cally on the far right of the table. This type of trivalent arises probably when pairing takes place between an inverted chromosome and the normal chromosome when they are oriented in opposite directions, in which case the homology of the two chromosomes for the inverted region is the same.

-- G. G. Doyle

6. Further evidence on the relationship between maize and teosinte.

The relative phylogenies of maize and teosinte have long been a matter of disagreement. Diploid hybrids between maize and teosinte made by Emerson and Beadle (Zeit. f. Ind. Abstmmgs. u. Vererbungslehre 62:305-315, 1932) and Arnason (Genetics 21:40-60, 1936) showed essentially normal rates of crossing over in marked regions. Cytological observation has shown chromosome pairing in 2N hybrids to be normal, and only small differences in length have been found. Cases of observed major failures in pairing and modification of crossing over in 2N hybrids can be traced to the presence of relatively inverted segments in some strains of teosinte. It must be concluded that study of 2N hybrids has failed to show significant differences between the genomes of maize and teosinte.

The next logical step in determining degree of relationship is the tetraploid hybrid test. Since there are two teosinte and two maize chromosomes present for each member of the set of 10 chromosomes, an opportunity for preference in pairing at meiosis is allowed. Therefore the tetraploid test should be a more sensitive test in determining degrees of chromosome homology. If pairing were strictly preferential, only bivalents would be formed, and recessive alleles introduced by the maize parent would not be expressed in the backcross progeny. Such a plant would be a stable amphidiploid. If pairing were random in the 4N hybrid, the frequency of recovery of recessives would be the same as in similarly marked autotetraploid maize controls. Therefore, preferential gene segregation from 4N "intergeneric" hybrid plants gives a measure of preference in chromosome pairing, and a measure of the degree of chromosome homology between maize and teosinte.

Seven sets of hybrids were made, using the tetraploid perennial form of teosinte and different tetraploid maize genetic stocks. F_1 hybrid plants used in backcrosses were determined from root tips to have 40 chromosomes, and from meiotic study to be balanced euploids. The backcross results are given in table 1.

TABLE 1. Percent of Recessives in Backcross Progenies of the 4N Hybrid of Maize and Perennial Teosinte, and of Corresponding Autotetraploid Maize Controls.

	4N Intergeneric Hybrid		Autotetraploid Maize	
Gene Marker	No.	Percent Recessive	No.	Percent Recessive
B	1952	6.4	2134	18.7
lg_1	1952	7.8	2134	21.6
lg_2	1640	9.9		
a_1	1640	11.6	4413[1]	20.7[1]
su_1	4213	4.9	2268	16.5
gl_3	4213	7.8	2268	21.9
Y	2021	2.8	2555	17.2
Pl	2021	4.4	2555	19.3
wx	9140	4.4	9008	16.5
sh_1	3019	4.6	4199	17.2
C	2317	3.3	4809	17.7
yg_2	2610	3.0	2391	22.9

1. Unpublished data kindly supplied by G. G. Doyle.

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.