THE EFFECTS OF IRRADIATION BY X-RAYS UPON THE QUANTITATIVE CHARACTERS OF AN INBRED STRAIN OF MAIZE

by

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INTRODUCTION

Considerable activity in genetic research in the last few years has been directed to the study of the effects of x-rays and other forms of radiant energy upon germ plasm. The occurrence of natural mutations has always emphasized the question of their cause. The discovery that x-rays do affect germ plasm has given at least a partial answer to that question of many years standing.

Following the initial discoveries of x-ray effects upon germ plasm by Muller (1927) on Drosophila and by Stadler (1928a) on barley, the latter being made independently and at nearly the same time as the former, a number of geneticists have studied the effects of x-rays on germ plasm in other organisms.

Muller and his co-workers (1927,1928,1929,1930) probably have made the most extensive study of x-ray effects on Drosophila of any group of investigators. These investigations include among other features cytologic and genetic studies of gene mutations, chromosomal abberrations, crossovers and linkage relations, and rate of change of hereditary factors.

Stadler has studied x-ray effects in barley, wheat, oats, and maize, and his investigations have included the effects of x-rays on linkage relations, crossovers, factor mutations, chromosomal irregularities, and cytological observations of some of these irregularities.

Blakeslee and co-workers (1928) (1929) have made extensive studies of gene mutations and chromosomal aberrations on radium treated Datura.

Goodspeed (1929b) has studied variants in tobacco and cotton produced by x-rays.

Hanson and Heys (1929b) (1930) have studied the relations of natural radiations to gene mutations in Drosophila.

Navashin (1931) has studied cytological evidence of chromosomal irregularities produced by x-rays in Crepis.

A. R. and P. W. Whiting (1929) have made studies of x-ray produced mosaics, gynandromorphs and other irregular types in Habrobracon and have made comparisons of natural and x-ray mutant types.

A complete list of the names of investigators would include many more than are given here, and the list of organisms which have been subjected to x-ray treatments would include a few more if all were given. These that

have been named, however, are the chief ones.

One generalization that can be made from the work of these various investigators is that the effects of x-rays upon the germ plasm of one form of life seem to be similar to those upon the other forms studied. The effects range from a very minutely localized effect such as the change of a single factor to a more general and extensive effect such as destruction of parts of chromosomes. Another generalization is that the gene mutations produced are in general the same ones which occur naturally . A number of the induced mutations have been tested and proved allelomorphs of known factors and identical with natural mutations. Some induced mutations differ from any known natural mutation, possibly because those particular natural mutations so far have escaped observation.

The work on x-ray effects upon germ plasm thus far is probably just a beginning in this type of investigation. Opinions vary as to the value of induced mutations. It seems likely, however, that the chief contribution of irradiation will be in the advancement of knowledge in the fields of genetics and cytology, and that at least for the present little practical or economic

use of induced mutations may be expected.

The studies have been limited to such phases as already have been named while very little work, if any, seems to have been done on the effects of x-rays on quantitative characters. Although quantitative characters have been studied in many organisms in the past, no one has studied effects of x-rays upon such characters.

OBJECT AND PLAN

The object of the experiment was to try to determine the effects produced on quantitative characters in maize by changes in the hereditary mechanism produced by x-ray irradiation of the reproductive and embryonic cells of a previous generation.

The plan of the experiment, stated briefly, was to irradiate with x-rays the reproductive cells and the resulting embryonic cells of an inbred strain of maize in one generation and then determine the effects of the treatment in following generations by observation and by comparing the measurements of quantitative characters of the treated lines with corresponding measurements of untreated lines of the same strain.

INBREDS AND OUTBREDS

An inbred strain was chosen for the experiment, not because it may or may not be more readily affected by x-rays than open-pollinated plants, but because its uniformity makes more feasible the identification of mutations or the determination of their occurrence. In a treated open-pollinated variety it would be difficult if not impossible to determine which of the variations appearing in later generations were due to changes in the germ plasm and which were merely the result of combinations of particular factors already existing in the variety before treatment. Corn is normally a cross-pollinated plant. There is therefore the possibility of fortuitous unions of factors in an almost unlimited variety of combinations, with corresponding effects upon the characters of the plants. The basis for this variation in an open-pollinated variety lies in the fact that a large proportion of the numerous factor pairs of the hereditary mechanism of the plant are in a heterozygous condition.

It would be desirable to have a pure line for an experiment with the object and purpose of this one, but because of the length of time required to be reasonably

certain of the production of a pure line, if ever, it is not practicable as Jones (1924) points out. Because strains which have been inbred five or more generations are to a large extent homozygous and consequently quite uniform, and because it is possible to determine from check lines the amount of variation to expect in the treated lines due to factor combinations among the remaining heterozygous factor pairs, a uniform inbred strain serves the purpose very well and such was used in this experiment.

THE EFFECTS EXPECTED OF IRRADIATION

In a pure line if a change of quality is effected in either member of a factor pair so that this factor becomes unlike its normal homologue, this factor pair thereby becomes heterozygous. When some change has occurred in the quality of a factor a mutation is said to have taken place. Within a pure line, therefore, one of the effects of the production of a mutation is to make heterozygous a pair of formerly homozygous factors. Strictly speaking, a mutation is a change in a factor; the changed character of the organism which may result later is only the outward expression of mutation. There

is a very remote possibility of both homologues being changed simultaneously and in the same way thereby remaining homozygous, even though of different quality than formerly. Muller (1929b) states that such an occurrence has not yet been observed.

That changes in the quality of factors do occur has been recognized for many years. These changes are considered to be of two kinds, natural and artificial, although the underlying cause may be the same in both cases.

One of the agencies producing artificially induced mutations is irradiation by x-rays as explained by Muller (1927). By irradiating the tassels and ears of maize in this experiment, the expentancy was to make heterozygous some factor pairs within either the gametes, zygote or embryonic cells of the inbred strain of maize. Because both tassels and ears were treated in two of the plants, II., III., it might be possible that a factor mutation would appear in the first generation following treatment, but the chances of such an occurrence are extremely small. It would be necessary for the x-rays to affect corresponding points or factors in what would later be homologous chromosomes and it would also be necessary to affect them in the same way. Even when as

intensely treated as possible and still have the organism survive, usually only a few of the many factors are affected.

Since induced mutations in maize are practically always recessive, as reported by Stadler (1930a), no evidence of the effect of factor mutation normally is expected in the first generation following treatment because each such mutated factor would be overshadowed in effect by its normal dominant homologue. An affected plant, however, would have the mutated factor in all its cells, hence one-half the sperm cells and half the egg cells produced by such a plant would be expected to contain the mutated factor. If the first generation plants are self-fertilized some of the mutated factors will be paired in fertilization, and because in that case there is then no normal homologue present in the cell, the recessive character of the plant governed by the mutated gene will become evident. It is the second generation, therefore, which is of chief interest and is the one in which may be established proof of change of quality of factors as a result of irradiation.

There are effects to be expected of irradiation other than making homozygous factor pairs heterozygous, some of

which will be recognizable in the first generation. These as a group are known as chromosomal aberrations, and include translocations, deletions, duplications, inversions, etc. Some of these are lethal in effect on the organism, others modify the appearance and measurable characters, while most produce sterility, either alone, or in addition to some of the other effects. While many are lethal or sterile they are of interest in that they show some of the immediate effects of irradiation by x-rays.

There is the possibility that many of the changes produced in factors are of a kind which in turn produce such a slight effect on a character that they are never detected.

So far only those possible x-ray effects have been mentioned which might affect a sperm cell, egg cell or fertilized egg cell. These effects would normally be expected in all cells of the resulting plant.

Because some of the ears were irradiated as late as the eighth day after pollination, when the embryo already may have reached a stage of several cells, it is expected that types will be produced with only a part of their structure descended from a mutated cell or cells. It is readily possible that one or more but not all of the cells

of the several-celled stage had a mutation produced in them. Only tissue formed from the mutated cell or cells would be abnormal. Several different combinations are possible: individuals with normal tissue except for a part of the somatic tissue, and those with part of the somatic and part of the reproductive tissue abnormal. Those "spotted" individuals with recessive factor mutations only in the somatic tissue would not be recognizable in the first generation, and as somatic tissue does not go into a second generation, would never be known. Some of those in which somatic tissue had chromosomal aberrations would be recognizable in the first generation. If only a part of the somatic tissue were affected these individuals would be chimeras.

Even though not recognizable phenotypically, there probably are many "genotypic chimeras" due both to chromosomal aberration and factor mutation. Some of those due to aberration might be detected cytologically.

DETERMINATION OF THE OCCURRENCE OF MUTATIONS

For color mutations visual observation can be depended upon to detect very slight variations. Usually the members of an inbred line of corn have a very uniform

color and slight deviations from this can be seen readily. Small variations of quantitative characters cannot be detected so readily. One reason for the difficulty is the natural variability due to soil heterogenity and other environmental factors. Another is the inability to average up quantitative characters by sight, especially when large populations are involved.

The statistical mean, however, does provide a fairly effective method of comparing different groups for quantitative characters.

However, the average or mean is limited in usefulness for unless the variation due to mutation were considerably larger than variation due to environment, the two could not always be distinguished from each other by this device. It is easily possible that the progeny of a heterozygous plant (made so by mutation) might grow upon soil more fertile on the average than that occupied by the checks. If the mutation is a deleterious one as most seem to be, the smaller average of the affected plants may just balance or cancel the higher average of the unaffected plants with the result that the average for the whole progeny is nearer the average of the checks than some of the individual check lines. Similarly a

favorable mutation (though a rare occurrence) might cancel the effects of a poor environment. Thus a quantative mutation might not be detected by comparing averages.

More sensitive devices for detecting mutations are measures of variability. Untreated inbred strains would be expected to be very uniform and to have a small value for the measure of variability. This is, of course, affected by the variability of the environment in the same proportion as the environment affects the uniformity of the individuals of a row or plot. But regardless of the variability due to environment, variation due to heredity would also affect the measure of varability and it is not likely that variation due to environment will cancel or offset that due to heredity. For this reason measures of variability are more sensitive and more reliable devices for detecting families segregating for quantitative characters than the average, or other measures of central tendency. A percentage of variability in a treated line significantly higher than in any of the checks would be a good indication of inherited variation in addition to variation due to environment, and hence a good indication of a hereditary change or mutation. There is a possibility that a natural mutation may occur and an

assumption in this experiment that hereditary changes in the treated lines were all due to irradiation would be false. However, because of the small number of plants involved, it is not likely that a natural mutation would be found in the treated population of this experiment as natural mutations in maize, according to Stadler (1926), occur very infrequently. Because natural mutations could occur in the untreated controls as well as in the treated plants, they would be more likely to be found in the checks because the untreated population was considerably larger than the treated.

MATERIALS

Treated and untreated seed corn of an inbred strain of Doctor M. T. Jenkins, Lancaster pedigree No. 317-3-1-2-5-4, was furnished for the experiment by Doctor L. J. Stadler of the United States Department of Agriculture and the University of Missouri. A description of the treatment by Doctor Stadler is as follows:

> "This strain of corn had been inbred six generations previous to the season in which the treatments were made .....
>
> "The tassel treatments were made at a target distance of 12 inches, the ear treatments at a target distance of 10 inches.

"The x-ray tube was a Coolidge tube of the self-rectifying radiator type, commonly known as the 5-30 tube.....

"Treatments were applied at a voltage corresponding to approximately 4.6 inches spark gap and no filter was used. The wave length spectrum under these conditions covers a rather wide range but does not include the very hard x-rays ..... Measurements made..... with the same machine (but different tubes) indicate the output under the same conditions to be about 46 r per minute at the 10-inch distance."

Three plants, each of which received a different amount of irradiation, furnished the treated seed for the experiment.

The tassel of the plant receiving the mildest treatment was not irradiated. The ear was irradiated four minutes daily for four days beginning the day after pollination (selfing), then eight minutes daily for four days. This plant and its progeny are designated in this experiment as No. I.

The tassel of the plant receiving the medium amount of treatment was irradiated nine minutes daily for three days. The plant was selfed on the fifth day after the beginning of treatment. Beginning on the sixth day the ear was irradiated four minutes daily for four days, then eight minutes daily for four days. This plant and its progeny are designated as No. II.

The tassel of the plant receiving the most severe treatment was irradiated twelve minutes daily for three days. The plant was selfed on the fifth day. Beginning on the sixth day the ear was irradiated four minutes daily for four days, then eight minutes daily for four days. This plant and its progeny are designated as No. III.

The three plants which in this experiment are designated as IV, V, and VI were untreated inbred checks.

The three progenies designated in this experiment as VII, VIII, and IX were the result of sib crosses between untreated plants of the same inbred strain, the crosses being made the same season that I, II, and III were irradiated.

PROCEDURE

First Generation

The following were planted, one seed to a jar, in four-gallon jars of clay loam in the greenhouse at Kansas State College, December 3, 1931.

