ABORTION OF MALE AND FEMALE GAMETES IN THE TOMATO DETERMINED BY ALLELIC INTERACTION¹

CHARLES M. RICK

Department of Vegetable Crops, University of California, Davis

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ANGIOSPERM gametogenesis, particularly on the male side, is highly susceptible to disturbance by either environment or genotype. Exemplary of environmental agents, sodium α,β -dichloroisobutyrate disrupts pollen development, the effect being sufficiently specific and complete to warrant use of this chemical for purposes of emasculation (EATON 1957). Instances of genetic control are commonplace; at least 30 genes are known in *Datura stramonium* that condition abortion of the microspores to which they segregate (AVERY, SATINA, and RIETSEMA 1959). In the presence of certain other genes, viable pollen grains may develop, but they fare poorly in competition with grains of other genotypes. Whatever the detrimental effect, segregation of linked genes can be distorted, the degree of distortion depending on the intensity of linkage. Genes affecting gametophyte development are often discovered, in fact, as a result of such distortion.

Interest in the present case intensified and the material was investigated in detail when it became apparent that it is exceptional in the following three respects: (1) male and female gametes are equally affected; (2) gametes abort only in certain hybrid combinations; and (3) the abortion factor behaves as if it were not completely penetrant.

MATERIALS AND METHODS

The first evidence of a gametophytic factor was encountered in F_2 ratios in certain combinations with wiry-4 (w_4), a spontaneous mutant of the tomato. This mutant had been discovered as an unfruitful plant in var. Pearson by M. P. ZOBEL of the Agricultural Extension Service, Woodland, California. Homozygotes for w_4 are distinguishable from normal at all stages of growth and correspond closely to the phenotype of w_1 (LESLEY and LESLEY 1928) except for less drastic foliar modification. Details concerning the phenotype of w_4 are given by RICK (1961). The F_1 , $w_1 \times w_4$, has normal phenotype, but F_2 segregation into an approximate $1 w_1 : 1 w_4 : 2 +$ and other linkage information indicate that these genes are tightly linked on chromosome 4. Other markers of chromosome 4 used in this study and their respective phenotypes are: *ful*₁, bright yellow-green foliage; *afl*, white cotyledons; *di*₁, whitish stems; *e*, entire leaves. Reference is made to the latest linkage summary for chromosome 4 by KHUSH (1965).

Counts of pollen abortion were made in the following manner: tiny pollen masses were carefully removed on the tip of a dissecting needle from the theca of an anther and mounted separately on a standard microscope slide; a limited amount of acetocarmine was then added and the preparation covered by a cover glass raised on three pieces of broken cover glass. The field

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was systematically scanned and aborted and normal staining grains counted. In this fashion, an exact count could be made of a completely confined sample without risk of differential loss of any kind of pollen.

Ovules were prepared for microscopic study of embryo sacs by fixation, imbedding, sectioning, and staining according to COOPER's (1931) method. Incipient seeds were examined and classified as normal or aborted (undeveloped ovules) by simple dissection of locules of ripe or nearly ripe fruit.

RESULTS

Inheritance: Crosses between w_4 and 20 different tomato stocks of varying origin yielded F_1 's of + phenotype, thereby revealing the recessive nature of the mutant. In F_2 's, however, an anomalous situation was encountered in which some families segregated in an approximately normal $3 + : 1 w_4$ fashion while others yielded an approximate $3 w_4 : 1 +$ ratio, suggesting a reversal of dominance (Table 1). A review of the pedigrees revealed that all of the exceptional segregations traced to matings between w_4 and stocks of *imb*₁, *inv*₁, *marm*₁, *pal*₁, and *pum*₁—all mutant genes induced by X rays in var. Condine (Kondine) Red (STUBBE 1957). On the other hand, the remaining, normal segregations had been sired by an assortment of stocks of many origins, including var. Pearson, within which w_4 had mutated. The 17 normal segregations listed in Table 1 show no evidence of heterogeneity, but, in total, show a slight but significant excess of w_4/w_4 (26.9%). Heterogeneity is revealed, nevertheless, for the combinations with Condine Red, and several of the families, as well as the total segregation (79.4% w_4/w_4), deviate markedly from 1:3. An analysis of the families reveals that most of the heterogeneity is contributed by two of the smaller families. The

