

THE EFFECTS OF CHROMOSOME SUBSTITUTION ON MALE BODY
WEIGHT OF *DROSOPHILA MELANOGASTER*

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THE manifestation of a quantitative trait is dependent upon the relationship of a number of genes in the same and different chromosome pairs. The nature of these relationships can be studied by comparing the effects of homologous chromosomes from different strains in a controlled genetic background. In experiments of this kind, the effects of the genes involved can be described in terms of effects of single chromosomes and of interaction between different chromosomes. A simplifying assumption which has been made frequently in the past is that there are a number of genes involved in the realization of the characters which act in a plus or minus direction. Depending on the balance of plus and minus genes in a particular chromosome, the chromosome itself will have a plus or minus effect. The plus and minus effects of different chromosomes would then determine the final value of a character. Additivity of groups of genes is the simplest assumption for this model, but other methods of synergy can be easily interpreted in this way.

It has, however, been shown that the action of genes affecting quantitative characters may depend on the genotypic environment, i.e. on other genes present in the same organism. In an organism with few chromosomes, such as *Drosophila*, it is possible to define the genotypic environment more closely by localizing the effects of the genotypic environment in one of the large chromosomes—the small fourth chromosome is usually neglected in studies of quantitative inheritance. The effect of the genic environment would then appear in the form of an interaction between different chromosomes. It is the purpose of the present paper to analyze the genetic determination of male body weight in four inbred strains of *Drosophila melanogaster* in terms of the action of the three major chromosomes.

In studies of this type, it is difficult to differentiate between the contributions of the hereditary and environmental components of variance to the phenotype of the population. However, if one component of variance can be eliminated, the other can be estimated from the remaining variation of the phenotype. The use of isogenic strains effectively eliminates genotypic variation. Thus, a group of isogenic individuals raised under defined environmental conditions will exhibit a range of phenotypes which leads to an estimate of the environmental effects under these conditions. The effects obtained from one isogenic strain under specific environmental circumstances are peculiar to that strain. Other isogenic

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strains raised under identical conditions may be more or less susceptible to those particular environmental influences and may show greater or smaller effects.

In studying the effects of selection on each major chromosome in *D. melanogaster*, MATHER and HARRISON (1949) used a method of chromosome assay which yielded a limited number of genotypic classes for the determination of the contributions of each chromosome to the number of chaetae. ROBERTSON examined the effects of different chromosomal combinations from selected and unselected strains on wing length (1954), thorax length (1954, 1961) and wing cell size (1961) in *D. melanogaster*. He observed dominance, additive effects and interactions in various genotypes. KELLER and MITCHELL (1962, 1964) found that inserting identical X chromosomes of *D. melanogaster* into different autosomal backgrounds resulted in a differential mean expression for several characters relating to morphology and viability.

For the analysis of chromosome differences between strains, a breeding method was devised which made it possible to create all possible combinations of major chromosomes between pairs of isogenic strains. The resultant substituted strains and the parental strains were raised in a single controlled environment. Any phenotypic differences observed among the strains must be due to genetic differences of the strains. Thus, the effects of chromosome substitution can be measured, interactions of chromosomes can be detected and compared and the effects of individual chromosomes on the quantitative trait can be determined.

MATERIALS

The isogenic strains used in this research are P_1 I Oregon-R, Ives Oregon-R, Canton-S and M Oregon-R (SEIGER 1958). P_1 I Oregon-R was obtained in 1956 at generation 236 and subsequently maintained for 119 generations. Ives Oregon-R, Canton-S and M Oregon-R were obtained in 1957 at generations 195, 14 and 201 respectively and subsequently were maintained for 106 generations. All the strains were maintained by single brother-sister pair matings each generation. The strain P_1 I Oregon-R was arbitrarily chosen as the standard strain whose chromosomes would be replaced by chromosomes from each of the other three strains. The homozygous chromosome pairs of P_1 I Oregon-R are designated by the single letters AAA, the three letters referring to the X, second and third chromosome respectively. The diploid designation A/A; A/A; A/A is used only in Figures 1, 2 and 3. For the sake of brevity the strain P_1 I Oregon-R is referred to as strain A. Strains Ives Oregon-R, Canton-S, and M Oregon-R are referred to as strains B, C, and D respectively and their chromosomes are indicated in the same way.

