

heterozygotes with  $\underline{r}^{\underline{G}_M^{st}}$  (test) and  $\underline{r}^{\underline{G}_+}$  (control). Because the three selections gave similar results the data have been bulked.

(a) Instability in the seedling. Five hundred seedlings of genotype  $(\underline{PI}^R \underline{Nc})_+ / \underline{r}^{\underline{G}_M^{st}}$  and 500 of genotype  $(\underline{PI}^R \underline{Nc})_+ / \underline{r}^{\underline{G}_+}$  were scored for presence of pigmented sectors in coleoptile and roots:

<u>Genotype</u>	<u>Seedlings with red sectors</u>	
	<u>Number</u>	<u>%</u>
$(\underline{PI}^R \underline{Nc})_+ / \underline{r}^{\underline{G}_M^{st}}$	77	15.4
$(\underline{PI}^R \underline{Nc})_+ / \underline{r}^{\underline{G}_+}$	21	4.2

The effect of  $\underline{M}^{st}$  was significant ( $P < 0.01$ ).

(b) Instability in the tassel. Separate populations of plants with genotypes identical to those in Part (a) were grown to maturity and the anthers scored for presence or absence of pigmented sectors:

<u>Genotype</u>	<u>Fraction of plants with anther sectors</u>
$(\underline{PI}^R \underline{Nc})_+ / \underline{r}^{\underline{G}_M^{st}}$	46/48
$(\underline{PI}^R \underline{Nc})_+ / \underline{r}^{\underline{G}_+}$	0/93

Anther sectoring occurred exclusively in the  $\underline{M}^{st}$  class. This supports the seedling observations in confirming that plant color instability of  $(\underline{PI}^R \underline{Nc})$  is of the same fundamental nature as seed spotting of  $\underline{R}^{st}$ .

Although anther sectors were small, encompassing four anthers at most, a one-generation test for  $\underline{M}^{st}$  in  $\underline{r}^{\underline{G}}$  stocks is now available.

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#### 4. Effect of hemizyosity on germinal mutation in the R-stippled and mutable R-Navajo systems.

In a limited test of plants hemizygous for  $\underline{R}^{st}$  (i.e., those having an  $\underline{R}^{st}$ -bearing standard chromosome 10 but the  $10^B$  chromosome of translocation B-10a in place of the normal homologue) Kermicle (1970\*) obtained a self-colored ( $\underline{R}^{sc}$ ) mutation frequency of  $39 \times 10^{-4}$ , while plants heterozygous  $\underline{R}^{st} / \underline{r}^r$  (W22 source) gave a value of only  $16.2 \times 10^{-4}$ . In neither case was mutation to  $\underline{R}^{sc}$  related to crossing over at meiosis.

This suggested that hemizygoty may lead to an increased rate of transposition of the element  $\underline{I}^R$  away from the  $\underline{R}$ -locus and, conceivably, this could be a general characteristic of transposable elements. Thus, an experiment was performed to compare the effect of hemizygoty on  $\underline{R}^{st}$  with that on the mutable-Navajo ( $\underline{mR}^{nj}$ ) system which is controlled by the transposable element, Modulator (I. M. Greenblatt, pers. comm.). The systems were tested in hemizygous condition and in heterozygotes with  $\underline{r}^G$ .

Plants hemizygous for the respective alleles were derived by pollinating  $\underline{R}^{st}\underline{M}^{st}$  and  $\underline{mR}^{nj}$  stocks of inbred W23 with material homozygous for translocation B-10a carrying  $\underline{R}_6^G$ . In the inbred W22 strain of B-10a employed, nondisjunction of the  $B^{10}$  element of the translocation occurs regularly at second pollen grain mitosis, giving one hypoploid and one hyperploid male gamete within the same male gametophyte. Since the  $\underline{R}$  locus is carried by  $B^{10}$ , one sperm lacks  $\underline{R}$  while the other carries two doses. Recognition of progeny kernels carrying hypoploid  $\underline{R}^{st}/-$  and  $\underline{mR}^{nj}/-$  embryos was facilitated by observation of their associated hyperploid endosperms marked by  $\underline{R}_6^G$ . Because the hypoploid plants so generated were W23 x W22 hybrids they were vigorous and, although retarded relative to normal plants and semi-sterile, nevertheless yielded on the average more than 225 kernels per ear.

Corresponding  $\underline{R}^{st}/\underline{r}^G$  and  $\underline{mR}^{nj}/\underline{r}^G$  heterozygotes were derived in a parallel fashion by use of W22  $\underline{r}^G$  pollen parents.

The hemizygous and heterozygous combinations were hand-pollinated with a W23  $\underline{ACr}^G$  stock.  $\underline{R}^{sc}$  and  $\underline{R}^{nj}$  selections from the resulting kernel population were grown and the mutant phenotypes tested for heritability by pollinating with a  $\underline{r}^G$  stock.

