

Replicated Selection for 21-day Pupa Weight of *Tribolium castaneum*

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Summary. Response to upward selection in 10 replicate lines was linear through 15 generations, had slowed considerably in many lines by generation 23 and continued in other lines through 30 generations. The lines tended to group into those which responded slowly during early generations and continued to respond through later generations and those which gave rapid early response and very low response later coupled with marked reduction in fitness. Response to downward selection was similar for 3 replicate lines but only 50% as great as that for the high lines. Response declined more rapidly in the low lines due to reduced fitness, declining selection differentials and a marked drop in phenotypic variance.

Theoretical deductions regarding the effects of selection are limited to the change in the population mean and strictly speaking apply only to response for one generation. By changing gene frequencies selection changes the genetic structure of the population. The changes in gene frequencies cannot be predicted since the effects of individual loci are unknown. The response to selection can be predicted only for as long as the genetic properties of the population remain unchanged.

If selection is applied to different samples drawn from the same population, the extent to which the samples vary in gene frequencies, both initially and during the course of selection, will determine how closely the results will agree from sample to sample. The results will then depend on the gene frequencies of the base population and the size of the populations during the course of selection. If most of the loci concerned have intermediate gene frequencies the response to selection is not likely to be influenced markedly by sampling variation. If on the other hand loci with fairly large effects on the character have genes at low frequency sampling variation, particularly for small samples, may appreciably influence the outcome of selection.

In a long term experiment designed to study the biochemical genetics of growth, a number of replicate selection lines of *Tribolium castaneum* were initiated from a single base population. The main purpose of the present investigation was to characterize the response to selection for 21-day pupa weight with particular reference to time trends in selection for high pupa weight.

Materials and Methods

A wild type foundation stock of *Tribolium castaneum* described previously (Gall 1970) was utilized as the base population. A large sample of eggs was taken from the population, allowed to develop for 21 days and pupae sexed. Twelve random samples of 25 males and 20 females each were weighed and designated as the generation 1 individuals of 12 replicate lines. The total sample of

300 males and 240 females was designated as generation zero yielding base population estimates for the mean and standard deviation of 21-day pupa weight of 2.45 mg and 0.305 mg, respectively. Selection was initiated by retaining, as parents of generation 2, the five heaviest males and all 20 females of the generation 1 individuals in each of 10 lines hereafter referred to as the high lines. In two randomly chosen lines, the five males were retained at random and these lines were designated as control lines 98 and 99.

Coincidental with generation 5 of the high lines, a second sample of eggs was drawn from the base population. At 21 days 4 random samples of 50 males and 75 females each were weighed and designated as the generation 1 individuals of 4 replicate lines. Three were designated as low lines for selection for low 21-day pupa weight and 5 males and 20 females were retained as parents of generation 2. The remaining sample was designated as control line 97 in which the 5 males and 20 females were chosen at random. The mean pupa weight and standard deviation for the total sample was the same as that for the high line sample and gave generation zero parameters. Consequently, the high and low sets of lines differed in that selection was practiced at a low intensity for males only in generation 1 of the high lines and the low lines followed the high lines by five generations or approximately a six month's time lag.

The selection intensity of 5 out of 50 males and 20 out of 75 females remained relatively constant through generation 23 for the high lines, generation 12 for the low lines and through generation 23 for control lines 98 and 99 and generation 16 for control line 97. However, due to reduced numbers of progeny selection was slightly more intense than described above in one or two generations for most lines during the first two-thirds of the experiment. The causes were most probably environmental. An incubator failure resulting in the loss of selected parents occurred in generation 13 for high lines 1, 4, 5, 9 and 10 and in generation 8 for low lines 1 and 2. In all cases the lines were continued with randomly selected pupae or adults from a reserve egg collection contemporary to the originally selected parents.

The culturing procedure for all lines consisted of setting the selected 21-day old pupae in a medium of 90% unbleached white flour and 10% dried brewer's yeast at a temperature of $33 \pm 1^\circ\text{C}$ and $70 \pm 1\%$ relative humidity. After a 14 day maturation and mating period the adults were transferred in mass to fresh medium for a two day egg laying period. Pupae were weighed on the 21st day, day zero being designated as the day egg collection was initiated. Weights were taken to the nearest

0.01 mg. Weighing dates for the 12 lines of the high set and the four lines of the low set were randomly distributed over a 30 day period.

A marked decline in the reproductive performance was observed in the high lines by generation 20. Although the number of pupae available at 21 days fell below the required number of 50 males and 75 females only on scattered occasions during generations 20–22, the margin of safety was small. Consequently, the decision was made at generation 23 to modify the selection procedure. The 10 high lines were evaluated, on data for generations 20 to 22, for the severity of the reproductive decline and for the magnitude of their selection response. Selection was suspended in 5 lines showing the lowest apparent reproductive rate and which had shown little or no response over the three generations. These lines were designated as Group B and consisted of high lines 1, 2, 4, 6 and 8. The remaining lines (3, 5, 7, 9 and 10) were designated Group A. The procedure for Group B, starting with generation 23 individuals, involved weighing in mass two samples of 10 male pupae, four samples of 10 female pupae and retaining all weighed individuals as parents of the next generation. Group A lines were continued on the original procedure with the provision that the selection intensity could be relaxed to the selection of 10 males and 30 females if the reproductive performance of a line declined sharply. The latter occurred for line 3 in generation 27–29, for line 5 in generation 29, line 7 in generations 25 and 27, line 9 in generation 23–25 and 28–29 and for line 10 in generation 29.

