VIVIPARY IN MAIZE[1]

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INTRODUCTION

The continuous development of a plant body from its unicellular inception to maturity, without the intervention of a period of dormancy, is called vivipary. In viviparous plants, the embryos develop into seedlings even while the seeds are still contained in the fruits of the parent sporophyte. Similarly, spores may develop into gametophytes without undergoing a period of dormancy.

Viviparous maize plants were described in an earlier publication (EYSTER 1924a) under the name "primitive sporophyte." This name was suggested by the fact that the sporophytes of all non-seed-bearing plants, which presumably are more primitive than seed-bearing plants, are normally viviparous. Since "primitive sporophyte" as well as such terms as "defective kernel" and "premature germination," which have been used in referring to maize sporophytes that apparently do not undergo a dormant period, are ambiguous and misleading, it seems best to use the botanically correct term in describing this phenomenon, namely, vivipary.

Viviparous maize plants first occurred in pedigreed cultures grown at the UNIVERSITY OF MISSOURI Agricultural Experiment Station, and with few

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exceptions lacked completely the chloroplastid pigments. The close association between vivipary and albino seedlings was regarded by EYSTER (1924a) as being due to separate but closely linked genes, while MANGELSDORF (1926) prefers to believe that physiological correlation is a more plausible explanation of the absence of chloroplastid pigments in the viviparous plants. That linkage and not physiological correlation is responsible for the close relationship between vivipary and albinism was demonstrated by self-fertilizing a large number of plants heterozygous for vivipary and albinism. Among the many albinotic viviparous seedlings occurred a few green viviparous seedlings which have been regarded as crossovers. When these green seedlings were removed to the soil, they grew to maturity and gave rise to a chlorophyll-bearing strain of viviparous maize.

In another paper by EYSTER (1924b) it was shown that at least two genes induce vivipary in maize.

While the first of the above-mentioned papers was in press, descriptions of what appear to be vivipary in maize were published by LINDSTROM (1923) in a paper concerned with "Endosperm defects" and by MANGELSDORF (1923) as "Germinating seeds." According to MANGELSDORF, "germinating seeds" are characterized by the failure of the embryo to go into the resting stage. Since germination implies dormancy, it is obvious that "germinating seeds" does not correctly apply to the character described.

Later MANGELSDORF (1926) adopted the term "premature germination" and differentiated genetically different types largely on the basis of the stage of endosperm development at which germination begins. Just how it was determined when dormancy began and ended in each case, and that dormancy was not completely inhibited by the gene which is assumed to produce premature germination is not stated.

More recently MANGELSDORF (1930) has presented a more extensive study of "premature germination." To explain the numerical results observed in various stocks, fifteen genes have been called into service. The descriptions of the different types of "premature germination" are based entirely upon time of germination and the degree of development of the chloroplastid pigments. To what extent these differences may have been caused by other genes and by environmental factors does not seem to have been determined.

ORIGIN AND DESCRIPTION OF VIVIPARY IN MAIZE

Vivipary has occured in a number of different and unrelated strains of maize. No attempts have been made to determine the nature of the origin of vivipary in any of the strains.

So far as observations have been made, viviparous maize plants have a continuous development from the fertilized egg to the mature plant so that dormancy and germination are not involved. The development of the

