# 4. The duplication of specific chromosome segments by crossing translocations involving the same chromosomes.

The technique for the duplication of specific chromosome segments was first proposed by H. J. Muller (Journal of Genetics 23:299-334) in 1930. In 1956, Gopinath and Burnham worked out the problem in great detail (Genetics 41:382-395).

Pairs of translocations suitable for the duplication of chromosome segments containing the y, wx, ae, or su, locus have been crossed with each other. It is hoped that the duplication of these loci will modify the chemical composition of the corn endosperm. Also some information about gene action should result from this work. If a recessive gene is an amorph, its duplication should have no effect. If a recessive gene is a hypomorph, then its duplication should result in a phenotype which approaches or exceeds the dominant phenotype.

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## 1. A new gene to mark the distal end of the short arm of chromosome 6.

In a previous newsletter (No. 33 p. 102) a recessive ragged seedling character here designated  $\underline{rgd}$  was shown to be on the opposite side of  $\underline{y}$  from  $\underline{ts}_8$  and later to be to the left of  $\underline{y}$ . For repulsion data were obtained from 9425 seedlings from 29 ears with the genotype  $\underline{rgd}$   $\underline{y}/+\underline{Y}$  classified as follows:

which indicates approximately 13% recombination and places  $\underline{rgd}$  very close to  $\underline{po}$ .

In 1960, one selfed ear from a plant with the genotype + po  $\underline{Y}$  + /rgd + y tsg and 3 from plants with the genotype + po  $\underline{Y}$  / rgd + y were obtained. Seeds were grown and plants which shed pollen were selfed. Plant classifications from these  $\mu$  F2 progenies are in Table 1.

Table 1

Phenotype	60-4108-3	60-4108-5	60-4108-6	60-4108-10
+ Y +	88	70	126	514
po Y +	45	28	48	32
+ Y ts8	2	- ,`	•	
- Y -*	54	<u>41</u>	40	33
+ y <sub>.</sub> +	Ò	17	41	15
роу+	0	1	1	. 3
+ y ts8	27	-		
- y -*	43	- 31	<b>3</b> 6	27
Sum	259	188-	292	164

\* Seeds did not germinate or plants did not emerge.

Plants in the phenotypic classes  $\underline{Y}$  and  $\underline{y}$  were selfed. The numbers of plants selfed in each progeny and their genotypes with respect to  $\underline{Y}$   $\underline{y}$  and  $\underline{rgd}$  as determined by seedling tests are in Table 2. The genotypes are designated by classes 1 to 6.

Table 2

Class	Genotype	60-4108-3	60-4108-5	60-4108-6	60-4108-10
1 2 3 4 5 6	Y + / Y + Y + / Y rgd Y + / y + Y + / y rgd y + / y + y + / y rgd	0 3 8 61 0	0 3 3 43 3 9	1 6 8 94 0 17	0 6 3 34 0 5
Total e	ears	72	61	126	48

The classes in Table 2 were established by germinating and classifying 20 seeds from Y Y and y y ears and 20 white seeds from each Y y ear. This procedure could result in placing Y rgd / y + ears in class 3. The data from white seeds of class 4 ears are in Table 3.

Table 3

1960 Ear	No. of 1961 progeny ears	+	rgd	Sum	% Recombinations
4108-3	61	404	768	1172	19.1
<b>-</b> 5	43	260	532	792	18.1
<b>-</b> 6	94	602	1193	1795	18.5
-10	34	158	473	631	13.4
Sum	232	<b>1</b> ]†5]†	2966	4390	17.8

<sup>\*</sup> p =  $1-\sqrt{\frac{d}{n}}$  where d = y rgd class

The recombination values are consistent around 17.8% indicating rgd to be to the left of po. Classes 1 and 5 of Table 2, however, provide the critical comparisons.

