THE EFFECTS OF A HETEROZYGOUS TRANSLOCATION BETWEEN CHROMOSOMES I AND V ON CROSSING OVER IN CHROMOSOME V OF *NEUROSPORA CRASSA*

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INTRODUCTION

The effects of translocations on crossing over have previously been studied in several organisms. In general, these studies have shown that translocations tend to decrease crossing over, particularly in regions brought nearer to a centromere by the translocation. Although several translocations which produce phenotypic effects have previously been reported in Neurospora, little attention has been given to their effects on crossing over in this organism. The difficulty encountered in establishing gene order in Neurospora suggests that translocations may affect crossing over in this organism differently from the way they affect it in the higher organisms, and that a study of the effects of a translocation on crossing over should be made.

The present investigation was conducted to determine the effects of a translocation between chromosomes I and V on crossing over in chromosome V; to map the location of the break in chromosome V, and to map the location of a mutant gene which produces the same phenotypic effects as the translocation.

LITERATURE REVIEW

Results of Previous Studies on Translocations

Dobzhansky (4) studied crossing over in *Drosophila melanogaster* heterozygous for translocations and found that the translocations reduced crossing over in the chromosomes involved in the translocations. In five of the cases studied, the third and fourth chromosomes were involved in reciprocal translocations. In three of the translocations (a, b and e, Table I), the break occurred in the left arm of chromosome three, proximal to the *cu* locus and in the other two cases (c and d) the break occurred in the right arm proximal to the *ca* locus. Several genetic markers are located within the region between the centromere and the distal loci involved so that Dobzhansky (4) was able to study the effects of the translocations on crossing over in several segments of chromosome III. As shown in Table I, the translocations produced major reductions in crossing over in the arm of the chromosome in which the break occurred, but crossing over was normal or even slightly increased in the other arm of the chromosome.

Dobzhansky also studied four translocations which involve a transfer of a section of the second chromosome

TABLE I

THE EFFECTS OF FIVE TRANSLOCATIONS ON CROSSING OVER IN VARIOUS SEGMENTS OF CHROMOSOME III OF DROSOPHILA MELANOGASTER, AS COMPARED TO THE CONTROL. (DOBZHANSKY, 4)

Interval	Control Value	TRANSLOCATIONS a	b	c	d	e
ru-h	23.7	-6.5	-2.5	+3.2	+5.4	-4.2
h-d	13.7	-10.8	-7.8	+1.7	+1.1	-2.1
d-th	1.1	-0.9	-0.9	+0.4	0.0	0.0
th-st	0.8	-0.6	-0.5	+0.1	+0.1	-0.3
st-cu	8.0	-1.4	-3.4	-3.5	-2.1	-2.9
cu-sr	15.4	+1.2	+1.7	-11.7	-2.8	+0.2
sr-es	10.3	+1.4	-0.3	-2.8	-1.4	+1.3
es-ca	31.0	0.0	0.0	-2.1	-11.8	0.0

TABLE II

THE EFFECTS OF FOUR TRANSLOCATIONS ON CROSSING OVER IN VARIOUS SEGMENTS OF CHROMOSOME II OF DROSOPHILA MELANOGASTER, AS COMPARED TO THE CONTROL. (DOBZHANSKY, 4)

Interval	Control Value	TRANSLOCATIONS a	b	c	d
Left Arm:					
al-dp	13.6	-3.0	-13.3	-13.3	+0.1
dp-b	31.0	-0.2	-30.2	-21.4	+1.5
b-pr	8.5	+0.1	-8.0	-2.4	+0.7
Right Arm:					
pr-c	21.3	-19.5	-1.9	+5.1	-7.6
c-px	23.8	-19.0	+2.8	+6.5	-13.8
px-sp	7.1	-3.3	+1.3	-0.2	-4.5

to the fourth chromosome. In two cases (a and d, Table II), the break occurred in the right arm of the second chromosome. In the other two cases (b and c, Table II), the break took place to the left of the centromere. In all four cases, a reduction in the frequency of crossing over was observed in the arm in which the translocation occurred but crossover frequencies were not affected in the opposite arm (Table II). A decrease in the frequency of crossing over was observed in the whole arm in which the break occurred but the strongest reduction in crossing over was observed near the point of breakage. In all four cases, crossing over was normal in the opposite arm.