A special strain was used in which the three major chromosomes contained inversions to suppress crossing over and dominant marker genes to keep track of the wild-type chromosomes from the isogenic strains during the course of chromosome substitution. VICTOR TINDERHOLT and I synthesized such a Complete Multiple Inversion (CMI) stock from three inversion stocks obtained from DR. E. B. LEWIS, California Institute of Technology. The three inversions are *FM6* (GRELL and LEWIS 1956), an X chromosome balancer containing Bar (*B*) yellow (γ), scute-8 (*sc⁸*) and diminutive (*dm*); *SM5* (MISLOVE and LEWIS 1955), a second-chromosome balancer containing Curly (*Cy*) as well as three recessive genes; *TM3* (LEWIS 1960), a third-chromosome balancer containing several recessive genes and an insertion of the normal alleles of yellow (γ^+) and achaete (*ac⁺*) transposed from the X chromosome to the left tip of the *TM3* chromosome. These transposed genes serve to detect crossing over in the tip of 3L. *FM6*, *TM3* individuals have a normal body color. If a crossover occurs in the tip of (3L), the γ^+ gene is no longer present and the body color of *FM6*, *TM3* is yellow. Thus, crossover progeny can be detected and discarded. The dominant gene Serrate (*Ser*), located approximately at 92.5 on the recombination

map where the largest of the inversions in *TM3* lies, was introduced by TINDERHOLT (1960) into *TM3* in the presence of *FM6* and *SM5* by a double crossover which occurred once in 20,000 gametes. Females homozygous for *FM6* are sterile. The inversions *SM5* and *TM3* are lethal when homozygous.

The CMI stock was designed to be a balanced lethal system. The dominant markers used on the balanced chromosomes are Hairy (*Hw*) on the X (which produces sterility when homozygous in females while leaving the homozygous males fertile); Sternopleural (*Sp*) and brown-dominant (*bw^D*) on 2 (*Sp* being lethal when homozygous and *bw^D* conferring a more easily recognizable phenotype); and Stubble (*Sb*) on 3 (lethal when homozygous). The interaction of all the inversions and marker genes, even in the most favorable conditions, produces a strain of low viability. When CMI individuals are inbred, only five out of 64 possible genotypes are viable and of these, only three are fertile. The fourth chromosome was left unbalanced, since it has few genes and these genes have little effect on the overall phenotype (ROBERTSON 1954; BELL 1956). The CMI stock is designated *Hw/FM6; Sp bw^D SM5; Sb/TM3*. The first chromosomes in males may be either *Hw/Y* or *FM6/Y*.

Method of substituting chromosomes: The breeding method shows how individual chromosomes in strain A are replaced by chromosomes from another strain. In the first generation (Figure 1), strain A females are crossed with CMI males. From this cross Curly Serrate males are collected and crossed with CMI females in Generation 2. Of the progeny of the second cross, only three different phenotypes can be used. These are Bar Sternopleural brown-dominant Stubble males, used to replace the strain-A X chromosome; Bar Sternopleural brown-dominant Curly Stubble males used to replace the X and second chromosomes; Bar Sternopleural brown-dominant Stubble Serrate males used to replace the X and third chromosomes. In the third generation, each of the three types of males is crossed with Curly Serrate females (Figure 3) in which strain B chromosomes are balanced. The Generation 3 crosses are made with as large a number of individuals as possible. From each of these three crosses, Bar Curly Serrate females

