The effects of mating systems and selection on pupa weight in *Tribolium**

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1. INTRODUCTION

Non-random matings may be made based on similar or dissimilar pedigrees (inbreeding, outbreeding), or they may be made based on somatic resemblance or non-resemblance (assortative, disassortative). The primary result in the former case would be a change in homozygosis, while in the latter case there may be little change in homozygosis.

Wright (1921*a,b*) set forth the theoretical expectations of inbreeding and outlined the expected effects on the variance, at a condition of equilibrium, of assortative and disassortative mating when all the variation is genetic. Wright's (1921*b*) formulation shows that genetic variation in a population should increase under inbreeding and assortative mating and should decrease under disassortative mating when compared with random mating. Under assortative mating, the realization of such increases in variation available to selection depends upon the correlation between genotypes of mates (m), which is based on $m = h^2 r_{pp}$ where h^2 is the heritability of the trait and r_{pp} represents the phenotypic correlation between mates.

Breese (1956) compared two generations of phenotypic assortative mating with random mating and inbreeding. That study revealed that phenotypic assortative mating increases gene combinations having extreme effects and reduces those combinations having intermediate effects.

Blair (1961), from an experiment designed similar to this study and on the same population, reported significant effects of mating systems upon the lowly heritable, highly heterotic trait of larva weight in *Tribolium*. However, when examined closely, it is evident that a large part of his significant mating systems effect was due to the depressing effect of inbreeding on larva weight.

McBride & Robertson (1963) reported consistent selective advantages in three assortatively mated lines as compared to randomly mated controls. However, the

advantages of the assortative lines were not great and do not appear that they would be significantly different from the random lines if they were tested statistically. These workers and Lush (1948) pointed out that phenotypic assortative mating as an aid to selection has its greatest effect when applied to traits of high heritability. Robertson (1960) has shown that intense selection applied to a trait of high heritability may rapidly increase inbreeding with a resulting decrease in fitness. However, it should be noted that most of the effect of assortative mating as an aid to selection should be realized in the early generations and therefore could probably be used effectively without bringing about fitness problems.

This study was designed to evaluate experimentally the effects of mating systems and selection upon an additive trait generally considered to be highly heritable.

2. EXPERIMENTAL METHODS

This experiment was conducted with a heterogeneous population of *Tribolium castaneum* formed by Blair (1961) by crossing four stocks collected from widely separated geographical areas. The trait studied was pupa weight measured 19 days after the egg was laid. Cultures were maintained in $\frac{3}{4}$ oz. glass creamers in control chambers at approximately 33°C. and 70% relative humidity. The culture media consisted of whole wheat flour with 5% dried brewer's yeast.

Two similar replications were maintained through six generations of selection. Each replication consisted of a mass selected and a randomly selected group. Within each of these groups there were five different lines, contrasted by different mating systems. Symbols used to designate selection methods and mating systems are shown in Table 1.

TABLE 1. *List of symbols used to designate the types of mating systems and selection methods*

Symbols	Description
M	Mass selection (based on 19-day pupa weight)
R	Random selection (entirely by chance)
i	Inbreeding (based on pedigrees of the individuals)
o	Outbreeding (based on pedigrees of the individuals)
a	Phenotypic assortative mating (based on somatic merit)
d	Phenotypic disassortative mating (based on somatic merit)
r	Random mating (matings made entirely by chance)

Each line, with the appropriate selection method and mating system applied, was propagated by twenty-two single pair matings per generation. An attempt was made to weigh individually three male and three female offspring, chosen at random, from each of twenty families per line for estimation of generation parameters. However, on some occasions, particularly in the inbred lines, fitness problems reduced the number of families available somewhat below twenty. When this occurred more pupa were weighed from the families that did reproduce giving

a total of sixty males and sixty females with sex ratios balanced within families. Selection intensity was 36·7%. Pupae were weighed in tens of micrograms and this unit of measurement was used throughout the experiment.

Coancestry values, as defined by Falconer (1960), between individuals of the same and different families were computed each generation for each line by the method of Emik & Terrill (1949). These values were essential for realization of maximum and minimum coancestry between mates in the inbred and outbred lines, and for calculation of inbreeding levels in the other lines.

Analysis of these data was by IBM 7090 computer and consisted generally of standard analysis of variance procedures applied to regression coefficients of generation mean pupa weight upon generation number. Phenotypic variances, coefficients of variation and variation among families (genetic variance) were calculated.