TABLE 1
Normal and deviating segregations of w_4

Combinations with Condine Red w_4					Combinations with other parents w_4				
Total	Number	Percent	(vs. 75 percent)	χ^2	Pistillate parent	Total	Number	Percent	(vs. 25 percent)
268	193	72.0	1.12		Hybrid†	2,412	659	27.3	6.93**
179	141	78.8	1.16		Hybrid	486	134	26.7	1.56
275	199	72.4	0.88		Hybrid	433	127	29.3	4.10*
177	147	83.1	5.70*		Hybrid	142	38	26.7	0.15
295	207	70.2	3.42		Hybrid	110	24	22.0	0.44
191	158	82.7	5.67*		Hybrid	220	54	24.5	0.01
200	181	90.5	24.81***		Lukullus	635	157	24.7	0.03
5,481	4,379	81.1	69.75***		Pearson	181	58	32.0	4.79*
1,275	1,016	79.9	14.68***		Primitive Cherry	135	41	30.4	1.80
					Rheinlands Ruhm	341	108	31.7	7.74**
					San Marzano	123	22	18.0	2.95
					XL Pearson	838	206	24.6	0.08
Total									
8,431	6,621	79.4	85.07***			6,056	1,628	26.9	11.45***
Heterogeneity			42.12*** (8 df)					(11 df)	19.13

* $P < 0.05$. ** $P < 0.01$. *** $P < 0.001$.

† Signifies lines of hybrid origin.

two largest families, which were scored more recently with the advantage of our greater familiarity with phenotypes, had proportions of w_4/w_4 (81.1, 79.9%) that were in remarkable agreement. The conclusion consequently is warranted that these deviations from 1:3 in the Condine Red combinations are real, consistent, and do not represent a reversal of dominance; nor would such an explanation be compatible with the normal phenotype of all F_1 hybrid combinations.

The problem was further illuminated, as well as confused, by results of F_3 tests. The complete ovule sterility and limited pollen fertility of w_4/w_4 preclude progeny tests of the latter, but $+F_2$ segregants can be selfed and their F_3 progeny grown to adduce the corresponding F_2 genotypes. When such a test was made of 86 $+$ segregants, every one was proven to be heterozygous, and 80 (92%) of the F_3 families segregated in the same distorted fashion as the F_2 , with a mean yield of 81.1% w_4/w_4 . Such an extreme deviation in favor of heterozygotes, although not ruling out differential zygotic elimination as a cause of the phenomenon, gave firm support to an explanation based on differential gamete elimination.

Since elimination of $+$ gametes of one sex would permit a maximum yield of only 50% w_4/w_4 in F_2 , an hypothesis based on gamete elimination would require effects on those of both sexes. The aforementioned sterility of w_4/w_4 precludes direct backcross tests of transmission, but the problem can be approached by crosses of the type $w_4/+ \times +/+$ and reciprocal, followed by progeny tests of the selfed offspring. In this fashion heterozygotes used as female parents yielded a gamete ratio of 27 $+$: 165 (85.9%) w_4 ; and as male parents, 18 $+$: 469 (96.3%) w_4 . Although the difference between these reciprocal yields is highly significant ($\chi^2 = 23.3$, 1 df), the F_2 proportion of w_4/w_4 expected from the product of these gamete ratios is 82.7%—a remarkably close approximation of the observed F_2 proportions. For abortion determined by the genotype of the gamete, such an effect on both sexes is far less frequent among higher plants than elimination limited to the male side.

The next aspect to be investigated was the genetic nature of the gamete eliminator. The F_2 tests (Table 1) already established that the eliminator can act only in certain combinations—for example, in the hybrid between var. Pearson and var. Condine Red. An F_1 hybrid between Condine Red and Pearson was mated as the pistillate parent with w_4/w_4 in its original Pearson background. The offspring of this cross—all of normal phenotype—were then selfed and progeny tested. Of the 148 progeny tests, 81 segregated with approximately normal ratios for w_4 , whilst 67 segregated for the high (ca. 80%) yield. Clearly, then, the eliminator itself segregates as if it were a single gene, and for purposes of expediency its locus is designated as *Ge* (Gamete eliminator), the Pearson “allele”, *Ge^p* and the Condine Red allele, *Ge^c*.

