the kernels of its progeny had reversed germs. In addition Country Gentleman sweet corn also was studied to some extent.

Conclusions (Joachim, in prep.) concerning the genetic behavior of the reversed germ character may be summarized as follows:

1. It behaves as a recessive mature plant character in both the Minnesota and the Canadian lines.
2. The genetic behavior of the Minnesota line may be explained by one major and one minor factor, either of which alone, or both together, produce the reversed germ character. The major factor is responsible for a higher frequency of such kernels than is the minor one.
3. Variability of percentage reversed germ kernels in the ears of the homozygous line was explained by varying genetic expressivity.

For purpose of classification of the orientation of the embryo in any single kernel, the kernel, whatever its shape, is assumed to be bounded by four imaginary planes, i.e. four sides. Two of these are perpendicular to the longitudinal axis of the ear, the one on the side

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of the kernel toward the tip of the ear is referred to as the upper plane, the corresponding one toward the base of the ear as the lower plane. The other two planes pass parallel to the longitudinal axis of the ear and are referred to as the side planes. Kernels whose scutellum lies in the upper plane were classified as normal and the rest as reversed germ kernels. The great majority of the latter had their germinal faces in the lower plane, but a very small number of them had the embryo in either of the two side planes. In identifying reversed germ kernels in the Minnesota line the location of the silk attachment point was helpful because in this line it generally occurs in the same plane as the scutellum. It cannot always be distinguished clearly with the naked eye, but when a magnifying glass is used and the surface of the kernel is probed with a needle it is clearly located as a small indentation. The silk attachment point was not a reliable supplementary criterion in the Canadian line.

Morphological and Ontogenetic Interpretation of the Character "Reversed Germ"

The ontogenetic development of the spikelet pairs as described by several workers (Bonnett, O. T., 1940; Kiesselbach, T. A., 1949; Miller, E. C., 1919; Randolph, L. F., 1936; Weatherwax, Paul, 1917, 1919; and others) may be summarized as follows: In the corn ear two spikelets (together constituting a spikelet pair) develop from a single branch primordium. Each spikelet contains one upper and one lower floret. In most corn varieties the ovary of the upper floret of each spikelet is functional and produces a mature kernel while the ovary of the lower one aborts. Since the spikelets occur in pairs, each pair originating from a single branch primordium, the rows on an ear of corn are usually in pairs.

It is known that in the sweet corn variety, Country Gentleman, all four florets of a spikelet pair are functional and produce mature kernels. Weatherwax (1919) explains the arrangement of kernels on such an ear as follows: "Since there is little or no compensation for the two grains in the length of the cob and insufficient difference in the size and shape of the grain, the ear is producing a larger volume of embryo and endosperm than is ordinarily produced in the same space. As a result of this crowded condition the straight rows are more or less obliterated for a more economical arrangement." According to the terminology used by the writer and in the literature, the kernel developing from the upper florets is normal in orientation while the one from the lower florets is "reversed." The sugary endosperm of Country Gentleman sweet corn made identification of the reversed germ character difficult. By using ears of Country Gentleman crossed with pollen of field corn, the resultant endosperm was nonsugary and made identification of orientation of the germ feasible. On each of several ears examined, about 50 per cent of the kernels were reversed, provided rows were absent. It may then be concluded that in such ears of Country Gentleman all the florets—both the upper and

the lower-ones are functional and develop into mature kernels. Occasionally definite rows were present toward the tip of the ear in these crossed ears. In those portions all of the kernels were normal.

Both the Minnesota and Canadian lines differ notably from Country Gentleman in one respect. With the exception of a few twin kernels, semi-connate and connate kernels in the Minnesota line which will be discussed later, both lines studied had distinct rows on the ears. This must be interpreted as indicating that either the upper or the lower, *but not both* of the florets of each spikelet, produce mature kernels, thus maintaining the definite rows. In contrast to Country Gentleman, ordinary field corn almost invariably has only the upper florets of each spikelet pair developing so that the orientation of the kernels is normal and the kernels fall in regular rows.

The material studied fell into three basic types of kernel arrangement and embryo orientation. These are described in Table 1.

