GENES IN MAIZE FOR POLLEN STERILITY

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INTRODUCTION

Studies of a group of genes in maize which have to do with pollen sterility are reported in the present paper. It should be pointed out that the type of sterility reported here is different from the phenomenon of self- or cross-sterility (EAST 1929) which is better characterized by the terms self- or cross-incompatibility (STOUT 1917). In the case of self- or cross-sterility, pollen of a given genetic constitution may or may not be capable of effecting fertilization depending on the genetic constitution of the plant to which it is applied. In other words, the pollen is functionally complete. In the present paper the term sterile is used to designate incompletely developed pollen which is incapable of effecting fertilization under any conditions.

Cases of pollen sterility in maize due to simple genetic factors have been reported. L. A. EYSTER (1921) described a simple recessive which is characterized by abortion of all the pollen. This character was given the name "male sterile" and the genetic symbol m_s. SINGLETON and JONES (1930b) have described a similar character. W. H. EYSTER recently (1931a, b) has reported two additional genes for male sterility. The writer (1930b, 1931, and in press) has studied three genes in maize which result in aberrant chromosome behavior and consequent pollen sterility.

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RHOADES (1931) has studied a type of pollen sterility in maize which is inherited maternally, presumably through the cytoplasm. Pollen sterility is known to result in maize from unfavorable environmental conditions, from chromosome unbalance, from chromosome deficiency and translocations, but these cases are outside the scope of this paper and are therefore only briefly mentioned.

In a number of cases the characters reported here have been studied cytologically. However it should be emphasized that such cytological observations as are mentioned are in no manner complete. It was desired merely to find at what stage of pollen development visible deviations from the normal could be easily detected by the use of simple and rapid methods.

MATERIAL AND METHODS

The pollen sterility characters reported in the present paper are all simple in inheritance, being in most cases differentiated from the normal by single genes. Unless otherwise stated, the characters reported here are simple recessives.

Several recessive pollen sterility characters have been reported in the literature of maize genetics. Since stocks of the male sterile reported by L. A. EYSTER were lost, SINGLETON and JONES (1930) designated the pollen sterility character which they described as male sterile-1 (m_{s1}). W. H. EYSTER (1931a, b) has given two additional male steriles the names male sterile-2 (m_{s2}) and male sterile-3 (m_{s3}). The writer has followed the terminology used by the above mentioned writers for phenotypically similar characters. In the case of pollen sterility characters phenotypically distinguishable from the "male steriles" distinctive names have been used.

The characters discussed in the present paper have been collected from various sources. A list of the various characters considered with the sources from which the writer obtained them is given as follows:

Variable sterile-2 (v_{a2})—Doctor R. A. EMERSON, CORNELL UNIVERSITY, Ithaca, New York. From a yellow dent grown for study of number of kernel rows.

Warty anthers (w_a)—Doctor R. A. EMERSON. From mosaic variegated pericarp strain originally obtained from Czechoslovakia.

Male sterile-1 (m_{s1})—Doctor W. R. SINGLETON and Doctor D. F. JONES, CONNECTICUT AGRICULTURAL EXPERIMENT STATION, New Haven, Connecticut. Reported by SINGLETON and JONES (1930). Male sterile-1 was also found in an inbred strain of white dent obtained from Doctor G. F. SPRAGUE of the UNITED STATES DEPARTMENT OF AGRICULTURE, Washington, District of Columbia.

Male sterile-2 (m_{s2})—Doctor W. H. EYSTER, BUCKNELL UNIVERSITY, Lewisburg, Pennsylvania. Reported by EYSTER (1931a).

Male sterile-3 (m_{s3})—Reported by W. H. EYSTER (1931b). This male sterile has not been grown by the writer.

Male sterile-4 (m_{s4})—Doctor R. G. WIGGANS, CORNELL UNIVERSITY, Ithaca, New York. From an inbred strain of a yellow dent.

Male sterile-5 (m_{s5})—Doctor R. G. WIGGANS. From an inbred strain of the Bloody Butcher variety.

Male sterile-6 (m_{s6})—Doctor R. G. WIGGANS. From an inbred strain of a yellow dent.

Male sterile-7 (m_{s7})—Doctor R. G. WIGGANS. From an inbred strain of a yellow dent.

Male sterile-8 (m_{s8})—Doctor R. A. EMERSON. From a genetic culture. Male sterile-8 was also found in an inbred strain of a yellow dent grown by Doctor R. G. WIGGANS.

Male sterile-9 (m_{s9})—Doctor R. A. EMERSON. Found in the progeny of a cross between Alberta flint and a South American variety. Male sterile-9 was also found in a native yellow dent variety.

Male sterile-10 (m_{s10})—Found in the F_2 generation of a cross between the Cornell-11 variety and a South American variety.

Male sterile-11 (m_{s11})—Found in a yellow dent strain grown by Doctor C. B. HUTCHISON while at CORNELL UNIVERSITY.

Male sterile-12 (m_{s12})—Obtained from Doctor C. R. BURNHAM, National Research Fellow at CORNELL UNIVERSITY. From the F_2 generation of a cross between a brown midrib character and iojap stripe.

