THE INHERITANCE OF DORMANCY AND PREMATURE GERMINATION IN MAIZE*

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INTRODUCTION

Seeds of maize and in fact those of the majority of spermatophytes normally do not germinate during their period of development. Dormancy during this period is as essential to the perpetuation of the species as the ability to germinate after development has been completed. In maize, however, it has been found that the presence in the germplasm of various genetic factors results in germination, before the seed is mature, in certain definite proportions of the seeds. This condition has been reported and described by LINDSTROM (1923), EYSTER (1924a, 1924b), and by the writer (MANGELSDORF 1923, 1926). In the paper last cited, evidence was presented to show that a number of genetic factors are involved in the inheritance of premature germination in maize; that these factors operate at various stages in the development of the seed and differ in some of their effects. All are alike, however, in forcing the seed to germinate before development has been completed and hence, under natural conditions, are ultimately lethal in effect.

The present paper represents further studies on the inheritance of

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several forms of premature germination previously reported; the verification of several hypotheses which had been tentatively presented; and a study of new types more recently discovered. The studies reported here were made at the CONNECTICUT EXPERIMENT STATION from 1921 to 1926 and at the TEXAS EXPERIMENT STATION from 1927 to 1929. Some of the stocks used were found to be unadapted to Texas conditions and rather than delay completion of the work until new stocks could be developed, most of the F_3 progenies were grown in New Haven, the self-pollinated ears being returned to Texas for classification. I take this opportunity of thanking Doctor D. F. JONES and Doctor W. R. SINGLETON for their kindness in growing and pollinating this F_3 material. I wish also to acknowledge the assistance of Mr. A. T. CHISHOLM in classifying some 54,000 individuals included in these studies.

ORIGIN AND DESCRIPTION OF CHARACTERS

The origin and description of a number of these characters has already been given in a previous paper (MANGELSDORF 1926); consequently only a brief resumé need be included here. The reader is referred to the above paper for further details.

g_{e1}

This is the first type of premature germination found. It was first noted in the second generation of inbreeding of a strain of Gold Nugget flint corn. Germination begins when the seeds are in the late milk stage and is associated with complete lack of color in the endosperm and chlorophyll in the plumule, except in the absence of light, when the plumule develops a faint tinge of bluish green. This character is inherited as a simple Mendelian recessive.

g_{e2}

This character was found in an inbred strain of Golden Bantam sweet corn. Germination begins when the seeds are in the dough stage. The endosperm color is slightly affected but the plumules are normal green. This character is associated with small seeds which are defective in appearance and it may be that the premature germination is merely a secondary effect of a factor for defective seeds, since early germination of some of the hereditary types of defective seeds is by no means uncommon.

g_{e3}

This stock was obtained from Doctor E. W. LINDSTROM and is the same one reported by him in 1923. It originated in an inbred strain of

Golden Bantam in the third generation of inbreeding. Germination begins at a very early stage and is almost completely associated with absence of color in the endosperm and lack of chlorophyll in the plumule. The g_{e3} type can be distinguished from g_{e1} only when both develop in darkness in which case the former is completely albinitic while the latter shows a faint greenish tinge. It is inherited as a simple recessive.

g_{e4}

An open-pollinated ear of flint corn of the Longfellow type received from Mr. T. B. MACAULAY of Montreal, Canada, gave rise to this type. Germination begins in the hard dough stage. Chlorophyll development is not affected and the endosperm color is only slightly diluted. The character is inherited as a simple recessive.

g_{e5}

This type of premature germination first appeared in the F_2 endosperm generation of a cross between g_{e1} and g_{e3}. It has since appeared in this same cross when repeated and in another cross in which g_{e3} was used as one of the parents. This situation is difficult to explain as the g_{e3} stock has always segregated in a normal 3:1 ratio. In appearance, g_{e5} differs in no discernible details from g_{e3}. Germination begins in the early milk stage and is associated with complete absence of endosperm and chlorophyll color.

g_{e6} g_{e7}

This character is due to the expression of duplicate factors. It was found in ears of an F_1 hybrid of two inbred strains of Canada Flint, neither of which had ever shown premature germination. Germination begins at the late dough stage. The plumule is green while the endosperm color is diluted only in small areas of the seed usually adjacent to the embryo. This character is inherited in a 15:1 ratio when both factor pairs are heterozygous; in a 3:1 ratio when one pair is homozygous recessive, the other heterozygous.

g_{e8} g_{e9} g_{e10}

A cross of an inbred strain of Sanford White flint with an unknown yellow flint gave rise to this stock. Germinating seeds were found in the F_2 endosperm generation in the ratio of 8:1. This was tentatively explained as the result of duplicate factors in the same linkage group. Later studies indicate that triplicate factors are involved and that two of these are linked. Germination begins at a very late stage and has no effect on chlorophyll development and practically none on endosperm color.

g_{e11}

This type of premature germination was first noted in the F_2 endosperm generation of a cross between two inbred stocks segregating for defective seeds, d_{e5} and d_{e11}, which later proved to be genetically identical. One parent was an inbred strain of Clarage Dent obtained from Mr. M. T. MEYERS, the other a strain of Reid's Yellow Dent from Doctor J. R. HOLBERT. Germinating seeds had never been noted in either of the parents, and since these were being studied especially for endosperm defects, it seems improbable that premature germination could have occurred without being noted. This type of premature germination is very striking in appearance, both the seed and plumule showing a pink color. The character appears to be inherited as a simple recessive.

g_{e12} g_{e13} g_{e14} g_{e15}

Ratios of 255:1 and 63:1 in several crosses indicate a set of quadruplicate factors all of which must be present in a homozygous recessive condition in order for premature germination to occur. Germination does not take place until the seed is practically mature and is later than in any of the other types described. The plumule seldom ruptures the pericarp and chlorophyll and endosperm color are not at all affected. The sprouting is so slight that the seeds must be rather carefully examined from the germ side in order to identify the recessives.

g_{ex}

This character is tentatively designated g_{ex} because little is known concerning it and it may prove to be identical with one of the types already described. It appeared in the F_2 endosperm generation of a cross between g_{e1} and g_{e6} g_{e7}, and was inherited as a simple recessive. In appearance it resembles g_{e4} rather closely and the two may prove to be genetically identical.

Peculiar origin of germinating seeds

An unusual fact regarding the origin of a large proportion of the types of premature germination is that they did not appear in the first generation of inbreeding when recessive characters are usually brought to light. Seeds of g_{e1} were first noted in the second generation; g_{e3} was discovered, according to LINDSTROM (1923), in the third generation; g_{e5} appeared only when g_{e3} was crossed with other stocks; g_{e11} resulted from a cross between two inbred strains which had never segregated for germinating seeds; and g_{ex} arose in a cross of g_{e1} g_{e6} g_{e7}. In addition g_{e6} g_{e7}, g_{e8} g_{e9} g_{e10}, and g_{e12} g_{e13}

g_{e14} g_{e15} were found in crosses, the parents of which had never shown these particular types of premature germination. These types, however, belong to a different category. They are the result of duplicate, triplicate, or quadruplicate factors and their occurrence in crosses is readily explained by assuming that the parents of the crosses were of such a genetic constitution that segregation could not occur. For example, the most simple explanation of the appearance of g_{e6} g_{e7} is that one parent was of the constitution $g_{e6}\,g_{e6}\,G_{e7}\,G_{e7}$, the other parent $G_{e6}\,G_{e6}\,g_{e7}\,g_{e7}$. Neither parent would segregate, nor would the F_1 seeds. In the F_2 generation, however, segregation in the ratio of 15:1 would be expected.

Such an explanation, however, does not account for the appearance of types which are inherited as simple recessives, such as g_{e1}, g_{e3}, g_{e5}, g_{e11} and g_{ex}. They might be the result of recent mutations but, if this is true, it is certain that mutations which result in premature germination are considerably more frequent than those of any other type so far observed in maize.

RESULTS OF CROSSING VARIOUS TYPES OF PREMATURE GERMINATION

The ultimate proof that all the types of premature germination, described above, are genetically distinct, must rest on the results of crosses in which the stocks are combined in all possible combinations. This program has not yet been completed but the data from such crosses as have been made, together with evidence of another nature, indicate rather convincingly that at least fifteen factors are involved in the inheritance of premature germination. The evidence for this conclusion is presented in the following pages.