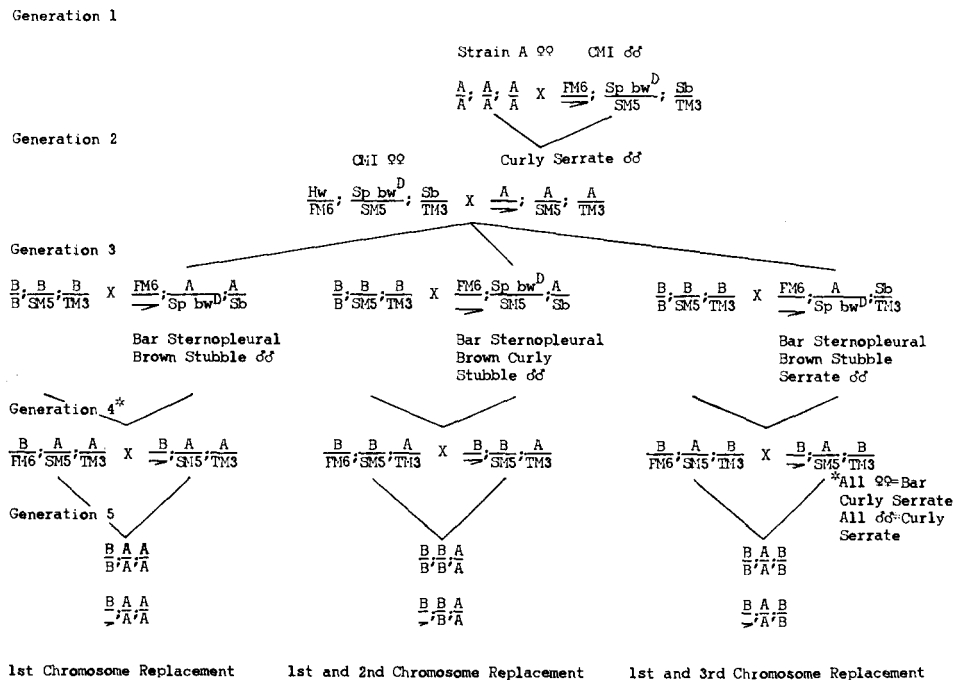


FIGURE 1.—Preparation of substituted strains: First-Chromosome combinations.

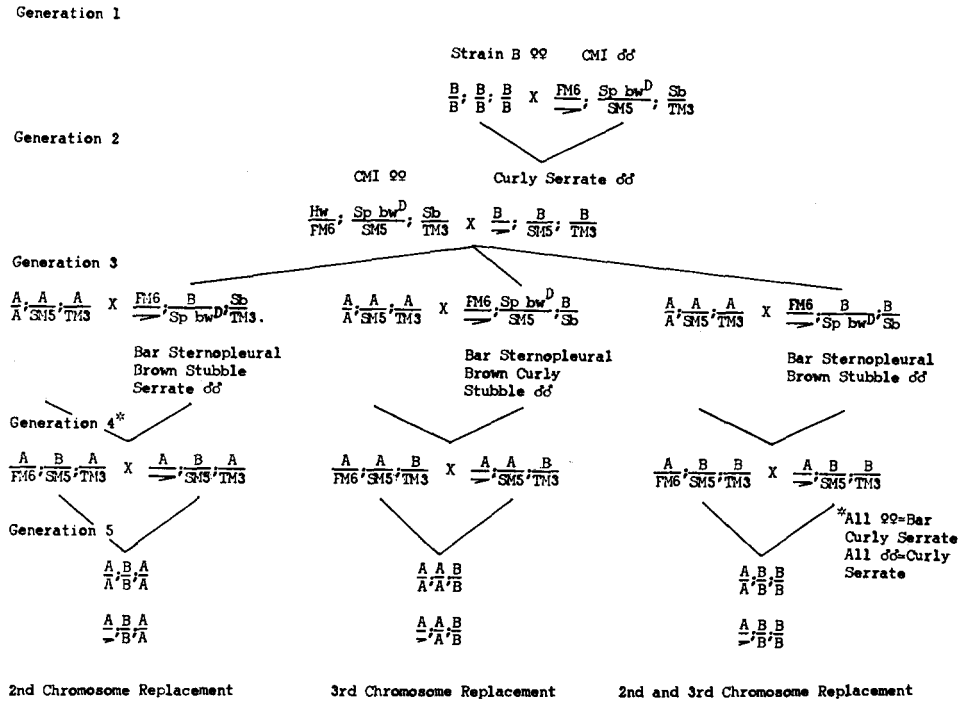


FIGURE 2.—Preparation of substituted strains: Autosomal combinations.