Male sterile-13 (m_{s13})—Doctor R. A. EMERSON. From a culture of white rice pop.

Male sterile-14 (m_{s14})—Found in a culture of Argentine flint.

Male sterile-15 (m_{s15})—Doctor M. T. JENKINS of the UNITED STATES DEPARTMENT OF AGRICULTURE and IOWA STATE COLLEGE, Ames, Iowa. From an inbred strain of a yellow dent.

Male sterile-16 (m_{s16})—Doctor M. T. JENKINS. From an inbred strain of a yellow dent.

The writer is grateful to the above mentioned persons who supplied the material for the studies reported here.

Many of the characters reported in the present paper were studied cytologically. These studies were made by means of the aceto-carmine method, a rapid and convenient method for the kind of preliminary survey desired. Material was killed in acetic alcohol (70 percent alcohol and 30 percent acetic acid) and stained with aceto-carmine or a mixture of aceto-

carmine and Ehrlich's haematoxylin as used by COOPER and BRINK (1931). In general, at least 3 plants of any one type were examined. In all cases the several plants of a given character showed essentially the same kind of behavior.

NORMAL POLLEN DEVELOPMENT

In order to describe the deviations from the normal that are found in the various cases of pollen abortion, it is necessary to have in mind the normal sequence of events during the course of pollen development. The meiotic divisions have been described and figured (RANDOLPH 1928, MCCLINTOCK 1929a). As the result of the two meiotic divisions, the microsporocyte is divided into four cells. These cells rapidly increase in size. After several days wall formation begins. Under ordinary growing conditions the microspore nucleus undergoes a vegetative division about a week after meiosis. During this division the chromosomes are large and have prominent constrictions (MCCLINTOCK 1929b). At this time the spore wall is well formed. Approximately a week later and a short time before the pollen is shed, one of the nuclei formed by the division just mentioned divides equationally to give rise to the two sperm nuclei which, at the time the pollen is shed, are crescent shaped. Thus the mature pollen grain contains three nuclei, one larger and more or less spherical and two smaller crescent shaped. Starch formation in the pollen grain takes place during a few days before shedding.

VARIABLE STERILE-2

Description

After the character variable sterile (v_a) was described (BEADLE in press) another character was found which is somewhat similar. It has been given the name variable sterile-2 and the symbol (v_{a2}).

Variable sterile-2 plants can be distinguished in the field by the fact that they shed but little pollen. Usually anthers are exserted but not systematically as they are in normal plants. The exserted anthers are usually rather sparsely scattered through the inflorescence. The anthers contain a variable amount of apparently good pollen. Anthers containing a high percentage of good pollen may dehisce and shed. However, most of the anthers fail to shed their contents presumably because there is insufficient pressure within the anther to cause the normal splitting of the suture at the tip of the anther. Variable sterile-2 plants are apparently completely female fertile.

Inheritance

Variable sterile-2 is a simple recessive character. As originally found, it appeared in about 25 percent of the plants. A v_{a2} plant crossed with homo-

zygous normal gave 12 normal plants. These backcrossed to v_{a2} plants gave a ratio of approximately 1 V_{a_2} to 1 v_{a_2}. A few progeny were grown from selfed seed of heterozygous variable sterile-2 plants. These were classified as 45 V_{a_2} and 14 v_{a_2}. Though the numbers are small, this is a close approximation to the expected 3:1 ratio. From crosses of v_{a2} by V_{a2} v_{a2} plants, 135 plants were grown. Among these, 72 were normal and 63 v_{a2}. This is in fairly good agreement with expectation. In all, the v_{a2} character has been under observation through 5 generations, and, although the num-

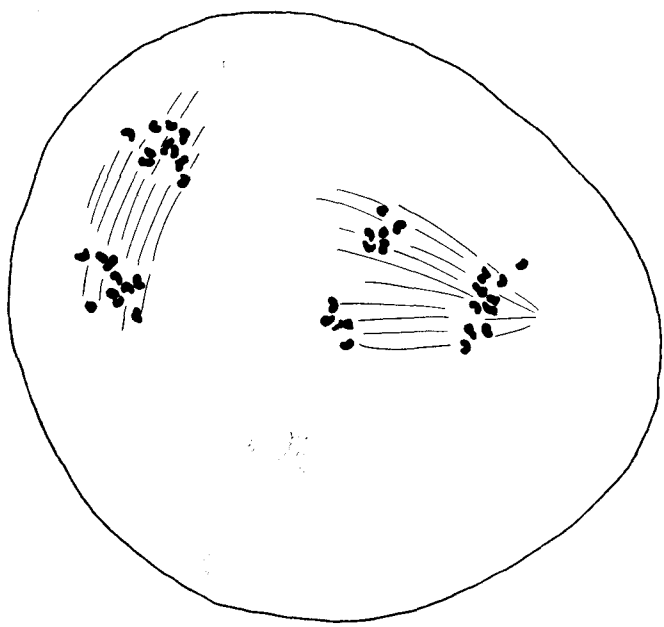

FIGURE 1.—Anaphase of the second meiotic division in v_{a2} plant in a cell in which cytokinesis failed to take place during the first division. There are two spindles and the distribution of chromosomes is apparently normal. (×775)

bers grown have been small, no significant departures from the expected behavior have been observed.