Four translocations which involve the second and third chromosomes were studied by Sturtevant and Dobzhansky (9). In two of these translocations, both the second and third chromosomes were broken at the spindle fiber. The left arm of the second and the left arm of the third chromosome united to form a 'new' chromosome, and the two right arms united to form another new chromosome. As a result of these changes in chromosome structure, crossover frequencies were decreased throughout the second and third chromosomes.

In another case, the third chromosome was broken at the spindle fiber and the second chromosome was broken to the left of its spindle fiber. The right arm of the third chromosome became attached to the longer fragments of the second chromosome, and the shorter

fragments of the second chromosome became attached to the left arm of the third chromosome. A reduction in crossing over was observed in the left arm of the second chromosome, and there was some reduction in crossing over in the whole third chromosome, but crossing over was normal in the right arm of the second chromosome. In the fourth translocation, a section of the left arm of the second chromosome became attached to but not at the end of the third chromosome. A striking reduction in crossing over was observed in the left arm of the second chromosome and in the left arm of the third chromosome, but crossing over was normal in the right arm of both chromosomes. Dobzhansky (4) has further studied a reciprocal translocation involving the X-chromosome and the second chromosome. The X-chromosome was broken at the bar locus and the second chromosome was broken at vestigial locus (right arm). Here again a reduction in crossing over was observed in the right arm of the second chromosome and part of the X-chromosome. On the other hand, the left arm of the second chromosome showed normal crossing over frequencies.

In another set of experiments, Dobzhansky (5) studied the effects of translocations and duplications on the frequency of crossing over. He mated yw males to females of the following constitution: translocation T_3-/sc-ec-cv-ct-v-g-f; translocation T_7/sc-ec-cv-ct-v-g-f. The frequencies of crossing over obtained in these

studies are shown in Table III. Crossing over was almost entirely suppressed in the y(sc)-ec interval. Further he crossed females that carried translocations T_7 and were also heterozygous for the second chromosome recessives al, dp, b, pr, c, px and sp to males of the constitution al, dp, b, pr, c, px, sp. The results of these experiments summarized in Table IV show that in the rearrangements crossing over was reduced in the px-sp interval but not in the other intervals. Reduction in crossing over in the px-sp interval was probably due to attachment of X-chromosome to the right of sp.

C. R. Burnham (2) studied crossing over in corn plants heterozygous for an interchange of a terminal piece of the short arm of chromosome 9 with a small terminal piece of the long arm of chromosome 5. He reported about two per cent recombination between the point of interchange and the waxy locus and about eight per cent with the shrunken locus. In plants heterozygous for the interchange yellow green-2 and shrunken gave eleven per cent, shrunken and waxy gave six per cent recombination, while the normal stocks were twenty-three and twenty per cent for the two intervals respectively. He observed that the greatest reduction took place in the region nearest the point of breakage.

G. W. Beadle (1) studied the effects of the spindle fiber on crossing over in Drosophila. Beadle used a translocation involving chromosomes III

TABLE III

FREQUENCIES OF CROSSING OVER IN THE X-CHROMOSOME OF FEMALES HETEROZYGOUS TO T_3 AND T_7 TRANSLOCATIONS AS COMPARED TO CONTROL.

	y-ec	ec-cv	cv-ct	ct-v	v-g	g-f
Control	4.07	7.22	6.37	13.64	12.38	9.70
Translocation T_3	0.42	0.64	2.80	10.57	11.38	13.41
Translocation T_7	0.0	1.34	3.25	11.67	10.39	9.35

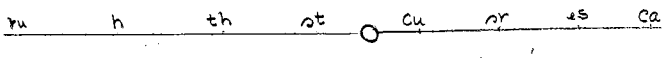
TABLE IV

THE EFFECT OF THE T_7 TRANSLOCATION ON FREQUENCIES OF CROSSING OVER IN THE SECOND CHROMOSOME AS A RESULT OF THE EFFECT OF TRANSLOCATION T_7 AS COMPARED TO CONTROL.