A similar but more severe and precipitous reproductive decline was observed for the low lines in generations 12 and 13. Since the number of pupae fell well below the required 50 males and 75 females all pupae were weighed. Only a small proportion of total number of individuals present were in the larval or adult stages and the number of pupae weighed was used to estimate reproduction (Table 1). In order to maintain these lines under continuous selection, the number of parents selected was increased to 10 males and 30 females for lines 1 and 2 at generation 14 and for line 3 at generation 13. The decision was based on the assumptions that the larger sample would reduce selection pressure, reduce the rate of inbreeding and increase the number of adults surviving through the egg laying period.

Table 1. *Reproductive performance of 3 lines selected for low 21-day pupa weight measured as the number of pupa weighed in generations 12 through 25. Maximum numbers required were 50 males and 75 females*

Lines Generation	1		2		3	
	♂♂	♀♀	♂♂	♀♀	♂♂	♀♀
12	50	75	50	75	30	65
13	34	34	30	34	10	30
14	18	29	33	34	50	64
15	15	26	39	47	50	71
16	50	69	50	61	50	58
17	23	23	32	32	25	25
18	36	45	45	44	50	75
19	50	75	50	71	50	75
20	50	59	50	75	50	75
21	31	30	50	75	50	74
22	50	42	50	75	50	75
23	50	75	35	39	50	75
24	38	52	50	62	50	75
25	50	62	50	75	50	75

Results and Discussion

The response in pupa weight to selection observed over the entire experiment is shown in Figure 1.

Group A and B lines, selected for high pupa weight showed similar responses during the early generations with the exception of line 7 of Group A which was consistently below the other nine lines. The lines began to show differentiation after generation 12. The precipitous drop in the mean for line 8, Group B at generation 10 cannot be explained. Following the decline to almost the initial value, the line responded to selection at a very rapid rate becoming the heaviest line at generation 12. Response then abruptly ceased at generation 14. The remaining Group B lines showed little or no response from generation 18 through 23 at which time selection was suspended.

The Group A lines showed a continuing linear response except for a moderate decline for line 3 between generations 20 and 24. It is of interest, however, that the average pupa weight of the Group B lines was equal to that of the Group A lines at generation 22. Line 9 (Group A) is also of interest in that its response was similar to the other lines through generation 18 after which it showed a marked increase in rate of response.

Selection response of the three Group L lines, selected for low pupa weight, was highly repeatable with very little segregation occurring in 25 generations. Lines 1 and 2 showed slight differentiation after generation 9 but remained parallel thereafter. This result may be confounded with the effect of random selection of parents to replace those lost in generation 8. The generally higher generation means for line 3 after generation 12 were also undoubtedly due to the loss of selection pressure in generations 12 and 13 caused by poor reproduction.

The performance of the control lines, Group C, was stable throughout the experiment. The mild decline in generation means during the early generations was most probably the result of small negative selection differentials. However, the effects of inbreeding and genetic drift could account for part of the change. Since there were no major shifts in the control lines, all analyses of performance of the selected lines was based on actual data rather than deviations from control.

The response of lines selected for high and low pupa weight was estimated for various intervals of the experiment by regression of pupa weight on generations using the techniques in which the generation number is repeated for each individual record. The latter method was chosen since it has been shown to be consistently more efficient than the method using means when the correlation between deviations from regression of individuals within a given value of the independent variable is small (Bohren, McKean and Yamada 1961; McKean and Bohren 1961).

Major asymmetry occurred for response in the upward and downward directions. The high lines showed an average total response of 2.30 mg in 23 generations as compared to only 1.25 mg in 25 generations for the low lines. Possible causes of asymme-

