

Since data are unavailable on the competitive disadvantage of the recessive ga10 allele, ga10 can tentatively be located 31 crossover units (15.4 x 2) from A2.

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The presence of En among some maize lines from Mexico, Colombia, Bolivia and Venezuela — In tests of an assortment of maize lines from Bolivia, Colombia, Mexico and Venezuela, five lines have been shown to possess En (Table 1). In the same tests the presence of r (or other distinguishable allele) and the color suppressor C-I was noted. The 23 lines tested can be grouped into five divisions with respect to the r allele, En and C-I (Table 2).

Table 2. Summary of the grouping of three characters.

	Presence of <u>r</u>	Presence of <u>C-I</u>	Presence of <u>En</u>	No. lines
1	Yes	Yes	No	12
2	Yes	No	No	3
3	Yes	Yes	Yes	4
4	R-st	No	Yes*	1
5	Yes	No	Yes*(a)	3
				23

\*Presence of En being confirmed.

(a) One of these already confirmed.

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Studies of a mutator locus on chromosome 10 — In the 1971 News Letter (45:81-87, 1971) I reported on an elevated spontaneous mutation rate that seemed to be under the control of a factor(s) at or near the y9 locus in chromosome 10. In genetic studies with y9 we had the opportunity to observe the self-progeny of numerous outcrosses involving heterozygous y9 plants as male parents; in these outcrosses there was an approximate 15-fold increase in mutation as compared to similar outcrosses not involving y9. The mutations occurred with equal frequency in outcross plants that received the y9 allele and those that did not; thus, they are not restricted to the chromosome carrying the y9 gene. A given outcross family frequently would have several plants that segregated for mutants which were quite similar in phenotype. If these represent identical mutants, it would suggest

Table 1. The distribution of En, r-allele and C-I among maize lines from various geographical areas.

Population	Origin	Race	Presence <u>r</u>	Presence <u>C-I</u>	Presence <u>En</u> **
Oaxaca 40	Tepalcingo, Morelos (Mexico)	Bolita	Yes	Yes	No
Chiapas 223	" " "	Zapalote Grande	Yes	Yes	No
Chiapas 225	" " "	Tepecintle	Yes	Yes	No
Chiapas 13	" " "	Oloton	Yes	Yes	No
Chiapas 171	" " "	Tehua	Yes	Yes	No
Nayarit 15	" " "	Reventador	Yes	Yes	Yes
Oaxaca 48	Tlaltizapan, Morelos (Mexico)	Zapalote Chico	Yes	Yes	No
Nayarit 72	" " "	Jala	Yes	Yes	No
Sonora 54	" " "	Harinoso de Ocho	Yes	No	No
Guanajuato 21	Leon, Guanajuato (Mexico)	Conico Norteno	Yes	Yes	No
Puebla 91	Chapingo (Mexico)	Arrocillo Amarillo	Yes	Yes	No
Mexico 72	" "	Conico	Yes	Yes	Yes
Mexico 55	" "	Palomero Toluqueno	Yes	Yes	Yes
Mexico 7	Batan (Mexico)	Cacahuacintle	Yes	Yes	Yes
Venezuela 341	Venezuela	Cariaco	Yes	No	No
Venezuela 870	"	Negrito	Yes	Yes	No
Santander Sur. 340	Colombia	Cacao	Yes	Yes	No
Choco 306	"	Chococeno	Yes	Yes	No
?	"	Chococeno	Yes	No	*
Bolivia 809	Bolivia	Pohoso	Yes	No	*
Bolivia 705	"	Cholito	Yes	No	No
Bolivia 707	"	Cholito	Yes	No	Yes
?	"	Cholito	<u>R-st</u>	No	*

\* Presence of En being confirmed.

\*\* Tests made with the standard En tester, a-m(r)/a-m-1 sh2.

? Population unknown.

that the mutator gene was acting in mitotic stages resulting in tassel sectors carrying a new mutation.

Three lines carrying y9 were observed in which limited tests seemed to indicate that there was not an elevated mutation rate. If these observations were confirmed, it would suggest either (1) that the mutator effect was controlled not by the y9 locus but by a separable factor or (2) that y9 is responsible for the mutator effect but can become inactive. The three lines tested consisted of one in which y9 had been crossed with the inbred M14 five times, one in which y9 had been crossed with the inbred W22 four times and one involving a cross to a bf2 stock. (In this report all lines tested were the result of crosses of heterozygous y9 plants as males to non-y9 lines; hence the tested family will consist of  $\frac{1}{2}$  heterozygous y9 plants and  $\frac{1}{2}$   $+/+$  plants). Plants of these lines (tested families) were grown, self-pollinated (to test for the presence of y9 and any new mutations) and outcrossed to a standard line (M14/W22). Only outcrosses from plants in which the selfed progeny did not segregate for new mutations were tested further. Fifty seeds from each outcross were planted, the resulting plants self-pollinated and the selfed ears seedling-tested for the presence of seedling mutations. The results of these tests are given in Table 1. For controls, selfs of outcrosses of M14, W22 and Standard (M14/W22) to Standard (M14/W22) were used. Since there was no obvious increase in mutation rate in these three y9 stocks, it would appear that y9 lines can lose the ability to induce mutation, either by recombination or by some inactivation of the mutator factor.

