

somewhat blunted leaves which are wider than normal siblings. The mature compact plant develops to at least three feet in height, or to nearly 50 per cent of the height of normal siblings; the internode number is the same, but the average internode length is two inches shorter than in the normal siblings. The shortened internode length is evident throughout the mutant plant and is not confined to those internodes below the ear node. The mutant plants have enlarged stalks. The ear is reduced in size and the tassel is compacted, but pollen is shed abundantly and ears are produced on most plants.

Intercrosses were made with thick-tassel-dwarf (ttd) in chromosome 5, Hy-rd and ct obtained from Dr. O. E. Nelson, none of which gave a positive allele test. Phenotypically the mutant appeared not to be similar to d₁ or d₂ in chromosome 3, or br₁ in chromosome 1.

The mutant was crossed to a waxy marked chromosome-nine translocation series involving all chromosomes and F₂ waxy seeds were screened. All F₂ populations showed normal 3:1 segregation except those involving the wx 1-9c (1S.48, 9L.22) and wx 1-9⁴⁹⁹⁵ (1L.19, 9S.20) interchanges in which the following data were collected. Waxy seeds from 4 families involving the cross with wx 1-9c gave 57 normal : 7 compact plants, and waxy seeds from 3 families involving the cross with wx 1-9⁴⁹⁹⁵ gave 74 normal : 14 compact plants. These data gave indications of linkage only with chromosome 1. This mutant is tentatively designated codw.

Dwarfs such as midget 8043, tiny 8446, dwarf 4963 and others have been associated with chromosome 1, but the codw phenotype is not similar. A test of allelism with br₁ has not been made. Its position in relation to the known markers on this chromosome is at present uncertain.

David V. Glover

PURDUE UNIVERSITY
Lafayette, Indiana
Department of Botany and Plant Pathology

1. Frequency of R^{st} to self colored (R^{sc}) aleurone mutations.

Early in the studies of paramutation at the R locus it was observed that Rst mutated to R^{sc}, and the frequency of such mutations has been reported by several investigators. The results from recent tests, together with some previously reported, are brought together in Table 1. The frequencies shown are the number of verified R^{sc} mutations over the number of stippled gametes tested. Where verification of self colored kernels was not accomplished the number of stippled gametes tested was proportionately reduced. The number of kernels scored was determined by actual counts or estimated from the weight of a sample of 500 to 1000 kernels from each family.

Certain of the allelic combinations have been tested more than once, and the number of tests and pooled frequency are shown in Table 1. Prior to pooling, the limits of expectation were calculated for each test and in

Table 1
 Frequency of mutation of R^{st} to R^{sc} when homozygous and when heterozygous
 with several other alleles and in male and female gametes

Allelic combinations	No. of tests	R^{sc} frequency	Rate $\times 10^{-4}$	Limits of expectation (P=.05)	
				lower	upper
<u>Female Gametes</u>					
$R^{st} M^{st}/R^{st} M^{st}$	2	41/ 23,830	17.2	12.3	23.3
$R^{st} + /R^{st} +$	3	129/ 60,576	21.3	17.8	25.3
$R^{st} M^{st}/R^{st} +$	1	67/ 30,898	21.6	16.8	27.5
Pooled		237/115,304	20.5	18.0	23.3
$R^{st} M^{st}/R^r +$	3	53/ 28,545	18.6	13.9	24.3
$R^{st} M^{st}/r^r +$	1	1/ 2,055	-	-	-
$R^{st} + /r^r +$	3	23/ 23,406	9.8		
Pooled		24/ 25,461	9.4	6.0	14.0
$R^{st} M^{st}/r^g +$	1	14/ 19,239	7.3	4.0	12.2
$R^{st} + /r^g +$	2	10/ 13,078	7.6	3.7	14.1
Pooled		24/ 32,317	7.4	4.8	11.0
<u>Male Gametes</u>					
$R^{st} M^{st}/R^{st} M^{st}$	3	390/ 92,122	42.3	38.2	46.7
$R^{st} M^{st}/R^r +$	1	59/ 30,400	19.4	14.8	25.0
$R^{st} M^{st}/r^r +$	1	53/ 30,236	17.5	13.1	22.9
$R^{st} M^{st}/R^{st} M^{st}/r^g +$ (trisomic)	1	132/ 29,710	44.4	37.2	52.7

no case did different tests of the same allelic combination give significantly different estimates of the mutation rate.