and Curly Serrate males are collected. It should be noticed that the haploid sets of wild-type chromosomes in each of the three crosses are of the desired constitution and that these chromosomes are balanced by the CMI inversions to prevent crossing over in the females. All the wild-type progeny of the fourth generation crosses are of the desired substituted type in which the wild-type haploid set of the previous generation has been duplicated exactly. For example, the wild-type progeny derived from the Bar Sternopleural brown-dominant Stubble males have had the X chromosomes from strain B substituted for the X chromosome of strain A and have the genotype B/B; A/A; A/A. The procedure for obtaining the rest of the chromosome substitutions is similar except that the crossing procedure is reversed (Figures 2, 3). The procedure for substituting chromosomes from strains C and D into a strain A background is identical to the above method. Thus three substituted series were obtained, each consisting of strain A and one other isogenic parental strain plus the six substituted strains derived from the two parental strains.

Experimental method. The four basic strains and the 18 substituted strains were expanded rapidly in mass culture in one generation. Ten pairs of flies from a strain were cultured at 25°C in a half-pint milk bottle containing fresh cornmeal, molasses, agar medium. The parents were discarded after four days. Upon emergence 50 males from each strain were collected at random. The males from each strain were put into vials containing optimal fresh medium and maintained without crowding at 25°C. When the males were three days old, they were transferred to empty vials and dried at 100°C for 24 hours. They were then stored in a dessicator until they could be weighed.

A weighing device was built and housed in a plastic body (SEIGER 1963). Each fly was removed from the dessicator and its weight determined by the deflection of the tip of a delicate quartz thread. Since the quartz thread has a constant Young's modulus, it can be readily calibrated and standardized for measuring small weights. The balance was calibrated by using

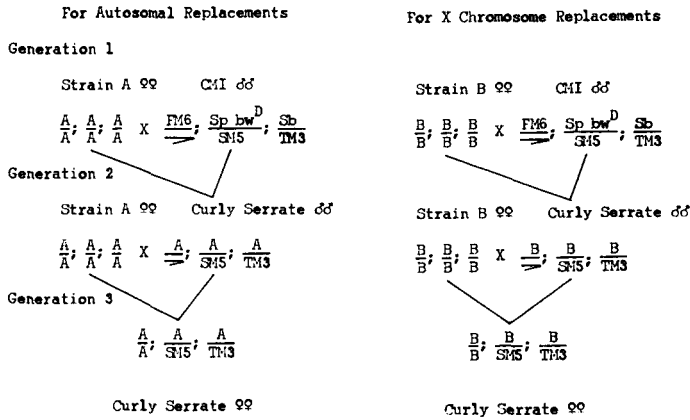


FIGURE 3.—Preparation of substituted strains: Derivation of Curly Serrate females.

standard microweights of 0.1 mg, 0.25 mg and 0.5 mg. During the course of the experiment the scale was repeatedly tested by reweighing the microweights and by comparing weights with those obtained from a sensitive Sartorius microbalance. The discrepancies were never more than ± 0.01 mg.

RESULTS

The mean male body weights for all strains are shown in Table 1. In general the substituted strains have lower body weights than the parental strains from which they are derived. Among all the substituted strains only strains ACA and CCA have significantly higher mean body weights than both of the parental strains.

Analyses of variance are used to compare the strains in each of the three substituted series to determine any significant differences between homologous

TABLE 1

Mean male body weights (mg) of the four parental isogenic strains and their substituted strains. $N = 50$

Strain	$\bar{X} \pm s_{\bar{x}}$	Strain	$\bar{X} \pm s_{\bar{x}}$	Strain	$\bar{X} \pm s_{\bar{x}}$
AAA	0.260 \pm 0.003	CCC	0.281 \pm 0.003	DDD	0.292 \pm 0.002
BBB	0.271 \pm 0.003	CAA	0.241 \pm 0.003	DAA	0.223 \pm 0.004
BAA	0.244 \pm 0.005	CCA	0.315 \pm 0.003	DDA	0.199 \pm 0.003
BBA	0.272 \pm 0.005	CAC	0.208 \pm 0.003	DAD	0.249 \pm 0.005
BAB	0.227 \pm 0.004	ACA	0.308 \pm 0.004	ADA	0.208 \pm 0.003
ABA	0.234 \pm 0.003	AAC	0.206 \pm 0.001	AAD	0.241 \pm 0.003
AAB	0.219 \pm 0.004	ACC	0.261 \pm 0.004	ADD	0.260 \pm 0.004
ABB	0.266 \pm 0.004				