5 kernels each of the three treated lines
I - 1 to 5, II - 1 to 5, III - 1 to 5.

3 kernels each of the three untreated check selfs
IV - 1 to 3, V - 1 to 3, VI - 1 to 3.

2 kernels each of the three sib crosses
VII - 1 and 2, VIII - 1 and 2, IX - 1 and 2.

Later seven replants, 3 II's, 2 III's, and 2 IX's, were made by sprouting seeds in an incubator, then transferring them to the jars. Of this planting and replanting, seven treated and nine untreated plants grew to maturity. Of the most severe treatment (series III) only one plant, a dwarf, was obtained. It produced no seed. Of the medium treatment, No. II, three plants were obtained, one of which produced no seed. Of the mildest treatment, No. I, three plants were obtained, one of which produced no seed. The nine untreated plants all produced seed.

These 16 plants were measured for height once a week until mature. The measurement taken was that from the surface of the soil in the jar to the tip of the tallest outstretched leaf or to the tip of tassel when it was the taller. The plants were all selfed and the dates of first pollen shedding and first silk appearance recorded. When the plants were mature the roots, nodes, and number of rows of kernels per ear were counted and recorded. Table I shows weekly measurements of height of each of the first generation plants and Figure 1 shows the growth curves of the treated plants and the tallest, shortest and average of the untreated.

TABLE I. DATA FOR FIRST GENERATION PLANTS GROWN IN THE GREEN HOUSE.

Pedigree		No. of roots	No. of nodes	No. of rows of kernels per ear	No. of days from planting date to first pollen shedding	No. of days from planting date to silk appearance	Weekly measurements of height in inches										
							Dec.	Jan.				Feb.				Mar.		
							18	8	16	22	29	6	12	19	28	5	12	19
I-1	Irradiated	26	17	12	84	87	3.75	16.25	22.88	29.00	33.37	40.12	45.62	55.37	58.37	60.37	60.37	60.62
I-3	"	28	16	12	85	88	2.50	13.75	20.75	28.75	35.88	39.62	47.12	50.88	58.88	63.12	63.37	
I-5	"	28	16		85	91	3.25	13.75	20.62	27.75	32.12	37.75	42.12	46.37	56.62	65.12	65.07	
II-1	"	25	16		88	94	0.25	15.00	20.00	26.37	29.25	35.25	42.75	46.50	55.00	60.50	61.75	
II-2	"	25	15	12	90	96	Replant	4.00	6.00	10.00	14.00	18.50	27.37	35.00	44.00	49.25	55.50	64.75
II-4	"	28	17	14	91	94	2.25	11.50	17.50	24.00	29.75	34.62	42.00	46.75	55.75	65.75	69.50	
III-2	"	6	15				Replant	2.00	3.00	5.00	8.75	12.25	18.50	23.00	30.00	33.00	35.62	39.12
IV-1	Untreated selfed	27	16	12	85	88	4.25	14.50	22.37	30.00	37.50	43.75	50.25	54.75	66.75	73.25	73.25	
IV-3	"	25	16	12	82	86	4.00	17.25	25.00	32.62	39.50	47.25	52.75	55.75	65.75	67.25	67.25	67.50
V-1	"	28	16	14	83	88	2.00	14.00	21.75	30.00	36.50	45.62	51.75	55.88	63.12	67.88	68.12	
V-2	"	25	16	12	83	86	3.00	16.00	24.00	32.12	39.12	47.50	53.00	57.00	64.00	67.25		
VI-1	"	26	16	14	82	86	4.50	16.00	23.37	32.37	37.12	46.50	53.00	56.00	66.00	68.50	69.25	
VI-3	"	25	16	14	84	88	3.25	16.50	22.50	30.00	34.00	43.62	50.12	55.12	64.50	71.12	71.62	
VII-2	Untreated sib cross	25	15	12	82	86	3.25	16.00	23.25	31.12	38.00	45.50	50.50	54.75	64.00	66.50	67.00	
VIII-1	"	25	16	12	83	86	4.50	16.00	22.50	31.00	38.25	45.37	50.88	55.00	65.50	69.00		
VIII-2	"	25	16	12	82	86	4.12	17.00	22.75	30.75	38.50	45.50	50.00	52.62	60.62	63.12	63.62	

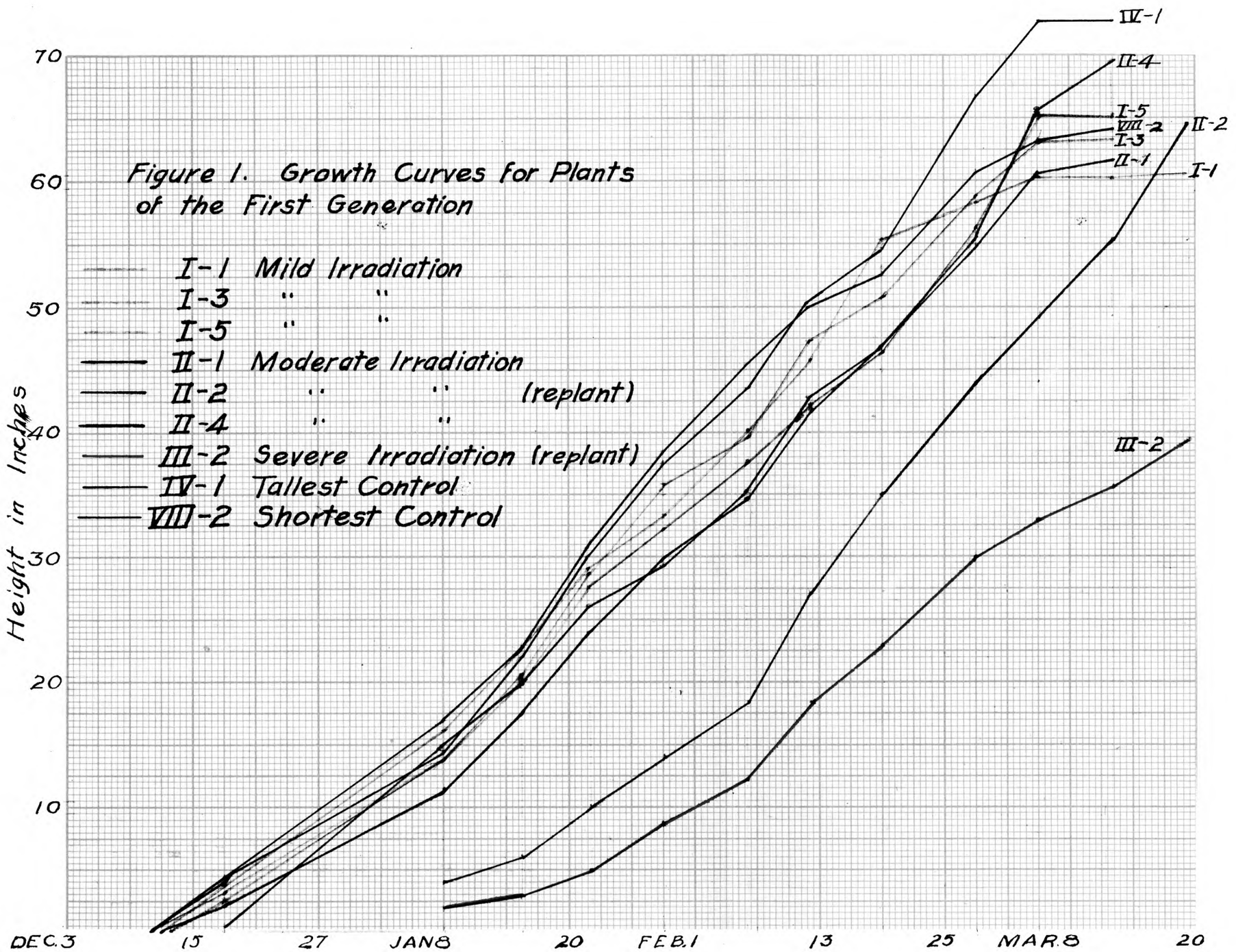


Figure 1. Growth Curves for Plants of the First Generation
I-1 Mild Irradiation
I-3 " "
I-5 " "
II-1 Moderate Irradiation
II-2 " " (replant)
II-4 " "
III-2 Severe Irradiation (replant)
IV-1 Tallest Control
VIII-2 Shortest Control
Height in Inches
70
60
50
40
30
20
10
DEC. 3
15
27
JAN 8
20
FEB. 1
13
25
MAR. 8
20
IV-1
II-4
I-5
VIII-2
I-3
II-1
I-1
II-2
III-2

Second Generation

The seed produced by the greenhouse crop (first generation) was planted on Kaw River bottomland near Fall Leaf, Kansas, May 23, 1932. The plants were spaced 20 to 24 inches apart in 42 inch rows. The arrangement of rows is shown on the map in Figure 2. The field in which the plat was laid out had been planted to corn about two weeks previously. The field corn was chopped out with a hoe and the experimental corn planted in the same listed furrows. Because the furrows were not of uniform depth, grade stakes were set in each to aid in determining the original level in the furrow after rains and cultivation started to fill the furrows. The border rows were at least 80 inches from any corn plants in the surrounding field. The plat was kept free from weeds and the furrows slowly filled by cultivation.

The plants were measured for height once a week until mature. Height was measured from the original level in the bottom of the furrow to the end of the tallest outstretched leaf or tassel when the latter was the taller. The fifth and tenth leaves were marked by cutting off the end of the leaf to aid in counting the number of

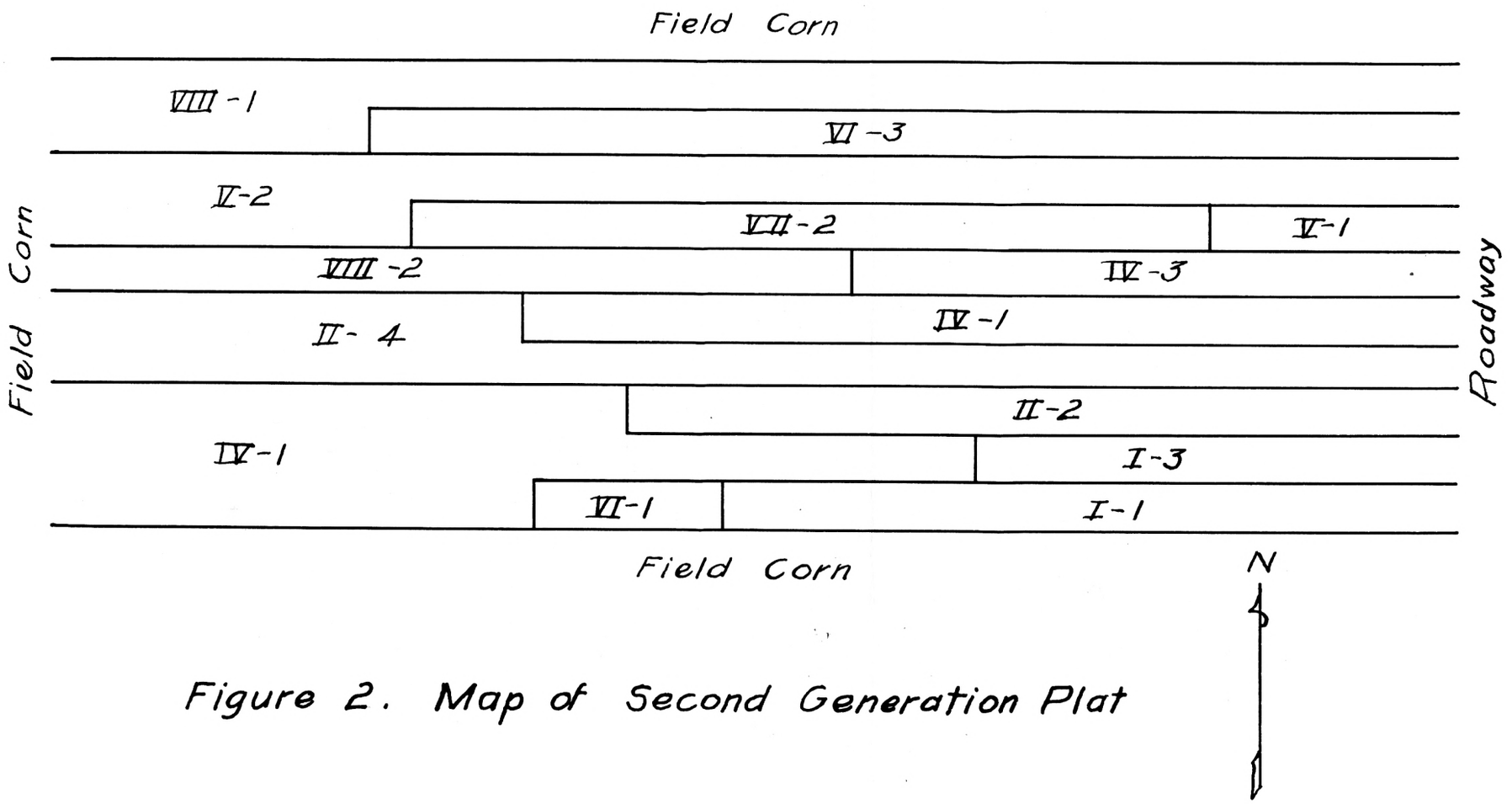


Figure 2. Map of Second Generation Plat

nodes of the plant. This later proved ineffective as the leaves were torn by the wind so much that the marked leaves could not be recognized with certainty. The dates of first pollen shedding and first silk appearance were marked on tags which were attached to the plants and later the readings were recorded from these tags. When the plants were mature the numbers of rows of kernels per ear were recorded for each plant, the upper and lower ear readings being kept separate. The plants were then dug up with a spade and roots stripped off close to the stem with a knife, the dirt jarred out of the root stubs, and the root stubs and nodes counted and recorded.