Method of making crosses

Perhaps a word should be said here regarding the method used in crossing the stocks. Since all these characters are lethal they can be perpetuated only in the heterozygous condition. When dormant seeds from a segregating ear are planted, part of the plants thus produced are heterozygous; the remainder are homozygous dormant, the proportion depending upon the number of heterozygous factor pairs involved in the expression of the recessive condition. There is no way of distinguishing the two genotypes until several weeks after pollination. Consequently, the practice has usually been to pollinate at random at least five plants of one parent with pollen collected at random from five or more plants of the other parent. This practically insures that heterozygous plants of both parents are included but renders it impossible to predict the proportions in which the various types of segregating progenies should appear in F_2 of any particular cross.

Method of presenting data

In all cases where crosses have been made, the two parental types of premature germination have reappeared in the F_2 endosperm generation which is borne on F_1 plants. The data from this generation are presented in detail and there appears to be no necessity for including the data on inheritance of the same characters in the parental stocks. The latter are therefore omitted except in the case of g_{e11} which has not yet been used in crosses.

When several types of segregating progeny occur in F_2 the different progenies have been grouped according to the Mendelian ratio which they fit most closely. Such an arbitrary grouping may be subject to errors, as SIRKS (1926) has pointed out, and the chief object in presenting the F_2 data in detail is that of demonstrating how large a proportion of the progenies fit a certain ratio within the limits of sampling errors, but differ significantly from other ratios which occur in the same population.

The fact that the segregation in any given progeny fits a particular Mendelian ratio does not, of course, prove that this ratio is the true expression of the segregation. Data collected at random are almost certain to fit one of the many possible Mendelian ratios within the limits of sampling errors. The behavior of the F_3 progenies, however, should show definitely whether any F_2 progeny has been correctly classified. F_3 progenies have been grown from F_2 populations representative of almost every ratio which occurred.

In tabulating the F_3 data it has not been considered necessary to present the data from each progeny separately. The progenies have been grouped, by simple inspection, according to the ratios which they appear to fit most closely. Some of the progenies might fall into either of two groups almost equally well but in general the groups have been well-defined with little overlapping. In addition the "goodness of fit" of each array has been calculated and with few exceptions was found to be reasonably close. The F_3 data indicate that such F_2 progenies as were tested had been correctly classified with regard to Mendelian ratios.

Results in F_2

$g_{e1} \times g_{e3}$

Since both of these characters are simple recessives it would be expected that the F_2 endosperm generation should produce two types of segregating progenies, some segregating 3:1 and others segregating 9:7. In a previous cross of these two characters (MANGELSDORF 1926) these two types reappeared in F_2, but in addition a third group, segregating in a ratio of 27:37, also occurred. This is difficult to explain since both parental stocks had previously segregated in a ratio of 3:1. The cross was, therefore, repeated with the results shown in table 1. The situation is almost identical to that found previously. Three types of segregating progeny appeared and these grouped themselves definitely into 3:1, 9:7, and 27:37 ratios. We must conclude that three factors for premature germination are involved in this cross. These are apparently independent in their inheritance, no evidence of linkage being exhibited. The third factor is presumably the one which has already been designated as g_{e5}. Its effects are practically identical to those of g_{e3}

Ratios of 3:1 and 9:7 are expected from this cross if two pairs of complementary factors are involved. Table 2 shows that these requirements

TABLE 1

Segregating F_2 progenies of the cross $g_{e1} \times g_{e3}$.

EAR NUMBER	GENETIC FACTORS	PROBABLE RATIO	TOTAL SEEDS	NUMBER GERMINATING	THEORETICAL NUMBER GERMINATING	DEVIATION
2986	g_{e1}, g_{e3}, or g_{e5}	3:1	259	63	64.8	−1.8± 4.7
2987	“	“	281	75	70.2	4.8± 4.9
2990	“	“	271	76	67.8	8.2± 4.8
2991	“	“	251	57	62.8	−5.8± 4.6
2993	“	“	268	67	67.0	.. ..
2994	“	“	221	53	55.2	−2.2± 4.3
2995	“	“	192	42	48.0	−6.0± 4.1
Total			1743	433	435.8	−2.8±12.2
2988	g_{e1} and g_{e3} or g_{e5}	9:7	270	111	118.1	−7.1± 5.5
2996	“	“	199	84	87.3	−3.3± 4.7
2997*	“	“	284	125	124.3	.7± 5.6
2988	“	“	203	89	88.8	.2± 4.8
Total			956	409	418.2	−9.2±10.4
2989+	g_{e1}, g_{e3}, g_{e5}	27:37	291	166	168.2	−2.2± 5.7
2992	“	“	224	132	129.5	2.5± 5.0
Total			515	298	297.7	.3± 7.6

* See table 12 for F_3 progenies of this ear.

\+ See table 13 for F_3 progenies of this ear.

$g_{e1} \times g_{e4}$

have been met. Three ears proved to be segregating for g_{e1}, two ears for g_{e4}, and the remaining three ears for both characters. The di-hybrid ears all show a close approximation to a 9:7 ratio, indicating that the two factors are independent in their inheritance. It is noted that two ears segregating in an approximate ratio of 255:1 are included in table 2. These are discussed later.

TABLE 2

Segregating F_2 progenies of the cross $g_{e1} \times g_{e4}$.

EAR NUMBER	GENETIC FACTORS	PROBABLE RATIO	TOTAL SEEDS	NUMBER GERMINATING	THEORETICAL NUMBER GERMINATING	DEVIATION
2969	g_{e1}	3:1	303	71	75.8	−4.8±5.1
2972	"	"	237	48	59.3	−11.3±4.5
2977	"	"	249	68	62.3	5.7±4.6
Total			789	187	197.3	−10.3±8.2
2970	g_{e4}	3:1	342	86	85.5	.5±5.4
2978	"	"	269	78	67.2	10.8±4.8
Total			611	164	152.7	11.3±7.2
2971	g_{e1}, g_{e4}	9:7	279	130	122.1	7.9±5.6
2973	"	"	221	91	96.7	−5.7±5.0
2975	"	"	315	145	137.8	7.2±5.9
Total			815	366	356.6	9.4±9.6
2974*	g_{e12}, g_{e13}, g_{e14}, g_{e15}	255:1	268	1	1.05	−.05±.69
2976	"	"	266	2	1.04	.96±.69
Total			534	3	2.09	.91±.97

* See table 18 for F_3 progenies of this ear.

$g_{e1} \times g_{e6} g_{e7}$

Since g_{e6} g_{e7} are duplicate factors which result in ratios of 15:1 when both pairs are heterozygous, this cross should produce three types of segregating progenies; 3:1, 15:1, and 45:19. The last is actually the trihybrid ratio 45:15:3:1 in which the three last terms are combined because the three phenotypes are so nearly alike that accurate classification is difficult. Occasionally it has been possible to separate the g_{e1} and g_{e6} g_{e7} seeds on the same ear but generally all germinating seeds have been grouped together into a single class.

The results of this cross are set forth in table 3. It is evident that all three types of segregating progenies have appeared and hence the two stocks are distinct in their factors for premature germination. The close agreement between the theoretical and actual ratios indicates further that these three factors are independently inherited.

TABLE 3

Segregating F_2 progenies of the cross $g_{e1} \times g_{e6} g_{e7}$.

EAR NUMBER	GENETIC FACTORS	PROBABLE RATIO	TOTAL SEEDS	NUMBER GERMINATING	THEORETICAL NUMBER GERMINATING	DEVIATION
2954	g_{e1}	3:1	185	48	46.2	1.8±4.0
2955	"	"	256	58	64.0	−6.0±4.7
2958	"	"	105	22	26.2	−4.2±3.0
2964	"	"	272	70	68.0	2.0±4.8
Total			818	198	204.5	−6.5±8.4
2950	g_{ex}	3:1	284	72	71.0	1.0±4.9
2957	"	"	281	74	70.2	3.8±4.9
Total			565	146	141.2	4.8±6.9
2949	g_{e6} g_{e7}	15:1	205	13	12.8	.2±2.3
2953	"	"	227	13	14.2	−1.2±2.5
2961	"	"	132	10	8.3	1.7±1.9
2962	"	"	129	12	8.1	3.9±1.9
Total			693	48	43.3	4.7±4.3
2948	g_{e1}, g_{e6}, g_{e7}	45:19	297	92	88.2	3.8±5.3
2951	"	"	348	100	103.3	−3.3±5.8
2956	"	"	169	57	50.2	6.8±4.0
2960	"	"	33	12	9.8	2.2±1.8
Total			847	261	251.5	9.5±9.0
2947*	g_{e1}, g_{ex}, g_{e6} g_{e7}	135:121	233	114	110.2	3.8±5.1
2952†	g_{e12} g_{e13} g_{e14} g_{e15}	255:1	281	1	1.10	−.10±.71
2963	"	"	171	1	.67	.33±.55
Total			452	2	1.77	.23±.89

* See table 16 for F_3 progenies of this ear.

