MAR 14 1967

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H.C. \$ 3.00 MN 65

C00-1512-3

MASTER

APPLICATION OF BIOMETRICAL GENETIC 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

Technical Progress Report 1966-67
Contract No. AT(11-1)-1512

by

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RELEASED FOR ANNOUNCEMENT
IN NUCLEAR SCIENCE ABSTRACTS

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INTRODUCTION

The radiation quantitative genetic investigations initiated at the University of Nebraska in 1965 have been conducted according to the original proposal as amended by the proposed technical program for 1966-67. In general the 1966 growing season was a very favorable one for plant growth and for nursery pollinations. Excellent seed sets were obtained in the nursery in spite of seven successive days with temperature exceeding the 100 degree mark. Likewise excellent yield levels were achieved in all experiments grown on the Agronomy Farm. The availability of an irrigation system to supplement normal rainfall has played a major role in the success of this project.

Analyses of experiments conducted in 1965 have been completed and are included in this report. Some results obtained in 1966 are also included, but most of the analyses and interpretations are yet to be done. Each experiment planned and conducted is presented and discussed individually.

HAYS GOLDEN MASS SELECTION STUDY

The Hays Golden variety of corn was chosen as the base population for one phase of our investigations. The variety is quite well adapted to the corn-growing regions of Nebraska, and it is believed to approximate a random-mating equilibrium population, which make it ideally suited for

the proposed studies.

The primary objective of the investigation was to induce genetic variation for quantitative traits in the population by using recurrent thermal neutron radiation, to eliminate deleterious mutations by mass selection based on yield of the individual phenotype, and hopefully to demonstrate that greater progress could be made in an irradiated population than in a non-irradiated one. A drastic reduction occurred in yield in the first generation following the initial radiation treatment of seeds in 1955. (Gardner, 1961). Consequently no irradiation was used in the next generation, but a second, lower dose was applied in 1957. No additional radiation has been used on the thermal neutron treated population. Mass selection of the highest yielding 10 percent of the plants using special stratification techniques has continued through the years on the Irradiated population (I) and the Control population (C). In one year no selections were possible in the Control population, so in 1966 the Irradiated population underwent the 12th cycle of selection and the corresponding Control population underwent the 11th.

Selection over the years has resulted in a fairly steady gain of about 3 percent per generation for both the Irradiated population and the Control, which is slightly less than the 3.9 percent reported by Gardner (1961) for the first 4 cycles of selection. Results of yield trials involving the original Hays Golden variety and the Irradiated and Control selected populations in 1965 and 1966 are reported in Tables 1 and 2.

Table 1. Mean values for grain yield and other agronomic traits of Hays Golden and some cycles of selection of the Control and Irradiated mass-selected populations tested in ten replications at Lincoln, Nebraska, 1965.

Population ^{1/}	Grain Yield ^{2/}		Moisture at harvest		Stalks lodged		Dropped ears	
	Metric tons per hectare	% of HG	%	% of HG	%	% of HG	%	% of HG
HG	3.79	100.0	17.0	100.0	30.4	100.0	2.9	100.0
C6	4.06	107.1	18.7	110.0	47.1	154.9	3.3	113.8
C6 relaxed	4.13	109.1	18.3	107.6	43.7	143.7	4.6	158.6
C7	4.02	106.2	19.3	113.5	39.6	130.3	4.2	144.8
C7 relaxed	4.24	111.8	19.4	114.1	53.7	176.6	5.4	186.2
C8	4.05	107.0	19.0	111.8	53.3	175.3	6.7	231.0
C8 relaxed	3.94	104.2	19.5	114.7	55.0	180.9	1.7	58.6
C9	4.48	118.4	20.0	117.6	51.7	170.1	7.5	258.6
I6	4.48	118.4	17.7	104.1	41.7	137.2	3.7	127.6
I7	4.56	120.4	17.7	104.1	50.4	165.8	2.5	86.2
I8	4.51	119.2	18.3	107.6	52.1	171.4	4.2	144.8
I9	4.41	116.6	17.5	102.9	57.5	189.1	3.7	127.6
I10	4.43	117.0	17.4	102.4	50.4	165.8	2.9	100.0
Nebr. 501D (check)	5.84	154.4	16.5	97.1	12.9	42.4	3.3	113.8

^{1/} HG = Hays Golden parent population; C = Control mass selected; I = Irradiated mass selected; 6, 7, 8, 9 and 10 indicate cycles of selection involved; relaxed indicates no selection in that generation; and Nebr. 501D is a check hybrid used in the evaluation.

^{2/} Standard error of a mean = .16 metric tons/hectare.
Standard error of a difference between any two means = .23 metric tons/hectare.

Table 2. Mean values for grain yield and other agronomic traits of Hays Golden and some cycles of selection of the Control and Irradiated mass-selected populations tested in ten replications at Lincoln, Nebraska, 1966.

Population ^{1/}	Grain Yield ^{2/}		Moisture at harvest		Stalks lodged		Dropped ears	
	Metric tons	% of	%	% of	%	% of	%	% of
	per hectare	HG		HG		HG		HG
HG	6.04	100.0	15.8	100.0	40.3	100.0	1.9	100.0
C7 relaxed	7.04	116.5	17.3	109.2	51.5	127.9	1.1	58.5
C8	7.49	124.1	18.0	114.0	52.2	129.7	1.9	97.6
C8 relaxed	8.11	134.3	17.8	112.9	44.8	111.3	4.4	234.1
C9	8.11	134.3	18.2	114.9	55.9	138.9	2.6	136.6
C9 relaxed	7.83	129.7	18.1	114.6	48.1	119.5	3.0	156.1
C10	7.70	127.6	18.1	114.4	53.3	132.4	1.9	97.6
I9	7.69	127.4	16.6	105.3	57.0	141.6	2.2	117.1
I10	7.92	131.3	15.9	100.7	52.2	129.7	2.2	117.1
I11	8.12	134.5	16.2	102.8	56.7	140.7	0.7	39.0
Nebr. 501D (check)	8.40	139.0	14.4	90.9	24.4	60.7	3.0	156.1

^{1/} HG = Hays Golden parent population; C = Control mass selected; I = Irradiated mass selected; 6, 7, 8, 9 and 10 indicate cycles of selection involved; relaxed indicates no selection in that generation; and Nebr. 501D is a check hybrid used in the evaluation.

^{2/} Standard error of HG mean (20 replications) = .23 metric tons/hectare.
Standard error of any other mean (10 replications) = .32 metric tons/hectare.
Standard error of a difference between HG and any other mean = .39 metric tons/hectare.
Standard error of a difference between any other two means = .45 metric tons/hectare.

Response to selection is shown graphically in Figures 1 and 2. Since seed viability decreases with age after a few years, we are now testing only the most recent generations of selection and the original variety maintained to evaluate progress.