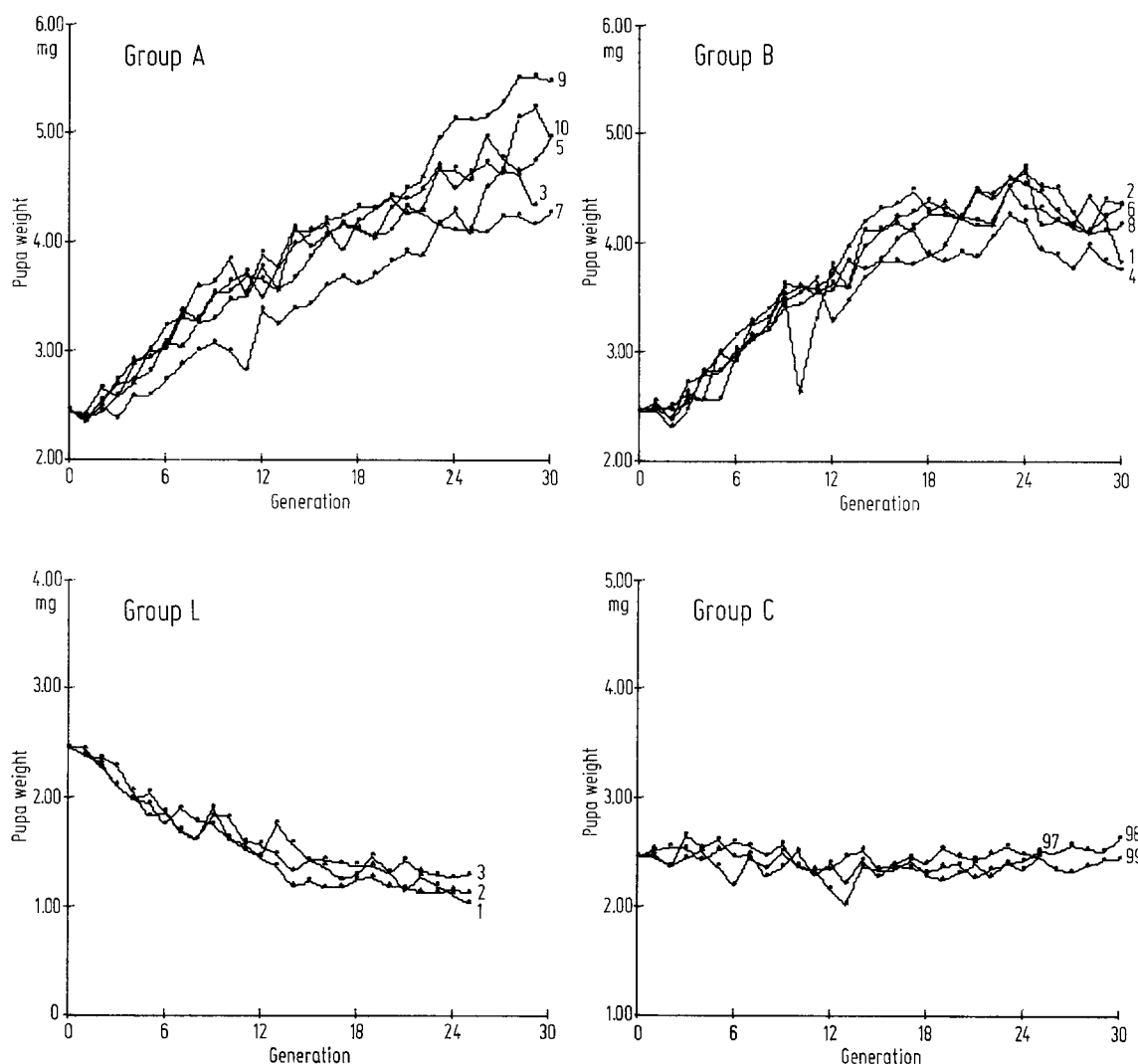


Fig. 1. Response to selection for 21-day pupa weight. Group A — 30 generations of upward selection. Group B — 25 generations of upward selection followed by 5 generations of suspended selection. Group L — 25 generations of downward selection. Group C — random selected controls: line 97, 25 generations contemporary to Group L; lines 98 and 99, 30 generations contemporary to Group A and B

try have been discussed elsewhere (Falconer 1960). Although replication was disproportionate, the data suggested that response to downward selection was much more uniform among lines than upward selection. Control lines 98 and 99 showed a small but significant downward response. This, however, can be accounted for by the small negative selection pressure inadvertently applied to these lines. Control line 97 did not change significantly over 25 generations and the average selection differential was zero.

The extent to which selection response and the genetic properties of each line changed as the duration of selection increased were estimated for the high lines by considering response observed over generation intervals 1 through 10, 1 through 15, 1 through 23 and over the entire experiment (Table 2). Generation zero was omitted from the analyses as differences between generations 0 and 1 reflect pri-

marily effects of sampling. For the first 10 generations of selection there were no significant deviations from the linear regression of response on generations and the selection differentials were very similar for all lines. Therefore, response during the first 10 generations would give an accurate estimate of the available additive genetic variability of each line. During the first 10 generations, average response (Table 2) ranged from a low of 0.09 mg per generation in line 7 to a high of 0.18 mg in line 10, a difference of 100%. The remaining 8 lines tended to scatter along this range although five were more intermediate. With the exception of line 10, average response per generation suggested that the Group B lines responded more rapidly than the Group A lines (0.13 mg vs. 0.15 mg) during the early generations. Such a result would indicate that the frequencies of favorable alleles in the Group B lines were more

Table 2. Regression coefficients of 21-day pupa weight (mg) on generations for high weight selected lines

Group	Line	Generation Interval			
		1-10 <i>b</i> ± s.e.	1-15 <i>b</i> ± s.e.	1-23 <i>b</i> ± s.e.	0-30 <i>b</i> ± s.e.
A	3	0.13 ± .003†	0.11 ± .002	0.09 ± .001	0.07 ± .001 ^s
	5	0.13 ± .003	0.11 ± .002	0.09 ± .001	0.08 ± .001
	7	0.09 ± .003	0.08 ± .002	0.08 ± .001	0.07 ± .001
	9	0.11 ± .003	0.10 ± .002	0.10 ± .001	0.11 ± .001
	10	0.18 ± .003	0.13 ± .002	0.10 ± .001	0.09 ± .001
	Average	0.13 ± .003	0.11 ± .002	0.09 ± .001	0.08 ± .001
B	1	0.14 ± .003	0.11 ± .002	0.09 ± .001	—
	2	0.13 ± .004	0.11 ± .002	0.10 ± .001	—
	4	0.14 ± .003	0.10 ± .002	0.08 ± .001	—
	6	0.15 ± .003	0.14 ± .002	0.12 ± .001	—
	8	0.17 ± .004††	0.12 ± .003	0.09 ± .002	—
	Average	0.15 ± .003	0.12 ± .002	0.10 ± .001	—
C	98	-.013 ± .004**	-.017 ± .002	-.010 ± .001	-.009 ± .001
	99	-.007 ± .003*	-.027 ± .002	-.014 ± .001	-.013 ± .001
	Average	-.010 ± .004*	-.022 ± .002	-.012 ± .001	-.011 ± .001

† All coefficients greater than zero at $P < .001$ except as indicated; ^{ns}not significant, * $P < .05$, ** $P < .01$.

†† Based on generations 1-9 only.

^s Line 3 completed only 29 generations.

