Tribolium castaneum which is utilized in quantitative genetical studies is the insect commonly known as the rust-red flour beetle. The adult is about 3.5 mm in length and 1.0 mm in width. The egg size is about 0.6 mm in length and 0.4 mm in diameter and weight per 100 is about 4.0 mg. Larva hatches 3½ days after oviposition. Larvae continue their growth until 15-16 days of age. Maximum larval weight is attained in 1-1½ days before pupation. There is no fixed number of larval instars, the number being variable with environments and populations ranging from 5 to 10. Pupation takes place under most laboratory conditions in 17-18 days after hatch. Pupae are white but darken as they approach to the time of emergence. The average duration of pupal stage is about 5 days. Sexes are easily distinguished by the appearance of the ventral surface of the terminal abdominal segment in pupal stage. The dark spot on the forelegs of the male is sometimes used for sexing. The newly emerged adult reaches its minimum live weight on the third day and restores a stable weight within a week after emergence. Then, the female starts egg production. The peak egg production appears at 10-15 days after emergence and the number of eggs per day runs from 10-20. It is easy to run a selection experiment with 4-week generation cycles.

Tribolium castaneum has 10 pairs of chromosomes including XY sex chromosomes. Recombinations take place in both sexes and segregation ratios are normal. Mating is polygamous in nature. This species is easily cultured on diets containing wheat flour with additive of dry yeast and thus is readily observed at any stage of development. It has very wide range of humidity and temperature tolerances but is raised normally in the optimum of 33°C and 70% R.H. in most

laboratories. Adult beetles maintained at a low temperature can live as long as one year. Thus, parents can be stored over several generations for subsequent repeat matings.

Disadvantages of the species are 1) small chromosomes which make cytological studies of chromosomes difficult, 2) cannibalism in motile stages (larval and adult) on eggs and pupae, and 3) lack of enough knowledge of physiology of the insect which makes difficult to assess the relevance of the conclusion drawn from selection experiments to higher animals. The last one is however inevitable nature for any laboratory animal to extrapolate the finding to farm animals, because each species has its own specificity in any way.

THE TRAITS STUDIED IN VARIOUS SELECTION EXPERIMENTS

Quantitative characters so far studied in Tribolium are listed in Table 1, with appropriate genetic information and references.

Rather than attempting to make a through review of literatures on selection responses in Tribolium, my discussions will be concentrated in two subjects: 1) Changes in growth characteristics by selection, and 2) Relative efficiencies of alternative breeding methods for exploiting additive and non-additive genetic effects.

CHANGES IN GROWTH CHARACTERISTICS BY SELECTION

Since the material had been introduced to Purdue, many selection experiments for changing some components of growth and development have been conducted extensively by Bell’s group for the past decade. Much effort was made to test the validity of quantitative genetic theories with special references to the effectiveness of selection for a single trait. Most early works dealt with pupal weight almost exclusively. When pupal weight was chosen as the trait for selection in early studies the nature of pupal weight, especially the absence of non-additive gene action, was not known. Accordingly, the trait was taken as the selection criterion for testing relative efficiencies of reciprocal recurrent selection (RRS) in comparison with conventional methods. Not many of early selection experiments for pupal weight were published by recent years except in abstract forms. These are summarized by Bell and Moore (1972) and will be discussed later in connection with RRS.

The first detailed report on selection for pupal weight appeared by Bray et al. (1962) on the efficiencies of control populations to separate genetic and environmental effects in selection experiments. The problem is basic to study selection response. Thus, control populations of some kind are incorporated in most selection experiments involving either laboratory animals or economic species of livestock. The most interesting finding which gave some stimulation to later studies was a GE interaction disclosed by selection.