† See table 18 for F_3 progenies of this ear.

In addition to the expected ratios, three types of segregating progenies, which had not been anticipated, were encountered in this cross. Two ears were found to be segregating in a ratio of 3:1 for a character which obviously was not g_{e1}. The recessive seeds on these ears did not lack endosperm color as do seeds of g_{e1}, but resembled more nearly the recessive seeds of g_{e6} g_{e7}. This situation might be readily explained by assuming that part of the plants of the original g_{e1} stock were homozygous recessive for either the g_{e6} or g_{e7} factor pair. This explanation is not tenable, however, because of a second unexpected progeny, Ear No. 2947, which segregates in a ratio of 135:121. This ratio does not differ significantly from a 9:7 but the F_3 progenies presented later show beyond doubt that the segregation is not 9:7.

This cross, then, as did that between g_{e1} and g_{e3}, has resulted in the unexpected appearance of a new type of premature germination not previously observed in either parent. The new character is tentatively designated as g_{ex} until it can be studied further. In appearance it is practically identical to g_{e4} and may prove to be the same genetically.

TABLE 4

Segregating F_2 progenies of the cross $g_{e4} \times g_{e3}$.

EAR NUMBER	GENETIC FACTORS	PROBABLE RATIO	TOTAL SEEDS	NUMBER GERMINATING	THEORETICAL NUMBER GERMINATING	DEVIATION
3008	g_{e3}	3:1	216	52	54.0	−2.0±4.3
3009	"	"	258	61	64.5	−3.5±4.7
3012	"	"	194	61	48.5	12.5±4.1
3016	"	"	300	76	75.0	1.0±5.1
3017	"	"	186	43	46.5	−3.5±4.0
3019	"	"	242	57	60.5	−3.5±4.5
Total			1396	350	349.0	1.0±10.9
3013	g_{e4}	3:1	259	71	64.8	6.2±4.7
3014	"	"	142	42	35.5	6.5±3.5
3015	"	"	252	63	63.0	..
3018	"	"	101	35	25.2	9.8±2.9
3020	"	"	239	71	59.8	11.2±4.5
3021	"	"	304	78	76.0	2.0±5.1
Total			1297	360	324.3	35.7±10.5
3010	g_{e3} g_{e4}	9:7	272	120	119.0	1.0±5.5
3011	"	"	130	51	56.9	−5.9±3.8
Total			402	171	175.9	−4.9±6.7

This cross, too, has produced two ears segregating in a ratio of approximately 255:1. These are discussed later.

$g_{e3} \times g_{e4}$

Two types of segregating progenies, approximating 3:1 and 9:7 ratios, are expected from this cross. Both of these types have been obtained as shown in table 4. The ears segregating in a 3:1 ratio have been further subdivided into two groups, those segregating g_{e3} and g_{e4}. Such a separation is possible in this cross because of the marked phenotypical difference in the two characters.

The only significant deviation in the data is a slight excess of recessives in the six ears which segregate for g_{e4}. One of these ears shows a deviation of 3.4 times the error and the deviation for the group is also 3.4 times the error. With this exception the data are in close agreement with the theoretical ratios and indicate that g_{e3} and g_{e4} are genetically distinct and independently inherited.

TABLE 5

Segregating F_2 progenies of the cross $g_{e6}\ g_{e7} \times g_{e3}$.

EAR NUMBER	GENETIC FACTORS	PROBABLE RATIO	TOTAL SEEDS	NUMBER GERMINATING	THEORETICAL NUMBER GERMINATING	DEVIATION
3046	g_{e3}	3:1	198	44	49.5	−5.5±4.1
3045	$g_{e6}\ g_{e7}$	15:1	230	13	14.4	−1.4±2.5
3048*	"	"	268	13	16.8	−3.8±2.7
3050	"	"	276	14	17.2	−3.2±2.7
3052	"	"	257	11	16.1	−5.1±2.6
3053	"	"	260	9	16.2	−7.2±2.6
3056	"	"	268	15	16.8	−1.8±2.7
Total			1559	75	97.4	−22.4±6.4
3049	g_{e3}, $g_{e6}\ g_{e7}$	45:19	246	82	73.0	9.0±4.8
3051	"	"	285	105	84.6	20.4±5.2
3055	"	"	246	76	73.0	3.0±4.8
3057	"	"	240	70	71.3	−1.3±4.8
Total			1017	333	302.0	31.0±9.8
3047	$g_{e3}\ g_{ex}$	9:7	243	99	106.3	−7.3±5.2
3054	"	"	137	61	59.9	1.1±3.9
Total			380	160	166.2	−6.2±6.5

* See table 14 for F_3 progenies of this ear.

$g_{e3} \times g_{e6}\ g_{e7}$

The results of this cross should be similar to those from the cross $g_{e1} \times g_{e6}\ g_{e7}$ in producing Mendelian ratios of three types, 3:1, 15:1, and 45:19. One ear of the first, six of the second, and four of the third were found, as shown in table 5. These were identified not only by the proportion of recessives but also by phenotypical differences in the two types of premature germination. The data show only a fair agreement with the theoretical ratios. Each of the six ears segregating in a 15:1 ratio shows a slight but not significant deficiency of recessives, while the total deviation for the group is 3.5 times the error.

This excess in ears which are segregating for all three factors may indicate linkage between g_{e3} and one member of the $g_{e6}\ g_{e7}$ pair, especially

TABLE 6

Segregating F_2 progenies of the cross $g_{e4} \times g_{e6}\ g_{e7}$

EAR NUMBER	GENETIC FACTORS	PROBABLE RATIO	TOTAL SEEDS	NUMBER GERMINATING	THEORETICAL NUMBER GERMINATING	DEVIATION
3044A	g_{e4}	3:1	285	71	71.2	−.2±4.9
3030	$g_{e6}\ g_{e7}$	15:1	255	17	15.9	1.1±2.6
3032	"	"	260	26	16.2	9.8±2.6
3034	"	"	52	4	3.3	.7±1.2
3035	"	"	226	20	14.1	5.9±2.5
3036	"	"	180	12	11.2	.8±2.2
3038	"	"	267	25	16.7	8.3±2.7
3039	"	"	294	12	18.4	−6.4±2.8
3040	"	"	259	20	16.2	3.8±2.6
3043	"		269	20	16.8	3.2±2.7
Total			2062	156	128.9	27.1±7.4
3033*	g_{e4}, $g_{e6}\ g_{e7}$	45:19	262	87	77.8	9.2±5.0
3037	"	"	92	27	27.3	−.3±3.0
3044B	"	"	212	68	62.9	5.1±4.5
Total			566	182	168.0	14.0±7.3
3031	$g_{e12}\ g_{e13}\ g_{e14}$	63:1	90	1	1.4	−.4±0.8
3041†	"	"	122	2	1.9	.1±0.9
3042	"	"	219	5	3.4	1.6±1.2
Total			431	8	6.7	1.3±1.7

* See table 15 for F_3 progenies of this ear.

† See table 17 for F_3 progenies of this ear.

in view of the fact that ears of the same cross, but segregating for either character alone, were deficient in recessives.

This cross has, like that of $g_{e1} \times g_{e3}$, yielded an unexpected type of ratio. Two ears are clearly segregating in a ratio of 9:7 and all of the recessives on these ears are of the g_{e3} type. Apparently the g_{e5} factor postulated in the cross of $g_{e1} \times g_{e3}$ is also present in this cross. Since both crosses have g_{e3} in common as one parent it seems very probable that this extra factor is in some way contributed by the g_{e3} stock.

