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PROGRESS REPORT

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"Theoretical and Experimental Aspects of Selection
as Applied to Biological Groups."

I. Introduction

The population genetics group (Drs. Clay, Griffing and Young) within the Genetics Department at the Ohio State University is involved in a mission-oriented research program which is concerned with the human population problem in general, and with particular emphasis on the theoretical aspects of increasing the world food potential. The key project in this research program is that funded by the AEC, with Contract number AT(11-1)-1761, for which this project report is written. Under the auspices of this project, new population theory is developed and then tested by plant material (Arabidopsis thaliana) and animals (Drosophila melanogaster). For ease of presentation the theoretical and experimental aspects will be discussed separately.

II. Theoretical considerations

Biological group theory provides a new attack on problems in which genotypes may interact in any manner whatsoever. This establishes a foundation for describing interactive systems within, as well as between, species. Hence theoretical considerations can be conveniently divided into those in which the biological groups are generated by 1) a single base population and 2) two or more base populations.

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The studies summarized in the first seven papers in the series entitled "Selection in Reference to Biological Groups" are devoted entirely to the situation in which the groups are generated by a single base population. The objectives in those studies were to (i) ensure that positive selection resulted in a non-negative response in the population mean, and (ii) to devise new selection procedures which were highly efficient in changing the population mean. These considerations led to the use of selection index theory in random groups and to the use of non-random groups.

The seven studies all pertained to breeding populations which are subject to random mating. Investigations are already underway to consider the situation in which members of the breeding populations are self-fertilized. This is important because many of the world's food crops are self-fertilized species. Because of the non-orthogonality of the situation, computer simulation must be an integral part of the theoretical approach to the problem.

Another very important aspect of biological groups generated by only one base population, is that concerning stable and unstable equilibria. For example, it can be shown that with genotypic interaction, stable equilibrium conditions are possible, and highly probable, for individual loci which do not exhibit overdominance in either direct or associate effects.

Turning attention to the biological situation in which groups of interacting genotypes are generated by two or more

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different base populations (or species), an entirely new area of theoretical research is opened up. The biological group approach permits a genetic analysis of inter-specific population dynamics. Some theoretical progress has already been made, and several computer programs have been written to help explore this rich field.

III. Experimental studies

(a) Plant experiments

As mentioned in the previous section, attention is being directed toward the development of biological group theory as it relates to self-fertilized organisms. Dr. Roger E. Clay is biologically testing this theory with the test-organism, Arabidopsis, which is reported to be an obligatorily, self-fertilized species. If all facets of the procedure are successful, it will provide an excellent example of our basic approach which consists of developing new theory algebraically with models, elaborating and testing certain aspects of the theory with computer analysis, and then finally testing the new concepts and theories with a biological system.

Dr. Clay's experimental procedure involves simultaneous individual and group selection within pure and mixed groups of size two generated by two populations each of which was initially a different F_2 generation. Although the procedure must terminate after a relatively few generations (because of rapid fixation of genes due to selfing), the actual time taken for each generation is greatly extended. This is due to the fact that plants must be grown, weighed and then the selected individuals replanted in order that seed may be collected. Several generations have been completed, and the experiment will be continued in the future.

In addition Dr. Clay is examining the interactions which occur between competing individuals under different environmental regimes. All possible pairwise combinations of eight races of Arabidopsis are being grown under different temperature and nutritional regimes. This experiment is near completion and it is hoped that the results will indicate the types of environmental regimes which maximize or minimize these interactions. It may then be possible to predict the type of environment under which heterogeneous groups will give greater yields than homogeneous groups.

In the experimental paper by Griffing and Zsiros (1970) an extensive study was made of the influence of various environmental variables on the manifestation of heterosis as expressed in relation to the races WS and WIL and their hybrid. This study yielded a great deal of detailed information concerning the growth of this particular biological system. The same approach is being used with the races PI, DI and their hybrid. The purpose is to provide backup data for material used in the selection experiments conducted by Dr. Clay. Three temperatures (19°, 25° and 31°C) and three levels of nutrient solution (N = normal, 1/4 N and 1/16 N) are used. Plants are grown in cabinets under a regime which is identical to those used in the selection experiment.

(b) Animal experiments

(i) Selection for coexistence of two Drosophila species.

There is some evidence in the literature that the ability of one group of organisms to compete with another may evolve by selection within a few generations. Investigations concerning

competition between Tribolium species (by Lerner and his co-workers at Berkeley) and housefly and blowfly (by Pimentel at Cornell) have shown that one group of organisms could, in a few generations, eliminate a competing group. On the other hand, selection for coexistence of two Drosophila stocks appears to be feasible, also within a few generations (Seaton and Antonovics in Heredity:22). The present experiment aims to investigate the consequences of selection for coexistence in two species of Drosophila.

Initial experiments were concerned with the task of finding suitable genetic material. In these preliminary experiments five Drosophila species were reared in different pair-wise mixed cultures. The species involved were Drosophila melanogaster, D. virilis, D. pseudoobscura, D. hydei, and D. funebris. The aim of these preliminary experiments was to find two species which would be suitable for the selection experiment. The species suitable for the experimental design must possess the following characteristics: (1) They must have similar generation times, and (2) One species must dominate the other at the initial generation. The results of the preliminary experiment showed that D. hydei and D. virilis satisfied the above specifications.

