3 ef
RF Project 2592

Report No. C00-1761-15

MASTER

FINAL

REPORT

By

THE OHIO STATE UNIVERSITY
RESEARCH FOUNDATION

1314 KINNEAR RD.
COLUMBUS, OHIO 43212

To U. S. ATOMIC ENERGY COMMISSION
Chicago Operations Office
9800 South Cass Avenue
Argonne, Illinois 60439
Contract No. AT(11-1)-1761

On THEORETICAL AND EXPERIMENTAL ASPECTS OF SELECTION
AS APPLIED TO BIOLOGICAL GROUPS

For the period February 1, 1968 - January 31, 1972

Submitted by Dr. Bruce Griffing
Department of Genetics

Date 13 January 1972

NOTICE

This report was prepared as an account of work sponsored by the United States Government. Neither the United States nor the United States Atomic Energy Commission, nor any of their employees, nor any of their contractors, subcontractors, or their employees, makes any warranty, express or implied, or assumes any legal liability or responsibility for the accuracy, completeness or usefulness of any information, apparatus, product or process disclosed, or represents that its use would not infringe privately owned rights.

DISTRIBUTION OF THIS DOCUMENT IS UNLIMITED
ef

DISCLAIMER

This report was prepared as an account of work sponsored by an agency of the United States Government. Neither the United States Government nor any agency Thereof, nor any of their employees, makes any warranty, express or implied, or assumes any legal liability or responsibility for the accuracy, completeness, or usefulness of any information, apparatus, product, or process disclosed, or represents that its use would not infringe privately owned rights. Reference herein to any specific commercial product, process, or service by trade name, trademark, manufacturer, or otherwise does not necessarily constitute or imply its endorsement, recommendation, or favoring by the United States Government or any agency thereof. The views and opinions of authors expressed herein do not necessarily state or reflect those of the United States Government or any agency thereof.

DISCLAIMER

Portions of this document may be illegible in electronic image products. Images are produced from the best available original document.

FINAL REPORT

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

OUTLINE

I. INTRODUCTION

II. DISCUSSION OF PROJECTS HAVING TO DO WITH THE THEORETICAL, SIMULATION AND EXPERIMENTAL ASPECTS OF BIOLOGICAL GROUPS.

A. Theoretical Aspects of Biological Groups

1. Intra-population dynamics

a. Unordered groups

- Project 1. Individual and group selection applied to unordered groups of arbitrary size.
- Project 2. Consequences of selection in groups of one size when evaluated in groups of a different size.
- Project 3. Generalized results from individual and group selection in terms of parent-offspring covariances.
- Project 4. Application of selection index theory to biological groups.
- Project 5. Analyses of random groups exhibiting family structure.
- Project 6. Analyses of full-sib groups exhibiting family structure.
- Project 7. Use of extreme forms of non-random groups to increase selection efficiency.
- Project 8. Individual and group selection involving a base population subject to self-fertilization.
- Project 9. Viability and fecundity selection as applied to groups generated by an autogamous base population (i.e. a population made up of different homozygous forms).

UTLINE CON'T

b. Ordered groups

Project 10. Various selection procedures applied to ordered groups generated by a random mating base population.

Project 11. Various selection procedures applied to ordered groups generated by an autogamous base population.

2. Inter-population dynamics

Project 12. Individual and groups selection applied to ordered groups generated by different base populations which do not interbreed.

B. Computer Simulation of Biological Groups

1. Intra-population dynamics

a. Unordered groups

Project 13. Individual, group and index selection for random groups.

Project 14. Individual and group selection for random groups and for non-random groups which include inbred, clonal, inbred-clonal and full-sib groups.

Project 15. Selection involving random groups generated by a base population subject to self-fertilization.

Project 16. Individual and group selection for groups generated by an autogamous base population.

b. Ordered groups

Project 17. Individual, group and modified group selection for ordered groups of size three.

Project 18. Individual, group and modified group selection for ordered groups of size three generated by an autogamous base population.

2. Inter-population dynamics

Project 19. Computer programs involving groups generated by different base populations.

OUTLINE CON'T

C. Experimental Testing of Biological Groups

1. Plant (Arabidopsis thaliana) Projects

- Project 20. Analysis of heterosis in relation to groups containing competitive or cooperative members.
- Project 21. Detailed analysis of temperature--nutrient interactions involved in heterosis of plant yield.
- Project 22. Attempts to detect cross-feeding between root systems of closely associated plants.
- Project 23. Comparison of individual and group selection with self-fertilized base populations.
- Project 24. Effect of different environmental regimes upon the interaction between competing members of a group.
- Project 25. Use of different species of Arabidopsis to form inter-population groups.
- Project 26. Development of cultural methods which enhance interaction between plants.
- Project 27. Development of an aqueous cultural technique for Arabidopsis.

2. Animal (Drosophila) Projects

- Project 28. Direct and associate effects of body weight and larval viability in Drosophila melanogaster.
- Project 29. Heterosis in relation to density, temperature and biotic associations.
- Project 30. Further investigation of the dependence of heterosis on environmental conditions.
- Project 31. Selection for positive and negative associate effects.
- Project 32. Selection for coexistence of two Drosophila species.
- Project 33. Further experiments on competition between Drosophila species.
- Project 34. Individual versus group selection.
- Project 35. Optimum phenotype in biological groups.

OUTLINE CON'T

III. REFERENCES

IV. INVITED SEMINARS IN THE AREA OF POPULATION GENETICS BY B. GRIFFING

V. GRADUATE STUDENTS ASSOCIATED WITH PROJECT

FINAL REPORT

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

(AEC Contract Number AT (11-1)-1761)

I. INTRODUCTION

New theoretical approaches to provide a greater understanding of intra- and inter- population dynamics are urgently needed. Such theory can be of value to the population biologist in his endeavor to preserve natural living resources while at the same time reconstructing biotic communities so that maximum use can be made of them in terms of aesthetic, as well as, material values. Newly developed population genetic theory is also essential to the agriculturist in his efforts to produce ever-increasing yields on ever-decreasing farm lands.

These and other problems requiring the manipulation of a single species or a community of species are becoming increasingly troublesome due to the pressures of the world's exploding human population. Time is running out for the population biologist to learn how to control and maintain his biotic environment.

In the past, theoretical population genetics dealt primarily with intra-population dynamics, i.e. with changes brought about by forces acting within a single population. The extension to inter-population dynamics (changes occurring among two or more populations)

has not been successfully made. Moreover, the classical theory of the past deals almost entirely with models in which interactions between genotypes are assumed to be absent. However, in the real world, individuals do interact with members of their own and other species. Competition and symbiosis are commonplace phenomena throughout the plant and animal kingdoms.

Hence the broad goal of this research program is to extend the non-interactive, classical population genetics approach so that it can accommodate genotypic interactions within and among populations.

In most situations of the real world an individual interacts with only a few other individuals. For example, a plant competes with only close neighbors; animals often form small social groups within which most interactions occur, etc.. To accommodate interactions among genotypes in small groups, the first step is to replace the conceptual, non-interacting base population of the classical approach with a new base population containing a group structure. Then the second step is to extend the classical gene model for a given genotype to include not only 'direct' effects due to its own genetic constitution but also the 'associate' effects due to genotypes of the other members of the group.