$g_{e4} \times g_{e6}\ g_{e7}$

This cross, like the one immediately preceding, should produce three types of segregating progenies; 3:1, 15:1, and 45:19. All of these occur and the data agree fairly well with the theoretical ratios (see table 6). In this case, however, there is a significant excess of recessives among the ears segregating 15:1, in contrast to a deficiency of about the same magnitude in the preceding cross. Three ears segregating in a ratio of 45:19 indicate that three distinct factors are involved in this cross and that these are independently inherited.

$g_{e8}\ g_{e9}\ g_{e10}$

In a previous paper (MANGELSDORF 1926) the writer recorded the segregation for premature germination on three ears, two of which segregated in a ratio of approximately 8:1, the third in a ratio of 41:1. It was suggested that the 8:1 ratio might be the result of linked duplicate factors with approximately 33.3 percent of crossing over, while the third ear might represent linked duplicate factors in the repulsion phase or a set of triplicate factors, two of which were linked with approximately 33.3 percent crossing over. In addition to making a slight arithmetical error in calculating the ratios that might be expected when F_3 progenies of this ear were grown, I neglected to point out that the possibility of Ear No. 2178 being the result of linked duplicate factors in the repulsion phase was very remote indeed, and that the hypothesis of triplicate factors with linkage between two members of the set was far more plausible. In this case the 8:1 ratios would also presumably be the result of triplicate factors, the independent factor pair being homozygous recessive. Such a combination, in the absence of linkage, should have given 15:1 ratios.

It was realized that such an interpretation could be no more than tentative since any conceivable ratio can be explained by assuming a sufficient number of factors with appropriate degrees of linkage between certain members of the set. If, however, the 8:1 ratios are the result of two linked factors with crossing over of approximately 33.3 percent, then we should expect to find in F_3 the following types of progenies in the proportion shown:

1. 8 ears segregating 3:1
2. 8 ears segregating 8:1
3. 2 ears segregating 35:1
4. 14 ears not segregating.

Seventeen ears of the F_3 endosperm generation were obtained with the results shown in table 7. Six of these ears were segregating for germinating seeds and it is noted that these ears fall into two distinct groups with regard to the proportion of recessive seeds. All of them deviate by significant amounts from a 3:1 ratio and four deviate significantly from a 15:1 ratio. On the other hand four of the ears fit an 8:1 ratio rather closely and the remaining two approximate a 35:1 ratio fairly well. Both of these ratios should be expected if linked duplicate factors with 33.3 percent crossing over are involved. The 8:1 ratios represent the coupling phase; 35:1 ratios the repulsion phase. Ratios of 3:1, resulting from a homozygous recessive condition of one of the pairs of factors which are also expected in F_3, did not occur. The distribution as a whole, however, is in fairly satisfactory agreement with expectation. In a population of

TABLE 7

F_3 progenies from an ear (Number 2179) segregating in an 8:1 ratio in F_2. Theoretical results calculated on the basis of duplicate factors with 33.3 percent crossing over.

EAR NUMBER	EXPECTED RATIO	NUMBER OF PROGENIES		TOTAL SEEDS	NUMBER GERMINATING	THEORETICAL NUMBER GERMINATING	DEVIATION
		Theoretical	Actual				
	3:1	4.25	0				
3098	8:1			287	25	31.9	−6.9±3.59
3100	"			126	16	14.0	2.0±2.38
3099	"			225	30	25.0	5.0±3.18
3095	"			115	19	12.8	6.2±2.27
Total		4.25	4	753	90	83.6	6.4±5.81
3096	35:1			208	3	5.8	−2.8±1.60
3097	"			51	1	1.4	−.4± .79
Total		1.06	2	259	4	7.2	−3.2±1.78
Not segregating		7.44	11				

seventeen ears the four types of progeny are expected in ratio of 4.25:4.25:1.06:7.44. They are found in the ratio of 0:4:2:11. Applying the formula for goodness of fit we find that $X^2=6.78$ and $P>0.05$.

F_3 progenies from the ear which segregated in a ratio of 41:1 were also grown. If we assume that this ratio is the result of a set of triplicate factors with linkage and 33.3 percent crossing over between two members of the set, then the following types of progenies are expected in F_3:

1. 16 ears segregating 3:1
2. 10 ears segregating 8:1
3. 16 ears segregating 15:1
4. 12 ears segregating 35:1
5. 3 ears segregating 71:1
6. 83 ears not segregating.

Unfortunately the plants grown from this ear were rather weak and only fifteen self-pollinated ears were obtained. Twelve of these did not segregate; the segregation of the remaining three is shown in table 8. With so small a number of segregating ears it is naturally impossible for all the expected types to occur. Yet the agreement with expectancy is fairly close, X^2 being 3.47 and $P>0.5$.

TABLE 8

Segregating F_3 progenies from an ear (Number 2178) segregating in a 41:1 ratio in F_2.

EAR NUMBER	PROBABLE RATIO	TOTAL SEEDS	NUMBER GERMINATING	THEORETICAL NUMBER GERMINATING	DEVIATION
3081	8:1	196	25	21.8	3.2±2.97
3082	15:1	167	10	10.4	– .4±2.11
3080	35:1	141	3	3.9	– .9±1.32
Total		504	38	36.1	1.9±3.90

In lieu of a larger population the best proof that three factors instead of two are involved is the appearance of a progeny segregating in a ratio of 15:1. It would be impossible for such ears to occur if only two linked factors were involved because so long as both factor pairs remained heterozygous only ratios of 8:1 resulting from the coupling phase and ratios of 35:1 resulting from the repulsion phase could occur. If a third factor, not linked with the other two, were involved, however, ratios of 15:1 would be expected in every case that either of the linked factor pairs be-came homozygous recessive. It may be noted that Ear No. 3082 in table 8 fits a 15:1 ratio very closely. Furthermore, the segregation in this ear deviates from an 8:1 ratio by an amount equal to 3.13 times the error and from a 35:1 ratio by 3.75 times the error. The occurrence of this ear is rather convincing evidence that three factors are involved in this family.

Still another test may be made to determine whether two or three factors are involved in this stock and whether the linked factor hypothesis explains the situation. If a progeny which segregated in a ratio of 8:1 is crossed with an unrelated stock, then the heterozygous hybrid should segregate in a ratio of 8:1 if linked duplicate factors are involved. No ratios other than this could possibly be produced. If three factors are involved, however, and two of these are linked, then only ratios approximately 35:1 could occur in F_2. This ratio is identical with that produced by two factors with the same degree of linkage in the repulsion phase, but by crossing with a totally unrelated stock it is assumed that one of the parents carries none of the recessive factors for premature germination and, hence, the coupling phase is the only one possible.

To make this test an F_4 plant from Ear No. 3081 was crossed by Yellow Creole, a southern variety quite different from the New England stock. Approximately half of the ear was self-pollinated, the other half crossed, the two types of seed being separated by xenia. The segregation among the self-pollinated seeds was 39 dormant:7 germinating; a ratio of 5.6:1. The crossed seeds on the same ear were all dormant. From these, three non-segregating and two segregating ears were obtained in the next generation (F_2 endosperm). The segregation on the latter is shown in table 9. It is noted that the ratios in the two ears are practically alike, 27.5:1 and 28.9:1. Both show a significant deviation from an 8:1 ratio but approach a 35:1 ratio rather closely.

These facts, considered in connection with previous data, furnish rather

TABLE 9

Segregating F_2 progenies from a cross of Ear Number 3081 ($G_{e8}\,g_{e8}\,G_{e9}\,g_{e9}\,G_{e10}\,g_{e10}$) × *Yellow Creole* ($G_{e8}\,G_{e8}\,G_{e9}\,G_{e9}\,G_{e10}\,G_{e10}$).

EAR NUMBER	PROBABLE RATIO	TOTAL SEEDS	NUMBER GERMINATING	THEORETICAL NUMBER GERMINATING	DEVIATION
5648	35:1	371	13	10.3	2.7±2.13
5649	"	359	12	10.0	2.0±2.10
Total		730	25	20.3	4.7±2.99

convincing evidence that a set of triplicate factors is involved in this stock and that two of these, arbitrarily designated as g_{e8} and g_{e9}, are linked while the third, g_{e10}, is inherited independently of the other two. All must be present, however, in a homozygous recessive condition in order for premature germination to occur.

Although all calculations of theoretical numbers have been based on an assumption of 33.3 percent crossing over between g_{e8} and g_{e9}, a tabulation of all available data would indicate that the percentage is somewhat lower than this and is probably nearer 30 percent.