Subsequent studies of selection for a single trait, pupal weight, were made by Wilson et al. (1965), and from other laboratories by Enfield et al. (1966), Rumball and Rae (1968) and Gall (1971). Selection studies for developmental time were made by Dawson (1965) and Engler and Bell (1970). Selection for two traits (larval and adult weights) simultaneously by use of restricted selection index

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### TABLE 1

**Quantitative traits of Tribolium castaneum studied in various selection experiments**  
(Modified from Bell, 1968)

<table>
<thead>
<tr>
<th>Trait</th>
<th>Relative heritability</th>
<th>Degree of heterosis</th>
<th>Genetically correlated</th>
<th>References *</th>
</tr>
</thead>
<tbody>
<tr>
<td>Larval weight (LW)</td>
<td>medium</td>
<td>moderate</td>
<td>PW +</td>
<td>2, 13, 14, 15,</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>AW +</td>
<td>19, 21, 23, 26,</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>DT +, —</td>
<td>27, 33, 34.</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>EN +, —</td>
<td></td>
</tr>
<tr>
<td>Pupal weight (PW)</td>
<td>high</td>
<td>slight</td>
<td>PW +</td>
<td>2, 4, 8, 12,</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>LW +</td>
<td>20, 31, 33, 34,</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>DT +, —</td>
<td>36.</td>
</tr>
<tr>
<td>Adult weight (W)</td>
<td>high</td>
<td>slight</td>
<td>PW +</td>
<td>2, 13, 26, 27,</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>LW +</td>
<td></td>
</tr>
<tr>
<td>Developmental time (DT)</td>
<td>medium to high</td>
<td>moderate</td>
<td>PW +, —</td>
<td>11, 13, 14, 15,</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>LW +</td>
<td>33, 34,</td>
</tr>
<tr>
<td>Egg number (EN)</td>
<td>low to medium</td>
<td>high</td>
<td>LW +</td>
<td>23, 30.</td>
</tr>
</tbody>
</table>

* The number stands for the order of references.
was done by Okada and Hardin (1967, 1970), and similar selection with three traits by Scheinberg et al. (1967). Independent culling level selection was made by Bell and Burris (1973). Most of these studies support the theory in general except asymmetrical responses in directly selected or indirectly selected characters were observed almost in all experiments.

Since Falconer (1952) had indicated his idea for the choice of environments in a selection experiment and provided experimental results with mice, the first study on the GE interaction was initiated in 1958 by Bell and McNary (1963) involving selection for increased pupal weight in each of two humidity environments. The significant finding from this study is that selection on pupal weight in the dry environment gave a correlated response in the wet equals to the direct response in the wet, but the reverse was not true. This indicates that the effective genetic correlation between pupal weights in a population under two environments is a function of which trait is selected or which environment is used for selection. This is analogous to the fact that the effective heritability for a single trait is a function of direction of selection to yield asymmetrical responses in two-way selection, which have been observed in all selection experiments cited before. This finding stimulated strongly later experimentations on GE interactions.

To make clear the conditions, which contribute to genetic asymmetry, further studies were made on Tribolium growth in two nutritional environments. Thirteen-day larval weight ($W_L$) was chosen for observation. Larval weight in the good nutrition was about twice of that in the poor (Hardin and Bell, 1967). After 8 generations of selection for both positive and negative selection, consistent results obtained over 4 replications agreed with Falconer's (1960) mice experiments, which yielded the conclusion that for maximum gain in a single environment, selection should be made in that environment and maximum average over two environments resulted from selection in a sub-optimum environment. Asymmetry in the realized heritabilities and genetic correlations was the rule, although these genetic parameters pooled over both directions and environments agreed with the initial parameters in the base population. It is hardly convinced that these genetic asymmetries were resulted from genetic sampling or drift because all replications were consistently in the same way.

A more extensive study with an additional refinement to avoid any possible effect of maternal nutrition on progeny was conducted by Yamada and Bell (1969). Asymmetrical responses were again observed to be dependent on the environments of selection. When selection was based on performance in the good, the asymmetry was observed toward small size. This situation in the poor level was completely mirror image. Environmentally dependent asymmetry could hardly result from directional gene frequencies or directional dominance, which was inferred from the theory by Falconer (1954) for two-way selection and Boiren et al. (1966) for genetic correlation. Physiological limits in the manifestation of the observed trait appear to be a more plausible cause, because the observed distributions of the trait in two environments showed opposite skewness toward less efficient response side.