The extension of classical population genetics theory to include small groups of interacting individuals is the rationale for calling the new approach 'Biological Group Theory'.

The population biologist is not concerned merely with the description of a static population, whether it consists of isolated

individuals or of groups of individuals. What is of fundamental importance is the study of changes in the structure of the population (reflected primarily in changes in means and variances) when various forces are applied to the population. Since the main interest in this research is man's intervention in the evolution of a single species or a community of species, the force of principal interest is that of selection.

The theoretical objectives of this study, then, are to study the consequences of applying different selection procedures to populations of groups which are generated in a variety of different ways. However, in the mathematical treatment of this theoretical objective restrictions on the gene model and approximations in the derivation of results are usually required. Therefore, a second objective of this research is to check and augment the theoretical considerations by computer simulations. Finally, any biological theory ultimately must be put to test with living organisms. Hence the final objective of the total integrated research program is to test biologically various aspects of the theory. This is accomplished by two different organisms especially chosen to yield maximum information for minimum amount of work. The organisms are: Arabidopsis thaliana (a self-fertilized plant that can be grown in test tubes), and Drosophila melanogaster.

In the time period of the AEC grant, a total of 35 individual projects were initiated. Some projects were discontinued for one reason or another, some were completed and reported in manuscript form, and others are still being continued. The remaining portion of this report discusses each project separately, as it fall into one of

the three major aspects of biological group theory: (i) Theoretical, (ii) Computer Simulation and (iii) Experimental.

II. DISCUSSION OF PROJECTS HAVING TO DO WITH THE THEORETICAL, SIMULATION AND EXPERIMENTAL ASPECTS OF BIOLOGICAL GROUPS.

A. Theoretical Aspects of Biological Groups

As stated in the introduction, the overall theoretical objective of this research program is to study the consequences of applying different selection procedures to various sorts of populations of groups containing genotypes which may interact in any way whatsoever. The design problem is to construct the conceptual population and the associated gene models so that the analyses are applicable to that area of complexly inherited phenomena termed "quantitative inheritance".

The theoretical studies are concerned first and foremost with identifying selection procedures which ensure that positive selection produces a non-negative change in the population mean. Once this has been accomplished, the emphasis is then to construct selection procedures which are efficient.

1. Intra-population dynamics (Groups generated by a single base population)

a. Unordered groups (positions in the group do not influence the interaction pattern)

Project 1. Individual and group selection applied to unordered groups of arbitrary size.

In this first study, the ground work was laid for the model built around the concept of small groups of interacting genotypes.

Random groups were generated as combinatorial products of appropriate base populations. Consequences of individual and group selection were determined for populations of constant group size. It was discovered that individual selection was unbalanced in the sense that positive selection could result in a negative response in the population mean. It was shown that this dilemma could be overcome by transferring the basis of selection from that of the individual to that of the group, i.e. group selection was shown to be balanced and, as such, invariably led to desirable results.

The project was completed; written in manuscript form and published (Griffing 1967).

Project 2. Consequences of selection in groups of one size when evaluated in groups of a different size.

Consequences of individual and groups selection were examined for the case in which selection operated with regard to groups of one size and the effects of selection measured with regard to groups of a different size. It was demonstrated that neither individual nor groups selection could ensure that positive selection would result in a non-negative change in the population mean.

A practical case in which groups of different sizes are often involved in a selection procedure is that of pasture plant breeding. In this case, it is common practice to select among spaced nursery plants under the assumption that the desired response will be exhibited by the progeny grown under sward conditions. This assumption

is not warranted, especially for those traits that are subject to competition stress. Perhaps this is one reason why breeding for pasture crops in the past has not resulted in greater fulfillment of objectives.

It was also shown in this study that selection among sets of randomly associated groups is less efficient than selection among individual groups. Also it was demonstrated that if individuals within groups are independent, group selection is less efficient than individual selection.

This project was completed; written in manuscript form and published (Griffing 1968a).

Project 3. Generalized results from individual and group selection in terms of parent-offspring covariances.

In the previous studies, consequences of selection were examined for groups of genotypes generated by an arbitrary number of alleles at a single locus. These results were illuminating in that they showed the nature of response to selection in terms of direct and associated additive genetic effects. However two further extensions of the theory are necessary before the total response pattern can be determined, and before the theory can be used practically. The first extension has to do with generalizing the gene model to include an arbitrary number of loci in order to evaluate the total response to selection. The second extension deals with the practical problem of stating the consequences of selection in terms of parameters that can be estimated directly.

Both of these problems were solved in this study by transferring the model-building unit from that of the gene to that of the individual genotype. This permitted the consequences of selection to be formulated in terms of covariances among relatives. These covariances are directly estimable and can be interpreted in terms of gene models of any degree of complexity.

This project was completed; written in manuscript form and published (Griffing 1968b).

Project 4. Application of selection index theory to biological groups.

Previously it was shown that the dilemma of negative response to positive individual selection could be overcome by transferring the basis of selection to the group. However, it was also shown that under certain circumstances group selection, although a "safe" procedure, could be an inefficient form of selection. Hence in this study the optimum selection method, that of the selection index, was investigated. Indices were developed which combined individual and groups selection in such a way as to invariably yield the maximum possible non-negative change in the population mean.

This project was completed; written in manuscript form and published (Griffing 1969).

- Project 5. Analyses of random groups exhibiting family structure.
- Project 6. Analyses of full-sib groups exhibiting family structure.
- Project 7. Use of extreme forms of non-random groups to increase selection efficiency.

These three projects are discussed together since they are closely related and collectively explore the use of non-random groups.

The first four projects dealt with the simplest types of biological groups, namely those in which individuals from an unstructured base population were associated at random. A more general, and certainly a more realistic model, includes different classes of individuals (such as those occurring in a typical family structure) in a group, and allows for the case in which individuals are associated in a non-random manner.

The fifth project is concerned with the consequences of selection in relation to groups in which offspring are associated at random but the parental influences are included. Project 6 extends the above situation to the case in which each biological group is taken to be a family unit (i.e. the offspring are full-sibs). These groups are of particular interest since the family unit is a widespread form of grouping among social animals, including human. Also, in the applied areas of plant and animal breeding, family groups are frequently used in selection programs.

With the consideration of family structure, two additional levels of complexity are introduced into the mathematical analyses: (i) increase in the number of different classes of individuals; and (ii) non-random association of group members. As a result, mathematical analyses become non-orthogonal and hence more difficult. In full-sib groups (Project 6), it was shown that associate progeny effects enter into the changes of gene frequencies when selection is on an individual basis. This is not true with random groups. Therefore, individual selection involving full-sib groups offers greater safety over individual selection with random groups in terms of genetic progress.