TABLE 10

Segregating progenies of g_{e11} stock.

EAR NUMBER	GENETIC FACTORS	TOTAL SEEDS	NUMBER GERMINATING	THEORETICAL NUMBER GERMINATING	DEVIATION
3205	g_{e11}	549	158	137.2	20.8±6.8
3206	"	340	85	85.0	.. ..
3207	"	245	71	61.3	9.7±4.6
3208	"	458	112	114.5	−2.5±6.3
3209	"	524	132	131.0	1.0±6.7
Total		2116	558	529.0	29.0±13.4

g_{e11}

No crosses have yet been made with this stock. The character is reported as a distinct type of premature germination because it differs phenotypically in several respects from all other types. As noted in the preliminary description the plumules are pink in color and there is also a pink tinge in the endosperm. In no other types of premature germination has such a condition been found and it seems safe to assume that g_{e11} is genetically distinct from the other types of premature germination, which have been described. The data in table 10 show that this character is inherited as a simple recessive.

G_{e12} g_{e13} g_{e14} g_{e15}

In a study on the inheritance of defective seeds, another type of endosperm character in maize, (MANGELSDORF 1926) it was found that the ratios were subject to slight errors due to the occurrence of non-hereditary defectives of various types on almost every ear. That a similar situation might obtain in the case of premature germination was suggested by the fact that one or two germinating seeds were occasionally found in ears ordinarily classed as non-segregating. Consequently, all seeds from "non-segregating" ears of the F_2 population were carefully examined with the result that one or more germinating seeds were found on seven ears from the crosses $g_{e1} \times g_{e4}, g_{e1} \times g_{e6}\, g_{e7}$ and $g_{e4} \times g_{e6}\, g_{e7}$. The segregation on these ears has already been shown in tables 2, 3, and 6. When the data on these ears are combined as in table 11 it is found that the segregation in three of the ears approaches a 63:1 ratio rather closely, while in the remaining four ears the data do not differ significantly from a ratio of 255:1.

TABLE 11

Ratios of 63:1 and 255:1 from "non-segregating" ears of various crosses.

EAR NUMBER	GENETIC FACTORS	PROBABLE RATIO	TOTAL SEEDS	NUMBER GERMINATING	THEORETICAL NUMBER GERMINATING	DEVIATION
3031	$g_{e12}\ g_{e13}\ g_{e14}$	63:1	90	1	1.4	−.4±0.8
3041	"	"	122	2	1.9	.1±0.9
3042	"	"	219	5	3.4	1.6±1.2
Total			431	8	6.7	1.3±1.7
2952	$g_{e12}\, g_{e13}\, g_{e14}\, g_{e15}$	255:1	281	1	1.10	−.10±.71
2963	"	"	171	1	.67	.33±.55
2974	"	"	268	1	1.05	−.05±.69
2976	"	"	266	2	1.04	.96±.69
Total			986	5	3.85	1.15±1.32

Had only the latter ratios occurred, the matter should probably have been given no further thought. The average number of seeds on the ears of these three crosses is approximately 235, and if one germinating seed occurred as the result of accident or other causes, a ratio approximating 255:1 would be inevitable. The fact, however, that ratios approaching 63:1 also occurred, that all these segregating ears were found in crosses of the same three stocks and that the non-segregating ears from all other crosses were completely free of germinating seeds, suggested with considerable force that genetic factors might be involved in the occasional appearance of these germinating seeds. Paradoxical though it may seem, the fact that the data do not exactly fit 63:1 and 255:1 ratios but show an excess of recessives, may be regarded as additional evidence of genetic segregation in those ratios. With the ears comprising an average total of 235 seeds it would be almost inevitable, as a result of random sampling, that some of the ears from heterozygous plants should show no recessive seeds. As these ears cannot be identified they are not included as segregating ears and their omission is a constant source of error which tends to raise the proportion of recessives among the ears classed as segregating. How great this error may be in the present case cannot be determined because no record was made of the number of seeds on the non-segregating ears. However, if their average number is the same as that of the segregating ears in the same family, that is, 235, then if one non-segregating, though heterozygous, ear is included the ratio becomes 243:1. If two ears are included the ratio becomes 290:1.

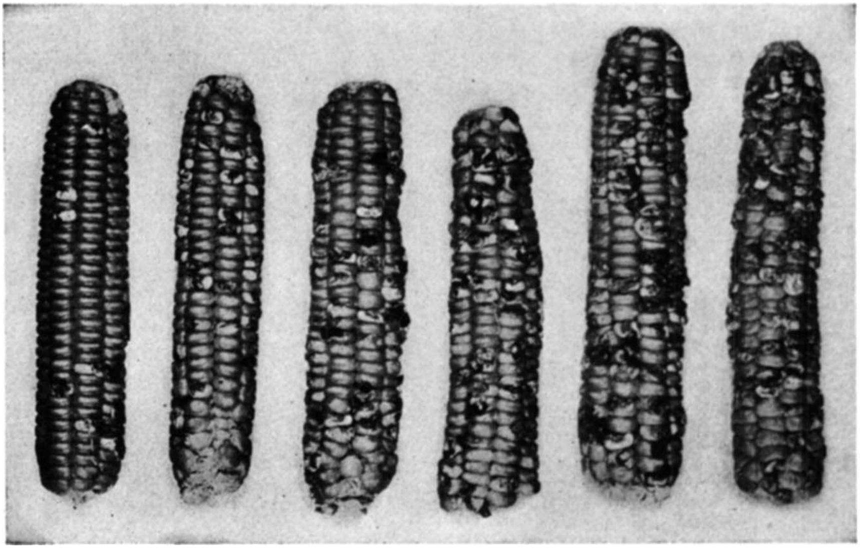

Figure 1.—Ears representing some of the ratios which occur in the inheritance of premature germination. From left to right the ratios are 15:1, 3:1, 45:19, 9:7, 135:121 and 27:37. Ears segregating 63:1, 255:1, and 225:31 were also found but were not photographed.

Ears segregating in a ratio of 63:1 are naturally subject to the same error though in a lesser degree. It may be of interest to note, in this connection, that Nilsson-Ehle (1909) in his study of the inheritance of seed coat color in wheat encountered precisely this error in a very marked degree. All of the 384 F_2 plants from a cross between red-seeded and white-seeded parents were red seeded. However, when 78 F_3 progenies were grown, ratios of 63:1, 15:1, and 3:1 were found. The failure of white-seeded plants to occur in F_2 appears to have been merely the result of random sampling, although the odds against the chance occurrence of this combination are approximately 75:1.

F_3 *progenies from various* F_2 *ratios*

In undertaking a study of segregation in F_3, it was obviously impossible, due to limitations of time and space, to grow F_3 progenies from any very large proportion of the F_2 ears, and it was considered more advisable to obtain F_3 progenies of the various ratios encountered in F_2 regardless of the parents involved rather than to grow F_3 progenies from each F_2 ear of any particular cross. In other words it seemed more important to learn, for example, how the F_3 progenies from an ear segregating in a 45:19 ratio in F_2 differed from those segregating 9:7 in F_2, than to attempt to prove that each ear which had been classified as segregating in a 9:7 ratio actually belonged in this category. Consequently, F_3 progenies have been grown from at least one ear representing each of the Mendelian ratios found in F_2 with the exception of the 3:1 ratio. The segregation for premature germination in various ratios is illustrated in figure 1.

Before proceeding with a discussion of the data it should be mentioned that classification in many of the F_3 progenies was subject to an unavoidable error as the result of accidental cross-pollination which inevitably reduces the proportion of recessives. This population came into bloom during a period of rainy weather and as a result many of the bags over the ear shoots were torn and the silks exposed for a brief period to cross-pollination. How great a percentage of cross-pollination occurred is impossible to estimate but the fact that many of the ears bore purple seeds as a result of pollination with other stocks in the vicinity is proof that it did occur. All purple out-crossed seeds were discarded in making the classifications but there were undoubtedly many other out-crossed seeds which could not be identified by color, and which, being classified as dormant, would tend to produce an excess of this class.

9:7 Ratio

Theoretically the dormant seeds from an ear segregating in a ratio of 9:7 should produce the following three types of progenies in the proportions shown:

1. 4 ears segregating 3:1
2. 4 ears segregating 9:7
3. 1 ear not segregating

An ear from the cross of $g_{e1} \times g_{e3}$ shown in table 1 was used to test this hypothesis. The results are shown in table 12. Thirty-five F_3 progenies were obtained. With this number the three types of progenies are expected

TABLE 12

F_3 progenies from Ear Number 2997 (9:7 ratio in F_2) $Ge_3\ g_{e3}\ G_{e5}\ g_{e5}$.

