1-1-1925

The Development and Inheritance of a Defective Endosperm in Maize

B. L. Wade

Follow this and additional works at: https://researchrepository.wvu.edu/wv_agricultural_and_forestry_experiment_station_bulletins

Digital Commons Citation

Wade, B. L., "The Development and Inheritance of a Defective Endosperm in Maize" (1925). *West Virginia Agricultural and Forestry Experiment Station Bulletins*. 197.
https://researchrepository.wvu.edu/wv_agricultural_and_forestry_experiment_station_bulletins/197

This Bulletin is brought to you for free and open access by the Davis College of Agriculture, Natural Resources And Design at The Research Repository @ WVU. It has been accepted for inclusion in West Virginia Agricultural and Forestry Experiment Station Bulletins by an authorized administrator of The Research Repository @ WVU. For more information, please contact ian.harmon@mail.wvu.edu.

West Virginia University Libraries

3 0802 100663713 5

EVANSDALE LIBRARY
WEST VIRGINIA
UNIVERSITY

--	--	--

Agricultural Experiment Station

College of Agriculture, West Virginia University

HENRY G. KNIGHT, Director

Morgantown

The Development and Inheritance of A Defective Endosperm in Maize

BY

B. L. WADE

AGRICULTURAL EXPERIMENT STATION STAFF

FRANK B. TROTTER, A. M., LL. D.....	President of the University
GEORGE R. LYMAN, Ph. D.....	Dean of the College of Agriculture
HENRY G. KNIGHT, Ph. D.....	Director of the Experiment Station
WALTER C. SCHNOPP, B. S. Agr.....	Agricultural Editor
JOHN C. JOHNSTON.....	Chief Clerk

AGRONOMY

R. J. Garber, Ph. D. Agronomist
 T. E. Odland, M. S. Associate Agronomist
 T. C. McIlvaine, Ph. D.† Assistant Agronomist
 K. S. Quisenberry, M. S. Junior Agronomist
 B. L. Wade, M. S. Agr. Graduate Assistant in Agronomy

ANIMAL HUSBANDRY

E. A. Livesay, M. S. Animal Husbandman
 Chas. V. Wilson, M. S. Assistant Animal Husbandman
 E. C. Stillwell, M. S. Assistant Animal Husbandman
 R. H. Tuckwiller, B. S. Agr.* Assistant Animal Husbandman

CHEMISTRY

Henry G. Knight, Ph. D. Chemist
 R. B. Dustman, Ph. D. Assistant Chemist
 Chas. E. Weakley, Jr., B. A., Assistant Chemist
 T. B. Leith, B. A.** Assistant Chemist
 T. J. Cochran, B. S. Junior Chemist

DAIRY HUSBANDRY

Ernest L. Anthony, M. S. Agr. Dairy Husbandman
 H. O. Henderson, M. S. Agr.*** Associate Dairy Husbandman
 Warren Gifford, B. S. Agr. Junior Dairy Husbandman
 G. M. Trout, M. S. Assistant in Dairy Husbandry

ENTOMOLOGY

L. M. Peairs, Ph. D. Entomologist
 W. E. Rumsey, B. S. ** Assistant Entomologist

FARM ECONOMICS

A. J. Dadisman, Ph. D. Farm Economist
 Paul A. Eke, Ph. D. Junior Farm Economist
 F. D. Cornell, M. S. Junior Farm Mechanician
 W. W. Armentrout, M. S. Junior Farm Economist

HORTICULTURE

M. J. Dorsey, Ph. D. Horticulturist
 H. L. Crane, M. S. Agr. Associate Horticulturist
 H. E. Knowlton, Ph. D. Associate Horticulturist
 K. C. Westover, M. S. Agr. Assistant Horticulturist
 Ernest Angelo, B. S. Agr. Junior Horticulturist
 L. F. Sutton, B. S. Agr.† Assistant Horticulturist
 Troy M. Currence, B. S. Agr. Assistant in Horticulture
 Lewis G. Stark, B. S. Agr. Graduate Assistant in Horticulture

PLANT PATHOLOGY

N. J. Giddings, Ph. D. Plant Pathologist
 Anthony Berg, B. S. Assistant Plant Pathologist
 L. H. Leonian, Ph. D. Assistant Plant Pathologist
 E. C. Sherwood, M. S. Assistant Plant Pathologist

POULTRY HUSBANDRY

Horace Atwood, M. S. Agr. Poultry Husbandman

SOILS

E. P. Deatrick, Ph. D. Associate Soil Technologist

*In co-operation with the U. S. Department of Agriculture, Washington, D. C.

