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1. An investigation of abberant transmission associated with the etched locus in maize.

The mutant etched allele of chromosome three is sometimes associated with viability effects which in certain backgrounds cause an upset in progeny ratios (Rhoades, M.G.C.N.L., 1957). Rhoades (M.G.C.N.L., 1961) observed that the elimination of etched individuals, in response to a "zygotic semi-lethal" system, varies in different genetic backgrounds. The complete elimination of etched individuals was not reported in this study.

In the present study self-pollination of a plant of the A Et/a et genotype produced an ear totally devoid of etched kernels. The absence of etched kernels is demonstrated to be conditioned by the action of a previously unreported modifier, M^{et}, (modifier of etched). Individuals homozygous for the modifier are defined as full strain. Because of the close linkage (12 units) of the color factor A_1 to the etched locus, self-pollination of A Et/a et (full strain) individuals produces ears having distorted colored to colorless ratios indicative of the complete elimination of all expected etched individuals (Table 1; Experiment 1). When these full-strain plants are used as pollen parents with colorless, etched testers (a et/a et), normal etched transmission is observed. The use of full-strain plants as pistillate parents, as in the cross A Et/a et; M^{et} M^{et} X a et/a et; ++, produces ears that indicate the elimination of all normal etched kernels. Some (53%) of the ears resulting from this cross possess vestigial etched kernels in varying frequencies and sizes. The other 47%, although they possessed the same genetic background, were entirely devoid of these abortive etched kernels. These reduced kernels are viewed as etched individuals able to develop at least partially in this background. If these reduced kernels are ignored in the scoring of ears the data indicate the total elimination of etched individuals (Table 1; Experiment 2). The cross A Et/a et (full-strain) X a Et/a Et yields results that indicate that the system of aberrant etched transmission is based on the zygotic elimination of etched individuals (Table 1; Experiment 3).

All the kernels produced by a cross between M^{et} M^{et} (full-strain) plants and nonrelated plants (+/+) are defined as half-strain, $+M^{et}$. Self-pollination of any half-strain A Et/a et individual produces an ear having 50 per cent of the expected etched kernels (Table 1; Experiment 4). It is possible to demonstrate the survival of 50 per cent of the expected etched kernels as a result of the testcross A Et/a et(half-strain) X a et/a et(table 1; Experiment 5). When any half-strain individual of the A Et/a et

Table 1
Outline of experimental results.

Experiment	Model	Cross	Frequencies expected (A:a)	Kernels A	Kernels a	X^2	Probability
1.	No survival of et individuals	$\frac{A\ Et}{Met}/\frac{a\ et}{Met}$; ⊗	0.92A: 0.08a	2887	225	2.51	≅0.12
2.	No survival of et individuals	$\frac{A\ Et}{Met}/\frac{a\ et}{Met}$ X $\frac{a\ et}{+}/\frac{a\ et}{+}$	0.88A: 0.12a	2764	341	3.12	≅0.08
3.	1A:1a ratio expected	$\frac{A\ Et}{Met}/\frac{a\ et}{Met}$ X $\frac{a\ Et}{+}/\frac{a\ Et}{+}$;	0.50A: 0.50a	2889	2777	2.14	≅0.16
4.	Survival of 50% of et individ's.	$\frac{A\ Et}{Met}/\frac{a\ et}{+}$; ⊗	0.82A: 0.12a	15810	3424	0.51	≅0.48
5.	Survival of 50% of et individ's.	$\frac{A\ Et}{Met}/\frac{a\ et}{+}$ X $\frac{a\ et}{+}/\frac{a\ et}{+}$;	0.63A: 0.37a	8704	5303	1.25	≅0.28
6.	Survival of 50% of et individ's.	$\frac{A\ Et}{Met}/\frac{a\ et}{+}$ X $\frac{A\ Et}{Met}/\frac{a\ et}{Met}$;	0.82A: 0.18a	850	160	3.20	≅0.07
7.	No survival of et individuals	$\frac{A\ Et}{Met}/\frac{a\ et}{Met}$ X $\frac{A\ Et}{Met}/\frac{a\ et}{+}$;	0.92A: 0.08a	1629	124	1.98	≅0.18

Table 2

Classification of ears produced by tests of F_2 individuals from self-pollinated half strain A Et/a et. Also shown is the chi-square value testing the fit of these data to a 1:2:1 ratio.