It is of interest to point out that Projects 5 and 6 are of particular importance to ecologist and behavioral biologists. This follows from the fact that the family unit is the primary sub-unit in populations of humans and of some animals and plants. In such groups the total gene effect may be partitioned into several components and thereby provides theoretical solutions to some of the genetic paradoxes in the past. For example, positive associate effects may more than compensate for a negative direct effect and thus a genetic explanation for the evolution of altruistic behavior is provided.

Having shown that the full-sib family group is an efficient structure in selection, attention was turned to groups with an even higher degree of homozygosity and/or homogeneity. The seventh project explored the efficiency of using extreme forms of non-random groups. These groups were assumed to be populations generated by

clonal propagation or by a population of isogenic inbreds produced by doubling haploid individuals. It was shown that if these groups were used as units of selection, a spectacular increase in efficiency of selection was possible. Of the two types of extreme groups, the groups generated by clonal propagation were shown to be more powerful in selection procedures.

All three projects have been completed and manuscripts have been written (Griffing 1972a, 1972b, 1972c). However the manuscripts are being revised in order to add greater detail and reduce problems of notation.

Project 8. Individual and group selection
involving a base population subject
to self-fertilization.

In previous studies the base population was assumed to randomly mate. This study concerns groups generated by a base population which is self-fertilized. The importance of considering this form of reproduction is that some of the most important food-crop species are predominantly self-fertilized, i.e. wheat, rice, barley, oats, etc..

Because of the non-orthogonality of the conceptual population framework, the algebraic treatment is difficult. For a single locus model, the change in mean involves the inbred mean itself together with a complex series of cross-products of genotypic effects.

An approach which appears to have some promise, is that of simulating the genetic system on the computer. Therefore, a computer program has been written for this purpose (see section on computer simulation). This is a continuing project, which will be integrated with computer simulation studies and biological testing using the self-fertilized organism, Arabidopsis thaliana.

Project 9. Viability and fecundity selection as applied to groups generated by an autogamous base population.

In the last few years considerable attention has been directed toward a number of phenomena which are brought together in this study. The basic conceptual framework studied was that of groups of size 'n' generated by a single base population consisting of a number of different homozygous genotypes with arbitrary frequencies.

Natural selection in the form of differing viability and/or fecundity parameters, was brought to bear on individuals within groups and on the groups themselves. It is interesting that prediction of expected changes in the population mean can be made with a completely general genetic model and with a minimum of approximations.

Another interesting aspect of the study is that the usual "frequency-dependent selection" phenomena can be viewed as a special case of the more general theory covered in this study.

The theoretical analyses are completed and the material is being prepared in manuscript form.

Project 10. Various selection procedures applied to ordered groups generated by a random mating base population.

The theoretical consequences of individual, restricted group, entire group and modified group selection procedures have been determined for the situation of ordered groups. The simplest example of an ordered group (in which position in the group modifies interaction between individuals) is that in which plants are arranged in linear order, as in a row. In this case a particular plant at a given position is influenced mostly by individual plants on either side and to a lesser extent by plants further removed.

The gene model is more complex than that for unordered groups, as it must now differentiate between different associate classes. With all forms of selection, the changes in population mean are complicated and involve matrices of variances and covariances. The only method of selection that is completely balanced (invariably results in ~~4:70~~) is "modified group" selection. In this procedure the entire group is selected on the basis of its mean, however, gametes are collected from only the central individual in the group.

This theoretical study is completed. It provided the major part of an invited lecture to the National Association of Forestry Geneticists (summer 1970). It is now being prepared in manuscript form.

Project 11. Various selection procedures applied to ordered groups generated by an autogamous base population.

In this project the theoretical consequences were determined for selection operating on ordered groups generated by a single autogamous base population. Hence this is an extension of the un-ordered case discussed in Project 9. The gene model and consequently the response to selection were more complex than in the case of unordered groups. This is due to the increase in the number of classes of associate effects which must be differentiated.

Preliminary work on this project has been completed but more work has yet to be done.

2. Inter-population dynamics

Project 12. Individual and group selection applied to ordered groups generated by different base populations which do not interbreed.

This project directs attention to the biological situation in which groups of interacting genotypes are generated by two or more different base populations. Such an approach permits a genetic analysis of inter-population dynamics. Consequences of individual and group selection have been derived theoretically for groups of an arbitrary size, 'n' (i.e. groups generated by 'n' different base populations). The analyses require a separate gene

model associated with each of the 'n' base populations. Responses to selection necessarily involve $n \times n$ matrices of variances and covariances.

Preliminary work on this project has been completed but more work needs to be done.

B. Computer Simulation of Biological Groups

A variety of computer programs have been written by Mrs. Ann Dudgeon (a Graduate Student in the Arabidopsis laboratory) to complement the theoretical aspects of biological group theory. The programs will be discussed as individual or collective projects arranged in approximately the same order as those in the theoretical area.

1. Intra-population dynamics (Groups generated by a single base population).

- a. Unordered groups (Positions in the group do not influence the interaction pattern).

- Project 13. Individual, group and index selection for random groups.

A program has been written to investigate individual, group and index selection as it operates within the framework of random groups of size two. The program utilizes a general gene model involving up to six alleles, with arbitrary frequencies, at a single locus. It should be remembered that although a single locus is under consideration, a two-locus gene model is actually involved because of the fact that there are two members of the group. This two-locus model is generalized to include not only arbitrary dominance patterns for direct and associate genotypes but also arbitrary epistatic parameters which jointly involve the direct and associate genotypes. The program repeats the selection procedure through any number up to 50 cycles. The population mean, gene frequencies and genotypic variance components are printed out for each cycle. Finally the population mean is plotted for the entire computer run.

The program is completed and has been put into operation. It complements the theoretical studies described in Project 1 and 4.

Project 14. Individual and group selection for random groups and for non-random groups which include inbred, clonal, inbred-clonal and full-sib groups.

Two programs have been written in this project area which complement the theoretical studies involved in Projects 5, 6, and 7.

The first program is limited to groups of size three, but includes a completely general genetic model. The second program generates groups of arbitrary size, 'n', but is restricted to only an additive gene model. For each cycle both programs print out the population mean, gene frequencies, direct and associate effects and variances. The population mean and gene frequencies are plotted for the entire-computer run.

Both programs are completed and have been used.

Project 15. Selection involving random groups generated by a base population subject to self-fertilization.

This program has been written to complement the theoretical studies reported in Project 8. Up to six alleles with arbitrary frequencies are permitted at the single locus under study. A general gene model is used. Group size is two and up to 50 cycles of selection can be run. The population mean and gene frequencies are printed out at each cycle and these statistics are plotted for the entire run.

The program is completed and preliminary studies have been made.

Project 16. Individual and group selection for groups generated by an autogamous base population.

The program written for this project complements the theoretical studies discussed in Project 9. An autogamous population is merely a population of homozygous genotypes with arbitrary frequencies. The program accommodates groups of size three. At each cycle the print-out includes values for the population mean, genotypic frequencies, direct and associate effects and variances. Plots over the entire run are made for the population mean as well as for the genotypic frequencies.

The program is completed and working.

- b. Ordered groups (Positions in the group influence the interaction pattern).

