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APPLICATION OF BIOMETRICAL GENETICS TECHNIQUES TO IRRADIATED AND NON-IRRADIATED POPULATIONS OF CORN TO PROVIDE INFORMATION ON NATURE OF GENE ACTION INVOLVED IN THE INHERITANCE OF QUANTITATIVE TRAITS AND IN HETEROSIS

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INTRODUCTION

Almost all traits of economic importance in agriculture and those involved in the evolutionary process in nature are quantitatively inherited. Such traits are controlled by many genes, which cannot be identified and manipulated independently, and whose effects involve many physiological processes that are also greatly influenced by environment. Needless to say, quantitatively inherited traits are difficult to study, and geneticists can easily find more productive avenues of investigation. Consequently, relatively little is known about the exact nature of gene action involved.

The plant and animal breeders have little choice. They must work with the whole organism, the phenotype, which is the result of the action and interaction of many genes with the environment in which the organism develops. If plant and animal breeders are to meet the needs in a world where human population expansion threatens to exceed our ability to produce the needed food, information on how genes act and interact to produce genetic variation and quantitative differences in populations is essential.

The purpose of this research was to extend out quantitative genetic investigations into some of the more basic aspects of genetic variation and heterosis observed in irradiated and non-irradiated populations of corn in order to determine more precisely how genes do act and interact to produce their observed cumulative effects.

Our general approach used in these investigations has been to use biometrical genetic techniques and develop appropriate genetic models and mating designs which could be used effectively to obtain useful genetic information from different kinds of populations. Thermal neutrons, X-rays and ethyl methanesulfonate (EMS) have been used as mutagenic agents to induce mutations and hence, genetic variation in populations undergoing selection. In a few cases, mutations affecting quantitative traits have been found to result from single gene effects and have been studied in detail.

Emphasis has been placed upon measurable morphological traits, particularly grain yield and its component parts. Yet we realize that many physiological processes, e.g. photosynthesis and respiration, and many chemical attributes, e.g. percent protein and lysine, are also affected by many genes and are inherited in a quantitative manner. Unfortunately, plant physiologists and biochemists have not yet developed techniques and methods of measurement that can be applied on a population basis. Until this is accomplished, the plant breeder will be somewhat handicapped in his attempts to improve the quantity and quality of agricultural products.

In the writing of this report, the major accomplishments are summarized with respect to (1) research results, (2) publications, (3) student training, and (4) theses completed or in progress. Although the contract with AEC has been terminated, the project will not be terminated and as many as possible of the long-term experiments are being conducted.

RESULTS OF RESEARCH

Effect of Thermal Neutron Irradiation and Recurrent Mass Selection on Random Mating Populations of Corn

The objectives of this experiment were (1) to demonstrate that considerable additive genetic variance does exist in adapted open-pollinated varieties of corn, (2) to evaluate the effect of thermal neutron irradiation of seeds on population means and on additive and non-additive genetic variation, (3) to reevaluate mass selection procedures as a method for grain yield improvement and for eliminating undesirable genetic changes following seed irradiation, (4) to study any shifts that occurred in relationships among morphological traits as a result of seed irradiation and selection, and (5) to assess the value of mutation breeding as a method of corn improvement.

The open-pollinated variety Hays Golden, which was thought to be quite well adapted to most of the corn-growing regions of Nebraska, was chosen for these studies. It tends to be somewhat drouth tolerant but lacked resistance to root lodging. In 1955, two samples of seed were taken. One was exposed to thermal neutrons; the other served as a control. Populations grown from this original seed have undergone mass selection for high grain yield each year using special refined techniques described by Gardner (1961, 1968, 1969a, 1969b).
Seeds of the treated population were exposed to thermal neutrons again in 1957, but no additional treatments have been given.

The original parent population has been maintained by growing a large sample in isolation every 3 to 4 years and has been used as the base from which population change has been measured.

Effect on grain yield mean.

A summary of the changes that have occurred in grain yield means of successive generations of the Control (C) and Irradiated (I) populations are presented in Figures 1 and 2, respectively. In the Control, mass selection has resulted in a remarkably linear response of 2.93% per generation. After 13 generations, there is no evidence of a plateau effect. In the treated population, and upward trend in also indicated, but, in the early generations, thermal-neutron treatment reduced grain yield even though selection was practiced. No improvement had been realized after the first 3 generations. Beginning with the fourth cycle (after radiation was discontinued), a linear increase in grain yield has been realized, with no evidence of a plateau after 14 generations.

In comparing Irradiated and Control populations, a question arises as to how to evaluate and interpret the response of the treated one. If measured as a linear response as we did for the control, a gain of 2.90% per generation is indicated, but the data do not fit such a curve well. If one assumes that no progress was made up through generation 3, a linear response from that point on gives a very good fit suggesting a gain of 4.38% per generation. This is somewhat more than in the Control but is consistent with genetic variance data and predicted gains. If we look at Figure 3 where responses of both populations appear on the same graph, the similarity of the two responses from generation 4 on tends to lead to the conclusion that genetic effects induced by thermal-neutron irradiation of seeds are primarily deleterious in nature, and that the mass-selection procedure provided and effective means of eliminating such effects. Clearly, the population means do not differ now; however, genetic variance and predicted gains suggest greater future gains in the treated population. Only by continuing this very important experiment for several years in the future can a complete interpretation be given. If thermal-neutron treatment of seeds does induce some favorable mutations for high grain yield and if mass selection techniques developed do effectively eliminate deleterious genetic effects and at the same time increase the frequency of favorable alleles, mutation breeding in allogomous species may have promise not previously recognized.

The response curves do conclusively demonstrate that additive genetic variance does exist in the Hays Golden variety and that Mass selection as modified for this study was an effective way to increase grain yield. Presumably, frequencies of favorable alleles are increased and those of less favorable ones are decreased. Gross chromosome abnormalities which lead to partial or complete sterility and reduced yield are quickly eliminated.

We see no reason to believe that mass selection will not be equally effective in other corn populations possessing additive genetic variability. The failure of the method to be effective in experiments conducted in the first quarter of this century can easily be traced to faulty techniques or inadequate evaluation. Other breeders such as Johnson (1963) who have adopted our techniques have had excellent success, particularly in developing countries of the world. One failure reported by Hallauer and Sears (1969) may be the result of using a high plant population density in the isolated nursery where selection is practiced. Our aim is to maximize genotypic expression of each plant and minimize competitive effects between plants; hence, we grow slightly less than 20,000 plants per hectare. As plant population density increases, the opportunity for the individual plants to exhibit their genotype diminishes and inter-plant competitive effects increase. We currently have some investigations under way to test this hypothesis.

Correlated responses

Selection for high grain yield has resulted in a number of correlated responses. The most notable of these has been increased number of ears per plant. Thermal neutron seed treatment together with mass selection increased multiple earedness more rapidly than mass selection alone. Although the data are not exactly comparable, some ear counts have been taken recently in isolated nurseries where mass selection is being practiced. These data are summarized in Table 1. A more precise comparison is available from data presented in Table 2. These data are from a replicated yield trial planted at 17,222 plants per hectare, slightly less than the rate used in the isolated nurseries.

Irradiation has resulted in more multiple-eared plants, but even more important is the fact that it has resulted in more multiple-eared main stalks without tillers when compared to the Control. From the standpoint of commercial corn production, multiple ears on a single stalk are preferable to multiple ears produced on tillers.

Selection has also resulted in later maturing plants and in taller and more vigorous plants. In days to flower, the Control selected population is 4 to 5 days later and the Irradiated Selected one is 3 to 4 days later than Hays Golden. At harvest time, the grain moisture is about 2 percentage points higher in the Control and 1 percentage point higher in the Irradiated population when compared to Hays Golden. Both selected populations tend to be 10 to 12 inches taller than the parent variety and have correspondingly higher ear placement.

Effect of Mass Selection for Prolificacy on a Random Mating Population of Corn

Since mass selection for high grain yield, particularly following seed irradiation, resulted in increased numbers of ears per plant, a logical question was what would happen if we selected for high numbers of ears instead of for high grain yield? Dr. J. H. Lonnquist initiated such a study in Hays Golden in 1961. At first, even two-eared plants were scarce, but the frequency of multiple-eared plants increased rapidly. This year only four-eared plants were selected for the next generation and over 90% of the plants had multiple ears,

The effect of selecting for prolificacy on grain yield has been most surprising. Yield response shown in Figure 4 indicates an increase in grain yield of 5.24% per generation, substantially more than has been realized by selecting directly for yield. This would suggest that number of ears per plant is a more reliable indicator of yield potential than is yield itself. Consequently, many population improvement programs now being conducted at the University of Nebraska and elsewhere emphasize selection for prolificacy. Prolific populations are particularly useful in a reciprocal full-sib selection program to develop superior hybrids.

Although some delay in maturity and increased plant height has occurred, the Prolific selected population tends to be intermediate between Hays Golden and the two populations mass selected for high grain yield.

Effect of Recurrent X-ray Seed Treatment and Mass Selection on a Random Mating Population of Corn

After the Control selected population had been mass selected for high grain yield for 9 generations, a sample of seed from that population was used to initiate a new program involving recurrent X-irradiation of seed and mass selection for high grain yield. Although some progress appears to have been made in improving the x-ray treated population, the untreated one is improving at a faster rate. Relative yields in percent of

Hays Golden are given in Table 3. Based upon our observations in the early generations of our thermal neutron treated population, we thought that we might not be able to make any increase in yield at all as long as we continued x-raying the seeds. The dose currently in use (10,000 r) seems to permit some progress. Eventually we will discontinue the treatment and assess the effect of treatment on genetic variation in the population. In some respects, this population looked very good in the isolated nursery in 1970.

Effect of Thermal Neutron Irradiation and Mass Selection on Genetic Variation and Genetic Correlation in the Hays Golden Variety and Selected Populations.

Results of genetic variance studies have been reported in publications by Lonnquist, Cota and Gardner (1966) and by Gardner (1968, 1969). The first study conducted after 6 generations of mass selection in the Control and Irradiated populations indicated that 6 generations of selection had not caused any detectable decrease in additive genetic variance in yield or other quantitative traits studied. Thermal neutron treatment of seeds in early generations did increase additive genetic variance for grain yield and ears per plant but had little, if any, effect on days to flower and ear height.

A second study conducted after 10 generations of mass selection was in general agreement with results obtained earlier. In 1967, which was a favorable growing season, results indicated no appreciable decline in additive genetic variance for yield due to selection and substantially increased additive genetic variance in the Irradiated selected population. In 1968, a somewhat less favorable growing season, both selected populations were lower in additive genetic variance for yield than the original variety. The explanation lies in the number of ears produced per plant. In 1968, the selected populations failed to develop as many second ears as in 1967, thus reducing additive genetic variance for both ears per plant and yield. The original variety produces relatively few second ears (See Table 2) and lacks the capacity to respond to a favorable environment.