The 1965 yields (Table 1 and Figure 1) were not nearly as favorable as those obtained in 1966 (Table 2 and Figure 2). Although yields in any one test tend to be erratic, the trend still seems to be upward. When a ceiling is imposed on yields by some environmental factor, the response to selection is not so evident as it is under more favorable circumstances such as existed in 1966. Based on 1965 results, one might be tempted to conclude that the Irradiated mass-selected population had reached a plateau and that selection was still effective in the Control mass-selected population. However, the 1966 results suggest the opposite situation. Also 1965 results suggest an average gain of approximately 2% per generation whereas the 1966 results indicate more nearly 3% per generation.

Selected populations are later maturing than the Hays Golden variety indicating that selection has been for plants that take full advantage of the growing season. Less change has taken place in the Irradiated population than in the corresponding control.

Stalk lodging has increased in the selected populations. Perhaps this result is directly related to increased yields putting more stress on the stalk in windstorms. Also the plant and ear height has increased which would increase the stress. An interesting experiment would be to

Figure 1. Yield of the Control mass-selected population and the Irradiated mass-selected population in % of the parent Hays Golden variety at Lincoln, Nebraska, 1965.

Figure 2. Yield of the Control mass-selected population and the Irradiated mass-selected population in % of the parent Hays Golden variety at Lincoln, Nebraska, 1966.

Table 3. Mean values for grain yield and other agronomic traits of Hays Golden, even numbered cycles of selection in both the Control and Irradiated populations, crosses between corresponding cycles of the Control and Irradiated populations and crosses of each selected cycle with the parent Hays Golden. Lincoln, Nebraska, 1965.

Population ^{1/}	Yield		Moisture at Harvest		Flowering Date		Ear Height		Stalk Lodging	Dropped Ears
	Metric tons per hectare	% of HG MP	%	% of HG	Day in July	% of HG	Meters	% of HG MP	%	%
HG	5.463	100		14.47	100	17.6	1.048		22.9	2.5
C2	5.732	105		16.28	112	19.4	1.103		25.4	3.8
C4	6.611	121		15.68	108	18.5	1.172		24.2	5.8
C6	6.662	122		16.77	116	18.6	1.150		36.7	6.7
C8	7.972	146		15.97	110	20.0	1.368		41.7	8.3
I2	5.936	109		15.16	105	19.2	1.161		35.0	3.3
I4	6.260	115		15.29	106	19.3	1.205		40.0	4.2
I6	6.526	119		15.02	104	19.1	1.220		37.1	3.3
I8	7.649	140		15.79	109	20.2	1.337		52.5	5.8
C2 x HG	5.778	106	103	15.98	110	17.2	1.142	109	29.6	4.2
C4 x HG	6.396	117	106	15.45	107	18.5	1.153	110	27.5	1.2
C6 x HG	6.469	118	107	15.09	104	18.4	1.208	115	27.9	5.8
C8 x HG	6.503	119	97	16.17	112	18.3	1.196	114	35.0	3.3
I2 x HG	5.880	108	103	14.78	102	17.8	1.139	109	28.8	5.0
I4 x HG	5.698	104	97	15.35	106	18.1	1.096	105	20.0	3.3
I6 x HG	6.566	120	110	14.94	103	18.4	1.199	114	34.6	8.8
I8 x HG	6.469	118	99	15.26	105	18.2	1.222	117	39.6	4.2
C2 x I2	5.931	108	102	15.50	107	18.2	1.161	111	27.1	4.6
C4 x I4	6.396	117	99	15.37	106	18.0	1.180	113	32.1	3.8
C6 x I6	7.105	130	108	15.42	107	18.3	1.201	115	37.1	3.8
C8 x I8	7.825	143	100	16.61	115	19.8	1.282	122	37.1	3.8

^{1/} HG = Hays Golden parent variety; C = Control mass-selected population; I = Irradiated mass-selected population; 2, 4, 6 and 8 are cycles of selection; MP = Mid-parent value (average of 2 parents)
Hays Golden mean is based on 20 plots, all other means on 10 plots.

Table 4. Analysis of variance of grain yield of Hays Golden, even numbered cycles of selection in both the Control and Irradiated populations, crosses between corresponding cycles of the Control and Irradiated populations and crosses of each selected cycle with the parent Hays Golden. Lincoln, Nebraska, 1965.

Source of variation	Degrees of freedom	Mean square
Blocks	9	2.1956*
Entries	21	15.6286**
Among Hays Golden Checks	1	0.6845
Among Cycled Generations	7	18.9436**
C vs I	1	1.4311
Within C	3	26.4990**
Linear	1	39.0728**
Quadratic	1	37.2490**
Cubic	1	3.1752
Within I	3	17.2256**
Linear	1	45.4104**
Quadratic	1	4.9702*
Cubic	1	1.2961
Among Cycles x Hays Golden	7	4.1717**
C x HG vs I x HG	1	1.1044
Within C x HG	3	3.6429*
Linear	1	7.8804**
Quadratic	1	2.6522
Cubic	1	0.3961
Within I x HG	3	5.7229**
Linear	1	10.8112**
Quadratic	1	0.0562
Cubic	1	6.3012**
Among Cycle Intercrosses	3	21.3656**
Linear	1	63.5064**
Quadratic	1	0.5062
Cubic	1	0.0841
HG vs Cycles x HG	1	28.5156**
Cycles vs Cycle Intercrosses	1	1.7510
(HG + Cycles x HG) vs (Cycles + Cycle Intercrosses)	1	71.3440**
Error	189	1.0372
Total	219	

* = significant at the .05 level of probability.

** = significant at the .01 level of probability.

Figure 3. Relative yield (% of Hays Golden) of selected cycles of the Control and Irradiated mass-selected populations, crosses between corresponding cycles, and crosses between selected cycles and Hays Golden. Lincoln, Nebraska, 1965.

Fig. 1. Relationship (%) of Hays Golden to selected populations of the Control and irradiated mass-selected populations and crosses between corresponding generations of the two selected populations. Lincoln, Neb., 1966.

initiate a selection study for the improvement of stalk strength.

A further evaluation of progress realized from mass-selection and from irradiation with mass selection and also an evaluation of the nature of the populations developed by mass selection were obtained in an experiment involving even numbered cycles of selection and the parent Hays Golden. The populations C2, C4, C6, C8, I2, I4, I6 and I8 as well as Hays Golden (HG) were included in the experiment. Each selected generation was crossed with HG, and corresponding cycles of the Control and Irradiated populations were crossed with each other, i.e. C2 x I2, C4 x I4, etc. The objectives were (1) to estimate gain realized from mass selection and from mass selection plus irradiation, (2) to observe the different responses when selected generations are crossed with the parent variety and with each other and to interpret the results in terms of gene effects. This research was conducted primarily by Fernando Arboleda-Rivera in fulfilling his requirements for an M.S. degree. The results are presented in Tables 3 and 4 and Figure 3.