**In co-operation with the State Department of Agriculture, Charleston, W. Va.

***On leave of absence.

†In charge of the Reymann Memorial Farms, Wardensville, W. Va.

‡In charge of the Maggie Sub-Station, Maggie, W. Va.

*The Development and Inheritance of a Defective Endosperm in Maize**

During the past two decades extensive genetic investigations have been carried on with maize. This is owing partly to the economic importance of the crop and partly to the ease with which pollination may be controlled.

Maize is naturally cross pollinated and hence highly heterozygous. One of the most striking facts which has been discovered about corn in recent years is the great number of undesirable characters which may be carried indefinitely in the heterozygous condition. Many of these characters when isolated in a homozygous condition by continued self fertilization become lethal or semi-lethal. The question naturally arises whether these characters or rather the factor differences which give rise to them interfere with normal metabolism and growth when in a heterozygous condition. One of the first steps in the study of such a character is to determine its manner of inheritance.

The present study was made to determine the manner in which a certain defective endosperm in maize is inherited; and also, to determine the stage of development in which defective seeds may be differentiated from normal seeds.

REVIEW OF LITERATURE

Emerson (1912) pointed out that there are many abnormalities in maize. Among the defects mentioned are: dwarf, hermaphrodites, yellow leaves, white seedlings, erect leaves due to the absence of the auricle, irregular kernel rows, inability to stand erect, and zigzag stalk. Most of the abnormalities are recessive characters. The dominant abnormalities listed are: fasciated, bifurcated, and branched ears; and staminate spike-

*The writer wishes to express his appreciation to Dr. R. J. Garber, head of the Agronomy department, under whose direction the present investigation was carried out.

lets intermingled with pistillate flowers.

Zapparoli (1923) reports that abnormalities are common. Some of the Italian farmers select deformed ears, believing that the kernels of such ears are harder and that they produce a greater yield. Kempton (1921, 1923a, 1923b) has studied three abnormal types of maize; brachytic, branched ears, and dead leaf margins.

Chlorophyll defects have received much attention. Lindstrom (1921) reported three types of chlorophyll defects in seedlings of maize. They are: albino, virescent, and yellow. Brunson (1924) has worked with a lethal, pale green seedling condition which behaves as a simple Mendelian recessive showing a single factor difference. Stroman (1924) gives a factorial explanation of three chlorophyll defects, yellow white (the reverse of virescent), white-base-leaf, and seedling zebra. Hayes and Brewbaker (1925) point out that mutations for chlorophyll deficiencies may occur quite frequently.

"Germless seeds" is a character which has been investigated by at least two persons. Demerec (1923) reported that germless seeds were found in the majority of commercial varieties of which selfed progenies were examined. Wentz (1924) has done further work with germless or miniature germ kernels.

Jones (1923) has investigated a case in which the development of the embryo and endosperm is stopped completely or greatly reduced shortly after fertilization. However, the pericarp continues to develop. The character is rather variable in its manifestations ranging from completely empty pericarps to seeds that are not at all shriveled but have a dull opaque appearance.

Hutchinson (1921) states that shrunken endosperm as it occurs in flour corn gives a 3:1 ratio. Richey (1923) reports that defective seed is not a new character. An ear obtained from an Indian grave in Peru, at least 300 years old, shows defective seeds, exhibiting, externally at least, the same kind of defective seeds as are now found in abundance in many types of maize.

Lindstrom (1923) has worked with two endosperm defects, one in sweet corn and the other in flint corn. Each defect is usually lethal in effect and when an occasional seedling is produced it is an albino. Pollen sterility has prevented an accurate analysis of the inheritance of these characters but a single factor

difference is thought to control the inheritance of each character. However, the deviations from a 3:1 ratio are wide.