Project 17. Individual, group and modified group selection for ordered groups of size three.

This program has been written to complement the theoretical study reported in Project 10. The random mating base population generates groups of size three. A general gene model is used. At each cycle the population mean, gene frequencies, direct and associate effects and variances are printed. The population mean and gene frequencies are plotted for the entire computer run.

The program is completed and working.

Project 18. Individual, group and modified group selection for ordered groups of size three generated by an autogamous base population.

The difference between this program and the one described in Project 17 is that the groups involved in this program are generated by an autogamous base population, whereas those in Project 17 are generated by a random mating base population. At each cycle genotypic frequencies, population mean, direct and associate effects and variances are printed. The population mean and genotypic frequencies are plotted for the entire computer run.

The program is completed and working.

2. Inter-population dynamics (Groups generated by different base populations).

Project 19. Computer programs involving groups generated by different base populations.

The previous programs deal with infinite population theory and involve a single base population which has taken various forms in the different projects (i.e. random mating, self-fertilizing, or autogamous base populations). These programs were written to explore intra-population dynamics.

Mrs. Dudgeon has also written new programs (or modified previous ones) which involve more than a single base population. Such programs permit the exploration of inter-population dynamics and augment the theoretical studies reported in Project 12. These

programs also utilize random mating, self-fertilizing and autogamous base populations.

A particularly interesting program is one which generates groups from two different base populations and investigates the dynamics of the group system under the restriction of small (finite) population sizes. The problem of computer simulation with finite population sizes is much more difficult and complicated than simulation with infinite populations. Random sets of genotypes are generated from two pairs of synthesized chromosomes, each containing 20 loci. Then random sets of groups are formed, and values for the genotypes and phenotypes are calculated. After selection, the chosen individuals are mated. This requires producing random gametes from the selected parents. A Poisson recombination model is used to simulate crossing-over in the meiotic process. Once the offspring are formed, the cycle is repeated.

This program, together with other computer programs discussed in this section of the report, provide the tools for Mrs. Dudgeon's Ph.D. dissertation.

C. Experimental Testing of Biological Groups

One of the main objectives of the research project is to test biologically various aspects of the theory. The tests have been carried out using a self-fertilized plant (Arabidopsis thaliana) and a cross-breeding animal (Drosophila melanogaster). These organisms are chosen specifically because they yield a great deal of biological information for a minimum amount of time and effort.

The experimental projects are grouped according to the organism used. Each project is discussed separately in the remainder of this section.

1. Plant (Arabidopsis thaliana) Projects.

Arabidopsis is not as well known an experimental organism as Drosophila. Therefore it is worth while to list the advantages of this self-fertilized crucifer:

- (i) Arabidopsis plants may be grown aseptically in ordinary test tubes on nutrient solution solidified with agar. (See Figure 1.)
- (ii) Since a plant may grow, flower and set seed in a test tube, a large number of plants can be grown in a relatively small environmentally controlled space. Thus a growth cabinet with 3-1/2' x 6-1/2' tray area can accommodate 5000 plants with normal sized test tubes; more with smaller tubes.

- (iii) Under optimal conditions, the plant grows and flowers very rapidly, the fastest races flowering 10-14 days after germination. Hence, up to 10 generations may be obtained in a year. In the usual experimental procedure, a growing period of 14 days is sufficient. This feature of fast generation time and short duration of experiments is an important characteristic of Arabidopsis.
- (iv) Arabidopsis plants are fully self-fertile, each setting about 150 seeds when grown in test tubes. Crossing may be performed using test-tube plants.
- (v) Considerable genetic variability is available in the form of naturally occurring races. A collection of about 50 ecotypes is available in our laboratory. These were collected from an area bounded by Holland in the west and Japan in the east, and by the Arctic Circle in the north and North Africa in the south.
- (vi) The haploid chromosome number is five.

The test-tube culturing technique of Arabidopsis is ideally suited to the establishment of well-defined groups of low order. Thus, groups of size 'n' are obtained by planting 'n' seeds per tube. Groups of larger order can be obtained by using larger containers. In fact, 'swards' of Arabidopsis can be grown in crystallizing dishes.

Project 20. Analysis of heterosis in relation of groups containing competitive or cooperative members.

The exploitation of heterosis is one of the most important applications of genetics in terms of present day agriculture.

However, the phenomenon of heterosis remains a genetic enigma. In the past, the manifestation of heterosis was almost always regarded as a genetic phenomena alone. In more recent years, however, it has been shown that diverse environments can cause drastic changes in the heterotic response. Thus heterosis must be viewed as due to the interaction between genetic and environmental stimuli.

With this more complex pattern of stimuli and response, the question naturally arises with regard to biological groups, as to whether the influence of groups members may alter the heterotic expression. To investigate this question, several experiments have been designed to which Arabidopsis races and their hybrids are reared as groups of size two in well-defined and quantitatively related environments.

In the experiment reported in this project, two races WS and WIL and their F_2 hybrid were used. The F_2 generation was included instead of the F_1 because of the difficulty of obtaining sufficient quantity of F_1 seed.

The environmental factors, which were varied in a controlled manner, were: (i) plant density (one or two plants per tube); nutrient level (normal and 1/16 normal strength); temperature level (25° , 28° and 31° C); and stage of plant development as reflected in four consecutive harvest dates.

When two plants per tube were planted, all possible pair-wise combinations were made in terms of the parents and their hybrid. Thus six combinations were produced which included pure stands $\{(WS, WS), (F_2, F_2) \text{ and } (WIL, WIL)\}$ and mixtures $\{(WS, F_2),$

(WS, WIL) and (F_2 , WIL) } . This planting design, which generates groups of size two, permitted the opportunity of measuring heterosis in three different ways (i.e. in terms of pure stand contrasts, 'direct' genotypic contrasts, and 'associate genotypic contrasts').

The results indicated that different kinds of heterosis were definable depending on how the heterotic phenomenon was influenced by facets of the physical as well as the biotic environments. In general, the heterotic responses were found to be dependent on nutrition, temperature, developmental-time and plant associations within groups. With particular reference to heterosis as influenced by the group phenomenon, the following points may be made:

- (i) Strong interaction among group members influenced the manifestation of heterosis:
- (ii) The heterotic contrasts, based on direct and associate effects, tended to be negatively correlated; and,
- (iii) Heterosis in general may be considerably influenced by the physical and biotic environments in which the material is grown.

The project outlined above has been completed and published (Griffing and Zsiros, 1971). Further studies involving another set of races is being completed.

Project 21. Detailed analyses of temperature-nutrient interactions involved in heterosis of plant yield.

Since, temperature- and nutrient-dependent forms of heterosis were found to be important in the experiment described in the

previous project, it was decided to investigate these phenomena in greater detail.