3. RESULTS

(i) *Response to selection*

Mean pupa weights by lines, generations and replications are shown in Fig. 1 and Table 2. Mass selection (M), based on individual phenotype, was quite effective in increasing pupa weight in the M lines. The randomly selected lines (R) deviated to some extent from the starting weights, but these deviations do not seem to
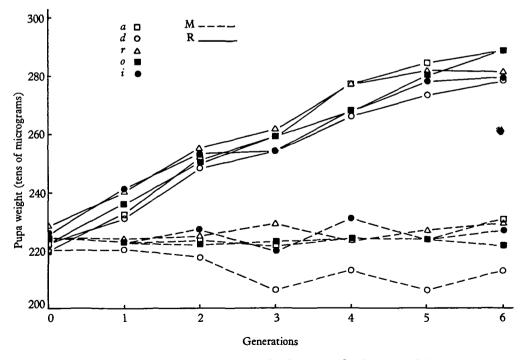

Fig. 1. Response curves of mass selected (M) and randomly selected (R) lines averaged over replications.

Table 2. *Mean pupa weights by generations, lines and replications in tens of micrograms*

Rep. I

Generations

Line	0	1	2	3	4	5	6
Ra	220	226	226	223	234	237	238
Rd	223	213	209	205	216	212	218
Rr	229	230	230	233	227	235	236
Ro	228	224	219	217	229	235	214
Ri	227	222	229	215	228	225	222
Ma	224	234	254	260	274	287	294
Md	218	228	242	242	263	269	275
Mr	231	245	260	259	278	281	281
Mo	226	237	249	261	274	283	293
Mi	236	248	258	254	269	278	282

Rep. II

Generations

Line	0	1	2	3	4	5	6
Ra	218	221	220	211	214	212	226
Rd	218	227	225	210	212	203	208
Rr	219	220	220	225	220	220	222
Ro	221	222	224	218	222	215	221
Ri	222	217	227	226	234	223	232
Ma	217	232	249	259	280	283	282
Md	224	235	255	266	269	278	283
Mr	228	236	251	265	276	283	281
Mo	221	235	250	258	264	277	283
Mi	216	236	250	255	267	279	276

have been directional in nature. Response in the M lines was somewhat more rapid in the early generations; however, this early, rapid response did not seem to be confined to any particular lines but was rather consistent for all lines.

When generation means were regressed upon generation number (Table 3), the within replication coefficients of the R lines showed only small inconsistent deviations from each other; while among the M lines, the Ma line showed the steepest slope in each replication. In replication I the Mi line failed to show as rapid response to mass selection as the other lines, but this trend was not evident in replication II and there is no obvious explanation.

An analysis of the variation among the regression coefficients of generation mean pupa weight on generation number was performed using a mixed model with selection methods and mating systems fixed and replications random (Table 4). This analysis revealed a significant effect of selection methods ($p < 0.05$), and a possible replication × mating system effect ($p < 0.25$). Other components did not approach significance.

Table 3. *Estimates of regression coefficients of generation mean pupa weight on generation number*

					Line					
	Ra	Rd	Rr	Ro	Ri	Ma	Md	Mr	Mo	Mi
Rep. I	3·0	− 0·4	1·0	− 0·4	− 3·0	12·1	9·8	8·6	11·4	7·5
Rep. II	0·0	− 3·3	0·3	− 0·6	1·8	11·7	9·9	9·9	10·1	10·1

Table 4. *Analysis of variance of the regression coefficients of generation mean on generation number over selection methods and replications*

Source	d.f.	Mean Square	Significance
Selection methods	1	524·60	0·05
Replications	1	0·01	
S × R	1	1·03	
Mating systems	4	4·75	
S × Ms	4	1·61	
R × Ms	4	4·81	0·25
S × R × Ms	4	1·33	

The above described analysis does not make the desired test of mating systems within selection methods; therefore, it was decided to analyze the data within selection methods and use the replication by mating system interaction as an error term (Table 5). From this analysis, there was no indication of a significant mating system effect among the R lines; however, there was slight indication of differential response among the M lines ($p < 0.25$). Duncan's New Multiple Range Test (Table 5) was then applied to these regressions averaged over replications and showed no differences among the R lines. Among the M lines, Ma was significantly different from the Mi line at the 5% level. However, this difference is partially explained by the fact that the Mi line in replication I responded very poorly to selection. No other comparisons were different at the 0·05 probability level.

Table 5. *Analysis of variance of multiple range tests, within selection methods, of regression coefficients of generation mean on generation number*

Source	d.f.	Random sel. mean square	Mass sel. mean square
Rep.	1	0·43	0·62
Mating systems	4	3·24	3·12*
R × Ms	4	4·98	1·16

* Significant at the 0·25 probability level.

