

## 2. Stability of $Dt_1$ .

In the same population of self-pollinated ears from which  $Dt_1^T$ 's were derived, % of the ears possessed dotless kernels present either in a very low percentage or accounting for 1/4 of the total. Tests of dotless kernels of different origin are shown in Table 2. Dotless kernel No. 1 proved to have an altered state of  $Dt_1$  activity showing a greatly reduced frequency of aleurone mutations such that frequently no dots were found on an individual kernel. Crosses of plants from dotless kernels Nos. 2-8 with  $dt\ dt$  plants carrying the standard  $a_1$  allele or the highly mutable  $a_1^{m-1}$  found by Nuffer (Nuffer, M. G. 1961. Genetics 46: 625-640) produced only dotless kernels; when crossed with  $a_1^s\ Dt_1$  (the  $a_1^s\ Dt_1$  stock has dotless aleurones since  $a_1^s$  does not mutate in the presence of  $Dt_1$ ), all of the dotless stocks gave  $F_1$  kernels with aleurone mutations with the exception of family No. 6 which produced ears with all dotless kernels, ears segregating for dotted and dotless, and ears with only dotted kernels. Thus, a dotted  $a_1$  allele was present in the dotless stocks and the loss of mutability was attributed to loss of  $Dt_1$  activity. Additional crosses involving family No. 6 substantiated the finding that both a mutable and a stable  $a_1$  allele were present. It is possible that the loss of  $Dt_1$  activity was coincident with a mutation of  $a_1$  to  $a_1^s$ . It is not known whether the families 2-8 have an inactive  $Dt_1$  allele or whether they experienced an actual physical loss of  $Dt_1$ . Numerous sib crosses of the dotless stocks (Table 2) as well as self-pollinations and crosses with  $a_1^{m-1}\ dt$  have produced no reactivation of  $Dt_1$ . The chromosomes 9 of these families, when observed at pachynema, appeared to be normal and had the small terminal knob characteristic of  $Dt_1$  stocks. Several losses of  $Dt_1$  and one mutation of  $a_1$  to  $a_1^s$  accounted for the occurrence of dotless kernels on otherwise  $a_1\ a_1\ Dt_1\ Dt_1$  ears. The apparent discrepancy between this result and those of Rhoades (Rhoades, M. 1941. Cold Spring Harbor Symp. Quant. Biol. 9: 138-144) and Peterson (Peterson, F. 1953. Maize Gen. Coop. News Letter 27: 61), who attributed the dotless kernels to mutations of  $a_1$  to  $a_1^s$ , is probably the result of sampling errors inherent in small populations. It is also possible that the stocks used contained different states of the  $a_1$  and/or  $Dt_1$  alleles, where changes to the inactive  $a_1^s$  and losses of  $Dt_1$  occurred at different rates.

A number of crosses of the type  $a_1\ a_1\ Dt_1\ Dt_1\ \text{♀} \times a_1\ a_1\ dt\ dt\ \text{♂}$  were made. Four ears in a total of about 40 had dotless kernels which were randomly distributed and not in clusters. The proportion of dotless kernels was high on some ears but never accounted for half the kernels. Dotless kernels were also observed on ears of the reciprocal crosses. Thus, in these plants independent losses of  $Dt_1$  (or loss of  $Dt_1$  activity) must have occurred after divergence of the cell lines forming individual ovules in the female parent. In the pollen parent, however, one cannot distinguish between frequent independent losses of  $Dt_1$  and a single event involving a sector of the tassel. The rate of  $Dt_1$  losses cannot be accurately determined since the majority of the ears showed no losses of  $Dt_1$  whatsoever, whereas a few ears had several dotless kernels. A similar distribution was observed with the self-pollinated ears.