The frequency distributions of the various characters measured for the different lines are shown in Tables III to X.

Calculations

From the recorded data the following constants were calculated for each line:

Average height for June 11, July 7, and the maximum height attained.

Average number of roots.

Average number of nodes.

Average number of rows of kernels per ear (upper ears).

Average number of days from planting date to the date of first pollen shedding.

Average number of days from planting date to the date of first silk appearance.

Average number of days of lag between first pollen shedding and first silk appearance.

Average number more of rows of kernels on the upper than on the lower ear.

The probable error for each of the above averages except for height on June 11 and on July 7.

The standard deviation for all the characters except height on June 11 and July 7.

The probable error of all the standard deviations.

The above constants are shown in Tables III to X.

The readings of all plants were included in the computations except those for plants which proved to be suckers, as shown by post mortem examination, and those for plants which were known to have been injured by wind, insects, etc., previous to the measurement in question. For instance, the readings of height for plant (II-4) 45 were used in determining the average height for all weekly averages up to and including July 1, but not for July 7 because it had been broken over by the wind shortly after July 1.

The lag in days between first pollen shedding and first silk appearance was determined separately for each plant, then these individual lags added together to determine the average lag for the line. Similarly the excess of rows of kernels on the upper ear of a pair was determined separately for each plant, then these differences were treated as a frequency distribution.

All the biometrical constants were calculated according to formulas given in "Statistics in Psychology and Education" by Henry E. Garrett, except probable errors of coefficients of variation which were calculated from formulas in"Breeding Crop Plants" by Hayes and Garber.

In addition to the sixteen lines, two other groups were carried through the same computations and are added at the end of the tables for the different constants calculated. These two groups are IV-1a, the group containing the first 20 plants (1-20) of the IV-1 line, and IV-1b, 20 plants (116-140 minus skips) also of the IV-1 line. The plants of both groups are included in the calculation of the IV-1 totals. The "a" group was located at the east end of the fifth row from the south (Fig. 2) and the "b" group at the west end of the second row from the south. As nearly as could be determined by casual

observation, one of these groups grew on the best soil, the other on the poorest in the area occupied by the whole IV-1 line, and incidentally also of the whole experimental plot. These were included to show the amount of variation in quantitative characters found within the same untreated line, due to soil, location, and other possible environmental effects.

In addition to the above calculations, the percentage of seedling deaths and the percentage of seeds of all those planted which did not germinate were calculated for each line. These percentages are shown in Table II.

OBSERVATIONS AND DEDUCTIONS

Comparisons in the First Generation

The growth curves of the first generation plants (Fig. 1) show that the treated plants averaged less in height than the checks.

Only one plant, III-2, was obtained from seven seeds planted from the line receiving the most severe treatment. It was a dwarf and produced no seed. It did not even produce a rudimentary ear although there were long silks on the tassel. Its root system appeared very much the same as the rootless plants described by Jenkins (1930).

TABLE II. PERCENTAGES OF SEEDLING DEATHS AND BLANKS.

Pedigree	Per cent of seedling deaths of the number of seeds which germinated	Per cent of seedling deaths of the number of seeds planted	Per cent of seeds planted which did not germinate	Per cent of seedling deaths plus per cent of seeds which did not germinate of all the seeds planted
I-1	17.2	11.6	32.6	44.2
I-3	8.7	5.9	32.3	38.2
II-2	4.6	4.0	17.7	21.7
II-4	2.0	2.0	4.8	6.8
IV-1	4.4	3.8	14.5	18.3
IV-3	2.8	3.0	2.8	5.8
V-1	8.3	5.0	40.0	45.0
V-2	4.2	4.0	8.7	12.7
VI-1	0.0	0.0	18.0	18.0
VI-3	9.4	8.6	8.6	17.2
VII-2	5.2	4.0	27.0	31.0
VIII-1	8.3	8.0	3.0	11.0
VIII-2	12.8	11.1	13.3	24.4

The rest of the plants, both treated and untreated, had root systems quite uniformly of about 25 roots each while III-2 had six. III-2 was a replant but so also was II-2 which reached a height as great as some of the checks and produced seed. The fact that only one plant, a defective, was obtained from seven seeds indicates this line received an amount of treatment near the limit of tolerance and that probably many of the embryos were so badly injured that they were unable to germinate.

The average height of the plants of the medium treated line was somewhat below that of the average of the untreated. II-1 produced no pollen and consequently no seed. The tassel had a white or blighted appearance from the time it first appeared until it dried up, though it did not appear to be diseased.

All plants of the I line (mildest treatment) were also somewhat below the average of the checks in height, and were even shorter than the II group. I-5 had a white margin on the third leaf about one-fifth to one-fourth the width of the leaf and extending the length of the leaf. I-5 also produced few silks and these did not protrude from the husk. This plant produced no seed. The second leaf of I-4 formed an enclosed sheath around the later

leaves and the plant died as a seedling. To offset this character as evidence of x-ray effects, IV-2, a check, also had a coarse, thick second leaf and the plant died as a seedling.

While the indications are good that each line of the treated plants was affected by x-rays, the evidence is not conclusive with so few plants.

Since in the first generation plants no evidence of factor mutations is expected, chromosomal irregularities probably account for any abnormalities produced by x-rays. The sterility of three treated plants and the low viability of seeds and seedlings fit in well with this hypothesis.

The white margin on the third leaf of I-5 indicates x-ray effects on some cell of the embryo after several cell divisions had taken place since only a part of the plant was affected.

Comparisons in the Second Generation

Contrasted with the variety of characters displayed by treated plants in the first generation, the second generation was relatively free from such abnormalities. One of the seven treated plants in first generation had a

color mutation while in the second generation there was observed no color mutation of any kind in the 194 descendants of treated plants. There were a number of dwarf plants in the second generation as there was one in the first generation treated lines but the proportions of dwarf to normal sized plants in the treated lines was little different from that in the controls. There was no evidence of sterility in the treated second generation plants while two control plants produced no pollen so far as known. Viability of seeds and seedlings in the treated second generation was little different from that in the controls. The second generation plants were therefore distinctly free from variants such as appeared in first generation.

An examination of the data in Tables III to X and the graphic display of Figs. 3 to 10 shows considerable variation in the averages calculated for the various characters studied both in the checks and in the irradiated lines. Even greater differences exist among the standard deviations, both for the checks and for the treated lines. The size of these differences or spreads in the averages for the various characters in control lines indicates that a large amount of the variation is due to

environment, if it can be assumed that the inbred strain used in the experiment was largely homozygous and that the different lines are equally pure. This it seems can be assumed because within some of the check lines certain sections can be chosen which show noticeably greater uniformity than the whole line of which they are a part. The view that environmental differences are the chief cause of variation is strengthened by the fact that larger standard deviations are more often found in the controls than in the treated lines.

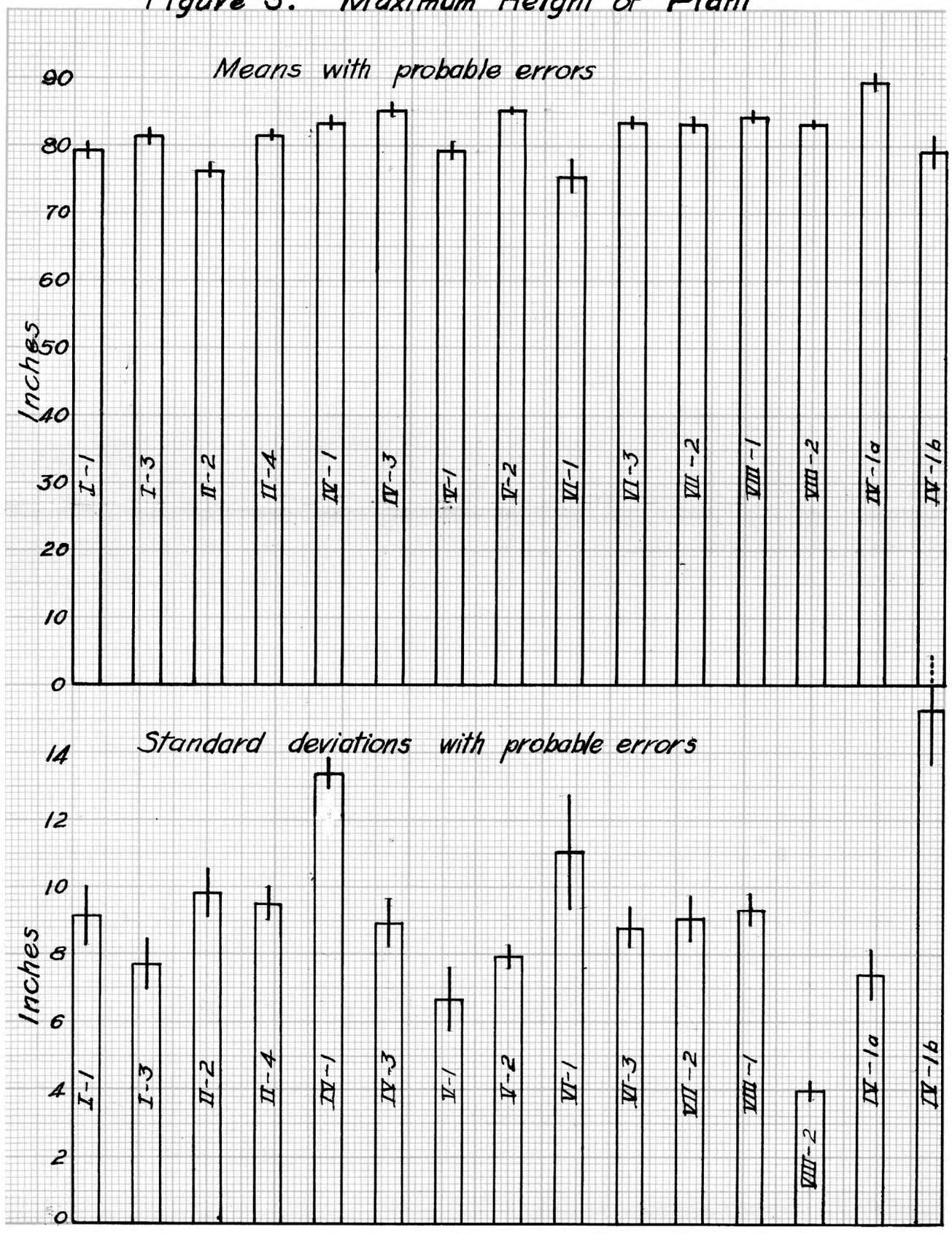
In the introduction and the paragraph on number of kernels per ear in Part II further evidence and discussion of the comparative purity of the various lines are given. One effect of the large amount of variation is that it precludes the detection of mutations on quantitative characters studied except those mutations which produce large effects.

Maximum Height. The differences between the average maximum heights for the various control families are greater than those of the treated lines. As may be seen in Table III and in figure 3, there is not much difference among the standard deviations calculated for the treated lines while there is considerable among those

TABLE III. FREQUENCY DISTRIBUTIONS FOR MAXIMUM HEIGHT.

