A higher proportion of tests of divergence between homologous segments was observed to be significant ($p \leq 0.05$) when the genome contained large segments of heterochromatin (B chromosome or K10). This proportion was greatly reduced by removing the extra heterochromatin, or by raising the temperature. While the proportion of significant tests of concordance was relatively low, it remained independent of the presence of extra heterochromatin.

While the tests themselves have been deemed valid, we are still assessing the objectivity of the test criteria in terms of the more general hypothesis of synchrony. We are extending our study to include specific translocation stocks as an experimental input to provide a further, more vigorous test of synchrony and autonomy of DNA replication.

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1. Effect of $\underline{M}^{st}$ on mutation of $\underline{R}^{st-f}$, a modified form of the $\underline{R}^{st}$ (Wisconsin) allele.

The effect of $\underline{M}^{st}$ (modifier of $\underline{R}^{st}$) on $\underline{R}^{st}$ to $\underline{R}^{sc}$ (self-colored) mutation in the aleurone is to increase the frequency of late occurring mutational events. Kernels with equal dosage of $\underline{R}^{st}$ appear much darker if they also carry $\underline{M}^{st}$ in the genome than if they don't. On the other hand, the frequency of corresponding colored aleurone and colored embryo kernels (a class which includes mutations of $\underline{R}^{st}$ to $\underline{R}^{sc}$ occurring from meiosis up to and including the second megagametophyte division) does not appear to be influenced by $\underline{M}^{st}$. Likewise, the available data do not show any effect of $\underline{M}^{st}$ on the frequency of kernels having non-corresponding aleurone and embryo phenotypes (a class representing mutations of $\underline{R}^{st}$ to $\underline{R}^{sc}$ at any of the three megagametophytic divisions). Therefore, the control of mutation of $\underline{R}^{st}$ to $\underline{R}^{sc}$ exerted by $\underline{M}^{st}$ appears to be limited to a specific tissue (the aleurone) and a specific time in the development of this tissue (late divisions).

Several derivatives of $\underline{R}^{st}$ showing a heritably modified aleurone phenotype have been isolated. One of these responds to $\underline{M}^{st}$ in an

altered fashion: $\underline{R}^{st}$ to $\underline{R}^{sc}$ mutations in the aleurone tend to be suppressed until a very late developmental stage. As a consequence, kernels with the modified $\underline{R}^{st}$ and $\underline{M}^{st}$ show only small, fine spots in the aleurone. This new form of $\underline{R}^{st}$ has been designated $\underline{R}^{st-f}$ ($\underline{R}$-stippled fine). The effect of $\underline{M}^{st}$ upon $\underline{R}^{st-f}$ is no longer limited to a specific time in the development of the aleurone since it now displays an early suppressing effect in addition to its standard late-mutating effect.

With the intent of studying the effect of $\underline{M}^{st}$ on megagametophytic mutation of $\underline{R}^{st-f}$ to $\underline{R}^{sc}$ the following crosses were performed:

$$\underline{R}^{st-f}\ \underline{M}^{st}\ \underline{+}^{\varphi} \times \underline{r}^{g}\ \underline{+}\ \sigma^{\prime}$$

$$\underline{R}^{st-f}\ \underline{+}^{\varphi} \times \underline{r}^{g}\ \underline{+}\ \sigma^{\prime}$$

The results are reported in the following table.

Phenotype of selection	Origin	Embryo classification by progeny test		Effective population
		$\underline{R}^{sc}$	$\underline{R}^{st}$	
Colored aleurone	$\underline{R}^{st-f}\ \underline{M}^{st}$	57 (17.2)[1]	1 (0.3)	33,510
Unselected embryo	$\underline{R}^{st-f}\ \underline{+}$	78 (33.8)	48 (20.8)	23,075
Stippled aleurone	$\underline{R}^{st-f}\ \underline{M}^{st}$	- (nil)	- (nil)	44,200
Colored embryo	$\underline{R}^{st-f}\ \underline{+}$	8 (4.1)	3	19,415

[1]Numbers in parentheses represent frequencies x 10^{-4}.

Two major observations can be made from the data reported in the table:

1) Kernels of non-corresponding aleurone and embryo phenotypes are essentially not recovered in the progeny from $\underline{R}^{st-f}\ \underline{M}^{st} \times \underline{r}^{g}\ \underline{+}$ crosses, whereas they occur quite frequently in the progeny from $\underline{R}^{st-f}\ \underline{+} \times \underline{r}^{g}\ \underline{+}$ crosses.

2) The frequency of corresponding colored aleurone and embryo kernels is much higher when the female parent is $\underline{R}^{st\text{-}f}$ $\pm$ than when it is $\underline{R}^{st\text{-}f}$ $\underline{M}^{st}$.

Both observations suggest that the effect of $\underline{M}^{st}$ is to eliminate mutation of $\underline{R}^{st\text{-}f}$ to $\underline{R}^{sc}$ in the female gametophyte. A comparison of the frequencies of the different kernel classes lends support to this interpretation. Mutation of $\underline{R}^{st\text{-}f}$ $\pm$ to $\underline{R}^{sc}$ at the third megagametophyte division should account for all the cases of stippled aleurone, colored embryo kernels and for twice as many colored aleurone, stippled embryo kernels. Thus, of the 20.8 cases of the latter per 10,000 kernels, 8.2 would be accounted for by mutation at the third division and 12.6 by mutation at either the first or second division. Likewise, since mutation of $\underline{R}^{st\text{-}f}$ $\pm$ to $\underline{R}^{sc}$ at either the first or second division should account for an equal number of the two classes of colored aleurone kernels (with corresponding embryo and non-corresponding embryo), 12.6 cases of the corresponding colored aleurone and embryo class for every 10,000 kernels would be due to mutation at either of the two early divisions. This leaves a residue of 21.2 cases of the latter class per 10,000 kernels to be explained. Since $\underline{R}^{sc}$ mutations do not occur in clusters in the ears, the most likely explanation for these remaining cases is that they arise during meiosis. The residual frequency of 21.2×10^{-4} agrees with the frequency of corresponding colored aleurone and embryo kernels obtained from $\underline{R}^{st\text{-}f}$ $\underline{M}^{st}$ (17.2×10^{-4}). This comparison suggests that all such mutants have a meiotic origin in $\underline{R}^{st\text{-}f}$ $\underline{M}^{st}$ females and lends support to the belief that few to no megagametophytic mutations occur in $\underline{R}^{st\text{-}f}$ $\underline{M}^{st}$ plants. However, if the above value represents the true frequency of $\underline{R}^{st\text{-}f}$ to $\underline{R}^{sc}$ meiotic mutations, then this frequency has been significantly increased above that normally obtained in standard $\underline{R}^{st}$ (Wisconsin) homozygotes.

The change of $\underline{R}^{st}$ to $\underline{R}^{st\text{-}f}$ appears, therefore, to have brought an increase in the frequency of $\underline{R}^{sc}$ mutations of meiotic origin in homozygotes and a new response to the action of $\underline{M}^{st}$, namely the complete suppression of post-meiotic $\underline{R}^{sc}$ mutations till a very late stage in aleurone development. Possibly, $\underline{R}^{st\text{-}f}$ represents a new relationship between the Sc and I^R components of the $\underline{R}^{st}$ allele.

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