

Effect of trisomy 4 on intergenic recombination
in chromosome 9 of maize

We are using monosomic analysis as a probe to analyze the maize genome. In a monosomic of a diploid species, an entire chromosome is present in the hemizygous condition. By comparing a plant monosomic for a specific chromosome with its disomic siblings, one compares one and two copies of all genes on an entire chromosome simultaneously. If a gene that exhibits dosage effects is present on the monosomic chromosome then a difference will be found between these two plant types for the experimental parameter being measured. In this way, one screens simultaneously all gene loci on a given chromosome by gene dosage comparisons. With this new method of analyzing the genome, one analyzes each gene locus on a given chromosome without inducing gene mutations. We are currently screening the maize genome with this approach to detect factors affecting genetic recombination.

I recently found (Weber, submitted for publication) that intergenic recombination in the sh-wx region of chromosome 9 in monosomic-4 plants testcrossed as males ($11.2 \pm 0.8\%$) is less than half of that found in comparable crosses with diploid control plants ($23.0 \pm 0.8\%$). A significant but smaller reduction in recombination was also found in monosomic-8 plants ($17.1 \pm 0.9\%$) but not in monosomic 7 plants ($21.8 \pm 1.8\%$). Therefore, monosomy per se does not cause a reduction in recombination in the sh-wx region.

To further explore the recombinational alteration detected in monosomic 4 plants, I initiated a series of experiments to compare the amount of recombination in this same region (sh-wx) of chromosome 9 in trisomic 4 plants with that occurring in diploid sibling plants. A trisomic 4 stock (from G. Doyle) was planted, and a trisomic 4 plant from this stock was crossed as a female parent with the same sh wx inbred that was used in the monosomic study described above. This sh wx stock was originally obtained from M. M. Rhoades.

Trisomic and diploid sibling plants from this cross were identified from somatic chromosome counts of root tips. The trisomics and diploids were each test-crossed both as male and female parents. The results are given in Tables 1 and 2.

Table 1. Recombinational frequency in the sh-wx region of chromosome 9 where heterozygous trisomic 4 and diploid sibling plants were testcrossed as male parents.

Plant	Plant type	No. kernels scored	% recombination in <u>sh-wx</u> region	$\bar{X} \pm SE$
75-603-1	Trisomic 4	530	22.6	
75-603-6	Trisomic 4	256	28.1	
75-603-12	Trisomic 4	230	26.1	25.6 ± 1.6
75-602-9	Diploid	805	21.6	
75-602-13	Diploid	504	23.6	
75-602-6	Diploid	712	22.1	$22.4 \pm .6$

Recombinational frequencies in the four classes (trisomics crossed as males, trisomics crossed as females, diploids crossed as males, and diploids crossed as females) were each found to be homogeneous by means of a Chi square test for homogeneity of binomial proportions, and a pooled frequency was calculated for each class.

Table 2. Recombination frequency in the sh-wx region of chromosome 9 where heterozygous trisomic 4 and diploid sibling plants were testcrossed as female parents.

Plant	Plant type	No. kernels scored	% recombination in <u>sh-wx</u> region	$\bar{X} \pm SE$
75-603-1	Trisomic 4	141	21.3	
75-603-11	Trisomic 4	207	22.2	
75-603-12	Trisomic 4	288	19.1	20.9 \pm .9
75-602-6	Diploid	478	19.5	
75-602-13	Diploid	456	19.5	
75-603-9	Diploid	426	17.6	18.9 \pm .6

A highly significant ($p < .005$) increase in recombination in the sh-wx region occurred in males (pooled trisomics and diploids) over that which took place in females (pooled trisomics and diploids). Numerous other investigators have also found that recombination in male maize flowers is higher than in female flowers (reviewed by Phillips 1969, Genetics 61:117, and Ghidoni 1975, Genetics 81:253).

When all diploid crosses (both as male and female parents) are compared with all trisomic crosses (both as male and female parents), the data are nearly significantly different ($p = .06$). Therefore, recombination appears to be higher in trisomic 4 plants than in diploid plants. Although the recombinational frequency in male flowers of trisomic 4 plants ($25.6 \pm 1.6\%$) is higher than that in their sibling diploids ($22.4 \pm .6\%$), the increase was not statistically significant ($p = .12$). The increase in recombination in the female flowers induced by the addition of an extra chromosome 4 (from $18.9 \pm .6\%$ to $20.9 \pm .9\%$) was smaller ($p = .37$). Ghidoni (1975, Genetics 81:253) found that trisomy of chromosome 6 increased recombination in the sh-wx region in both sexes of maize by approximately the same amount.

As noted before, I testcrossed heterozygous monosomic 4 and control diploid maize plants as males to determine if monosomy could alter recombination in the sh-wx region. Monosomic 4 plants had only $11.2 \pm .8\%$ whereas diploid control plants had $23.0 \pm 0.8\%$. Therefore, monosomic 4 plants had only approximately half the amount of recombination found in their diploid controls. If the amount of recombination in the sh-wx region in chromosome 9 was proportional to the number of chromosomes 4, then a recombinational frequency in the trisomic 4 plants male flowers would be expected to be 1-1/2 times that found in the diploid siblings (or $1.5 \times 22.24\% = 33.36\%$). This obviously was not the case because the recombination frequency increased to only 25.61%. It therefore appears that a plateau in recombinational alteration is being reached. These data indicate that monosomic-diploid comparisons are a far more sensitive system for measuring this continuously variable quantitative trait, and presumably other quantitative traits, than disomic-trisomic comparisons.

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The homeostatic nature of the acid extractable amino acids (free amino acid pool) in leaves

Since the acid extractable amino acid pool (free amino acid pool) is an intermediate, and not an end-product of a series of reactions involved in protein