Yield responses indicated for the mass-selected Control and Irradiated populations are quite linear and do not differ significantly. Gain appears to be nearly 5% per generation. The response indicated for the crosses $C_j \times I_j$, $j = 2, 4, 6$ and 8 , is very linear and generally tends to be intermediate between the yields of the parent populations. No evidence of heterosis in the crosses was observed; hence, one can conclude the selection has simply increased the frequencies of the same favorable genes

in both populations. The irradiated population does not appear to possess genes favorable for yield that are not also in the control population in about the same frequency. We had hoped that some distinct differences might be reflected.

Yields of crosses between selected generations and Hays Golden tended to approach more closely to the selected parent except in cycle 8 where the cross is strictly intermediate in yield. Such responses suggest selection for dominant favorable genes for yield in the early generations and selection of strictly additive genes in later generations.

The linear nature of the response curves shown in Figure 3 indicates that selection has been and is continuing to be effective. Since there is no evidence of a decreasing rate of increase with cycles of selection, we can conclude that additive genetic variance has not been greatly reduced and continued progress should be expected in future generations. This in turn is evidence of a relatively large number of genes involved in the inheritance of grain yield.

The effect of selection for yield upon other traits is of interest. Simple correlation coefficients between yield and the traits ear height, moisture in grain at harvest and flowering date were 0.91, 0.44, and 0.68, respectively. As yield has been increased by selection, the plants in the populations have become taller and later maturing.

A more elaborate study has been initiated involving the same initial populations as used by Arboleda. A complete diallel cross involving the

9 populations was produced. Plants in each of the 9 parent population and in each of the 36 F_1 crosses were self-pollinated to produce selfed progenies, and each F_1 was also advanced to the F_2 generation by random mating. The 126 populations were grown in a yield trial in the field in 1966 and will be grown again in 1967. The data will be analyzed according to the general model for genetic effects developed by Gardner and Eberhart, and valuable information on additive, dominance and epistatic gene effects and on heterosis and inbreeding depression will be obtained. A detailed report of 1966 results will be included in the next annual report; however, yield data for the selected generations and their intercrosses at each cycle are shown in Figure 4. These data are in agreement with those of Arboleda and indicate a gain of 3.4% per generation. This particular study is being conducted by Mr. Albert Hornbrook, Graduate Assistant working toward his Ph.D. degree.

A sample of seed from the 9th generation of the Control mass-selected population was exposed to 15,000r. X-radiation and the population was grown in isolation in 1965. The same mass-selection procedure followed in the past was used on the new X-ray treated population. Seed from selected plants was again exposed to 15,000r. X-radiation in 1966 and the selection procedure was repeated. The highest yielding 10% is selected from each block in the field each year. The recurrent radiation and selection procedure will be repeated each generation. After a few cycles of selection, progress will be evaluated by yield tests grown from seeds

kept in cold storage to retain their viability. The effect of selection on yield and the effect of X-radiation of seeds on genetic variability in the population will be assessed. Also resistance to radiation damage will be evaluated.

EFFECT OF IRRADIATION AND SELECTION ON FREQUENCY OF DELETERIOUS RECESSIVE ALLELES

An investigation to determine the presence and frequency of deleterious recessive alleles (those that cause chlorophyll deficiencies primarily) in the Hays Golden population and in the C9 and I9 selected generations was conducted by Robert Schaffert, Graduate Research Assistant. Many such alleles should be lethal in homozygous condition but they are maintained in the population at a low frequency in heterozygous condition. Others such as the virescents are not lethal but might have an effect on grain yield. If any of the deleterious recessive alleles tended to reduce yields in the heterozygote compared to the homozygous normal or if the homozygous recessive genotypes survived but produced lower yields relative to the heterozygous and homozygous normal types, then mass selection should be somewhat effective in reducing the frequency of such alleles. On the other hand, thermal neutron irradiation is known to induce mutations causing chlorophyll deficiencies. Since selection is somewhat slow in eliminating deleterious recessive alleles when the frequency is low, the I9 population, though having undergone the same number of generations of mass selection, should be expected to have

a higher frequency of such alleles than the corresponding C9 population. The C9 population should be somewhat lower than the parent Hays Golden variety.

In order to detect the presence of deleterious recessives generally masked by the dominant normal allele, 120 plants chosen at random from each of the three populations were self-pollinated in 1965. In the case of a simply inherited trait where a 3:1 segregation would be expected in the S_1 family, 16 plants should be examined to have a 99 percent chance of including at least one homozygous recessive, assuming that all genotypes are equally viable. If 30 plants are observed, one has a .9999 chance of including at least one homozygous recessive when the 3:1 ratio is expected and a very high probability (.85) of including at least one of the double homozygous recessives where duplicate genes are involved giving a 15:1 ratio. Therefore, 30 seeds of each S_1 family were planted in sand in the greenhouse bench in the winter of 1966. Daytime temperatures of 90 to 95 degrees Fahrenheit were maintained, so the seedlings emerged in about 4 days and grew very rapidly. Counts of kinds and numbers of chlorophyll deficient phenotypes were recorded for each S_1 family. The results are reported in Table 5. Since some families contained plants of more than one chlorophyll deficient phenotype, the total number of families exhibiting abnormal phenotypes is not the sum of the numbers of families in each class.

The results indicate that selection has not reduced the frequency

Table 5. Number of S_1 families showing each kind of chlorophyll deficiency in the Hays Golden variety (HG), the 9th generation of the mass-selected Control (C9), and the 9th generation of the mass-selected Irradiated population (I9) together with percentage seed germination and total number of families showing chlorophyll deficiencies in each population. Lincoln, Nebraska, 1966.

Chlorophyll deficient seedling class	Population		
	HG	C9	I9
	Number of families having designated deficiency		
White	4	4	5
Cream	8	2	11
Gold (yellow)	0	3	2
Light green	13	7	13
Lethal necrotic left blotch	2	3	4
Other chlorotic abnormalities	14	20	17
Other deleterious effects	0	1	0
Total abnormal families	41	40	52
% abnormal families	34.2	33.3	43.3
% seed germination	86.8	87.5	83.1

of plants carrying deleterious recessive alleles suggesting that the frequency of any particular allele is probably quite low in the population and that a number of loci are involved. If such is the case, mass selection should not be expected to be very effective. On the other hand, thermal neutron irradiation has induced mutations which fall into the deleterious recessive class. The I9 mass-selected population exhibited approximately 10 percentage points more families having chlorophyll deficiencies of one type or another than either of the other populations. The relationship between the frequency of deleterious recessive genes and the magnitude of the genetic variances needs further investigation.

The distribution of the relative numbers of families exhibiting the different kinds of chlorophyll deficient phenotypes in each of the three populations is essentially the same (Chi-square test for independence = 13.6, d.f. = 12 and $0.25 < P(x^2 \geq 13.6) < .50$).