It is possible that dotless kernels are the reciprocal product of  $Dt_1$  transpositions; i.e., after a transposition has occurred in a homozygous

Table 2  
Phenotypes of kernels resulting from crosses between dotless types of different origin and tester strains. The dotless types were derived from the selfed progeny of homozygous  $\underline{Dt}_1$  stocks

No.	Dotless families	X $\underline{a}_1^* \underline{sh}_2 \underline{dt}$	X $\underline{a}^m - 1^* \underline{dt}$	X $\underline{a}_1^s \underline{Dt}$	X sib (No. of crosses)
1	741	a few kernels dotted	a few kernels dotted	all kernels dotted	-----
2	743	----	dotless	dotted	dotless (6)
3	744	dotless	dotless	dotted	dotless (4)
4	745	dotless	dotless	dotted	dotless (3)
5	747	dotless	dotless	dotted	dotless (7)
6	748	dotless	dotless	dotless or dotted+	dotless (2)
7	749	dotless	dotless	dotted	-----
8	1255	dotless	dotless	dotted	dotless (2)

\* $\underline{a}_1$ , the standard allele that responds to  $\underline{Dt}$

$\underline{a}^m - 1$ , a highly mutable  $\underline{a}_1$  allele described by Nuffer (1961)

$\underline{a}_1^s$ , an  $\underline{a}_1$  allele that does not respond to  $\underline{Dt}$

+The ears testing individual sib plants were completely dotted, completely dotless, or segregated 1:1.

Dt<sub>1</sub> cell line, ¼ of the gametes derived from the line would contain no Dt.

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### 3. Activation Cycles of Dt<sub>1</sub><sup>TB</sup>

Kernels sectored for dotted expression were first observed among the back-cross progeny of a Dt<sub>1</sub> Yg<sub>2</sub>/dt yg<sub>2</sub>, Dt<sub>1</sub><sup>TB</sup> dt<sup>TB</sup>, a<sup>m-1</sup> a<sup>m-1</sup> plant. Several kernels had no dots at all in the aleurones but were heavily dotted in the scutella. Whereas three-fourths of the kernels were expected to have fully dotted aleurones, the ear contained 172 kernels with uniformly dotted aleurones, 117 completely dotless types, and 96 with dots found in sectors of the aleurone and/or dotted scutella. The aberrant types from the latter class were grown and crossed with tester strains to determine the cause of the altered dotted expression in these kernels.

Self-pollinations of plants grown from sectored kernels produced kernels having basically colorless aleurones, some of which had well-defined dotted sectors; the dotting in the scutella, when it occurred, was uniform (color in the scutellum requires additional genes which were not being followed here). A very few kernels were dotted throughout the aleurone. A plant arising from a kernel with reduced Dt activity was selected for intensive study and used as pollen parent in a variety of crosses. All the kernels on an ear from a cross between this plant and an a<sub>1</sub><sup>s</sup> a<sub>1</sub><sup>s</sup> Dt<sub>1</sub> Dt<sub>1</sub> stock (colorless aleurone) were uniformly and highly dotted. Since a<sub>1</sub><sup>s</sup> does not respond to Dt, the only source of a mutable a<sub>1</sub> allele was the plant being tested; thus, the presence of two normally mutable a<sup>m-1</sup> genes in the pollen parent was established.

The activity of Dt was studied by crossing the test plant to an a<sub>1</sub><sup>s</sup> a<sub>1</sub><sup>s</sup> dt dt (colorless aleurone) female parent. The resultant ear showed that Dt was inactive in most of the aleurones but occasionally became active, producing sectors of a<sub>1</sub> mutability. The same behavior was observed in a similar cross to an a<sup>m-1</sup> a<sup>m-1</sup> dt dt plant.

An independent modifier of Dt activity could not have caused the sectoring since the Dt from the a<sub>1</sub><sup>s</sup> Dt<sub>1</sub> stock was not affected. A modifier linked to Dt whose influence is restricted to genes in the same homologue might be postulated, but it seems more likely that induction of Dt activity and inactivity was autonomous.

Since the tested plant was homozygous for the highly mutable a<sup>m-1</sup>, sectors of Dt reactivation were clearly defined. The reactivation sectors on self-pollinated ears were larger than on outcrossed ears, where only one Dt was present in the triploid endosperm. It is possible that Dt reactivation in these kernels was dose-dependent; i.e., the inactive Dt's acted synergistically to reactivate other inactive alleles. According to this explanation, the combined action of the Dt's caused earlier reactivation realized by larger sectors of Dt activity.

One ear from the cross a<sub>1</sub><sup>s</sup> a<sub>1</sub><sup>s</sup> dt dt X a<sup>m-1</sup> a<sup>m-1</sup> dt Dt<sup>in-ac</sup> ("Dotted, inactive-active") segregated 1:1 for kernels with dotted and colorless scutella (Table 3, No. 1). Kernels in the two classes were scored for