Table 3. Regression coefficients of 21-day pupa weight (mg) on generations for low weight selected lines

Group	Line	Generation Interval		
		1-10	1-16	0-25
L	1	-.07 ± .003†	-.06 ± .001	-.05 ± .001
	2	-.08 ± .003	-.08 ± .001	-.05 ± .001
	3	-.08 ± .003	-.06 ± .001	-.04 ± .001
	Average	-.08 ± .003	-.07 ± .001	-.05 ± .001
C	97	-.005 ± .003 ^{ns}	-.001 ± .001 ^{ns}	-.001 ± .001 ^{ns}

† All coefficients greater than zero at $P < .001$ except Group C; ^{ns} not significant.

intermediate than in Group A, a factor which must be considered in an explanation of the early plateau observed for the Group B lines. An average response of the lines in each group was used since the similarity of standard errors did not warrant a more sophisticated pooling technique.

There was a definite drop in the rate of response as selection progressed. Lines showing the largest response initially declined the most rapidly. Lines 8 and 10, for example, declined from 0.17 and 0.18 mg per generation through generations 9 and 10, respectively, to 0.09 and 0.10 mg by generation 23. Lines 7 and 9 on the other hand changed from initial 10 generation responses of 0.09 and 0.11 mg to a respectable 0.07 and 0.11 mg by generation 30. An exception to this general trend was line 6 which maintained a high response for a longer period. The latter response suggests that at least some favorable alleles were at a relatively low initial frequency in this line.

Similar time trends were observed for the three low lines over intervals of generations 1 through 10,

1 through 16 and over the entire 25 generations (Table 3). Since the lines gave very similar responses and the response was low in comparison to the high lines any effect of initial conditions on subsequent performance is unclear, except that there was a decline in response as selection continued.

An estimate of realized heritability (h^2) was calculated as the regression over generations of pupa weight on observed accumulated selection differential by the technique described for regression on generations (Table 4). Again the results over the first 10 generations can be taken as estimates of initial conditions. With the possible exception of lines 2 and 10, Group B lines initially demonstrated higher realized heritabilities than the Group A lines and individual lines which gave larger initial estimates tended to decline the most rapidly. Group B lines declined from an average h^2 of 0.40 over the initial 10 generations to 0.26 over 23 generations whereas the Group A lines which gave a lower average initial value of 0.34 declined to a very similar value of 0.25 after 23

Table 4. Regression coefficients of 21-day pupa weight (mg) on observed accumulated selection differentials (realized heritabilities) for high weight selected lines

Group	Line	Generation Interval			
		1-10	1-15	1-23	0-30
A	3	.34 ± .009†	.26 ± .005	.21 ± .003	.17 ± .002 ^S
	5	.36 ± .010	.31 ± .006	.27 ± .004	.22 ± .002
	7	.24 ± .009	.22 ± .005	.23 ± .003	.21 ± .002
	9	.30 ± .009	.28 ± .006	.25 ± .003	.28 ± .002
	10	.47 ± .009	.34 ± .006	.29 ± .004	.23 ± .002
	Average	.34 ± .009	.28 ± .006	.25 ± .003	.23 ± .002
B	1	.41 ± .010	.35 ± .006	.30 ± .004	—
	2	.32 ± .009	.26 ± .005	.23 ± .003	—
	4	.41 ± .009	.31 ± .006	.24 ± .003	—
	6	.42 ± .010	.37 ± .005	.29 ± .004	—
	8	.43 ± .012††	.28 ± .007	.22 ± .004	—
	Average	.40 ± .010	.31 ± .006	.26 ± .004	—

† All coefficients greater than zero at $P < .001$.

†† Based on generation 1-9 only.

^S Line 3 completed only 29 generations.

Table 5. Regression coefficients of 21-day pupa weight (mg) on observed accumulated selection differential (realized heritabilities) for low weight selected lines

Group	Line	Generation Interval		
		1-10	1-16	0-25
L	1	.25 ± .010†	.27 ± .005	.26 ± .003
	2	.29 ± .010	.30 ± .005	.25 ± .003
	3	.24 ± .008	.21 ± .005	.18 ± .003
	Average	.26 ± .010	.26 ± .005	.23 ± .003

† All coefficients greater than zero at $P < .001$.

Table 6. Regression of observed accumulated selection differentials and generation standard deviations on generations and average standard deviations for high 21-day pupa weight selected lines. (Group A - generations 0-30†; Group B - generations 0-23)

Group	Line	Selection Differential	Standard Deviation	
		$b \pm \text{s.e.}$ (mg)	$b \pm \text{s.e.}$ (mg × 10 ⁻²)	$\bar{X} \pm \text{s.e.}$ (mg)
A	3	.42 ± .005††	.77 ± .12**	.362 ± .016
	5	.36 ± .005	.14 ± .09 ^{ns}	.309 ± .008
	7	.33 ± .002	.05 ± .08 ^{ns}	.267 ± .007
	9	.38 ± .004	.13 ± .15 ^{ns}	.321 ± .013
	10	.35 ± .004	.24 ± .08**	.292 ± .008
	Pooled	.37 ± .004	.25 ± .06**	.310 ± .012
B	1	.30 ± .005	.38 ± .16*	.292 ± .012
	2	.42 ± .007	.41 ± .13**	.310 ± .011
	4	.31 ± .004	-.20 ± .10*	.261 ± .007
	6	.37 ± .006	.22 ± .20 ^{ns}	.308 ± .014
	8	.39 ± .006	-.02 ± .20 ^{ns}	.321 ± .010
	Pooled	.36 ± .006	.16 ± .08*	.298 ± .005

† Generations 0-29 for line 3.

†† All coefficients this column greater than zero at $P < .001$; ^{ns}not significant, * $P < .05$, ** $P < .01$.

generations. From these results it can be concluded that initially the additive genetic variance was in general higher in the Group B lines than in the Group

A lines suggesting that a larger number of favorable alleles were at intermediate frequencies in the Group B lines. The results reported here for 10 generations agree well with those of Enfield, Comstock and Braskerud (1966) who observed realized heritabilities of 0.37 and 0.34 in two replicate lines of *Tribolium castaneum* selected for high pupa weight for 12 generations.