The results obtained by mass selection in Hays Golden are strikingly different from those obtained by recurrent selection for general combining ability in Krug Yellow Dent (Table 7 Final Report to the Atomic Energy Commission, Contract No. AT(11-1)-352, 1960). In the recurrent selection for general combining ability procedure, S_1 families are selected based upon half-sib family performance in yield trials. The one generation of selfing each cycle is quite effective in eliminating the deleterious recessive alleles from the population. After 2 cycles of inbreeding, selection and synthesis, only 6.25 percent of the plants carried deleterious

recessive alleles compared to 37.5 percent of the plants in Krug Yellow Dent. A Krug Yellow Dent population after 3 cycles of ultraviolet irradiation of pollen had 56.2 percent of its plants carrying such recessives.

If deleterious recessive alleles causing chlorophyll deficiencies are a contributing factor to genetic variance and to generally lower yields, perhaps a generation of self-fertilization should be considered occasionally in the mass selection program for population improvement.

EFFECT OF IRRADIATION AND SELECTION ON GENETIC VARIANCES

Investigations were conducted to evaluate the kinds and amounts of genetic variation in the C6 and I6 populations compared to the original Hays Golden population from which they were derived. The results were reported in Crop Science 6:330-332.1966 (Technical Information Document C00-1512-1). Additive genetic variance for yield in the I6 was more than double that of the original variety and was nearly double that of the C6 indicating that thermal neutron irradiation probably did increase additive genetic variance against which mass selection is effective. The two selected populations have been shown to be at about the same yield level now, but the additional additive genetic variance observed in the I6 population indicates that progress in yield improvement in future generations should be higher in that population than in the C6. A substantial increase (255%) in additive genetic variance for ears per

plant, one of the components of yield, was also noted. No differences in days to flower or ear height variances were evident. Estimates of dominance variances indicated no differences among the populations; therefore one must conclude that the kinds of mutations induced by thermal neutron irradiation of seeds and affecting genetic variation in yield and number of ears per plant are quite largely additive in their effects.

In 1966 a new experiment was initiated to study genetic variation after 10 generations of mass selection. Random full-sib and half-sib matings were made in the Hays Golden, C10 and I10 populations and will be grown in yield trials in 1967 and 1968.

In another approach to study the genetic structure of the original Hays Golden and mass selected populations and to evaluate the kinds and amounts of genetic variation in these populations, a selfing program was initiated in 1965 to develop random inbred lines from Hays Golden and the C9 and I9 selected generations. The random S_1 progenies were used to check on the presence and frequency of deleterious recessive alleles as indicated earlier in this report. They were also planted in the nursery in 1966 and advanced to the S_2 generation. Each original randomly chosen S_0 plant will be maintained as a line each generation by random choice of one self-pollinated plant in that line, unless the line is eliminated by natural selection. At the present time we have about 150 lines of the C9 and I9 populations and about 200 of the Hays Golden variety.

Inbreeding of randomly chosen plants in the C10, I10 and Hays Golden populations was also initiated in connection with genetic variance studies in 1966.

EFFECTS OF THERMAL NEUTRON IRRADIATION OF SEEDS AND ULTRAVIOLET IRRADIATION OF POLLEN ON HOMOZYGOUS LINES OF CORN

Starting with seeds from a single plant of long-time inbred lines, sets of sub-lines were developed by two methods: (1) Prior to self-pollination each year, pollen was exposed to ultraviolet irradiation for four successive generations. (2) Seeds were exposed to thermal neutron irradiation at the beginning of the experiment. Comparable control lines were developed in each case. Studies involving two sets of these lines in partial diallel crosses have been conducted by Robert F. Mumm for his Ph.D. thesis. The results are now being analyzed and will be reported in his thesis in the near future. A discussion of the results will be included in the next annual report.

GENETIC INVESTIGATIONS OF THREE MUTANT TYPES INDUCED IN INBRED LINES OF CORN BY IRRADIATION TECHNIQUES

Three mutant types observed to be distinctly different from their parent lines in one particular trait were chosen from the sets of lines described above to be studied in detail by Albert R. Hornbrook for his M.S. thesis. One mutant type exhibited necrotic lesions (blotches) on the leaves of fully developed plants. At first, the plants were believed

to be diseased but no causal organism could be found. Therefore, we concluded that the abnormality was probably genetically controlled. The sub-line came from inbred line N25 seed treated with $8.03 \times 10^{12} \text{ N}_{\text{th}}/\text{cm}^2$. The other mutant phenotypes were distinctly shorter in stature but were not dwarfs or brachyitics. They were simply reduced in height. One line came from N25 seed treated with $8.03 \times 10^{12} \text{ N}_{\text{th}}/\text{cm}^2$, and the other came from inbred line N6 which had undergone 4 successive cycles of pollen irradiation with ultraviolet light prior to self-pollination.

Reciprocal crosses were made between mutant types and their normal parent inbred line, the F_2 generations were produced by selfing F_1 plants, and one first backcross generation was produced by crossing each F_1 with the mutant parent. The backcross of the F_1 to the normal parent would have provided additional information but it was not produced because the traits were believed to be controlled by simple recessive alleles. The following symbols will be used to represent populations as indicated:

P_1 = normal parent.

P_2 = mutant parent.

$F_{1.12}$ = F_1 generation with P_1 as female and P_2 as male.

$F_{1.21}$ = F_1 generation with P_2 as female and P_1 as male.

F_1 = $(F_{1.12} + F_{1.21})/2$.

$F_{2.12}$ = F_2 generation produced by self-fertilization of $F_{1.12}$.

$F_{2.21}$ = F_2 generation produced by self-fertilization of $F_{1.21}$.

F_2 = $(F_{2.12} + F_{2.21})/2$.

$B_{1.122}$ = Backcross of $F_{1.12}$ (female) to P_2 (male).

$B_{1.212}$ = Backcross of $F_{1.21}$ (female) to P_2 (male).

$B_{1.2} = (B_{1.122} + B_{1.212})/2$.

The various populations produced were grown in yield tests at the Agronomy Farm in 1965. Segregating generations (F_2 and B_1) were duplicated in two tests and triplicated in the other. Data were taken on yield of grain, plant height, days to flower, number of internodes per plant (plant height mutant populations only), and number of ears per plant (N6 reduced mutant populations only).

Blotched Mutant.

Individual plants in populations involving the blotched mutant were classified either as normal or as blotched. The results are presented in Table 6. There can be no doubt about the inheritance of the blotched trait. It is controlled by a single locus and the normal allele is completely dominant to the blotched mutant allele. The data on yield of grain, plant height and days to flower are presented in Table 7. The population means differ in grain yield and in plant height, but no differences in days to flower were detectable.

The blotched mutant yielded strikingly less than the normal N25 line and was two inches taller. No difference in flowering time could be demonstrated. While at first glance the yield data suggest a maternal effect, there is not much statistical evidence to support such a hypothesis. A detailed analysis of the distributions of plant heights given in Table 8, causes one to question whether real differences exist for this trait. Some extreme observations in the normal line are surprising and account

Table 6. Frequency distribution of blotched and normal plants in normal N25, a blotched mutant, and the F_1 , F_2 , and backcross generations and goodness of fit Chi-square tests applied to F_2 and backcross generations assuming inheritance is controlled by a single locus with the normal allele completely dominant. Lincoln, Nebraska, 1965.

