In all cases, significant preference in pairing was found. Markers close to the centromere were recovered less frequently than those more distant, indicating that some "intergeneric" crossing over takes place. Genes on some chromosomes were recovered much more frequently than those on other chromosomes, indicating that the degree of homology between maize and teosinte differs from one chromosome to another.

Morphological characteristics which have been chosen as "differentiating" between Zea and teosinte can be considered suspect, since nearly all of them are characters which would come under strong selection pressure during the domestication of maize. A fresh approach to the problem of relationship could be had by simply comparing preferential segregation and chromosome behavior in doubled maize-teosinte hybrids with that in doubled hybrids between species and genera in other plants whose phylogenies are not in dispute.

Intergeneric hybrids in other plants as a rule cannot be made. Of those which yield successful seedlings, most fail to flower. In those which reach maturity, sterility is usually complete. In the maize-Tripsacum intergeneric hybrid, offspring are rarely produced, and then only by apomixis. When intergeneric hybrids are doubled, even here most are infertile. Notable fertile exceptions are Raphanus - Brassica hybrids, and hybrids of Triticum with related genera. Preference in pairing, however, in these few physiologically normal intergeneric hybrids has been found to be perfect, or nearly so.

Clearly, the polysomic test indicates that maize and teosinte are much more closely related than other forms considered to be in separate genera.

Doubled interspecific hybrids have been studied within the genera Gilia, Gossypium, Nicotiana, Primula, and Rubus (Grant, 1954, El Aliso 3:19-34; Beasley, 1942, Genetics 27:25-54; Gerstel & Phillips, 1958, C.S.H.S.Q.B. 23:225-237; Clausen & Goodspeed, 1925, Genetics 10:278-284; Upcott, 1939, Genetics 39:79-100; Crane and Darlington, 1927, Genetica 9:241-274). In every genus, at least most of the doubled interspecific hybrids showed more preference in chromosome pairing and gene segregation than the maize-teosinte hybrid of the present study.

Clearly, the polysomic test indicates that the degree of chromosome affinity between maize and teosinte is intermediate to the degree of chromosome affinity between species within 5 other genera.

The present work provides support for the argument that the relationship between maize and teosinte is co-generic.

-- Donald L. Shaver

7. A simple method of measuring linkage in tetraploids.

Because of double reduction and numerical non-disjunction, calculation of linkage in autotetraploids is exceedingly difficult. No satisfactory method of calculating linkage in duplex tetraploid hybrids has yet been proposed. Mather (Jour. Gen. 32:287-314, 1936) has concluded that linkage calculations in duplexes are meaningless unless the two gene markers are within 15 units of each other, and the centromere distance is known. Even if these qualifications are met, his formula does not consider numerical non-disjunction. Fisher (Phil. Trans. Roy. Soc. London 233:55-88, 1947) has developed formulae for determining linkage, but has concluded that both repulsion and coupling data must be obtained, and that each member of the backcross progeny must be progeny-tested. Because these procedures are impossible in many cases and always require great expenditure of land resources, it seems desirable to propose a practical method for estimating linkage.

The theoretical backcross ratio from a duplex autotetraploid is 5:1. Double reduction and numerical non-disjunction modify this ratio to a different degree for each gene. In diploid studies, crossover values are based upon the frequency of recombinant strands for a given region. In autotetraploids, only one assumption is needed to simply estimate this parameter from backcross data, namely, that the consummation of a crossover in the region under study does not affect the frequency of double reduction for the region. Because of the possibility, however remote, that this factor could bias tetraploid values and therefore tetraploid values made not strictly comparable to diploid values, the tetraploid statistic is given the designation β, the coefficient of tetraploid linkage.

For coupling, the formula is:

$$\beta = 1 - \frac{Xy + xY}{(a \times B) + (A \times b)}.$$

For repulsion, the formula becomes:

$$\beta = 1 - \frac{xy}{a \times b},$$

where a = freq. of gametes phenotypically x,
where A = freq. of gametes phenotypically X,
where b = freq. of gametes phenotypically y,
where B = freq. of gametes phenotypically Y, and where, for example, the combination xy represents the frequency of gametes phenotypically xy. Both formulae simply relate the observed frequency of crossover gametes to expected frequency based on independence of genes x and y.

If linkage is complete, β takes a value of unity, and if linkage is absent, β becomes zero. Intermediate values are linear if the assumption for the formulae is true.

TABLE 2. Comparison of Diploid Recombination Values of Tetraploid β Values.

Region	Usual Diploid Recomb. Value	Tetraploid β Value	Progeny Size
B - lg_1	34	.119	2134
su_1 - gl_3	34	.184	2268
Y - Pl	28	.505	2555
wx - C	26	.567	2602
wx - sh_1	21	.547	4199
wx - yg_2	41	.347	2391

β values are not always of magnitudes predictable from diploid data, but a moment's reflection upon the differences between tetraploid and diploid meiosis shows that a host of unknown must be experimentally resolved before one can say whether this predictability should obtain.

At present, it seems best to treat tetraploid genetics as a subject by itself with parameters which have not been compromised by attempts to make values comparable between diploids and tetraploids.

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