Cytological observations

Meiotic chromosome behavior was studied in 4 variable sterile-2 plants and was found to be somewhat similar to that of variable sterile-1 (BEADLE in press). Chromosome behavior seems to be quite normal during the course of the first division. Diakinesis, metaphase, anaphase and telophase stages have been observed. As in v_{a1} plants a variable percentage of the

microsporocytes fail to undergo cytokinesis during division I. Five to ten percent might be considered a fair estimate of the percentage of micro-

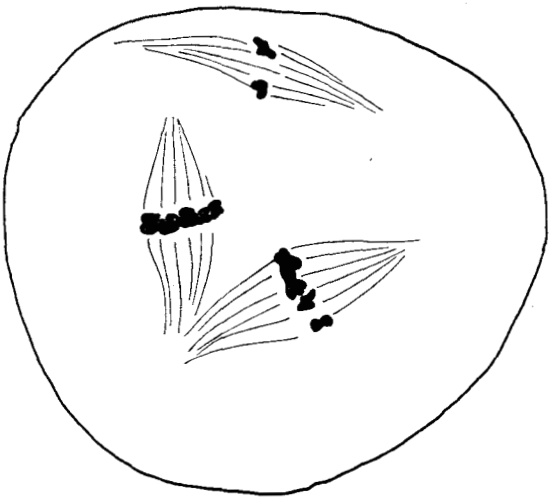

FIGURE 2.—Metaphase II in a v_{a2} plant in which there was no cytokinesis during division I. Three spindles are evident. (×775)

sporocytes which show such behavior. In the cells which divide normally during the first division, the second division is usually normal and pro-

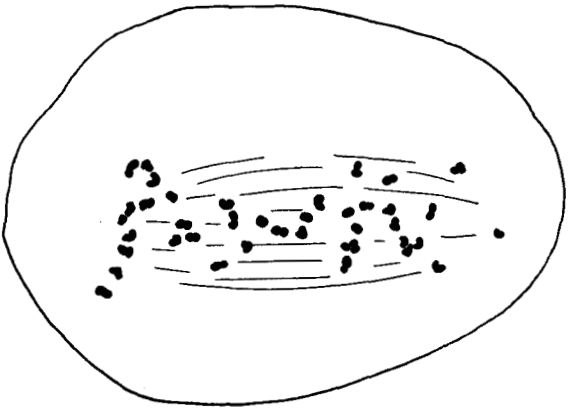

FIGURE 3.—Anaphase II in a v_{a2} plant in which there was no cytokinesis during division I. There is much lagging of chromosomes. (×775)

duces a normal appearing group of four spore cells. In the cells in which cytoplasmic division fails to take place during division I, the second divi-

sion is often aberrant. Two spindles each containing ten chromosomes can be observed in some cells (figure 1). In other cells more than two spindles can be seen (figure 2). In still other cells only one spindle may be formed. In such cases the chromosome distribution may be fairly regular, twenty chromosomes going to each pole, or there may be a great deal of lagging which results in an unequal distribution (figure 3). In variable sterile-1 plants it was found that cytokinesis usually fails to take place during the second division in those cells in which it fails during the first division. In contrast to this behavior, cytokinesis often takes place in the second division in variable sterile-2 plants in cells in which it failed during the first division. Groups of variable numbers of unequal-sized spore cells may result from aberrant second divisions (figure 4). In such cells as are illustrated in figure 3 in which there is a great deal of lagging of chromosomes, the division is usually not completed. Often no metabolic nuclei are formed, the cells degenerating with the chromosomes in the condensed

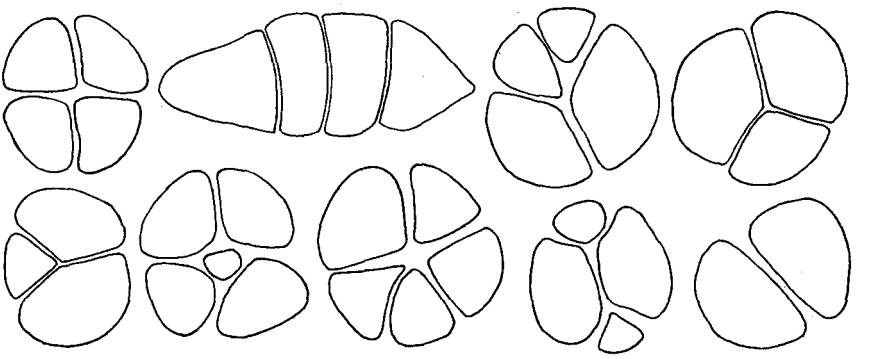

FIGURE 4.—Groups of spore cells from a v_{a2} plant showing variations in number, arrangement and size.

form. During the degeneration, the individual chromosomes form spherical vesicles of weakly staining chromatin.