Phenotype	No. of plants observed (O)					No. expected (E)		Contribution to chi-square (O - E) ² /E	
	P ₁	P ₂	F ₁	F ₂	B _{1.2}	F ₂	B _{1.2}	F ₂	B _{1.2}
Normal	75	1	145	233	80	228	77.5	.11	.08
Blotched	0	75	0	71	75	76	77.5	.33	.08
						Chi-square		.44	.16
						Probability of a larger Chi-square		.50	.70

Table 7. Mean grain yield, plant height and days to flower observed for normal N25, a blotched mutant and populations developed from them. Lincoln, Nebraska, 1965.

Population	Grain yield (gms./plant)	Plant ht. (inches)	Days to flower
P ₁	101.0	71.2	42.6
P ₂	82.1	73.3	43.2
F ₁ .12	109.4	71.8	42.8
F ₁ .21	107.8	72.1	42.6
F ₂ .12	93.6	71.4	43.0
F ₂ .21	93.1	70.7	42.9
B ₁ .122	90.3	72.2	42.9
Standard error of a mean			
Parents and F ₁	4.45	0.53	0.19
F ₂ and backcross	3.15	0.38	0.14

Table 8. Frequency distributions of plant heights (inches) in three sets of populations involving three different induced mutant phenotypes.. Lincoln, Nebraska, 1965.

for much of the lower mean height.

Since the necrotic lesions on the leaves reduce the photosynthetic area and provide an entry for disease organisms, some yield reduction should be expected in the blotched mutant line. However, the heterosis exhibited for yield of grain in the F_1 hybrid (18.6% relative to the mid-parent and 7.5 relative to the high (normal) parent) is indeed surprising. Is it possible that such a deleterious recessive gene could contribute something to the heterozygote to cause it to be superior to the normal N25 line? Or is it more likely that mutations have taken place at other loci affecting yield and that the heterosis observed is a result of gene effects and possibly interactions of several loci? To get a better understanding of the inheritance of grain yield in the cross, the model proposed by Hayman (1958) for the analysis of generation means and modified to fit this particular set of data was used to estimate cumulative additive effects, cumulative dominance effects, and cumulative epistasis effects. The estimates of the parameters are possible only by assuming dominance x dominance epistasis to be zero, because the first backcross to the normal parent is lacking. The parameters estimated are given in Table 9 for grain yield, plant height, and days to flower. The analyses of variance are reported in Table 10. The amount of total variance in each trait attributable to additive gene action, dominance and epistasis is indicated in Table 11.

In the case of grain yield, most of the variance is attributable

Table 9. Unweighted least squares estimates of the mean (m), cumulative additive effects (a), cumulative dominance effects (d), cumulative additive x additive epistasis effects (aa) and cumulative additive x dominance epistatic effects (ad) and their standard errors estimated from population means in three sets of populations involving three different induced mutants.^{1/}

Population and trait	Estimates of parameters indicated				
	m	a	d	aa	ad
N25 blotched					
Plant Height (m.)	71.056±0.243	-1.166±0.748	1.892±0.686	2.168±0.594	-0.141±0.786
Grain Weight (gms.)	93.336±0.646	12.904±1.991	30.278±1.827	13.833±1.582	3.321±2.093
Days to flower	42.921±0.065	-0.107±0.200	-0.512±0.183	-0.285±0.159	0.185±0.210
N25 reduced					
Plant Height (m.)	67.072±0.419	9.954±1.005	3.151±1.451	-1.819±1.108	1.654±1.088
# Internodes	11.999±0.116	0.134±0.279	-0.064±0.403	-0.459±0.307	-0.205±0.302
Grain Weight (gms.)	101.612±0.958	12.429±2.297	9.159±3.319	-1.079±2.535	-4.439±2.489
Days to flower	42.593±0.110	0.048±0.264	0.220±0.381	0.235±0.291	-0.256±0.286
N6 reduced					
Plant Height (m.)	62.498±1.043	11.888±3.256	6.240±3.612	-2.760±2.759	1.203±3.419
# Internodes	13.610±0.000	0.068±0.000	-0.457±0.000	-0.065±0.000	0.005±0.000
Grain Weight (gms.)	85.402±2.305	31.479±7.198	10.784±7.985	-23.482±6.099	-15.249±7.558
# Ears	1.112±0.007	-0.099±0.022	0.012±0.024	0.474±0.019	0.343±0.023

^{1/} Since the backcross to the normal parent was not evaluated, all the parameters defined by Hayman (1958) could not be estimated. Dominance x dominance epistasis was assumed to be lacking.

Table 10. Unweighted analyses of variance of population means in three sets of populations developed from 3 different induced mutants. Lincoln, Nebraska, 1965.

Population	Source of Variation	D.F.	Mean Squares			
			Yield of Grain	Plant Height	Days to flower	# Internodes
N25 blotched						
	Additive (a)	1	2271.1309**	22.3061**	1.7192*	
	Dominance (d)	1	2704.3802**	.7618	.5153	
	aa	1	678.1111	15.7237*	.2421	
	ad	1	21.0136	.0379	.0655	
	Residual ^{1/}	2	8.3454	1.1777	.0841	
	Error	72	198.2618	2.8598	.37611	
N25 reduced						
	Additive (a)	1	7123.297**	1982.7997**	2.0436**	2.36983**
	Dominance (d)	1	992.516*	222.2762**	.0071	1.98036**
	aa	1	6.836	9.9197	.1616	.77676**
	ad	1	70.070	9.7326	.2326	.14976
	Residual	2	22.032	4.2119	.2906	.32418
	Error	99	150.755	5.189	.23569	.087039
N6 reduced						
	Additive (a)	1	26145.6498**	1489.3741**	No. of ears 2.0774**	.06552
	Dominance (d)	1	6300.1887**	370.4348**	1.2850**	.62196
	aa	1	1006.5742*	12.5810	.4137**	.00696
	ad	1	259.5728	1.6162	.1311	.00000
	Residual	1	63.7623	13.0459	.0006	.00000
	Error	55	233.84261	14.77713	.03562	.21340

* Significant at .05 level of probability.

** Significant at .01 level of probability.

All values not marked by asterisks are considered non-significant.

^{1/} The residual source of variation arose from differences between reciprocal F₁'s and F₂'s.

Table 11. Percentage of total variation among population means attributable to additive gene effects (a), dominance effects (d), additive x additive effects (aa), additive x dominance effects (ad), and deviations from the model in three sets of data involving induced mutants. Lincoln, Nebraska, 1965.

