8. Modifying factor.

The segregation of white and mosaic seedlings on the same ear indicate that the mutable condition is controlled by a modifying factor that can be separated from the vp-2 locus. This modifier must be closely linked to the vp-2 locus or widely spread in our stocks since most outcrosses of mosaic to standard lines give only mosaic seedlings.

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1. Continued study of stability of location of Spm.

The mode of operation of the a_1^{m-1} - Spm system was outlined in the last two issues of this News Letter and evidence was presented indicating that the Spm element undergoes frequent changes in location. To obtain further evidence of the degree of stability of location of Spm, two additional tests were conducted this past summer. Each involved determination of Spm constitution and linkage relations in the progeny of a plant having one Spm whose location was known. In both cases, the location of Spm in the chromosome complement differed from that of other determined locations of it. In one parent plant, Spm was linked with Wx in chromosome 9. In the other parent plant, it was located close to Y in chromosome 6. The history of the first mentioned parent plant is referable to a culture grown in the summer of 1954. The plants in this culture were Wx/wx and either a_1^{m-1}/a_1^{m-1} or a_1^{m-1}/a_1 in constitution. In one plant of this culture, two independently located Spm elements were present, one of which was linked with wx. When pollen of a plant homozygous for a_1^{m-1} and wx and having no Spm (standard Spm tester stock) was used on the silks of an ear of this plant, there appeared 130 pale colored kernels (no Spm) and 335 kernels that had A_1 spots in a colorless background (Spm present), indicating the presence in this plant of two independently located Spm elements. From the ratio of Wx to wx in each class (100 Wx : 30 wx in the no Spm class and 123 Wx : 212 wx in the Spm class) it was evident that one of the two Spm elements was located in the wx carrying chromosome of this plant. In order to obtain plants with a single Spm element located in a chromosome 9 carrying Wx, and to test for its stability in this location, 29 plants derived from the variegated, Wx class of kernels on the above described ear were again tested by crossing them with plants that were homozygous for a_1^{m-1} and wx but in which no Spm was present. The first ear on the main stalk was always used for this test and when possible, other ears of the plant were so used. Among these 29 plants, 1 had no Spm; 20 plants had one Spm but it was not linked with Wx; 4 plants had two Spm elements that were not linked to each other but in 3 of these plants, one of the two Spm elements was linked with Wx. One plant had three independently located Spm elements. In the remaining 3 plants, a single Spm element was present and it was linked with Wx. Among the 1918 kernels appearing on five ears obtained from these three plants, the following types appeared: 1 A_1 wx, 1006 uniformly pale colored (no Spm) of which 222 were Wx and 784 were wx, and 911 in which spots of A_1 appeared in a colorless background (Spm present) of which 747 were Wx and 164 were wx. Linkage of Spm with Wx is obvious and the value of the "recombinant" classes is 20.1%.

Thirteen plants derived from the Spm Wx class of kernels on one of the five above mentioned ears were grown this past summer under culture number 7285. Each was used as a female parent in crosses with plants homozygous for a_1^{m-1} and wx and carrying no Spm, and all fertile ears produced by each plant were so used. One of the 13 plants had no Spm but in the remaining 12 plants, one or two Spm elements were present. The number of ears obtained from each plant, the Spm constitution in the cells that produced each ear, and the linkage relations of Spm and Wx, are indicated in table 1. The tiller ear produced by one plant had no Spm but in the remaining 25 ears obtained from these twelve plants, one or two Spm elements were present. In 16 ears, one Spm element, linked with Wx, was present. In 5 ears, two Spm elements were present, one of which was linked with Wx. In 4 ears, one Spm was present but it was not linked with Wx. The ratio of kernel types appearing on these ears is given in table 2 for each of these three categories of Spm constitution and location. From table 1, it may be seen that correspondence in Spm constitution and location is shown in the cells that produced the 1st and 2nd ears on the main stalk. Differences with respect to this were expressed only in tillers. This suggests that the mechanism responsible for change in number and location of Spm elements was operating relatively early in development of these plants.