TABLE 2
Results of analyses of variance for male body weight

Source of variation	Degrees of freedom	B series	C series	D series
1st chromosomes	1	10.71**	1.40	0.60
2nd chromosomes	1	77.86**	778.80**	2.60**
3rd chromosomes	1	6.86**	351.20**	288.00**
1st and 2nd chromosomes	1	23.29**	24.20**	32.20**
1st and 3rd chromosomes	1	0.86	15.00**	95.00**
2nd and 3rd chromosomes	1	71.57**	0.20	236.60**
1st, 2nd and 3rd chromosomes	1	29.57**	0.80	0.20
Within Mean Square		0.0007	0.0005	0.0005

** P value significant at the 1% level.

chromosomes (Table 2). The within mean squares for series B, C and D are respectively 0.0007, 0.0005 and 0.0005. This would indicate that the experimental errors for the three series are negligible. Where primary differences exist between pairs of homologous chromosomes, additional analyses of variance are performed to show the contributions to variance of the genetic background of the four strains containing one or the other of the homologous chromosomes. The estimate of the effect of a given chromosome is determined by the formula:

$$\hat{\Phi}(i) = (MS_i - MS_w) / na$$

Where $\hat{\Phi}(i)$ = the estimate of variance of a given chromosome or combination of chromosomes, MS_i = the mean square value for a given chromosome or chromosome combination, MS_w = the within mean-square, n = the number of flies measured per strain, and a = the number of strains containing a particular chromosome or chromosome combination. In Table 3 $\hat{\Phi}$ is presented as a percentage of the total $\hat{\Phi}$.

Figure 4 shows comparisons of male body weights between strains differing only by one chromosome. A substituted series is arranged into two groups, each group containing strains having a specific chromosome in common. The body weights of pairs of strains differing only by one chromosome can then be compared. For example, to compare the effects of homologous first chromosomes in the B series, strain AAA is compared with strain BAA, ABA with BBA, etc. These comparisons show that a parental strain is almost always heavier than a substituted strain differing from it by one chromosome regardless of the general trend which that particular chromosome substitution establishes between pairs of chromosomes.

Comparison of chromosomal effects: In the C substituted series, strain C flies are heavier than strain A flies. When single chromosomes of strain A are replaced by their strain C homologs, C_2 increases body weight strongly, but substitution of the first and third chromosomes results in a lower weight. Among the substi-

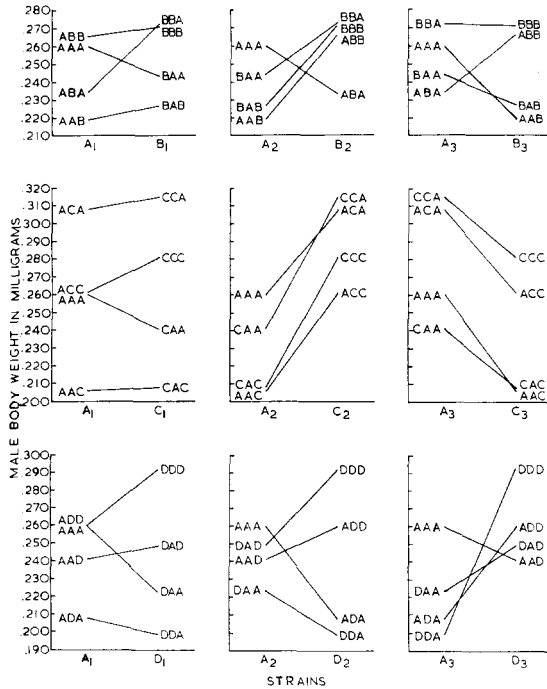


FIGURE 4.—Comparison of male body weight between strains differing by one chromosome. Each graph shows the strains in one series divided into two groups, one group containing one specific chromosome from strain A and the other group containing the homologous chromosome from the second parental strain.