Inches	Families														
	I-1	I-3	II-2	II-4	IV-1	IV-3	V-1	V-2	VI-1	VI-3	VII-2	VIII-1	VIII-2	IV-1a	IV-1b
96					15			2						3	
92	2			1	27	9		19		5	1	18		9	1
88	2	6	2	31	44	13	2	32	1	18	16	37	7	6	8
84	6	6	7	29	30	6	2	12	1	14	9	16	18	1	5
80	5	5	13	19	12	1	2	14	4	4	8	7	7	0	2
76	3	2	10	5	6	1	1	2	1	2	1	2	1	0	1
72	3	0	2	5	2	0	2	0	0	0	0	3	0	0	0
68	0	1	4	2	1	1	1	1	0	1	1	0	1	0	0
64	0	0	0	0	1	0		2	0	2	0	0		0	0
60	1	0	0	0	2	1		1	1	1	0	1		1	0
56	0	0	2	1	0	0		0	0	0	0	1			0
52	1	1	0	1	2	1		0	1	0	0	1			0
48			0	0	3			0		1	0	1			1
44			0	0	2			1			0	1			1
40			0	1	2						0				1
36			0	0	0						1				
32			1	0	2										
28				1											
Total	23	21	41	96	147	33	10	86	9	48	37	88	34	20	20
Mean	79.13 ±1.28	81.14 ±1.13	76.19 ±1.03	81.54 ±0.65	83.37 ±0.72	85.21 ±1.05	79.20 ±1.41	85.30 ±0.57	75.55 ±2.48	83.25 ±0.84	83.13 ±1.00	84.59 ±0.66	83.29 ±0.45	89.40 ±1.11	79.20 ±2.29
Standard deviation	9.13 ±0.90	7.70 ±0.79	9.83 ±0.72	9.52 ±0.45	13.18 ±0.51	8.98 ±0.74	6.64 ±0.99	7.96 ±0.40	11.06 ±1.75	8.77 ±0.60	9.06 ±0.70	9.32 ±0.47	3.93 ±0.31	7.40 ±0.78	15.26 ±1.62

Figure 3. Maximum Height of Plant



of the checks. Family IV-1, the most variable check line, has a coefficient of variation of 15.18, while family II-2, the most variable treated line, has a coefficient of variation of 12.89. This relation is the opposite of what would be expected on the basis that factor mutations affecting height had been produced in any of the treated lines. This comparison, however, is not as significant as at first might appear. Family II-2 is a fairly small population and consequently did not extend over a very large area of soil. Its variability may have been due largely to heredity. This seems not at all to be the case with IV-1. Instead the large variability shown by IV-1 seems most plausibly explained as being due to environment. IV-1 is the largest population of any line and an examination of the map, Fig. 2, shows the area occupied by this line extended from the east end of the experimental plot to the west center of one row and approximately occupied the west half of three other rows. Judging from the behavior of other lines nearest the various sections of IV-1 in maximum height and time of maturity, this area happens to fall on about as variable a soil as is in the experimental plot. Families II-4 and IV-3 indicate the soil was quite favorable for plant

growth near the east end of the plot and VI-1, although a small population, indicates conditions were poor near the south and west end of the plot. The standard deviation calculated for IV-1 would therefore be large due to environmental effects alone. The fact that IV-1a, 20 consecutive plants in a row, is approximately 50 per cent as variable as the whole IV-1 line indicates that soil differences cause the great amount of variation. Again in IV-1b, 20 consecutive plants in a row, planted from the same parent ear, had a standard deviation over twice as great as IV-1a. Consequently not much significance can be attached to a comparison of IV-1 with another line. While the other lines all represent smaller populations and consequently do not range through such a wide variety of soil conditions, some at least have constants which are affected similarly to those of IV-1 although to a lesser degree, and the same caution must be used as with IV-1 in attaching significance to comparisons with others.

IV-3, the next most variable check line, is a fairly small population and does not extend over as large a variety of soil as IV-1. Its coefficient of variability is 10.5 or 2.39 smaller than II-2. The difference between standard deviations of the two is slightly larger

than the probable error of the standard deviation of either one. While it is not possible to separate or distinguish the one kind of variation from the other in the case of a quantitative character, it can be assumed that environmental variation in II-2 is as great as in IV-3 or any other of the control lines. The small amount by which II-2 is more variable than IV-3 and the small difference between standard deviations of the two does not warrant any assumption but that environment accounts for the differences. From comparisons made among the lines of the second generation, no evidence can be found which might indicate segregation as the cause of any of the variation and hence no evidence of x-ray effect upon maximum height.

A comparison of the maximum height of plants in the first generation with the mean maximum height of their respective progenies in the second generation was made to determine if the relative height in the first generation is maintained in the second generation. The coefficient of correlation of the relative position was calculated by the rank difference method and found to be .19, indicating practically no correlation at all when the whole series of lines is considered. This indicates

that environment is the cause of most of the variation and supports the contention previously made as to the cause of the large amount of variability in both checks and treated lines.

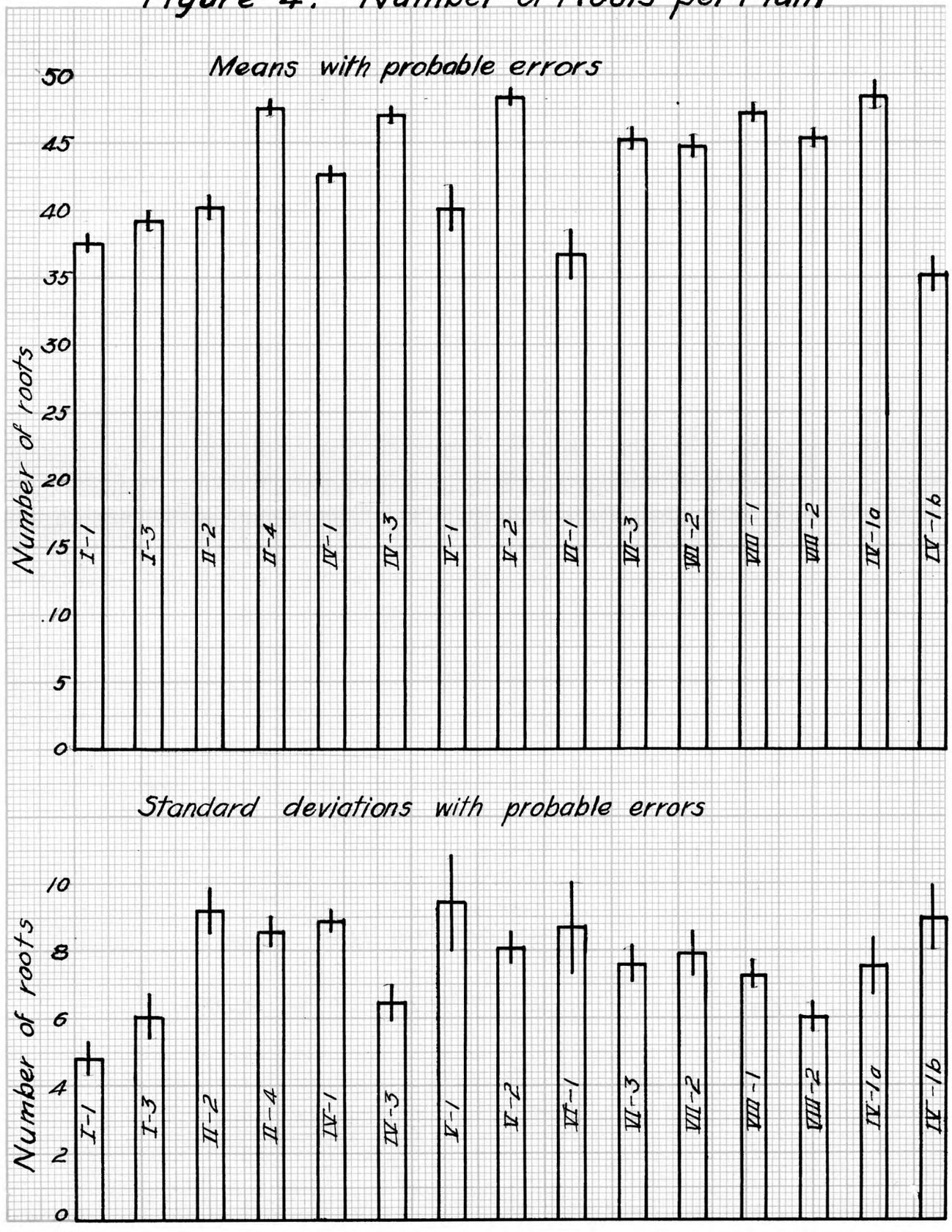
Since practically no correlation exists between ranks in the two generations, and in view of the facts that more variability is found in the checks than in the treated lines and that the widest range in averages and nearly the widest range in variability were found within a single line, it can be assumed that little of the large amount of variation is due to hereditary changes. Because x-ray effects on quantitative characters can only be distinguished as variation due to segregation that they might make possible in the second generation, the large amount of environmental variation precludes the finding of any x-ray effects except those producing considerably large variations than produced by the environment. In this experiment no such evidence is present for maximum height and the conclusion is that no large mutations were produced by the irradiation and it is not possible to learn of smaller ones, if any were prèduced.

Roots. As will be found in Table IV and figure 4, the checks show greater differences between the

TABLE IV. FREQUENCY DISTRIBUTIONS FOR THE NUMBER OF ROOTS PER PLANT.

Number	Families I-1	I-3	II-2	II-4	IV-1	IV-3	V-1	V-2	VI-1	VI-3	VII-2	VIII-1	VIII-2	IV-1a	IV-1b
64								1							
62				1	1			2		1				1	
60				3				1				1			
58			1	6	2			5			1	2		2	
56			1	12	2	4		14		6		7	1	1	
54			2	9	9	4	2	9			2	13	1	2	
52		2		9	8	3		4	1	6	6	11	3	4	
50		1	4	10	11	4		4		1	3	9	4	1	1
48	2		5	8	21	1	1	11		5	5	9	6	3	
46			4	4	13	4	1	10		5	3	9	7	4	1
44	1	1	4	6	13	6		5		7	2	6	4		3
42	1	2	2	9	12		1	1		2	5	7	2		4
40	6	3	3	6	8	1		5	3	4	3	4	1	1	
38	3	3	3	4	12	1	2	5	2	2	4	1	1	1	1
36	3	5	5	5	9	3		3	1	2	1	2			3
34	4	2	1	1	6	1		3	1	3		3	2		2
32			1	1	3					1		1	1		0
30	1	2	1		6		1	1		2			1		2
28	2				1			2				1			
26					1		1				1	2			
24			1		1		1								1
22															
20			3		3										1
18				1											
16				1	1										
14					1				1		1				1
12					1										
Total	23	21	41	96	145	32	10	86	9	47	37	88	34	20	20
Mean	37.65 ±0.67	39.23 ±0.88	40.48 ±0.97	47.89 ±0.59	42.64 ±0.50	47.25 ±0.77	40.00 ±1.76	48.27 ±0.59	36.77 ±1.96	45.19 ±0.75	44.70 ±0.76	47.38 ±0.52	45.41 ±0.69	48.50 ±1.14	36.40 ±1.34
Standard deviation	4.83 ±0.48	6.02 ±0.63	9.26 ±0.69	8.66 ±0.42	8.99 ±0.35	6.49 ±0.55	9.47 ±1.42	8.14 ±0.42	8.73 ±1.38	7.64 ±0.53	7.95 ±0.62	7.29 ±0.37	6.02 ±0.49	7.59 ±0.81	8.93 ±0.95

Figure 4. Number of Roots per Plant



averages for the number of roots than do the treated lines. The reverse is true for standard deviations. This indicates that a large amount of the variation is due to environment. The two groups IV-1a and IV-1b differ more widely than any two of the thirteen lines, IV-1a having a larger average number and IV-1b a smaller average number of roots than any other line. As in the previous paragraph on maximum height, this indicates that all the variation found in any line could be attributed to environment. II-2, the most variable irradiated line, has a coefficient of variation of 22.82. This is not significantly different from IV-1, the most variable check, which has a coefficient of 21.10. Further, IV-1b has a coefficient of variation of 24.50 which exceeds that of any whole line. Even though variation due to segregation may be present, there is too much variation due to environment present for the former to be discernible. The only conclusion that can be made concerning possible x-ray effects upon factors affecting the number of roots is that no evidence of large effects on the character is present and that the character is too widely influenced by differences in environment to make feasible the detection of smaller ones.

Nodes. The number of nodes is a character which, unlike the former two discussed, does not fluctuate widely. Table V shows the range in averages for the treated lines is .62 nodes while that of the check lines is .60 nodes. The difference between families IV-1a and IV-1b, the two which differed so widely for some of the other characters, is only .20 nodes. Environmental differences at least do not produce such wide differences in this as in other characters. It is possible though that the same proportion of the variations may have been produced by environment as were caused by it in the other characters. Characters affected mildly by differences in environment may also be affected mildly by differences in heredity.

The average of averages of all thirteen lines is 19.78. Families IV-1a and IV-1b, which were at opposite extremes of the range of averages shown for two other characters, are remarkably near the mean of the entire population for this character, differing by only .08 in one case and .12 in the other. This would indicate that the variations were not due to the same causes as in the other characters. If environment is responsible it must be some other part of the environment than in the case of the other two characters, otherwise IV-1a and IV-1b should

have varied more for they must have been at extremes of environmental conditions which affect the other two characters. It is possible that the number of nodes is determined within a shorter period of time than are maximum height and number of roots so that the kind of environment during the short period of time may differ considerably from an average of environmental conditions over a longer period.

Using the means of all thirteen lines, correlations calculated by the rank difference method give a coefficient of 0.43 between number of nodes and maximum height and one of 0.23 between number of nodes and number of roots. These coefficients indicate some tendency for concomitant variation, although the number of nodes is affected much less by soil heterogeneity than are the other characters.