Reciprocal crosses between stocks of *Ge^c* and *Ge^p* revealed transmission of the respective alleles, thereby ruling out any cytoplasmic differences that might account for the observed results.

Subsequent tests revealed severe distortion in the segregation of another closely linked marker, *ful₁*, a mutant induced in var. Condine Red. The two stocks—the original wiry-4 (w_4 *Ge^p*) and fulgens-1 (*ful₁* *Ge^c*)—can then be used as testers

to ascertain the nature of the *Ge* allele in any other parent. Thus, the presence of *Ge^p* in a line can be detected by the extremely low yield of *ful₁/ful₁* in the *F₂* of crosses with the latter, and of *Ge^c*, by high yields of *w₄/w₄* in crosses with the former. With this pair of testers a group of tomato varieties has been surveyed without finding any other source of *Ge^c*, but *Ge^p* was detected in several Californian varieties (Early Santa Clara and others) all of which are known to be related to var. Pearson. Additionally, some lines, including var. San Marzano, yielded normal segregations when mated with both testers, thereby revealing the presence of a third, neutral allele, designated *Geⁿ*.

All stages of meiosis in the critical *F₁* hybrids were studied cytologically. No abnormality was observed in any aspect of chromosome behavior, and no evidence was found for heteromorphy in the paired homologues of chromosome 4 at pachytene, diplotene, diakinesis, or metaphase. Neither nondisjunction nor meiotic drive could therefore account for the observed deviations.

Inspection of the original *F₂* and *F₃* segregations from the mating of $+ Ge^c \times w_4 Ge^p$ reveals a curious situation. Distorted segregation in the majority of *F₃* progenies of $+$ segregants proves that the latter received *Ge^c* chromosomes. The mechanism for elimination of *Ge^c* therefore cannot be 100% effective. In an attempt to ascertain the degree of effectiveness of the eliminator mechanism, various models were tested assuming equal elimination of male and female gametes, varying degrees of penetrance for the eliminator, and varying crossover values between *Ge* and *w₄*. The results of these estimations are presented graphically in Figure 1, in which observed values and their 5% fiducial limits are compared with curves representing expected values for the proportion of $+/+$ and *w₄/w₄* in the *F₂* and for the fraction of $+/w_4$ that were also *Ge^c/Ge^p* (i.e., that yielded distorted segregations in *F₃*). For such comparisons the $+/+$ data discriminate much less effectively than those of $+/w_4$ and *w₄/w₄* because ex-

FIGURE 1.—Proportions of various genotypes of *w₄* in progeny of *Ge^c + / Ge^p w₄* as ascertained by *F₃* progeny test. Curves represent values expected with various levels of abortion of both male and female gametes. Shaded areas represent 5% fiducial limits of observed values, those for $+/w_4$ and $+/+$ being calculated according to STEVENS (1942).

pected and observed values cover a very narrow range. As to the proportion of w_4/w_4 , 40% abortion can be ruled out because observed and expected lines do not intersect. The intersection for 45% abortion occurs in the 0 to 2% crossover range, while that for 47.5% falls in the 4 to 7% crossover range. The same analysis applied to the $+w_4$ data reveals interception for 47.5% abortion in the 0 to 1% crossover range, and for 45% abortion in the 0.5 to 2% range. Therefore, the only curve among those represented in Figure 1 that provides a satisfactory fit is that for 45% abortion. The intercepts indicate crossing over between 0 and 2%. The data also discriminate against abortion values higher than 46% and lower than 44%.

Test for transmission of Ge^c : If Ge^c gametes are occasionally transmitted by Ge^c/Ge^p heterozygotes, it should be possible to detect the presence of Ge^c by progeny tests in later generations. The following experiment was accordingly designed to test the above formulated hypothesis concerning the action of Ge . The purposes of such a test are served much better by a recessive marker linked with Ge^c than with Ge^p . A test was therefore prepared with ful_1 , which, as mentioned, is closely linked with w_4 and Ge . An F_1 , $ful_1 Ge^c/+ Ge^p$, was allowed to self-pollinate and the progeny were grown. As anticipated from the linkage relationships and behavior of the Ge alleles, the yield of ful_1/ful_1 was low—five plants in a total F_2 of 1,318.