tuted strains in general, the presence of C₂ or A₃ produces individuals of higher body weights. Indeed, the combination C₂A₃ (ACA = 0.308 mg, CCA = 0.315 mg) seems to have a synergistic effect on body weight. Individuals of this genotype, regardless of the origin of the first chromosome, have body weights significantly higher than either of the parental strains. Conversely, those strains with the lowest body weights contain the chromosomal combination A₂C₃ (AAC = 0.206 mg, CAC = 0.208 mg). The origin of the first chromosome does not influence the action of the second and third chromosomes very much, but a significant influence of the first chromosome in this series is indicated by the data in Table 2.

In the D series, strain D is much heavier than strain A, but any single D chromosome substituted for its strain A homolog lowers body weight, especially D₂. In combinations, D₁ has little effect on the action of D₂ and D₃; but replacement of the homologous A chromosomes by D₂D₃ results in a body weight equal to that of strain A. While each single substitution of a D chromosome for an A chromosome lowers body weight, in combination they cause a sharply increased body weight.

In the B substituted series, pure strain B individuals are slightly but significantly heavier than strain A individuals. However, the replacement of any single

TABLE 3
*The amount of variance attributed to the component chromosomes of the genetic background
 in the presence of one specific chromosome (in percent)*

Strain	A_1 common	B_1 common	A_2 common	B_2 common	A_3 common	B_3 common
Strain B substituted series	$\hat{\phi}(II) = 3.65$	$\hat{\phi}(II) = 88.83$	$\hat{\phi}(I) = 0.54$	$\hat{\phi}(I) = 36.94$	$\hat{\phi}(I) = 6.80$	$\hat{\phi}(I) = 1.33$
	$\hat{\phi}(III) = 0.36$	$\hat{\phi}(III) = 4.83$	$\hat{\phi}(III) = 75.45$	$\hat{\phi}(III) = 18.47$	$\hat{\phi}(II) = 0.00$	$\hat{\phi}(II) = 98.67$
	$\hat{\phi}(II \times III) = 95.99$	$\hat{\phi}(II \times III) = 6.34$	$\hat{\phi}(I \times III) = 24.01$	$\hat{\phi}(I \times III) = 44.59$	$\hat{\phi}(I \times II) = 93.20$	$\hat{\phi}(I \times II) = 0.00$
	$MS_w = 0.0006$	$MS_w = 0.0008$	$MS_w = 0.0006$	$MS_w = 0.0007$	$MS_w = 0.0007$	$MS_w = 0.0006$
Strain C substituted series	No significant variance due to A_1 vs. C_1					
			$\hat{\phi}(I) = 3.00$	$\hat{\phi}(I) = 9.21$	$\hat{\phi}(I) = 0.69$	$\hat{\phi}(I) = 2.74$
			$\hat{\phi}(III) = 87.41$	$\hat{\phi}(III) = 87.58$	$\hat{\phi}(II) = 91.45$	$\hat{\phi}(II) = 93.83$
			$\hat{\phi}(I \times III) = 9.59$	$\hat{\phi}(I \times III) = 3.21$	$\hat{\phi}(I \times II) = 7.86$	$\hat{\phi}(I \times II) = 3.43$
		$MS_w = 0.0004$	$MS_w = 0.0007$	$MS_w = 0.0005$	$MS_w = 0.0005$	
Strain D substituted series	No significant variance due to A_1 vs. D_1					
	No significant variance due to A_2 vs. D_2					
			$\hat{\phi}(I) = 23.20$	$\hat{\phi}(I) = 24.87$	$\hat{\phi}(II) = 61.04$	$\hat{\phi}(II) = 59.90$
			$\hat{\phi}(I \times II) = 15.23$	$\hat{\phi}(I \times II) = 15.75$	$MS_w = 0.0005$	$MS_w = 0.0006$

chromosome in strain A by a B chromosome results in lowered body weight as compared to strain A (Table 1; Figure 4). Individuals with a higher weight are produced among the substituted strains by substituting the first and second chromosomes of strain B for the first and second chromosomes of strain A. The combinations B_1B_2 and B_2B_3 produce the heaviest individuals in the series ($BBB = 0.271$ mg, $BBA = 0.272$ mg, $ABB = 0.266$ mg).