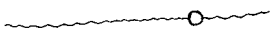
Interval	al-dp	dp-b	b-pr	pr-c	c-px	px-sp
Translocation T_7	11.83	27.47	10.08	19.68	18.75	3.76
Control	10.94	25.92	6.01	19.63	20.20	5.88

and IV, which was obtained in homozygous state. In this translocation, the section of the third chromosome including the curled locus and the regions to its right were brought nearer the centromere of chromosome IV while the region to the left of the curled locus remained unchanged relative to the centromere of chromosome III. The configuration of the normal and translocation chromosomes are illustrated by the following diagram:

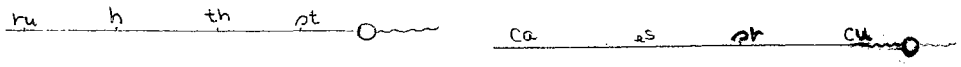
Normal III



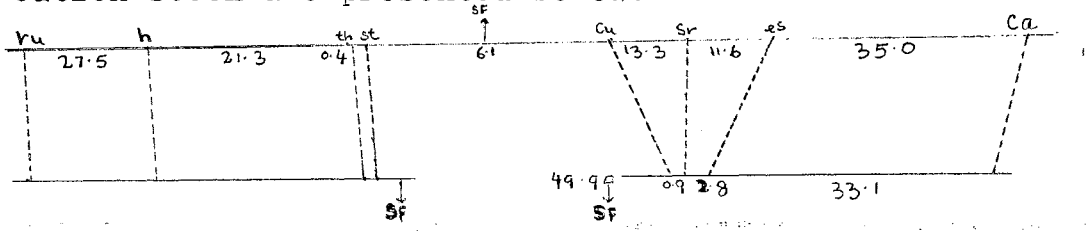
Normal IV



Translocation Chromosomes



The experiment was designed so as to compare the frequency of crossing over in the homozygous translocation stocks with that in the normal stocks carrying the same genetic markers. The comparative crossover frequencies in the control and in the homozygous translocation stock are presented below:



The above data indicate, rather conclusively, that the regions displaced nearer to the proximity of the chromosome IV centromere exhibited markedly reduced crossover frequencies, while those that remained unchanged relative to distance from the centromere

showed little change in the frequency of crossing over.

The information presented above in this literature review may be summarized as follows:

1. In the case of translocation heterozygotes; if a chromosome is broken between its centromere and its end, or if a fragment of another chromosome becomes attached to it, a reduction in the frequency of crossing over in this chromosome occurs.

2. The strongest reduction in crossing over occurs in the intervals near or at the point of the breakage or attachment.

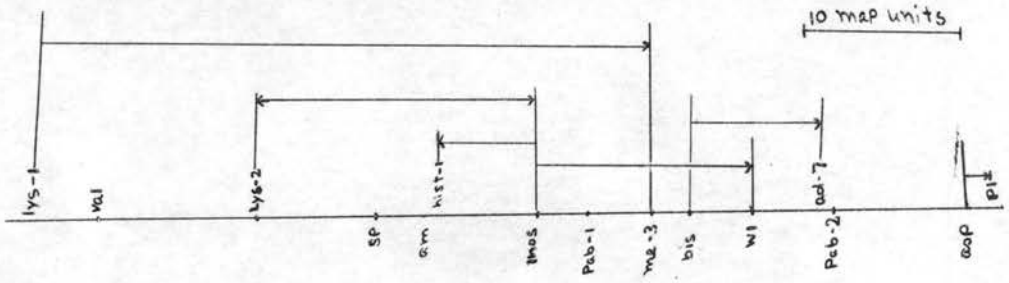
3. In V-shaped chromosomes, crossing over in one arm need not be influenced by events taking place in the opposite arm.