Table 1. Mutation rate in apparent non-mutator y9 lines.

Line	No. of outcrosses tested	Total plants for all outcrosses	No. of mutations	% mutation
M14/ <u>y9</u>	17	755	4	0.5
W22/ <u>y9</u>	14	685	1	0.1
bf2/ <u>y9</u>	13	565	3	0.5
Control	20	880	2	0.2

The observations reported in the 1971 News Letter were made only incidentally to linkage studies that were being carried on at the time, and there was thus a possibility that some mutations might have been overlooked. In 1971 three lines that had shown increased mutation rates were tested again by the procedure outlined above for the non-mutator lines. The three lines tested derived from

crosses of y9 to purple aleurone (pl aleur), g and bf2 (not the same bf2 line listed above). The results of tests involving the outcrosses of plants heterozygous for y9 from the tested families are given in Table 2. Column 4 includes all mutations that occurred. When more than one ear of an outcross family segregated for a mutant of a given phenotype, it was assumed that these were derived from a single mutational event that gave rise to a tassel sector.

Table 2. Mutation rates in mutator y9 lines heterozygous for y9.

Line	No. of outcrosses tested	Total plants for all outcrosses	Total mutants	Total mutants %	Total different mutants	Total different mutants %
<u>pl</u> aleur/ <u>y9</u>	7	280	34	12.1%	20	7.1%
<u>g</u> / <u>y9</u>	4	168	16	9.5%	6	3.6%
<u>bf2</u> / <u>y9</u>	3	119	18	15.1%	10	8.4%
Total mutator	14	567	68	12.0%	36	6.3%
Control	20	880	2	0.2%	2	0.2%

Such mutants were counted only once in determining the number of different mutants that had occurred (column 6). For example, in one outcross family one plant segregated for a yellow-green necrotic mutant, another segregated for a pale yellow mutant and two plants segregated for a yellow-green mutant. The total number of mutants observed was 4 (column 4), but there were only three different mutants (column 6). The assumption that mutants with similar phenotypes are derived from the same mutational event has not been proved, since for the most part such mutants have not been tested for allelism. However, one test in 1972 involving two albinos segregating in sibling ears of one outcross family did prove that they were allelic, so the assumption is not unreasonable. There is always the possibility of two mutants with similar phenotypes arising independently; since this undoubtedly occurs, the mutation rate based on total different mutants (column 6) is a minimal estimate. An increase in mutation rate is obvious in these lines; there is an 18- to 42- fold increase in mutation over the control lines with a 31.5-fold increase observed for the total mutator progeny.

In the tests reported in the 1971 News Letter only the outcrosses of plants that were heterozygous for y9 were considered since we were concerned only with following this gene. However, in 1971 outcrosses from sibling plants of the

tested families not carrying y9 were tested as well; the results of these tests are given in Table 3. It is obvious that the non-y9-bearing plants have a mutation rate of the same magnitude as that observed in the y9-bearing plants.

Table 3. Mutator rates from plants not carrying y9 (siblings of plants listed in Table 2).

Line	No. of outcrosses tested	Total plants for all outcrosses	Total mutants	Total mutants %	Total different mutants	Total different mutants %
p1 aleur/ <u>y9</u>	9	352	40	11.4%	16	4.5%
g/ <u>y9</u>	3	131	14	10.7%	8	6.1%
bf2/ <u>y9</u>	<u>1</u>	<u>38</u>	<u>4</u>	<u>10.5%</u>	<u>4</u>	<u>10.5%</u>
Total mutator	13	521	58	11.1%	28	5.4%
Control	20	880	2	0.2%	2	0.2%