Ra	Rr	Ro	Ri	Rd	Ma	Mo	Md	Mr	Mi
1·52	0·66	− 0·46	− 0·58	− 1·80	11·92	10·75	9·84	9·25	8·79

** Any two mean regression coefficients not underscored by the same line are significantly different at the 0·05 level.

(ii) *Effects on variances*

The Bartlett test for homogeneity of variances was applied within selection methods and revealed that phenotypic variances among lines were not different; however, there were some noticeable trends among variances. The general trend in both replications was for a decline over generations of phenotypic and genetic variation in the M lines (Tables 6, 7). This trend was rather consistent across mating systems.

Among the randomly selected lines there seemed to be a tendency for a decline in phenotypic variance (Table 6); however, this did not hold true for the estimates

Table 6. *Estimates of phenotypic variances (var.) and coefficients of variation (c.v.), pooled over sexes, by replication, line and generation*

Rep. I

		Line									
Gen.	Item	Ra	Rd	Rr	Ro	Ri	Ma	Md	Mr	Mo	Mi
0	var.	1446	1168	1061	1035	1230	851	1009	1205	1232	791
	c.v.	0·17	0·15	0·14	0·14	0·15	0·13	0·15	0·15	0·16	0·12
1	var.	1015	1023	1070	1109	946	1269	821	1018	1007	937
	c.v.	0·14	0·15	0·14	0·15	0·14	0·15	0·13	0·13	0·13	0·12
2	var.	983	974	1035	1104	1030	783	835	775	978	835
	c.v.	0·14	0·15	0·14	0·15	0·14	0·11	0·12	0·11	0·13	0·11
3	var.	1063	856	708	1492	845	701	691	847	733	627
	c.v.	0·15	0·14	0·11	0·18	0·14	0·10	0·11	0·11	0·10	0·10
4	var.	1174	1051	1189	1075	1017	717	512	763	867	987
	c.v.	0·15	0·15	0·15	0·14	0·14	0·10	0·09	0·10	0·11	0·12
5	var.	880	1265	812	847	753	745	706	732	727	738
	c.v.	0·12	0·17	0·12	0·12	0·12	0·10	0·10	0·10	0·10	0·10
6	var.	1131	924	846	1088	808	802	613	630	513	662
	c.v.	0·14	0·14	0·12	0·15	0·13	0·10	0·09	0·09	0.08	0·09

Rep. II

		Line									
Gen.	Item	Ra	Rd	Rr	Ro	Ri	Ma	Md	Mr	Mo	Mi
0	var.	838	1012	790	952	1047	1000	1087	1145	1020	884
	c.v.	0·13	0·15	0·13	0·14	0·15	0·15	0·15	0·15	0·14	0·14
1	var.	1014	884	898	1029	821	1128	1349	1170	862	1188
	c.v.	0·14	0·13	0·14	0·14	0·13	0·14	0·16	0·14	0·12	0·15
2	var.	1157	849	866	884	1039	1178	1156	1094	804	998
	c.v.	0·15	0·13	0·13	0·13	0·14	0·14	0·13	0·13	0·11	0·13
3	var.	1166	638	1000	890	1026	809	1057	863	793	689
	c.v.	0·16	0·12	0·14	0·14	0·14	0·11	0·12	0·11	0·11	0·10
4	var.	1163	841	767	991	1140	831	1026	733	1019	748
	c.v.	0·16	0·14	0·13	0·14	0·14	0·10	0·12	0·10	0·12	0·10
5	var.	1778	903	1322	925	806	714	1030	648	917	579
	c.v.	0·20	0·15	0·17	0·14	0·13	0·09	0·12	0·09	0·11	0·09
6	var.	1362	711	1011	875	970	722	810	593	817	523
	c.v.	0·16	0·13	0·14	0·13	0·13	0·10	0·10	0·09	0·10	0·08

Table 7. *Estimates of the variation among families (genetic variance),*
pooled over sexes, by replication, line and generation

Rep. I

Generation

Line	0	1	2	3	4	5	6
Ra	323·4	162·4	322·6	319·9	523·3	304·5	577·6
Rd	132·6	122·9	212·3	56·5	142·7	386·6	104·1
Rr	274·6	307·5	216·7	−34·0	327·4	79·9	246·4
Ro	243·2	338·2	399·6	700·4	163·9	283·5	284·6
Ri	287·5	423·7	333·7	132·9	400·1	222·8	210·0
Ma	258·0	401·0	37·8	76·5	229·3	277·5	221·7
Md	324·3	208·7	134·1	209·1	85·9	246·1	57·8
Mr	358·1	69·7	10·3	132·9	132·2	123·6	101·7
Mo	307·2	168·5	206·6	134·8	199·7	126·4	205·8
Mi	97·9	383·6	92·5	182·9	440·0	313·9	218·7