EXPECTED RATIOS	NUMBER PROGENIES		TOTAL SEEDS	NUMBER GERMINATING	THEORETICAL NUMBER GERMINATING	DEVIATION
	Theoretical	Actual				
3:1	15.6	21	3295	757	823.8	−66.8±16.8
9:7	15.6	14	2559	1027	1119.6	−92.6±17.0
Not segregating	3.9	0				
Total	35.1	35	5854	1784	1943.4	−159.4±24.3

in a ratio of 15.6:15.6:3.9. They occurred in a ratio of 21:14:0. The agreement with expectancy is reasonably close, X^2 being 5.93 and $P > 0.05$. The recessive seeds in both the 3:1 and 9:7 groups show a marked deficiency which is undoubtedly due to contamination.

27:37 Ratio

Four types of progenies are expected from this ear in the proportions indicated.

1. 6 ears segregating 3:1
2. 12 ears segregating 9:7
3. 8 ears segregating 27:37
4. 1 ear not segregating

TABLE 13

F_3 progenies from Ear Number 2989 (27:37 ratio in F_2) $Ge_1\ g_{e1}\ G_{e3}\ g_{e3}\ G_{e5}\ g_{e5}$.

EXPECTED RATIOS	NUMBER PROGENIES		TOTAL SEEDS	NUMBER GERMINATING	THEORETICAL NUMBER GERMINATING	DEVIATION
	Theoretical	Actual				
3:1	7.6	9	1549	382	387.3	−5.3±11.5
9:7	15.1	16	2433	1021	1064.4	−43.3±16.5
27:37	10.1	7	1221	659	705.9	−46.9±11.6
Not segregating	1.3	2				
Total	34.1	34	5203	2062	2157.6	−95.6±24.0

Thirty-four progenies were obtained from Ear No. 2989, which had segregated in a ratio of 27:37 and was presumably heterozygous for g_{e1}, g_{e3}, and g_{e5}. With a population of this size the four types of progeny are expected in the ratio of 7.6:15.1:10.1:1.3. As shown in table 13, they occurred in the ratio of 9:16:7:2. The results are in close agreement with expectancy, X^2 being 1.64 and $P > 0.50$.

15:1 Ratio

Progenies from plants segregating in a ratio of 15:1 should fall into three groups in the following proportions:

1. 4 ears segregating 3:1.
2. 4 ears segregating 15:1
3. 7 ears not segregating.

TABLE 14

F_3 progenies from Ear Number 3048 (15:1 ratio in F_2) G_{e6} g_{e6} G_{e7} g_{e7}.

EXPECTED RATIOS	NUMBER PROGENIES		TOTAL SEEDS	NUMBER GERMINATING	THEORETICAL NUMBER GERMINATING	DEVIATION
	Theoretical	Actual				
3:1	8.5	7	1605	326	401.3	−75.3±11.7
15:1	8.5	6	1188	40	74.2	−34.2± 5.7
Not segregating	14.9	19				
Total	31.9	32	2793	366	475.5	−109.5±13.4

Thirty-two progenies were grown with the results shown in table 14. The theoretical distribution of 32 ears among these three groups is 8.5:8.5:14.9. The actual distribution is 7:6:19. The two distributions are in close agreement, X^2 being 2.14 and $P > 0.30$. In this case as in those already presented there is a deficiency of recessive seeds in both classes of segregating progeny, probably due to cross-pollination.

45:19 Ratio

A ratio of 45:19 is presumably the product of 3:1 and 15:1 ratios; one pair of complementary and a set of duplicate factors being involved. Consequently, five types of progenies are expected in F_3 in the following proportions:

1. 18 ears segregating 3:1
2. 4 ears segregating 15:1
3. 8 ears segregating 45:19
4. 8 ears segregating 9:7
5. 7 ears not segregating.

The 9:7 ratios are expected from plants that are heterozygous for the complementary factor and heterozygous for one pair of duplicate factors but homozygous recessive for the other pair.

TABLE 15

F_3 progenies from Ear Number 3033 (45:19 ratio in F_2) $G_{e4}\, g_{e4}\, G_{e6}\, g_{e6}\, G_{e7}\, g_{e7}$.

EXPECTED RATIOS	NUMBER PROGENIES		TOTAL SEEDS	NUMBER GERMINATING	THEORETICAL NUMBER GERMINATING	DEVIATION
	Theoretical	Actual				
3:1	14.4	11	1989	480	497.3	−17.3±13.1
15:1	3.2	5	722	50	45.1	4.9± 4.4
45:19	6.4	5	652	198	193.6	4.4± 7.9
9:7	6.4	7	1049	440	458.9	−18.9±10.9
Not segregating	5.6	8				
Total	36.0	36	4412	1168	1194.9	−26.9±19.9

Thirty-six F_3 progenies were obtained with the results set forth in table 15. With a population of this size the five types of progeny are expected in a ratio of 14.4:3.2:6.4:6.4:5.6. They occurred in a ratio of 11.5:5:7:8. The agreement with expectation is very close, X^2 being 3.21 and $P > 0.50$. In this case the segregation within each group is also very close to expectation, there being no significant deviations.

135:121 Ratio

This ratio is presumably the product of 9:7 and 15:1 ratios. If this is true, four factor pairs are involved; two pairs of complementary factors and a set of duplicate factors. Seven classes of F_3 progenies are expected in the following proportions:

1. 32 ears segregating 3:1
2. 44 ears segregating 9:7
3. 16 ears segregating 27:37
4. 4 ears segregating 15:1
5. 16 ears segregating 45:19
6. 16 ears segregating 135:121
7. 7 ears not segregating.

Table 16 shows that with a population of 46 ears all the expected types of progenies, with the exception of those segregating in a ratio of 27:37, have occurred. With a population of this size the seven types are expected in a ratio of 10.9:15.0:5.5:1.4:5.5:5.5:2.4. They occurred in a ratio of 21:7:0:4:10:2:2. This array differs significantly from the theoretical,

X^2 being 34.31 and $P < 0.01$. The segregation within each class, however, is in very close agreement with expectancy in every case.

TABLE 16

F_3 progenies from Ear Number 2947 (135:121 ratio in F_2) G_{e1} g_{e1} G_{ex} g_{ex} G_{e6} g_{e6} G_{e7} g_{e7}.

EXPECTED RATIOS	NUMBER PROGENIES		TOTAL SEEDS	NUMBER GERMINATING	THEORETICAL NUMBER GERMINATING	DEVIATION
	Theoretical	Actual				
3:1	10.9	21	3911	970	977.8	−7.8±18.2
9:7	15.0	7	1087	459	475.5	−16.5±11.0
27:37	5.5	0				
15:1	1.4	4	903	56	56.4	−0.4± 4.9
45:19	5.5	10	1926	595	571.8	23.2±13.5
135:121	5.5	2	456	225	215.5	9.5± 7.2
Not segregating	2.4	2				
Total	46.2	46	8283	2305	2297.0	5.0±27.5

Since a ratio of 135:121 seldom differs significantly from a 9:7 ratio, probably the best proof that the parent ear of these progenies segregated in the former ratio and not the latter is the appearance of 15:1 ratios in F_3. It would be impossible, as the result of recombination, for such a ratio to appear in the progenies of an ear segregating 9:7. The same holds true for the 45:19 ratios. The fact that both of these have appeared in F_3 is ample evidence that the F_2 ratio could not have been 9:7 in spite of the fact that the seven types of progeny have not appeared in the proportions expected from a ratio of 135:121.

63:1 and 255:1 Ratios

Ratios of 255:1 are presumably the result of a set of quadruplicate factors, all four factor pairs being heterozygous. The 63 : 1 ratios are assumed to be due to the same factor complex except that one of the four factor pairs is homozygous recessive. The latter should produce four types of progenies in the following proportions:

1. 6 ears segregating 3:1
2. 12 ears segregating 15:1
3. 8 ears segregating 63:1
4. 37 ears not segregating.