The thermal neutron treatment definitely increased additive genetic variance in ears per plant, which in turn also increased additive genetic variance in yield in a situation where limiting factors did not exist. Selection alone also tended to increase additive genetic variance in ears per plant. which helps to explain in part the lack of decrease in additive genetic variance for yield in the selected Control.

The Prolific selected population after 5 generations of selection for high number of ears per plant was also included in the second genetic variance study. Additive genetic variance for grain yield was higher in both 1967 and 1968 than in Hays Golden, but when combined over years, the difference was no longer evident. Genotype x environment interaction is obviously important. In ears per plant, the Prolific population was comparable to the selected Control, greater than Hays Golden but less than the Irradiated population.

In the maturity traits, days to flower and grain moisture at harvest, and in ear height, the 4 populations differed very little in additive genetic variance.

Dominance variance estimates were obtained but were found to be quite low in precision and were rather meaningless. No definite conclusion can be drawn from them.

Genetic correlations, which have not been previously presented or published are given in Table 4. Correlations between other traits and yield tend to be higher in the Control than in other populations. Lower genetic correlations between yield and ears per plant in the Irradiated and Prolific populations compared to the parent variety and the selected Control may be explained by the fact that they are uniformly more prolific, so that prolificacy is less of a factor in determining yield. Correlations between yield and grain moisture at harvest tend to be high except in Hays Golden. This is probably due to the fact that Hays Golden may be a little early for the Lincoln area and variation in maturity is not an important factor in yield. Selection has shifted the populations toward later maturity and later genotypes can take advantage of the longer growing season; hence, the increased relationship and higher genetic correlation.

Estimation of Heterosis, Inbreeding Depression and other Genetic Parameters in Hays Golden and Selected Generations of Control and Irradiated Populations.

The Gardner-Eberhart model (Gardner and Eberhart (1966) and Eberhart and Gardner (1966)) to estimate genetic parameters in random-mating, equilibrium populations was used to evaluate changes that had taken place in genetic parameters as a result of irradiation and selection in the Hays Golden variety. A diallel cross involving the base population and the 2nd, 4th, 6th and 8th generations of selection in each of the two selected populations was developed. From each of the 9 populations and the 36 F_1 crosses, S_1 progenies were developed. From the 36 F_1 crosses, the 36 F_2 generations were developed by random mating among F_1 plants. Such a set of material permits estimation of cumulative effects of homozygous loci and of heterozygous loci and estimation of heterosis effects and inbreeding depression. Although grain yield is the most important trait studied, ears per plant, days to flower, ear height and plant height were also studied. Results have been reported in a Ph. D. thesis by A. R. Hornbrook and will be published soon. Only a brief summary is included here.

As in other studies, yield responses were found to be linearly related to generations of selection. Yield increases of 3.31% and 3.95% per generation were noted for the Control and Irradiated populations, respectively. In the crosses, if we plot yield against average generations of selection for the two parent populations, gains of 4.07% and 3.24% per generation are indicated for Control and Irradiated populations, respectively.

Heterosis

Although the analyses of variance indicated statistically significant heterosis effects, the effects were very small and were consdiered biologically unimportant. As indicated in previous reports, if we examine crosses between corresponding generations of selection in the Control and Irradiated populations (C-2 x I-2, C-4 x I-4, C-6 x I-6 and C-8 x I-8), we find the F_1 crosses to be almost exactly intermediate. Likewise, crosses of selected generations of each population with the base population gave F_1 crosses that tended to be intermediate between their two parents. The average yield of all F_1 crosses was 286 grams compared to 285 grams, the average yield of the 9 parent populations used in the diallel cross. Hence, we are lead to the conclusion that heterosis is negligible in the population crosses.

In the absence of epistasis, a lack of heterosis can result from either a lack of dominance or from essentially equal gene frequencies in the parents. Since improvement in grain yield has occurred, the frequencies of favorable genes must have increased; therefore, a lack of dominance or a low degree of dominance seems to be the most logical conclusion.

If epistasis does exist and selection has been for favorable epistatic combinations, heterosis due to epistasis would not be so likely in crosses between random-mating, segregating populations, and crosses could be intermediate if several different kinds of epistasis involving many loci were operating.

Inbreeding depression

Inbreeding in parents and in F_1 crosses resulted in substantial losses in vigor and yield. In the 9 parents, the average reduction due to one generation of inbreeding was nearly 35% and was essentially the same for Irradiated generations as for Control. In the F_1 crosses, average yield reduction due to one generation of self-fertilization was 33.4%, but it was only 29.8% in crosses between Control generations compared to 34.5% in crosses between Irradiated generations and to 34.9% in crosses between Control and Irradiated generations. The greatest inbreeding depression resulted from selfing crosses between the most highly selected generations. In other words, it appears that selection is increasing the frequency of some genes which tend to be deleterious in homozygous condition but which confer a selective advantage in heterozygous condition. Perhaps in early generations selection was for genes which behaved in an additive manner with partial to complete dominance, but in later generations selection may be for genes having an overdominant effect or for those which interact with genes at other loci in a dominant x dominant or additive x dominant manner.

If individuals within an F_1 cross of two random-mating populations are random mated, a decrease in yield equal to one-half the heterosis value should result providing epistasis is not an important factor. However, since there was little evidence of heterosis in the crosses, we should not expect much decrease from random mating within F_1 families. Average yields of F_1 crosses random mated was 285 grams compared to 286 grams from F_1 crosses and 285 grams for parent populations.

Predicting performance

Parent population yields were reasonably good predictors of their S_1 progeny yields using a simple linear regression equation. Correlations between Control generations and their S_1 progenies was .92 compared to .95 for that between Irradiated generations and their S_1 progenies. On the other hand, yields of S_1 progenies of F_1 crosses could not be accurately predicted from their F_1 parents. Correlations were .50 for F_1 crosses and S_1 progenies involving Control generations only, .37 for those involving Irradiated generations only and .55 for those involving a Control and an Irradiated generation. The F_1 cross yields and those of their random mated progenies were quite highly correlated - .96 for Control, .86 for Irradiated and .85 for Control x Irradiated.

Generations of selection also proved to be a good predictor of yields using a simple linear regression equation. Correlations between generations of selection (or average generations of selection in the case of F_1 crosses) and yields were all quite high except in the cases involving S_1 progenies. Regression coefficients of yield on generation of selection and corresponding correlation coefficients are given below for the various population types within and between Control and Irradiated generations used in this study:

Population	Correlation coefficient	Regression coefficient
Parents in Control	.98	8.2 ± 1.0
Parents in Irradiated	.98	9.8 ± 1.2
S_1 progeny of Parents in Control	.94	5.4 ± 1.2
S_1 progeny of parents in Irradiated	.94	6.0 ± 1.3
F_1 crosses in Control	.96	10.1 ± 1.0
F_1 crosses in Irradiated	.87	8.0 ± 1.6
S_1 progeny of F_1 crosses in Control	.45	2.2 ± 1.6
S_1 progeny of F_1 crosses in Irradiated	.40	2.4 ± 1.9
F_2 progeny of F_1 crosses in Control	.94	8.1 ± 1.0
F_2 progeny of F_1 crosses in Irradiated	.87	7.4 ± 1.5
F_1 crosses of Control x Irradiated	.88	7.3 ± 1.0
S_1 progeny of F_1 crosses of Control x Irradiated	.49	2.5 ± 1.2
F_2 progeny of F_1 crosses of Control x Irradiated	.74	6.5 ± 1.6

The genetic parameters estimated using the Gardner - Eberhart model for the 126 populations derived from the Hays Golden variety provide the best basis for predicting performance of the populations grown in different environments. Correlations between predicted yield values calculated from data obtained in one year with observed yields were .969 and .972 for the 126 populations. On the other hand, the estimates of the parameters seemed somewhat inconsistent with some results already discussed above.

Modification of the Gardner - Eberhart Model to Evaluate Changes in Genetic Parameters Resulting from Selection

When a diallel cross and its related populations are derived from a random-mating, equilibrium population and selected cycles of that parent population obtained by some systematic selection scheme, the original Gardner - Eberhart model should be modified. Details of the modified model are presented in Technical Information Document COO-1512-12 and in the Ph. D. thesis of James J. Hammond. Only a brief summary is presented here.

Basically, the modified model permits estimation of parameters in selected generations in terms of those in the parent population. Changes in the parameter due to cumulative effects of homozygous loci, in one due to culmulative effects of heterozygous loci and in heterosis parameters may be linear, quadratic, cubic or higher order polynomial. When data on the diallel cross and appropriate related populations are available, parameters can be estimated and the nature of the response to selection can be determined. The modified model also permits estimation of the frequency of favorable alleles at the start of selection and the change that takes place with generations of selection. The endpoint of selection or number of cycles before plateau can also be determined. However, it should be pointed out that selection must be over a relatively long period of time to obtain such estimates.

Data collected by Hornbrook were reanalysed making use of the modified model. A linear change in the parameter measuring cumulative effects of homozygous loci was indicated but was shown to be negative instead of positive as expected. This suggests that the frequency of favorable genes in homozygous state may have actually decreased with selection and perhaps selection favors the heterozygote, which agrees with Hornbrook's results. If so, then overdominance may be operating in some genes controlling yield. On the other hand, the increased yields with the advance in generations in each of the two selected populations and in the S_1 progenies developed from the different generations within each population certainly indicate an increase in the frequency of favorable alleles controlling grain yield. The regression in the parameter measuring cumulative heterozygous effects should be curvilinear assuming some degree of dominance of genes controlling yield, however, over the span of eight generations, no curvilinearity could be detected. Perhaps this is much too short a period for any curvilinear effect to be observed.

Some computer simulation of a parent population and selected generations, which were then put into a diallel cross from which related populations were developed, was carried out to test the theoretical model. Possible biases due to linkage and random-mating disequilibrium resulting from selection were considered. In general, the model appears to be satisfactory and serious biases were not detected; however, only a limited number of combinations of gene models, gene frequencies and differences in gene frequencies were possible.

Computer simulation work revealed some flaws in the IBM random number generator and considerable work was involved in modifying the program for genetic simulation work.

Computer simulation of a variety diallel cross and related populations also revealed some interesting facts concerning the mechanics used to produce the "related populations", and the procedures used to sample segregating populations. In order to save nursery space, time and money in developing the diallel cross and related populations for Hornbrook's study, plants were frequently used as a male more than once. The same plant could provide pollen for selfing to produce the S_1 progenies, for crossing to produce varieties random mated, or for crossing to produce the F_1 cross to another variety. Such a procedure results in correlations between types of progenies which are assumed to be independent in the model.

Computer simulation results indicated that when a plant is used more than once as a male or female, the means are unbiased but the within population variances for crosses, crosses selfed and crosses random mated were much larger than the theoretical expectation. When the program was modified so that a plant could be used only once and populations were completely independent with respect to sampling, all variances were found to be well within the range expected in view of the random sampling errors. Although the procedure used by Hornbrook gave unbiased estimates of means, which are the values needed to estimate genetic parameters, the means lacked the precision of estimation that could have been obtained by proper sampling to assure complete independence of the different populations developed.