In many of the spore cells in variable sterile-2 plants there is an apparent tendency toward a precocious division. Very soon after the second meiotic division is completed the chromatin begins to change from the typical metabolic form and assume the form of visibly identifiable chromosomes. This prophase-like condition is very similar to the prophases observed in polymitotic maize plants during the first supernumerary division of the spore cells (BEADLE 1931). Apparently the spore cells in v_{a2} plants do not go beyond the prophase stage of a division. They usually degenerate in a rather early prophase-like condition. In a few cells the chromosomes condense to a stage such as is illustrated in figures 5 and 6,

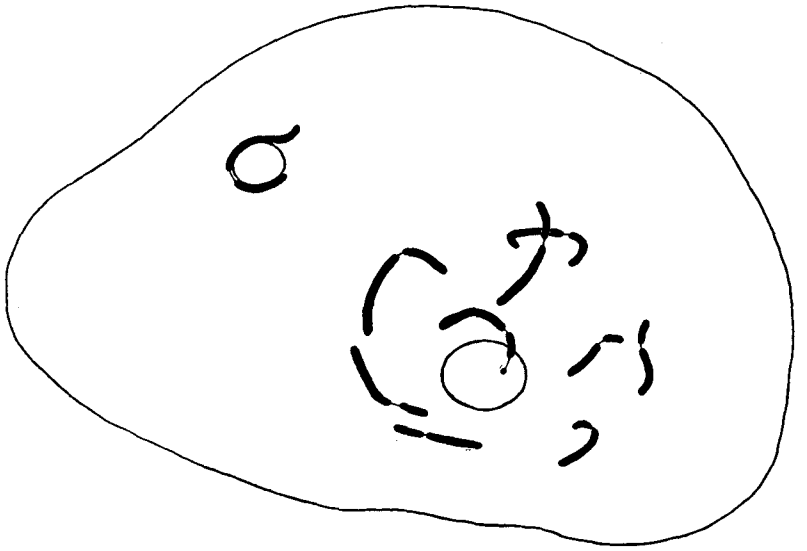

FIGURE 5.—Precocious condensation of chromosomes in a haploid spore cell of a v_{a2} plant. (×1560)

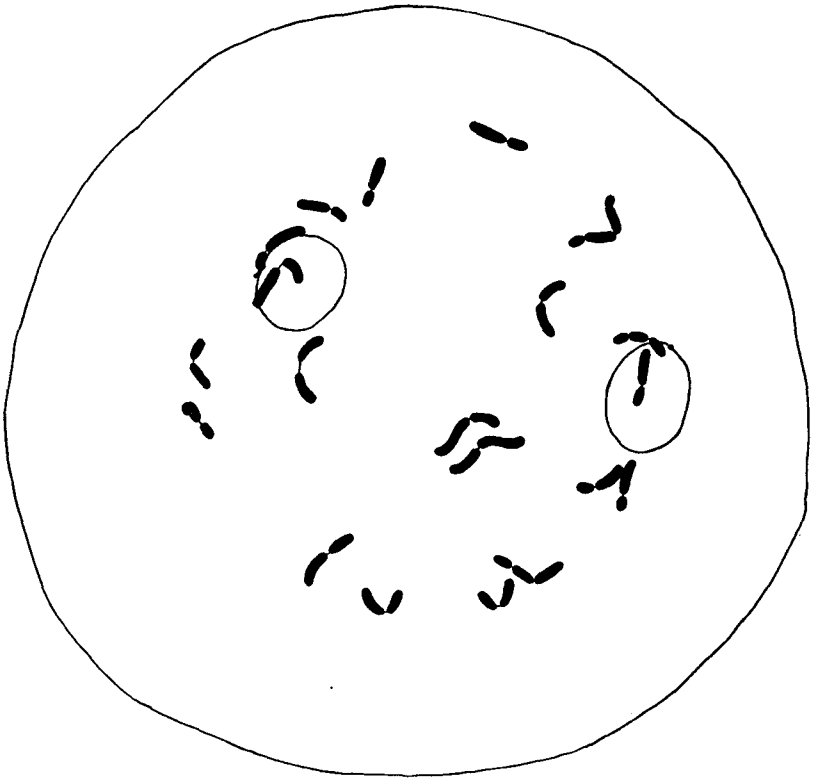

FIGURE 6.—Precocious condensation of chromosomes in a diploid spore cell of a v_{a2} plant. (×1560)

both diploid and haploid cells showing this tendency (figures 5 and 6). The constrictions are very prominent in these prophase-like stages. The relative lengths of the chromosomes and the position of the spindle attachment constrictions is clearly evident in such cells (figure 5). In general these stages are similar to the prophase stages of the first vegetative division of the microspore nucleus (McCLINTOCK 1929b).