After the termination of this selection for 16 generations, entire growth patterns of these selected populations in the two environments were studied, in terms of average weight of 100 individuals from each population in each environment at a given date regardless of their metamorphic stages and developmental time.
by use of 50% pupation time and 50% emergence time (Yamada, 1973). A part of the results are presented in Figure 1. As is seen, these two environments did not result an appreciable difference for all maximum larval weight, pupal weight and adult weight, while rather a large difference in developmental time was observed under two environments. Accordingly $W_a$ was very much affected by environments. Growth patterns of these selected populations in the two environments changed drastically, in particular with respect to developmental time. For example, PL lines selected for large in the poor environment grew faster in both environments than GL lines selected for large in the good environment and the difference of 50% pupation time between two environments was smaller in PL than in GL. Selection for small direction was reverse. Unexpectedly the weight characters at

Fig. 1.—Growth patterns of selected populations under two nutritional environments.
the same physiological ages of developmental time were all at the same levels in these two nutritional environments. These were the causes of magnified GE interaction in later generations of selection.

Weight of an animal at a given time during growth, $W(t)$, is in general expressed as a function of ultimate weight ($W$) and the time to the maximum ($T$). The weight in the $i^{th}$ environment may be written in a linear form after appropriate transformation of the variables as: $W(t) = W_i - b_i (T_i - t)$. Although $W(t)$ is the primary trait for selection, it must be understood that $W(t)$ is casually the dependent variable on both $W$ and $T$. The increment of $W(t)$ in a given environment can be made either by increasing $W$ with no change in $T$, or decreasing $T$ with no change in $W$, or increasing $W$ and decreasing $T$ simultaneously.

As selection pressure applies to $W(t)$, $W$ and $T$ change proportionally to the genetic covariances of these major components with $W(t)$. The selected trait $W(t)$ of the next generation may not be the same to that in the preceding generation, because the time $t$ is fixed rather than adjusted and the relationships of $W(t)$ with $W$ and $T$ have to be changed by selection. As an extreme, when $t$ approaches to $T$, then $W(t)$ approaches to $W$ in the positive selection.

Physiological basis of $W(t)$ in two environments may be different depending on how much retardation in developmental time takes place in the poor environment compared with that in the good. This is equivalent to say that the coefficient or the relative weight $b_i$ given to $T$ varies with environments. The weighting factor $b_i$ in two environments in a given generation may differ substantially between generations, depending on the constitution of the selected trait of these two major characters and their variabilities. Consequently, differential changes in $W$ and $T$ by selecting for $W(t)$ in two environments will be observed. Nevertheless, such differential responses in $W$ and $T$ are not predictable unless the experimentalist has necessary genetic and phenotypic information to calculate the $b$ value every generation (Yamada, 1970).

In connection to the above argument, it is interesting to cite the data presented by Englert and Bell (1969) on the changes of growth components by selection. Figure 2 illustrates the divergence of populations selected for either pupal weight or pupation time, early or late. Since all of these populations were selected for a single trait from Purdue «+» Foundation stock, any concomitant change in not selected trait is regarded as the correlated response. Consequently, realized genetic correlations between $W$ and $T$ were completely inconsistent.

It is impossible to interpret such divergences of selected populations with respect to $W$ and $T$ from the theory of correlated response. Realized genetic correlations range from negative to positive. As a plausible explanation, I have introduced a concept of unintentional secondary selection which is caused by unseen processes by the experimentalist. Major causes of such secondary selection arise from directional technical errors, or non-normal distributions of the variables concerned. Details will be published elsewhere.