Basically the sampling procedure used by Hornbrook affects actual sample size. When the variances obtained were adjusted for sample size, they were found to be close to the expected values based on theory. In all future work of this kind, we recommend that a plant be used only once to develop one kind of population. Since the populations involved are extremely heterozygous and heterogeneous, sample size is important in producing selfed and random mated progenies as well as in producing crosses. Perhaps the best procedure is to make individual plant crosses, but bulking of n plants to pollinate n other plants is satisfactory and might save time and expense. If the latter procedure is used, the effective sample size is somewhat less than n. Further work is needed to determine the minimum acceptable sample size in work of this kind.

Effect of Plant Population Density on Quantitative Traits in Irradiated and Selected Populations Compared to Hays Golden and a Hybrid Check

Isolated nurseries of our selected populations are planted at a low rate (19,375 per hectare) in order to permit maximum expression of the genotype with minimum competition effects. We believe that such a rate is essential to progress from mass selection. Breeders argue that we are selecting at an unrealistic rate of planting in view of the fact that maximum farm yields are obtained at planting rates of 50,000 to 60,000 plants per hectare. We do evaluate our selected generations at a planting rate of 51,666 plants per hectare and find that the most advanced generations are approximately equal to a check hybrid, Nebr. 501D.

In order to check the response of yield and other agronomic traits to varying rates of planting, an experiment was designed using the most advanced generation of selection in the Control (C-12), Irradiated (I-13) and the Prolific (P-7) selected populations, the parent Hays Golden and the hybrid check Nebr. 501D. Planting rates were 1, 2, 3 and 4 plants per hill or 17.2, 34.4, 51.7 and 68.9 thousand plants per hectare.

Response in yield to plant population density is shown in Figure 5. The optimum density was 51.7 plants per hectare and the highest density resulted in decreased yields. At the lowest density, selected populations had a distinct advantage because they produced second and third ears which the parent variety and the hybrid check were incapable of doing. At higher rates the check hybrid exceeded the selected populations but differences were not significant. Hays Golden increased from the lowest to the second density but stayed level from there on. The hybrid and the Control and Irradiated selected populations averaged essentially the same and exceeded Hays Golden by over 50%. The Prolific population performed well considering that it had been selected only 7 cycles compared to 12 and 13 for the Control and Irradiated populations.

Yield responses are explained by number of ears per plant (Figure 6), the percent of plants producing two or more ears (Figure 7) and percent barren plants (Figure 8). Maturity as measured in days to flower was delayed a total of 1 to 1½ days by increased density.

Selection at low population densities has not affected the relative performance of selected populations compared to the hybrid at higher densities. At lower densities, their prolific nature gives them a distinct advantage. In areas where rainfall is limiting, use of a multiple-eared genotype planted at a lower population density may have an advantage in the long run.

In developing corn populations for high yield when planted at high densities, some form of family selection based on the family's yield performance should have an advantage over mass selection.

Evaluation of the Effects of Thermal Neutron Irradiation and Selection on Corn Populations as Measured by Random S_1 Lines and Their Testcrosses to Related and Unrelated Single Cross Testers

After 9 generations of mass selection in Control and Irradiated populations developed from Hays Golden, random S_1 lines were developed from each population and from the parent variety. If population improvement resulted from an increased frequency of favorable alleles with no more than complete dominance, the selective advantage should be reflected in the S_1 lines and in testcrosses of the S_1 lines to single-cross testers. Details will be reported in an M.S. thesis by R. E. Harris, so only major findings are reported here.

Population means are reported in Table 5 and genetic variances are reported in Table 6 for the three kinds of progenies from the three populations.

The S_1 families obtained by self-fertilizing randomly chosen plants one generation should provide the best evaluation of the selected populations relative to the parent variety. In testcross families one-half the germ plasm is common to all families. If high yielding testers are used, they are likely to possess many dominant favorable genes which mask deleterious recessives and make discrimination among genotypes within populations as well as the detection of differences between populations more difficult.

Substantial increases in grain yield in selected populations are indicated by the means. The C-9 and I-9 S_1 families exceeded HG families by 34.7 and 32.1%, which represents gains of 3.86 and 3.57% per generation. These data compare favorably with gains of 3.32 and 3.66% per generation calculated from yields of S_1 progenies of the 2nd, 4th, 6th and 8th cycles of Control and Irradiated populations studied by Hornbrook.

Yield results from testcrosses to the related single cross were somewhat surprising in that C-9 and I-9 testcross progenies exceeded HG testcross progenies by 31.2 and 34.2%, almost the same as noted for S_1 lines per se. Since half the germ plasm is the same in the three sets of progenies, even greater superiority of the C-9 and I-9 populations over Hays Golden is indicated than noted in S_1 progenies. Yield results from testcrosses to the unrelated single cross indicated an advantage for C-9 and I-9 progenies over HG of 15.2 and 17.6%. If this measures half the difference, then increases of 30.4 and 35.2% for C-9 and I-9 progenies over HG are indicated.

For C-9 and I-9, the two single cross testers produced approximately the same yield, which exceeded S_1 yields by 55 to 60%. For Hays Golden, however, testcrosses to the related tester exceeded S_1 yields by 57% but those to the unrelated tester exceeded S_1 yields by 80%.

Yield results are interpreted to indicate that the increases in grain yield in selected populations have resulted from an increase in frequency of favorable alleles controlling yield. It appears that dominance is either lacking or is relatively low.

Selection has resulted in populations quite different from the Hays Golden variety as indicated by the differential responses to the two testers. The alleles in the related tester exist in a relatively high frequency in Hays Golden compared to the selected populations. The relationship between the related tester and the selected populations appeared to be no greater than that between the unrelated tester and the selected population.

In other traits, selected populations have more ears per plant, higher shelling percent, higher grain moisture at harvest, later flowering dates, higher ears and taller plants. Greatest differences are reflected in S_1 families and least differences are reflected in crosses to the unrelated tester. Crosses to the related tester indicated differences in between the other two types of progenies but more like those of the unrelated testcrosses.

Genetic components of variance in Table 6 indicate that the greatest genetic variance in yield exists in Hays Golden. Selection has reduced genetic variability and the Irradiated population does not appear to be more variable than the Control. The parent population is also more variable in number of ears per plant. Differences in other traits are not great.

The reduced genetic variance in yield noted here for selected populations and the failure of the Irradiated one to exceed the control tend to support the idea that irradiation induced mutations and other effects which were primararily of a deleterious nature and which were eliminated by mass selection. The two populations may now be essentially the same having had a number of favorable alleles increased in frequency or fixed by the selection procedure. The advantage in additive genetic variance and the higher predicted gain from selection indicated in other genetic variance studies for the Irradiated population need to be re-examined and checked in additional experiments.

Development of Homozygous Lines from Hays Golden and Selected Populations for Genetic Studies.

Two kinds of homozygous lines are being developed from Hays Golden and from selected populations. One set involves the development of random homozygous lines to be used in genetic variance studies. Each line developed traces back to a single open-pollinated (S_0) plant. Lines from generations 9 and 10 of the Control and Irradiated populations and from Hays Golden have been advanced to the S_6 and S_5 generations, which means that they are sufficiently homozygous to initiate genetic studies next year.

A second set of lines are being developed from Hays Golden, the Irradiated population after 13 cycles of selection, the Control population after 12 generations of selection and the Prolific population after 7 cycles of selection. In this set, standard breeding procedures are being used to develop selected sets of lines to see is superior lines can actually be selected out of the improved populations. Approximately 1,000 plants of each were planted in 1968 and the best appearing plants were self-pollinated. In 1969, lines were self-pollinated and selection was practiced between and within S_1 progenies at both pollination time and harvest time. In 1970 lines were again self-pollinated and selection was again practiced between and within the S_2 lines. The S_2 lines were also topcrossed onto two testers - Ohio 43 and N7A x N7B. In 1971, the inbreeding and selection program will be continued and topcross progenies will be grown in replicated yield trials. Additional selection will be done based on topcross progeny performance. We also plan to form new populations from superior topcrosses to shorten the population, to make it earlier maturing and to gain strength in the root system.

Effect of Thermal Neutron Irradiation, Recombination and Selection on Means and Genetic Variation in Populations Developed from a Cross of Two Inbred Lines

The base material for this experiment was two very good inbred lines of corn N6 and N15. The two lines were crossed and the F_1 seed was divided into two parts. One part was exposed to thermal neutron irradiation (1.28×10^{13} N_{th} /cm^2); the other served as a control. The F_1 plants were all self-pollinated. The control F_2 is designated population R1. It had only minimum opportunity for recombination to break down linkages. One sample of the control F_2 was advanced to the F_3 and F_4 generation by random mating and is designated R3 because there were three opportunities for recombination. Another sample of the control F_2 was advanced to the F_4 but only the agronomically best appearing plants were intercrossed and the best 20% based on yield (or yield potential) and other agronomic traits were harvested each year. This population is designated R3S because there were three opportunities for recombination and selection was practiced. The thermal neutron population was intercrossed and selected like R3S and it also received a second but lower dose of thermal neutrons (8.66×10^{12} Nth /cm^2) between the F_2 and F_3 generations. It is designated NR3S. Results of this study were reported by Gardner (1968) and have been included in annual reports. They are briefly summarized here.

In order to evaluate these 4 populations, random sets of inbred lines (S_6 generation) were developed from each and were crossed using a cross-classified or Design II mating system of Comstock and

Robinson (1948).

Highest yielding hybrids came from lines in the NR3S population where irradiation was used. Hybrids from lines of the F_2 generation (R1) and from the selected R3S population were about equal and averaged less than NR3S hybrids. The lowest yielding group was those hybrids from lines where recombination without selection was used (3R). A frequency distribution of all lines involved in hybrids yielding more than 270 grams per plant was formed. More high-yielding lines came from the treated population and the highest-yielding hybrids also came from that population. The F_2 generations had the second highest number of good lines. Since no hybrids exceeded the original N6 x N15, it appears that favorable epistatic combinations were an important factor in the heterosis observed in the original hybrid. Many of the favorable epistatic combinations were undoubtedly preserved in the F_2 because there was little opportunity for crossing over and recombination. The value of the selection practiced was also evident in the means and distribution of hybrids.

The thermal neutron treatment substantially increased additive genetic variance for yield. Selection seems to have reduced additive genetic variance, and recombination has increased it. A high ratio of dominance variance to additive genetic variance observed in the F_2 generation indicates considerable repulsion-phase linkage of dominant favorable genes controlling yield. The overdominance effect disappears when recombination is permitted. There was some indication that selection without irradiation tended to hold some linkage groups together.

The ears-per-plant components followed a pattern very similar to that for yield. Additive genetic variance of traits related to measures of maturity (days to flower and grain moisture) was higher in the irradiated population than in the others. Also there was no evidence of linkage bias, thus supporting our hypothesis that these maturity traits are controlled by relatively few genes that are largely additive in their effects. Increased additive genetic variance in plant and ear height was evident in the irradiated population with the most additive genetic variance. Some linkage bias was evident in the F_2 plant and ear height data.