4. If a V-shaped chromosome breaks into two equal parts (ie, if the breakage occurs near the spindle fiber), crossing over in the resulting fragments may or may not be affected.

5. Studies on the effect of the spindle fiber on crossing over indicate that the spindle fiber interferes with crossing over in its immediate neighborhood.

Markers on linkage group V of Neurospora

Strickland, et al. (11), recently presented the following map of chromosome V of Neurospora Crassa:



In addition to the markers placed on chromosome V by Strickland, et al., Murray (7) has placed the translocation (pk-1) and gene mutation (pk-2) used in the present study on chromosome V, approximately 26 units from the centromere. Murray made no attempt to establish gene order in chromosome V.

MATERIALS AND METHODS

Stocks

The translocation stock utilized in the present investigation was isloated from wild-type *Neurospora* by Murray (7) after treatment of conidia with beta-propiolactone. Because of the effect this translocation produces on the phenotype, Murray (7) described the translocation stock as *peak* and proposed for it the gene symbol of *pk-1*. *Pk-1* was found to be the result of a translocation, as shown by linkage to both linkage groups I and V.

For studying the effects of the translocation on crossing over along chromosome V and for studying the linkage of the translocation; the following chromosome V markers were obtained from Dr. David Perkins of Stanford University: *methionineless-3* (*me-3*), *histidineless-1* (*hist-1*), *adenineless-7* (*ad-7*), *inositolless* (*inos*). A gene mutation (*pk-2*) with morphological effects similar to those of *pk-1* and located on chromosome V was also utilized in the present study as a marker. Since Murray (7) was unable to obtain recombination between *pk-1* and *pk-2*, it was concluded that *pk-2* is a gene mutation near the locus where the translocation break occurred in chromosome V. *Pk-2*

was also isolated from wild type after treatment with beta-propiolactone by Murray (7).

Medium

Minimal Fries medium supplemented to support growth of the biochemical mutants was used throughout the study, except for crossing. Fries medium has the following composition in grams per liter:

ammonium tartrate	5
ammonium nitrate	1
monobasic potassium phosphate	1
magnesium sulfate ($7H_2O$)	0.5
trace element solution	1 ml
biotin	5 x 10-6
calcium chloride ($2H_2O$)	0.10
sucrose	2.0

The trace element solution contains the following per liter:

boric acid H_3BO_3	30.0 mg
or $K_2B_4O_7 \cdot 5H_2O$	160.0 mg
$CuCl_2$ (Cuprice)	125.0 mg
$FeCl_3 \cdot 6H_2O$	500.0 mg
$MnSO_4$	30.0 mg
molybdic acid	170.0 mg
or $(NH_4)6Mo_7O_{24} \cdot H_2O$	12.4 mg
$ZnCl_2$	2,000.0 mg
or $ZnSO_4$	2,600.0 mg

The concentration of each of the amino acids used in this study to support growth of the various amino acid requiring mutants used as genetic markers was 10 mg per 100 ml of medium. The concentration of inositol and adenine sulfate used to support the growth of the inositol and adenine requiring mutants was 5 mg of the respective compound per 100 ml of medium.

Crosses were made on water agar medium containing one per cent corn meal. Culture of the isloates

and the identification of the biochemical markers were carried out in the manner described by Beadle and Tatum (3).

RESULTS AND DISCUSSION

As previously stated, the objective of this investigation was to determine whether a translocation between chromosome I and chromosome V has any effect on the frequency of crossing over in several segments of chromosome V. The difficulty encountered in assigning gene order in *Neurospora* compared to that encountered with higher organisims (Mitchell 6) suggests that the crossing over mechanism may be somewhat different in *Neurospora* and that such a study might yield vital information concerning the genetic system of this organism.