Because macronutrient requirements of plants vary within large limits, there has been considerable interest in determining the optimum combination of these elements. As early as 1910 a "triangular" system was introduced for the study of the effects of varying the quantities of nitrogen, phosphorous and potassium. The vertices of the triangle represented 100 percent of NH_3 , P_2O_5 and K_2O . The intermediate points within the triangle represented various combinations of the fertilizer constituents. This method was criticized by various workers on the grounds that no single ion in the nutrient solution could be varied alone. In 1961 a method (Steiner Method) was proposed to overcome the weakness of the triangular system. In this method the nutrient amount is represented as milligram ions per liter, or milliequivalents per liter, or parts per million or as a percentage of the total anions or cations present in the solution. The Steiner Method enables the construction of nutrient solutions which contain a desired anion and cation ratio together with a certain total ionic concentration and desired pH level.

In Project 21, then, the Steiner Method was used to make up 10 solutions with different percentages of nitrogen, phosphorus and sulfur, which collectively constituted the anionic portion of the nutrient solution.

In order to find suitable genetic material for this project, eight races of Arabidopsis were grown in various temperature and

nutritional combinations. From the results of this experiment, the races of RLD, EST, BLA and DA were selected. These races and their F_2 hybrids, then, were used in further genetic experiments.

The results showed that heterotic responses were significantly influenced by both the genetic and environmental main effects as well as by their interactions. In addition, a genotype-dependent form of heterosis was found to be large and important.

The data demonstrated that genotype-environment interactions were represented by linear fractions of percent nitrogen in solution and that heterotic responses to different nitrogen concentrations varied with the genetic material. Furthermore, specific combinations of parental types yielded higher or lower amounts of hybrid vigor than expected over a range of environments.

Temperature-dependent heterosis was evident, and the results appeared to be consistent with a genetic model involving dominance of alleles producing relatively heat-stable enzymes.

The above investigation was conducted by P. J. Mikolaj under the supervision of B. Griffing. The results of this investigation were reported in a Ph.D. thesis submitted by Mr. Mikolaj (1970).

Project 22. Attempts to detect cross-feeding between root systems of closely associated plants.

Although this project was not completed successfully, it is reported here because of the unusual interest in plant interactions (see NAS-NRC symposium entitled "Biochemical Interactions Among Plants", published in 1971).

In Project 20, which involved planting two plants per tube, evidence for the unexpected phenomenon of cross-feeding between root systems of closely associated plants was detected at high temperatures. Hence a rotational type of experiment was conducted in this project in order to more clearly demonstrate the phenomenon and to pin-point exactly the form of interaction taking place. The experiment started by planting two parents and their hybrid singly in vials. The plants were grown under optimal conditions. After approximately three weeks, the tops were removed and weighed, but the roots were allowed to remain undisturbed in the agar. Tubes from each class of genotypes of the first planting were divided into three parts and each part replanted to one of the three genotypes. The nine sets of second plantings were divided equally into two parts. One part was put into optimal growing conditions and the other part into a high temperature stress regime. The possibility of cross-feeding with regard to the alleviation of high temperature lesions was to be determined by comparing appropriate responses.

Although the procedure was attempted several times, the cultural problems inherent in the system (keeping agar substrate in vials for a long period of time) prevented a satisfactory completion of the experiment. It is hoped that the detection of cross-feeding can be realized using a different (aqueous) cultural technique (see Project 27).

Project 23. Comparison of individual and group selection with self-fertilized base populations.

In Project 8, biological group theory is being developed as it relates to self-fertilized base populations. The theory is augmented by computer simulation studies in Project 15. Finally in the present project, Dr. Roger E. Clay is biologically testing certain aspects of the theory with Arabidopsis.

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 the selected plants must be replanted in order that seed may be collected. Several generations have been completed, and the experiment will be continued in the future.

If all facets of the procedure in Projects 8, 15 and 23 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 simulation and then finally testing the new concepts and theories with a biological system.

Project 24. Effect of different environmental regimes on the interaction between competing members of a group.

Dr. Clay is examining the nature and magnitude of interactions between competing individuals within groups under different environmental conditions. All possible pairwise combinations of eight Arabidopsis races are grown under different temperature and nutritional regimes. It is hoped that the results will indicate the types of environmental conditions which maximize or minimize these interactions. It may then be possible to predict the type of environment under which heterogeneous (mixed) groups will give greater yields than homogeneous (pure) groups. The project is not yet completed.

Project 25. Use of different species of Arabidopsis to form inter-population groups.

The main species of Arabidopsis used experimentally in our laboratory is Arabidopsis thaliana. We have approximately 50 races of this one species. Seed collections for three other species have been made over the last two years. These species are A. Griffithiana, A. Pumila and A. Korshinskyi. Invariably the seed collections for each species produced a variety of growth types. Hence the sorting out process has been time consuming. However studies are now being planned which will involve two different species. One such experiment is to select for mixing ability among segregating A. thaliana plants when grown pairwise with a single tester species other than A. thaliana. It would be interesting

to know if mixing ability can be changed. If it can be changed, is the change specific to the tester used or is it of a more general nature?

This and other experiments involving two different species of Arabidopsis are planned for the future.

Project 26. Development of cultural methods which enhance interactions between plants.

A great deal of effort has been devoted to exploring new cultural methods which maximize interactions between plants within short growth periods. Normally plants are reared on about 8 ml of nutrient solution solidified by agar in standard test tubes. When two plants grow in a single test tube, it is found that the root systems may be largely independent and there is apparently little movement of nutrient ions in the agar matrix. This means that to obtain a strong competitive interaction, the plants need to be grown for a long period of time. Such a procedure is undesirable for at least two reasons: (i) it prolongs the experiments and makes it almost impossible to conduct a sequence of growing operations; and (ii) it forces the experiment to include the flowering as well as the vegetative growth phases. Therefore a search for different culturing systems seemed necessary in order to discover new techniques which produce strongly competitive interactions in a short growth period.

Various techniques, not all unrelated, were tried. These included, dilution of the medium, planting more than two plants per tube, using less medium, and using small-sized tubes.

Dilution of the medium, in itself, did not entirely solve the problem; it resulted in miniature plants with relatively the same competitive interactions. Planting more plants per tube was found to be impractical because the probability of obtaining tubes in which all seeds germinated and produced desirable plants was low; this resulted in an impossibly high discard rate.

After considerable experimentation, varying the tube size and the quantity of nutrient medium proved most successful and provided some unexpected results. Two interesting points are summarized as follows:

- (i) Arabidopsis plants can be grown through the entire life cycle to produce viable seed in the smallest tubes available to us. These tubes have dimensions 6x50 mm. The plants will go through a life cycle in these tubes on (1/8) ml of nutrient solution, which in less exact terms, is about a drop of liquid! (See figure 2)
- (ii) For a 14 day growth period, plants will grow on 2 ml of nutrient in 10 mm (3/8") diameter tubes to a size comparable to, or even greater than, plants grown on 8 ml of nutrient solution in the standard 18 mm tubes.

A paper embodying these results has been published (Mikolaj and Griffing 1971). In this paper it is postulated that a favorable spatial dimension, which leads to satisfactory root development, is important to plant growth.

Project 27. Development of an aqueous cultural technique for Arabidopsis.