Full Strain ($M^{et}M^{et}$)	Half Strain ($+ M^{et}$)	Normal ($++$)	X^2(2 d.f.)	Probability range
8	15	7	0.066	.95-.99

Table 3

A résumé of the various crosses performed in the course of this investigation, the resulting genotypes in terms of the modifier M, and the corresponding effects on the survival of the mutant etched allele.

Cross	Zygote	Endosperm	Progeny
$M^{et}M^{et}$ ⊗	$M^{et}M^{et}$	$M^{et}M^{et}M^{et}$	No et kernels
++ X $M^{et}M^{et}$	$+ M^{et}$	$+ + M^{et}$	Normal et survival
$M^{et}M^{et}$ X ++	$M^{et} +$	$M^{et}M^{et}+$	No normal et (reduced only)
$+ M^{et}$ ⊗	$+ M^{et}$ $+ +$ $M^{et}M^{et}$ $M^{et}+$	$+ + M^{et}$ $+ + +$ $M^{et}M^{et}M^{et}$ $M^{et}M^{et}+$	50 per cent of the expected etched individuals survive
$+ M^{et}$ X ++	$+ +$ $M^{et}+$	$+ + +$ $M^{et}M^{et}+$	50 per cent of the expected etched individuals survive
++ X $M^{et}+$	$+ +$ $+ M^{et}$	$+ + +$ $+ + M^{et}$	Normal etched survival

++ = Nonrelated Tester; $M^{et}M^{et}$ = Full Strain; $+ M^{et}$ = Half Strain genotype is used as a pollen parent with a nonrelated etched tester, normal phenotypic frequencies are observed.

If the modifier which conditions the zygotic elimination of etched individuals is independent of the etched locus, self-pollination of F_1 half-strain individuals should express this factor in a 1:2:1 (full-strain:half-strain:normal) ratio among the resulting kernels. This distribution was demonstrated by tests of the F_2 population. (Table 2).

Reciprocal crosses between full-strain and half-strain A Et/a et plants indicate the operation of an endosperm dosage phenomenon as the causal factor of etched elimination. The zygotic genotypes produced by these reciprocal crosses are the same. However, when full-strain plants were used as the maternal parent in these crosses no normal etched kernels were produced. But when half-strain plants were used as the pistillate parents, 50 per cent of the expected etched kernels were observed (Table 1; Experiment 6 and 7). The inequality in the results of these reciprocal crosses infers the existence of an endosperm dosage phenomenon.

An interesting relationship between the endosperm dosage of M^{et} and the survival of etched kernels can be illustrated for all the levels of aberrancy thus far reported. Table 3 presents a résumé of the zygotic and endosperm genotypes which were obtained as a consequence of these studies.

The genotypic relationships presented in Table 3 imply that endosperm dosage of the M^{et} factor causes the elimination of etched individuals. It is interesting to note that at any given level of aberrancy, where a nonrelated tester (++) is used as the maternal parent, normal phenotypic frequencies are produced on the resultant ears. These findings imply that under the conditions of this type of cross, the etched individuals survive because they never receive more than one dose of the modifier. The zygotic elimination of etched individuals is apparently based on the maternal contribution of the factor, M^{et}, to the products of double fertilization.

Developmental studies were undertaken to determine the histological basis of the zygotic elimination of etched individuals. Self-pollinated, full-strain ears of the A Et/a et genotype demonstrated a 3:1 ratio for full:reduced developing kernels as early as eight days after pollination. Both full and reduced kernels were fixed and sectioned at 8, 10, and 15 days after self-pollination. These sections demonstrated normal development for a given full-sized developing caryopsis. The reduced kernels, although they were obviously postzygotic, maintained a juvenile appearance consisting of only a proembryonic axis embedded in a nondifferentiated endosperm.

These studies, both histological and genetic, demonstrate that the aberrant transmission under investigation is due to the zygotic elimination of etched individuals which is conditioned by the action of an independent modifier.

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