Whether the variations are caused by environment or heredity or both, any variation due to segregation of mutant factors would have to produce effects in the character larger than those due to environment in order to be recognized. The treated lines would then show more variation than the check lines. This is not the case, for VII-2 has a coefficient of variation of 2.88 while

Figure 5. Number of Nodes per Plant

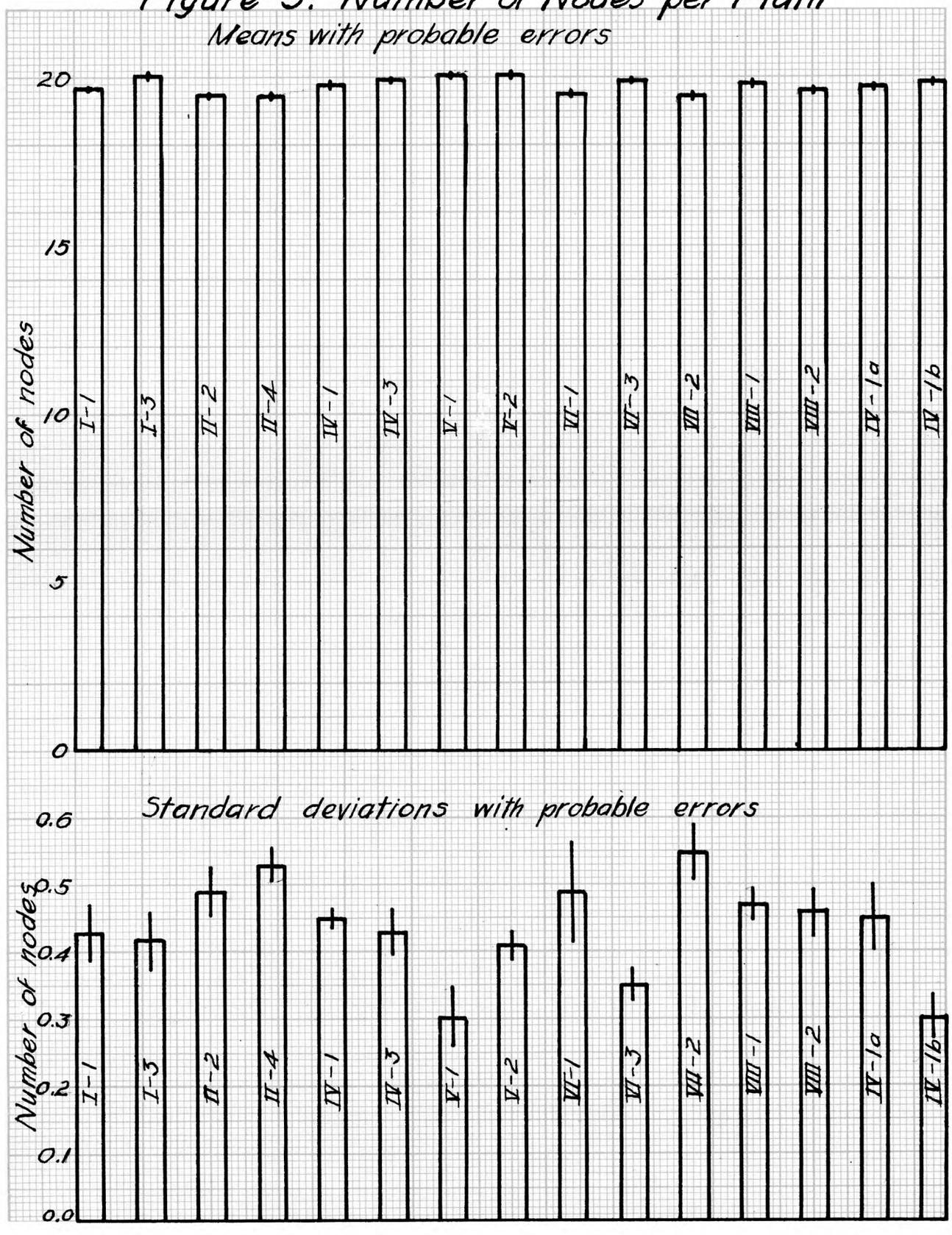


TABLE V. FREQUENCY DISTRIBUTIONS FOR THE NUMBER OF NODES PER PLANT.

Number	Families I-1	I-3	II-2	II-4	IV-1	IV-3	V-1	V-2	VI-1	VI-3	VII-2	VIII-1	VIII-2	IV-1a	IV-1b
22								1							
21		3		1	1	3	1	10		2	1	5			
20	17	17	22	45	109	26	9	73	5	41	17	67	23	14	18
19	6	1	19	49	34	3		2	4	4	19	16	11	6	2
18				1	1										
Total	23	21	41	96	145	32	10	86	9	47	37	88	34	20	20
Mean	19.73 ±0.06	20.09 ±0.06	19.53 ±0.05	19.47 ±0.03	19.75 ±0.02	20.00 ±0.05	20.10 ±0.06	20.11 ±0.03	19.55 ±0.10	19.95 ±0.03	19.51 ±0.06	19.87 ±0.03	19.67 ±0.05	19.70 ±0.07	19.90 ±0.04
Standard deviation	0.43 ±0.043	0.42 ±0.044	0.49 ±0.037	0.53 ±0.026	0.45 ±0.017	0.43 ±0.036	0.30 ±0.045	0.41 ±0.021	0.49 ±0.079	0.35 ±0.024	0.55 ±0.043	0.47 ±0.024	0.46 ±0.038	0.45 ±0.049	0.30 ±0.032

II-4, the most variable treated line, has a coefficient of variation of 2.77. There is therefore no indication of x-ray effects upon factors affecting the number of nodes per plant.

Rows of Kernels per Ear. The number of rows of kernels per ear does not vary much in the inbred strain used in this experiment. In this respect it resembles the number of nodes per plant as a character. Unlike the variation shown by the latter, however, the variation in number of kernel rows seems to be due mostly to environment. There are several sources of evidence to support the above hypothesis, namely, variation shown between two sections of the same line, correlation between the character and several others which are affected appreciably by environment, and comparisons of row number in the first generation plants with those in their respective progenies in the second generation.

As will be observed in Table VI, IV-1a has an average number of kernel rows .34 larger than the highest average among the thirteen lines, while IV-1b in a range of 1.18 for all thirteen lines is only .19 larger than the smallest average. The two sections therefore have a greater range between averages than any two of the

Figure 6. Number of Rows of Kernels per Ear

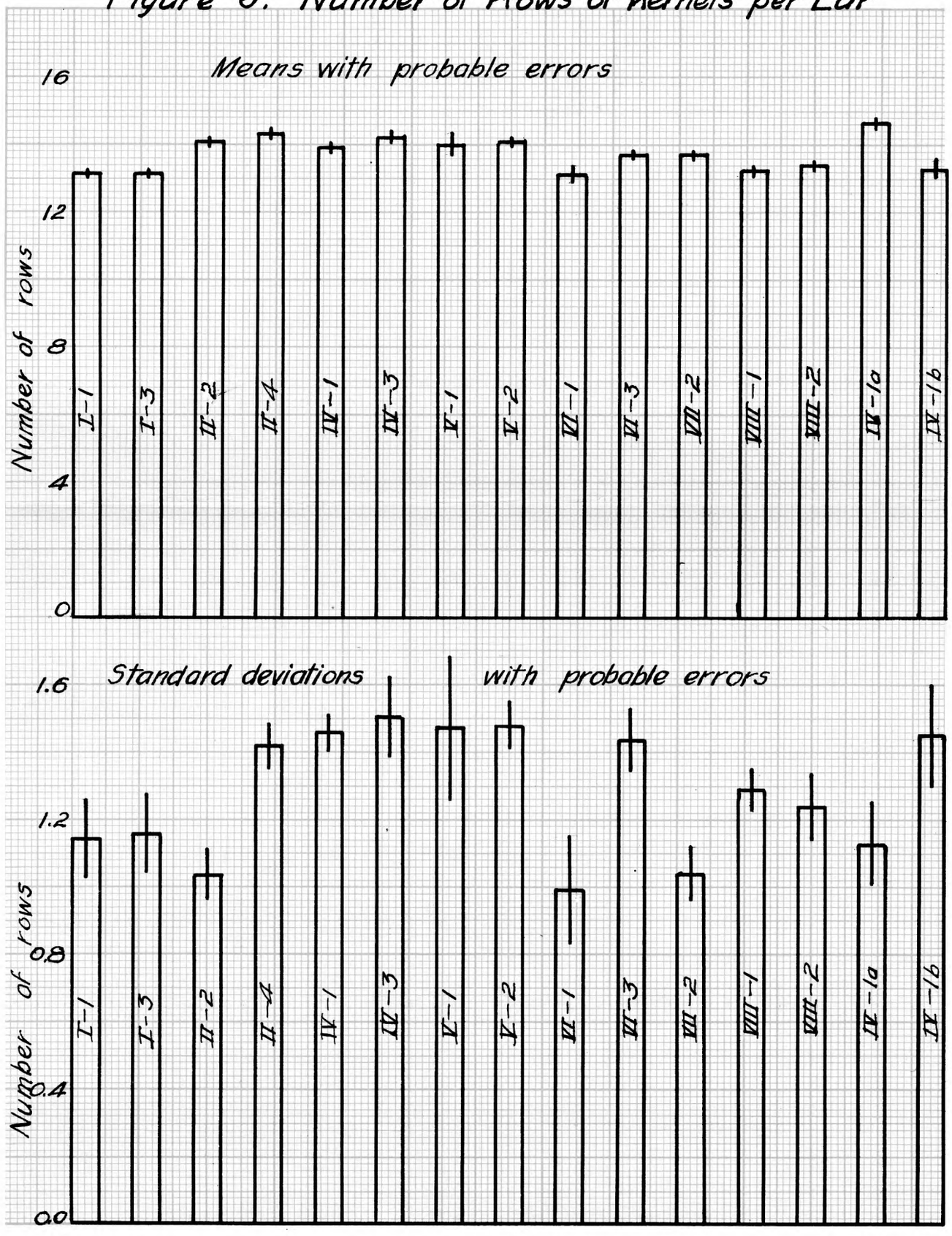


TABLE VI. FREQUENCY DISTRIBUTIONS FOR THE NUMBER OF ROWS OF KERNELS PER EAR.

	Families														
Number :	I-1:	I-3:	II-2:	II-4:	IV-1:	IV-3:	V-1:	V-2:	VI-1:	VI-3:	VII-2:	VIII-1:	VIII-2:	IV-1a:	IV-1b
18				1	1	1		1							
16	1	1	6	29	32	10	3	25		9	3	6	3	7	2
14	11	10	29	47	76	14	5	41	5	25	25	44	18	11	10
12	11	10	5	17	34	8	3	20	4	12	7	35	13	1	7
10					2					1		2			1
Total	23	21	40	94	145	33	11	87	9	47	35	87	34	19	20
Mean	13.13 ±0.16	13.14 ±0.15	14.05 ±0.10	14.29 ±0.09	13.94 ±0.08	14.24 ±0.17	14.00 ±0.29	14.16 ±0.10	13.11 ±0.22	13.78 ±0.14	13.77 ±0.11	13.24 ±0.09	13.41 ±0.14	14.63 ±0.17	13.30 ±0.22
Standard deviation	1.15 ±0.11	1.16 ±0.11	1.04 ±0.07	1.42 ±0.06	1.46 ±0.05	1.50 ±0.12	1.47 ±0.21	1.48 ±0.07	0.99 ±0.16	1.44 ±0.09	1.04 ±0.08	1.29 ±0.06	1.24 ±0.10	1.13 ±0.12	1.45 ±0.15

thirteen lines. This evidence for environmental effect fits in well with the potentiality for variation of the IV-1 line on account of location which has been described in the paragraph on maximum height.

The coefficient of correlation, calculated by the rank difference method, between the number of kernel rows and (1) maximum height is .41, (2) number of days from planting date to first pollen shedding .67, and (3) number of roots .70. While not nearly perfect the correlation does ascend in the order in which the three characters seem to be affected by environment and therefore indicates the variation in the number of kernel rows is due mainly to environment.

A comparison of the number of kernel rows in the ears of the first generation plants and the average number in their respective progenies indicates the environment in the second generation was generally more favorable than for the first generation. The average of the thirteen first generation ears is 12.62 while the average of averages in the second generation is 13.71. All averages in the second generation are above 13.11 and five are 14 or above. Four ears of the first generation had 14 kernel rows and the progenies of three of these each had an aver-

age of 14 or above. The other 14-kernel row ear had the progeny with the lowest number, 13.11. However, the population of this line was the smallest of any, consisting of only nine plants, and this second generation population grew upon the poorest soil of the experimental plot as shown by some of the other characters such as maximum height, number of days to pollen, and number of roots. The difference between the first and second generations appears to be due to environment also, but nothing very conclusive can be said about it because the difference is too small to be significant when only thirteen comparisons are involved.