The second test of stability of location of Spm was conducted with the progeny of a plant having a single Spm element located close to Y in chromosome 6. The parent plant was one of 5 in a culture and it was the only plant in this culture that showed close linkage of Spm with Y. This plant was homozygous for a_1^{m-1} and heterozygous for Y, Pr, and Wx. It was used as a female parent in a cross with a plant that was homozygous for a_1^{m-1}, y, pr, and wx, and had no Spm. The ear this cross produced had a small, well defined sector in which Spm was absent. All the kernels within this sector were uniformly pale colored (no Spm); 21 were Y and 26 were y. Among the other 329 kernels on this ear, 167 were uniformly pale colored (no Spm) and 162 showed A_1 spots on a colorless background (Spm present). In the pale colored class, 10 were Y and 157 were y. In the variegated class, 153 were Y and 9 were y. It could be concluded, therefore, that a single Spm element was present in the part of the plant that produced most of this ear and that this element was closely linked with Y (5.6% "recombinants"). No linkage with Pr or with Wx was expressed. This past summer, 17 plants derived

Table 1.

Table 1.

Plant Number in culture 7285	Number of ears tested per plant	Position of ear on plant	Spm constitution and linkage with Wx
A-6, B-1, and B-6	1	1st ear, main stalk.	1 Spm; linked with Wx (each ear)
B-4	1	"	2 Spm; one linked with Wx
A-5	2	1st and 2nd ear, main stalk.	2 Spm; one linked with Wx (both ears)
B-2 and B-5	2	1st ear, main stalk; tiller ear.	1 Spm; linked with Wx (all four ears)
A-1	3	1st and 2nd ear, main stalk; tiller ear.	1 Spm; linked with Wx (1st and second ear, main stalk) 1 Spm; not linked with Wx (tiller ear)
A-3	3	"	2 Spm; one linked with Wx (1st and 2nd ear, main stalk) 1 Spm; linked with Wx (tiller ear)
A-4	3	"	1 Spm; not linked with Wx (all three ears)
A-2	3	1st ear, main stalk; ear on each of 2 tillers.	1 Spm; linked with Wx (1st ear, main stalk; 1 tiller ear) No Spm (1 tiller ear)
A-7	4	1st and 2nd ear, main stalk; ear on each of 2 tillers.	1 Spm; linked with Wx (all four ears)

Table 2.

Spm constitution of tested plants (Culture 7285)	A_1	Phenotype of kernel: Pale color (No Spm)		Colorless with spots of A_1 (Spm present)		Total
		Wx	wx	Wx	wx	
1 Spm; linked with Wx	1	418	1539	1512	356	3826*
2 Spm; one linked with Wx	0	79	267	594	323	1263
1 Spm; not linked with Wx	0	190	168	140	174	672

* 20.2% are "recombinants".

from the variegated, Y, Pr, Wx class of kernels on this ear were tested for Spm constitution and location. The silks of all fertile ears produced by each plant received pollen from plants that were homozygous for a_1^{m-1}, y, pr, and wx and had no Spm. One ear was obtained from 3 plants, two ears were obtained from 4 plants, three ears were obtained from 7 plants, and four ears were obtained from 3 plants. That a single Spm element was present in all tested parts of each plant was indicated by the approximate 1 : 1 ratio of presence and absence of Spm among the kernels on each of the 44 ears. And, in 43 of these 44 ears, linkage of Spm with Y was expressed. Only on the ear produced by a tiller of one plant was evidence of this linkage absent. The proportion of kernel types with respect to presence and absence of Spm and to Y and y among the kernels appearing on the ears of 15 of the 17 plants is given in A of table 3. One plant, number 17, was small and defective in appearance. The ear it produced was partially sterile and from the ratio of kernel types on this ear, it was evident that the Y chromosome carrying Spm was not being transmitted normally. Nevertheless, close linkage of Spm with Y is indicated (B, table 3). The types of kernels appearing on each of two ears produced by plant number 2 is shown in C of table 3. On the 1st ear of the main stalk, linkage of Spm with Y was clearly expressed. However, the ratio of kernel types that appeared on the ear produced by a tiller of this plant gives no evidence of such linkage. Also, there was no evidence of linkage of Spm with either Wx or Pr.