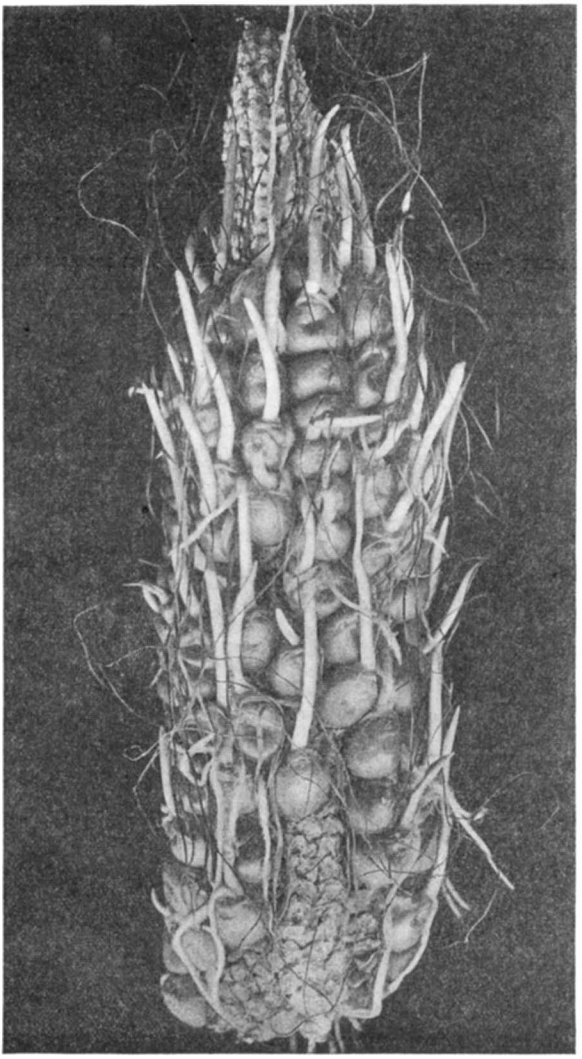

FIGURE 1.—An ear of maize homozygous for vivipary$_1$ showing the viviparous embryos in various stages of development.

chloroplastid pigments as well as other plant pigments is conditioned by other genetic factors in viviparous plants exactly as in non-viviparous plants. When viviparous seedlings of such genetic constitution that the

plastid pigments develop normally are transferred to soil, they develop into mature plants. A maturing ear of a homozygous viviparous plant is shown in figure 1. Although the embryos of all kernels are homozygous for vivipary, they are in different stages of development. Some of the em-

FIGURE 2.—Mature plants which are homozygous for $vivipary_1$.

bryos are hurrying into the seedling stage, while others are still so small that the kernels appear to contain non-viviparous embryos. It would be impossible to characterize vivipary in maize on the basis of a definite relationship between a stage in endosperm development and the appearance

of the plumule and radicle of the developing seedling as has been done by MANGELSDORF in differentiating the different types of "premature germination."

Viviparous maize plants have been growing continuously through consecutive generations, without a period of dormancy in the seed stage, for three years. The fourth continuous generation of viviparous maize$_1$ is shown in figure 2. These viviparous plants apparently grew as vigorously as non-viviparous plants belonging to the same strain.

INHERITANCE OF VIVIPARY IN MAIZE

Vivipary in maize is inherited as a simple Mendelian recessive character, and is brought into expression by a number of different genetic factors. The genes for vivipary which have been studied are indicated by the symbols V_{p1}, V_{p2}, V_{p3}, and V_{p4}. The effect of each of these genes is to inhibit dormancy and cause the sporophyte to undergo continuous development from the fertilized egg to the mature sporophyte, as is characteristic of the sporophytes of non-seed-bearing plants. The time of the appearance of the plumule and radicle outside of the pericarp varies with changes in the genetic constitution of the individual. Vivipary$_1$ has been studied in pure cultures and in various hybrid combinations, and it has been found that in some stocks the seedlings are quite large at the time of maturity of the ear, while in others they are so small that they often do not even burst through the pericarp at the time of kernel maturity.

In F_2 progenies segregating vivipary$_1$, 24026 kernels were classed as having normal and 8336 as having viviparous embryos. These results show a deviation of 220 ± 53 kernels from the expected frequencies. Backcross progenies involving vivipary$_1$ yielded 1709 kernels with normal and 1726 kernels with viviparous embryos. The deviation between the observed and expected frequencies in these backcrosses is 8.5 ± 51 kernels.

Vivipary$_2$

F_2 progenies segregated 2625 kernels with normal and 959 kernels with viviparous kernels. This is a deviation of 63 ± 17.5 kernels from the expected frequencies. Intercrosses between vivipary$_1$ and vivipary$_2$ yielded normal plants, which, when self-fertilized, produced normal and viviparous kernels in the relation of 9:7. These results indicate that vivipary$_1$ and vivipary$_2$ are caused by genes having their loci in different chromosomes.