Population	Source of variation	% of variation explained for trait indicated			
		Yield of grain	Plant ht.	Days to flower	
N25 blotched	a	39.9	54.2	63.5	
	d	47.5	1.8	19.0	
	aa	11.9	38.2	8.9	
	ad	.4	0.1	2.4	
	Deviations	.3	5.7	6.2	
N25 reduced					No. of internodes
	a	86.5	88.8	67.5	40.0
	d	12.0	10.0	.2	33.4
	aa	0.1	.4	5.3	13.1
	ad	0.9	.4	7.7	2.5
	Deviations	0.5	.4	19.2	10.9
N6 reduced					No. of ears
	a	77.4	78.9	53.1	9.4
	d	18.6	19.6	32.9	89.6
	aa	3.0	.7	10.6	1.0
	ad	0.8	.1	3.4	0.0
	Deviations	0.2	.7	0.0	0.0

to additive gene effects and dominance. There is some evidence of additive x additive epistasis, though statistically non-significant, suggesting that more than the blotched locus may be involved in determining yield. An examination of the frequency distributions (Table 12) suggests the possibility of bimodal curves for the F_2 and $B_{1.2}$ populations. Perhaps the blotched locus has the major effect but modifying factors may exist at other loci. If the blotched locus plus environmental effects are responsible for the results observed, then one would have to assume overdominance to account for the heterosis noted in the reciprocal F_1 crosses. Further investigation is needed to determine the genetic mechanism involved in the effect of the blotched locus on yield.

Days to flower is primarily additive but some dominance (non-significant statistically) is indicated. Plant height results indicate additive gene action with additive x additive epistasis, again suggesting that at least 2 loci may have mutated, but further investigation is needed.

N25 Reduced Mutant.

The frequency distribution of plant heights measured in the 5 kinds of populations are presented in Table 8. Apparently one major gene determines plant height in this set of data; however environmental variations and possibly modifying factors tend to cause overlapping of the distributions.

Mean values of the various traits measured and associated standard errors are presented in Table 13. The reduced mutant is 23.1% shorter than the normal parent, has slightly more internodes, yields 29.3% less, and

Table 12. Frequency distributions of grain yields (gms./plant) in the various sets of populations involving three different mutants. Lincoln, Nebraska, 1965.

Class Mid- points	N25 Blotched					N25 Reduced					N6 Reduced				
	P ₁	P ₂	F ₁	F ₂	B _{1.2}	P ₁	P ₂	F ₁	F ₂	B _{1.2}	P ₁	P ₂	F ₁	F ₂	B _{1.2}
0 ^{1/}	2		2	18	7	1	2	4	7	2		17		25	21
5	2	2	3	5	1	0	1	0	0	1		10		14	14
10	1	0	0	2	1	0	1	0	0	0		9		1	8
15	0	1	0	0	2	1	0	0	0	0	2	1	1	4	3
20	1	1	2	1	0	1	1	0	0	0	0	3	0	1	0
25	1	0	0	3	2	0	1	0	0	1	0	0	0	1	2
30	2	1	0	0	1	0	1	1	1	1	0	2	0	3	0
35	0	0	2	5	5	0	0	0	1	2	0	0	1	0	3
40	0	2	0	5	4	0	0	0	0	1	1	1	0	1	1
45	0	1	0	8	3	0	1	0	2	3	0	1	0	2	2
50	1	1	1	6	6	1	4	1	2	1	2	0	2	2	0
55	0	1	2	8	7	0	4	4	9	1	0	0	2	7	0
60	0	5	0	4	3	1	2	2	8	2	0	1	0	2	0
65	0	8	2	8	3	1	4	5	8	8	3		1	5	2
70	2	6	6	5	7	0	3	1	11	8	2		0	7	0
75	2	7	1	8	4	3	7	4	14	11	2		4	8	5
80	0	3	4	12	11	2	6	3	16	4	0		1	12	3
85	3	5	6	11	5	6	8	9	22	15	2		3	11	4
90	3	6	9	12	7	1	8	7	17	14	0		1	11	3
95	6	6	3	13	4	7	8	12	17	12	1		2	13	1
100	3	2	5	17	6	5	5	13	26	9	2		3	11	3
105	6	2	6	14	6	5	6	12	27	9	1		1	20	7
110	7	2	12	23	4	3	2	15	20	12	1		4	19	6
115	5	2	9	23	5	6	4	23	24	7	4		1	12	10
120	5	3	10	16	4	7	2	18	34	7	2		2	21	10
125	1	0	11	10	13	5	1	13	23	9	6		1	21	3
130	6	3	11	21	5	5		8	21	9	4		2	12	4
135	4	4	15	14	4	7		13	12	9	1		1	13	3
140	3	1	9	13	8	6		6	8	2	4		1	5	1
145	3	0	8	6	6	10		5	5	1	2			2	1
150	6	1	0	8	5	4		2	4	1	1			1	1
155			2	3	3	2		1	6	1					
160			2	1	0				1	1					
165			2	1	1				0						
170					2				0						
175									0						
180									1						

^{1/} Midpoint 0 is from only 0 to 2.5 grams.

Table 13. Mean plant height, number of internodes, yield of grain and days to flower observed for normal N25, a reduced mutant and populations developed from them. Lincoln, Nebraska, 1965.

Population	Plant ht. (inches)	No. of internodes	Yield of grain (gms./plant)	Days to flower
P ₁	72.0	11.9	112.8	43.0
P ₂	55.4	11.2	79.7	42.4
F ₁ ·12	69.0	12.0	110.8	42.8
F ₁ ·21	68.2	11.9	102.2	42.7
F ₂ ·12	67.3	11.9	101.7	42.6
F ₂ ·21	66.8	12.1	101.9	42.6
B ₁ ·122	62.5	12.0	97.5	42.8
B ₁ ·212	61.1	11.7	93.8	42.5
Standard error of mean				
All except F ₂	0.66	0.085	3.54	0.14
F ₂ populations	0.46	0.060	2.51	0.10

flowers slightly earlier. There is some slight indication of a maternal effect in the data for the F_1 , F_2 and $B_{1.2}$ populations. Heterosis in percent of the mid-parent was observed for plant height (7.7%), yield (10.6%) and number of internodes (3.5%) indicating dominance or epistasis or both to be operating in the inheritance of those traits. An examination of the set of means suggests that a single gene pair with partial dominance could explain the results observed for plant height. In the case of yield, at least 2 or 3 loci appear to be operating. Frequency distributions of grain yields are presented in Table 12.

Least squares estimates of genetic parameters according to Hayman (1958) as modified because of the missing $B_{1.121}$ and $B_{1.211}$ populations are given in Table 9. The analyses of variance are given in Table 10 and the percent of the total variance among population means explained by each source of variation is given in Table 11. Plant height and grain yield variation is explained largely by additive effects with some dominance and days to flower is explained by additive effects. The number of internodes data suggest both dominance and additive x additive epistasis operating.

N6 Reduced Mutant.

The frequency distribution of plant heights measured in the five kinds of populations involving the N6 reduced mutant are presented in Table 8. Similar frequency distributions for grain yield are given in Table 12. Means of the various traits measured are given in Table 14.

Table 14. Mean plant height, number of internodes, yield of grain and number of ears observed for normal N6, a reduced mutant, and populations developed from them.

