

does not compete on equal terms with the normal pollen. The depression of the a Sh class relative to the A sh class is probably because the a Sh markers are in the duplication segment in the short arm and generally the a Sh gametes are actually a Sh-a sh.

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8. A telocentric trisome and its potential use in the production of commercial hybrid corn using genic male sterility.

A telocentric trisome ($2n + t6L$) arose spontaneously in a culture of primary trisome 6 probably by the transverse division of a univalent chromosome 6 at meiosis. One telocentric trisome in an otherwise normal progeny was recognized by a peculiar ratio of Y kernels to y kernels on the ear. There were 90 Y kernels or 25.9% and 248 y kernels or 74.1% instead of 38.2% Y and 61.8% y as found in a simplex primary trisome. In addition all the Y kernels were noticeably smaller than most of the y kernels. Cytological examination of this progeny revealed the presence of a telocentric chromosome consisting of the long arm of chromosome 6, along with the normal complement.

At the pachytene stage of meiosis this telocentric chromosome is frequently paired nonhomologously with itself. At diakinesis the trivalent frequency has been found to be 34.6%. Only 133 cells have been observed so this is a rough estimate. The pattern of chromosome disjunction can be determined by examining the quartet stage of meiosis. Since the telocentric chromosome 6L does not have a nucleolar organizer, spores which have only this chromosome instead of a normal chromosome 6 have a diffuse nucleolus. The frequency of quartets with two spores with diffuse nucleoli has been found to be only 3.15% (50 out of 1,585 quartets). This indicates that the two normal chromosomes 6 generally disjoin from each other. If the disjunction of the chromosomes of the trivalent were at random then we would expect the frequency of quartets with two spores with diffuse nucleoli to be 11.5% ($1/3 \times 34.6$).

Spores with only the telocentric are inviable. The resulting pollen abortion is very small ($1/2 \times 3.15\%$ or 1.58%). Background pollen abortion would prevent the identification of the telocentric trisome by pollen abortion rate. There is no noticeable semi-sterility on the ears

of telocentric trisome plants.

The telocentric chromosome (t6L) is transmitted when a normal chromosome 6 is also present. The transmission rates can be studied easily because the telocentric is marked with Y and the normal chromosomes are marked with y. The Y₁ locus is very close to the centromere and, since there is reduced pairing of the telocentric and the normal chromosome, there is less chance of crossing over. See Tables 4 and 5.

Table 4. Transmission rates of hyperploid gametes n + t6L

Cross	No. of plants	Number of kernels				Transmission rates	
		<u>Y</u>	<u>Y-y</u> mosaics	<u>y</u>	Total	% <u>Y</u>	% <u>Y-y</u> mosaics
<u>y/y</u> X t6L <u>Y/Y/Y</u>	36	331	30	19,149	19,510	1.70	0.15
t6L <u>Y/Y/Y</u> X <u>y/y</u>	90	4,774	3	18,494	23,271	20.51	0.01

There were a number of kernels which were mosaic for Y and y (generally half and half). The telocentric chromosome is apparently frequently lost in the development of the endosperm. The difference in the frequency of mosaic kernels in the reciprocal crosses reflects the different constitutions of the two endosperms, of course. In the first case it is t6L Y/y/y/y and in the second case it is t6L Y/t6L Y/y/y/y. The frequency of mosaic kernels when the female parent is the telocentric trisome theoretically should be the square of the frequency of mosaic kernels when the telocentric trisome is the male parent.

The results of progeny tests of plants grown from Y kernels are given in Table 5.