The general procedure in all tests of female gametes was to pollinate with an $\underline{r} \underline{r}$ stock carrying a marker gene or genes at other loci to aid in identifying mutant phenotypes attributable to pollen contamination. The self colored kernels were grown out to verify a germinal mutation. In tests of female gametes only about 50% of the self colored kernels proved to be germinally $\underline{R}^{\text{sc}}$, the remainder being $\underline{R}^{\text{st}}$. $\underline{R}^{\text{sc}}$ mutations also are known to occur only in the germ, giving a kernel with an $\underline{R}^{\text{sc}}$ germ but a stippled aleurone; no mutations of this exceptional type are included in the Table 1 data. It is assumed that self color mutants borne singly on an ear result from mutations in the basal megaspore, or during or just prior to megasporogenesis, and that kernels with noncorresponding endosperms and germs result from mutations which occur during formation of the female gametophyte. Rarely, mutations to $\underline{R}^{\text{sc}}$ occur in somatic tissue to give ear sectors of $\underline{R}^{\text{sc}}$ tissue; such sectors were not included in the mutation rate data.

$\underline{R}^{\text{sc}}$ ear sectors were readily apparent on all but $\underline{R}^{\text{r}} \underline{R}^{\text{st}}$ ears but tassel sectors were not and are a possible source of inflated mutation rate estimates in tests of male gametes. In five of the six tests of male gametes, numbered plants were tested individually without bulking pollen, and mutation rates could be calculated for each plant. The number of gametes tested from each plant was necessarily small, and, consequently, the limits of expectation were large. No significant differences were found between individual male plants in any of the tests, but one $\underline{R}^{\text{r}} \underline{R}^{\text{st}}$ plant gave a mutation rate sufficiently greater than that of other plants in the test so as to make tassel mosaicism suspect; mutations from this plant were not included in the data reported.

Indications of $\underline{R}^{\text{sc}}$ ear sectors on $\underline{R}^{\text{r}} \underline{R}^{\text{st}}$ ears can be obtained by noting the frequency of $\underline{R}^{\text{sc}}$ mutants recovered from each ear. Ears scored in these three tests totaled 191 from which 53 mutants were recovered; one ear yielded three mutants, six ears yielded two, and the remaining 38 mutants occurred singly. There is no evidence in these data of large somatic sectors, and if it were assumed that all mutants had an independent origin, the frequency of ears with more than one mutant does not appear to be greater than would be expected from chance alone.

The tests involved both "stippled" ($\underline{R}^{\text{st}} \underline{M}^{\text{st}}$) and "light stippled" ($\underline{R}^{\text{st}} \underline{+}$), which differ only in the presence or absence, respectively, of a modifier six units distal to the \underline{R} locus. Early data suggested that $\underline{M}^{\text{st}}$ had no effect on the frequency of germinally recoverable $\underline{R}^{\text{st}}$ to $\underline{R}^{\text{sc}}$ mutations, and this is substantiated by the data in Table 1: compare lines 1 and 2, and lines 9 and 10. In the absence of any effect of $\underline{M}^{\text{st}}$ the data from tests of stippled and light stippled were pooled and used to compute a single mutation rate for the various allelic combinations.

In female gametes, $\underline{R}^{\text{st}}$ mutated to $\underline{R}^{\text{sc}}$ more frequently when homozygous than when heterozygous with \underline{r}^{r} or \underline{r}^{g} (lines 4, 8, and 11). The rate in $\underline{R}^{\text{r}} \underline{R}^{\text{st}}$ plants (line 5) was about the same as in $\underline{R}^{\text{st}} \underline{R}^{\text{st}}$ plants and greater than in $\underline{R}^{\text{st}} \underline{r}^{\text{r}}$ and $\underline{R}^{\text{st}} \underline{r}^{\text{g}}$ plants, although the difference between $\underline{R}^{\text{r}} \underline{R}^{\text{st}}$ and

$\underline{R}^{st} \underline{r}^r$ was not quite statistically significant.