Population	Plant ht. (inches)	No. of internodes	Yield of grain (gms./plant)	No. of ears
P ₁	67.6	13.8	102.8	1.2
P ₂	46.0	13.7	9.6	2.0
F ₁₋₁₂	65.3	13.3	90.0	1.1
F ₂₋₁₂	61.6	13.6	83.3	1.1
F ₂₋₂₁	63.5	13.6	87.5	1.1
B ₁₋₁₂₂	56.0	13.5	64.1	1.3
Standard error of mean				
P ₁ , P ₂ , and F ₁	1.57	0.19	6.24	.08
F ₂₋₁₂ , F ₂₋₂₁ and B ₁₋₁₂₂	.91	0.11	3.60	.04

The N6 reduced mutant type was over 20 inches shorter and yielded less than 10% of the normal N6 yield. Because of its low yield, multiple shoots with relatively few kernels each tended to develop, so number of ears per plant is higher in the mutant type. Some type of partial female sterility appears to have been involved.

Plant height appears to be controlled by a single locus with the normal type completely dominant over the recessive mutant type. The same locus controlling height is probably responsible for grain yield differences noted too.

Genetic parameters estimated using a modification of Hayman's (1958) model are presented in Table 9, analyses of variance are given in Table 10, and the percent of the total variation among population means attributable to the different parameters is given in Table 11. Additive gene effects with dominance explain most of the variance among population means.

CHEMICAL MUTAGENIC STUDIES IN CORN

In 1965 pollen of plants of a long-time inbred line N6 were exposed varying lengths of time to vapor from ethyl methane sulfonate (EMS) to induce mutations in grain yield and other quantitative traits. The same line has already been used in extensive studies involving the use of ultraviolet light and thermal neutron irradiation of pollen and seeds, respectively.

Pollen from plants designated as males was collected and half was

treated with EMS vapors and half was not treated. Treated pollen was used to fertilize one female plant of the same line and untreated pollen was used to fertilize another, the control. M_1 and C_1 plants were grown in the Florida nursery and were self-fertilized to produce the M_2 and C_2 generations, which were grown in the field and evaluated in 1966. Analysis of the data has not been completed.

Seeds of N6 were also treated with EMS or a combination of EMS and thermal neutrons and were planted in the greenhouse in late 1965. Plants produced were self-fertilized. Selfed progenies were evaluated in the field in 1966 along with the pollen-treated lines.

In 1966 treatment of pro-embryos in the single-cell stage was done on N6 plants in the corn nursery, and good seed sets were obtained.

All sub-lines developed from the various EMS treatments were advanced a generation by self-fertilization in the nursery in 1966.

The chemical mutagenic work is being supervised by Dr. N. K. Chatterjee, who will use this phase of the program as part of his Ph.D. thesis (His original Ph.D. was obtained in India and he wishes to have a Ph.D. from an American university).

SOME OBSERVATIONS ON QUANTITATIVE TRAITS OF ARABIDOPSIS THALIANA GROWN IN THREE DIFFERENT ENVIRONMENTS

The use of field crops for radiation quantitative genetic investigations has not been entirely satisfactory because of the time required per generation, the magnitude of experiments needed to arrive at sound

conclusions, the expense involved in such experiments, and our inability to control the environment. Although we recognize that many types of experiments must involve field crops to reach satisfactory answers, we still feel that a small laboratory plant with a short life cycle and one that can be grown in a controlled environment might be used to answer basic questions in radiation quantitative genetics. Arabidopsis thaliana (L.) Heynth. of the Cruciferae family is one such plant that might prove useful.

Preliminary studies were initiated to study genetic variation in some measurable traits in a single Arabidopsis line under 3 different environments. Environment 1 was a growth chamber where day temperatures were 75 to 80° F., night temperatures were 65 to 70° F., and a light program of 750 foot candles from 9:00 a.m. to 4:00 p.m. was maintained. Environment 2 was also a growth chamber where temperature was maintained at 60 to 70° F. at all times, and the light program was 980 foot candles from 7:00 a.m. to 5:00 p.m. Environment 3 was the greenhouse where temperatures ranged from 85 to 95° F. during a 24 hour period and light intensity was governed by normal Nebraska weather conditions during the period from late December to the end of February. Since we had no growth chambers of our own, we had to use space wherever it was available, and we had no control over the light and temperature regime used. The environments used were not the best for Arabidopsis, but we believed that they were suitable for such preliminary investigations.

Seeds from a single plant of Arabidopsis were obtained from

Dr. G. P. Redei of the University of Missouri. Five plants were chosen at random from a small sample of plants grown from the seed supplied by Dr. Redei. Seeds harvested from each plant were planted and one random plant of each line was grown to maturity. Seed harvested in this generation was used to initiate the experiment involving the 5 lines. The original seed received was assumed to be a pure line and genetic variation should not have been expected.

A plot consisted of a 5.5" x 4" plastic flat containing a mixture of 2 parts of autoclaved soil, 1 part fine sand, and 1 part peat moss. Depth of the growth medium was about 2". Six plants of a line were grown in a plot. Five replications of each line in a 5 x 5 Latin square design were grown in each environment. A double rate of planting was used and if both seeds grew, one plant chosen at random was removed so that each plot always had 6 plants uniformly spaced. Data were taken on 30 plants of each line in each environment.

Traits measured were days to flower, plant diameter (cm.) at flowering time, number of fruits and seed weight (gms.). Means of each line in each environment and overall means are given for each trait in Table 15. Plant-to-plant variances within plots for each line in each environment and pooled plant-to-plant variances for lines and for environments are given in Table 16. Experiment means, the component of variance due to genetic differences among lines within an environment, the plot component of variance and the within plot component of variance are shown for each trait in each environment in Table 17. The

Table 15. Mean values of four quantitative traits measured on each of five lines in each of three environments and the combined means of the five lines averaged over the three environments. Lincoln, Nebraska, 1966.

Trait	Line	Environment			Combined mean
		1	2	3	
Days to flower	1	55.3	68.3	58.7	60.8
	2	51.1	69.8	57.5	59.5
	3	51.1	71.6	60.2	60.9
	4	52.5	67.2	62.4	60.7
	5	53.9	65.7	57.7	59.1
	Mean	52.8	68.5	59.3	60.2
Plant Diameter (Cms)	1	4.0	6.9	9.2	6.7
	2	4.3	6.3	10.2	6.9
	3	5.4	5.5	10.3	7.1
	4	5.5	7.1	9.3	7.3
	5	6.5	6.7	9.5	7.6
	Mean	5.1	6.5	9.7	7.1
No. of fruits	1	67.7	230.0	242.3	180.0
	2	61.5	196.6	266.8	175.0
	3	77.3	144.2	264.5	162.0
	4	89.0	229.0	178.6	165.5
	5	100.7	192.7	218.2	170.5
	Mean	79.2	198.5	234.1	170.6
Seed weight (gms)	1	0.026	0.129	0.063	0.072
	2	0.025	0.103	0.060	0.062
	3	0.029	0.077	0.066	0.058
	4	0.041	0.121	0.055	0.072
	5	0.038	0.096	0.050	0.061
	Mean	0.032	0.105	0.059	0.065

Table 16. Variation among plants within plots of five *Arabidopsis* lines measured in three environments and pooled over the three environments. Lincoln, Nebraska, 1966.