TABLE I. – BASIC TYPES OF KERNEL ARRANGEMENT AND EMBRYO ORIENTATION

Type	Description	Rows vs. No Rows
1	All four florets of the spikelet pair develop: the embryos in the upper florets are normal, the embryos in the lower florets are reversed. This type is represented by Country Gentleman sweet corn.	No Rows
2	The two upper florets of the spikelet pair develop: the embryos in these florets are normal, the two lower florets are aborted. This type is represented by normal field corn.	Rows
3	The two lower florets of the spikelet pair develop: the embryos in these florets are reversed, the two upper florets are aborted. This type is represented by the Canadian reversed germ line.	Rows

In these basic types the right and the left florets of the spikelet pair are alike. Figures 2, 3, and 4 illustrate diagrammatically these types. It is recognized by the writer that occasional deviations from these types may occur.

The Minnesota reversed germ line represents a mixture of these three types because different basic types may occur in a single spikelet pair or in adjacent spikelet pairs. Table II shows the possible recombinations of basic types in the Minnesota line.

TARLE II. – RECOMBINATIONS OF BASIC TYPES OF KERNEL ARRANGEMENT AND EMBRYO ORIENTATION IN THE MINNESOTA REVERSED GERM LINE

Types	Left (or right) side of spikelet	Right (or left) side of spikelet
1 and 2	*normal*	normal
	reversed	aborted
1 and 3	*normal*	aborted
	reversed	reversed
2 and 3	normal	aborted
	aborted	reversed

BASIC TYPES OF KERNEL ARRANGEMENT
AND EMBRYO ORIENTATION

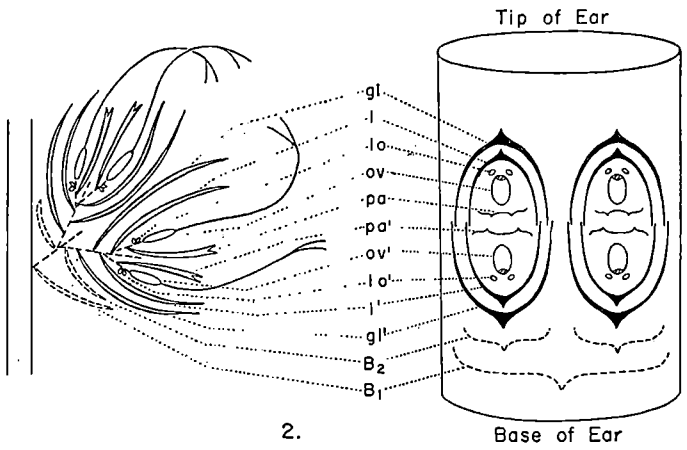

Fig. 2. Spikelet pair with the upper and the lower floret in each spikelet functional as in Country Gentleman sweet corn.

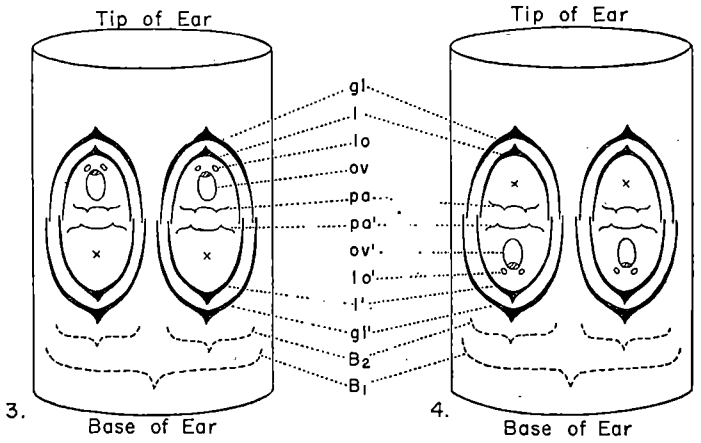

Fig. 3 Spikelet pair with the upper floret in each spikelet functional and the lower one abortive as in ordinary field corn.

Fig. 4. Spikelet pair with the upper floret in each spikelet abortive and the lower one functional as in the Canadian Reversed Germ Line.

The abortive ovaries are indicated by x's.

Legend to figures 2, 3 and 4.

gl	upper glume	ov	upper ovary	gl'	lower glume	ov'	lower ovary
l	upper lemma	pa	upper palea	l'	lower lemma	pa'	lower palea
lo	upper lodicule			lo'	lower lodicule		

B_1 primary bract
B_2 secondary bract

The kernels are arranged in rows with exception of the cases in italics where two kernels develop in the place of one.

Since Type 2 is the normal field corn type, the varying frequency of Type 3 would be responsible for the varying percentages of reversed germ kernels in the Minnesota line. The rare occurrence of Type 1 in the cases shown in italics would account for the twin, semi-connate and connate kernels found in this line which will be discussed later.