Manglesdorf (1922) describes a condition that he calls mealy endosperm, in which the starch grains are normal. In the mealy seed he found a small but normal embryo. The character proved to be a simple Mendelian recessive. In crosses with other defectives it was found that the recently discovered defective was genetically distinct. It is a lethal condition linked with albinism.

In another paper Manglesdorf (1923) takes up defectives in general. Defective seeds are defined as heritable characters in maize in which the endosperm is lacking or is incomplete or abnormal in its development. Defective seeds have appeared in all the sub-species of maize with the possible exception of *Zea mays tunicata*. The defectives were roughly classified into: (1) Complete defectives, those in which the development of the ovule is arrested shortly after fertilization, (2) Partial defectives, those in which a certain amount of endosperm is laid down, and (3) Germinating seeds, those in which the mature seed fails to go into the resting stage.

Garber and Wade (1924) in a preliminary paper on a certain defective endosperm in maize report that the character is apparently controlled by a single factor difference. The present paper deals with a continuation of the study of this defective endosperm.

MATERIAL AND METHODS

In 1922 a selfed ear segregating for defective endosperm was harvested, together with five non-segregating ears from a strain of Leaming corn which had been selfed for three years. The corn was obtained originally from Geo. S. Strosnider near Waynesburg, Pennsylvania. This segregating ear had 284 normal and 96 defective seeds.

In 1923 all the seeds from this ear were planted at the rate of a single seed every 15 inches in rows $3\frac{1}{2}$ feet apart. All the planting was done at one time. In 1924, 2203 seeds from the previous generation were planted at the same rate as in 1923, except that single seeds were spaced 30 inches apart. Of the seeds planted 1125 were for a classification of certain doubtful

seeds, 247 were crossed seeds, and the remainder were for miscellaneous purposes. In order to have available matured pollen at the proper time, deferred plantings of crossed seed and homozygous normal seed were made. In 1924, as in 1923, seeds classified as normals and taken from a single segregating ear were planted.

The usual methods of pollinating were used. In 1923 most of the plants were selfed. Attempts to self defectives or to cross defectives with defectives were not successful. Several back crosses of normals to the recessives were made and one large ear and several small ones obtained. In 1924 about 30 plants from the segregating ear were selfed. The F_1 plants were pollinated with a pollen mixture and with pollen from homozygous defective plants.

The material for the histological study was killed and fixed with chromo acetic acid and imbedded in paraffin. The sections were stained with Heidenhain's iron-alum haematoxylin and destained with a solution of ferric ammonium sulphate.

The first year (1923) pistillate florets from each of the three different kinds of plants, homozygous normal, heterozygous normal, and homozygous defective were collected and killed before fertilization. Material also was collected and killed, after fertilization, at two week intervals for a period of eight weeks. Homozygous defectives were not included in these later collections on account of the fact that attempts at selfing them were unsuccessful.

During the second year, material was collected as in the first year, except that after fertilization the samples were taken at two day intervals. In 1924 florets and immature seeds from an F_1 individual back crossed to a homozygous defective were collected and killed. Prepared sections of all material collected before pollination and during the six days subsequent to fertilization were very satisfactory as the details of cell structure were clearly shown. The methods employed did not give satisfactory sections of the older material.

When necessary and desirable, variability was measured statistically. If the numbers involved were small Bessel's formula was used but in all other cases the ordinary formula was employed.

DESCRIPTION OF THE DEFECTIVE SEEDS AND PLANTS

The matured seeds classified as defective were generally undersized and variable in the expression of the character. Some of the defectives were almost as plump as normal seeds and would have been classified as such except for a milky opaque appearance at the crown. In typical cases however, from one-half to three-fourths of the normal amount of endosperm had de-

Fig. 1.—A Homozygous Normal and a Segregating Ear, Natural Size

veloped. In practically all cases the pericarp attained approximately normal size. Normal seeds in general, have a bright yellow color typical of the Leaming variety, but the defective seeds are dull and without lustre. (See Figure 1)

The breeding records show a striking variation in the expression of the defective character. Among 25,492 seeds produced in 1923 on segregating ears, there were 1106 seeds of such appearance that they could not satisfactorily be placed in either class, i. e. normal or defective. Since space was not available for planting all of these, 375 doubtful seeds from nineteen ears were planted, and an equal number of normal and defective seeds from the same respective ears, in parallel rows, on either side of the defectives.