The Arabidopsis laboratory, primarily through the efforts of Mrs. Ann Dudgeon, is working on a project in which Arbidopsis plants are grown submerged in a liquid nutrient solution. Our efforts are a modification of an unpublished technique developed by Dr. John Langridge, Division of Plant Industry, C. S. I. R. O., Australia.

The procedure now used in our laboratory utilizes a humidifying flask, a growth flask, and a discharge flask connected by appropriate filters.

A stream of air, generated by a pump, is bubbled through water in a 400 ml humidifying flask, then it is filtered and passed into the growth flask by means of a gas dispersion tube, the end of which is submerged in the sterilized nutrient solution contained in the 400ml discharge flask where moisture in the form of liquid drops is trapped. Finally the air is discharged from the system by passing it through a filter. The entire apparatus is sterilized, and surface-sterilized seed is placed in the growth flask under aseptic conditions. Growth takes place under appropriate fluorescent lighting.

If only nutrient solution is used, the seed germinate but do not grow. However if sucrose is added the plants grow amazingly well (See figure 3)!

The aqueous system should be valuable for at least the following reasons:

- (i) The amount of dry weight actually produced per unit of time is far greater than that for test-tube culture;
- (ii) the method converts a diploid flowering plant into a growth system analogous to that of a microbial (single cell) growth system in so far as producing biomass growth curves is concerned;
- (iii) with the method it is easily possible to add metabolites and anti-metabolites to the plant environment in order to study their effects on plant growth;
- (iv) the method allows a study of possible cross-feeding between different genotypes thereby providing a solution to the cultural problem described in Project 22; and
- (v) by culturing the entire plant, the method provides a new approach to the physiological studies of heterosis which have been attempted in the past with tissue (root in particular) culturing techniques.

The difficulties which are yet to be solved are the high rate of contamination and the repeatability of performance in different runs. For example it would appear that the air pressure is critical for consistent runs. This project is continuing.

2. Animal (Drosophila) Projects

Drosophila was chosen to be the model organism for experiments pertaining to animal populations. The various advantages of using Drosophila in genetics work, namely the short generation interval, the ease of stock maintenance and well documented studies on morphological and biochemical variability are well known. An added advantage is that several species of Drosophila are readily available for experiments involving interspecific competition. The experiments supported directly or indirectly by the present project are listed below.

Project 28. Direct and associate effects of
body weight and larval viability
in Drosophila melanogaster.

When genotypes coexist in a common environment they may interact in a variety of ways. Probably the most frequently observed interaction is that of competition in which the success of some genotypes is accompanied by the failure of others. Another form of genotypic interaction is known as facilitation, here the simultaneous presence of two different genotypes are mutually beneficial. Still another form is the opposite of facilitation, inhibition, where the presence of two different genotypes are detrimental to both. In the first theoretical paper, (Griffing 1967), direct effects were defined as those gene effects due to the genotypes themselves, and the associate effects as the contributions due to other members of the same group. Associate effects can be positive or negative and thus account for different forms of interaction. In this way competition and facilitation are expressed in quantitative terms which are, then, incorporated into population genetic models.

The present experiment was designed to detect the presence of genotypic interactions and to estimate sizes of associate effects among five genotypes (sc, e, gt v, B and +) in Drosophila melanogaster. Two traits were observed in this study; body weight and larval viability. Body weight is a metric character not directly connected with fitness while larval viability is a component of fitness.

First instar larvae of the five genotypes were reared in shell vials, with four cc. of food. Mixed and pure cultures were established. The environmental variables included four temperatures and six densities. Within each temperature-density combination 15 mixed and pure cultures were synthesized. In this way a total of 24 combinations of each of 15 cultures were observed.

It was found that the overall associate effects among genotypes for both body weight and viability were small and non-significant. However, some associate effects in certain physical and biotic environments were large and significant. The direct and associate effects of various genotypes for body weight were frequently found to be different from similar effects for larval viability.

In this study it was also possible to compare the differences in interaction between genotypes in pure and mixed cultures. For body weight, inhibition is the mode of genotypic interaction. In contrast, facilitation is usually found in the viability data. As a result of interactions, the overall mean body weight is higher in pure cultures than in mixed cultures. On the other hand, mean viability is higher in mixed than in pure cultures.

It was concluded that a knowledge of genotypic interaction concerning a trait not directly connected with fitness does not permit inferences to be made concerning interactions affecting fitness characters.

A paper embodying results of this experiment has been published in Genetics (Young 1970).

Project 29. Heterosis in relation to density, temperature and biotic associations.

This experiment is a parallel experiment, in animals, to that discussed under Project 21. Briefly the aim of the experiment was to investigate the influence of the environment on the manifestation of heterosis using a factorial design approach. However, in this experiment it was possible to measure a fitness trait (larval viability) in addition to the weight of the organism.

The experimental design is similar to that discussed under Project 28. The environmental conditions included three temperatures and six densities, so that 18 environmental regimes were created in all. The genetic material consisted of two stocks of Drosophila melanogaster, coiled and Bar eye, as well as the F_1 hybrid between the parental stocks. Within each environmental regime all possible combinations of pure and mixed cultures of first instar were made. Larval viability and body weight of adult flies were recorded.

The performances of F_1 's were compared with mid-parent values in two ways; comparisons of direct heterotic effects, and comparisons of associate heterotic effects. The latter measured the competitive ability of the F_1 relative to the average competitive ability of the parents.

The heterotic responses for the two traits were quite different in different environmental regimes. The superiority of the F_1 in viability was uniformly large over all environments. This was, however, not the case for body weight data. The performance of the F_1 flies depended markedly on temperature. At the optimum temperature of 25°C, no hybrid vigor was observed, while at the extreme temperatures of 16°C and 30°C, the F_1 's were clearly superior.

Heterotic contrasts in associate effects for the two traits were also different. The contrasts for body weight changed with changing density-genotype combinations while those for viability varied with densities.

It was concluded that within a special environment the types of heterosis termed 'euheterosis' and 'luxuriance' are manifested in different manners by the same organism.

A paper reporting the findings has been published in Genetics (Young, 1971).

Project 30. Further investigation of the dependence of heterosis on environmental conditions.

The experiment described under Project 29 showed that the manifestation of heterosis in body weight was dependent on temperature while hybrid vigor for larval viability was more or less uniform over all the environmental regimes used in the experiment. It was postulated that the hybrid vigor of "luxuriance" traits may be more susceptible to variations in environmental conditions as compared with "euheterotic" traits. If the hypothesis were true then it may have far reaching effects, both in the exploitation of heterosis in agricultural production and in the interpretation of

the role of heterozygosity in evolution. An experiment was designed to further explore this hypothesis. In this experiment two different traits will be measured: these are a fitness character "emergence time" and a metric trait "abdominal bristle count". The latter is a quasi-continuous variable with no apparent relationship with fitness. The experimental design is the same as that described under Project 29.

The experiment is under way and it is hoped that the work will be completed before the end of January 1972.

Project 31. Selection for positive and negative associate effects.

A preliminary experiment to investigate the feasibility of selection for positive and negative associate effects, using two D. melanogaster stocks, (e,+), were conducted. Three lines were established in the experiment, and these were:

1. Facilitation line - selected for positive ability to coexist;
2. Competition line - selected for negative ability to coexist; and
3. Control line - no selection.