Realized heritability for the low lines was about 70% of that observed for the high lines when estimated over the first 10 generations (Table 5). These estimates were maintained through generation 16

in contrast to the high lines which had shown a drop in realized heritability between generations 10 and 15. Consequently, the loss of response was proportionately lower over 25 generations in the low lines than it was over 23 generations in the high lines.

The observed differences in selection response and differential realized heritabilities of the lines could be due to differences in selection pressure and/or phenotypic standard deviation. That such is the case for the comparison of the high and low lines but not for comparisons between the two groups of high lines is shown in Figure 2 and Tables 6 and 7.

Estimated as regression of accumulated selection differential on generations, the average selection differentials for the high lines were 60% larger than for the low lines and accumulated linearly over the entire period of selection. In the low lines selection pressure accumulated linearly for the first eight generations, showed a marked leveling during gene-

Table 7. Regression of observed accumulated selection differentials and generation standard deviations on generations and average standard deviations for low 21-day pupa weight selected lines and control lines. (Group L - generations 0-25; Group C - lines 98 and 99, generations 0-30, line 97, generations 0-25)

Group	Line	Selection Differential	Standard Deviation	
		$b \pm \text{s.e.}$ (mg)	$b \pm \text{s.e.}$ (mg × 10 ⁻²)	$\bar{X} \pm \text{s.e.}$ (mg)
L	1	-.18 ± .008†	-.59 ± .06	.183 ± .010
	2	-.21 ± .007	-.54 ± .06	.196 ± .010
	3	-.23 ± .008	-.38 ± .08	.212 ± .008
	Pooled	-.21 ± .006	-.50 ± .04	.198 ± .005
C	97	-.001 ± .002 ^{ns}	-.04 ± .10 ^{ns}	.258 ± .008
	98	-.013 ± .003	-.27 ± .12*	.250 ± .012
	99	-.011 ± .002	-.83 ± .13	.204 ± .018
	Pool (98, 99)	-.012 ± .002	-.55 ± .10	.227 ± .011

† All regression coefficients greater than zero at $P < .001$ unless otherwise indicated; ^{ns}not significant, * $P < .05$.

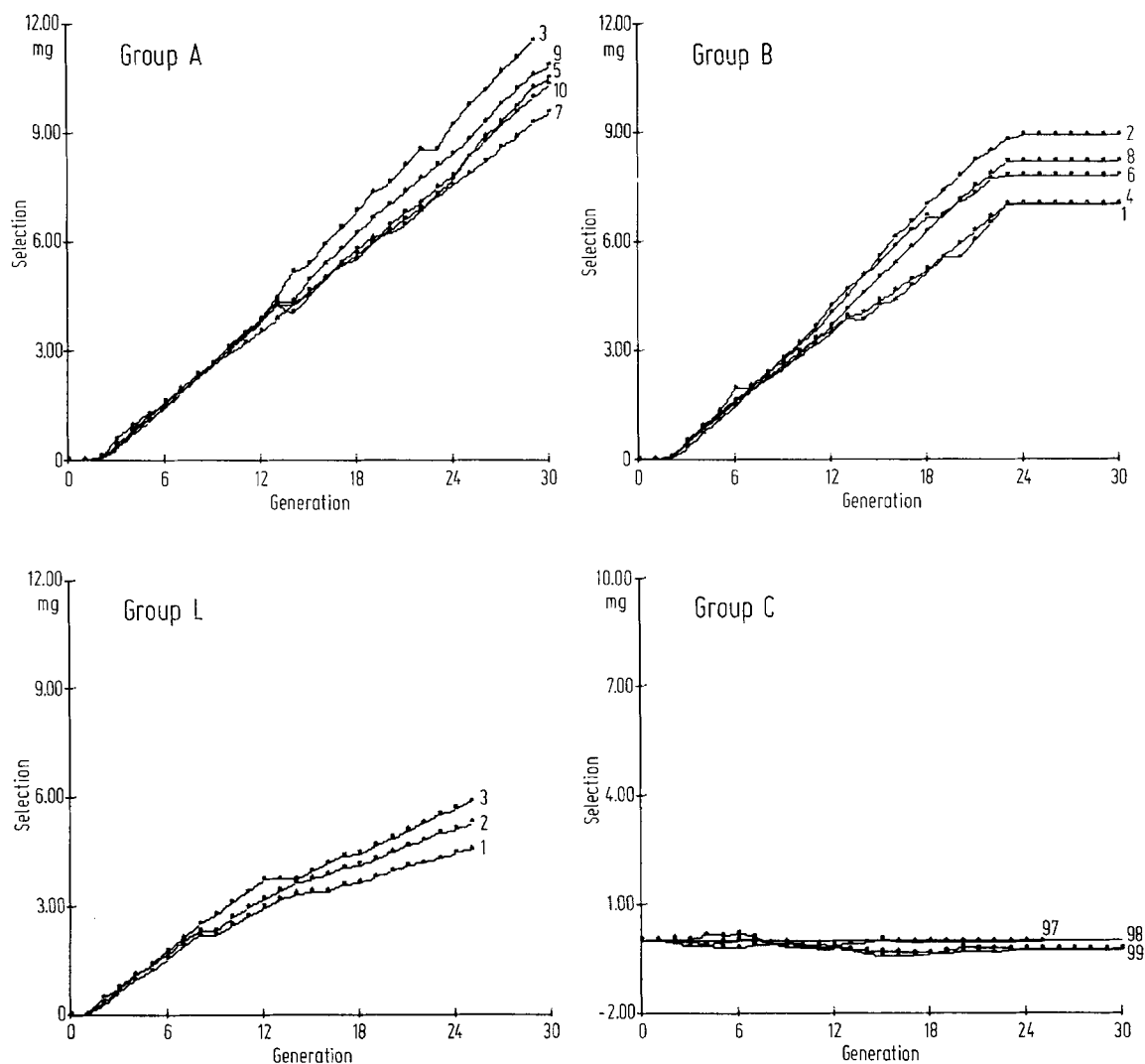


Fig. 2. Selection differentials for 21-day pupa weight, accumulated over generations. Groups defined as in legend of Figure 1