In order to determine the effect the translocation has on crossing over, several stocks carrying various markers along chromosome V were crossed with a stock carrying a translocation between chromosomes I and V (*pk-1*) and with a stock carrying a point mutation (*pk-2*) at the locus at which the translocation break occurred in chromosome V. The results from these two types of crosses were compared for cross over frequency.

Linkage position of pk on chromosome V

Although data are presented here from only two three-point crosses, the linkage position can be fairly well established from these data and from data pre-

sented by Strickland, et al. (11). The data presented in Tables V and VI show that in three point crosses involving pk, inos and hist-1, pk and hist-1 are further removed from each other than either is from inos, indicating that inos is located between the pk locus and the hist-1 locus. Since Strickland, et al. (11) have shown inos to be distal to hist-1, then pk must be distal to inos. This order is consistant with the frequency of recombinant classes. The other three point crosses presented here are crosses involving pk, me-3 and ad-7. Me-3 has been placed distal to inos and ad-7 is distal to me-3. The data from three point crosses presented in Table VII and Table VIII show that me-3 is between pk and ad-7, since it is nearer to both pk and ad-7 than ad-7 and pk are to each other. The lack of the recombinant classes that would represent double crossover products for this order substantiates this conclusion.

Considering the data presented above and the data presented by Strickland, et al. (11), the following gene order can be established for the loci used in this study: hist-1 - inos - pk - me - ad-7.

The conbined data presented in Tables V and VI show that inos and hist-1 are 7.92 map units apart and that inos and pk are 12.02 map units apart. The combined data presented in Tables VII, VIII and XIII indicate that pk and me-3 are 3.31 units apart

TABLE V

NUMBERS OF INDIVIDUALS OCCURING IN THE VARIOUS GENOTYPIC CLASSES FROM THE CROSS PK-1a x HIST-1 INOS A

pk + +	182
+ inos hist	274
pk inos hist	32
+ + +	33
pk + hist	42
+ inos +	0
pk inos +	0
+ + hist	0
	563

TABLE VI

NUMBERS OF INDIVIDUALS OCCURING IN THE VARIOUS GENOTYPIC CLASSES FROM THE CROSS PK-2a x HIST-1 INOS A

pk + +	118
+ inos hist	305
pk inos hist	33
+ + +	34
pk + hist	34
+ inos +	11
pk inos +	0
+ + hist	0
	535

TABLE VII

NUMBERS OF INDIVIDUALS OCCURING IN THE VARIOUS GENOTYPIC CLASSES FROM THE CROSS PK-1-ME-3A x AD-7a

pk + +	151
+ me ad	215
pk me ad	13
+ + +	9
pk + ad	34
+ me +	3
pk me +	0
+ + ad	0
	425

TABLE VIII

NUMBERS OF INDIVIDUALS OCCURING IN THE VARIOUS GENOTYPIC CLASSES FROM THE CROSS PK-2-ME-3A x AD-7a

pk + +	234
+ me ad	210
pk me ad	12
+ + +	3
pk + ad	21
+ me +	4
pk me +	0
+ + ad	0
	484

and Tables VII and VIII indicate that me-3 and ad-7 are 6.82 units apart.

Effects of the translocation, pk-1, on crossing over

The data for comparing the frequency of crossing over in crosses involving a heterozygous translocation with the frequency of crossing over in non-translocation crosses are presented in Tables IX to XIII. In order to determine whether the translocation has any significant effect on the frequency of crossing over in chromosome V, the data were analysed to determine whether the progeny from the crosses involving the translocation contained the same proportions of parental and of non-parental genotypes as did the progeny from the same crosses involving non-translocation stocks. This comparison was made by the use of the heterogeneity chi-square as described by Snedecor (10). Heterogeneity chi-square values were also calculated for the entire spectrum of genotypic classes resulting in each cross in order to determine whether the data from the two types of crosses were homogeneous throughout. In three cases, when all of the classes were considered, the data from the crosses involving the heterozygous translocation were not homogeneous with those from the same crosses lacking the translocation. In two of these cases, the heterogeneity was produced by an inconsistency in the frequency of one parental class (tables IX and XII). In the other case where the data