Plants from the normal seeds were of ordinary height of a bright green color, while those from defective seeds were very short and possessed a somewhat lighter green color. Figure 2 shows the difference in height between the two kinds of plants.

Planting was done on May 12, 1924 and stand notes taken at three different dates. In September the plants were measured for height, recounted, and classified. The data are presented in Table I.

TABLE I.—Stand Notes of Plants Grown in 1924 from Seeds Planted for Classification Purposes.

Kind of Seed	No. of Plants June 12	Per cent of Total * June 12	No. of Plants June 26	Per cent of Total June 26	No. of Plants July 23	Per cent of Total July 23	No. of Plants Sept. 5	Per cent of Total Sept. 5
Defective	161	42.9	127	33.9	91	24.3	74	19.7
Doubtful	178	47.5	186	49.6	161	42.9	53† } 155	41.3
Normals	313	83.5	305	81.3	301	80.3	102 } 289	77.1

*375 seeds

†53 defectives, 102 normals.

The delay until September in classifying the plants was due to the difficulty in distinguishing defective and normal plants in the early stages. Even at later stages classification was difficult. The chief difficulties encountered were variation in diameter and in height of plants since there was a tendency for the two strains

Courtesy Journal of Heredity.

Fig. 2.—Plants from Normal and Defective Seeds Ten Weeks After Planting.

to overlap in these characteristics. The defective plants matured pollen about two weeks later than the normal plants.

Of the 375 doubtful seeds planted 155 plants survived until September and 53 of these were defectives and 102 were normals. By means of the relative number of the normal plants and the relative number of the homozygous defective plants that survived, it was calculated that 37.6 per cent of the seeds classified as doubtful were normal, and 62.4 per cent were defective.

The mean, the standard deviation, and the coefficient of variability of height of plants from normal seed and from defective seed are shown in Table II. The mean height of the former is 69.90 ± 0.34 and that of the latter is 32.42 ± 0.69 . The coefficients of variability between the two classes of plants show a difference of 20.90 ± 1.51 . When measured by means of this statistical constant, it is apparent that the variability of the plants from the defective seed is approximately two and one-half times that from normal seed. The extreme deviation of some of the plants made it difficult to classify them.

An instance of the variability of the expression of defective endosperm was shown by a certain ear, grown in 1923. This ear had 102 normal seeds, no defective seeds, and forty unfilled pericarps. A breeding test in 1924 showed that the ear should be classified as segregating for the defective condition.

Further evidence of the variability of the expression of the defective character is found in the fact that among the plants from defective seeds grown in connection with the classification study in 1924 were five normals, while among the plants from normal seed were ten which appeared like defective plants. The normal plants among defectives may have come from seeds erroneously classified as defective due to crowding on the ear, or seed in an unfavorable position for development. The plants which resembled defectives and appeared among what were supposed to have been normals may have been due in part at least, to root rot, which was known to be present in this particular field.

The variability of defective endosperm suggests the possibility that a modifying factor (or factors) is present and conditions the expression of the character. It would be necessary to make further breeding tests to determine if such is actually the case.

TABLE II.—Variability in Height of Plants Grown in 1924 from Defective and Normal Seeds.