Vivipary$_3$

F_2 progenies segregated 723 kernels with normal and 208 kernels with

viviparous embryos. This is a deviation of 25 ± 8.91 kernels from the expected frequencies.

Vivipary$_4$

Up to the present time a single F_2 progeny involving vivipary$_4$ has been studied. This progeny included 214 kernels with normal and 109 kernels with viviparous embryos. These results represent a deviation of 28 ± 6.85 kernels from the frequencies that were to be expected.

The identity of the different genes for vivipary has been determined by their linkage relations as is shown in a later section of this paper.

SPURIOUS RATIOS OF NORMAL VERSUS VIVIPAROUS KERNELS

The wide variation in the stage of development of the viviparous embryos at the time of the maturity of the ear as indicated by the hardened endosperm is due in part to inherent genetic factors and in part to external environmental factors, especially moisture. By harvesting homozygous viviparous ears prematurely and drying them by blowing air over them by means of an electric fan, it has been possible to induce some or all of the embryos of such ears to become dormant. So, also, when the maturing ears of normal strains of maize are exposed to abnormally moist conditions, there is a tendency for the embryos to continue their development. Whether the embryos actually undergo a period of dormancy under these conditions is an open question.

There appears to be a greater tendency for the kernels which are heterozygous for vivipary than for the homozygous normal kernels to germinate on ears which are maintained under moist conditions. Accordingly, when ears which are heterozygous for vivipary are exposed to moist conditions, there may be an excess of viviparous kernels due to the germination of some of the heterozygous kernels which, under drier conditions, would have remained dormant.

In the study of the effect of premature drying on viviparous embryos, *R*-testers homozygous for shrunken endosperm and vivipary$_1$ were used. The self-fertilized ears of these plants were harvested and dried while the kernels were still immature. Accidental contaminations by pollen from other plants in the field could be recognized by (1) non-shrunken endosperm, and (2) colored aleurone.

The self-fertilized ears of plants which are homozygous for vivipary$_1$ and the *R*-aleurone color factor and homozygous for the other genes necessary for the development of colored aleurone bear, with rare exceptions, normal kernels with colored aleurone and viviparous kernels with colorless aleurone. The recombinations of these characters, due to crossing over,

occurred with a frequency of less than two per thousand kernels. In the study of the effects of premature drying and of increased moisture, respectively, the colored kernels from the self-fertilized ears could be regarded as homozygous non-viviparous and heterozygous viviparous, while the colorless kernels were, with rare exceptions, homozygous for vivipary.

Induced dormancy of viviparous kernels under dry conditions and germination of normal kernels under moist conditions give rise to all sorts of numerical ratios between normal and viviparous kernels, even when vivipary_1 alone is concerned. The spurious ratios thus obtained varied from 328 non-viviparous : 1 viviparous to 1 non-viviparous : 2.3 viviparous kernels. These results emphasize the importance of exercising extreme caution in the liberal and wholesale assumption of multiple factors, with and without linkage, in explaining observed numerical relationships.

The viviparous kernels, which have been forced into dormancy by artificial drying, germinate when they are exposed to suitable growth conditions. A number of viviparous plants which had undergone a period of induced dormancy were grown to maturity and, when self-fertilized, produced viviparous kernels exclusively, thus showing that they actually were homozygous for vivipary_1.

In like manner, germinating kernels with colored aleurone in which vivipary was induced by maintaining the maturing ear under moist conditions were transferred to soil and the plants grown to maturity. The self-fertilized ears of these plants produced kernels with dormant and viviparous embryos in the relation of 3:1, thus indicating that vivipary had been induced in heterozygous plants.

SUMMARY OF GENES USED IN THIS STUDY

The genes referred to in this study belong to linkage groups as indicated below.