The frequency of \underline{R}^{sc} mutations was significantly greater in male than in female gametes in $\underline{R}^{st} \underline{R}^{st}$ plants (line 4 vs. 12), approached significance in $\underline{R}^{st} \underline{r}^r$ plants (line 8 vs. 14), and was clearly not significant in \underline{R}^r plants (line 5 vs. 13).

The frequency of \underline{R}^{sc} mutations was the same in male gametes from $\underline{R}^{st} \underline{R}^{st} \underline{r}^g$ (trisomic) as from $\underline{R}^{st} \underline{R}^{st}$ plants (line 12 vs. 15), which indicates that the greater mutability of \underline{R}^{st} when homozygous than when heterozygous with \underline{r}^g is due to interaction between \underline{R}^{st} alleles in the homozygote rather than to a mutation inhibiting action of \underline{r}^g in the heterozygote.

R. B. Ashman

2. Gene linkages in translocation T9-10a heterozygotes.

Translocation T9-10a (9L.14--10L.92) has been used as a distal marker for \underline{R} in several of our genetic studies, and a test was made to determine the linkage between the translocation and \underline{R} and \underline{M}^{st} on chromosome 10 and \underline{Wx} on chromosome 9.

Kernels from the following cross were classified for stippled and waxy:

$$\begin{array}{c} \underline{r} + \underline{N} \underline{wx} \\ \underline{r} + \underline{N} \underline{wx} \end{array} \quad \times \quad \begin{array}{c} \underline{R}^{st} \underline{M}^{st} \quad \underline{T9-10a} \quad \underline{wx} \\ \underline{r} \quad + \quad \underline{N} \quad \underline{Wx} \end{array}$$

The number of kernels in the two parental classes was 1067 $\underline{R}^{st} \underline{wx}$ and 989 $\underline{r} \underline{Wx}$, and in the two crossover classes 291 $\underline{R}^{st} \underline{Wx}$ and 204 $\underline{r} \underline{wx}$. An excess of \underline{R}^{st} kernels was noted in both the parental and crossover classes. The uniformity of the data was tested in a 2 X 2 contingency table, and the chi-square value was highly significant, indicating inconsistencies within the class frequencies. The excess of $\underline{R}^{st} \underline{Wx}$ kernels is very likely due to the functioning of some $\underline{R}^{st} \underline{Wx}$ duplicate-deficient gametes, since these gametes are deficient for only about 8% of 10L. The $\underline{r} \underline{wx}$ duplicate-deficient gametes would be much less likely to function, since they are deficient for about 86% of 9L. If it is assumed that $\underline{r} \underline{wx}$ duplicate-deficient gametes do not function, the $\underline{r} \underline{wx}$ kernels result only from crossing over, and the percentage of $\underline{R}^{st} \underline{Wx}$ kernels resulting from the functioning of duplicate-deficient gametes can be estimated as $291-204/291=30\%$. Also, if alternate and adjacent-1 disjunction are assumed to occur with equal frequency, it can be estimated that about 7% of the $\underline{R}^{st} \underline{Wx}$ duplicate-deficient gametes produced function through the pollen, even though in competition with normal gametes.

Kernels in the two crossover classes were grown out and the ears classified for the translocation (semi-sterility). Ears from the $\underline{R}^{st} \underline{Wx}$ kernels were also classified for \underline{M}^{st} , which is scorable only in the presence of \underline{R}^{st} . Kernels in the two parental classes ($\underline{R}^{st} \underline{wx}$ and $\underline{r} \underline{Wx}$) were not grown out so no data were obtained on the frequency of double crossovers.

Two adjustments were made in the data before crossover per cents were calculated: (1) the total population was adjusted for the proportion of