Effect of Thermal Neutron Irradiation of Seeds and of Ultraviolet Irradiation of Pollen on Homozygous Lines of Corn

Starting with seeds from single plants of long-time inbred lines of N6 and N25, sets of sub-lines were developed using two types of irradiation. In one case pollen was exposed to ultraviolet light just prior to self-pollination for 4 successive generations. In the other, seeds were exposed to thermal neutron irradiation and resulting plants were self-pollinated. Sub-lines were developed in both lines treated by the two methods and comparable sets of control sub-lines were also developed. Lines were evaluated in testcrosses and in the Design II mating system. Details are given in a Ph. D. thesis by R.F.. Mumm and in publications by Gardner (1968, 1969). Only a brief summary is included here.

Studies indicated that substantial increases in genetic variability in yield and other quantitative traits could be induced by irradiation treatment. Much of the increased variation in yield, however, could be attributed to partial sterility caused by heterozygous translocations. When families with partial sterility were eliminated from the analyses, we could show no significant difference between treated sub-lines and control sub-lines.

Genetic Study of 'Necrotic Leaf Spot' Mutation Induced by Thermal Neutron Irradiation

Seeds of a long-time inbred line of corn N25 were divided into two samples. One received 8.03×10^{12} thermal neutrons per square centimeter; the other served as the control. Plants grown from both samples were self-pollinated for two generations to form sub-lines. All control sub-lines appeared normal, but segregation for induced mutants was evident in many sub-lines from irradiated seeds.

Two sub-lines, descended from different M_1 plants, segregated for what appeared to be susceptibility to some kind of leaf-blotching disease, similar, in some respects, to Helminthosporium turcicum. Careful examination failed to reveal any causal organism so the leaf blotching was believed to be inherited. One line was thoroughly studied genetically and the results have been published by Hornbrook and Gardner (1970).

The necrotic leaf spot symtom was found to be controlled by a single locus and is caused by a recessive allele in homozygous condition. When compared to 'Zebra necrosis' mutants obtained from the Missouri and Illinois Agricultural Experiment Stations, our leaf spot necrosis appeared to be quite different, both in time of expression and in the symptoms exhibited. Zebra necrosis results in necrotic areas developing parallel to the leaf veins wheareas leaf spot necrosis causes irregular blotches which often coalesce. The patterns are not at all regular like zebra necrosis. However, when our leaf spot necrosis mutant was crossed with the zebra necrosis mutants, all F_1 plants had necrotic spots on the leaves. We have concluded that leaf spot necrosis is controlled by a different allele but it is at the same locus as zebra necrosis.

Single mutant genes such as this one often have pleiotropic effects. In this case, mutant plants are taller than normal ones and are substantially lower yielding. Fortunately such alleles are strongly selected against in population improvement programs, but in studies designed to evaluate the effects of mutagenic treatment on genetic variability, such genes do play an important role.

There is some evidence that the heterozygote may exceed the normal parent in yield. Studies are being conducted to determine whether or not the heterozygote has a selective advantage, and to determine whether the differences in observed symptoms are due to different alleles or to different genetic backgrounds.

Genetic Studies of Plant Height Mutants Induced by Thermal Neutron Irradiation and Ultraviolet Light Treatments

Two plant height mutants were observed in sub-lines of N25 and N6. The N25 seeds had been exposed to thermal neutron irradiation as described above to develop sub-lines. The N6 mutant resulted in a sub-line developed by recurrent irradiation of pollen preceeding self-fertilization of the long-time inbred N6. Genetic studies of these mutations are reported in detail by A. R. Hornbrook in his M.S. thesis.

The N25 reduced height mutant was only 77% as tall as normal N25, and it had fewer internodes. The height reduction was found to be controlled by a single locus and resulted from the homozygous recessive condition. The noraml allele was only partially dominant over the mutant allele. Internode number and grain yield were also reduced but each trait seemed to be governed by two or more loci.

The N6 reduced height mutant was only 68% as tall as normal N6 but no difference in internode number could be detected. Number of ears per plant was higher on the mutant but total grain yield was greatly reduced, probably as a result of induced partial sterility. The height reduction in N6 was also found to be controlled by a single locus and occurred in the homozygous recessive. The normal allele was completely dominant over the mutant. Grain yield and number of ears each seemed to be controlled by more than one gene.

Effect of the Chemical Mutagen Ethyl Methanesulfonate (EMS) on Genetic Variation in Quantitative Traits of Corn Sorghum and Arabidopsis

The objective of this research was to investigate the effectiveness of EMS in inducing favorable genetic variability in quantitative traits in both self- and cross-pollinating species. Details of this research are give in the Ph.D. thesis of N. K. Chatterjee. Only the main points are summarized in this report.

Corn research

N6, a long-time inbred line previously used in thermal neutron and ultraviolet irradiation studies, was chosen for this study. Pollen was treated in the laboratory with EMS vapors just prior to pollination. Seeds produced were planted in our winter nursery and the resulting plants were self-pollinated. A total of 89 sub-lines of treated N6 and a corresponding 89 control sub-lines were produced and were evaluated in a replicated experiment.

EMS treatment reduced grain yield about 7% and plant height about 1%. No change in days to flower or ear height were detected. Frequency distributions and estimates of genetic variances indicate that EMS nearly doubled the genetic component of variance for grain yield, but most of the increased variance was in the direction of reduced yield. However, two sub-lines of N6 yielded more than the best control sub-line. One was significantly higher yielding than the control and is being checked further to get a better evaluation.

Genetic variation in days to flower was nearly tripled, in plant height doubled and in ear height quadrupled. No sub-lines earlier than control sub-lines were obtained.

Sorghum research

An inbred line called Redlan was used for this study. Seeds of a single self-pollinated head were divided into two samples of 150 seeds each. One sample was soaked in EMS solution for two hours, a dose approximately equivalent to the LD_{40} level. The other was soaked in the buffer solution to serve as a control. Plants grown from treated and untreated seeds were self-pollinated. A replicated yield trial involving 100 sub-lines or families from the treated seeds and another 100 from untreated seeds was conducted.

EMS reduced grain yield 8% but did not alter days to flower, flag leaf area, plant height or head length. Genetic components of variance were increased 11% for grain yield, 9% for days to flower, 388% for flag leaf area, 626% for plant height and 222% for head length by EMS treatment. Frequency distributions indicate that two EMS treated sub-lines exceeded in yield the best control sub-lines. Unfortunately, all of the seed of the highest yielding one was used to conduct the experiment and cannot be rechecked.

Arabidopsis research

Seeds of a supposedly homozygous line of *Arabidopsis thaliana*

(L.) Heynth. were used for this experiment. One batch of seeds was soaked in EMS solution using an LD_{40} dose and the other batch was soaked in buffer only to serve as a control. A total of 72 sub-lines were developed and evaluated in the treated group and in the control group.

EMS reduced seed yield 61%, decreased days to flower 4%, increased fruits per plant 16% and reduced plant diameter 29%. Genetic components of variance were increased 380% for seed yield, 169% for number of fruits per plant, and 2,663% for plant diameter. No treated sub-lines produced as much seed as the best control sub-line and relatively few even exceeded the mean of the control sub-lines. Earlier flowering was induced in several EMS sub-lines.

Analyses of Two Enzyme Proteins in Some Genotypes of Corn

Two enzyme proteins, alcohol dehydrogenase (ADH) and esterase, were analyzed electrophoretically and kinetics measurements were made for ADH in two exotic varieties of corn, some elite inbred lines and their hybrids, and two mutant lines. This work is discussed in detail in the Ph.D. thesis of N. K. Chatterjee and in Technical Information Document COO-1512-19.

Starch gel electrophoresis in a discontinuous buffer system for the two enzymes indicated the existence of the enzymes in multiple molecular forms in the genotypes studied. All of the inbreds except one had two anode-migrating isozymes of ADH, one of which was fast and the other slow moving. Of the two mutants induced by EMS and thermal neutron treatment of N6, only one (EMS) showed an isozyme pattern different from the original N6. All single and double crosses showed the presence of hybrid enzyme in addition to the parental enzymes.

Specific activity values of ADH were lower in all the hybrids except one when compared to parental averages. K_m's for ethanol in crude enzyme preparations of the hybrid were lower than those of the parents of the hybrids. K_m's of the two mutants were higher than that of the control.

Three of five anode-migrating isozymes of esterase were found in the different genotypes. The EMS mutant showed an isozyme pattern different from the control. No hybrid enzyme for esterase was found in the hybrids.

We believe that isozyme studies in populations and in lines developed from them would be useful if they could be conducted on a large enough scale and related to yield and other quantitative traits.

Opportunities for Mutation Breeding in Allogamous Species Such as Corn

Mutation breeding has never enjoyed the popularity among breeders of allogamous species that it has among breeders of autogamous species. Relatively few plant breeders have attempted mutation breeding in allogamous species and many of those who did were disappointed and soon abandoned the approach. The problem was simply that expectations were too great. Many breeders thought that they could simply irradiate seeds (or other plant parts) and select out genotypes superior to the parent genotype in yield and other measurable traits. Needless to say, this is not the case. Mutation breeding is simply a method which can be used by the plant breeder to speed up the mutation process that exists in nature. Most mutations are deleterious in nature as far as grain yield is concerned and they vary considerably in the magnitude of their effects. Most of them probably have very small effects but a few have relatively large effects. Chromosome abberations resulting from irradiation often have very large effects. Favorable mutations with small effects on grain yield would be difficult, if not impossible, to identify. Therefore, mutation breeding must be combined with other breeding methods to be successful and the tedious work of hybridization, observation, screening, selecting and testing generation after generation cannot be avoided.

If mutation breeding for the improvement of grain yield and other quantitative traits is to be successful, mutagenic treatment of seeds or other plant parts must simply be a part of a regular plant-breeding program. To be more specific, a systematic approach involving selection and recombination of selected genotypes on a cyclic basis is essential. Recurrent selection is essential to eliminate undesirable mutations and deleterious chromosomal abberations, and recombination is essential to bring together favorable mutations induced in different plants.

Where mass selection can be used, it provides an excellent screening technique to eliminate undesirable genotypes. It is easy to use, requires minimum time, is inexpensive and has been effective in corn breeding. Systems of family selection (S_1 families, full-sib families, half-sib-families or reciprocal full-sib-families) can also be used effectively in recurrent selection programs. In many instances they are more effective than mass selection.

Recombination in allogamous species is no problem if an isolated nursery can be found. Natural cross pollination among progenies of selected individuals or families can be used. Controlled recombination with some selection being practiced can also be done but requires considerably more work.

Research done on this project indicates that mutation breeding in allogamous species does have promise for the improvement of yield and other quantitative traits, but more research is essential to prove that it can be successful. Financial support for a long-range program should be provided by the Atomic Energy Commission.