The diploid microspore cells which show a tendency to undergo a precocious division are interesting in that the chromosomes show no visible split and do not pair, as might be expected on the basis of DARLINGTON'S (1931) theory of synapsis. However, the chromosomes might well be

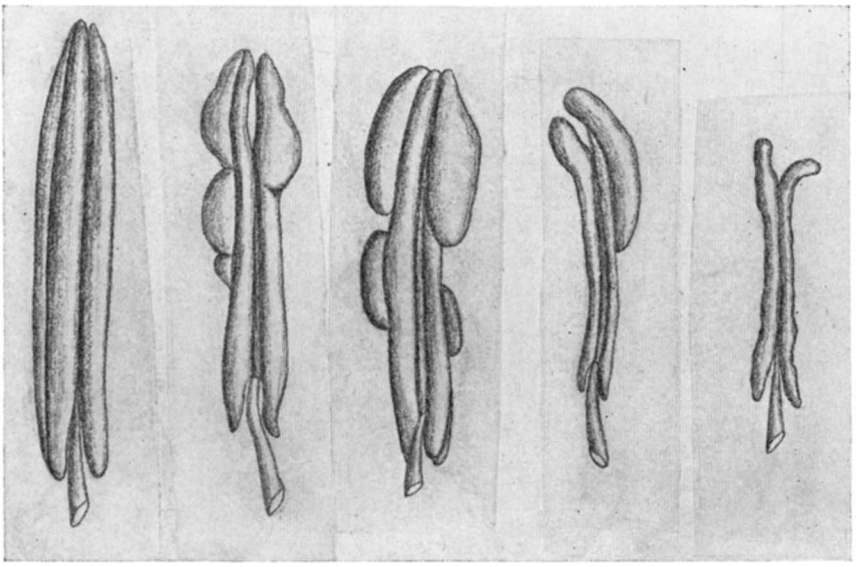

FIGURE 7.—Anthers of a normal (to the left) and a warty anther plant (4 anthers to the right) showing the characteristic shape and the variability of anthers from w_a plants.

actually but not visibly split which would prevent pairing on DARLINGTON'S theory. Furthermore these cells must be abnormal since they very soon degenerate. The case is therefore not a critical test of DARLINGTON'S theory.

Variable sterile-2 plants resemble variable sterile-1 plants in their meiotic chromosome behavior. The apparent tendency of the spore cells to undergo a precocious division is suggestive of the condition observed in polymitotic maize plants.

WARTY ANTHERS

Warty anther plants usually exsert very few anthers and shed little or no pollen. The anthers are very much shriveled except in certain regions which develop normally. The anthers have a very characteristic appearance (figure 7). Very few of the anthers dehisce. However if the tip of the anther is well developed dehiscence may take place and pollen be shed. Tests have shown that at least some of this pollen is functional. Warty anther plants are completely female fertile.

The warty anther (w_a) character is inherited as a simple recessive.

An examination of the young anthers of w_a plants shows that in the shriveled parts of the anther the sporogenous cells degenerate very early. The exact time of degeneration with reference to meiotic stages was not established. It is possible to say, however, that this degeneration begins somewhere near the time of synapsis. In maize synapsis takes place a relatively long time before metaphase of the first division. At this stage the anthers are usually less than one mm long. In the very young anthers of w_a plants the swellings which mark the regions in which the sporogenous tissue does not degenerate are evident. By the time the chromatin threads begin to loosen up after synizesis the cells are in an advanced stage of disintegration. In some anthers all of the sporogenous tissue may degenerate. In others only the tissue in certain sections of the anther degenerates while that in other sections develops normally and gives rise to normal pollen grains. It is difficult to understand why the tissue in certain parts of an anther should so completely break down while adjacent tissue develops quite normally.

MALE STERILES-1 TO -16

Male steriles are of relatively frequent occurrence in maize. The writer has collected such characters from over thirty sources. Doctor M. T. JENKINS (unpublished) has collected male steriles from eighteen sources. Only a representative group of the available male steriles is considered in the present paper.

All of the characters to which the name male sterile has been given are similar in that they are partially or completely pollen sterile and completely egg fertile.

Male sterile-1 (m_{s1})

Male sterile-1 was reported by SINGLETON and JONES (1930). It is a simple recessive character. The gene concerned is located in the Y-P_l chromosome within a few crossover units of the Y (yellow endosperm) gene. It is not known whether m_{s1} lies in the direction of the P_l (purple

plant color) gene, or in the opposite direction. Male sterile-1 plants may exsert a few scattered anthers but no pollen is shed.

Cytological examinations of m_{s1} plants by the writer show that the two meiotic divisions are completed in a normal manner. The spore cells grow to almost normal size, develop a wall but degenerate before the nucleus goes through the first division and before starch formation begins.

Male sterile-2 (m_{s2})

Male sterile-2 was reported by Doctor W. H. EYSTER (1931a). EYSTER showed that the m_{s2} gene is located in the chromosome which contains, among others, the well known genes *C* (aleurone color), s_h (shrunken endosperm) and w_x (waxy endosperm). The m_{s2} gene gives about 23 percent of crossing over with s_h but it is not known on which side of s_h it lies.

No cytological examinations of m_{s2} plants have been made by the writer.