The problem then centered on the nature of the Ge alleles present in the ful_1/ful_1 segregants. Test crosses were therefore made between them and a line of $+ Ge^p$ (var. Pearson). Five or ten F_1 plants of each hybridization were selfed and small F_2 progenies were grown from each. The $+:ful_1$ ratios in the latter families could then give a clue as to the Ge alleles in the respective ful_1/ful_1 grandparents. Normal ratios would signify a $ful_1 Ge^p$ combination, severely depressed ratios, $ful_1 Ge^c$. Two of the groups gave only normal segregations, whereas three included normal and aberrant ones, the latter in the minority. It follows from this test that of the ten Ge alleles in the five original plants at least three were Ge^c . Since in Ge^c/Ge^p hybrids only 10% of Ge^c are expected to survive, the number of F_1 plants tested was too small to detect the presence of Ge^c with certainty; the test consequently does not eliminate the possibility that as many as 5 of the 10 alleles were Ge^c . Thus, although the data have little quantitative value, they do prove that Ge^c gametes can be transmitted from such hybrids.

Gamete abortion: Preliminary examination of Ge^c/Ge^p pollen samples revealed consistent abortion at an approximate 50% level. The above predictions concerning the nature of gamete elimination, however, prompted a closer examination. For this purpose a group of 48 plants of the genotype $w_4 Ge^p/+ Ge^c$, as verified by a high proportion of w_4/w_4 in their progeny, were sampled, and well defined pollen abortion was found in each. Exact counts on 19 plants made in the manner outlined in MATERIALS AND METHODS gave a mean of 46.1% pollen abortion with no evidence of heterogeneity and a highly significant departure from 50% abortion (Table 2).

TABLE 2

Frequencies of normal and aborted pollen in different plants of Ge^c/Ge^p

Total number	Aborted		χ^2 (vs. 50 percent)	Total number	Aborted		χ^2 (vs. 50 percent)
	Number	Percent			Number	Percent	
341	140	41.1	10.92**	378	191	50.5	0.04
255	108	42.3	6.0 *	290	129	44.5	3.52
265	140	52.8	0.84	323	141	43.7	5.2 *
244	119	48.8	0.14	228	104	45.6	1.75
381	182	47.8	0.76	538	242	45.0	5.4 *
292	140	47.9	0.58	324	149	46.3	2.08
281	140	49.3	0.01	244	118	48.3	0.26
182	73	40.1	7.12**	233	100	42.9	4.66*
233	98	42.1	5.88*	294	138	46.9	1.1
				344	162	47.1	1.16
Total				5,670	2,614	46.1	34.45***
Heterogeneity $\chi^2 = 22.88$ (18 df; $P = 0.1-0.2$)							

* Conventional significance levels, as in Table 1.

For an estimate of female gamete abortion, ovules developed following manual self-pollination in nearly ripe fruits were subjected to exact counts on 16 of the same 19 plants. The analysis again indicated no detectable heterogeneity between plants and gave a mean value of 45.7% defective seeds, which again falls significantly below 50% (Table 3).

Although ovule abortion will result in defective seeds, failure of fertilization or of postsyngamic development could lead to the same result. A more precise estimate of female gamete abortion was made by directly counting embryo sacs in sectioned ovaries of the same material. As with pollen samples, aborted embryo sacs were clearly defined, conforming to the "collapsed" type described in previous studies (Rick 1946). Counts made on six samples of *Ge^c/Ge^p* and five of the

TABLE 3

Frequencies of normal and defective seeds in different plants of Ge^c/Ge^p

Total number	Defective		χ^2 (vs. 50 percent)	Total number	Defective		χ^2 (vs. 50 percent)
	Number	Percent			Number	Percent	
115	68	59	3.84*	131	69	53	0.38
118	41	35	11.00**	135	61	45	1.26
138	56	41	4.90	128	62	48	0.12
104	45	43	1.88	126	57	45	1.14
119	54	45	1.02	144	64	44	1.78
127	57	45	1.32	130	54	41	3.72
116	59	51	0.04	136	55	40	5.01*
96	44	46	0.66	101	51	51	0.01
Total				1,964	897	45.7	14.72***
Heterogeneity $\chi^2 = 23.35$ (15 df; $P = 0.05-0.10$)							

* Conventional significance levels, as in Table 1.