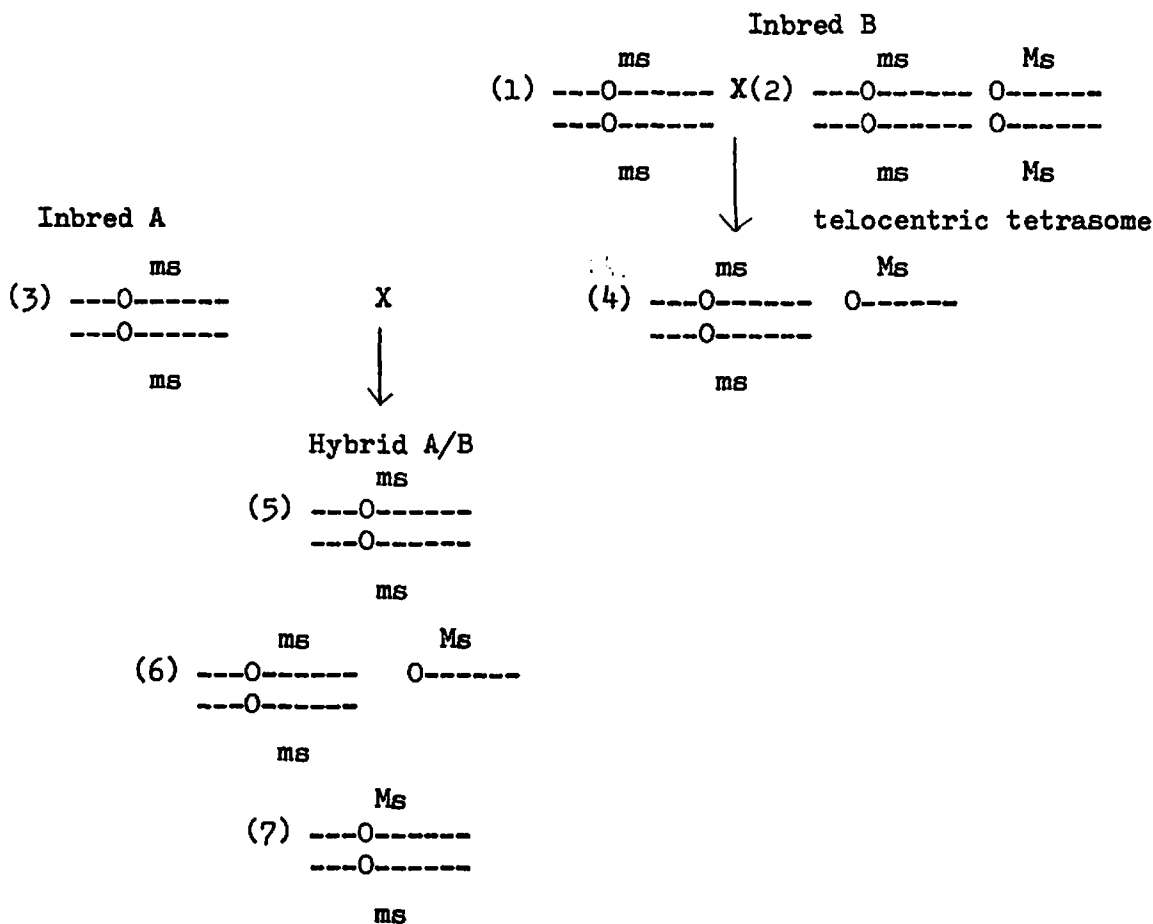
Table 5

Cross	Number of plants with constitutions of					Total	% "cross-overs"
	t6L <u>Y</u> / <u>Y</u> / <u>Y</u>	<u>Y</u> / <u>Y</u> / <u>Y</u>	<u>Y</u> / <u>Y</u>	<u>Y</u> / <u>y</u>	<u>y</u> / <u>y</u>		
(t6L <u>Y</u> / <u>Y</u> / <u>Y</u> X <u>y</u> / <u>y</u>) X <u>y</u> / <u>y</u>	108	0	1	2	111	0.92	
(<u>y</u> / <u>y</u> X t6L <u>Y</u> / <u>Y</u> / <u>Y</u>) X <u>y</u> / <u>y</u>	21	0	2	0	23	8.70	

There were two cases when the telocentric trisome was the female parent in which the progeny of Y kernels was all y. Probably the telocentric was lost somatically. The data are inadequate but it appears that there is a very low crossover rate between the Y locus and the centromere when the telocentric trisome was the female parent. When it was the male parent, there is a much higher apparent crossover rate, but this is not accurate because we are selecting for crossover events when Y kernels are used. The Y gene can be transmitted through the pollen only when it has crossed over on to a normal chromosome or is in hyperploid gametes which seldom function. If we multiply the frequencies of crossover events in the Y kernels times the frequencies of Y kernels in the total progeny and multiply this times two, the crossover frequencies are 0.38% for the female (20.52 X 0.92 X 2) and 0.32% for the male (1.85 X 8.70 X 2).

These data suggest the possibility of using this telocentric trisome in the commercial production of hybrid corn involving genic male sterility. A male sterile locus (ms₁) is very closely linked to the Y locus; the crossover rate is less than 1%. Since the hyperploid gametes are transmissible through the pollen, it is possible to get the telocentric trisome in different cytoplasms. Commercial hybrid corn could be produced by the following procedure.

Procedure for producing hybrid corn



Stock (1) can be maintained by crossing it as the female with stock (4), the telocentric trisome. Stock (2) can be produced by selfing the telocentric trisome. The telocentric tetrasome should be fairly stable. It probably can be recognized by a distinctive phenotype. It has not been isolated yet. The progeny (4) of a tetrasome and a disome should be mostly trisomic. The genic male sterile inbred A (stock 3) [which is maintained in the same fashion as stock (1)] is crossed with the telocentric trisome of inbred B (stock 4). The resulting hybrid should be mostly stock (5), which can be used as the female parent in a cross with another inbred for a three way cross, or with a hybrid produced by detasseling, by cytoplasmic male sterility, or by one using another genic male sterile and another system for maintaining male sterile lines. The double cross hybrids would all be fertile. The

frequency of stock (7) is so low as to be tolerable. The telocentric trisome, stock (6), which would also occur in stocks (1) and (3), could probably be removed from the field before pollination. If its phenotype is not distinctive enough to be recognized, then it is possible to translocate any dominant gene marker onto the telocentric. If white hybrids are desired, it is possible to eliminate most of the trisomes by using the Y_1 gene marker. Some of the telocentric trisomes could be eliminated by using only the heavier seed.

This procedure has some advantages over the method proposed by Dr. Earl Patterson in which a duplicate-deficient chromosome is used to carry the M_s allele. The duplicate-deficient chromosome is not transmitted through the pollen and it remains in the cytoplasm in which it was produced. Thus, if this method is widely used, it would lead to homogeneity of cytoplasm which would be dangerous since a new mutant form of a pathogen could arise to attack lines with this cytoplasm. (This difficulty could be overcome by crossing the duplicate-deficient line with a tetraploid. The resulting triploid could then be crossed as the male parent onto diploids and after a few generations the trisomic progeny could be removed from the population leaving the duplicate-deficient chromosome in new cytoplasmic backgrounds.) Since the telocentric is transmitted at a low frequency through the pollen we do not have this problem.

However, the main advantage of the telocentric trisome system is that the pollen parent (4) of the initial commercial cross would be almost all of the desired type, whereas in the duplicate-deficient system only half of the plants in the pollen parent rows would be male fertile.

The disadvantage of the telocentric system is the transmission of the hyperploid gametes through the pollen; while the frequency is low (1.85%), it is not tolerable. It should be possible by selection and structural modification of the telocentric by irradiation to lower this frequency.

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