Male sterile-3 (m_{s3})

Male sterile-3 was reported by W. H. EYSTER (1931b). It was found to be linked with the c_r (crinkly leaves) gene with about 30 percent of crossing over. Its position is not known with respect to other genes in this chromosome which contains a_1 (aleurone and plant color), t_{s4} (tassel seed-4), d_1 (dwarf-1) and others (BRINK and SENN 1931).

EYSTER reports that the anthers of m_{s3} plants contain many walled starchless microspores which have a single nucleus. In a few cases two nuclei were found. It seems, therefore, that degeneration takes place in m_{s3} plants, for the most part, before the microspore nucleus goes through the first division.

Male sterile-4 (m_{s4})

Male sterile-4 is a completely pollen sterile type which does not exsert anthers.

Examination of the anthers of m_{s4} plants established that the two meiotic divisions are normal. Pachytene, diakinesis, metaphase I, telophase I, prophase II, metaphase II and anaphase II stages were observed. A few of the spore cells show the beginnings of wall formation but most of them degenerate before any wall formation is detected.

Male sterile-5 (m_{s5})

Male sterile-5 plants are completely pollen sterile and do not exsert anthers.

Cytological studies show that the meiotic divisions are normal. Cells in pachytene, diplotene, diakinesis, telophase I, prophase II, metaphase II and anaphase II stages were observed. The microspore cells reach the

stage of wall formation, but the nucleus probably does not undergo the first vegetative division. This latter point was not established for certain.

Male sterile-6 (m_{s6})

Male sterile-6 appears to be a simple recessive though because of the variability of the character this has not been established for certain. It is a partially sterile type. Usually the exserted anthers are sparsely distributed through the inflorescence though occasionally anther exsertion is practically normal. The tips of the anthers tend to be empty and therefore have a pinched appearance (figure 8). Such anthers do not dehisce, pre-

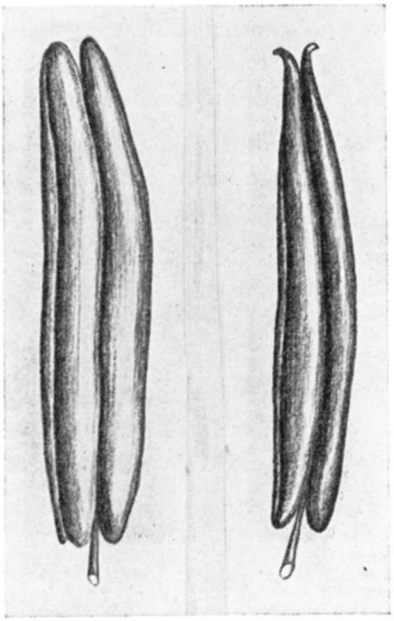

FIGURE 8.—Anther from a normal (left) and from an m_{s6} plant (right) showing the pinched tip characteristic of the anthers of m_{s6} plants.

sumably because of insufficient pressure at the tip where the split in the suture normally occurs. Many anthers contain abundant pollen and in certain plants a small amount of it may be shed.

Cytological examinations of m_{s6} plants show considerable degeneration of microsporocytes before, during and after metaphase of the first meiotic division. The two meiotic divisions are completed in a normal manner in many cells. Apparently a variable percentage of cells degenerate in m_{s6} plants in any one of several stages ranging from before metaphase I to pollen maturity.

Male sterile-7 (m_{s7})

Male sterile-7 is completely pollen sterile and no anthers are exserted. The character is inherited as a simple recessive.

A study of microsporogenesis in m_{s7} plants reveals that the two meiotic divisions are normal. Pachytene, early and late diakinesis, metaphase I, anaphase I, metaphase II, and anaphase II stages were examined. Degeneration of the spore cells takes place after wall formation but probably before the first division of the microspore nucleus. The contents of the anthers are almost completely disintegrated by the time pollen is shed by normal sib plants.

Male sterile-8 (m_{s8})

Male sterile-8 plants are completely pollen sterile and exsert no anthers. The anthers are very much shriveled and their contents have completely degenerated by the time pollen is shed by normal sibs.

Meiosis is rarely completed in m_{s8} plants. Degeneration of the microsporocytes takes place during pachytene or later stages of meiosis. The cytoplasm disintegrates before the chromatin. A few microsporocytes complete meiosis but the resulting spore cells degenerate very soon thereafter. In many of the cells which complete meiosis there is a failure of cytokinesis during the first division and large cells with 40 chromosomes similar to those found in v_{a1} and v_{a2} plants are found. However this behavior in m_{s8} plants differs from that in variable sterile plants in that the cells concerned in m_{s8} plants show distinct signs of degeneration.

Male sterile-8 has been tested with a considerable number of characters in known chromosomes but no good indication of linkage was found. Most of the data were from F_2 cultures. The characters with which m_{s8} was tested and the number of individuals classified are as follows:

s_h	110	f_1	534	P	209	a_1	855
w_x	110	B	1129	b_r	357	t_{s4}	550
R	304	l_g	857	f	273	d_1	380
g_1	1178	Y	822	r_a	408	c_r	427
s_u	348	P_l	1022			P_r	575
T_u	144						

The m_{s8} gene probably lies at the untested end of the r_a or of the P_r chromosome or in the linkage group which probably contains the C_h (chocolate pericarp) gene (ANDERSON and EMERSON 1931).

