Table 1. Heritable variations of the plastids in relation to genotype.

Cross	Normal Seedling	White Seedling
ij/ij r/r x +/+ r/r	6,513	173
	Normal progenies	Segregating progenies
(ij/ij r/r x +/+ R/R) x +/+ r/r	417	0

$X^2 = 11$; $P < 0.001$

Applying to the above results a test of significance by means of a 2 x 2 contingency table we obtain that the heritable variation of the plastids induced by the ij gene appears to be reversible to normality by the action of the R-r or R-g gene, by means of a structural change of the plastids that would normalize them hereditarily.

The interpretation of this phenomenon of the heritable variations of the plastids (mutation and reversion) produced by genes can be the following one if we base our opinion in the knowledge of molecular genetics.

Mazoti (M.N.L. 40:62, 1966; 41:87, 1967; 49:66, 1975; Publ. No. 88 Inst. Fitotec., 1975.) formulated hypotheses based on free replication of DNA to interpret cases of inheritance in corn that deviate from the Mendelian mechanism. The same hypothesis based on free replication of DNA will be useful to us to elaborate our hypothesis on the action of the ij gene over the plastids. Thus, if the ij gene produces its replica, this replica would have the quality of hybridizing with the plastid DNA, in a specific segment; and it will produce heritable variations in the plastids if it acts as an episome. The "mutational" frequency of all the plastids of a cell will depend on the number of free DNA replicas and on the degree of affinity with the plastid DNA.

If we consider that the R gene would also produce its replica, this hypothesis would also interpret the reversion of plastid mutations by the R gene. This replica would be, at least in part, homologous with the ij segment in its nucleotide sequence, and it would produce a segmental trisomy of DNA: R/ij/plastid. Stability of this synaptic state in a small chromosomal segment is rather improbable, because the synapsis of homologous chromosomes in trivalents is partial; and when the pairing of two chromosomes is produced in one segment, the homologous segment of the third one tends to get free. By means of the mechanism mentioned before, plastid reversion to normality would be produced because of the ij replica becoming free from the association.

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A dominant color allele, A-m(r), responsive to a specific En (Spm)

In the course of investigations of the Fcu controlling element system (Abstracts 1975 International Maize Symposium) two ears segregating an unexpected class of spotted kernels resulting from the cross of a-m(r)/a-dt sh2 plants by an a2 bt/a2 bt tester stock were found. The progeny included 75% solid colored and 25% spotted kernels, leading to the initial interpretation that perhaps a change in state had occurred in the components (r-cu or Fcu or both) responsible for the aleurone color variegation in kernels from the Cuna tribal maize from Colombia (MGNL 48:66-68). Test crosses of the spotted progeny by an r/r tester invalidated the initial

interpretation of an r change since these plants were homozygous for a dominant R allele.

Crosses by a-dt sh2/a-dt sh2, however, gave a strong indication that the spotting behavior was due to an En responsive A allele. This is based on results of the following series of crosses (Table 1). It is evident that one of the ear cultures (4 1140-1) segregated colorless shrunken (a-dt sh/a-dt sh) kernels which had

Table 1. Percent progeny segregation of plants from spotted kernels crossed by an a-dt sh2/a-dt sh2 tester stock.

Cross	Round			Shrunken	Genotype
	Colored	Spotted	Colorless	Colorless	
'4 1140-1/1167	24.68	25.22	0	50.10	A/a-dt sh2
-2/1167	27.68	47.00	25.32	0	A/a-m(r)*
-3/3623	20.93	51.86	27.21	0	A/a-m(r)
-4/1170	24.97	52.06	22.97	0	A/a-m(r)
-5/1202	25.55	45.74	28.71	0	A/a-m(r)

*a-m(r) is an allele known to respond to En. In the absence of En a colorless phenotype is produced but in its presence spots appear on a colorless background.

absolutely no dots, indicating that the cause of the spotting was not a Dt-like element. This ear showed 25% spotted kernels. The remaining 4 ears segregated approximately 25% colored, 50% spotted and 25% colorless round kernels, with the spotted ones showing two different patterns: fine, very high, clear (f, v.hi, cl = small spots with a very high frequency on a clear background) and fine, medium, pale (f, m, pale - small spots with a medium frequency on a pale to dark background). It is hypothesized that the spotting is due to an En (Spm) element to which both a-m(r) and a particular A allele (originating from the a2 bt/a2 bt tester stock) are responsive.

The involvement of En in this spotting behavior was confirmed by the following crosses, utilizing a-m(r) --a specific tester for En. Plants from colorless-round kernels isolated from 4 1140-2/1167 when crossed by numbered a-dt sh2/a-dt sh2 plants from 4 1140-1/1167, which were tested for En presence with a standard En tester, a-m(r)/a-m(r), showed that each case of confirmed En activity was associated with spotted kernels. Conversely, when En was absent no spotted progeny were obtained.