Group	*Gene*	*Character*
I	c	Colorless aleurone
	sh	Shrunken endosperm
	v_{p4}	Viviparous embryo
II	g	Golden plant
	r	Colorless aleurone
	v_{p1}	Viviparous embryo
III	su	Sugary endosperm
	v_{p3}	Viviparous embryo
V	P_l	Plant color
VIII	P_r	Purple aleurone
	r_{e1}	Reduced endosperm
	r_{e2}	Reduced endosperm
	sc_1	Scarred endosperm
	v_{p2}	Viviparous embryo
	Y_2	Yellow endosperm

SUMMARY METHOD OF PRESENTATION OF THE DATA

The data are presented in summary form only, and are grouped into tables, where possible, to save space. The detailed data are on file in the laboratory of the writer and will be furnished upon request.

LINKAGE RELATIONS OF VIVIPARY$_1$

The gene for vivipary$_1$ is very closely linked with the *R* aleurone color gene as shown by the data in table 1 and the illustration in figure 3.

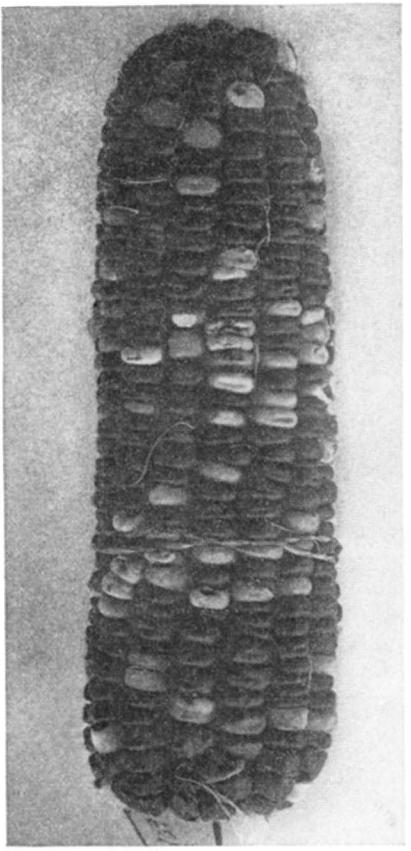

FIGURE 3.—A self-fertilized ear of a plant which was heterozygous for vivipary$_1$ and colored aleurone. Note that the colored kernels have dormant and the colorless kernels viviparous embryos due to the very close linkage between the *R*-aleurone color factor and the V_{p1} factor for vivipary.

Vivipary$_1$ and colored aleurone

Plants heterozygous for V_{p1} and *R* and homozygous for all other genes which are necessary for the development of colored aleurone were back-

crossed reciprocally with homozygous viviparous *R*-testers. The results of these backcrosses are given in table 1 A. Only 5 kernels among the 3435 which resulted from the backcrosses had the segregating characters in recombinations. These results indicate a linkage with 0.15 percent crossing over.

TABLE 1

Tests involving vivipary$_1$ and aleurone color factors.

PART	NATURE OF THE TESTS	COLORED ALEURONE		COLORLESS ALEURONE	
		V_{p1}	v_{p1}	V_{p1}	v_{p1}
A	Backcross involving *R* and V_{p1}	1707	3	2	1723
B	F_2 progenies involving *R* and V_{p1}	6070	23	19	2092
C	F_2 progenies involving *R*, *C*, and V_{p1}	5783	27	1871	2670
D	F_2 progenies involving *R*, *C*, *A*, and V_{p1}	5326	39	4957	3485

The close linkage shown by the backcross data is substantiated by F_2 data involving (1) *R* and V_{p1} as given in table 1B, (2) *R*, *C*, and V_{p1} as given in table 1C, and (3) *R*, *C*, *A*, and V_{p1} as given in table 1D.

Vivipary$_1$ and golden plant

According to LINDSTROM (1917, 1918), there is approximately 23 percent crossing over between *R* and *G*. As V_{p1} is very closely linked with *R*, it should show approximately the same linkage with *G* as *R* does.

As yet only limited data on the relationship between V_{p1} and *G* are available and are given in table 2A and B. The data in table 2A represent an F_2 progeny in the coupling series, while the data in table 2B represent a

TABLE 2

Further linkage tests involving Vivipary$_1$.