Male sterile-9 (m_{s9})

Male sterile-9 plants are completely pollen sterile and exsert no anthers.

Cytologically m_{s9} was found to be very similar to m_{s8}. Degeneration takes place during the same stages and apparently in much the same way.

Male sterile-10 (m_{s10})

Male sterile-10 plants are completely pollen sterile and exsert no anthers.

Meiosis is normal in m_{s10} plants. Pachytene, diplotene, metaphase I, anaphase I, metaphase II, and anaphase II stages have been examined. Visible signs of degeneration of the microspore cells make their appearance at about the time of wall formation.

Male sterile-11 (m_{s11})

Male sterile-11 is a completely pollen sterile type that does not exsert anthers. It has not been examined cytologically.

Male sterile-12 (m_{s12})

Male sterile-12 is a simple recessive character that is not completely pollen sterile. Some plants exsert a few anthers some of which dehisce and shed pollen. It has not been examined cytologically. Since m_{s12} is partially sterile it may not be of the same type as the other characters described under the name "male sterile."

Male sterile-13 (m_{s13})

Male sterile-13 plants are completely pollen sterile and exsert no anthers.

Male sterile-13 plants show normal chromosome behavior at meiosis. Very soon after meiosis the spore cells show signs of degeneration. A few cells may reach the stage of wall formation.

Male sterile-14 (m_{s14})

Male sterile-14 is completely pollen sterile and exserts no anthers.

Meiosis is normal in m_{s14} plants. The microspore cells degenerate after wall formation and probably before the first division of the microspore nucleus.

The ms_{14} gene was found to be linked with the s_b (slit leaf blade) gene (BEADLE 1930a). Evidence was presented showing that these two genes are located in the Y-P_l linkage group. Since the above cited paper was written some additional data involving the s_b, Y and P_l genes have been obtained. These data are not sufficient to be conclusive but do not substantiate the earlier data in indicating the s_b is linked with Y and P_l. The conclusion that m_{s14} is located in the Y-P_l chromosome is therefore somewhat doubtful.

Male sterile-15 (m_{s15})

Male sterile-15 is a recessive character obtained from Doctor M. T. JENKINS. Most of the material involving this character grown by the writer has been heterozygous and it is therefore not possible to describe it in any detail. It has not been examined cytologically.

Male sterile-16 (m_{s16})

This character, a simple recessive, was also obtained from Doctor M. T. JENKINS. It is a completely pollen sterile type that does not exsert anthers. It has not been examined cytologically.

OTHER MALE STERILES

A number of male steriles other than those considered above have been studied. Some of them are simple recessive characters but are not considered for the reason that intercrosses have not been completed. Others gave indications of a more complex type of inheritance. In two cases ratios suggested that duplicate recessive genes were concerned. However, these cases were not satisfactorily analyzed as it was decided to study the simpler cases first.

Cytological studies of a simple recessive male sterile obtained from one of Professor R. A. EMERSON'S linkage testers showed that the microsporocytes degenerate during synizesis or pachytene stages. This behavior differs from that of any of the other male steriles which have been studied cytologically and it is probable therefore that the gene concerned is different. However, this male sterile may be the same as some of those considered above which were not examined cytologically. It has not been intercrossed with other male steriles.

INTERCROSSES OF POLLEN STERILE CHARACTERS

Since most of the characters under consideration are completely pollen sterile, it is necessary in intercrosses to use as pollen parents plants heterozygous for the desired genes. In many cases heterozygous plants were also used as female parents. In all cases the female parent of heterozygous plants used in intercrosses was homozygous for the m_s gene under study.

The data from the intercrosses which have been made are presented in table 1. With the exception of m_{s3}, which the writer did not have, the intercrosses of the male steriles are practically complete. The strain of m_{s13} used was found to be cross sterile as female parent with certain unrelated strains. This behavior is probably the same as that reported by DEMEREC (1929) and explains the absence of intercrosses of m_{s13} with m_{s12}, m_{s15} and

m_{s16}. Variable sterile-1 may not be different from m_{s12} or m_{s15}. With the above mentioned exceptions the data show that the m_s genes concerned are non-allelomorphic.

TABLE 1

Intercrosses of v_{a_1}, v_{a_2}, w_a and male steriles-1 to -16. B indicates normal progeny from a cross between plants homozygous and heterozygous for m_s genes (m_{sx} $m_{sx} \times M_{sy}$ m_{sy}). F indicates normal progeny from a cross between plants heterozygous for m_s genes (M_{sx} $m_{sx} \times M_{sy}$ m_{sy}). C indicates phenotypic of cytological difference. L indicates that genes are located in different chromosomes.