Trait	Line	Environment			Pooled variance
		1	2	3	
Days to flower	1	28.7934	12.6600	9.0268	16.8267
	2	23.4334	26.8663	18.9601	23.0866
	3	14.6534	16.9201	9.4267	13.6673
	4	16.5601	39.6934	26.9201	27.7245
	5	29.3134	28.3168	150.1734	69.2679
	Pooled	22.5507	24.8913	42.9014	30.1145
Plant diameter (cm.)	1	.8625	1.6398	2.6756	1.7260
	2	1.0889	.7906	1.7454	1.2083
	3	1.3007	1.6071	5.1642	2.6907
	4	1.0487	1.2659	2.4986	1.6044
	5	1.2734	.5738	1.7930	1.2134
	Pooled	1.1148	1.1754	2.7754	1.6885
No. of fruits	1	1935.0533	5112.0672	14885.7744	7310.9649
	2	730.7334	2788.6989	8573.7130	4031.0484
	3	805.0334	3996.0741	10683.2408	5161.4494
	4	929.3802	10709.5341	7310.8744	6316.5962
	5	1246.3869	3690.6607	3459.7272	2798.9249
	Pooled	1129.3174	5259.4070	8982.6660	5123.7968
Seed wt. (gm.)	1	.0003	.0018	.0010	.0010
	2	.0001	.0012	.0004	.0006
	3	.0002	.0008	.0009	.0006
	4	.0002	.0040	.0007	.0016
	5	.0002	.0017	.0003	.0007
	Pooled	.0002	.0019	.0007	.0009

Table 17. Experiment means ($\bar{X}$), genetic component of variance ($\sigma_{g,1}^2$)^{1/}, error component of variance (σ^2) and within plot component of variance (σ_w^2) for four traits measured on five lines of Arabidopsis grown in three environments.

Trait	Component	Environment		
		1	2	3
Days to flower	$\bar{X}$	52.7666	68.5200	59.3333
	$\sigma_{g,1}^2$	1.1533	3.8031*	1.3533
	σ_e^2	7.2997**	-4.8876	6.9942*
	σ_w^2	22.5507	67.5250	42.9013
Plant diameter	$\bar{X}$	5.1470	6.5033	9.7203
	$\sigma_{g,1}^2$	0.1541	0.3198*	-0.4496
	σ_e^2	4.1618**	0.3210	3.2134
	σ_w^2	1.1149	1.2084	2.7754
No. of fruits	$\bar{X}$	79.2266	198.4666	234.1133
	$\sigma_{g,1}^2$	-274.6776	978.7402*	306.2219
	σ_e^2	2447.8808**	324.6015	3713.9670**
	σ_w^2	1129.3180	5460.1350	8982.6640
Seed weight	$\bar{X}$	0.0319	0.1053	0.0591
	$\sigma_{g,1}^2$	-0.0000	0.0003*	-0.0000
	σ_e^2	0.0004**	0.0002	0.0001**
	σ_w^2	0.0003	0.0020	0.0001

* Significantly different from 0 at the .05 level of probability.

** Significantly different from 0 at the .01 level of probability.

^{1/} The genetic component is completely confounded with the genotype x environment interaction component, i.e.

$$\sigma_{g,1}^2 = \sigma_g^2 + \sigma_{ge}^2 \quad (\text{See Table 19})$$

pertinent portions of the combined analyses of variance are given in Table 18. The overall mean, the component of variance due to genetic differences among lines, the genotype x environment interaction component, the pooled error component and the pooled within plots components are given for each trait in Table 19.

An increase in temperature caused increased vegetative growth as indicated by greater plant diameter at fruiting time and by an increased number of fruits. However, at the higher temperature fruits were frequently empty or contained only rudimentary seeds. The lowest temperature with the longest light period (Environment 2) gave the greatest seed production. No significant difference could be detected among lines averaged over environments but a significant line x environment interaction was indicated for all traits except plant diameter. The lines reacted differently relative to one another in the different environments. This suggests genetic differences among the lines which would not be possible if Arabidopsis was strictly a self-pollinating species. More research is needed to evaluate so-called pure lines of Arabidopsis and to determine the frequency of out-crossing if it occurs. Special care may have to be taken to avoid out-crossing in irradiated or chemically treated populations. This work has been supervised by Dr. N. K. Chatterjee.

Table 18. Pertinent portions of the analyses of variance of four traits measured on plants of five lines of *Arabidopsis* grown under three environmental conditions. Lincoln, Nebraska, 1966.

Source of variation	Degrees of freedom	Mean squares			
		Days to flower	Plant diameter	No. of fruits	Seed weight
Lines	4	64.3473	9.6683	4659.90000	.04392
Lines x environments	8	157.1813*	21.1676	40069.4250*	.057196**
Error	36	63.1385	17.0920**	18163.6047**	.002421*
Plants in plots	375	30.1145	1.6996	5123.7968	.0009

* Significantly different from 0 at the 0.05 level of probability.

** Significantly different from 0 at the 0.01 level of probability.

Table 19. Overall mean ($\bar{X}$), genetic component of variance (σ_g^2), genotype x environment interaction component of variance (σ_{ge}^2), pooled error component of variance (σ_e^2) and pooled within plot component of variance for four traits measured on five lines of Arabidopsis grown in three environments. Lincoln, Nebraska, 1966.

Trait	$\bar{X}$	σ_g^2	σ_{ge}^2	σ_e^2	σ_w^2
Days to flower	60.2066± 1.3215	- 1.0315	3.1347*	3.1354	30.1145
Plant diameter	7.1235± 0.4850	- 0.1277	0.1358	2.5654**	1.6996
No. of fruits	170.6018±21.1001	-393.4391	730.1940*	2162.1498**	5123.7968
Seed weight	0.0654± 0.0080	- 0.0002	0.0018**	0.0002*	.0009

* Significantly different from 0 at the 0.05 level of probability.

** Significantly different from 0 at the 0.01 level of probability.

MUTAGENIC STUDIES IN ARABIDOPSIS THALIANA

Arabidopsis seeds have been exposed to X-rays, thermal neutrons, and ethyl Methane sulfonate (EMS) and have been observed and measured in a number of pilot studies. Attempts have been made to establish the dose rate at which half the seeds fail to grow (LD50), so that comparable doses of the three mutagens could be used in studies designed to evaluate their effectiveness in causing favorable mutations for quantitative traits against which selection might be effective. The LD50 has been reasonably well established for X-rays and EMS but additional data are needed on thermal neutron irradiation. Dr. N. K. Chatterjee has supervised this research.

LITERATURE CITED

- Hayman, B. I. 1958. The separation of epistatic from additive and dominance variation in generation means. *Heredity* 12:371-390.