Finally, the plant breeder must make some choices as to the best methods to use for developing his breeding populations from which he expects to extract superior genotypes to release as varieties, hybrids or other forms. In establishing his basic gene pool, he can use locally adapted material or he can introduce germ plasm from other areas and from foreign countries. Some introduced material may be fairly well adapted while some may not be. Nevertheless, the latter may possess some desirable genes that would be useful in one way or another. Even related species or genera might be used. The use of mutagenic agents to induce genetic variability should not be overlooked. Perhaps the use of adapted material with mutagenic treatment will provide the needed genetic variation with less reduction in the population mean than is sometimes experienced when unadapted germ plasm is introduced.

In the case of corn, there is already a great deal of genetic variation in existence throughout the world. Corn breeders have not felt the need for the use of mutagenic agents to obtain genetic variability. This is probably also true for other allogamous species.

Use of Quantitative Genetic Procedures in Studying Populations Treated with a Mutagenic Agent.

When irradiation or chemical mutagen treatments are used, genetic variability is introduced. The distributions of the initial populations are not likely to be normal. Therefore, the use of quantitative genetic techniques which are based on normal distributions must proceed with caution and a good deal of common sense. For example, the equation for predicting progress from selection in populations is based on truncation selection of the highest performing individuals in a normal distribution. If the population is anormal and is badly skewed to the left by induced deleterious effects, the prediction equation would indicate progress from selection that could not be realized. By the use of screening techniques such as mass selection, the poorest yielding genotypes are eliminated and then the population is likely to be approximately normal and quantitative genetic methods based on the normal distribution can be utilized.

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Table 1. Percent prolific plants observed in populations grown in isolated nurseries, 1967-1970.

Population	Percent multiple-eared plants 1967	1968	1969	1970	Percent multiple-eared main stalk, 1970
Control selected	22.2	48.3	45.8	62.8	46.6
Irradiated (N_{th}) selected	57.6	66.4	70.6	77.2	74.2
Prolific selected	43.9	71.6	60.0	91.2	68.8
X-rayed selected	--	53.6	--	70.8	67.8

Table 2. Percent prolific plants observed in populations grown in a replicated yield trial in 1968 and 1969 (17,222 plants per hectare).

Population	Percent multiple-eared plants 1968	1969	Percent multiple-eared main stalks, 1969
Hays Golden	5.1	13.2	10.0
Control selected	43.2	75.6	60.9
Irradiated (N_{th}) selected	52.6	78.8	70.7
Prolific selected	36.7	69.0	61.0

Table 3. Grain yield in percent of Hays Golden estimated for four generations of recurrent X-irradiation of seeds and mass selection compared to selection alone.

Generation	X-ray treatment with selection	Selection alone
0		128.8
1	123.0	128.5
2	126.9	136.0
3	134.2	142.0
4	137.9	143.2

Table 5. Mean values of quantitative traits measured in S_1 and Testcross progenies of the parent variety Hays Golden (HG), the selected Control (C-9) and the Irradiated Selected population (I-9). Lincoln, Nebr., 1968.

Type of progeny	Population	Means						
		Grain yield q/ha	Ears per plot No.	Shelling %	Grain moisture %	Days to flower	Ear height cm	Ear height cm
S_1 families	HG	42.0	23.4	75.9	16.8	74.6	96	239
	C-9	56.6	27.3	76.1	18.8	76.8	115	264
	I-9	55.5	28.2	77.2	18.0	76.7	119	265
Testcrosses to related tester N6 x N6G	HG	65.8	25.8	78.4	16.5	72.2	106	268
	C-9	86.3	26.5	79.7	17.2	73.2	119	290
	I-9	88.3	28.0	80.2	16.9	73.2	120	289
Testcrosses to unrelated tester WF9 x H49	HG	75.5	26.5	80.6	16.3	72.6	114	278
	C-9	87.0	26.8	80.9	16.9	73.4	123	293
	I-9	88.8	27.5	81.2	16.5	73.6	129	295

Table 5. Mean values of quantitative traits measured in S_1 and Testcross progenies of the parent variety Hays Golden (HG), the selected Control (C-9) and the Irradiated Selected population (I-9). Lincoln, Nebr., 1968.

Type of progeny	Population	Means						
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	I-9	55.5	28.2	77.2	18.0	76.7	119	265
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	C-9	86.3	26.5	79.7	17.2	73.2	119	290
	I-9	88.3	28.0	80.2	16.9	73.2	120	289
Testcrosses to unrelated tester WF9 x H49	HG	75.5	26.5	80.6	16.3	72.6	114	278
	C-9	87.0	26.8	80.9	16.9	73.4	123	293
	I-9	88.8	27.5	81.2	16.5	73.6	129	295

Table 6. Genetic components of variance for quantitative traits measured in S_1 and testcross progenies of the parent variety Hays Golden (HG), the selected Control (C-9) and the Irradiated selected population (I-9). Lincoln, Nebr., 1968

Type of progeny	Population	Genetic components of variance						
		Grain yield q/ha	Ears per plot	Shelling %	Grain moisture %	Days to flower	Ear height cm	Plant height cm
S_1 families	HG	234	20.9	21.7	3.06	3.29	40.1	93.1
	C-9	157	14.1	24.2	6.61	2.28	23.6	44.1
	I-9	171	12.0	12.7	5.04	4.31	34.9	58.8
Testcross to related tester N6 x N6G	HG	113	3.0	2.9	.80	.22	6.7	14.3
	C-9	73	1.8	.7	.90	.45	9.7	16.0
	I-9	36	.9	2.5	1.74	.39	7.9	16.9
Testcross to unrelated tester WF9 x H49	HG	147	4.2	4.1	.76	.05	10.0	33.7
	C-9	57	2.4	1.7	.80	.45	11.9	22.0
	I-9	58	1.2	3.3	1.08	.75	11.2	21.2

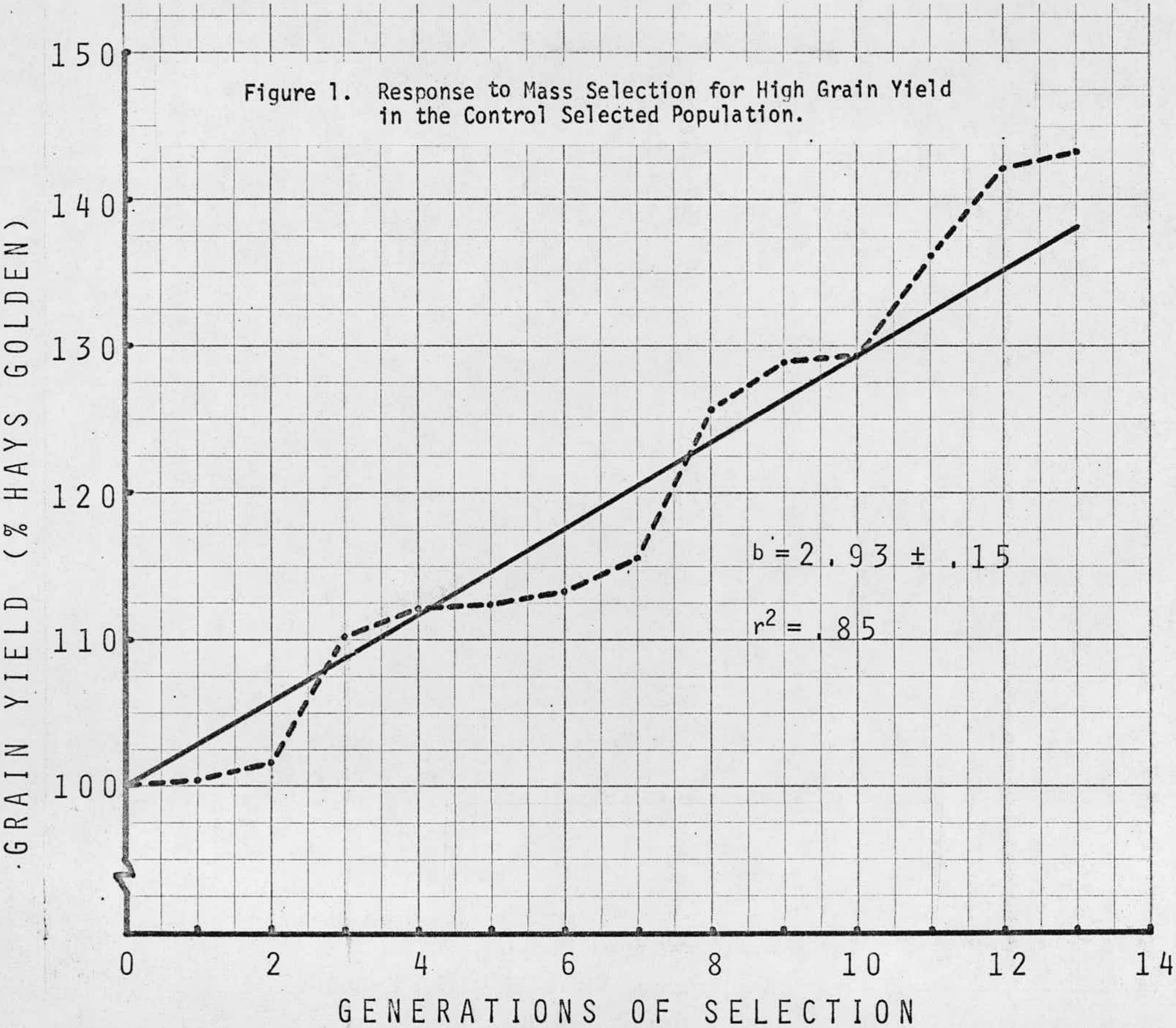


Figure 1. Response to Mass Selection for High Grain Yield in the Control Selected Population.