TABLE IX

COMPARATIVE FREQUENCY OF CROSSING OVER BETWEEN INOS AND HIST-1 IN CROSSES INVOLVING PK-1 AND PK-2

	Frequency			
	pk-1 (cross pk-1a x hist-inos A)		pk-2 (cross pk-2a x hist-inos A)	
Genotype	Obs.	Cal.	Obs.	Cal.
parental:	498	495.3	468	470.6
pk +	224	192.8	152	183.1
+ inos	274	302.6	316	287.3
non-parental:	65	67.7	67	64.3
+ +	33	34.3	34	32.6
pk - inos	32	33.3	33	31.6

Heterogeneity $x^2 = 16.119^{**}$
parental-non-parental heterogeneity $x^2 = 0.049$ p=.97-.99

TABLE X

COMPARATIVE FREQUENCIES OF CROSSING OVER BETWEEN INOS AND HIST-1 IN CROSSES INVOLVING PK-1 AND PK-2

	Frequency			
	pk-1 (cross pk-1a x hist-inos A)		pk-2 (cross pk-2a x hist-inos A)	
Genotype	Obs.	Cal.	Obs.	Cal.
parental:	521	518.39	490	492.6
inos-hist	306	330.0	338	314.0
+ +	215	188.0	152	178.0
non-parental:	42	44.6	45	42.39
inos +	0	6.0	11	5.0
+ hist	42	39.0	34	37.0

Heterogeneity $x^2 = 25.226^{**}$
parental-non-parental heterogeneity $x^2 = 0.324$ df = 1
p = 0.500 - 0.250

TABLE XI

COMPARATIVE FREQUENCY OF CROSSING OVER BETWEEN AD-7 AND ME-3 IN CROSSES INVOLVING PK-1 AND PK-2

	Frequency			
	pk-1 (cross pk-1 me-A x ad a)		pk-2 (cross pk-2 me-A x ad a)	
Genotype	Obs.	Cal.	Obs.	Cal.
parental:	403	407.7	469	464.2
pk +	185	205.4	255	234.0
+ me	218	201.7	214	229.8
non-parental:	22	17.2	15	19.7
+ +	9	5.6	3	6.3
pk - me	13	11.6	12	13.3

Heterogeneity $x^2 = 10.541$ p = .01 - .025
parental-non-parental heterogeneity $x^2 = 2.563$
p = 0.100-0.050

TABLE XII

COMPARATIVE FREQUENCY OF CROSSING OVER BETWEEN AD-7 AND ME-3 IN CROSSES INVOLVING PK-1 AND PK-2

	Frequency			
	pk-1 (cross pk-1 me-A x ad a)		pk-2 (cross pk-2 me-A x ad a)	
Genotype	Obs.	Cal.	Obs.	Cal.
parental:	388	396.01	459	450.98
ad me	228	210.15	222	239.40
+ +	160	185.39	237	211.20
non-parental:	37	28.98	25	33.01
+ ad	34	25.68	21	29.26
me +	3	3.26	4	3.72

Heterogeneity $x^2 = 14.414^{**}$
parental-non-parental heterogeneity $x^2 = 4.466$
p = 0.05-0.028

TABLE XIII

COMPARATIVE FREQUENCY OF CROSSING OVER BETWEEN *ME-3* AND *PK* IN CROSSES INVOLVING *PK-1* AND *PK-2*

	Frequencies			
pk-1 (cross *pk-1A* x *me-a*)			*pk-2* (cross *pk-2A* x *me-a*)	
Genotype	Obs.	Cal.	Obs.	Cal.
parental:	563	562.9	666	666.03
pk +	292	299.9	363	354.35
+ *me*	271	262.8	303	310.53
non-parental	16	16.03	19	18.9
+ +	0		0	
pk - *me*	16	16.03	19	18.9

Heterogeneity $x^2 = 0.955$ $p = .75 - .90$

parental-non-parental heterogeneity $x^2 = 0.000$

were not homogeneous, the inconsistency in the frequency of parental types was also present, but in addition one of the non-parental classes was missing altogether in the translocation cross (table X).