Rep. II

Generation

Line	0	1	2	3	4	5	6
Ra	158·1	309·5	696·9	726·8	578·2	1396·6	771·1
Rd	144·9	248·9	217·3	197·9	232·5	204·4	88·2
Rr	98·7	338·7	177·0	322·4	213·8	593·1	220·3
Ro	584·2	293·7	301·0	395·1	46·4	220·4	129·7
Ri	426·4	133·3	354·2	321·4	459·0	259·3	441·6
Ma	412·6	193·2	428·0	413·1	209·5	10·4	228·7
Md	236·7	130·4	213·6	88·9	−26·7	206·3	134·7
Mr	417·0	163·5	142·3	263·2	127·4	50·4	173·6
Mo	384·2	359·7	175·9	28·1	218·7	308·0	200·4
Mi	205·7	539·3	211·4	29·6	73·8	18·5	209·8

of genetic variance (Table 7). In both replications, the randomly selected, assortatively mated lines showed increases over generations in estimated genetic variance (Table 7).

(iii) *Inbreeding*

Levels of inbreeding, at the sixth generation, in the assortatively, disassortatively and randomly mated lines were quite similar within selection methods (Table 8). The outbred lines, where minimum coancestries between mates were realized, averaged approximately 4% and the inbred lines averaged slightly above

Table 8. *Sixth generation inbreeding coefficients by line and replication*

Line

	Ra	Rd	Rr	Ro	Ri	Ma	Md	Mr	Mo	Mi
Rep. I	0·06	0·07	0·07	0·04	0·31	0·11	0·06	0·10	0·06	0·33
Rep. II	0·07	0·08	0·07	0·04	0·31	0·09	0·09	0·13	0·04	0·39

33%. In most cases, mass selected lines showed somewhat higher coefficients of inbreeding than the randomly selected lines.

Six generations of full-sib matings would be expected to produce offspring that are 73·4% inbred. However, since matings were of selected offspring, it was possible to average approximately fourteen full-sib matings per line and generation. The other eight matings were made up of individuals as closely related as possible, but their coancestry values were much lower than the full-sib matings. Under these conditions expected inbreeding levels were approximately 60% for generation 6, provided each mating contributed equally to the following generation. In actuality inbreeding levels, as shown above, were far below those expected. This was brought about when matings with high coancestry values were in many cases sterile, thus eliminating those matings as parents of the next generation.

(iv) *Selection differentials and heritabilities*

Selection differentials, weighted by the number of offspring measured per mating and averaged over generations, were quite similar in the Ma, Md, Mr and Mo lines; however, in each replication the Mi lines showed the lowest value (Table 9). This can be explained by the fact that the Mi line in each replication showed somewhat smaller phenotypic variances, beginning with the zero generation and continuing through the experiment. The weighting procedure used adjusts selection differentials for differences in fertility of the parents and viability of the offspring to the time of measurement.

Table 9. *Average weighted selection differentials and realized heritabilities*
by line and replication

	Rep. I Line					Rep. II Line				
	Ma	Md	Mr	Mo	Mi	Ma	Md	Mr	Mo	Mi
Sel. diff.	32·2	27·1	28·5	30·1	26·2	31·2	33·5	31·1	32·8	28·3
Real. h²	0·35	0·35	0·29	0·37	0·30	0·35	0·29	0·28	0·31	0·35

Heritability estimated from the zero generation of the entire population, by regression of offspring on mid-parent, was $0·46 \pm 0·09$. Within line, realized heritabilities, over six generations, ranged from 0·28–0·37 for the M lines (Table 9). Realized heritabilities calculated over the first four generations of selection ranged from 0·31–0·46 and averaged 0·38 versus 0·32 for those calculated over six generations. Bartlett (1961) working in this laboratory with a different population of *Tribolium* reported realized heritabilities of 0·51–0·67.