In the substituted strains of all three series, A_1 consistently lowers the value to the level of strain A. Chromosome A_2 lowers body weight strongly in all experiments while A_3 increases body weight in the B and C series and decreases it in the D series. The presence of A_1A_2 and A_2A_3 consistently lowers body weight among all the substituted strains. The combination A_1A_3 lowers body weight in series B and D substituted strains while increasing weight values in the C series.

Differences between homologous chromosomes can be further defined by considering the contributions to variance of the components of the genetic background (Table 3). In the C substituted series most of the variance in both the A_2 and C_2 groups is due to differences between third chromosomes while differences between second chromosomes contribute most of the variance in the A_3 and C_3 groups. In the D series, the difference between second chromosomes is the most important source of variance in both the A_3 and D_3 groups. The B series is unique among the three substituted series because in comparing strains having one chromosome in common, the contribution to variance of the other chromosomes does not correspond in the case of alternate homolog series being compared to each other. In the A_3 common and B_3 common comparison, for example, the second chromosome alone is responsible for most of the variation in the latter, while in the A_3 group of values it is the interaction of first and second chromosomes. Similarly, among the strains containing A_1 in common most of the variance is due to the interaction of second and third chromosomes while among the strains carrying B_1 most of the variance is due to differences between second chromosomes. Most of the variance in the group containing A_2 is contributed by differences between third chromosomes while in the B_2 group the contributions to variance are mainly attributable to differences between first chromosomes and to interaction of first and third chromosomes.

DISCUSSION

It is immediately apparent that the results do not lend themselves to a simple description. As Figure 4 shows, only the chromosomes C_2 and C_3 have consistent effects when they are substituted for A_2 and A_3 ; C_2 may be said to act in the plus direction while C_3 may be said to carry minus modifiers. Since C_1 has little effect in two substituted genotypes, the whole C series could be explained on the basis of plus and minus genes if C_1 did not have different effects in the remaining two genetic backgrounds. One might "overlook" this exception if only this case was available, but in the other two series dependence of the effect of a particular chromosome substitution on the other two chromosomes appears to be the rule rather than the exception. It is, for instance, impossible to say whether the chro-

mosome B_3 contains genes for higher or lower body weight, if compared to A_3 ; in two of the possible combinations it seems to have "minus" genes, in a third one "plus" genes, while in the fourth combination it has no measurable effect. It is also impossible to explain the high weight of DDD on the basis of the effects of the single chromosomes.

Little of the variance uncovered by chromosome substitution is additive. Even in those cases where there are no first order interactions between homologous pairs of chromosomes (Table 2), there are second order interactions. This indicates that the differences between the pairs are not additive. Even in the C series the second order interactions show that the substitution into different genetic backgrounds gives rise to disparate results and a departure from the additive action of the A_1 and C_1 blocks of genes.

The results presented here are in agreement with those of ROBERTSON (1954) who demonstrated that the substitution of a homozygous pair of chromosomes from one unrelated, unselected inbred line to another may increase or decrease thorax and wing lengths depending upon the genetic background. ROBERTSON found significant deviations from additiveness and found substantial interactions between genes on nonhomologous chromosomes in several cases. These tended to be greatest when chromosomes from unrelated strains were combined.

KELLER and MITCHELL (1962), inserting identical X chromosomes into different autosomal backgrounds, found that the expression of the morphological traits studied was affected by nonallelic interactions (epistasis). KELLER and MITCHELL (1964) also found that the viability traits were modified to a greater extent by interchromosomal interaction than the morphological traits. They state that this is consistent with the concept of an integrated genome being most important in characters related to fitness.