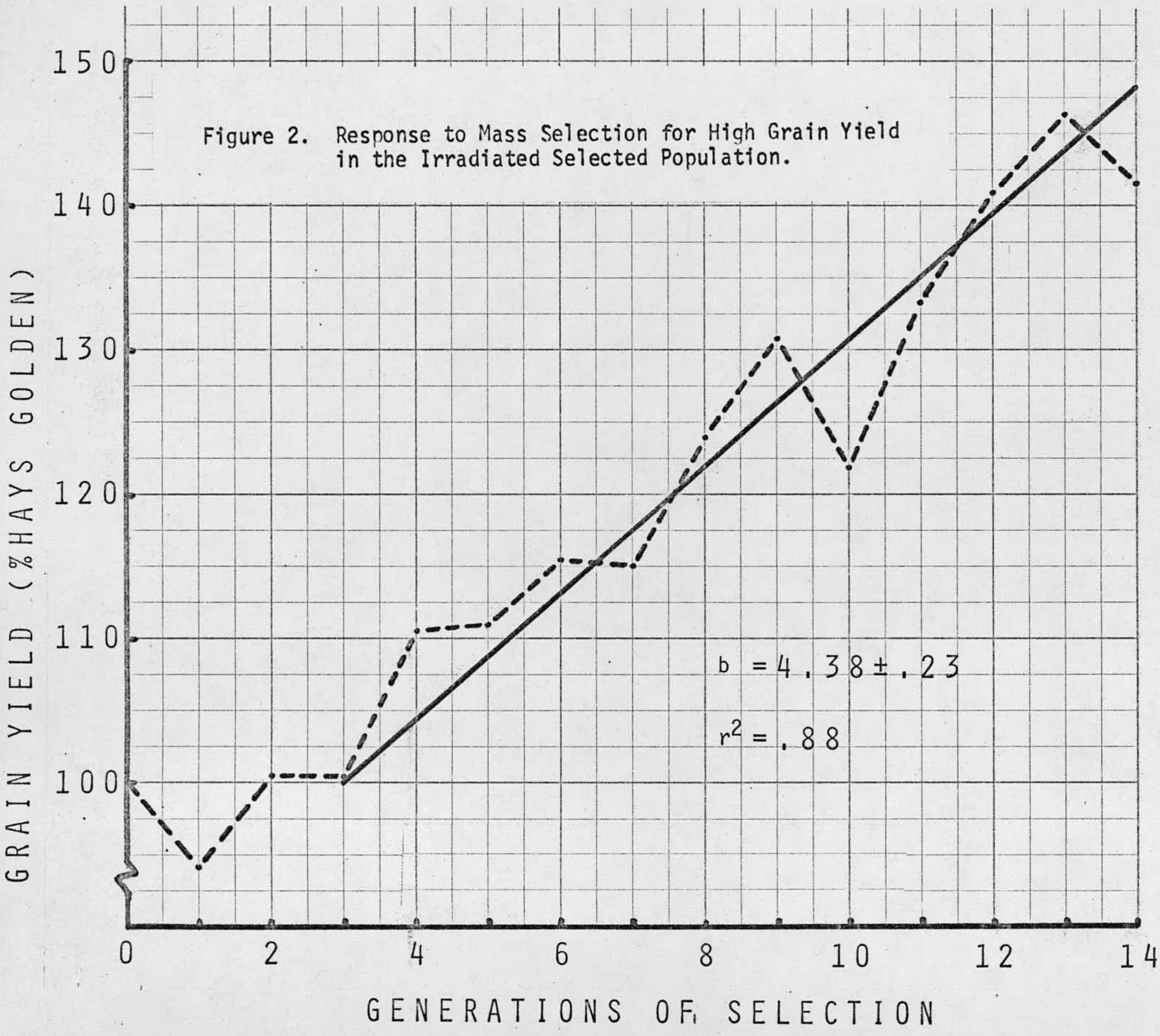
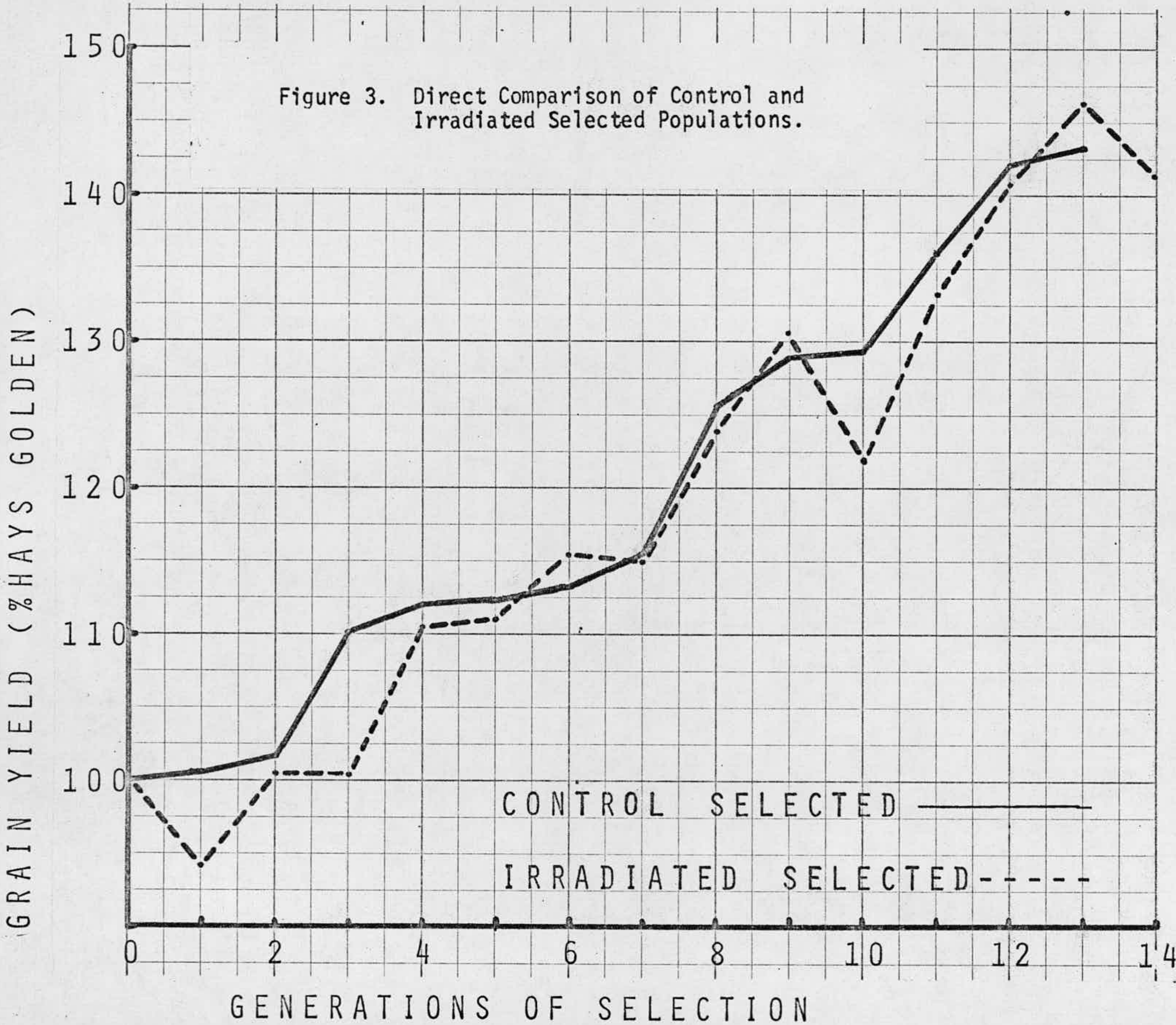


Figure 2. Response to Mass Selection for High Grain Yield in the Irradiated Selected Population.

Figure 3. Direct Comparison of Control and Irradiated Selected Populations.



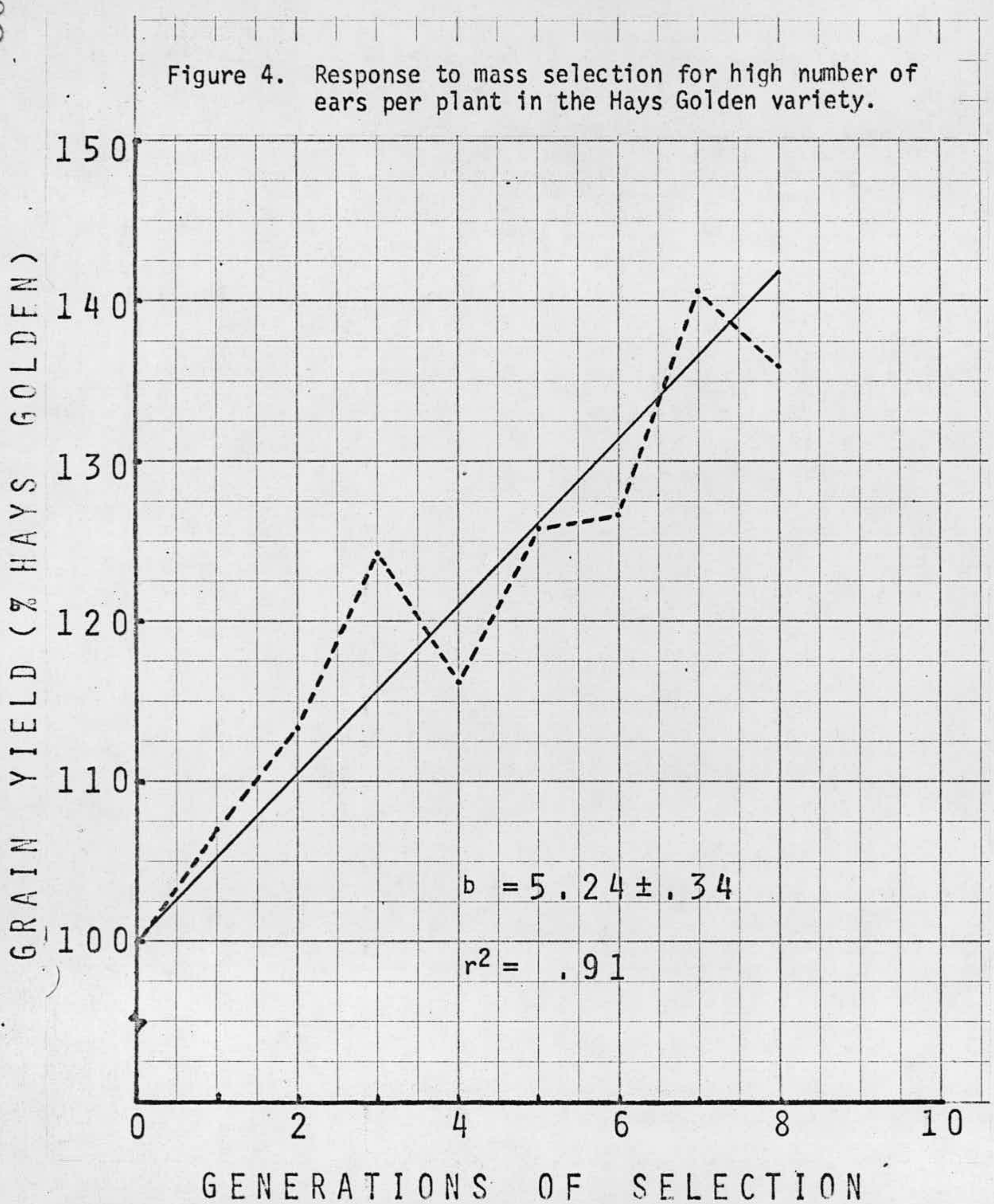


Figure 4. Response to mass selection for high number of ears per plant in the Hays Golden variety.

Figure 5. Changes in grain yield in response to plant population density observed for selected populations, their parent variety and a hybrid check.