rations 9 through 14 and then continued at a slower but linear accumulation through generation 25. Generation 14 coincides with the time at which parent population size of the low lines was increased from 5 males and 20 females to 10 males and 30 females. Thus, increasing parent population size or reducing selection intensity was effective in preventing a continuation of deteriorating selection pressure.

The effect of selection on the phenotypic standard deviation of the lines selected for low pupa weight was marked and consistent (Table 7). Selection caused an average reduction in standard deviation of 0.005 mg per generation which was equivalent to 1.5% of the initial value per generation. A major cause of the low absolute response in these lines was thus a combination of decreasing variability and declining selection differentials. The extent to which reduced fitness of parents effected the latter cannot be estimated since progeny were not observed for individual parents.

The effect of selection on standard deviation for lines selected for high pupa weight was inconsistent (Table 6). Pooled regression of generation standard deviations on generations for the five Group A lines gave an estimate of an increase of 0.0025 mg per generation for 30 generations and a similar estimate for the five Group B lines showed them to have increased 0.0016 mg per generation for 23 generations. However, five of the 10 lines showed no significant change and the change for the other five lines ranged from -0.0020 mg for line 4 to $+0.0077$ mg for line 3. Since there was no apparent relationship between the change in standard deviation and the selection pressure applied it is improbable that changes in standard deviation had any marked effect on the responses observed for the high lines.

Two of the three control lines showed a significant reduction in phenotypic standard deviation (Table 7). These two lines, 98 and 99, also had small negative average selection differentials suggesting that selec-

tion may have been partly responsible. The fact that line 97 did not show a significant change eliminates inbreeding as a major factor. The mean standard deviation for 30 generations pooled for control lines 98 and 99 (Table 7) was significantly lower than the comparable estimate for the high lines (Table 6). If the reduction in control line standard deviation was due to an environmental time trend the regression of standard deviation on generations may be an underestimate of the effect on phenotypic standard deviation of selection for high pupa weight. Such would be true only if the observed change in the control lines

was unique to the methods or procedures used in selection rather than some random phenomenon such as genetic drift. The contrasting performance of control line 97 suggests a chance phenomenon.

The effect of suspending selection for the Group B lines was compared to the effect of continued selection for the Group A lines (Table 8) from generation 23 through 30. Average pupa weights for each line were calculated from the generation means of generations 21 through 23 and generations 28 through 30 to remove generation to generation fluctuations. The effect of selection was estimated as the difference between these averages. The Group B lines decreased an average of 0.21 mg over the seven generation period and the decrease was relatively consistent from line to line. The Group A lines, which were continued under selection at a reduced intensity showed an average increase of 0.45 mg over the same period, a per generation value equal to one-half of that experienced during the first 10 generations. The latter increase was due primarily to line 9 which gave a response of 1.5 to 4 times that of the other four Group A lines.

A further understanding of the response to selection for high pupa weight can be contained from an examination of the shape of the response curve over generations. This was done by fitting first and second degree polynomial regressions of 21-day pupa weight generation means on generation number and calculating the arithmetic average of the regression coefficients for each group of lines (Figure 3). A comparison of the regression coefficients and coefficients of determination for linear and quadratic equations fitted to data for the first 15 generations (Table 9) demonstrated that the response was linear in all

lines except line 10. Two lines (4 and 9) gave quadratic coefficients significantly different from zero at the 90% probability level.

Line 10 was unique in that the quadratic coefficient was highly significant and positive. Consequently, line 10 generation means were increasing at an increasing rate through generation 15. In addition, line 10 showed the highest initial linear response (Table 2) and the highest realized heritability (Table 4). One explanation is that this line had a greater degree of additive genetic variance than the other lines but also carried favorable alleles at low frequency, most likely alleles with rather large effects. The latter effect could also have occurred in line 9 but to a lesser extent.

Table 10 shows the coefficients for quadratic equations

Table 8. Response of Group A lines to continued selection and response of Group B lines to suspended selection for 21-day pupa weight from generations 23 to 30 based on the difference in average generation means for 3 generation intervals

Average 21-day pupa weight (mg)				
Group Line		Generations 21—23	Generations 28—30	Difference
A	3	4.32	4.53†	.22
	5	4.40	4.78	.38
	7	3.98	4.22	.24
	9	4.67	5.50	.83
	10	4.52	5.11	.59
	Ave- rage	4.38	4.83	.45
B	1	4.27	4.05	— .22
	2	4.54	4.27	— .27
	4	4.06	3.85	— .21
	6	4.51	4.34	— .18
	8	4.30	4.12	— .18
	Ave- rage	4.34	4.13	— .21

† Line 3 completed only 29 generations.