PART	PROGENY	FACTORS INVOLVED		*AB*	*Ab*	*aB*	*ab*	LINKAGE
		A	*B*					
A	F_2	*G*	V_{p1}	242	58	58	42	Yes
B	F_2	*G*	V_{p1}	40	28	28	0	Yes
C	F_2	S_h	V_{p1}	14043	4847	5090	996	No
D	F_2	S_u	V_{p1}	374	123	96	39	No
E	F_2	P_r	V_{p1}	959	0	352	0	No

repulsion series. These results indicate a linkage between V_{p1} and *G* with approximately 35 percent crossing over. The data here presented are too limited to be of value other than to substantiate the linkage which was to be expected.

Vivipary$_1$ and shrunken endosperm

The results of F_2 progenies which segregated vivipary$_1$ and shrunken endosperm are given in table 2C. There is a marked tendency for homozygous viviparous embryos to become dormant in the seed stage when the endosperm is homozygous shrunken, and this may be caused by a more rapid withdrawal of water from the embryo as the kernel approaches maturity. By allowing for the tendency of shrunken endosperm to inhibit vivipary, we find the data indicate that vivipary$_1$ and shrunken endosperm are inherited independently.

Vivipary$_1$ and sugary endosperm

Vivipary$_1$ is inherited independently of sugary endosperm as indicated by the F_2 data given in table 2D.

Vivipary$_1$ and purple aleurone

F_2 data on the relationship between V_{p1} and P_r are given in table 2E. Since all of the kernels which had viviparous embryos had colorless aleurone due to the very close linkage between V_{p1} and R, they could not be classified with respect to the P_r gene. The relation of P_r to p_r among the kernels which have non-viviparous embryos and colored aleurone indicates that P_r and V_{p1} are inherited independently.

LINKAGE RELATIONS OF VIVIPARY$_2$

Vivipary$_2$, so far as can be determined by ordinary observation, is phenotypically indistinguishable from vivipary$_1$ and is the expression of a gene in chromosome VIII.

Vivipary$_2$ and purple aleurone

The results from F_2 progenies which segregated viviparous embryos and red aleurone color are given in table 3A and B. A represents V_{p2} and P_r in

TABLE 3

Linkage tests involving vivipary$_2$.

PART	PROGENY	FACTORS INVOLVED		AB	Ab	aB	ab	LINKAGE
		A	B					
A	F_2	V_{p2}	P_r	269	66	47	24	Yes
B	F_2	V_{p2}	P_r	216	95	76	4	Yes
C	F_2	V_{p2}	R_{c1}	2058	190	252	620	Yes
D	F_2	V_{p2}	S_{c1}	300	21	16	68	Yes
E	F_2	V_{p2}	R_{c2}	257	0	4	72	Yes
F	F_2	V_{p2}	S_h	236	62	72	16	No
G	F_2	V_{p2}	Y_2	250	2	16	81	Yes

coupling series and B in repulsion series. These results indicate a linkage between V_{p2} and P_r with approximately 30 percent crossing over.

Vivipary$_2$ and reduced endosperm

Reduced endosperm$_1$ and reduced endosperm$_2$ are genetic variations in kernels of maize in which the amount of endosperm which is formed is greatly reduced, and are the expressions of genes which have their loci in chromosome VIII as shown by EYSTER (in press).

The results of F_2 progenies segregating vivipary$_2$ and reduced endosperm$_1$ are given in table 3C, and indicate a linkage between these characters with approximately 15.5 percent crossing over.

Vivipary$_2$ and reduced endosperm$_2$

F_2 progenies involving vivipary$_2$ and reduced endosperm$_2$ are given in table 3E. These data indicate a linkage between V_{p2} and R_{e2} with 1.2 percent crossing over.

Vivipary$_2$ and scarred endosperm$_1$

This pair of characters was found to be linked with 9.6 percent crossing over as shown by the F_2 data given in table 3D. This linkage is in agreement with the genetic correlation between S_{c1} and P_r previously reported by EYSTER (1926).

Vivipary$_2$ and shrunken endosperm

A single F_2 progeny which segregated vivipary$_2$ and shrunken endosperm indicates that the genes for these two characters segregate independently. The observed frequencies of this progeny are given in table 3F.

