3. Inheritable instability of the B^4 chromosome.

When individuals of the genotype 4su, 4su, + B^4Su were crossed as the male parent to a su_1 tester, about 16% of the progeny showed the Su phenotype as the result of the transmission of the supernumerary B^4 chromosome marked with Su (see M.N.L. 42, p. 70, 1968).

While most of these kernels appeared uniform (starchy and round), a number of them showed single su sectors of various sizes resulting from the loss, in the endosperm tissue, of the dominant marker which is present in the supernumerary chromosome. The nature of the loss observed in the form of sharp sectors is not known, although the indications are that this phenomenon is the result of chromosomal behavior rather than of genic instability. Chromosome lagging, non-disjunction, or breakage (proximal to Su) would be equally able to produce the same effect. Sectors were obtained on progeny kernels of plants grown from any Su kernels, whether or not their endosperm showed su sectors, and the variation observed in the frequency of the appearance of sectors is possibly due to the influence of several factors (background and/or environment).

A different phenotype, however, was found in some of the kernels which appeared as Su/su mosaics. In these cases the Su phenotype was frequently lost during endosperm development. Some of these kernels were planted in the summer of 1966 and later to be crossed to a su_1 tester. An examination of their progeny revealed the following facts which are summarized below:

cross: su_1 ♀ x 4su,4su, + B^4Su ♂ Phenotype of the male parent: mosaic Su/su	No. of ears
Transmission of stable Su with a typical frequency	4
Transmission of stable Su at a very low rate	8
Transmission of Su/su mosaics (at a very low rate)	5
No transmission of Su (su only recovered)	10
Total No. of ears	27

The appearance of mosaics in the progeny of mosaic kernels of the type described above (which was reported at the Maize Genetics Conference, Allerton, 1969) showed the inheritability of this phenomenon. The results obtained with the B^4 chromosome compare well with unstable B^9 derivatives obtained by W. Carlson (personal communication, and M.N.L. 43, p. 79, 1969).

progeny of unstable B^4Su		progeny of unstable B^9C	
Stable Su	12	Solid color C	12
Mosaics Su/su	5	Mosaics C/c	7
su only	10	c only	12
Total	27		31

A common feature is that mosaics are recovered from one out of every 4 or 5 plants grown from a mosaic kernel. When mosaics are not recovered, the chromosome apparently either regained its stability or was lost with nearly equal frequencies. It seems that events of breakage are detected and selected for. In the case of B^4 the frequency of transmission of stable Su types was rated either "typical" or "low." In the first case, the event that led to the mosaicism was probably limited to the endosperm. In the second case, a breakage distal to Su which occurred during or after meiosis possibly started a breakage-fusion-bridge cycle which continued in the endosperm tissue, while the embryo had a modified B^4 chromosome whose broken end healed. This chromosome could be either deficient or have deficient + duplicate regions resulting from the b-f-b cycle, and this change in its structure would be responsible for the low recovery which has been observed through both male and female gametes.

The transmission of mosaics is certainly due to an unstable chromosome structure whose behavior is similar in many regards to that of ring chromosomes. In root tip cells it is difficult to study the structure of the supernumerary chromosome involved, which is much smaller than the original B^4; this observation supports the idea that breakage was responsible for the mosaic phenotype. Pachytene also is of little help since this chromosome is a single one and appears backfolded on itself. However, in premeiotic prophases where the cells are large and the chromosomes are in a favorable stage for observation, a ring structure was clearly seen in the only plant so far investigated.

The recovery of su only, from mosaic kernels, was found in a high number of cases. Noncorrespondence between embryo and endosperm is often due to nondisjunction in the 2nd microspore division when B or B^A chromosomes are involved. But this is apparently not the case, since no 4^B is present (Roman found 4^B necessary for the nondisjunction of B^4) and, moreover, the endosperm showed a mosaic phenotype indicating a chromosomal instability which led to the loss of the dominant Su in one of the sperms. Heterofertilization in ten out of 27 mosaics is unlikely. Finally, transmission of su only occurs in a few cases from mosaics of the inheritable type, and, in reciprocal crosses, the unstable structure is recovered much more frequently through the pollen than through the egg. This was seen in 20 of the 22 plants so far tested. The two exceptional cases unfortunately were lost.

The formation of a ring chromosome requires two breakages, one in each arm if the centromere is to be included. Since the B^4 chromosome is subtelocentric, only a high frequency of breakage in the very short arm could account for the high frequency of ring formation. The finding of these spontaneously formed unstable structures (which are inheritable) with such a high frequency is unprecedented and remains unexplained. However, the chromosome involved is a supernumerary one and therefore not necessary to the viability. The cells where this chromosome undergoes breakage, disintegration, or rearrangement are then easily detected if the phenomenon occurs in the germ line.

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