TABLE 4

Frequencies of normal and aborted embryo sacs of Ge^c/Ge^p and parents

Source	Total (number)	Aborted (number)	Aborted (percent)	χ^2	
F_1 (Ge^c/Ge^p)	88	38	43	1.64	(vs. 50 percent)
	64	25	39	3.07	(vs. 50 percent)
	100	39	39	4.83*	(vs. 50 percent)
	114	42	37	8.27**	(vs. 50 percent)
	105	45	43	2.14	(vs. 50 percent)
	133	53	40	5.48*	(vs. 50 percent)
Total	604	242	40.1	23.91***	(vs. 50 percent)
Heterogeneity				1.42	(5 df)
Parents					
Condine Red	106				
(Ge^c/Ge^c)	195	3	1.5		
Pearson	76	3	4.0		
(Ge^p/Ge^p)	124	1	0.8		
	155	4	2.6		
Total (both parents)	656	11	1.7		
F_1 versus parents				185.45***	(1 df)

* Conventional significance levels, as in Table 1.

parental Ge^c/Ge^c and Ge^p/Ge^p are summarized in Table 4. Internal consistency of the data for the heterozygotes is indicated by the nonsignificant χ^2 for heterogeneity, and their mean embryo sac abortion, 40.1%, deviates very significantly from 50% and parental control values. This figure is lower than the 45.7% measured for ovules in ripe fruit, as expected because it is not subject to environmental causes of infertility. The lower abortion rate of embryo sacs than that of pollen also agrees with the difference found between sexes in transmission of w_4 by Ge^c/Ge^p hybrids.

All three of these statistics of gamete abortion are probably overestimated because all are subject to varying degrees of environmentally induced failure of gametogenesis. That these nongenetic sources of variation are inconsequential, however, is intimated by the uniformity of test conditions as verified in the nonsignificant values for heterogeneity. In any event, the total abortion was not high enough in any of the tests to be confused with semisterility and in this respect is concordant with the 45% abortion estimated from the genetic data.

Linkage studies: The affiliation of w_4 with chromosome 4 first became evident when hybrids between stocks of Ge^p and ful_1 , which was previously known to be a marker of that chromosome, showed exceedingly depressed ratios in crosses with stocks of Ge^p . It is therefore of interest to compare the linkage distances predicted for various markers based on the degree to which their F_2 ratios are distorted in Ge^c/Ge^p combinations with those estimated from standard linkage tests. Such comparisons must be made, not with map distances that have been compiled from the sum of the component short intervals between the two points in question, but with distances estimated directly for the segregation of genes at

the two points, shortened as they must be by double crossovers. Also, for the purpose of such comparisons, it is assumed from the foregoing analysis of distorted segregations that the loci of w_4 and ful_1 lie very close to that of Ge . All distances were reckoned from the locus of ful_1 .

Two estimates of the distance from ful_1 were made, one based on 90% elimination of Ge^c gametes (45% abortion), the other on 100% elimination (50% abortion). For recessive markers linked with Ge^p , the recombination value for 90% elimination is $(4.5 - 5\sqrt{a})/4$, and for those linked with Ge^c it is $(5\sqrt{a} - 0.5)/4$, where a is the proportion of recessive homozygotes. Estimates are summarized in Table 5. It can be seen that neither level of elimination provides a basis for closely approximating all the known linkage values. The discrepancies, nevertheless, are not excessive when account is taken of the fact that the two sets of estimates were made with lines of different genetic backgrounds and under different environmental conditions. The facts, *per se*, that the degree of distortion is exceedingly different for each mutant and that it conforms roughly to linkage distances from ful_1 , rule out any explanation of the observations based on conversion or other mutational phenomena, as does also the close relationship with observed gamete abortion. It can be safely concluded that the degree of ratio distortion corresponds roughly with known linkage distances from the locus of Ge .

DISCUSSION

Parallel examples in the literature: The information presented above demonstrates conclusively that the gamete aborter Ge^c (1) affects male and female gametes equally; (2) acts only in heterozygous combinations with a specific allele, Ge^p ; and (3) behaves as if incompletely penetrant. In each of these three aspects it differs unequivocally from the great majority of gamete aborters in higher plants, which generally (1) affect only pollen viability; (2) act in all tested combinations; and (3) uniformly condition abortion in all microspores to which they segregate.