Vivipary$_2$ and yellow endosperm$_2$

One of the progenies which segregated normal and viviparous kernels also segregated yellow and white endosperm. A striking feature of this progeny was that practically all of the yellow kernels were non-viviparous while almost all of the kernels with white endosperm were viviparous, thus suggesting a linkage between the factors for vivipary and white endosperm. The F_2 data on this relationship, as given in table 3G, indicate a linkage between V_{p2} and Y_2 with approximately 5.3 percent crossing over.

Vivipary$_2$ and colored aleurone

F_2 progenies involving the R and C aleurone color factors and V_{p2} are given in table 4A, and others involving the A, R, and C aleurone color factors with V_{p2} are given in table 4B. These results indicate that V_{p2} is segregated independently of all aleurone color factors.

TABLE 4

F_2 progenies involving colored aleurone and various chromosome VIII characters.

PART	FACTORS INVOLVED		*AB*	*Ab*	*aB*	*ab*
	Colored Aleurone *A*	Chromosome VIII Character *B*				
A	*R* and *C*	V_{p2}	318	226	97	85
B	*A*, *R*, and *C*	V_{p2}	164	157	32	52
C	*A*, *R*, and *C*	S_{c1}	151	45	165	44
D	*A*, *R*, and *C*	Y_2	188	59	171	47

Scarred endosperm$_1$ and colored aleurone

One of the pedigrees which segregated for scarred endosperm$_1$ also segregated kernels with colored and colorless aleurone in the ratio of 27:37, thus showing that all three factors for aleurone were involved. The data, which are given in table 4C, indicate that S_{c1} segregates independently of the aleurone color factors.

Yellow endosperm$_2$ and colored aleurone

One of the progenies which segregated yellow endosperm$_2$ also segregated colored and colorless aleurone in the ratio 27:37, thus showing that the *A*, *C*, and *R* aleurone color genes had been involved. The observed frequencies, given in table 4D, indicate that yellow endosperm$_2$ is inherited independently of aleurone color.

Scarred endosperm and purple aleurone

The data given in table 5A, representing an F_2 progeny which segregated scarred endosperm$_1$ and purple aleurone, indicate a linkage between S_{c1} and P_r with approximately 20.7 percent crossing over.

Reduced endosperm$_1$ and shrunken endosperm

The F_2 data on this relationship are given in table 5B, and indicate that R_{c1} and S_h segregate independently. It is difficult to distinguish between non-shrunken and shrunken endosperm when the kernels are homo-

TABLE 5

Miscellaneous linkage tests involving chromosome VIII characters.

PART	FACTORS INVOLVED		*AB*	*Ab*	*aB*	*ab*	LINKAGE
	A	*B*					
A	S_{c1}	P_r	105	46	43	2	Yes
B	R_{c1}	S_h	939	294	346	66	No
C	R_{c2}	S_h	198	63	55	17	No
D	R_{c1}	Y_2	243	15	22	68	Yes

zygous for reduced endosperm$_1$. This difficulty is responsible for the wide deviation between the observed and expected frequencies of reduced kernels with non-shrunken and shrunken endosperm as given in table 5B.

Reduced endosperm$_2$ and shrunken endosperm

F_2 data showing that these two characters are inherited independently are given in table 5C.

Reduced endosperm$_1$ and yellow endosperm$_2$

Since both of these characters are linked with vivipary$_2$, it was to be expected that they would show a linkage with each other. F_2 data on this relationship are given in table 5D, and indicate a linkage between R_{e1} and Y_2 with about 11.3 percent crossing over.

The yellow endosperm referred to above is phenotypically and genotypically different from the pale yellow endosperm which has been shown by EYSTER (1924a) to be linked with vivipary. It is obviously different also from the yellow endosperm described by CORRENS (1901) and more recently by others, as the latter has its locus in chromosome V as indicated by its linkage relations with P_l and other genes known to be located in this chromosome. The yellow endosperm described in this paper for the first time has been named yellow endosperm$_2$ and the gene conditioning its development is designated by the symbol Y_2.