Such results could be expected if the female parents (non-y9) of the tested families were homozygous for a mutator gene. When heterozygous y9 plants were crossed with such a line, all the plants (whether or not they received y9) would exhibit an increased mutation rate. This seems to be an unlikely explanation since three genetically unrelated lines were used as female parents in these crosses (i.e., g, bf2 and purple aleurone). Included in the 1971 report was the finding of mutability in a line in which the female parent carried T9-10b; in this case at least four different lines would have had to be homozygous for a mutator factor. The one thing these four tested lines had in common was that the male parent of each was heterozygous for y9, and it would seem that mutability is being transmitted in association with y9. Since only 13 plants not segregating for y9 were involved in these tests, since two of the 13 plants tested had no mutations and since we have shown that the mutable locus can be separate from y9, the 11 plants with an elevated mutation rate may represent crossovers in which the mutator gene has been transferred to the non-y9 chromosome in the heterozygous y9 parent of the tested families. Larger numbers of non-y9-bearing plants will have to be tested to determine if they consistently exhibit an increased mutation rate. If they do, it is possible that the y9-bearing chromosome is having an effect that is transmitted to the next generation through the non-y9 gamete. If such is the case, the effect may be either permanent or transitory. Further

tests will be necessary to distinguish between the two possibilities. If the mutator phenotype is the result of a cytoplasmic factor that is pollen transmissible, non-y9 mutator plants would be expected. Although male transmission of cytoplasmic factors has been demonstrated in other plants, it has not been established in corn.

If the mutability is associated with y9, the individual plants of the tested families should segregate for new mutations when self-pollinated. This would be expected since these families have been produced by outcrossing heterozygous y9 plants. Samples of the tested families were grown and self-pollinated and the resulting ears scored for the segregation of new mutants. The results are given in Table 4 along with the results of the mutation tests of the outcrosses of the tested families. It is obvious that the mutation rate within the tested families is of the same order of magnitude as that observed when these families are outcrossed. These results demonstrate that the elevated mutation rate has remained constant for at least two generations.

Table 4. Mutation rates found in the families of plants tested for the transmission of mutations (compared with the mutation rate found in the outcrosses of these families).

Tested progeny	Results from selfs of tested families			Results from selfs of outcrosses of tested families (Tables 2 & 3 combined).		
	No. of plants tested	Total different mutants	Total mutants %	No. of plants tested	Total different mutants	Total different mutants %
p1 aleur/ <u>y9</u>	56	3	5.4%	271	18	6.6%
p1 aleur/ <u>y9</u>	68	3	4.4%	361	18	5.0%
<u>g/y9</u>	109	7	6.4%	299	14	4.7%
<u>bf2/y9</u>	73	5	6.8%	157	14	8.9%
Total	306	18	5.9%	1088	64	5.9%

If a mutator factor is closely associated with y9, homozygous y9 plants might be homozygous for the factor; such homozygosity might result in a higher mutation rate. Four homozygous y9 plants were self-pollinated and outcrossed to standard; the resulting outcross plants were self-pollinated and their ears scored for the segregation of new mutants. The results are presented in Table 5. The outcross

Table 5. Mutations in outcrosses of homozygous y9 plants.

Family	Total plants	Total mutants	Total mutants %	Total different mutants	Total different mutants %	Total different mutants from outcrosses of ear parent providing the homozygous <u>y9</u> %
7501-02	85	0	0	0	0	0
7503-04	85	3	3.5%	3	3.5%	8.9%
7505-06	58	10	17.2%	4	6.9%	7.1%
7507-08	<u>89</u>	<u>13</u>	<u>14.6%</u>	<u>7</u>	<u>7.9%</u>	<u>2.3%</u>
Total	317	26	8.2%	14	4.4%	6.9%

of one plant produced no mutations, while the outcrosses of the rest had three or more different mutants. There is no consistent evidence that homozygous y9 plants have a higher mutation rate than heterozygous y9 plants. If the mutator factor is loosely linked to y9, it may be that three of these homozygotes have lost the factor by crossing over in one of the two gametes and the fourth from both. In the homozygous y9 families, most plants were weak and were not usable for selfing and outcrossing; only the stronger plants were used in these tests, and these might have lost, through crossing over, one or more of the mutator factors. Homozygosity for the mutator factor might be responsible for the weakness exhibited by many homozygous y9 plants.

Donald S. Robertson

A new compound A-B translocation, TB-5S,1L(8041) — Several compound A-B translocations have been produced by crossing over between the original set of A-B translocations produced by Roman (Roman and Ullstrup, Agron. J. 43:450-454, 1951) and selected reciprocal A translocations. Rakha and Robertson (Genetics 65:223-240, 1970) describe eight such translocations. These translocations have a portion of two A chromosomes attached to the B centromere; proximally there is a piece of the A chromosome carried by the original A-B translocation and distally a segment of one of the A chromosomes which was involved in the reciprocal A translocation.

In 1973,  $F_1$ 's between TB-1a (1L.2) and T1-5(8041) (1L.80,5S.10) were crossed as males to an a2 tester. Many of the ears on the a2 plants segregated for small yellow seeds, which ranged in size from very small, almost empty, pericarps to seeds about one-eighth the size of the plump purple seeds on the ear. It was assumed that these seeds were the result of fertilizations by gametes from a