Defectives										n	M	σ	C
Class (Inches)	0-5	5-10	10-15	15-20	20-25	25-30	30-35	35-40	40-45	45-50	50-55		
Frequency	0	3	8	6	17	14	22	17	16	14	5	11.33±0.49	34.95±1.12
Normals													
Class (Inches)	40-45	45-50	50-55	55-60	60-65	65-70	70-75	75-80	80-85	85-90	90-95	95-100	100-105
Frequency	4	8	21	29	47	70	83	66	47	8	2	0	1
												9.82±0.24	14.05±1.02

DEVELOPMENT OF THE PISTILLATE SPIKELET

Weatherwax (1916) states that the upper pistillate flower has a pistil, three rudimentary stamens but no lodicules. The secondary flowers have lodicules. Miller (1919) traced the de-

a = base of silk
 b = outer integument
 c = embryo sac with one of the nuclei
 d = palea of fertile flower
 e = palea of sterile flower
 f = lemma of sterile flower

g = sterile flower
 h = outer glume
 l = lemma of fertile flower
 m = outer glume
 n = outer integument
 o = inner integument

Fig. 3.—A Projection Drawing of a Developing Corn Floret Showing One Nucleus of the Embryo Sac.

velopment of the pistillate spikelet in a detailed manner. He found that in the development of the embryo sac all four of the megasporos are functional. Within 36 hours after fertilization the cells of the endosperm completely fill the embryo sac. Illustrations of extremely young and more mature florets are shown.

In the present investigation possible differences between the developing florets of normal and of defective plants were sought. A projection drawing of an unfertilized defective floret showing one nucleus of the embryo sac is presented in Figure 3. This drawing is typical of either normal or defective florets before fertilization. The palets of the fertile and infertile flowers are side by side while the lemmas occupy opposite sides of the flowering branch. The embryo sac differentiates at the same time that the ovule is inverting and during the growth of the integuments. The integuments on one side of the ovule usually grow more rapidly than the integuments on the opposite side. The result of this difference in rate of growth is shown in the drawing.

Careful examinations and comparisons of the slides prepared in 1923 and 1924 showed that: (1) No difference could be seen between normal and defective flowers before fertilization, (2) There was no apparent difference in the embryo sacs of the normal plants and those of the defective plants, (3) Up to six days after fertilization no differences were detected in the development of the endosperm of homozygous normals, heterozygous normals and homozygous defectives.

Illustrations of a mature normal seed and of a mature defective seed are shown in Figure 4. These diagrammatic drawings were made from sections of seeds under a dissecting binocular microscope and show a difference in the appearance of the starch laid down in the two kinds of seeds and a difference in the degree of development of the endosperm. The endosperm of defective seed is made up of soft starch and that of normal seed is made up of both hard and soft starch. Although the pericarp of the defective seed is developed to almost the same extent as that of the normal seed, the former contains considerably less endosperm. There is apparently no difference in the embryos.

POLLEN ABORTION

In 1923 the anthers of normal and defective plants were examined for pollen abortion. To detect the presence of aborted grains the common method of staining with a mixture of acid fuchsin and lactic acid was employed. Counts were made to determine whether pollen from defective plants is as viable as that from normal plants.

Table III shows that the average amount of pollen abortion for pollen from normal plants expressed in percentage is 2.64 ± 0.47 while that from defective plants is 2.18 ± 0.32 . The difference is 0.46 ± 0.33 and therefore not significant.

Fig. 4.—Diagrammatic Drawings to Show the Difference Between Mature, Normal and Defective Corn Seeds.

TABLE III.—Pollen Abortion Among Plants Grown in 1923 from Normal Seed and from Defective Seed.

Normal Plants			Defective Plants		
Plant No.	Abortive Grains		Plant No.	Abortive Grains	
	in 1000	Per cent		in 1000	Per cent
201 - 7	18	1.80	207 - 9	33	3.30
201 - 10	24	2.40	207 - 18	29	2.90
201 - 15	27	2.70	207 - 20	19	1.90
201 - 17	14	1.40	207 - 23	17	1.70
201 - 18	76	7.60	207 - 24	21	2.10
201 - 50	8	0.80	207 - 29	12	1.20
201 - 61	22	2.20	Average	21.8	2.18±0.32
201 - 62	53	5.30			
201 - 104	20	2.00			
201 - 110	7	0.70			
201 - 142	13	1.30			
201 - 146	15	1.50			
201 - 149	35	3.50			
201 - 238	36	3.60			
201 - 241	35	3.50			
Average	26.4	2.64±0.47			

INHERITANCE OF THE DEFECTIVE SEED

In 1923 the selfed normal (homozygous and heterozygous) plants produced one hundred and fifty-three ears. In 1924 fifteen additional ears were obtained. The results for the two years are shown in Table IV. Considering the two years together the total number of ears produced is 168 of which 61 are non-segregating and 107 segregating ears. There is a deviation from the expected monohybrid ratio of 5 ± 4 which is only 1.3 times its probable error and therefore not significant.