Twenty-eight F_3 progenies were obtained with the results shown in table 17. With a population of this size the four classes are expected in a ratio of 2.7:5.3:3.6:16.4. They occurred in the proportion of 0:2:3:23. Although no ears segregating in a ratio of 3:1 were obtained, the observed array as a whole shows a reasonably close agreement with the theoretical array, X^2 being 7.52 and $P > 0.05$. The segregation within each class is also in agreement with expectation, the deviations being less than three times the error in both types of segregating progenies.

TABLE 17

F_3 progenies of Ear Number 3041 (63:1 ratios) $G_{e12}\ g_{e12}\ G_{e13}\ g_{e13}\ G_{e14}\ g_{e14}\ G_{e15}\ g_{e15}$.

EXPECTED RATIOS	NUMBER PROGENIES		TOTAL SEEDS	NUMBER GERMINATING	THEORETICAL NUMBER GERMINATING	DEVIATION
	Theoretical	Actual				
3:1	2.7	0				
15:1	5.3	2	431	18	26.9	−8.9±3.39
63:1	3.6	3	505	7	7.9	−.9±1.88
Not segregating	16.4	23				
Total	28.0	28	936	25	34.8	−9.8±3.92

From an ear segregating 255:1, the following F_3 progenies are expected:

1. 8 ears segregating 3:1
2. 24 ears segregating 15:1
3. 32 ears segregating 63:1
4. 16 ears segregating 255:1
5. 175 ears not segregating.

TABLE 18

F_3 progenies of Ears Numbers 2974 and 2952 (255:1 ratio) $G_{e12}\ g_{e12}\ G_{e13}\ g_{e13}\ G_{e14}\ g_{e14}\ G_{e15}\ g_{e15}$.

EXPECTED RATIOS	NUMBER PROGENIES		TOTAL SEEDS	NUMBER GERMINATING	THEORETICAL NUMBER GERMINATING	DEVIATION
	Theoretical	Actual				
3:1	2.3	1	216	23	54.0	−31.0±4.29
15:1	7.0	4	482	28	30.1	−2.1±3.58
63:1	9.3	6	1224	11	19.1	−8.1±2.93
255:1	4.6	4	1005	4	3.9	0.1±1.33
Not segregating	50.8	59				
Total	74.0	74	2927	66	107.1	−41.1±6.86

F_3 progenies from two F_2 ears were grown and 74 self-pollinated ears were obtained. With this population the five classes are expected in the ratio of 2.3:7.0:9.3:4.6:50.8. Table 18 shows that they occurred in the proportions of 1:4:6:4:59. The agreement is reasonably close, X^2 being 4.60 and $P > 0.30$. It is noted, however, that the segregation within the classes is not particularly close to expectation. The progenies segregating 3:1 and 15:1 both show a significant deficiency of recessive seeds. Progenies segregating in a 63:1 ratio also show a slight deficiency, while those segregating 255:1 are almost in perfect agreement with the theoretical ratio. In the latter case a slight excess of recessives would be expected, as has previously been pointed out, due to the exclusion of ears, which though heterozygous for all four factors pairs, produce no germinating seeds as the result of the operations of random sampling.

These consistent deficiencies of recessives in all four classes of segregating ears are probably due to contamination. Purple outcrossed seeds were particularly numerous in these progenies and other out-crossed seeds which could not be identified by color were probably just as numerous, or more so, as stocks with purple aleurone were further removed than other unrelated stocks with colorless aleurone.

In spite of this unfortunate error the evidence supporting a four factor hypothesis seems to be rather convincing. A consideration of the combined results of F_2 and F_3 leaves little doubt that the premature germination on these ears is inherited and that at least four recessive factors in a homozygous condition are necessary for premature germination to occur.

Although no crosses have been made between this stock and others which segregate for germinating seeds, it is not difficult to demonstrate that a different set of genetic factors is probably involved. It is fairly certain that the character is distinct from g_{e1}, g_{e2}, g_{e3}, g_{e4}, g_{e5}, and g_{e11} and because the latter are in each case governed by a single pair of complementary factors. The character is undoubtedly distinct from g_{e8} g_{e9} g_{e10} because in this set of triplicate factors two of the genes are apparently linked while the data on g_{e12} g_{e13} g_{e14} g_{e15} indicate independent inheritance. Finally, this character is probably distinct from that produced by the duplicate factors g_{e6} g_{e7} because several ears of the latter have been found which were also segregating for g_{e12} g_{e13} g_{e14} g_{e15}. When these two types occurred on the same ear they could be readily separated, as the former produced a well developed plumule, while the latter showed only a slight elongation of the plumule beyond the region of the germ. To give but one example of the segregation of both types in the same ear, an F_3 progeny from Ear No. 2947 bore 273 dormant seeds, 22 seeds of the g_{e12-15} type and 26 seeds of the g_{e6-7} type. Apparently both types were segregating in a ratio of 15:1 so that the complete ratio would be 225:15:16. With a population of 321 seeds the theoretical distribution is 282:19:20. This agrees fairly well with the observed results, X_2 being 2.55 and $P > 0.20$.

Summary of segregation

Table 19 brings together in compact form practically all of the available data from each type of Mendelian ratio that has appeared in these studies. In making up this summary the data from tables 12 and 14 have been omitted because every class of segregating progeny included in these two tables shows a marked deficiency of recessives that cannot be attributed to chance and is undoubtedly due to accidental cross-pollination.

With the exception of the 9:7 and 45:19 ratios the data are in close agreement with expectation. No cause is known for the significant deficiency of recessives in the former and significant excess in the latter, although in the case of the 9:7 ratios part of the deficiency may be partly accounted for by cross-pollination.

TABLE 19

Summary of segregation classified according to Mendelian ratios.

FACTOR COMBINATIONS	THEORETICAL RATIOS	TOTAL SEEDS	NUMBER GERMINATING	THEORETICAL NUMBER GERMINATING	DEVIATION	DEV. / P.E.
1 pair complementary	3:1	20430	5074	5108	−34±41.7	.8
2 pairs complementary	9:7	10521	4420	4603	−183±34.3	5.3
3 pairs complementary	27:37	2545	1444	1471	−27±16.8	1.6
1 set duplicate	15:1	7873	491	492	−1±14.5	.1
1 set triplicate	63:1	2160	26	34	−8± 3.9	2.0
1 set quadruplicate	255:1	1991	9	8	1± 1.9	.5
1 set duplicate: 1 pair complementary	45:19	5008	1569	1487	82±21.8	3.8
1 set duplicate: 2 pairs complementary	135:121	689	339	326	13± 8.8	1.5
Totals		51217	13372	13529	−157±67.3	2.3

Considering the population of 51,217 seeds as a whole, it is found that the total number of germinating seeds does not differ significantly from the theoretical number determined by totalling the calculated numbers for each class. The deviation is −157±67.3.

The percentage of recessives in this population has varied from 0.39 percent in the 255:1 ratios to 57.81 percent in the 27:37 ratios, with intervening values ranging between these two extremes. The situation would have been hopelessly confusing had all these varying percentages appeared in a single population but occurring as they did in unrelated stocks, their analysis proved to be relatively simple.

These data furnish an excellent example of the tremendous complexity that may be expected from simple Mendelian combinations behaving in an orthodox fashion. When the disturbing effects of linkage and differential pollen-tube growth are also considered, it is evident that almost any percentage of recessives from 0–100 might occur. Even without these disturbing influences it is theoretically possible with the factors already studied to obtain a combination showing 92.49 percent of germinating seeds.

NUMBER OF DISTINCT FORMS OF PREMATURE GERMINATION.

The fifteen genetic factors for premature germination represent nine different types of premature germination. The evidence, though not complete, is sufficient to indicate that all of these are genetically distinct. That g_{e1}, g_{e3} and g_{e5} are genetically different is shown by the 27:37 ratios which are found when all three types occur in the same progeny. The marked phenotypical differences between g_{e4} and the types just mentioned are almost sufficient to prove that g_{e4} is different from the remaining three. In addition crosses of g_{e4} with g_{e1} and g_{e3} show the former to be genetically unlike the latter. The genotype g_{e2} has been crossed only with g_{e1} (MANGELSDORF 1926). Since the germination in g_{e2} is not always clear cut, this stock has been discarded, and the only evidence that it is different from the other stocks is of a morphological nature. This is also true of g_{e11}.