With the genotype + po Y /  $\underline{rgd}$  +  $\underline{y}$  and assuming the order and distances to be  $\underline{rgd}$ - $\underline{h}$ - $\underline{po}$ - $\underline{lh}$ - $\underline{y}$ , a class 5 ear may be obtained by union of two gametes each with a single crossover, one of which must be in region 1. This will occur with an expected frequency of  $\underline{l}$ % of the selfed  $\underline{y}$  y ears to give  $\underline{+}$  po  $\underline{y}$  /  $\underline{+}$  +  $\underline{y}$  or  $\underline{+}$  +  $\underline{y}$  /  $\underline{+}$  +  $\underline{y}$  genotypes. With the positions of  $\underline{rgd}$  and  $\underline{po}$  reversed, only  $\underline{.}$ 17% of selfed  $\underline{y}$   $\underline{y}$  ears are expected to breed true for  $\underline{Rgd}$  and this only if no chromosome interference is assumed. The observed proportion was  $3/3\underline{l}_1$  or almost 9%.

The single ear in class 1 is equally interesting. With  $\underline{rgd}$  to the left of  $\underline{po}$  a noncrossover and a double crossover are required as a minimum to give  $\underline{+} + \underline{Y} / \underline{+} \underline{po} \underline{Y}$ . The expected frequency is 1% of the selfed  $\underline{Y}$   $\underline{Y}$  ears. With  $\underline{po}$  and  $\underline{rgd}$  reversed a noncrossover gamete and a region  $\underline{I}$  crossover gamete will give  $\underline{po} + \underline{Y} / \underline{+} \underline{Y}$  and two gametes each

with a single crossover in region 1 will give + + Y / + + Y. The combined expectation of these two genotypes is 22% of selfed Y Y ears. The observed frequency is 1/19 or about 5%.

Thus both classes 1 and 5 in Table 2 as well as the recombination percentages in Table 3 agree in placing rgd distal to po on the short arm.

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## Synthesis of hybrid esterase enzymes in E heterozygotes.

By investigating newly synthesized enzymes that are still associated with the template on which they were synthesized, we have been able to establish that in the heterozygotes the new hybrid enzymes are synthesized as such on the ribosomes and do not result from random dimerization of previously synthesized monomers. We have been able to rule out the possibility that the particle-bound enzymes represent nonspecific adsorption of free enzymes to the ribosomes. The hybrid enzymes very probably result from interaction between two messenger RNA molecules specified by the two alleles, each of which contributes some information to the specificity of the hybrid enzyme.

Drew Schwartz

## 2. Regulatory mutant at the E locus.

The esterase enzymes specified by the E alleles are normally synthesized in the maternal tissue, endosperm, and embryo of the developing kernel as well as in the young seedling. A mutant has been found which affects the distribution of the enzyme in these tissues. Normal amounts of enzyme are synthesized in the diploid tissue but synthesis of the enzyme in the endosperm is almost completely blocked. The mutant, designated  $\mathbf{E}^F$ , controls the synthesis of an F type enzyme that shows the same electrophoretic mobility as the F type enzyme produced by the normally behaving  $\mathbf{E}^F$  allele. In heterozygotes the  $\mathbf{E}^F$  allele is not influenced by and does not affect the homologous allele so that, for example, in  $\mathbf{E}^F$  / $\mathbf{E}^F$  endosperm only N type enzyme is detected electrophoretically and in the amount expected from a single dose of the gene.

Since the E gene is not active throughout the life cycle of the plant, we propose that the E locus is compounded of a regulatory and structural gene. According to this hypothesis, E<sup>F</sup> has a mutant regulatory gene which fails to "turn on" the structural gene in the endosperm tissue. The regulatory gene is similar to the operon in the β-galactosidase case described by Jacob and Monod in that it operates only in the cis condition controlling the structural gene on the same chromosome, and is very closely linked to the structural gene. No crossovers have been found in over 2000 tested endosperms. Since the E alleles can be distinguished only by the electrophoretic migration rate of the esterase enzymes which they specify, the test involves individual electrophoresis of single, immature endosperms.

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