4. Studies of instability of chromosome behavior of components of a modified chromosome 9.

A preliminary study was made of a modification affecting the organization of chromosome 9. This modified chromosome is composed of two independent segments. One segment includes the distal third of the short arm and will be called the fragment chromosome. The other segment is composed of the proximal two-thirds of the short arm and all of the long arm and will be called the deficient chromosome. The distal end of the fragment terminates in a knob and its proximal end is composed of a centromere from which a short piece of very deep-staining chromatin extends. These two independent segments carry the full genic complement of chromosome 9. The locus of C is carried in the fragment chromosome. That of Sh is very close to the end of the short arm of the deficient chromosome. The deficient chromosome is transmitted through the female gametophyte but its transmission through the pollen occurs only when the fragment chromosome is also present in the tube nucleus. Study of this modification was undertaken because the fragment chromosome undergoes many changes in constitution in somatic cells: "misdivision" of its centromere leading to loss or non-disjunction of the fragment; loss of the deep-staining component adjacent to the centromere or duplications of this component; ring chromosome formation; deletion of segments of chromatin composing the fragment; attachment of the fragment at its centromere region to the end of another chromosome, its own centromere being lost in the process; attachment of its centromere to that of another chromosome resulting in loss of an arm of the other chromosome; etc. These events affecting the fragment chromosome appear to be regulated in a manner somewhat similar to that which controls mutation at a "mutable locus." This is made evident in some isolates by the patterns produced by patches of colorless aleurone in a colored background that appear in kernels having one or two normal chromosomes 9 carrying c and a fragment chromosome carrying C. The colorless patches represent those areas in which C has been lost from the cells. The broken end of the deficient chromosome also initiates modifications that affect its own organization and also that of other chromosomes of the complement but the frequency of occurrence of such events appears to be lower.

In structural heterozygotes, crossing over occurs between the locus of C and the centromere of the fragment chromosome and isolates having c in the fragment chromosome have been obtained as well as isolates in which the C from the fragment has been introduced into a normal chromosome 9. Several sets of data suggest that a segment carrying sh and bz may be included in the fragment. If so, the constitution of this modification includes a duplication of the segment that carries the loci of sh and bz for both Sh and Bz are present in the deficient chromosome. Plants carrying Bz both in the normal chromosome 9 and in the deficient chromosome and also a fragment chromosome, when crossed to plants homozygous for bz have produced ears on which kernels showing the bz phenotype have appeared in constant proportions. This is made evident in B of the following table:

A. $_{m}$ C sh bz wx/C sh bz wx x $_{h}$ sh Bz wx; normal chromosome,
Sh Bz Wx; deficient chromosome
No Fragment.

B. $_{m}$ C sh bz wx/C sh bz wx x $_{h}$ Same as A but fragment present.

| Phenotype of kernel | A. | B. Plants 1 to 5 | | | | | Totals for B |
|---|---|---|---|---|---|---|---|
| | | 1 | 2 | 3 | 4 | 5 | |
| Sh Bz Wx | 0 | 81 | 141 | 147 | 169 | 249 | 787 |
| Sh Bz wx | 0 | 4 | 15 | 12 | 27 | 33 | 91 |
| sh Bz Wx | 71 | 65 | 81 | 95 | 147 | 154 | 542 = 19% of sh Bz class |
| sh Bz wx | 367 | 357 | 335 | 454 | 480 | 602 | 2229 |
| sh bz Wx | 0 | 2 | 1 | 1 | 3 | 2 | 9 = 21.9% of sh bz class |
| sh bz wx | 0 | 5 | 3 | 6 | 6 | 12 | 32 |
| Totals | 438 | 514 | 576 | 716 | 832 | 1052 | 3690 |
| % bz among sh class | 0 | 1.6 | 0.95 | 1.2 | 1.4 | 1.8 | 1.4 |

Substantiating evidence of inclusion of sh and bz in the fragment chromosome was obtained from crosses of several plant shaving a normal chromosome 9 carrying c sh Bz wx, a fragment chromosome 9 carrying C, and a deficient chromosome 9 carrying Sh Bz Wx. When crossed by plants homozygous for c, sh, bz, and wx, the following phenotypes appeared among the kernel on the ears of these plants: 84 C Sh Bz Wx, 4 C Sh Bz wx, 53 c Sh Wx, 12 c Sh wx, 1 C sh Bz Wx, 35 C sh Bz wx, 5 C sh bz wx, 18 c sh Wx and 294 c sh wx. Among the 41 sh kernels in which C, originally carried in the fragment chromosome, was present, 5 were bz in phenotype. The duplicated region must be very short for cytological evidence of it has been difficult to substantiate. Also, mutation at the locus of Bz in the normal chromosome 9 from some event at meiosis associated with synapsis of the fragment chromosome with its homologous segment in the normal chromosome cannot be excluded, for it is known from other studies of this modification that changes in expression of C, of Sh, and of Bz that cannot be accounted for by normal crossover processes, have occurred.

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