A point to be noted is that it is not necessary for the inbred lines to be derived from different base populations in order to display differences in the genetic control of a quantitative trait. Three of the inbred lines used in the experiment presented here were derived from Oregon-R and yet a comparison of homologous chromosomes from these strains shows that they have quite different effects. During the course of inbreeding, those genes had been fortuitously selected, and subsequently fixed, which should allow each of the parental strains to be fit in its environment. The results of obtaining isogenic strains from a base population is equivalent to taking a random sample of haploid sets of chromosomes and making each set diploid. The fixed loci will not be the same for each strain and the strains can be as different from each other as they would be from isogenic strains obtained from completely different base populations. For a series of isogenic strains obtained from a population, no pattern of fixation of alleles at given loci can be predicted unless selection is practiced. The isogenic strains used in these experiments were inbred without selection. Whether or not a strain survives depends on the chance fixation of genes at many loci which combine in their action to produce fit individuals which can survive and produce offspring for the next generation. The genome of such a fit strain is said to be coadapted. If we were to study only one strain, nothing could be said about the coadapted genome.

However, when pairs of strains are studied by crosses between them, some knowledge of the coadaptive processes between nonhomologous chromosomes can be gained.

In the environment in which the four basic strains were inbred, combinations of genes were fixed which gave rise to mean male body weights ranging from 0.26 mg to 0.29 mg. Most of the effects of replacing one chromosome of a basic strain by another were in the negative direction. In considering the 12 major chromosomes of these four strains, only two, A_3 in CCA and C_2 in ACA, result in higher weight when introduced into a parental strain. When the coadapted genomes of the parental strains produced by the selection in their entirety are disrupted by chromosome substitution, the body weights of the resulting substituted strains are usually, though not always, lower than those of the parental weights. From similar data concerning bristle number and body length KELLER and MITCHELL (1962) have suggested that there might exist interchromosomal "heterotic" mechanisms not related to allelic heterozygosity. However, the incorporation of A_3 in strain D led to a reduction in body weight and had no effect when in strain B. A_1 substituted for the X chromosome of the other heavier parental strains lowers the body weight in all three series to the level of strain A. It would seem that selection during inbreeding has been coadaptive for gene actions which result in relatively high body weight. Therefore, the individual chromosomes seem to act in a negative direction when considered singly. Yet these three apparently negative chromosomes, when selected together, act in concert with each other to produce a parental strain having a relatively high body weight. Despite the fact that isogenic strains may be aberrant genetically, they do have a balanced genome. Coadaptation seems to play a major role in the establishment of the parental strains.

It is a distinct pleasure to acknowledge the interest and counsel of DR. LEONARD BUTLER. His knowledge and patient guidance contributed a great deal to this work. I should also like to acknowledge the aid and cooperation of my late friend and colleague, VICTOR TINDERHOLT, with whom the special strains used in these experiments were developed. In our many discussions, MR. TINDERHOLT provided ideas and stimulation for the successful completion of this work. I am indebted to DR. G. S. WATSON for his instruction in analyzing the body weight data and to Drs. A. HANNAH ALAVA, A. A. BUZZATI-TRAVERSO, P. T. IVES and E. B. LEWIS for providing the *Drosophila* material. I also wish to thank DR. ERNEST CASPARI for his helpful criticisms of the manuscript. Finally I should like to express my gratitude to my wife, HAYDEE, for her technical assistance, her patience and her encouragement during the course of this project.

SUMMARY

A breeding method was devised to make all possible combinations of major chromosomes between two isogenic strains. Three substituted series, each consisting of the two parental strains and their six substituted genomes, were used to determine the genetic control of male body weight at the chromosomal level. The strain P_1 I Oregon-R was chosen as the standard strain and was used as a parental strain common to the three series.

Analyses for the contributions of chromosomes to male body weight were

carried out for each of the three substituted series. Very little of the variance resulting from chromosome substitution was due to additive effects. In almost every case, the replacement of a single chromosome from one strain by the homologous chromosome from another strain resulted in a lower weight. In only two cases were there definite directional effects when one chromosome was substituted for another. The second chromosome of the Canton-S strain substituted for the second chromosome of P₁ I Oregon-R resulted in flies having an increased body weight while the substitution of the third chromosome of Canton-S for the third chromosome of P₁ I Oregon-R resulted in a lower body weight. It is concluded that during the course of inbreeding the genome is selected in its entirety so that fit animals having body weights within certain limits survive. When that integrated genome is disrupted by chromosomal replacement, body weight is generally lowered.

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