	ms_{16}	ms_{15}	ms_{14}	ms_{13}	ms_{12}	ms_{11}	ms_{10}	ms_9	ms_8	ms_7	ms_6	ms_5	ms_4	ms_3	ms_2	ms_1	wa	va_2
va_1		C	C	C		C	86F	257F	95B	106F	89F	60B	77F	CL	CL	57B	40F	53F 54F
va_2	11B	21B	70F 31B	37F	37B	39B	56F 41B	139F 144B	174F 40B	88F	90F	99F	84F	C	38B	58B	56F	
wa	38B	*36F	104F	30F	36F	40B	100F	242F	101B	53B	53F	83B	67B	C	55F	52B		
ms_1	36B	36B	62B	39B	40B	68B	56B	202B	40F 136B	55B	50B	56B	56B	L	84B			
ms_2	34B	20B	38F 45B	46F	30B	38F	26F 31B	43F	87F 72B	70B	75F	69B	57B	L				
ms_3											C							
ms_4	20B	8B	90F	33B	39B	39B	114F	173F	137F 14B	88F	94F	85F						
ms_5	9B	24B	76B	42B	49B	45B	78B	143F 120B	141F 40B	94F	47F							
ms_6	21B	30B	101F	42F	38F	38F	116F	391F	187F	46F								
ms_7	29B	22B	56B	44B	20B	45B	96F	197B	172F 42B									
ms_8	35F 41B	44F 20B	40F 79B	29F	30F 30B	39B	40F 83B	70F 45B										
ms_9	51B	37B	316F	43B	51B	45B	214F											
ms_{10}	40B	17B	94F	37F	41F	36B												
ms_{11}	43F	38F	33F	34F	39F													
ms_{12}	22B	20B	39F															
ms_{13}			49F															
ms_{14}	12B	13B																
ms_{15}	24F																	

*One m_s plant observed in this cross. Possibly the result of an accidental self pollination of the female parent.

DISCUSSION

As has already been stated, no attempt has been made in the present paper to describe in detail the disintegration of the sporocytes or microspore cells in the various sterile types studied. Such a study would of course require the use of more refined methods than any that were used in the

course of the present study. In general the cytoplasm showed changes before any deviation from the normal was detected in the chromatin. The nature of the changes in the cytoplasm was not studied in detail but in advanced stages of degeneration it is completely broken down. In the sporocytes it tends to break away from the main body of the cell. In the walled microspores it breaks down completely, the amount of stainable cytoplasm being gradually reduced. The chromatin tends to accumulate in spherical droplets which appear to have a watery consistency during the late stages of the process of disintegration.

In most of the characters studied all the microsporocytes or microspore cells show the same changes at about the same time. Exceptions to this were observed in warty anther plants where the degeneration is confined to certain regions of the anthers and in male sterile-6 plants where the degeneration seems to take place at any stage over a comparatively wide range.

The question of what changes occur in the tapetal cells which are generally assumed to have a nutritive function is important. Some observations were made on these cells but the methods were unsuited to such a study and the observations themselves so limited in extent that it is not considered worth while to discuss them in more detail than to say that in many of the characters tapetal tissue was seen to be disintegrating at the time at which the anther contents were undergoing degeneration.

It seems reasonable to assume that degeneration takes place in the cells under consideration in male sterile plants because of some sort of nutritive disturbance.

Judging from the number of genes which affect them the processes of microsporogenesis and pollen development must depend on easily disturbed physiological conditions. The case is perhaps comparable to chlorophyll development which is likewise known to be frequently disturbed by genetic changes.

Genetic pollen abortion appears to be of much more common occurrence than megaspore or egg abortion, no cases of the latter unaccompanied by the former having to the writer's knowledge been reported. (In the character, silkless, reported by JONES [1925] and ANDERSON [1929], RANDOLPH [unpublished] has shown that the entire pistil aborts early in development. Anthers develop in the pistillate inflorescence of silkless plants. The character is comparable to the tassel seeds [EMERSON 1920] in which the stamens abort early in development and permit the development of pistils in the inflorescence that would normally be staminate.) The female sporocytes and spore cells probably have an advantage of position, as they are

imbedded in a rather large mass of sporophytic tissue during the entire course of their development.

SUMMARY

A study of fifteen genes for pollen sterility characters is reported. In all of these characters the development of megaspores and female gametophytes is normal.

In the character variable sterile-2 (v_{a2}) as in variable sterile-1 (previously reported), cytokinesis often fails to be completed during meiosis. The young spore cells in v_{a2} plants apparently have a tendency to go through precocious post meiotic division. The chromatin condenses as prophase-like chromosomes which show no signs of splitting. The cells degenerate without showing further progress of division.

A gene to which the name "warty anther" and the symbol w_a has been given is reported. In w_a plants the very young microsporocytes degenerate in certain regions of the anther but develop normally in other regions.

Thirteen additional genes for male sterility are reported. These have been given the names male sterile-4 to -16 and the symbols m_{s4} to m_{s16}. Intercrosses show that with one possible exception the genes concerned in the production of these male sterile characters are non-allelomorphic.

Cytologically the male steriles are characterized by degeneration of the microsporocytes or of the microspore cells. The time of degeneration may be the same or different in different male steriles and ranges from the synizetic stage of meiosis almost to pollen maturity.

In no case are the linkage relations known for the male steriles reported for the first time in this paper.

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