For the main experiment, three selection lines were derived.

- (i) Control line 1 - four pure cultures of D. virilis were used in every generation.
- (ii) Control line 2 - four pure cultures of D. hydei were used in every generation.

(iii) Selection line - 24 mixed cultures of the two species were established in each generation. Four bottles with the smallest differences between the numbers of emerged flies in each species were selected as parents.

Intense competition conditions were created by placing eight pairs of parents in each bottle.

At the first generation, D. virilis was clearly the dominant species. The number of virilis flies which emerged from the first unselected stock constituted about 82% of the total number of imagoes in the mixed cultures. However, this was followed by a rapid increase in hydei and at the fourth generation, hydei emerged as the dominant species. But the superiority was not maintained after the fifth generation. The experiment is now at the eighth generation and further work is under way.

The data clearly indicate that selection for competitive ability can be extremely effective. It shall be interesting to see if the two species reach an equilibrium state under the present regime of selection pressure. Also it shall be interesting to see if the result of previous selection is maintained upon relaxation of selection pressure. Another aspect of the study is to examine the changes in fitness traits of the species as a result of selection. This will be discussed in a later section.

(ii) Individual versus group selection.

Experiments are underway to test the theory that with competition, group selection may be more efficient than

individual selection, in terms of genetic progress.

Early experiments using a fixed number of larvae in a small quantity of food (2 cc in a shell vial) were abandoned because of high mortality of the larvae due to hardening of the food in the vials.

In the second experiment, a competitive environment was created by placing four pairs of parents in shell vials containing four cc of food. The flies were allowed to lay eggs for five days. Body weight of emerged flies was used as the trait under selection.

Three selection lines were established. The lines and the methods of selection were:

- (i) Mass selection line -- selection based on individual merit.
Two replicates.
- (ii) Group selection line - selection based on mean weight of
flies in each vial. Two replicates.
- (iii) Control line - no selection.

There were gains in all lines up through the third generation, but the gain in the Mass line was negligible from generation four to generation six. The Group line continued to increase in mean body weight up to generation six. Further selection showed no gain in both selection lines. It was felt that the lack of response to selection after only four and six generations might be due to a lack of genetic variability in the laboratory stock used in the experiment, as well as to a severe increase in the degree of inbreeding within each line. The experiment was terminated at generation 14.

A third experiment was designed. To ensure the presence of genetic variability in the initial stock, four wild type strains (Swedish D, Lausanne S, Sito and Wageningen) were crossed. The selection lines were established in the same manner as before, but the number of parents used in every generation was doubled.

Up to the present time, selection has been conducted for 14 generations. In the first seven generations, the Mass selection line showed no increase in mean body weight while substantial progress was made in the Group line. In later generations, the Mass line began to increase in mean body weight while the progress in the Group line ceased. However, at generation 13, the Group line began to show an increased gain. Further selection work is underway.

IV. Publications and manuscripts submitted for publication which are associated with AEC Project AT(11-1)-1761 since its inception in February, 1968.

Griffing, B. (1967). Selection in Reference to Biological Groups I. Individual and Group Selection Applied to Populations of Unordered Groups. Aust. J. Biol. Sci. 20:127-139. (Basis for original proposal)

Griffing, B. (1968). Selection in reference to biological groups II. Consequences of selection in groups of one size when evaluated in groups of a different size. Aust. J. Biol. Sci. 21:1163-1170.

Griffing, B. (1968). Selection in reference to biological groups III. Generalized results of individual and group selection in terms of parent-offspring covariances. Aust. J. Biol. Sci. 21:1171-1178.

- Griffing, B. (1969). Selection in reference to biological groups IV. Application of selection index theory. Aust. J. Biol. Sci. 22:131-142.
- Griffing, B. (1969). Selection in reference to biological groups V. Analyses of random groups exhibiting family structure. (Submitted for publication).
- Griffing, B. (1969). Selection in reference to biological groups VI. Analyses of full-sib groups exhibiting family structure. (Submitted to publication).
- Griffing, B. (1969). Selection in reference to biological groups VII. Use of extreme forms of non-random groups to increase selection efficiency. (Submitted for publication).
- Griffing, B. and E. Zsiros (1970). Heterosis associated with genotypic-environmental interactions. (Submitted for publication).
- Mikolaj, P. J. (1970). Manifestation of heterosis in Arabidopsis thaliana under varying temperature and nutritional regimes. Ph.D. Thesis. Ohio State University (Columbus, Ohio).
- Mikolaj, P. J. and B. Griffing (1970). The growth of Arabidopsis thaliana in miniature containers. (Submitted for publication).
- Young, S. S. Y. (1969). Direct and associate effects of body weight and viability in Drosophila melanogaster. Genetics. (in press).
- Young, S. S. Y. (1970). The effects of some physical and biotic environments on heterosis of direct and associate genotypes in Drosophila melanogaster. (Submitted for publication).