The ability or inability to coexist was judged by the number of flies of each stock which emerged in mixed cultures. In each generation virgin flies were collected from the bottles and mated with males of the same genotypes. Fertilized females were used to establish mixed cultures involving all lines in each generation.

Selection was discontinued after nine generations due to contamination of the stocks. The contamination occurred because of a lengthening of the time of emergence of the mutant stock, ebony. A delay of virgin collection resulted in crossing between stocks.

Since this work is of importance to ecological genetics, further experiments in this area are under consideration.

Project 32. 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 (Lerner and Ho 1961) and housefly and blowfly (Pimentel et. al. 1965) 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 Antonevics 1967). 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 in 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 D. 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 D. hydei and at the fourth generation, D. hydei emerged as the dominant species. But the superiority was not maintained after the fifth generation.

At generation 7, the numbers of D. virilis and D. hydei flies emerged from mixed cultures were approximately equal. The selection phase of the experiment was terminated. The selected and the control stocks were subjected to a series of tests with the view to provide some answers to two specific questions. These were:

- (i) Is the improved ability for the species to coexist, which has evolved by the current selection method, specific for the two stocks under selection?
- (ii) What are the correlated changes in fitness traits, if any, of the two species due to selection for coexistence?

Two series of tests were conducted. The first test consisted of an estimation of relative fitness between the two species. Individual females in each species were mated and placed in separate vials. The females were allowed to lay eggs for five days and then discarded. The average number of days required for the emergence of first five flies in each vial, together with the number of flies produced, were recorded. The second test consisted of competition experiments involving selected and unselected flies. The selected flies of the two species A and B were reared with the unselected flies a and b in pairwise mixtures. In this way 4 combinations aB, Ab, AB, and ab, each represented by eight mixed cultures, were established. The number of flies of each species emerged from each culture was recorded. Then the relative number of flies emerging from the mixed cultures were used to indicate any genetic change in competitive abilities in the selected stocks.

The experiments have been concluded and the analysis of data is underway.

Project 33. Further experiments on competition between Drosophila species.

The experiments described under Project 32 showed that selection for coexistence between two species of Drosophila may be relatively effective. It was decided to apply the same selection method to a different combination of species which exhibited an even larger initial difference in competitive ability when reared in mixed cultures. Earlier results showed that when D. virilis and D. funebris flies were reared in mixed cultures, more than 90-99% of the emerging flies belonged to D. virilis. Therefore these two species were chosen for the current experiment.

The experimental design and the method of selection were the same as those described under Project 32.

Selection for a higher proportion of D. funebris flies in mixed cultures was carried out for 13 generations. There was a general increase in the proportion of D. funebris flies up to the 5th generation. Further selection up to the 10th generation produced no further change in the relative frequency of the two species. Between the 5th to the 10th generation the mixed populations appeared to have stabilized at about 25% D. funebris and 75% D. virilis. However selection after the 10th generation resulted in an unexpected steady decline in the proportion of D. funebris flies.

At the 13th generation it was necessary to abandon the selection experiment because of insufficient number of D. funebris flies emerging from the mixed cultures. Fertility tests on D. funebris flies are now underway.

From the results obtained under Projects 32 and 33 it appears that coexistence between species is a function of the particular species involved in a given environment. Under suitable conditions coexistence between species may be evolved in a relatively short period of time.

It is anticipated that a paper discussing the findings will be submitted for publication in the near future (Young 1972).

Project 34. Individual versus group selection.

Three experiments were conducted 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 (two 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 conducted. 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.

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 Group line ceased. From the 9th to the 18th generation the Mass line overtook the Group line and at the end of the 18th generation the mean of the Group line was 7% lower than the Mass line.

There is thus a general agreement between experiments (2) and (3) in that group selection was more efficient than mass selection during the initial generations of selection but the relative efficiency changed with further selection pressure. One possible explanation for these results, is that selection under crowded conditions may result in a change in the covariance between the direct and the associate effects. If the change is appreciable, then under certain circumstances (Griffing 1967), the relative efficiency between group and mass selection may also be altered.

The experimental evidence therefore, appears to be insufficient to draw firm conclusions. Since the theory of group selection represent an entirely new approach to selection, it is important to continue the experimental phase of this work. Further studies involving new experimental designs appear to be important.

Project 35. Optimum phenotype in biological groups.

An optimum fitness model was proposed by R. A. Fisher and Sewell Wright in the 1930's. In this model it was suggested that organisms with intermediate phenotypes (or genotypes) were the fittest in the population. It was further suggested that the fittest phenotypes may be those with measurements most closely approximating the mean. The optimum model has been subjected to considerable theoretical analysis. However very little experimental evidence concerning the concept has been reported in the literature. Therefore two experiments were conducted to obtain information on this phenomenon which is of extreme importance in terms of natural selection. In these experiments, the relationships between a metric trait, body weight and fertility and between body weight and fecundity in Drosophila melanogaster were investigated. The relationships were examined in three temperatures (20°C, 25°C and 30°C) and in several genetic stocks.

In the first experiment, the mid-parent body weight was used as the metric trait, but in the second experiment female body weight was used. The genetic material used in both experiments involved high and low body weight lines, inbred and outbred lines and selected and unselected mutant (Ebony) stocks.

Within each genotype-temperature subclass, approximately 60 females (representing the whole range of body weight) were measured and allowed to produce offspring in single vials. In this way, about 3800 individual body weight and fertility records were available for analysis.

The relationship between body weight and fitness traits were examined within each temperature and within each stock. There were 60 genotype-temperature subclasses available and of these, 23 were found to have significant phenotypic optima. In view of the limited range of genetic variability of the laboratory stocks used in this study, it is speculated that phenotypic optima are probably more prevalent in natural populations. Each calculated optimum body-weight value was compared with the mean body weight of the subclass. Only four optima were found to be within the 95% confidence interval for the mean. There is however a slight (statistically non-significant) positive correlation between mean body weight and mean fitness. This is not surprising in view of the small number of means involved in the analysis.

It is tentatively concluded that the optimum weight, if it exists, does not coincide with the mean body weight. However, the two values may be positively correlated.

The above experiments were carried out by Dr. Thomas J. Glover under the supervision of S.S.Y. Young. The results of this project form the basis of a Ph.D. dissertation submitted by Glover (1971) to the Ohio State University. A paper embodying the results is to be submitted for publication (Glover and Young 1972).