From the cross initially segregating spotted progeny (a-m(r)/a-dt sh, A2/A2 x A/A, a2 bt/a2 bt) two classes of kernel pattern types observed among the spotted class were tested for a allele content by crossing by a-dt sh2/a-dt sh2. In all cases, those with the very high spot frequency were A/a-m(r) whereas those with the medium frequency were A/a-dt sh2, indicating a differential expression resulting from the two genotypes.

This En-responsive A allele is designated A-m(r) and the En is designated En-A-m(r). In the absence of En-A-m(r) the phenotype of A-m(r) is full-color, but in its presence the level of action of A-m(r) is reduced to a pale background. When a mutational event occurs full A expression results, producing a phenotype consisting of full-colored spots on a pale to dark background.

The origin of the En element was initially believed to be the Fcu-containing Colombia Cuna maize population known to possess a very weak En (small and very infrequent spots with standard a-m(r)) but which occasionally changes in activity resulting in a very high frequency of spots with a-m(r). However, this interpretation seems invalid for the following reason. When spotted progeny from the crosses listed in Table 1 are crossed by the a2 bt/a2 bt tester from which A-m(r) was extracted, spotted kernels are again isolated. When these spotted progeny are testcrossed by a-dt sh2/a-dt sh2, ears segregating what appears to be homozygous En are obtained. No such behavior is observed when only a-dt sh2/a-dt sh2 is

recurrently used. It appears, therefore, that this particular a2 bt/a2 bt stock is not only the donor of A-m(r) but also of the En. This is presently being tested.

A-m(r) is not responsive to all En elements as revealed by the negative results with a different En source, nor are all A alleles responsive to En-A-m(r). Thus, A-m(r)-En-A-m(r) represents a quasi-specific interaction.

Jaime Gonella and Peter A. Peterson

R-mo(cu), a new allele of the Fcu controlling-element system

In the course of investigations of the Fcu controlling-element system (Abstracts 1975 International Maize Symposium) a new allele at the R locus was uncovered. Of three crosses of the type C/c sh wx, R/r-cu x r/r, wx/wx (where the R allele in the female parent came from a previous cross by a c sh wx/c sh wx tester stock) one ear showed an unusual phenotypic segregation consisting of the following three kernel types: colorless, a variously expressed dilute, and mottled kernels. The first two classes were expected based on the variable expression of r-cu, which produces a continuous range of phenotypes from colorless to seemingly fully colored (MGNL 48:66-68 and the 4th section of this report). The mottled class, however, was not expected.

The three phenotypic classes from the unusual phenotypic segregation were used to test the basis for the allele conditioning the mottled behavior. The colorless progeny were testcrossed by r/r, wx/wx producing 14 progeny ears: 6 segregated dilute and colorless kernels (ear genotype r-cu/r); the other 8 showed mottled and colorless phenotypes (ear genotype R-mo(cu)/r). The test crosses of the dilute sibs gave only dilute and colorless kernels. The segregation of the mottled sibs is given in Table 1.

Table 1. Phenotypic segregation from testcrosses of mottled progeny, R-mo(cu)/r x r/r, wx/wx.

Cross	Colorless	Mottled	Total
'4 1037-1/1235	209 (78.28)	58 (21.72)	267
-2/36A36	309 (77.64)	89 (22.36)	398
-3/1235	421 (82.87)	87 (17.13)	508
-4/1238	330 (79.90)	83 (20.10)	413
-5/1235	245 (53.73)	211 (46.27)	456
-6/36A34	368 (67.28)	179 (32.72)	547
-7/1236	239 (64.77)	130 (35.23)	309
-8/1239	216 (70.36)	91 (29.64)	307

It can be observed from the table that no consistent segregations were obtained when the mottled class of kernels was tested. It was suspected, however, that the cause of the erratic behavior might be the particular r tester used. Accordingly, mottled progeny were selected and crossed by either W22 r-g/r-g or the r/r, wx/wx tester with the resulting data in Table 2. None of the crosses by W22 r-g/r-g gave a Chi-square value significant at the 0.05 level for a 1 mottled:1 colorless segregation. However, the deviations from 1:1 were very highly significant when the r/r, wx/wx tester was used. This R allele conditioning a mottled phenotype will be designated R-mo(cu), where mo identifies the mottled behavior and cu indicates that it responds to Fcu. Proof for this is now presented.

The possibility that R-mo(cu) responds to Fcu signals was tested by crossing mottled progeny (R-mo(cu)/r) by plants identified for the presence or absence of Fcu (determined with an Fcu tester stock - r-cu/r). The findings are presented in Table 3. The results show that the presence of Fcu in the male parent is associated with variegation and conversely, no variegation occurs when the male parent lacks Fcu. It is concluded that R-mo(cu) is an allele of the Fcu controlling-