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1. *En* at the mutable locus, a_1^m.

The identification of the regulatory element *En* at a mutable locus can be facilitated by the diversity of the forms of mutability that exist. Among the diverse mutable alleles, one that mutates to a readily identifiable mixture of pale and deep purple dots a_1^m (p and p) is available. Colorless forms, noted as $a^{m(r)}$, also exist and these respond to the presence of *En* in a predictably recognizable manner (Peterson, Genetics 1961). When a heterozygote is made between a_1^m (p and p) and $a_1^{m(r)}$ the resulting expression is a very heavily mutable form showing the effect of *En* on $a_1^{m(r)}$. Proof that it is the *En* of the $a_1^{m(p\text{ and }p)}$ allele that is causing the mutability is obtained by testcrossing the heterozygote (by *a1sh*/*a1sh*). The resulting progeny shows the separation of kernels -- 1/2 of which are pale and purple dotting and 1/2 are colorless, $a_1^{m(r)}$, since the *En* is coupled with the $a_1^{m(p\text{ and }p)}$ allele. A small percentage of exceptions appear and these will be discussed in the next section.

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2. Changes at the $a_1^{m(p\text{ and }p)}$ allele: The status of *En*.

Among the progeny arising from testcrosses (by *a1sh*/*a1sh*) of the $a_1^{m(p\text{ and }p)}$ allele, stable non-dotting pale types ($a^{p(nr)}$) and colorless types ($a^{m(nr)}$)* are observed. It has previously been reported (Peterson, 1961 Genetics) that the colorless types do not respond to the presence of *En* and are designated $a_1^{m(nr)}$. Similarly, the pales do not respond to the presence of *En* and are therefore *nr* (non-responding) types. If these derivatives are canvassed for the presence of *En*, it is found that they invariably do possess *En*. In crosses of $a^{p(nr)}$ and $a^{m(nr)}$ by $a^{m(r)}$ (*Cross #1*), mutability is observed in the heterozygote. In testcrossing these heterozygotes -- $a^{p(nr)}$*/$a^{m(r)}$* x *a1sh*/*a1sh* (*Cross #2*) -- a variable percentage of mutable kernels results. These mutable kernels represent the effect of *En* on the $a_1^{m(r)}$ allele. This would indicate that the *nr* kernels possess *En* in coupling $a_1^{p(nr)}$ *En* and the distance between $a_1^{p(nr)}$ and *En* is proportional to the frequency of mutable kernels that arose from *Cross #2***.

This position of En can be verified by resubmitting these mutable kernels to a further testcross -- Cross #3 (dotted kernels Sh/$a_1$sh x $a_1$sh/$a_1$sh). In the progeny of Cross #3 the frequency of colorless Sh kernels should equal the frequency of mutable kernels in Cross #2 described above.

Examples of Cross #2: a_1^{p} Sh/$a_1^{m(r)}$Sh x $a_1$sh/$a_1$sh

	(A) colorless Sh	(B) pale-stable Sh	(C) purple dots on colorless bkgd Sh	C / A + C %
3 92-3	45	69	9	16.6
3 92-4	58	68	6	9.4

Examples of Cross #3: dotted from column (C) above

	colorless Sh	%	dotted Sh	
4 107-3	10	5.05	168	from '3 923**
4 108-1	16	10.9	131	from '3 924

There is some agreement between the expected results from Cross #3 when related to those of Cross #2. This would indicate that En is relocated on the chromosome associated with the mutable locus following the change from a^{p} and p to pale-stable. This would agree with the results of previous workers on the probable site of the relocation of controlling elements following a mutation event (Van Schaik and Brink, 1959 Genetics) and (Greenblatt and Brink, 1962 Genetics).

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* Unless indicated (by sh) the kernel types are non-shrunken (Sh).

** The colorless sh kernels represent ½ of the segregating ear and are not included in the data. The a_1^{dt} does not respond to En. The reciprocal cross-over event yielding an a_1 sh En linkage cannot be detected in this cross.

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