Vivipary$_1$ and vivipary$_2$

The F_1 kernels between vivipary$_1$ and vivipary$_2$ contain embryos which become dormant in the seed stage. F_2 progenies yielded a total of 1492 kernels with dormant and 1034 kernels with viviparous embryos. These frequencies represent a deviation of 71 ± 16.8 kernels from the 9:7 ratio which was expected. These results indicate that vivipary$_1$ and vivipary$_2$ are genetically different though phenotypically alike, and that they are inherited independently.

LINKAGE RELATIONS OF VIVIPARY$_3$

Viviparous strains of maize, which are not phenotypically different from those which have already been described in which vivipary is linked with sugary endosperm, have been found recently in my cultures. The observed frequencies are as follows: 1107 kernels with starchy endosperm and dormant embryo, 175 kernels with starchy endosperm and viviparous embryo, 164 kernels with sugary endosperm and dormant embryo, and 274 kernels with sugary endosperm and viviparous embryo. These results are in close agreement with calculated frequencies on the basis of linkage between S_u and V_{p3} with 22 percent crossing over.

MANGELSDORF (1926) states that G_{e1}, one of his genes for premature germination, appears to be linked with sugary endosperm with about 40 percent crossing over. This linkage is, however, only inferred by him. It is possible that V_{p3} and the G_{e1} represent the same gene.

LINKAGE RELATIONS OF VIVIPARY$_4$

Vivipary$_4$ is the expression of a gene which has its locus in chromosome I at approximately 11.8 crossover units from the gene for shrunken endosperm. Unfortunately only a single F_2 progeny concerned with the relationship between vivipary$_4$ and shrunken endosperm are available at the present time. More extensive observations have been made but the data are not available. In the F_2 progeny there were 200 kernels with non-shrunken endosperm and dormant embryo, 22 kernels with non-shrunken endosperm and viviparous embryo, 14 kernels with shrunken endosperm and dormant embryo, and 87 kernels with shrunken endosperm and viviparous embryo. These results are in close agreement with calculated frequencies on the basis of linkage between V_{p4} and S_h with 11.8 percent crossing over.

THE OCCURRENCE AND NATURE OF VIVIPARY IN THE PLANT KINGDOM

The almost universal occurrence of vivipary among the most simple plants leads to the general conclusion that vivipary is a fundamental and primitive characteristic of plants, and that dormancy has been acquired as a result of genetic changes in the course of phylogenetic development. Plants which changed genetically in such ways that vivipary became inhibited by unfavorable growth conditions were able to survive periods which are unfavorable to vegetative growth. As a result of the genetic changes which made possible this adaptive response, plants have been able to invade and occupy terrestial habitats where the conditions are not always optimum, or even favorable, for growth.

The occurrence of vivipary in maize as an inherited character is direct evidence that vivipary and dormancy are controlled by genetic as well as environmental factors. The identification of four different genes for vivipary in maize in this preliminary study is evidence that dormancy has been induced by a large number of genes in the course of phylogenetic development.

Dormancy occurs in all of the great divisions of the plant kingdom, due, no doubt, to the interaction of genetic and environmental factors. It has been acquired in spores which develop into gametophytes, and in various sporophytic structures as (1) the zygote or fertilized egg in many algae and

fungi, (2) the embryo sporophyte as in most spermatophytes, and (3) modified stems as tubers of *Solanum tuberosum* and buds of trees and shrubs.

Vivipary is generally characteristic of both gametophyte and sporophyte of the liverworts. In Pellia and Fegatella, the spores even germinate within the sporangia.

In mosses the spores develop directly into gametophytes and fertilized eggs into sporophytes without the intervention of a period of dormancy. The spores of Dicnemon and Eucalptodon, two related genera of mosses, grow into multicellular plant structures while they are still within the sporangia. These structures are easily visible to the unaided eye, and are flat on one surface and three-pointed on the other. Similar multicellular bodies have been observed in *Cleistostoma ambigua*, *Cryphaea macrospora*, and *Cryphaea grecillinia*.