Several of the check lines have larger standard deviations than any of the treated lines. IV-3 has a coefficient of variation of 10.53 while the most variable treated line, II-4, has a coefficient of variation of 10.

Since environment seems to be responsible for most of the variation shown by this character, little variation can be due to segregation of new mutations. In either event, however, more variation would be found in the treated lines than the checks if x-rays had produced changes in factors affecting the character studied and since the opposite is true it is quite certain the changes,

if present at all, have produced effects too small to show above environmental variation.

Number of days from planting to first pollen shedding. Like most of the other characters considered, the number of days from the date of planting to the date of first pollen shedding seems to be greatly affected by environment. The better the environment, the shorter is the period from planting date to first pollen shedding. The coefficient of correlation, by the rank difference method, of this character with maximum height is -.70; with number of roots, -.94; and with the date of first silk appearance, .96. This indicates the influence of the same factors, whether hereditary or environmental, on all four characters. That the factors causing this effect are environmental is shown by the general appearance of thriftiness of the plants on what was judged to be the better soil, lack of thriftiness shown by those on the poorer soil, the gradual change of thrifty appearance from one to the other, and the gradual change in the size of the various characters from areas of better conditions to those of poorer conditions.

The fact that the II-4 line had the largest kernels of the first generation and happened to be planted in the

shallowest furrow parallels the fact that it had the shortest average period from planting date to first pollen shedding date, the largest average number of kernel rows per ear, and next to the largest average number of roots.

Table VII shows that in number of days to pollen shedding there are greater differences among averages for the treated lines but greater differences among standard deviations for the check lines.

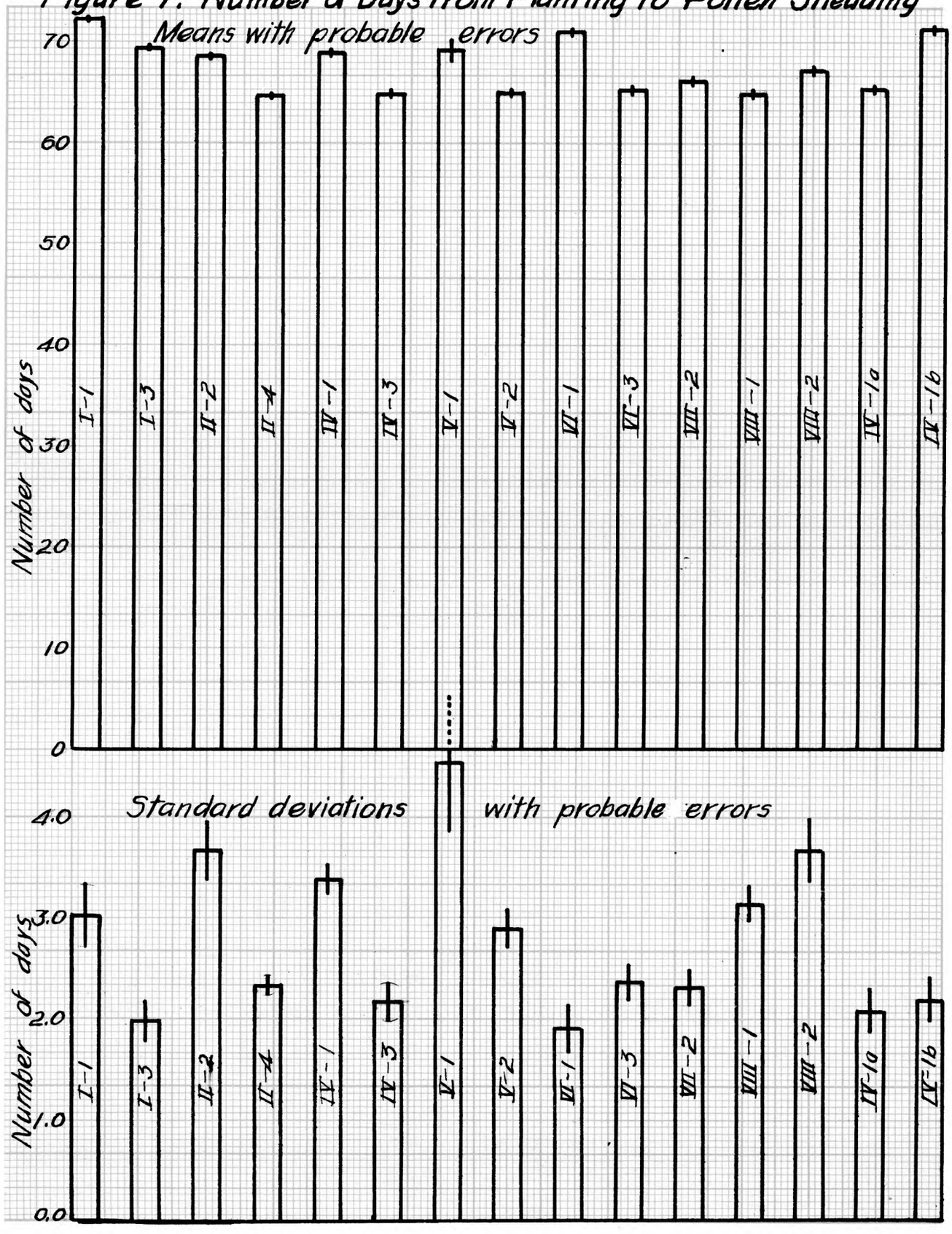
Family VIII-2 has a coefficient of variation of 5.43 while II-2, the most variable treated line, has a coefficient of variation of 5.34.

Since the date of first pollen shedding, like some of the quantitative characters previously discussed, is subject to large environmental variations, and since there were rather wide ranges of environmental conditions present in the experimental plot, variations due to segregation are difficult to detect. Because more variability is shown by check lines than by treated lines, the only conclusion that can be arrived at is that x-ray effects in the date of first pollen shedding, if present at all, were too small to be detected.

TABLE VII. FREQUENCY DISTRIBUTIONS FOR NUMBER OF DAYS FROM PLANTING DATE TO DATE OF FIRST POLLEN SHEDDING.

Number	Families														
	I-1	I-3	II-2	II-4	IV-1	IV-3	V-1	V-2	VI-1	VI-3	VII-2	VIII-1	VIII-2	IV-1a	IV-1b
84												1	1		
82	1		1												
81	0		0												
80	0		1		2										
79	2		0		2		1								
78	0		0		1		0								
77	0		0		0		0	1							
76	1		0		1		0	0	1						1
75	0	1	0		3		0	0	0						2
74	0	0	1	1	2		1	1	0						
73	2	0	1	0	2		0	0	0			1			1
72	4	1	0	0	8	1	1	2	1	1			2	1	2
71	6	4	2	1	17	0	1	1	2	2	3	3			6
70	1	2	5	2	21	0	1	3	5	1	1	1			7
69	4	4	5	2	13	1	0	4		3	6		3		
68	1	7	2	4	19	2	0	5		5	2	10	7	1	
67	1	1	10	7	17	2	0	6		6	4	1	4	4	
66		1	8	16	17	6	3	9		8	3	6	6	4	1
65			2	13	9	6	1	12		6	11	16	4	4	
64			3	23	8	9	1	20		9	6	22	3	4	
63				10	2	1		13		5	1	17	1	1	
62				12	1	5		8		2		7		1	
61				2				1				2			
Total	23	21	41	93	145	33	10	86	9	48	37	87	31	20	20
Mean	72.04 ±0.43	69.33 ±0.28	68.34 ±0.38	64.87 ±0.16	68.82 ±0.18	65.03 ±0.25	69.30 ±0.96	65.39 ±0.21	71.11 ±0.41	65.95 ±0.23	66.51 ±0.25	65.03 ±0.22	67.51 ±0.44	65.65 ±0.31	71.25 ±0.32
Standard deviation	3.04 ±0.29	1.96 ±0.20	3.65 ±0.27	2.27 ±0.10	3.34 ±0.13	2.16 ±0.17	4.54 ±0.67	2.89 ±0.15	1.85 ±0.29	2.38 ±0.16	2.27 ±0.17	3.11 ±0.15	3.67 ±0.31	2.08 ±0.22	2.16 ±0.23

Figure 7. Number of Days from Planting to Pollen Shedding



Number of days from Planting to First Silk Appearance. An examination of Table VIII shows that the number of days from date of planting to the date of first silk appearance closely parallels the character just described. This is most convincingly shown by the coefficient of correlation between the two of .96, calculated by the rank difference method.

Similar to number of days to pollen shedding, there are greater differences among averages in the treated lines and greater differences among standard deviations in the check lines.

Comparing the control line IV-1, having a coefficient of variation of 5.12, with II-2, the most variable treated line with a coefficient of variation of 5.08, rules out any indication of x-ray effect on this character.

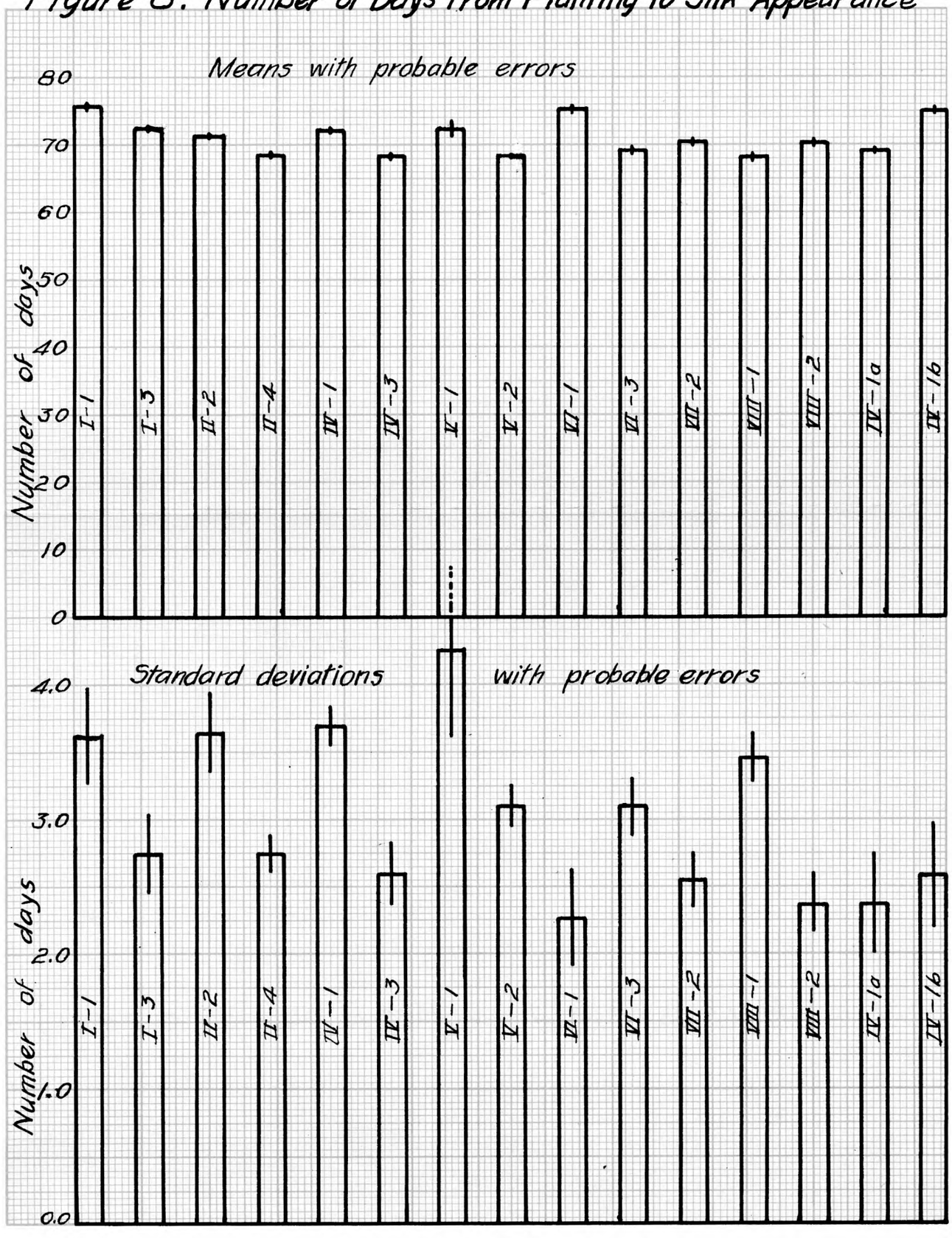
Lag of silk appearance after pollen shedding. Lag of silk appearance after pollen shedding is a rather variable character in this experiment, the standard deviation for a line nearly always being approximately one-third of the average. In no case was the lag a negative number. In two plants of the VIII-2 line, the silks appeared simultaneously with the shedding of pollen.

