

4. A suppressor-mutator system of control of genic action and mutational change.

Several systems that control genic action and mutational change, other than that of Ds and Ac, are being examined. One of them has received a considerable amount of study and its pattern of behavior is now apparent. It is the system associated with control of genic action and mutation at the a_1^{m-1} locus. (Designation refers to a mutable condition that arose at the A_1 locus in the Cold Spring Harbor cultures.) It was originally thought that a_1^{m-1} was an "autonomous" mutable locus. This now appears not to be true and for reasons that will be apparent. An independently located factor, designated Spm for Suppressor-mutator, is responsible for the observed behavior of a_1^{m-1} . When this factor is present, anthocyanin development in kernel and plant is suppressed until a mutational change occurs at a_1^{m-1} . These changes give rise to stable mutants distinguishable from one another by different levels of expression of anthocyanin pigmentation in kernel and plant. These range from no pigment formation to the apparent full A_1 expression. When Spm is removed from the nucleus, either by a somatic loss or transposition, or by means of meiotic segregations, the a_1^{m-1} locus can express itself, producing uniformly distributed pigment in both kernel and plant. This expression is stable in subsequent generations as long as Spm is absent from the nuclei. The degree of this expression varies with the particular state of a_1^{m-1} that may be present. Strikingly different states of a_1^{m-1} have appeared, one arising from the other through the influence of Spm on the a_1^{m-1} locus. They are characterized by the types of mutation that occur, by the time during development when these occur, and by the type of pigmentation that is expressed in the absence of Spm. This latter ranges from almost none to very intense. When through appropriate crosses, Spm is returned to the nucleus, the Suppressor-mutator action it induces at a_1^{m-1} is again apparent. The types of effects that it will produce are quite predictable if the state of a_1^{m-1} is known in advance.

The Spm factor behaves much like Ac in that it occupies a definite position in the chromosome complement but may be transposed to a new position, remaining at the new location until a subsequent transposition occurs. Several different positions of Spm within chromosome 6, within chromosome 5 and within chromosome 9 have been found. As long as Spm remains in a particular position, it gives clear-cut linkage relations with known factors. These are expressed directly in backcross tests or in progeny tests. It is in the progeny tests, however, that new positions of Spm are discovered. Unlike Ac, Spm does not give a sharply defined dose action. Therefore, when 3 or more independently located Spm factors are present in a plant carrying a_1^{m-1} , nearly all of the gametes carry one or more of them and, in test crosses, the a_1^{m-1} locus appears to be "autonomous" in its mutation control. Progeny tests are required to separate the different Spm factors and to determine the number present in the parent plant if more than 2 are present.

To summarize, Spm is a chromosomal element, subject to somatically occurring losses from some nuclei or changes in location in others, that suppresses the potential action at the a_1^{m-1} locus until a change occurs at this locus under the influence of Spm that produces either an altered type of

response to Spm in subsequent cell and plant generations (a change in stage of a_1^{m-1}) or a stable mutation that expresses a particular level of anthocyanin pigmentation in kernel and plant.