

The difference between the two populations is significant by the F test. These data do, however, support the contention that autotetraploid maize populations should remain stable within the range of 36 to 43 chromosomes.

-- Donald L. Shaver

10. Note on the problem of disjunction from autotetraploid quadrivalents.

In tracing the events giving rise to double reduction in autotetraploids, Mather (Jour. Gen. 32:287-314, 1936) has likened segregation from the tetraploid quadrivalent to segregation from the ring quadrivalent typical of diploid translocation heterozygotes. Mather's model has been widely followed, notably by Little (Bot. Rev. 11:60-85), Catcheside (Heredity 10:205-218, 1956), and others.

However, the two types of quadrivalents are basically different. In the translocation heterozygote, no chromosome region is present more than twice. In the tetraploid, each region is present in quadruplicate.

As a consequence of this basic difference, there are 10 ways for a tetraploid quadrivalent to be ordered at diakinesis. In maize, 8 of these types were found in scoring only 220 sets of homologues (Shaver, unpublished Ph.D. thesis). More than 2/3 of the arrangements were in some configuration other than rings or chains. Since any possible arrangement except rings and chains requires effective partner exchange within arms (see definition above), the concept of alternate vs. adjacent disjunction cannot be applied. Therefore the scoring of alternate vs. adjacent orientation of rings, as Venkateswarlu (cited by Catcheside, 1956) has done, does not provide an adequate basis for genetic inference, since rings are actually a minority class.

In the absence of information as to how the placement of chiasmata in a quadrivalent affects the mode of disjunction, it may be best at present to assume that disjunction from tetraploid quadrivalents is largely random. It is interesting to note that if Catcheside (1956) had assumed randomness, instead of drawing inference from the cytological data of Venkateswarlu, his calculated value for double reduction at the su_1 locus would have agreed closely with his experimental value. Instead the calculation was in disagreement by a factor of about 2.

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11. Evidence for homosynapsis of bivalents in 4n hybrids of maize and perennial teosinte.

In article (8) above, it was argued that if all heterosynaptic associations in an allotetraploid were in quadrivalents, then the same β could be used to compare strength of linkage in auto and allotetraploids during heterosynaptic events.

Chromosome 6 was followed cytologically in 242 cells of the "intergeneric" hybrid. It was found to form 2 bivalents at a frequency of .837, to form trivalent-plus-univalent at a frequency of .006, and to form a quadrivalent at a frequency of only .157.

Assuming random disjunction of quadrivalents and trivalents for reasons given in article (10) above, the expected frequency of recessive y progeny in a backcross population would be .026 (from quadrivalent disjunction) plus .001 (from numerical non-disjunction), plus about .001 (from trivalent-plus-univalents), or a total frequency of .028. The experimentally obtained frequency of y was .028, in perfect agreement with expectations from cytological data.

Since random disjunction from multivalents alone accounts for all of the recessive backcross progeny, it is logical to conclude that bivalents in the "intergeneric" hybrid are rarely or never heterosynaptic.

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12. The possible significance of a modified type of autotetraploid meiosis in perennial teosinte.

Meiosis was studied in a clonal derivative of the original collection of *E. perennis* made by Collins and Kempton in 1922. It was found that at pachynema, pairing was largely multivalent, as in autotetraploid maize. Many exchanges of pairing partners could be found in single cells.

However, a study of the diakinesis stage in 114 completely analysed cells revealed that quadrivalents were formed at a frequency of only .499, while two bivalents were formed at a frequency of .496. In autotetraploid maize, on the other hand, the quadrivalent frequency was .871, and the bivalent frequency was only .106. Since disjunction from bivalents is always regular, *E. perennis* may be expected to show much greater chromosome stability than autotetraploid maize.

Even more surprising was the fact that the quadrivalents of perennial teosinte were almost always restricted to two of the ten possible types, namely rings and chains of four, which are non-effective pairing (within arms) partner exchange types. Thus, in spite of the fact that exchange of pairing partners is very frequent at pachynema, some mechanism prevents these exchanges from being effective at diakinesis.

Possibly the simplest explanation for such a restriction in chiasma placement would be that the maximal chiasma number per arm in *E. perennis* is one (Chiasma interference is 100%). If this assumption is allowed, then at diakinesis, all of the chiasmata present can be detected. From cytological data from 110 cells (Shaver, unpublished Ph.D. thesis), it was calculated that the average frequency of chiasma per arm was .89. On the assumption of 100% chiasma interference, then, each chromosome arm takes part in a chiasma at a frequency of .89, and fails to do so at a frequency of .11.

The hypothesis of 100% chiasma interference within arms may be tested to see if it can satisfy the data. The hypothesis predicts ring-of-four formation at a frequency of $.89^4 \times 2/3 = .419$. The observed value was .410. The frequency of arms not taking part in a chiasma would be predicted as .110, while the observed frequency was .119. Hence, for two values, the hypothesis holds very well.

If the secondary hypothesis is made, that failures of chiasma formation are randomly distributed, further predictions can be made.¹ The predicted frequency of chains-of-four is .207 (observed was .067). Trivalent-plus-univalent is predicted at a frequency of .011 (observed was .003). Bivalent-plus-two-univalents is predicted at a frequency of .011 (observed was .001). Two bivalents are predicted at a frequency of .328 (observed was .494). Obviously the secondary hypothesis does not hold, and it seems likely that distribution of chiasma failure is not at random, but rather is directed to give an excess of bivalents at the expense of univalent formation. This localization can be explained by the hypothesis that the apparently strong chiasma interference within chromosome arms extends, to some degree, across the centromere.

It is therefore possible to explain all of the observed differences in meiotic behavior between perennial teosinte and 4N maize by the single hypothesis that chiasma interference is greatly increased in *E. perennis*, to 100% within arms, and to a lesser extent between arms. This apparently single

¹ The writer is indebted to G. G. Doyle for the method of calculation used here.