TABLE 5

Linkage distance of various markers of chromosome 4 from the locus of ful_1 estimated from distortion of monogenic ratios†

Segregation in <i>Ge^c/Ge^p</i>					Distance from <i>ful</i> ₁ (map units)		
Gene	Phase	Total	Mutant		Estimated from distorted ratios		Estimated from standard linkage tests
			Number	Percent	90 percent elimination	100 percent elimination	
<i>afl</i>	<i>afl-Ge^p</i>	1,015	519	51.1	23.4	28.7	20.0 ± 1.1‡
<i>di</i> ₁	<i>di</i> ₁ - <i>Ge^c</i>	276	34	12.3	31.4	35.1	40.1 ± 1.2‡
<i>e</i>	<i>e-Ge^c</i>	1,140	102	8.95	24.8	29.8	31.0 ± 1.1§
<i>w</i> ₄	<i>w</i> ₄ - <i>Ge^p</i>	5,481	4,379	81.1	— 0.8	9.3	0

† See text for method of computation.

‡ Data of KHUSH (1965).

§ Data of RICK and MARTIN (1961).

Two examples can be cited of parallel behavior: one in derivatives of *Nicotiana tabacum* $\times$ *N. plumbaginifolia* (CAMERON and MOAV 1957), the other in *Triticum aestivum* ssp. *vulgare* (LOEGERING and SEARS 1963). Gamete lethality in the former is clearly defined in introgressants having the normal complement of *tabacum* chromosomes (24_{II}) and a specific single extra chromosome from *N. plumbaginifolia*. Performance of this hybrid and segregation in its progeny reveal that part of the pollen is aborted and that nearly all of the functional pollen transmits the extra chromosome. These and other findings indicate that microspores lacking the extra chromosome are "killed" if they are produced by microsporocytes that carry the extra chromosome. In the latter example, the inheritance of a gene determining resistance to stem rust in hybrids between certain bread wheat varieties is best explained by assuming that a closely linked gene determines pollen abortion and does so only in certain hybrid combinations. Gene dosage studies in trisomic and tetrasomic hybrids suggest that abortion results from the interaction between the abortion gene in maternal tissue and a different allele in the microspore.

An element common to the present example and the two cited ones, is the dependence of the aborter for its activity on interaction with some other allele. The parallel with wheat is even closer, for in that case the presence has been ascertained of a third allele, which does not interact with the aborter; whereas in tobacco no exceptions have been reported that would suggest genetic differences within *N. tabacum* that affect the killer mechanism.

In respect to the other two unusual features of the tomato material mentioned above, the tobacco and wheat examples either disagree or behave in a variable fashion. Thus, as to sex, action of the tobacco and wheat killers is restricted to pollen. As to degree of killing in tobacco, 85% instead of 100% of the microspores lacking the extra chromosome are eliminated. The reduction is logically attributed to somatic instability of the extra chromosome, which is a common feature of the *tabacum-plumbaginifolia* hybrids. In the wheat instance, no evidence was found for a reduced degree of gamete killing.

Incomplete penetrance: What might account for the incomplete penetrance of Ge^c in the present material is not known. Somatic instability is not likely responsible because the proportion of gamete abortion is remarkably constant and no evidence has yet been detected of somatic instability for other genes segregating in the various tested Ge^c/Ge^p hybrids. Possibly significant is the nature of environs of the *Ge* locus. By cytological analysis at pachytene of several radiation-induced interstitial deficiencies, KHUSH (1965) has narrowed the locus of *ful*₁ to a small region within 1 μ of the very short heterochromatic region that flanks the centromere on the short arm of chromosome 4. Since *ful*₁, *Ge*, and *w*₄ are known to be tightly linked, *Ge* must lie in close proximity to, if not within, this heterochromatin. Perhaps some of the many phenomena peculiar to heterochromatin might account for the remarkably constant level of penetrance, estimated in these experiments at about 90%. Whatever the explanation, it cannot assume alteration of Ge^c because progeny tests have proved that a few Ge^c -bearing gametes

survive and that the transmitted Ge^c can cause typical gamete abortion in subsequently synthesized Ge^c/Ge^p heterozygotes.

Nature of the Ge^c Ge^p interaction: The cited examples of gamete abortion present interesting situations that require for their activity some kind of interaction between spores that receive one allele (non- Kl in tobacco, kl in wheat, and Ge^c in tomato) and tissue carrying a different allele or conditioned by it. The possibility of an antigenic interpretation is explored by CAMERON and MOAV (1957).