Because the character is dependent upon the differ-

TABLE VIII. FREQUENCY DISTRIBUTIONS FOR THE NUMBER OF DAYS FROM PLANTING DATE TO DATE OF FIRST SILK APPEARANCE

Number	Families														
	I-1	I-3	II-2	II-4	IV-1	IV-3	V-1	V-2	VI-1	VI-3	VII-2	VIII-1	VIII-2	IV-1a	IV-1b
87					1										
86	2														
85			1									1			
84					3							1			
83					1										
82			1	1	1										1
81	1				1			1	1						
80	1	1					1								
79					2										2
78							1	1		1					
77	2	1	1	1	7					1					2
76	4		2		7	1	2		2	1	1	1	2	1	
75	3	4		1	9			3	3		1	2			4
74	7	1	2		17	1		3	1	4	3				6
73	2	2	5	4	19	2	1	2	2	1	4	1	4		4
72	1	4	4	5	18			7		8	4	6	5	1	
71		2	7	7	18	1		6		2	2	4	7	3	
70		4	8	14	18	3	1	5		7	4	4	3	4	1
69		2	4	11	6	4	2	12		2	5	11	6	1	
68			3	21	5	8	2	13		7	8	14	4	4	
67			2	13	8	2		10		9	3	16	2	3	
66				5	3	9		16		3	1	15		2	
65				8		2		5		3		10	1		
64				2				1				1			
Total	23	21	41	93	144	33	10	85	9	48	36	87	34	19	20
Mean	76.17 ±0.51	72.61 ±0.40	71.80 ±0.38	68.80 ±0.19	72.61 ±0.20	68.33 ±0.30	72.70 ±0.90	68.66 ±0.22	75.33 ±0.51	69.85 ±0.29	70.30 ±0.29	68.40 ±0.25	70.47 ±0.27	69.21 ±0.36	75.00 ±0.39
Standard deviation	3.65 ±0.35	2.75 ±0.28	3.65 ±0.27	2.76 ±0.13	3.71 ±0.14	2.62 ±0.22	4.26 ±0.64	3.11 ±0.15	2.26 ±0.35	3.10 ±0.21	2.58 ±0.20	3.48 ±0.17	2.37 ±0.19	2.37 ±0.26	2.60 ±0.27

Figure 8. Number of Days from Planting to Silk Appearance



ence of two other characters, it would not necessarily be expected to have a close correlation with either. The coefficient of correlation calculated by the rank difference method of lag with number of days to pollen shedding is .32 and with silk appearance date, .46. This indicates only some tendency for the lag to increase with the increase in length of the period from planting date to silk appearance. Since the latter character is larger on poorer soil, so also is the lag greater on poor soil. I-1 and VI-1, both on poor soil, are the only lines in which the mean lag is greater than four days.

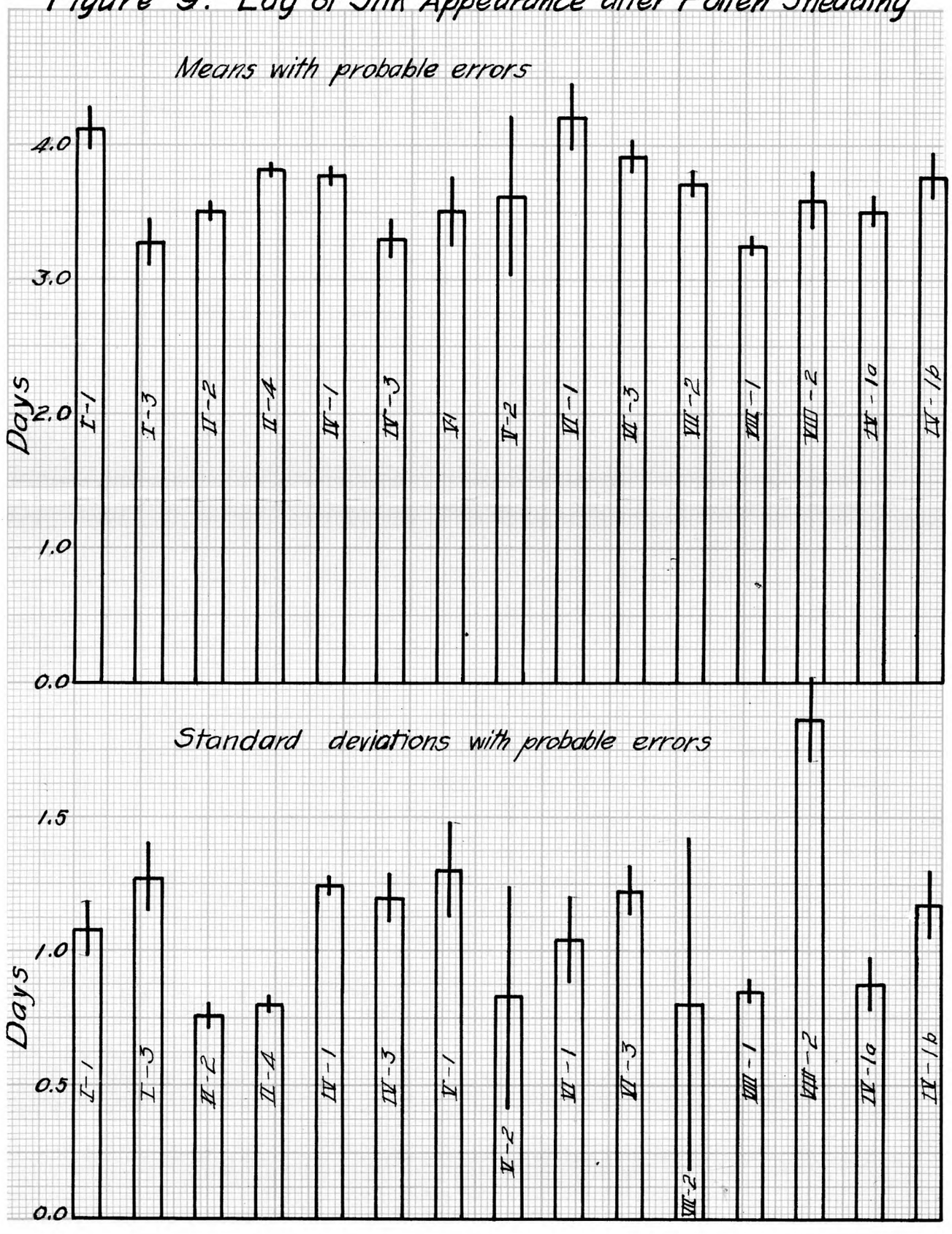
As in the two characters upon which lag depends, the most variable line, as shown in Table IX, was VIII-2, one of the checks and the same one which was most variable for date of pollen shedding. It has a coefficient of variation of 51.53, while the most variable treated line, I-3, has a coefficient of variation of 38.96.

Because no indication of x-ray effects was noted in the case of dates of pollen shedding and silk appearance, none would be expected in the case of the lag of one after the other. The comparison of coefficients of variation of VIII-2 and I-3 shows that no x-rays effects are in evidence.

TABLE IX. FREQUENCY DISTRIBUTIONS FOR THE LAG OF SILK APPEARANCE AFTER FIRST POLLEN SHEDDING.

Days	Families														
	I-1:	I-3:	II-2:	II-4:	IV-1:	IV-3:	V-1:	V-2:	VI-1:	VI-3:	VII-2:	VIII-1:	VIII-2:	IV-1a:	IV-1b
9					1			1							
8					2										
7	1				3					2			1		2
6		2	1	2	6	1		1	1	4	1		3		
5	8	1	3	15	12	3	3	5	3	6	4	5	7	2	
4	7	5	13	42	56	13	4	36	2	15	16	28	6	9	7
3	6	7	23	31	49	7	1	36	3	17	14	39	6	5	11
2	1	5	1	2	15	6	2	6		4	1	12	2	3	
1		1				3	1					2	2		
0													3		
Total	23	21	41	92	144	33	11	85	9	48	36	86	30	19	20
Mean	4.13 ±0.15	3.28 ±0.18	3.51 ±0.08	3.82 ±0.05	3.77 ±0.07	3.30 ±0.14	3.54 ±0.26	3.57 ±0.60	4.22 ±0.23	3.93 ±0.11	3.72 ±0.09	3.25 ±0.06	3.60 ±0.22	3.52 ±0.12	3.75 ±0.17
Standard deviation	1.08 ±0.10	1.27 ±0.13	0.76 ±0.05	0.80 ±0.03	1.24 ±0.04	1.21 ±0.09	1.30 ±0.18	0.82 ±0.42	1.04 ±0.16	1.23 ±0.09	0.80 ±0.63	0.85 ±0.04	1.85 ±0.16	0.88 ±0.09	1.17 ±0.12

Figure 9. Lag of Silk Appearance after Pollen Shedding



Number more of kernel rows on the upper ear than on the lower. The number more of kernel rows on the upper ear than on the lower ear is a character similar to the one just described in that it is dependent upon the relation of two other characters. It happens in this experiment that the lower ears usually have more rows of kernels than do the upper ears.

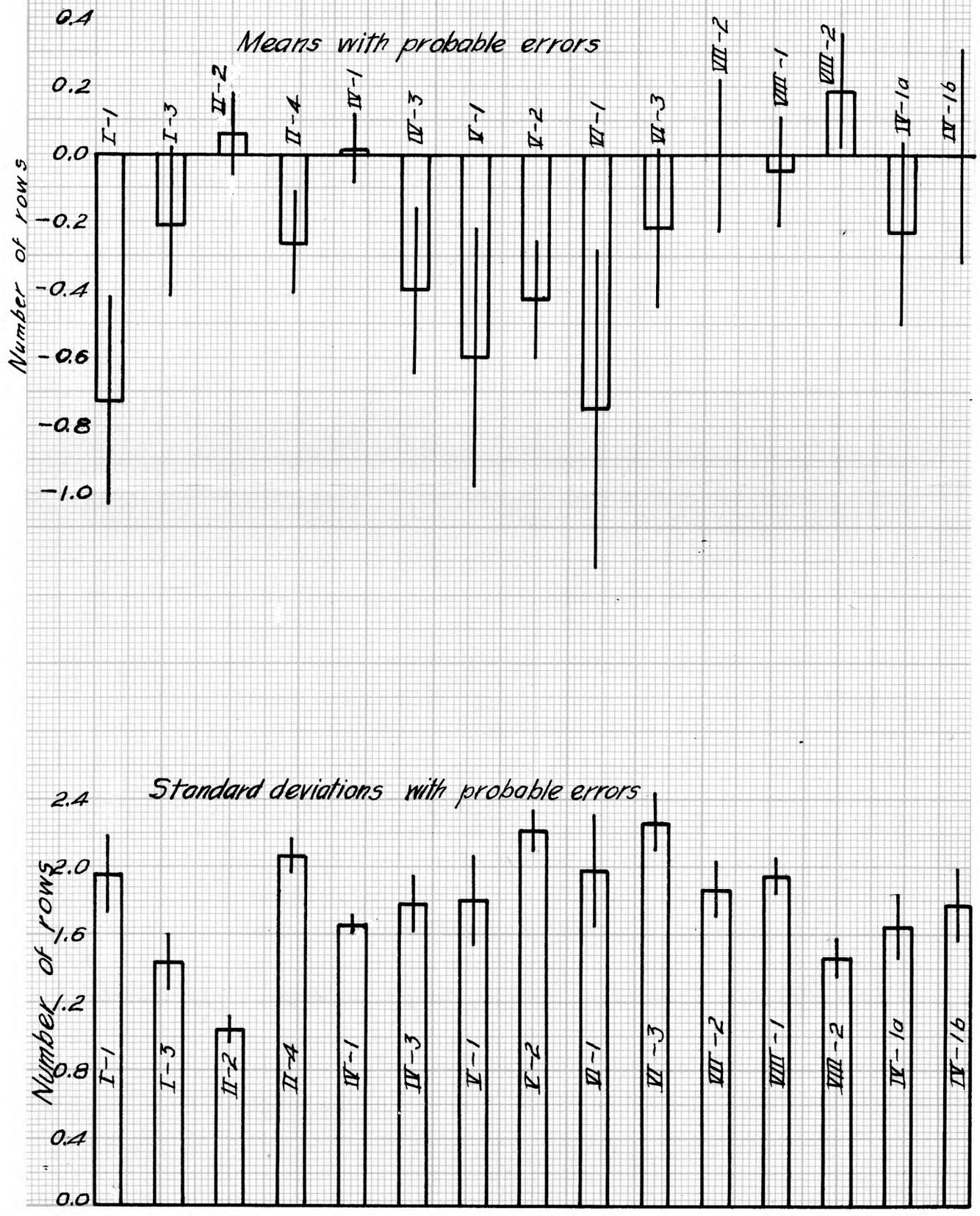
The coefficient of correlation by the rank difference method of this character with number of kernel rows per ear is .10, with date of pollen shedding is .25, with number of roots is .26, and with lag of silking is .37.

