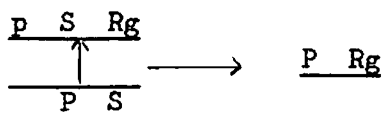
If we assume that S^{st} is a compound structure consisting of S plus an adjacent regulatory component (Rg), the most likely interpretation of these observations is that the R "mutant" originated from an intralocus recombination of the oblique type (Emmerling 1958) that gave rise to a crossover strand deficient for the S component and with the regulatory component (Rg) in coupling with P.

The event leading to the appearance of a similar strand is depicted below:



These observations, even though limited, seem to suggest that the mechanism leading to S instability can extend its action to the P component of R when both P and S are brought in coupling on the same chromosome.

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2. Mutability of the S component of the R locus.

As previously outlined, the S component of R^{st} is unstable. The instability consists of frequent changes of S from an inactive to an active state, leading to a variegated aleurone phenotype. If this change occurs in the germ line cells, it gives rise to a stable form of S. This form is symbolized S^{sc} (self colored) to distinguish it from the S components present in the R^{r} and R^{ch} gene complexes. S^{sc} in fact determines pigmentation in both the scutellum and aleurone and it conditions a full pigmentation of the aleurone even when present in a single dose (s s S^{sc}). The other two S components do not extend the pigmentation to the scutellum tissues and condition a mottled aleurone phenotype (S of R^{r}) or a pale phenotype (S of R^{ch}) when present in a single dose.

It is likely that these phenotypic differences reflect a difference in the structural organization of the genetic material at the R locus in the three different forms of R.

This possibility has been tested by comparing the frequency and spectrum of mutation of the S component of the three forms of R. The results obtained are reported in Table 1. The S^{sc} gametes analyzed were obtained from individuals heterozygous for two S^{sc} isolates of independent origin. In this way the mutational behaviour of 7 different $\underline{S}^{sc}$ isolates was studied.

The data presented in the Table indicate that while the $\underline{S}$ component of $\underline{R}^r$ and $\underline{R}^{ch}$ mutates to $\underline{s}$ (null level allele) with a frequency of about 1%, $\underline{S}^{sc}$ gives rise only to mutants conditioning an intermediate level of pigmentation with a very low frequency. No $\underline{S}^{sc} \longrightarrow \underline{s}$ mutation has been observed.

The mutational behavior of $\underline{S}^{sc}$ could be explained by assuming that $\underline{S}^{sc}$ consists of a series of reiterated $\underline{S}$ genes that originated through a process of gene duplication not associated with gene divergence. According to this hypothesis the mutation of $\underline{S}^{sc}$ to the null level $\underline{s}$ allele could arise through two or more succeeding steps. This would represent a rare event not easily observable in the sample of gametes we analyzed. On the other hand, the "mutation" to intermediate level alleles could be the result of unequal crossing over between either sister or nonsister strands with the production of a crossover strand lacking one or more $\underline{S}$ duplicates.

We are presently trying to obtain experimental evidence in favor of this hypothesis.

Table 1

Frequency and spectrum of mutation of $\underline{S}$ components of different origin.

Origin	n (no. gametes tested)	Colorless		Nearly colorless		Pale		Slightly pale	
		Isol.	Tested	Isol.	Tested	Isol.	Tested	Isol.	Tested
R^{sc} R^{sc}*	36,137	0	0	1	0	1	1	3	2
R^r R^r	24,207	24	18	0	0	0	0	0	0
R^{ch} R^{ch}	42,390	47	0	0	0	6	0	0	0

*$\underline{R}^{sc}$ indicates a form of $\underline{R}$ carrying a stable $\underline{S}^{sc}$, isolated from an unstable $\underline{S}$.

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