Table 9. Linear response estimated by simple linear regression and quadratic response estimated by second degree polynomial regression of 21-day pupa weight generation means on generation for first 15 generations of selection. (b , b_1 , linear regression coefficient; b_2 , quadratic regression coefficient; r^2 , coefficient of determination for linear regression; R^2 , coefficient of determination for quadratic regression)

Group Line		Linear		Quadratic		
		$b \pm$ s.e. (mg)	r^2	$b_1 \pm$ s.e. (mg)	$b_2 \pm$ s.e. (mg $\times 10^{-2}$)	R^2
A	3	.11 \pm .008†	.94	.15 \pm .032	-.24 \pm .19 ^{ns}	.95
	5	.11 \pm .008	.95	.15 \pm .032	-.24 \pm .19 ^{ns}	.95
	7	.08 \pm .007	.90	.08 \pm .031*	-.02 \pm .19 ^{ns}	.90
	9	.10 \pm .005	.97	.14 \pm .021	.25 \pm .13 ^a	.97
	10	.12 \pm .010	.92	.22 \pm .033	.62 \pm .20**	.96
	Average	.11 \pm .008	.94	.15 \pm .030	.07 \pm .18 ^{ns}	.95
B	1	.11 \pm .007	.95	.13 \pm .032**	-.13 \pm .19 ^{ns}	.95
	2	.11 \pm .006	.96	.12 \pm .030**	-.08 \pm .18 ^{ns}	.96
	4	.10 \pm .010	.89	.17 \pm .039	-.45 \pm .23 ^a	.92
	6	.14 \pm .006	.98	.11 \pm .024	.16 \pm .15 ^{ns}	.98
	8	.11 \pm .017	.77	.09 \pm .077 ^{ns}	.14 \pm .47 ^{ns}	.77
	Average	.12 \pm .009	.91	.13 \pm .040**	-.07 \pm .24 ^{ns}	.92

† Unless otherwise indicated coefficients greater than zero at $P < .001$; ^{ns}not significant, ^a $P < .10$, * $P < .05$, ** $P < .01$.

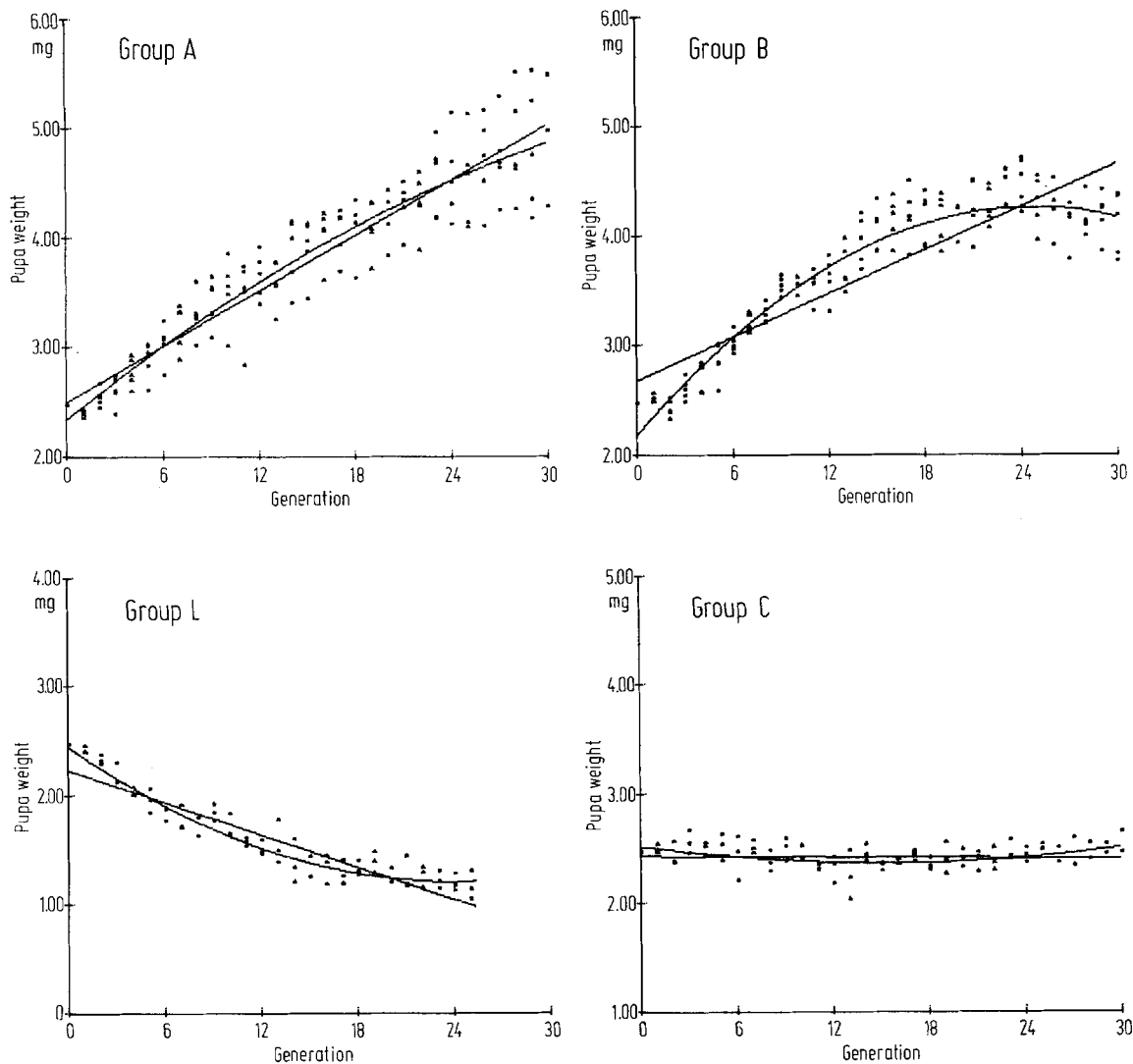


Fig. 3. Response to selection for 21-day pupa weight characterized by simple linear regression and second degree polynomial regression of generations means (*) on generation number. Groups defined as in legend of Figure 1

fitted to data through generations 23 and 30. Two of the Group A lines and only one Group B line gave nonsignificant quadratic regression coefficients through generation 23. Group B line 8 did not yield a significant quadratic coefficient due to erratic response as indicated by the large standard errors of estimates. Comparison of the average quadratic regression coefficient of $-.0018$ for the Group A lines to that of $-.0027$ for the Group B lines demonstrates that the Group B lines were approaching a plateau at a faster rate than the Group A lines. The linear coefficients coupled with the average initial responses (Table 2) and average initial realized heritabilities (Table 4) suggest that the Group B lines also gave a more rapid linear response than the Group A lines.