(v) *Correlations between mates*

Correlations between phenotypes (r) and genotypes (m) of mates are shown in Table 10. Phenotypic correlations between mates, averaged over generations, were 0·97 in each of the Ra lines and 0·94 and 0·96 in the Ma lines. These values for the Rd lines were $-0·92$ and $-0·93$ respectively, while in the Md lines they

Table 10. *Correlations between phenotypes* (r) *and genotypes* (m) *of mates, by line and replication, averaged over generations*

	Ra		Rd		Rr		Ro		Ri	
	r	*m*	*r*	*m*	*r*	*m*	*r*	*m*	*r*	*m*
Rep. I	0·97	0·45	−0·92	−0·42	−0·17	−0·08	−0·17	−08	0·26	0·12
Rep. II	0·97	0·45	−0·93	−0·43	0·05	0·02	0·03	0·01	0·00	0·00

	Ma		Md		Mr		Mo		Mi	
	r	*m*	*r*	*m*	*r*	*m*	*r*	*m*	*r*	*m*
Rep. I	0·94	0·33	−0·86	−0·30	−0·04	−0·01	0·08	0·03	0·18	0·05
Rep. II	0·96	0·34	−0·85	−0·25	0·19	0·05	−0·04	−0·01	0·04	0·01

were −0·86 and −0·85. Calculated m values were 0·45 in each of the Ra lines and 0·33 and 0·34 in the Ma lines. They were −0·42 and −0·43 in the Rd lines and −0·30 and −0·25 in the Md lines.

Estimated heritability of 0·46 was used to calculate m values for the R lines while the somewhat lower realized heritabilities were used in the M lines. This explains most of the discrepancy shown between m values of the two groups; however, phenotypic correlations between mates were less in magnitude in the Ma and Md lines than in the Ra and Rd lines.

4. DISCUSSION

The general formula of Wright (1921b) gives a precise value of 1·18 for the ratio of the standard deviation at equilibrium under assortative mating to that found under random mating when all variation is genetic, the number of loci is ten or more and $m = 0·30$. Bartlett (1961) has estimated the number of loci affecting pupa weight to be in excess of 100. Since Wright's work was not concerned with selection, its application would be something less than perfect; however, it would indicate that one could expect the effect of assortative mating as an aid to selection to be minor when heritability is not high, even though the phenotypic correlation between mates is nearly perfect.

It was expected at the beginning of the experiment that m values would be in the neighborhood of +0·5 and −0·5 for the Ma and Md lines respectively. In the light of actual m values approximating +0·3 and −0·3 in these lines, the small effect of assortative mating as an aid to selection does not seem greatly out of line with expectations. Phenotypic correlations between mates were slightly higher in the R than in the M lines. This can be attributed to a greater range of weights among potential parents in the R lines.

In view of the evidence that, in the M lines, there was a general decline in the estimates of phenotypic and genetic variance over generations, it seems evident

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that selection was the major force affecting those parameters. In the R lines, variation more or less followed expectations. This was particularly true of the Ra lines which showed increases in estimated genetic variance over generations.

The lack of conformity of estimates of variation to expectations, particularly in the M lines, may be partially explained by the large sampling variations associated with such estimates; however, a more plausible explanation seems to be that selection simply masked any effects on variation that mating systems might have had.

Response to mass selection seemed to decrease after generation 4 as evidenced by realized heritabilities being somewhat higher when calculated over the first four generations rather than over six generations.

Inbreeding had little if any effect on pupa weight as such, but there was a profound degenerate effect upon fitness when inbreeding reached approximately 30%. There was evidence that mass selection for pupa weight increased inbreeding in the Ma and Mr lines as contrasted to the Ra and Rr lines. However, in six generations of selection, the increase in homozygosis was not enough to cause fitness problems.

It appears, from the work of Blair (1961), McBride & Robertson (1963) and from this study, that for assortative mating to be effective as an aid to selection, heritability of the selected trait and the phenotypic correlation between mates must be high enough to produce an m value of at least 0·5. Under these conditions it seems that assortative mating does enhance selection but not greatly.

SUMMARY

An experimental evaluation of the effect of mating systems and selection upon an additive trait thought to be highly heritable was made. There were two similar replications. Each consisted of a mass selected and randomly selected group, with five mating systems within each group.

Realized heritabilities in the mass selected lines were considerably less than was expected prior to the initiation of the experiment, and averaged approximately fourteen percentage points less than heritability estimated from the zero generation. This in turn resulted in smaller correlations between the genotypes of mates than had been previously expected in the assortatively and disassortatively mated lines.

The average response of the mass selected, assortatively mated lines was slightly more than the mass selected, randomly mated lines, though not statistically significant. This result seems to conform to theoretical expectations.

In the mass selected lines, estimates of phenotypic and genetic variance declined regardless of mating systems. There was a tendency for phenotypic variances to decrease in the randomly selected lines, but this was not the case for estimates of genetic variance.

As an aid to selection, it seems that assortative mating would be of little value with traits of low or intermediate heritability but might be useful if the trait is highly heritable.

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