**Relative efficiencies of RRS and WLS**

Experimental approaches to compare relative efficiencies of RRS and conventional within-line selection (WLS) were first initiated with *Drosophila* by Bell et al. (1955). The results summarized were: 1) The largest response in egg size,
a highly heritable with little heterosis, was observed in WLS; 2) Egg number, a 
heterotic with medium heritability, showed the largest response in the early 
generation under WLS, while both RRS and recurrent selection (RS) with an
The results of these three experiments were in summary as follows:

1. **Selection for pupal weight.**

   Pupal weight in the base population was found to be highly heritable with little non-additive gene action. As expected on theoretical basis, the purebred selection method was definitely superior to the others. A nearly perfect genetic correlation existed between purebred and crossbred performance as evidenced by purebred responses within the reciprocal lines paralleling those observed for RRS crossbreds. No heterosis was observed for the inbred-hybrids (Bell and Moore, 1972).

2. **Selection for larval weight.**

   The second selection experiment involved a long term study of 13-day larval weight, a moderately heterotic with a heritability of about 20%, in two unrelated base populations, pearl \( p \) and black \( b \). An attempt to exhaust much of the additive genetic variance with purebred selection before initiating RRS was made by use of family selection based on purebred performance for 30 generations with crossbred performance test each generation as a correlated response. All lines were responding still in the later generation with no tendency toward plateaus. After 30 generations of selection, the four selected purebred lines were random mated without selection for 5 generations before starting a replicated comparison within each of selected lines of RRS versus continued purebred (WLS) for another 12 generations. Findings from this study are: 1) Both purebreds and crossbreds showed some decline in the selected trait during the 5 generations of relaxed selection, 2) Both RRS and WLS improved the crossbred performance without either method showing a consistent advantage, and 3) The most significant point is the suggestion that RRS and WLS are exploiting different kinds of gene effects. Without exception, the RRS purebred response was less than the WLS purebreds, yet RRS crossbred did as well or better on the average than WLS crossbreds (McNew and Bell, 1973).

   According to the theoretical study by McNew and Bell (1971), a negative covariance between purebred and crossbred performance can arise from epistasis as well as overdominance. The trends in the purebred-crossbred covariances observed suggest the hypothesis that RRS utilizes some kind of non-additive genetic variance, while response under purebred selection appears to be limited to additive gene effects. Whether or not such evidence are generally witnessed must wait for further examinations.

3. **RRS versus WLS for increasing the rate of egg production under optimum and stress environments.**

   The selection study by Orozco (1969) involved a replicated comparison over 9 generations of three methods of selection for performance in each of three environments \((38^\circ C\) as a mild stress, \(33^\circ C\) as optimum, and \(28^\circ C\) as severe stress). Heritability of egg production in the unselected base population was about 20% and was slightly related to the testing environments. Both RRS and WLS
methods were started from the same base population. In this discussion only
direct selection responses will be cited. The results are summarized as: 1) WLS
was superior to RRS in optimum and mild stress environments, yet average gain
from selection for performance under severe stress condition were significantly
greater for RRS; 2) Although the WLS and RRS populations were originated from
the same base population the initial selection responses favored WLS in every
case, yet in the terminal rate of response was greater for RRS; 3) Almost all
WLS response curves show negative tendency which is characteristic of most
single trait selection experiments within a closed population. The heritability of
purebred performance declined under WLS but that of crossbred performance
under RRS showed no decline to suggest the possible utilization of non-additive
gene effects; and 4) The most interesting point was that the magnitude of the GE
interaction variance was relatively small among RRS lines than among WLS lines.
This can be ascribed to the superior buffering abilities of the lines developed
under RRS systems.

CONCLUDING REMARKS

It is quite evident that Tribolium is a suitable biological model for quantitative
genetic studies and for comparing efficiencies of various breeding methods before
applying them to animal breeding practice. The most important contribution
from experimental studies with Tribolium is the disclosure of unexpected biological
phenomena which have been overlooked or ignored in the classical genetic
models.