Quadratic equations satisfactorily accounted for the response of all lines through generation 30. However, the equation obtained for Group A lines

was not greatly different than that seen for the response through generation 23 indicating again that the approach to a plateau in these lines was proceeding slowly. The effect of suspended selection was evident in the large quadratic coefficients obtained for Group B through generation 30.

In general the average response of lines selected in the upward direction was large and repeatable, however, there were marked differences among some of the lines in the nature of their response. The results suggested that differences in the genetic properties of the lines resulted from initial sampling, and that the nature of these differences is complex. Cessation of response occurred early in lines which had shown the most rapid response during early generations. Lines which appeared to be lagging during early generations maintained a linear response over a long period of time and in at least one instance became the largest line.

The hypothesis proposed by Falconer (1960) that early similarity between lines followed by later divergence results from early response being governed by genes at more or less intermediate frequencies and that in later stages genes at initially low frequencies come into play would explain a major portion of the observed differences between replicate lines. However, the unique response of line 10, that of showing

direction coupled with selection modifying the nature of genetic correlations between body weight and components of fitness (Bohren, Hill and Robertson 1966).

The results observed in this experiment agree in principle with those presented by Clayton and Robertson (1957) for selection for bristle number in *Drosophila melanogaster*. They found response had

Table 10. Response to selection for high 21-day pupa weight estimated by second degree polynomial regression of pupa weight generation means on generation. Group A — continuous selection through generation 30. Group B — selection suspended from generation 23 through 30. (b_1 , linear regression coefficient; b_2 , quadratic regression coefficient; R^2 , coefficient of determination for quadratic regression)

Group	Line	Through Generation 23			Through Generation 30†		
		$b_1 \pm$ s.e. (mg)	$b_2 \pm$ s.e. (mg $\times 10^{-2}$)	R^2	$b_1 \pm$ s.e. (mg)	$b_2 \pm$ s.e. (mg $\times 10^{-2}$)	R^2
A	3	.17 \pm .014††	-.35 \pm .06	.97	.14 \pm .011	-.24 \pm .04	.96
	5	.15 \pm .016	-.24 \pm .07**	.96	.13 \pm .010	-.16 \pm .03	.97
	7	.08 \pm .014	-.00 \pm .06 ^{ns}	.96	.09 \pm .009	-.07 \pm .03*	.97
	9	.10 \pm .015	+.01 \pm .06 ^{ns}	.98	.09 \pm .009	-.06 \pm .03*	.99
	10	.18 \pm .015	-.33 \pm .06	.97	.14 \pm .012	-.18 \pm .04	.97
	Average	.14 \pm .015	-.18 \pm .06	.97	.12 \pm .010	-.14 \pm .03	.98
B	1	.16 \pm .018	-.31 \pm .07	.96	.18 \pm .013	-.39 \pm .04	.94
	2	.14 \pm .013	-.15 \pm .05*	.98	.16 \pm .012	-.29 \pm .04	.96
	4	.15 \pm .018	-.29 \pm .07	.94	.15 \pm .011	-.32 \pm .04	.94
	6	.19 \pm .017	-.35 \pm .07	.97	.19 \pm .012	-.40 \pm .04	.96
	8	.15 \pm .034	-.23 \pm .13 ^{ns}	.86	.16 \pm .018	-.31 \pm .06	.89
	Average	.16 \pm .020	-.27 \pm .08	.94	.17 \pm .013	-.34 \pm .04	.94

† Line 3 completed only 29 generations.

†† All coefficients greater than zero at $P < .001$ unless otherwise indicated; ^{ns}not significant, * $P < .05$, ** $P < .01$.

a rapid initial response which increased in rate over the first 15 generations, suggests that the effects of genes with relatively large effects which have low initial frequencies must also be involved.

One can postulate that rapid response exaggerates the effect of selection on genetic homeostasis generating an extreme situation of gametic disequilibrium. A lack of sufficient time for favorable recombination could result in unfavorable fitness genes being carried with favorable body weight genes. In lines which respond slowly the assortment of chromosomes would be more near random increasing the chances of recombination breaking unfavorable linkage groups (see, for example, Fraser 1967).

A marked asymmetry occurred between selection in the upward and downward directions with response in the downward direction being less. The major cause of the relatively low response was reduced phenotypic variability and reduced selection intensity. The latter effect was undoubtedly influenced by natural selection since reproductive fitness declined rapidly in the low lines. It is conceivable that genes which act in an additive manner when selection is practiced in an upward direction act in a nonadditive manner when selection proceeds in the downward

slowed down considerably after 20 generations in many lines and that in many lines, the cessation of response was abrupt. They also observed the existence of additive genetic variance in both upward and downward selected, plateaued lines. They concluded that the variability was maintained by a complex of lethal genes, selection for heterozygotes, infertility of extreme females and heterozygosity for inversions. Brown and Bell (1961) did not observe similar characteristics in a study of a plateaued population of *Drosophila* selected for high fecundity and questioned the general validity of the conclusions of Clayton and Robertson (1957).

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