Germination of the spores within the sporangia of liverworts and mosses makes possible a shortening of the protonemal development outside the capsule. This is an important characteristic in epiphytic species since a multicellular body will lose water less rapidly than a filamentous protonema. It is probable that the germination of the spores while they are within the sporangium is caused by genetic factors, and has been retained as a permanent character in species which are aided thereby in the reproduction of new individuals.

In some species of pteridophytes the spores pass through a dormant period before developing into gametophytes, in others they germinate as soon as they are exposed to favorable conditions outside of the sporangium, while in still others the spores germinate within the sporangia. The development of the gametophytes within the sporangia is especially characteristic of the species which grow in moist situations. The sporophytes of the pteridophytes are normally viviparous, as the fertilized egg grows directly into a mature sporophyte without the intervention of a period of dormancy.

In the spermatophytes, the gametophytes are normally viviparous, as the spores develop directly into gametophytes without passing through a period of dormancy. The sporophytes, on the other hand, enter a period of dormancy while they are in an early embryonic stage in development. Since the spermatophytes are more familiar in their sporophyte stage, we have come to regard dormancy, as it occurs in seeds, as a normal characteristic of the seed plants. The fundamental nature of dormancy doubtless varies widely in the different categories of the spermatophytes, and, although it is determined by genetic factors, it is influenced by such environmental factors as moisture, temperature, and available oxygen.

Widely scattered among both monocotyledonous and dicotyledonous angiosperms occur plants which bear sporophytes which forego the period of dormancy in the embryonic stage of development. Only a few of the more outstanding examples can be mentioned here. According to GOEBEL (1923) this type of vivipary is characteristic of the genera Rhizophora, Bruigera, and Ceriops. The embryos of the species of Rhizophora are extraordinary because of the extreme development of the stock-like hypocotyl which in many plants is a half meter long. After the embryo is well developed, it drops off the parent plant and rapidly gains a foothold in the muddy ground. In other genera, as Avicenna, the embryos grow into seedlings within the maturing ovary and have stiff upwardly-bent hairs which serve to attach the seedlings to the soil.

Among the monocotyledonous angiosperms may be mentioned the aroid, Cryptocoryne. The ovules of this aroid have two integuments and the outer, after fertilization, grows into a body composed of loosely arranged parenchyma cells in which the continued development of the embryo takes place. The embryo finally falls from the parent plant enclosed by the thin outer integument and is prepared to make a rapid growth into the soil (GOEBEL 1897).

The occurrence of vivipary in maize as genetic variations indicates that this phenomenon is not limited to plants which normally grow in wet places, though viviparous plants have survival value only in habitats where the conditions for continued growth prevail.

SUMMARY

1. Vivipary, the continuous development of the sporophyte in maize, is determined by genetic factors and is strongly influenced in its expression by environmental factors.

2. Four genes for vivipary have been identified by their linkage relations. Data are presented which indicate that the locus of V_{p1} is in chromosome II, that of V_{p2} is in chromosome VIII, that of V_{p3} is in chromosome III, and that of V_{p4} is in chromosome I.

3. By varying the environmental conditions of the maturing ears of plants which are homozygous and heterozygous for a single factor pair for vivipary, normal and viviparous phenotypes have been produced in practically all possible numerical relationships. These results warn against the liberal assumption of multiple factors, with and without linkage, to account for unusual numerical ratios.

4. Data are given which indicate the approximate locus of each of the genes for vivipary, and show that the genes for reduced endosperm$_1$, re-

duced endosperm$_2$, scarred endosperm$_1$, and yellow endosperm$_2$ have their loci in chromosome VIII.

5. Vivipary is regarded as a primitive plant character which, by the interaction of genetic factors and unfavorable growth conditions, may be inhibited. This temporary inhibition of growth is called dormancy. The ability to pass through a period of dormancy has enabled plants to utilize habitats where unfavorable growth conditions alternate with favorable conditions and has been important undoubtedly in the successful invasion of plants from aquatic into terrestial habitats.

6. Vivipary occurs in all of the great divisions of the plant kingdom, but naturally persists only among plants which live in moist habitats. Viviparous plants are not adapted for passing through unfavorable growth periods and do not persist, therefore, among plants that are exposed to such conditions, as, for example, maize.

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