Because of the difference in mode of inheritance, it is almost certain that the genotype g_{e6} g_{e7} differs genetically from the five genotypes in which only one factor pair is involved. Crosses of g_{e6} g_{e7} with g_{e1}, g_{e3} and g_{e4} bear out this assumption, ratios of 45:19 having been observed in every case.

The genotype g_{e8} g_{e9} g_{e10} has not been tested in crosses. It is undoubtedly different from genotypes g_{e1}–g_{e5} because of the different mode of inheritance. Linkage of two members of this set of triplicate factors indicates that this genotype differs from g_{e6} g_{e7} and from g_{e12} g_{e13} g_{e14} g_{e15}, although there is a possibility that either, or both, of the latter may be homozygous recessive for an additional factor, which, if brought to light, would display linkage with one of those already known. This possibility is remote in the case g_{e6} g_{e7} as this character has been crossed with a number of unrelated stocks and no indication of additional factors has been found. The genotype g_{e12} g_{e13} g_{e14} g_{e15} has been shown to be distinct from g_{e6} g_{e7} by the segregation of both characters on the same ear. We may consider it, tentatively at least, to be different from g_{e8} g_{e9} g_{e10} because the latter exhibits linkage, the former not. The discovery of additional factors, however, in either set might possibly show the two characters to be the result of the same factor combination.

With the exception of g_{e2}, and perhaps g_{e11}, the evidence is fairly conclusive in showing nine distinct types of premature germination, involving 15 genetic factors, to have occurred in the course of these studies.

DISCUSSION

The inheritance of premature germination is but another demonstration of the large number of genetic factors involved in a relatively simple phenomenon. Dormancy of the seed during development is so general that it may almost be taken for granted. Yet we find that at least fifteen different genetic factors are involved in maintaining dormancy and we can scarcely suppose that this is more than a sample of the total number.

As has been the case in several other characters in maize, two types of inheritance involving complementary and multiple factors, respectively, have been encountered. It is a temptation to assume that these two types of genetic phenomena are associated with distinct types of physiological reactions involved in maintaining dormancy. We might postulate, for example, that a series of complementary factors governs the formation of a group of substances, enzymes or inhibitors, all of which must be present in order to maintain dormancy, while a series of duplicate factors is responsible for another group of substances any of which will inhibit germination. In the first case the seed will germinate prematurely whenever any one of the essential inhibitors is lacking; in the latter case it will germinate only when all are lacking.

There is, at present, no evidence in support of such an interpretation. It may be more than a coincidence, however, that all the types of premature germination in which complementary factors are involved, occur relatively early in the development of the seed, while those in which multiple factors are involved occur relatively late. There are six characters in the former category and three in the latter. The test for independence shows the odds against the chance occurrence of this combination to be large, P being considerably less than 0.01. Perhaps these odds should not be taken too seriously as only nine characters are being considered and there is no sharp distinction between "early" and "late."

Since the discovery of duplicate factors and the introduction of the multiple factor hypothesis which was formulated independently by NILSSON-EHLE (1908) and EAST (1910), many cases of inheritance which fall into the category of duplicate factors have been recorded and there has been no small amount of speculation regarding the origin of this hereditary mechanism.

The attractive, and very plausible, hypothesis of the origin of duplicate factors through doubling of the original chromosomes has met with several objections, two of which have been discussed in some detail by SHULL (1926). The first is that only certain characters exhibit the type of inheritance expected from duplicate factors, while other characters in the same race and even in the same linkage group are inherited as simple recessives. The second objection is that a doubling of the chromosomes would be expected to result, as MULLER (1914) pointed out some years ago, in ratios of 35:1 if the four homologous chromosomes assort at random. Ratios of 15:1 would not be obtained unless the four chromosomes should assort as two independent disomes rather than as a single tetrasome. SHULL (1926) states that deviations from a 15:1 ratio and approaching the tetrasomic ratio of 35:1 have occasionally been encountered in Bursa. In maize, DEMEREC (1923), working with albino seedlings, and the writer, in studies of premature germination, have observed ratios approaching 35:1. These have, however, been assumed to be the result of linkage of duplicate factors (repulsion phase) or linkage of two members of a set of triplicate factors. My own data from several generations fit the latter interpretation very well indeed, but there is always the possibility that additional studies will throw an entirely new light on the situation.

Probably a more serious objection to the chromosome duplication theory, at least as it applies to maize, is the occurrence of triplicate and quadruplicate factors. While these can be explained, as are duplicate factors involving two factor pairs, by additional doubling of the chromosomes, there is an arithmetical limit to the number of duplications which could have occurred to produce the present ten pairs. On the other hand it is by no means certain we have found the limit in the number of factors involved in the expression of a single simple character such as premature germination, although it is admittedly difficult to discover combinations larger than four factor pairs in population of the size ordinarily produced by single plants of maize.

If multiple factors have arisen through chromosome duplication, then the character g_{e12-15} which is the expression of four independent factor pairs accounts for four chromosomes, in the present complement of ten, which have originated from a single chromosome during the course of evolution of maize. If this were the case, perhaps we might expect that four of the present chromosomes would show considerable morphological resemblance. A recent paper by McClintock (1929) indicates that this is not the case. Miss McClintock is convinced that every chromosome in maize is morphologically identifiable, differing from every other in some essential feature.

It is possible that the hypothetical transition from tetrasomic to disomic inheritance, that is, from a tetraploid to a "double diploid," has been accompanied by discernible morphological changes in chromosomes that were originally identical and homologous. The fact remains, however, that at present there is very little, if any, critical evidence that multiple factors arise through chromosome duplications. The hypothesis remains a plausible one, however, particularly in view of the fact that duplicate factors and polyploidy are both of frequent occurrence in plants and of rare occurrence in animals.

Sirks (1926) suggests that some cases of inheritance attributed to duplicate factors are interpreted equally well by the molecular hypothesis of Correns (1919) which postulates that molecules in homologous chromosomes can exchange in either direction one or more of the atoms of which they are constituted. Thus, what appears to be a series of multiple factors might in reality be a series of multiple allelomorphs. Sirks' argument was partly based on the assumption that it had never been shown conclusively that certain Mendelian factors were linked with one of several members of a series of multiple factors and inherited independently of other members of the series. He was not familiar at that time, however, with the work of Warren (1924) on inheritance of egg size in Drosophila and Lindstrom (1926) on the inheritance of size of fruit in the tomato. Both of these writers have definitely localized in certain linkage groups one or more of the genes of a series of multiple factors.

In view of these facts, Sirks' argument loses much of its force. We must not overlook the possibility, however, of a more complex situation than simple re-combination of duplicate factors, particularly when the data show marked deviations from normal ratios, and appear, at first glance, to suggest linkage. Perhaps it is more than a coincidence that the ratios 8:1 and 27:1, which Demerec (1923) found in the case of white seedlings; the ratio of 10:1 which Stewart (1928) encountered in a study of inheritance of awns in several crosses of wheat; and the ratios of 7.5:1 and 35:1 in premature germination which I have recorded in this paper, are so closely alike. All have been interpreted on the basis of duplicate factors with linkage and crossing over of the order of 33 percent. This appears to be the most simple interpretation and is probably justified until more adequate linkage tests with other factors of the same linkage group, or data of another nature, show that it is no longer tenable.

SUMMARY

1. Premature germination is an inherited character in which the seeds fail to maintain dormancy during development and germinate before maturity.

2. This character has appeared in many different stocks of maize, in several cases when two stocks were crossed, and in others in the second and third generation of inbreeding.

3. At least fifteen different genetic factors and nine distinct characters are shown to be involved in the inheritance of premature germination. There are recognizable differences between some of the types in the time at which germination begins as well as in other phenotypical characteristics.

4. Six of the characters are the result of complementary factors and are inherited in ratios of 3:1, 9:7, and 27:37, depending on the number of factors involved in the cross.

5. Three characters are governed by duplicate, triplicate, or quadruplicate factors and are inherited in ratios of 15:1, 63:1, and 255:1.

6. Ratios of 8:1 and 35:1 are interpreted as a result of triplicate factors, two of which are linked with approximately 33 percent of crossing over.

7. Combinations of 3:1 and 15:1 ratios produce a ratio of 45:19. Combinations of 9:7 and 15:1 ratios result in a ratio of 135:121.

8. Practically all of the different Mendelian ratios encountered have been verified by the data from F_3 progenies.

9. The possible origin of duplicate factors through chromosome doubling is discussed in detail.

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