Table 3.

A. Plant number in culture 7260	A_1	Phenotype of Kernel: Pale color (No Spm) Y	Pale color (No Spm) y	Colorless with spots of A_1 (Spm present) Y	Colorless with spots of A_1 (Spm present) y	Total
1	0	25	345	360	18	748
3	0	16	308	272	9	605
4	0	14	389	387	9	799
5	0	2	55	48	2	107
6	1 Y	17	367	364	13	762
7	0	17	252	257	18	544
8	1 y	16	530	520	38	1105
10	0	19	318	295	11	643
11	1 y	20	468	436	13	938
12	0	28	548	540	12	1128
14	0	24	271	251	12	558
15	0	19	302	305	17	643
16	0	5	75	81	5	166
18	0	7	122	125	2	256
19	1 Y	18	358	310	13	700
Totals	4	247	4708	4551	192	9702*
B. Plant No. 17	0	1	91	20	1	113
C. Plant No. 2						
main ear	0	25	203	171	11	410
tiller ear	0	65	47	48	59	219

* 4.5% are "recombinants"

With regard to stability of location of Spm, the results obtained from the two experiments, outlined above, differ markedly. The first gave evidence of relatively frequent changes in location of Spm. This is in contrast to the experiment just described where an unusual degree of stability of location of Spm was made evident. Nothing is yet known about genetic or other factors that may be responsible for controlling the time during development of a tissue when change in location of Spm will occur, or the frequency of this.

2. Continued study of a structurally modified chromosome 9.

In last year's News Letter, a description was given of a modification affecting the organization of chromosome 9. Two chromosomes instead of one carry the substance of this chromosome. One of these is composed of the distal third of the short arm and it was referred to as the fragment chromosome. The centromere is situated at the proximal end of this component of chromosome 9. The longer segment is composed of the proximal two-thirds of the short arm of chromosome 9 and all of its long arm, and it was referred to as the deficient chromosome. Interest in this case was centered on the aberrant behavior of the fragment chromosome in somatic cells, and this was outlined briefly last year. Further examination of this case required more exact knowledge of the composition of the two components of this structural modification. Therefore, an extensive series of tests of this were continued during the past year. The fragment was known to carry the locus of C and preliminary evidence presented in the News Letter last year, suggested that it also carried the loci of sh and bz. Since the deficient chromosome was known to have the loci of Sh and Bz, with Sh situated very close to the end of its short arm, the genetic composition of the structurally modified chromosome 9 would then include a duplication of a segment composed of the region from the locus of sh to one that is proximal to bz. Recent tests have confirmed the presence of sh and bz in the original fragment chromosome and they also have revealed the relative length of the segment that extends from bz to the centromere of the fragment. It is equivalent to a segment in the normal chromosome 9 that is 5 crossover units proximal to Bz.

Genetic study of the constitution of the fragment and the deficient chromosome makes it clear that a segment in the fragment,--from the locus of sh to the centromere--, duplicates a segment in the deficient chromosome that is located at the very end of its short arm. Examination of the chromosomes at the pachytene stage in structural heterozygotes did not reveal the physical length of the duplicated segment with the desired degree of certainty. It can not include more than 1 or 2 small chromomeres, if matching chromomeres in synapsed regions may be used as a reliable criterion of homology.

In structural heterozygotes whose chromosome 9 components are appropriately marked for crossover studies (an example: normal chromosome 9 with I Sh Bz wx/ deficient chromosome 9 with Sh Bz Wx/ fragment