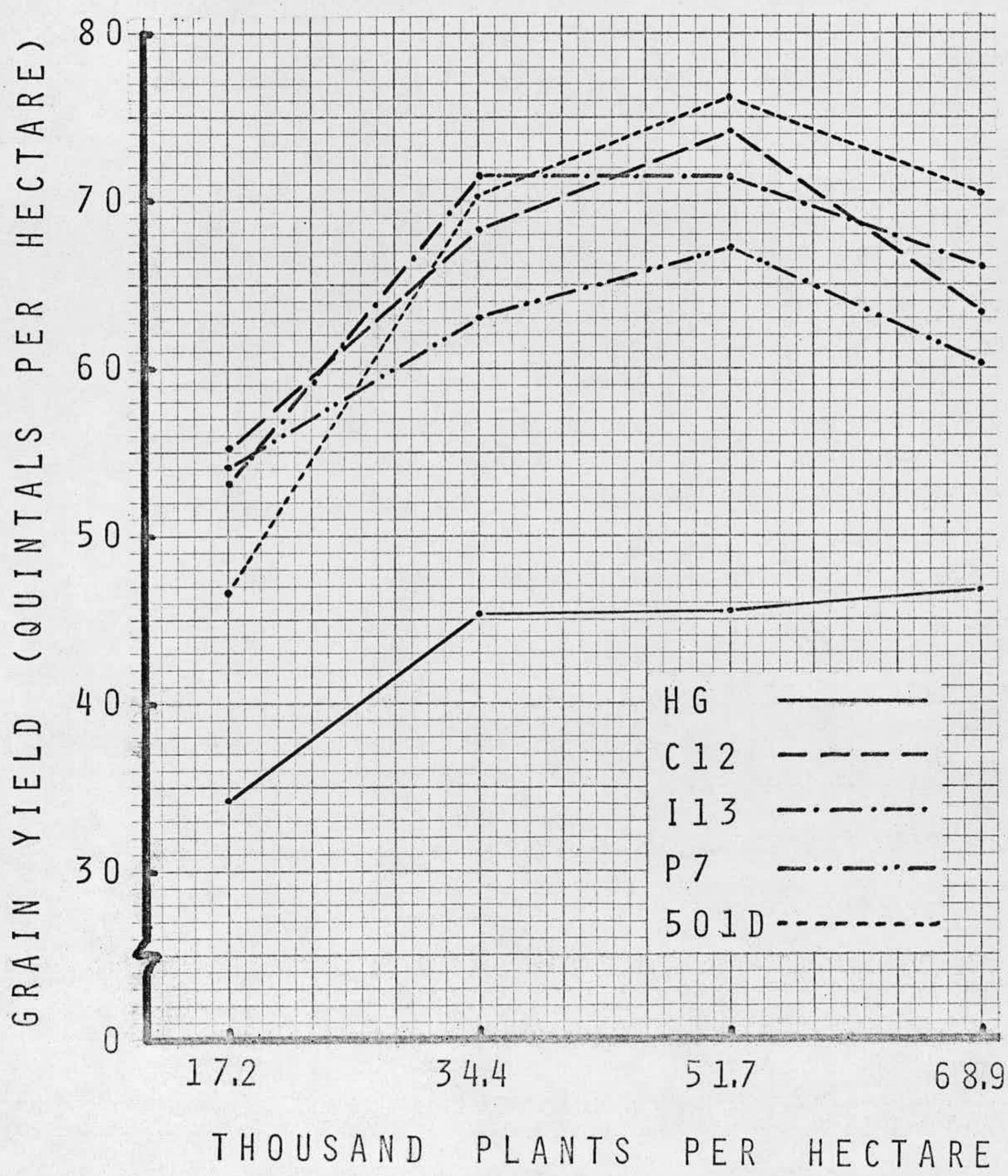


Figure 6. Changes in ears per plant in response to plant population density observed for selected populations, their parent variety and a hybrid check.

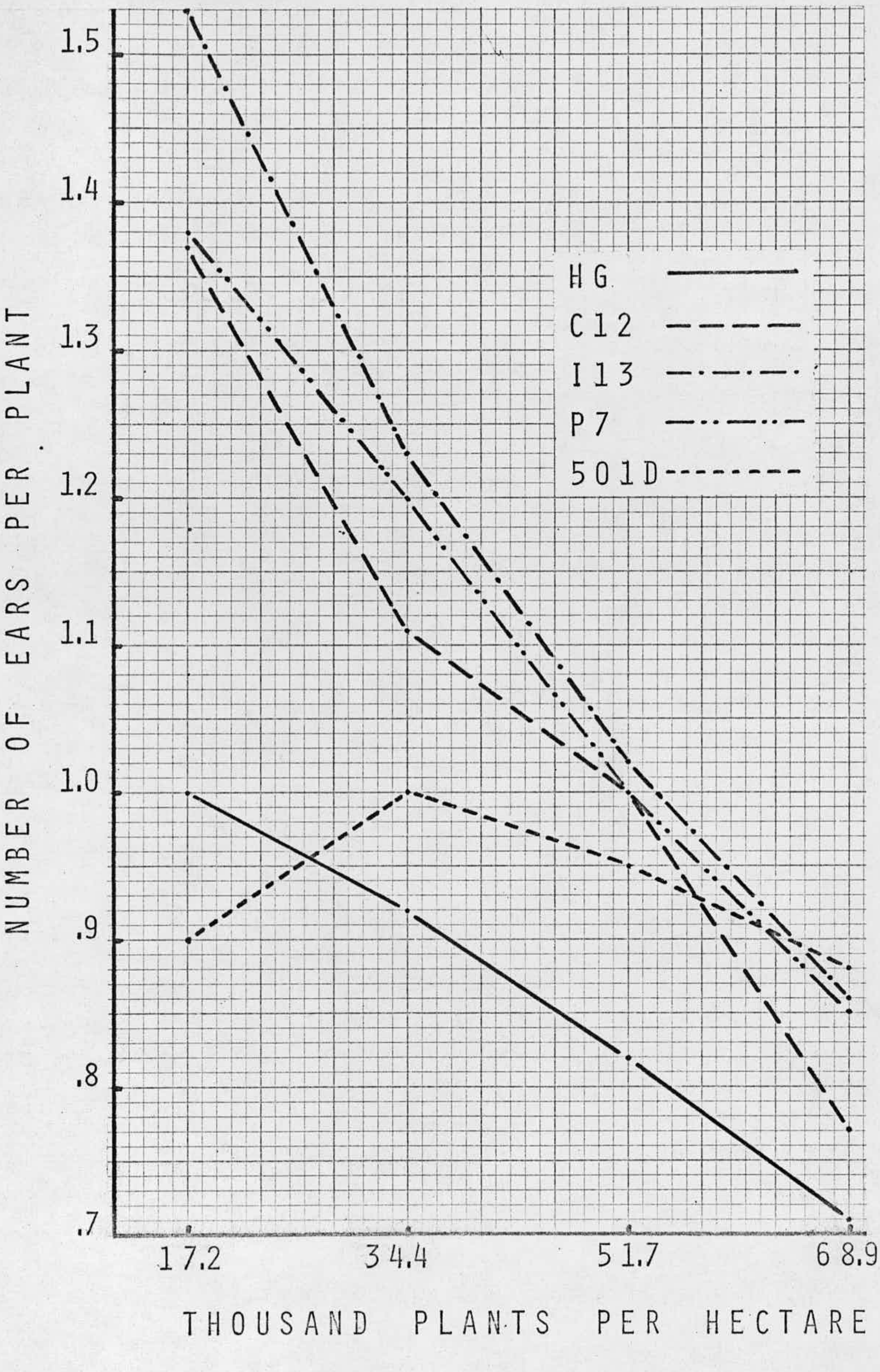


Figure 7. Changes in percent prolific plants in response to plant population density observed for selected populations, their parent variety and a hybrid check.