Participation of the subsequently aborted microspore in this interaction is beyond dispute, but the identity of the other tissue is not entirely clear, although the respective investigators proffer arguments for either the cytoplasm of the microsporocyte or surrounding maternal tissue. Since it has been reasonably well demonstrated in the tobacco example that survival of non- Kl microspores (those lacking the extra chromosome) results from somatic elimination of Kl , it follows that the interaction must take place only between the non- Kl microspore and the Kl -bearing cytoplasm of the microsporocyte. Maternal tissue is ruled out as the effective agent by situations in which, as a result of the loss of Kl from a small patch of cells, non- Kl microspores survive despite the presence of Kl in nearby maternal tissue. Levels of pollen abortion in various wheat trisomics and tetrasomics are best explained if it is assumed that interaction involves maternal tissue rather than cytoplasm of the microsporocyte or genotype of opposing microspores from a common microsporocyte.

With respect to the tomato example, action on the female side may shed light on the nature of the interaction, for here the Ge^c embryo sacs abort almost as frequently as Ge^c pollen. In tomatoes, as in the majority of angiosperms, three megaspores regularly abort and one survives to give rise to the embryo sac. Interaction between megaspores determining abortion might lead to elimination at this stage with no effect on female fertility but with modification of gene frequencies. On the other hand, interaction with maternal tissue could take place at a later stage subsequent to the normal elimination of megaspores. Interaction between a Ge^c nuclear product and a Ge^p factor in the cytoplasm could result in elimination at either stage. The observed high ovule abortion and strongly modified ovule ratios are therefore compatible with a hypothesis based on interaction with maternal tissue or cytoplasm.

Origin of the eliminator: Evidence presented here reveals the existence of three alleles or states of the eliminator. Some inkling as to varietal distribution of them is also gained, but their origins remain entirely a matter of speculation. In combination with the rather widespread neutral allele, Ge^n , neither Ge^c nor Ge^p affects gamete development. It is therefore entirely possible that the latter two alleles arose by spontaneous mutation, perhaps within cultivated tomatoes, and, having no apparent selective disadvantage, became fixed fortuitously, Ge^c in European forcing varieties and Ge^p in Californian processing varieties.

On the other hand, the presence of these alleles may signify a much earlier evolutionary development, possibly as a type of isolating mechanism. As they

function in our materials, Ge^c and Ge^p could tend to limit interbreeding of the parental types. From a survival standpoint their effect on pollen abortion is inconsequential because pollen is produced in excessive quantities, but the reduction of embryo sac—hence seed—fertility would put heterozygotes at a severe reproductive disadvantage. In many respects the model is similar to that of an interchange heterozygote except that it does not suffer the difficulty of semi-sterility inherent in the origin of the latter. As mentioned above, both Ge^c and Ge^p could arise by mutation from Ge^n without adverse effect on gamete fertility. If the three alleles were all inherited from ancestral species, in which they functioned as an isolating mechanism, a polyphyletic origin of the cultivated tomato would be implied. As a preliminary step in the investigation of this problem, appropriate crosses are being made to test the distribution of Ge alleles in species and primitive cultivars of *Lycopersicon*.

SUMMARY

Departures from Mendelian ratios for certain genes on chromosome 4 of the tomato are attributed to linkage with a gamete eliminator, Ge , located close to or within the proximal heterochromatin of that chromosome. Three alleles of Ge have been detected, elimination occurring only in Ge^c/Ge^p , in which Ge^c gametes are aborted. No abortion occurs in combinations with Ge^n or in Ge^c/Ge^c or Ge^p/Ge^p . The only known source for Ge^c is var. Condine Red; Ge^p exists in Pearson and related varieties; Ge^n appears to be widespread. The best fit to observed F_2 and F_3 segregations and to observed levels of pollen and embryo-sac abortion is provided by a model that assumes incomplete penetrance of the eliminator, specifically 90% elimination of Ge^c gametes of both sexes (causing 45% lethality of all gametes). When this model is applied to distorted ratios of *afl*, *di*, *e*, *ful*, and *w* in the F_2 of Ge^c/Ge^p combinations, the recombination distances thereby estimated correspond approximately with those estimated by standard methods.

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