III. REFERENCES

- Fisher, R. A. (1930). The Genetical Theory of Natural Selection. (Clarendon Press Oxford).
- Glover, T. J. (1971). An experimental examination of the optimum fitness model using body weight and some fitness traits in Drosophila melanogaster. Ph.D. Thesis, Ohio State University, Columbus, Ohio.
- Glover, T. J. and S. S. Y. Young (1972). The relationships between body weight and some fitness traits in Drosophila melanogaster. (to be submitted for publication)
- Griffing, B. (1967). Selection in reference to biological groups. I. Individual and group selection applied to populations of unordered groups. Aust. J. Biol. Sci. 20:127-39.
- Griffing, B. (1968a). 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. (1968b). 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. (1972a). Selection in reference to biological groups. V. Analyses of random groups exhibiting family structure. (Being revised).
- Griffing, B. (1972b). Selection in reference to biological groups. VI. Analyses of full-sib groups exhibiting family structure. (Being revised).
- Griffing, B. (1972c). Selection in reference to biological groups. VII. Use of extreme forms of non-random groups to increase selection efficiency. (Being revised).
- Griffing, B. and E. Zsiros (1971). Heterosis associated with genotype-environment interactions. Genetics 68:443-455.
- Lerner, I. M. and F. K. Ho (1961). Genotype and competitive ability of Tribolium species. Amer. Nat. 95:329-343.
- Mikolaj, P. J. (1970). Manifestation of heterosis in Arabidopsis thaliana under varying temperature and nutritional regimes. Ph.D. Thesis, Ohio State University, Columbus, Ohio.

REFERENCES - Continued

- Mikolaj, P. and B. Griffing (1971). Growth of Arabidopsis thaliana in miniature containers. Jour. Hered. 62:54-57.
- Pimentel, D., E. H. Feinberg, P. W. Wood and J. J. Hayes (1965). Selection, spatial distribution and the coexistence of competing fly species. Amer. Nat. 99:97-109.
- Seaton, A. P. C. and J. Antonovics (1967). Population inter-relationships 1. Evolution in mixtures of Drosophila mutants. Heredity 22:19-33.
- Wright, S. (1935). Evolution in populations in approximate equilibrium. J. Genet. 30:257-266.
- Young, S. S. Y. (1970). Direct and associate effects of body weight and viability in Drosophila melanogaster. Genetics 66:541-554.
- Young, S. S. Y. (1971). The effects of some physical and biotic environments on heterosis of direct and associate genotypes in Drosophila melanogaster. Genetics 67:569-578.
- Young, S. S. Y. (1972). Selection for coexistence of Drosophila species. (to be submitted for publication).

IV. INVITED SEMINARS IN THE AREA OF POPULATION GENETICS

By

B. Griffing

- 1967 - Seminar entitled, "Biological Group Theory", sponsored by the Department of Statistics, Iowa State University, Ames, Iowa.
- 1967 - Seminar entitled, "Temperature-Dependent Heterosis in Maize", sponsored by the Agronomy Department, Iowa State University, Ames, Iowa.
- 1967 - Two Seminars entitled, "Biological Group Theory" and "Temperature-Dependent Heterosis in Maize", sponsored by the Population Genetics Institute, Purdue University, Lafayette, Indiana.
- 1967 - Lecture entitled, "Selection Within and Between Groups when Genotype Influences Group Environment", sponsored by the National Poultry Breeders Roundtable, Kansas City, Missouri.
- 1968 - Seminar entitled, "Food for Billions", sponsored by the Agricultural Honors Colloquium, Ohio State University, Columbus, Ohio.
- 1968 - Seminar entitled, "Selection in Relation to Groups Containing Competitive or Cooperative Members", sponsored by the Department of Entomology and Limnology, Cornell University, Ithaca, New York.
- 1968 - Two seminars entitled, "Gene Model Construction and Selection in Relation to Groups Containing Competitive or Cooperative Members", and "Heterosis Analysis in Relation to Groups Containing Competitive or Cooperative Members", sponsored by the Graduate Committee on Genetics, University of Arizona, Tucson, Arizona.
- 1968 - Talk entitled, "World Food Crisis", delivered at the 1968 Ohio State University Research Foundation Board of Directors Meeting.
- 1968 - Talk entitled, "Selection in Reference to Groups of Related Individuals", sponsored by the Biometrics Society, The Ohio State University, Columbus, Ohio.
- 1969 - Two seminars entitled, "Heterosis Associated with Genotype-Environment Interactions", and "Selection with Reference to Biological Groups", sponsored by the Department of Genetics, University of California, Davis, California.

- 1969 - Seminar entitled, "Heterosis Associated with Genotype-Environment Interactions", sponsored by the Department of Genetics, University of California, Berkeley, California.
- 1969 - Talk entitled, " Competition Effects", sponsored by the 1969 Conference of Collaborators, Regional Swine Breeding Laboratory, Ohio State University, Columbus, Ohio.
- 1969 - Talk entitled, " Population Genetics and the Future of Mankind", sponsored by the Open Court, Ohio State University, Columbus, Ohio.
- 1970 - The talk entitled, " A Critique of the Genetical Aspects of the Jensen I. Q. Argument (as presented in the article written by A. R. Jensen, "How Much can We Boost I. Q. and Scholastic Achievement?")", was presented four times, i.e. to (i) The Population Group, (ii) Genetics Department Seminar, (iii) Phi Delta Kappa (honorary education society), and (iv) Psychology 663: Hereditary Components of Human Behavior, at Ohio State University, Columbus, Ohio.
- 1970 - Talk entitled, "Biological Group Theory", sponsored by the Annual Meeting of the Quantitative Forest Genetics Group, held at Michigan State University, E. Lansing, Michigan.
- 1971 - Seminar entitled, " Genetic Modeling to Accommodate Genotypic Interactions", sponsored by the Genetics Departmental Seminar, Ohio State University, Columbus, Ohio.
- 1971 - Seminar entitled, " Modeling of Genetic Selection with Regard to Biological Group Theory", sponsored by the Biophysics Departmental Seminar, Ohio State University, Columbus, Ohio.

V. GRADUATE STUDENTS ASSOCIATED WITH PROJECT

1. Dr. P. Mikolaj was a Ph.D. student of Dr. B. Griffing. He studied heterosis of plant (Arabidopsis) weight under varying environmental conditions. Dr. Mikolaj completed his Ph.D. degree in September 1970.
2. Mrs. Ann Dudgeon, who is responsible for the computer simulation studies in this report, is a Ph.D. student of Dr. B. Griffing. She has completed most requirements for the Ph.D. degree and expects to graduate in June, 1972.
3. Mr. C. M. Song is a Ph.D. candidate working with Arabidopsis under the supervision of Dr. B. Griffing.
4. Dr. T. J. Glover received his Ph.D. degree in December, 1971, under the supervision of Dr. S. S. Y. Young. Dr. Glover used Drosophila as the experimental organism.
5. Mr. Alan Katz is a Ph.D. candidate working with Drosophila under the supervision of Dr. S. S. Y. Young.
6. Mr. Sushil Prasad is a M.S. candidate working with wheat under the supervision of Dr. Roger Clay.

The graduate students received no direct support from the limited project budget. However they were supported indirectly, in varying degrees, by use of facilities provided under the AEC grant.

Figure 1. Flowering and seed setting of Arabidopsis plants grown in standard test tubes.

Figure 2. Seed setting of an Arabidopsis plant grown on 0.125 ml. of nutrient solution in a 6x50 mm. test tube.

Figure 3. Arabidopsis plants growing submerged in nutrient solution supplemented by sucrose.