

2. The smoky and light smoky derivatives of  $R^{st}$ .

## A. Genetic control of their phenotype

These two stippled alleles were first isolated on ears obtained from the cross  $R^{st}R^{st}lMp \times r^r r^r$ . Both the alleles, designated  $R^{sk}$  and  $R^{l.sk.}$ , breed true and are highly paramutagenic. They are easily distinguishable on the basis of their aleurone phenotype and of their frequency of reversion to  $R^{sc}$  in the germinal tissues ( $8.4 \times 10^{-4}$  for  $R^{sk}$  and  $0 \times 10^{-4}$  for  $R^{l.sk.}$ ). Since both these alleles were first isolated from an  $R^{st}$  line carrying  $M^{st}$ , the possibility arises that they are the result of a change of  $M^{st}$  rather than a change at the  $R$  locus.  $M^{st}$  is a Modifier of  $R^{st}$ , lying 5.7 units distal to it, whose presence increases the number of dark spots in the stippled aleurone. Loss of  $M^{st}$  through crossing over leads to a reduction in the number of spots, thus giving rise to a light stippled phenotype.

This possibility has been tested by crossing both  $R^{sk}$  and  $R^{l.sk.}$  with a homozygous  $g R^{st}m^{st}/g R^{st}m^{st}$  tester. The two heterozygous combinations have then been crossed with  $g rEm^{st}/g rEm^{st}$  plants. If the smoky and light smoky phenotypes reflect a change at the  $R$  locus, rather than a change of  $M^{st}$ , they should still carry an unchanged  $M^{st}$ . The presence of this Modifier can be inferred from the production of a few stippled recombinants among the light stippled segregants in the testcross ears. The results of the crosses performed are reported in Table 1.

Table 1  
Results of the crosses performed to establish whether  $R^{sk}$  and  $R^{l.sk.}$  carry an unchanged  $M^{st}$  along their chromosome

Pedigree	Pistillate parent genotype	Observed segregations	Estimated $R-M^{st}$ c.o. value (%)
g1314 x g1201A	$g R^{st} m^{st} / G R^{sk} (*)$	137 smoky 140 l.st. 10 st.	6.6
g1315 x g1313	$g R^{st} m^{st} / G R^{l.sk.} (*)$	276 l.smoky 257 l.st. 23 st.	8.2

\* $M^{st}$  presence to be tested.

The appearance of the recombinant stippled kernels, besides the two parental types, shows that both  $R^{sk}$  and  $R^{l.sk.}$  carry along their chromosome an unchanged  $M^{st}$  in its standard position. It then appears that the alteration in phenotypic expression of these two stippled derivatives reflects a change at the  $R$  locus. These observations also disclose a specificity of action of  $M^{st}$ .

B. Germinal transmission of the smoky derivatives of  $\underline{R}^{1.sk.}$ .

The aleurone of kernels carrying two or three doses of the  $\underline{R}^{1.sk.}$  allele often shows sectors of variable size exhibiting the darker phenotype conditioned by  $\underline{R}^{sk.}$ . In some cases these sectors cover the whole endosperm.

In order to test the germinal transmission of the smoky derivatives of  $\underline{R}^{1.sk.}$ , the following cross has been performed:  $\underline{G} \underline{R}^{1.sk.} / \underline{g} \underline{r}^g \times \underline{g} \underline{r}^g / \underline{g} \underline{r}^g$ . This cross gave 6739 light smoky kernels and 51 with the whole aleurone phenotypically smoky. Twenty-one of them have been progeny tested. The results of the progeny tests are shown in the table below.

Table 2  
Sporophyte constitution of 21 smoky derivatives of  $\underline{R}^{1.sk.}$  obtained from the cross  $\underline{G} \underline{R}^{1.sk.} / \underline{g} \underline{r}^g \times \underline{g} \underline{r}^g / \underline{g} \underline{r}^g$  as determined by progeny tests.

$\underline{g} \underline{R}^{1.sk.}$	$\underline{G} \underline{R}^{1.sk.}$	$\underline{g} \underline{R}^{sk.}$	$\underline{G} \underline{R}^{sk.}$
5	10	2	4

These results indicate that:

1. Germinal transmission of the smoky derivative is very low (28.57%). This suggests that a large percentage of the smoky derivatives shows a phenotypic change limited to the endosperm tissues. After correction for lack of germinal transmission the rate of origin of smoky in the sample tested is 0.21%.
2. The data also provide some evidence of the lack of association between the change from light smoky to smoky and proximal crossing over. In fact, assuming a crossover value of 14% between  $\underline{g}$  and  $\underline{R}$ , the expected number of recombinants in the sample tested would be 2.94 (the upper and lower limits of expectation, according to Stevens method, being 3.06 and 11.7). The observed number of recombinants is 7 out of 21.

The smoky derivatives of  $\underline{R}^{1.sk.}$  could be envisaged as either the result of a change at the  $\underline{R}$  locus or the consequence of recombination between  $\underline{R}^{1.sk.}$  and a closely linked Modifier. One needs suitable markers flanking  $\underline{R}$  to discriminate between these two possibilities and stocks are being prepared for this purpose.

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