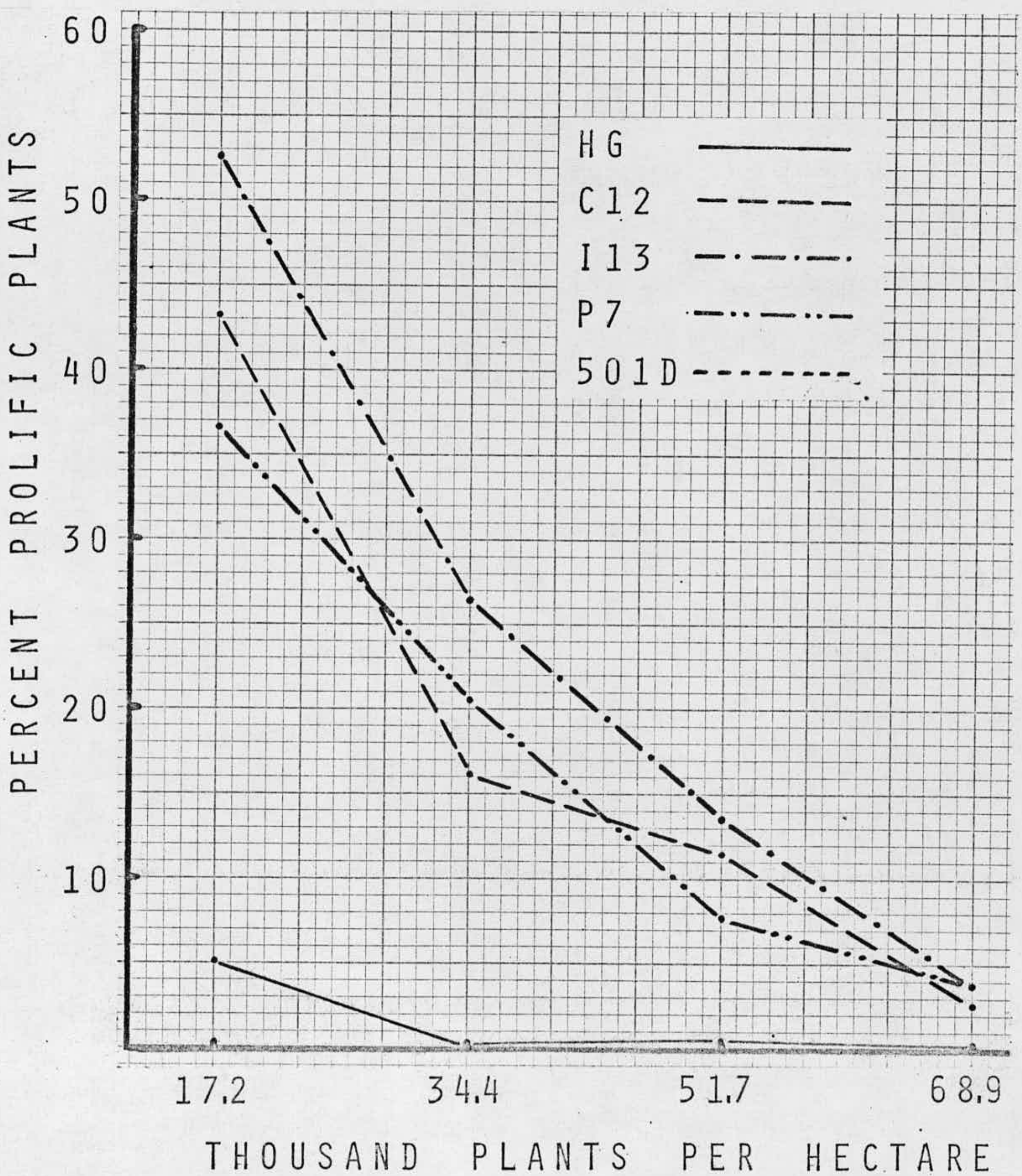
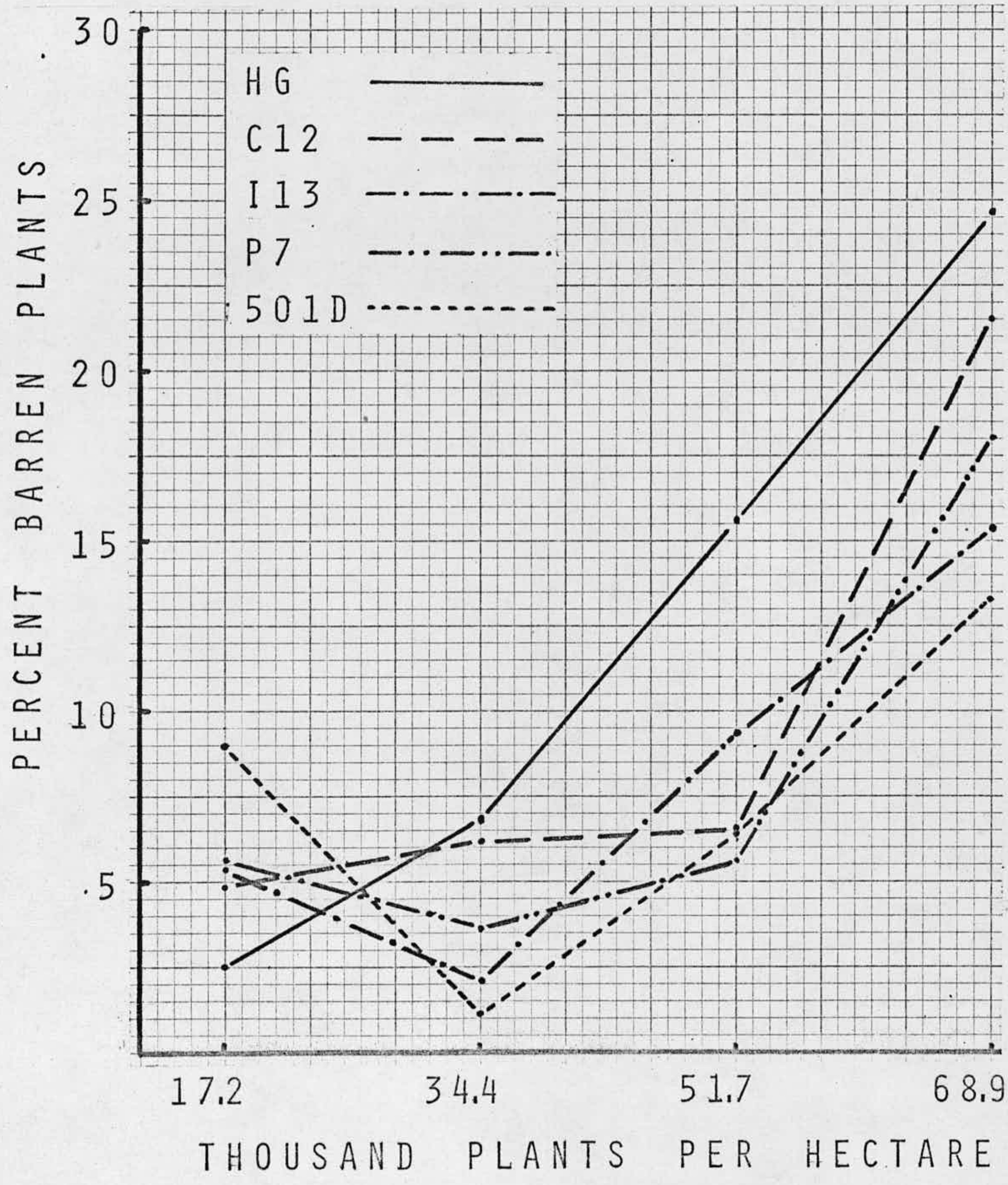


Figure 8. Changes in percent barren plants in response to plant population density observed for selected populations, their parent variety and a hybrid check.



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Hornbrook, A. R. and C. O. Gardner. Genetic study of two reduced plant height mutant genotypes induced in homozygous lines of *Zea mays* L. by irradiation techniques.

Chatterjee, N. K. and C. O. Gardner. Mutagenic effect of ethyl methanesulfonate on some quantitative traits in corn.

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Hammond, J. J. and C. O. Gardner. Modification of the Gardner - Eberhart model for evaluating cycles in a recurrent selection program.

Hammond, J. J. and C. O. Gardner. Effect of method of genetic sampling in finite populations on effective sample size.

SCIENTIFIC PAPERS PRESENTED AT NATIONAL AND INTERNATIONAL MEETINGS

Shauman, W. L. and C. O. Gardner. Effect of mass selection in three populations of an open-pollinated variety of corn. Paper presented at the American Society of Agronomy meetings, Tucson, Arizona, Aug. 23-27, 1970. Agron. Abstracts 62:19-20 (Tech. Inf. Doc. COO-1512-21).

Gardner, C. O. and W. L. Shauman. Effect of plant population density on grain yield and other agronomic traits in mass selected corn populations and in checks. Paper presented at the American Society of Agronomy meetings, Tucson, Arizona, Aug. 23-27, 1970. Agron. Abstracts 62:9-10 (Tech. Inf. Doc. COO-1512-20).

Gardner, C. O. The role of mass selection and mutagenic treatment in modern corn breeding. Paper presented at the American Seed Trade Association 24th Annual Corn and Sorghum Research Conference, Chicago, Ill., Dec. 9-11, 1969. (Tech. Inf. Doc. COO-1512-18).

Gardner, C. O. Genetic variation in irradiated and control populations of corn after ten cycles of mass selection for high grain yield. Paper presented at the International Symposium on the Nature, Induction and Utilization of Mutations in Plants, Pullman, Wash., July 14-18, 1969. (Tech. Inf. Doc. COO-1512-13).

Chatterjee, N. K. and C. O. Gardner. Analyses for two enzyme proteins in extracted embryos and seedlings of some inbred lines of corn, their hybrids and two mutant populations. Paper presented at the American Society of Agronomy meetings, New Orleans, La., Nov. 10-15, 1968. Agron. Abstracts 60:5. (Tech. Inf. Doc. COO-1512-10).

Gardner, C. O. Mutation studies involving quantitative traits. Paper presented at International Symposium on Present State in Mutation Breeding, Mito, Japan, Aug. 15-17, 1968. (Tech. Inf. Doc. COO-1512-9).

Gardner, C. O. Genetic changes resulting from mass selection in irradiated and control populations of an open-pollinated variety of corn. Paper presented at the XII International Congress of Genetics, Tokyo, Japan, Aug. 19-28, 1968. Proc. Int. Cong. of Genetics 1:269. (Tech. Inf. Doc. COO-1512-8).

Gardner, C. O. Population studies on variability, effects of irradiation and progress from selection in an open-pollinated variety of corn. Paper presented at the Seventeenth Annual National Poultry Breeders' Roundtable, Kansas City, Mo., May 3-4, 1968. (Tech. Inf. Doc. Coo-1512-7).

Gardner, C. O. and J. H. Lonnquist. Results of ten years of individual plant selection for high grain yield in an open-pollinated variety of corn. Paper presented at the VII Reunion Latinoamericana de Fitotecnia, Caracas, Venezuela, Sept. 17-23, 1967. (Tech. Inf. Doc. COO-1512-4).

REPORTS TO ATOMIC ENERGY COMMISSION ON RESEARCH ACCOMPLISHMENTS

Final Report 1965-1970. Technical Information Document COO-1512-22.

1968-69 Technical Progress Report. Technical Information Document COO-1512-12.

Comprehensive Summary Report 1965-1968. Technical Information Document COO-1512-6.

1967-68 Technical Progress Report. Technical Information Document COO-1512-5.

1966-67 Technical Progress Report. Technical Information Document COO-1512-3.

1965-66 Technical Progress Report. Technical Information Document COO-1512-2.

POST DOCTORAL STUDENTS TRAINED

Dr. Laures Empig	(Philippines)	1969-70.
Dr. Leslie Jones	(Australia)	1968-69.
Dr. Eli Cohen	(Israel)	1967-68
Dr. Noboru Mochizuki	(Japan)	1967-68
Dr. Nando K. Chatterjee	(India)	1966-67

GRADUATE STUDENTS TRAINED

Ph.D. level (Date of completion in parentheses).

Wendell L. Shauman (1971)

James J. Hammond (1969)

Nando K. Chatterjee (1969) (From India)

Albert R. Hornbrook (1968)

Fernando Arboleda (1972) (From Colombia)

Robert F. Mumm (1967)

Ibarra S. Santos (1966) (From the Philippines)

M.S. level

Randall Harris (1971)

Hernan Cortes (1971) (From Mexico)

Wendell Shauman (1970)

Robert Schaffert (1967)

Fernando Arboleda (1966) (From Colombia)

Albert R. Hornbrook (1966)

Oscar Cota (1964) (From Mexico)

THESES COMPLETED

Ph.D. theses

1969 Hammond, James J. Theoretical and computer simulation considerations of the variety diallel and related populations.

1969 Chatterjee, Nando K. Mutagenic effect of ethyl methanesulfonate on some quantitative traits of plants and the use of biochemical techniques to relate observed gene effects to biochemical activity in lines or populations.

1968 Hornbrook, Albert R. Influence of mass selection and thermal neutron irradiation on means and cumulative gene effects in a variety of corn (*Zea mays* L.).

1967 Mumm, Robert F. A comparison of genetic variances and estimated response to selection between the irradiated and non-irradiated groups in two inbred lines of maize.

1966 Santos, Ibarra S. Utilization of random homozygous inbred lines to evaluate genetic and environmental variations in an open-pollinated variety of corn.

M.S. theses

1970 Shauman, Wendell L. Effect of mass selection for yield improvement on yield and related quantitative traits in four populations of the Hays Golden variety of corn (*Zea mays* L.).

1967 Schaffert, Robert E. The effects of thermal neutron radiation, selection and recombination on genetic variance components of populations of maize derived from the cross of two homozygous lines.

1966 Hornbrook, Albert R. Genetic studies of three mutant genotypes induced in inbred lines of maize by irradiation techniques.

1966 Arboleda-Rivera, Fernando. Evaluation of progress from mass selection in two sub-populations of maize.

1964 Cota, Oscar. Effect of mass selection on genetic variances of the Hays Golden variety of corn.

UNDERGRADUATE STUDENTS TRAINED

Margaret Plank

Judith Boyle

Thomas Hoeggemeier

Kenneth Dolezal

Robert Schaffert

TECHNICIANS TRAINED

Donald N. Johnston

Clarmont Miller

Robert Hanson