$\underline{R}^{st}$  hemizygous plants ( $\underline{R}^{st}/-$ ) yielded  $\underline{R}^{sc}$  mutants at a frequency of 37 per  $10^4$  gametes, while  $\underline{R}^{st}/\underline{r}^G$  material produced 16.5 per  $10^4$  gametes. The difference was statistically significant ( $P < 0.001$ ):

<u>Parental genotype</u>	<u>Number of <math>\underline{R}^{st}</math> gametes tested</u>	<u>Number of confirmed <math>\underline{R}^{sc}</math> derivatives</u>	<u>Frequency of <math>\underline{R}^{sc}</math> mutation</u>
$\underline{R}^{st}/-$	37,940	142	$37.4 \times 10^{-4}$
$\underline{R}^{st}/\underline{r}^G$	46,560	77	$16.5 \times 10^{-4}$

As with  $\underline{R}^{st}$ , mutable-Navajo showed a higher yield of germinal mutants per gamete tested in the hemizygous state than in the heterozygous state although the relative difference was not as large. Analysis of the mutable  $\underline{R}^{nj}$  data was complicated by two factors not encountered in the  $\underline{R}^{st}$  study. First, a number of somatic sectors involving mutation from  $\underline{mR}^{nj}$  to  $\underline{R}^{nj}$  occurred. Any confirmed sector of three or more kernels in size was counted as a single event. Associations of two kernels were not regarded as sectors but were considered, for the purposes of this experiment, as two independent events. Fewer than five sectors occurred in each genotype. Secondly, besides parental-type kernels and  $\underline{R}^{nj}$  revertants there was, on each ear, a class of 'light' mutable-Navajo kernels. No quantitative separation of the 'light'  $\underline{mR}^{nj}$  kernels was made because the phenotype overlapped with the parental types. A sample was progeny tested and found to be a heterogeneous collection of types, mostly lighter in aleurone phenotype than standard  $\underline{mR}^{nj}$ . Tests of their capacities to cause  $\underline{Ds}$ -induced breakage in an  $\underline{IDs}$  tester stock revealed that such 'light'  $\underline{mR}^{nj}$  types carried a second dose of Modulator in their genomes and are thus the counterpart of light variegated pericarp in this respect. For the purposes of the present experiment these derivatives were included as part of the total population of gametes tested. No attempt was made to determine whether they were equally represented in the two test groups.

The material was grown in two separate tests in different years.  $\chi^2$  tests indicated that the  $\underline{R}^{nj}$  frequencies for each genotype in the two years were not significantly different. The data for the two tests were thus bulked. Hemizygous  $\underline{mR}^{nj}/-$  produced a significantly higher frequency of  $\underline{R}^{nj}$  mutants than did heterozygous  $\underline{mR}^{nj}/\underline{r}^g$  ( $\chi^2 = 6.55$ ;  $P < 0.025$ ):

	Parental genotype	Number of $\underline{mR}^{nj}$ gametes tested	Number of confirmed $\underline{R}^{nj}$ mutations	Frequency of $\underline{R}^{nj}$ mutation
First test	$\left\{ \begin{array}{l} \underline{mR}^{nj}/- \\ \underline{mR}^{nj}/\underline{r}^g \end{array} \right.$	3,280	182	$5.6 \times 10^{-2}$
		4,000	180	$4.5 \times 10^{-2}$
Second test	$\left\{ \begin{array}{l} \underline{mR}^{nj}/- \\ \underline{mR}^{nj}/\underline{r}^g \end{array} \right.$	2,437	110	$4.5 \times 10^{-2}$
		5,200	206	$4.0 \times 10^{-2}$
Total	$\left\{ \begin{array}{l} \underline{mR}^{nj}/- \\ \underline{mR}^{nj}/\underline{r}^g \end{array} \right.$	<u>5,717</u>	<u>292</u>	<u><math>5.1 \times 10^{-2}</math></u>
		<u>9,200</u>	<u>386</u>	<u><math>4.2 \times 10^{-2}</math></u>

It is apparent that hemizyosity has a marked effect on mutation of  $\underline{R}^{\text{st}}$  to  $\underline{R}^{\text{sc}}$ , and probably also causes an increase in mutation of  $\underline{mR}^{\text{nj}}$  to  $\underline{R}^{\text{nj}}$ . Further study to determine whether this is a response common to autonomous transposable elements would seem to be justified.

We do not know what property of hemizyosity is responsible for the observed effect. The mutations under study were mostly single kernel events - implying transposition at, or very near, meiosis. Conceivably then, the processes of meiotic chromosome pairing may be involved in some way. Further information on this point may be obtainable from more extensive study of the  $\underline{mR}^{\text{nj}}$  system, which gives a significant frequency of somatic sectors. If only meiotic chromosome pairing is involved then no effect of hemizyosity on somatic mutation rate should be found.

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##### 5. Tandem and displaced duplications in the distal end of 10L.

The  $\underline{R}$  locus, which is essential for anthocyanin pigmentation in certain plant and seed tissues, is located in the distal one-fifth of the long arm of chromosome 10. The first allele of this locus to be extensively studied,  $\underline{R}^{\text{F}}$  (Cornell or standard), was found to be associated with a tandem duplication. The proximal member of the duplication carries  $\underline{P}$ , the plant pigmenting determiner, while the distal member carries  $\underline{S}$ , the seed pigmenting determiner.

$\underline{Lc}$  is the designation given to a leaf color factor extracted from the  $\underline{R}^{\text{F}}$ -Ecuador 1172 strain.  $\underline{Lc}$  maps distal to the  $\underline{R}$  locus, and shows between 1 and 2% recombination with it. A large number of seedling and plant tissues are pigmented by the action of  $\underline{Lc}$ : coleoptile, blade joint, roots (weakly), nodes, silks, pericarp, and leaf blade. Strong pigmentation of the first blade joint allows one to screen for the presence or absence of  $\underline{Lc}$  at the seedling stage, even in the presence of  $\underline{P}$  of  $\underline{R}^{\text{F}}$ . One of the adult plant tissues, on the other hand, that is most conspicuously pigmented by  $\underline{Lc}$  is the leaf blade. Hence its name  $\underline{Lc}$  (leaf color). An extensive study aimed at fractionating the  $\underline{Lc}$  compound phenotype yielded negative results.