TABLE IV.—The Number of Ears Segregating and the Number of Ears Not Segregating in 1923 and 1924. A Ratio of Two Segregating Ears to One Non-segregating Ear is Expected.

Year	Number of Segregating Ears	Number of Non-segregating Ears	Deviation	D./P.E.
1923	98	55	4 ± 4	1.0
1924	9	6	1 ± 1	1.0
	<u>107</u>	<u>61</u>	5 ± 4	1.3

The relative numbers of normal defective seeds produced by the segregating ears were determined. The results are listed in Table V. In 1923 one of the segregating ears moulded before the seeds were counted so that counts are given for only 97 ears. These 97 ears produced a total of 23,353 seed of which 18,835 were normal, 5412 defective and 1106 of such appearance that a progeny test was necessary to determine their genetic constitution. As has already been mentioned on page 10 the breeding test showed that 37.6 per cent of the doubtful seeds should be classified as normal and 62.4 per cent as defective. By classifying these doubtful seeds according to the above percentage the ratio of the total number of normal seeds to the total number of defective seeds is 19,351 to 6,141. This does not give a very close fit to a 3:1 ratio. The deviation is 232 ± 47 , or a deviation 4.9 times its probable error. This deviation is significant but is probably due to improper classification of seeds.

Table V also shows the results for 1924. The deviation, the probable error, and the deviation divided by its probable error are given for each ear and the total. The deviations vary from 0.50 ± 1.1 to 21.3 ± 6.0 . Considering all the seeds produced by segregating ears a ratio of 1359 normal to 454 defective seeds was obtained. This is a very close fit to the expected 3:1 ratio, the deviation being only 0.8 ± 12.4 . In 1924 all seeds were definitely classified as normal or defective.

From these results it appears that a single main factor difference is responsible for the inheritance of the defective endosperm. Moreover this factor difference does not find expression in the endosperm only but in the resultant plant as a whole. Plants homozygous for the defective condition are shorter, more slender, later in maturing, and less vigorous than normal plants.

TABLE V.—The Breeding Nature and Number of Seeds Produced by Each Selfed Ear in 1924 and a Summary of Those Produced in 1923.

Selfed Ears Grown in 1924						
Number of Ear	Nature of Ear	Number of Normal Seeds	Number of Ear	Nature of Ear	Number of Seeds	
					Normal	Defective
3	Normal	288	2	Seg.	264	66
9	Normal	133	4	Seg.	159	45
10	Normal	148	5	Seg.	124	37
12	Normal	178	6	Seg.	159	62
14	Normal	36	7	Seg.	130	39
17	Normal	112	8	Seg.	293	126
			11	Seg.	101	41
			13	Seg.	10	4
			16	Seg.	119	34
Total		895	9		1359	454
						16.5±5.3
						6.0±4.2
						3.3±3.7
						6.8±4.3
						3.3±3.8
						21.3±6.0
						5.5±3.5
						0.5±1.1
						4.3±3.6
						0.8±12.4
						3.1
						1.4
						0.9
						1.6
						0.9
						3.6
						1.6
						0.5
						1.2
						0.1

Selfed Ears Grown in 1923			
55	Normal	15986	98*
			Seg.
			19351†
			6141
			232±47
			4.9

* The seeds from 97 ears only were counted as one ear was moulded.

† This represents the ratio of total normal to total defective seed s including the doubtful seeds which were classified on the basis of a progeny test in 1924.

HECKMAN
BINDERY INC.

JUNE 99

Bound-To-Please® N. MANCHESTER,
INDIANA 46962