It has already been mentioned that it is known that in normal field corn usually only the upper florets of the spikelets are functional, while both the upper and lower florets are functional in Country Gentleman sweet corn. From this study it cannot be concluded whether in the Minnesota reversed germ line all lower florets are potentially functional or only some of them. Even if all were functional there might be competition as to which floret of the spikelet gets fertilized first. Other interacting factors may also have some influence on the final outcome. It seems more likely that in the Canadian line potentially *all lower* florets are functional. This situation would be exactly opposite to that prevailing in normal field corn.

In summary it may then be concluded that the so-called reversed germ is actually not reversed in the ontogenetic sense but is the consequence of the development of the lower floret. Although the term reversed germ is somewhat ambiguous it has become so firmly established in the literature that no other name is suggested for it.

Interpretation of Twin Kernels, Connate and Semi-connate Seeds

Mildred Stratton (1923) working with the variety *polysperma* described three different types of kernels as follows:

(1) Separate or twin kernels: if both flowers of the spikelet are functional then the resulting kernels occur in pairs, the upper kernel having its embryo on the adaxial (upper) side and the lower kernel having it on the abaxial (lower) side. The two seeds are therefore said to be back to back, the lower being "inverted." Such kernels were also described by Kempton (1913), Weatherwax (1916), Kiesselbach (1925), and Randolph (1936).

(2) Connate seeds: Stratton considers these to be examples of pseudo-polyembryony. Both seeds are actually enclosed by a common pericarp forming what is really a two-seeded fruit or kernel. In *polysperma* the embryos in the double kernel are arranged opposite each other, but at the right and left edges of the kernels while in the Hopi variety they are arranged above and below with respect to the cob as an axis (Kempton, 1913).

(3) Semi-connate seeds: between the condition in which two entirely separate kernels develop from a single spikelet and that in which a two-seeded fruit develops from the two flowers of a single spikelet are a number of intermediate conditions in which the kernels show various degrees of coalescence. Blaringhem (1920) also reported fused and partly fused double kernels in *Zea mays var. polysperma*

and concluded that this was a case of inheritance of acquired characters.

In the Minnesota reversed germ line a total of three connate kernels were found and from one to three each semi-connate and twin seeds on each of several ears of the inbred line. The connate seeds were twice as large as normal kernels and the embryos were located at the right and left edges of the kernels as in the variety *polysperma.* The semi-connate seeds could be recognized by the location of the kernel pair, the division line between the two kernels being in the center of the otherwise clearly defined row, the location of the two embryos at 180° from each other—also at the right and left edges of the kernels—and finally from the common pedicel of both kernels. Twin kernels, connate, and semi-connate kernels found in the Minnesota line would represent the occasional occurrence of Type 1 either in the right or the left florets of a spikelet as was described earlier.

Summary

The reversed germ character is recognized phenotypically by the fact that the germinal face of the kernel is oriented toward the base of the ear.

Observations were made on a Minnesota inbred line of dent corn which has the reversed germ character, a Canadian inbred line with a similar character, and on Country Gentleman sweet corn.

The reversed germ character in the Minnesota line is recessive and is carried by a major and a minor gene (Joachim, in prep.). The percentage of reversed germ kernels in the Minnesota line varied from 4.4 to 63.7 per cent while in the Canadian line it was 60.6 to 97.8 per cent.

The morphological and the ontogenetical development of the spikelet pair in corn are reviewed. Country Gentleman sweet corn crosses were taken as the basis for the morphological analysis. Here, about 50 per cent of the kernels have reversed germs and there are no distinct rows. This is interpreted as indicating that the ovaries of all four florets of each spikelet developed into mature kernels, the upper florets into normal and the lower florets into reversed germ kernels. The resulting crowding of the kernels destroyed the arrangement in rows.

In the Minnesota and the Canadian lines of dent corn distinct rows are generally found. It was therefore concluded that in the Minnesota line the ovaries of *either* the upper or the lower florets while in the Canadian line, *more often the lower* florets, of any spikelet produced mature kernels.

In Country Gentleman sweet corn both the upper and the lower florets are functional while in normal field corn only the upper florets are functional. In the Minnesota line at least some of the lower florets must be functional; it seems that in the Canadian line most or all of the lower florets may be potentially functional.

It may then be concluded that the so-called reversed germ is actually not reversed in the ontogenetic sense but that it is the consequence of the development of the lower floret. However, since this name for the character has been used in the literature, no other name is suggested for it.

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