When the data were analysed only for their consistency in numbers of parental and of non-parental genotypes the crosses involving the translocation were homogeneous with those not carrying the translocation. This finding indicates, very strongly, that the heterozygous translocation has little if any effect on crossing over in chromosome V, at least in the regions tested.

Two possible explanations can be offered at this time for the three cases where the data from the two types of crosses were heterogeneous. The most logical explanation is the possibility of errors in the classification of the progeny. The second explanation might be that certain classes have differential viability because of linked genes. Nevertheless, even in view of the heterogeneity in three crosses, the consistency throughout the data in the proportions of the parental and non-parental in the two types of crosses in all of the marker combinations tested can lead to no other conclusions than that the effects of this translocation are very small indeed compared to the effects of the translocations studied in higher organisms.

In view of the large effects translocations have been found to have on crossing over in such higher organisms as Drosophila and Maize (4, 2), the results

presented here appear to indicate that the genetic system of Neurospora differs from those of the higher organisms just mentioned. Perkins (8) has reported similar findings with other translocations in Neurospora since the present study was initiated. In fact, Perkins (8) found indications that the translocation might have actually increased the frequency of crossing over in the chromosomes involved in the translocation. Although there is not sufficient data available at present to give definite explanations for the differences in the effects of the translocations in Neurospora compared to the effects of the translocations in higher organisms, some speculations might not be premature. It would appear possible that whereas the heterozygous translocations might prevent the chromosomes in the higher organisms from pairing in the vicinity of the translocation break, in Neurospora the chromosome might be fine enough or pliable enough to allow sufficient pairing for crossing over despite the presence of the translocation. On the other hand, the difficulty encountered in establishing gene order in Neurospora compared to the relative ease in the higher organisms suggests that the two genetic systems might be quite different in their behavior at meiosis and the lack of the effects of the translocation might be more complex than the mere ability of the Neurospora chromosomes to pair in the vicinity of the break.

A finding of equal interest is the apparent lack of any

influence by the centromere on crossing over. Murray (7) found that the segment of chromosome V is attached to chromosome I about two map units from the centromere and pk-2 is approximately 26 units from the centromere of chromosome V. Since the data presented here indicate that pk-1 is located between inos and me-3 the regions between pk-1 and me-3 and between me-3 and ad-7 must have been moved closer to a centromere through the translocation. In contrast to the absence of any significant influence of the centromere on crossing over in the case reported here, Beadle (1) found that crossing over is greatly reduced in Drosophila when a region is brought nearer to the centromere by a translocation. This finding also suggests that the differences between the genetic system of Neurospora and those of the higher organisms might be quite pronounced and that a knowledge of these differences would be of fundamental importance in understanding the nature of the hereditary material.

SUMMARY AND CONCLUSION

The present study was conducted to determine what effect a translocation between chromosomes I and V has on the crossing over in various segments of chromosome V, also the positions of the translocation (*pk-1*) and of a gene mutation (*pk-2*) with similar effects on the morphology were mapped on chromosome V.

Pk was found to be located on chromosome V between *inos* and *me-3* about 12.02 units apart from *inos* and about 3.31 units from *me-3*.

By the use of a homogenity chi-square test, the frequencies of non-parental segregants occuring in the progeny from crosses involving the translocation were compared to those from crosses not involving the translocation. In 5 comparisons, there was not a single case in which the cross involving the translocation differed signigicantly from the control cross. This indicates that the translocation (*pk-1*) has little, if any, effect on the frequency of crossing over in chromosome V of *Neurospora crassa*.

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Master of Science

Thesis: THE EFFECTS OF A HETEROZYGOUS TRANSLOCATION BETWEEN CHROMOSOMES I AND V ON CROSSING OVER IN CHROMOSOME V OF NEUROSPORA CRASSA

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