Perhaps the most promising future research in Tribolium will come from
dynamic studies on GE interaction. The reasons for this are as follows: 1) By use
of nutritional, physico-chemical environmental stresses or conditions, concealed
genetic variations which never be seen under a normal environment may be
disclosed. The gene, *cos*, which was found by Costantino *et al.* (1967, 1968) from
one of my selected lines is a typical example. This gene behaves as a major gene
in one environment but acts as one of polygenes in another environment. There
would be many such genes whose actions are not detected under the normal
environment but would be screened out in an appropriate environment; 2) A
complex metric character which is not separable into components under the normal
environment may be decomposed into a few but more simpler components
controlled by a single or a few genes by exposing the animal to various environments.
Orozco's (1970) experiment suggests that egg production of virgin females
may be separated into the stimulation by mating and the real potential of egg
production in the female, because virgin females selected for decreasing egg
production laid no egg without males in late generations, while fecundated females
produced enough fertile eggs and thus no difficulty for reproduction. On the
other hand, females selected for increasing egg number laid 100 eggs without
mating, compared with 20 eggs in the control lines. The genetic correlation of egg
production of virgin and fecundated females was originally 0.83 (Orozco and
Bell, 1973). The environment in this example is with or without stimulation by
males; and finally 3) By exposing to various environments, integrated steps in the
complex of physiological and developmental processes for manifesting a quanti-
tative character might be separated into essential and not essential biochemical

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pathways, each controlled by a single gene with varying its action and effect in different environments. Again, $cos$ is an example.

**SUMMARY**

Selection experiments with *Tribolium* have provided ample evidences that the species is a suitable biological model for quantitative genetic studies. Although results obtained by various selection studies support in general the validity of quantitative genetic theories, consistent evidences of asymmetrical direct and indirect selection responses suggest that some revisions of the classical genetic model should be made.

Evidences from reciprocal recurrent selection and within-line selection in *Tribolium* suggest that RRS and WLS are exploiting different kinds of gene effects. Consequently, the RRS purebred response was less than the WLS purebred response in early generations, yet RRS crossbreds did as well or better than WLS crossbreds in later generations.

The importance of genotype-environment interaction studies to understand the constitution of an integrated biological system is also discussed.

**RESUME**

Les experiences de selection realisees avec *Tribolium* ont verifie avec des preuves suffisantes que cette espece est un modele biologiquement convenable aux etudes de genetique quantitative. Bien que les resultats obtenus par les differentes etudes verifient en general la validite des theories de la genetique quantitative, d'autres decouvertes evidentes sur la selection symetrique directe ou indirecte suggèrent qu'on doit introduire quelques revisions dans le modele genetique classique.

Les preuves de l'existence de selection recourant reciproque, et dans les lignes de *Tribolium*, suggèrent que RRS et WLS sont des classes differentes d'exteriorisation d'effets geniques. Par consequence, la reponse en RRS de race pure fut moindre qu'en celle WLS de race pure, aussi dans les premières generations, tout en se conduisant encore les croisements RRS aussi bien ou mieux que ceux WLS dans les generations posterieures.

L'importance de l'interation genotye-milieu environnant pour comprendre la constitution d'un systeme biologique integre, est aussi discutee dans ce travail.

**RESUMEN**

Los experimentos de selección con *Tribolium* han aportado amplias pruebas de que esta especie es un modelo biológicamente conveniente para los estudios de genética cuantitativa. Aunque los resultados obtenidos por diversos estudios comprueban en general la validez de las teorías de la genética cuantitativa, otros hallazgos evidentes sobre la respuesta simétrica a la selección directa e indirecta sugieren que deben introducirse algunas revisiones en el modelo genético clásico.

Los resultados obtenidos en experimentos de selección recurrente recíproca (SRR) de estirpe cerrada (SEC) y en *Tribolium* sugieren que cada una de ellas utilizan genes de acción diferente.
Por consiguiente, la respuesta de las líneas puras en la SRR fue menor que en la SEC en las primeras generaciones, comportándose los cruces SRR tan bien o mejor que las líneas SEC en las generaciones posteriores.

La importancia de la interacción genotipo-medio ambiente para comprender la constitución de un sistema biológico integrado se discuten también en el presente trabajo.

REFERENCES