Because of the negative quantities involved in averages, coefficients of variation calculated for the different lines are not of much value. For that reason comparisons of variability are more satisfactorily made directly from the standard deviations. As will be seen in Table X, the check lines show more variation for the character than the treated lines, VI-3 having a standard deviation of 2.26, while II-4, the most variable treated line, has a standard deviation of 2.07. As in the other characters discussed, there is no evidence of x-ray effects upon factors which influence directly or indirectly the number more of kernel rows on the upper than on the

TABLE X. FREQUENCY DISTRIBUTIONS FOR THE NUMBER OF ROWS OF KERNELS PER EAR FOR UPPER AND LOWER EARS AND STANDARD DEVIATIONS OF THE NUMBER MORE OF KERNEL ROWS ON THE UPPER EAR THAN ON THE LOWER.

Upper: / Lower:		Families														
		I-1:	I-3:	II-2:	II-4:	IV-1:	IV-3:	V-1:	V-2:	VI-1:	VI-3:	VII-2:	VIII-1:	VIII-2:	IV-1a:	IV-1b
	18															
	16						1									
18	14					1			1							
	12				1											
	10															
	18						2									
	16			1	9	9	2	2	5		3			1	3	
16	14	1	1	3	14	17	3	1	12		3	1	4	2	3	1
	12				2	1			3		2	2	1			
	10															
	18				2				2		1					
	16			3	16	15	4	2	13	1	4	3	3	3	4	
14	14	6	6	19	19	39	6	2	19	2	9	13	14	6	5	6
	12	3	3	2	7	12	2	1	6	2	10	6	19	8	1	3
	10					1										
	18															
	16	3			6	4	2	1	9	1	6	1	5		1	2
12	14	5	6	1	8	12	1	1	8	2	3	6	12	4		
	12	1	3	4	2	9	2	1	1		2		7	7		3
	10					1							1			
	18															
	16															
10	14															
	12															
	10										1					
Total		19	19	33	86	121	25	10	78	8	44	32	69	31	17	15
Mean		-0.73 ±0.31	-0.21 ±0.21	0.06 ±0.12	-0.27 ±0.15	0.01 ±0.10	-0.40 ±0.24	-0.60 ±0.38	-0.43 ±0.17	-0.75 ±0.47	-0.22 ±0.23	0.00 ±0.22	-0.05 ±0.16	0.19 ±0.17	-0.23 ±0.27	0.00 ±0.31
Standard deviation		1.96 ±0.22	1.43 ±0.16	1.04 ±0.08	2.07 ±0.10	1.67 ±0.06	1.78 ±0.17	1.80 ±0.27	2.21 ±0.11	1.98 ±0.33	2.26 ±0.16	1.87 ±0.16	1.95 ±0.10	1.46 ±0.12	1.66 ±0.19	1.78 ±0.22

Figure 10. Number More Rows Kernels on Upper Ear



lower ear of a plant.

CONCLUSIONS

A summary of all the above comparisons shows that in no case was there more variability in any treated line than in the most variable check line for any character considered. In the case of number of roots per plant, the most variable check line has only ten plants and consequently is not very reliable, but even for this character the most variable treated line is not significantly more variable than the second most variable check line, which does have a large population.

From a consideration of the eight quantitative characters studied in this experiment, it must be concluded that there is no indication of any measurable change, due to irradiation by x-rays, in factors affecting these characters.

If any such factor changes were effected by x-rays, the plants were probably eliminated in the first generation through inability to germinate, grow or reproduce.

The fact that no color mutations were found in the second generation indicates that any such changes produced in the germ plasm also were lethal and were elimin-

ated before they had an opportunity to develop. The existence of a dwarf plant and of a striped leafed plant and of sterility of these two, in addition to sterility in another in the first generation, indicates that the irradiation was effective in producing changes in the germ plasm, and the lack of such evidence in the second generation, among the remaining lines, indicates elimination in the first generation of the individuals affected the most.

It is probable that quantitative characters are dependent on many factors for expression so that the possibility is slight of having the particular combination of factors affected which would be necessary to produce discernible changes by x-rays, without at the same time damaging the cell mechanism so severely that it cannot survive.

There is a possibility of mutations having occurred which in effect are lethal or semi-lethal when homozygous. The percentage of blanks and of seedling deaths, however, furnishes no conclusive evidence of such an occurrence.

It is possible that x-rays did affect some factors without elimination of the plants possessing them in the first generation, but in that case the effects were not

upon the particular quantitative characters studied.

Because of the small number of treated plants involved in the first generation, and since no significant difference was noted in any character between treated and untreated populations in the second generation, it appears that no conclusive statement can be made of the effects of irradiation by x-rays upon the quantitative characters of maize from the results of this experiment.

SUMMARY

Observations made on the first generation following x-ray treatment of the reproductive and embryonic cells of an inbred strain of maize, indicate strongly that the organisms were affected.

A dwarf plant, a striped plant and sterility in several plants, all found in the treated lines of the first generation with no such effects in the checks, indicates x-ray effects, but because of the small number of treated plants involved the evidence is not conclusive.

There was no evidence in the second generation of viable treated first generation plants of any effects of irradiation by x-rays upon the quantitative characters of maize.

The difference in results found in the first and second generations in irradiated lines of an inbred strain of maize indicates that if any plants were affected by the irradiation they also were eliminated by the end of the first generation.

No conclusive statement can be made from the results of this experiment on the effects of irradiation by x-rays upon the quantitative characters of an inbred strain of maize. It is possible that if a larger number of plants had been treated in order to produce a larger first generation than was obtained in this experiment, some x-ray effects on quantitative characters might have been obtained in the second generation. Because of the damaging effects of x-rays upon the treated organism generally, the method appears impractical as a means of inducing quantitative changes which might be found useful in crop improvement work.

PART II

QUANTITATIVE CHARACTERS AS INDICES OF HOMOZYGOSITY

In some experimental problems pertaining to crop improvement it is necessary to use strains and varieties of plants of approximately known degrees of purity. The only practical means of learning the extent of purity or homozygosity attained by an inbred strain is through observation, or study of the behavior of certain characters while the plant is growing under controlled conditions. The efficiency of each of such characters studied as an index of homozygosity must be known with some certainty in order to make estimates of purity of strains that can be considered reliable.

It is possible that observation of the behavior of some one character may be more reliable as a criterion of homozygosity than an examination of a number of other characters. If the more useful or reliable character-indicators are known their use will simplify the amount of experimental work involved as well as permit more accurate estimates to be made. It is, therefore, desirable and worth while to determine the comparative value of characters as such indices. Because usefulness of such characters depends upon their relative freedom from

environmental effects, a preliminary problem is to determine which of a number of characters is least affected by environment.

In crop improvement work, the characters known as quantitative characters are often of greatest importance. Yields of crops are among the most important quantitative characters and no doubt are dependent upon or influenced by other quantitative characters. Yield of corn may be dependent upon the size of the leaf area of the plant or upon the number of roots or upon both and many others. It is, therefore, important to learn the genetic background or genetic composition of some or all of these quantitative characters. Not much is known of them so far except that they are much more complex than qualitative characters such as colors of pericarp, aleurone, etc.

While yields of crops may be the most important of the quantitative characters, it may not lend itself satisfactorily to experimental studies. For that reason knowledge of quantitative characters may possibly be determined first from characters other than yield which of themselves may not necessarily be useful in determining or influencing yield but which are more readily analyzed. For such studies, characters which are least affected by

environment appear to be most useful. In this phase of research, as in the one previously mentioned, the preliminary problem is to determine the relative effects of environment upon a number of quantitative characters.

No such preliminary studies or determinations seem to have been made of quantitative characters for corn. Because data originally obtained for Part I of this problem are also applicable to a study of quantitative characters as indices of homozygosity, use has been made of them for such investigation in Part II.

There are several reasons why the data, although applicable, are not ideal for the study. Two of these are, the lack of proper replications and the small numbers in some of the lines involved. Another reason is the lack of evidence with which to determine accurately the purity of the strain upon which the characters are being tested. Any one or more of a number of degrees of purity can exist in the strain and about which only estimates can be made. Each of the untreated lines could be (1) pure to the same degree for all the characters studied; (2) pure to the same degree for some but not all of the characters studied; (3) pure to the same degree for no two of the characters. A certain line could be

60 per cent pure for each of the eight characters while another line might be only 50 per cent pure for each of the characters.

While all the above possibilities must be considered when attaching reliability to the conclusions arrived at, it will simplify the problem and furnish a starting point or basis for it, to assume that the untreated strain is equally pure for all characters considered. This assumption is not made without some foundation. The strain was inbred six generations before separation into the paired lines. While not enough generations for attaining the highest practical degree of homozygosity, a high degree of uniformity is usually attained in six generations of inbreeding and selection. The data obtained in this experiment also indicate that a high degree of uniformity was attained in the six generations of inbreeding. This has been fully discussed in Part I in the paragraphs describing each of the eight characters.

All of the characters for which data are available are quantitative characters. While this is more or less an arbitrary classification it is probable that most "quantitative" characters are controlled or determined by hereditary mechanisms of considerable complexity. Student

(1933) has shown that several quantitative characters most probably are dependent upon hundreds or possibly thousands of factors. The factors undoubtedly each affect the character in varying degrees. Six generations of inbreeding would tend to eliminate the majority of heterozygous combinations. The few remaining heterozygous factors would not tend to cause much variation in the line, due to segregation, in the following generation. From an illustration by Student (1933) theoretically only one in 100 million individuals would be likely to exceed either extreme of a middle range less than one third the possible range of variation produced by 400 factors having small but cumulative effects. If quantitative characters are dependent upon the large number of factors as surmised by Student rather little variation is expected due to segregation, and this view or theory lends support to the assumption that the strain used in this experiment probably is equally pure for all the characters studied.

If the lines are equally pure the same amount of variation due to heredity will be expected for any character in any line or portion of a line (provided large enough numbers are involved) regardless of the kind of environment the line or portion was subjected to.

Differences in variability displayed among the different characters of an inbred strain will, therefore, be measures of the extent to which these characters are influenced by environment. Knowing that, the comparative value of a number of characters as indices of homozygosity and the relative value of these characters as subjects for the study of genetic composition of quantitative characters may then be determined. Consequently, the immediate problem is to determine how much each of the characters for which data are available is affected by environment.

CALCULATIONS

Because it was assumed that the untreated lines were all equally pure, the untreated population was considered as a single inbred strain. This strain, however, was made up of two parts; the sib crosses, lines VII-2, VIII-1, and VIII-2 being placed in one group and the untreated selfs, lines IV-1, IV-3, V-1, V-2, VI-1, and VI-3 in the other. The averages, standard deviations, and coefficients of variation were calculated for each of the two groups for the eight different characters studied. These constants are shown in Table XI. The averages are true averages but the standard deviations

TABLE XI. RELATIVE VARIABILITY OF EIGHT QUANTITATIVE CHARACTERS OF AN INBRED STRAIN OF MAIZE.

		Number of days from planting date to first pollen shedding date		Number of days from planting date to first silk appearance date		Lag in days of silk appearance after pollen shedding.		Number more of kernel rows on upper ear than on lower	
Number of Variates	Selfs	331		329		330		286	
	Sibs	155		157		152		132	
Mean	Selfs	67.21	±0.11	70.83	±0.124	3.69	±0.041	-0.2237	±0.077
	Sibs	65.87	±0.165	69.28	±0.165	3.43	±0.061	0.0166	±0.107
Standard Deviation	Selfs	3.01	±0.078	3.37	±0.088	1.14	±0.029	1.95	±0.055
	Sibs	3.06	±0.116	3.08	±0.116	1.12	±0.043	1.83	±0.075
Coefficient of Variation	Selfs	4.48	±0.11	4.75	±0.12	30.84	±0.88	8.7	
	Sibs	4.64	±0.17	4.44	±0.16	32.79	±1.39	109.5	

		Maximum height (in inches)		Number of roots		Number of nodes		Number of rows of kernels per ear	
Number of Variates	Selfs	333		329		329		332	
	Sibs	159		159		159		156	
Mean	Selfs	83.69	±0.399	44.68	±0.311	19.90	±0.015	13.98	±0.053
	Sibs	83.97	±0.449	46.33	±0.385	19.74	±0.026	13.39	±0.060
Standard Deviation	Selfs	10.81	±0.281	8.38	±0.220	0.428	±0.010	1.46	±0.037
	Sibs	8.40	±0.317	7.21	±0.272	0.491	±0.018	1.23	±0.046
Coefficient of Variation	Selfs	12.91	±0.33	18.77	±0.51	2.15	±0.05	10.46	±0.27
	Sibs	10.00	±0.37	15.56	±0.60	2.48	±0.09	9.19	±0.35

were obtained by using the deviations of the individuals from the averages of their respective lines, before regrouping, and not from the averages of the whole group considered. The coefficients of variation consequently are also affected.

COMPARISON OF CHARACTERS

An examination of Table XI shows that the regrouped populations indicate considerable soil differences in the area occupied by the untreated lines. The averages for the two groups, as would be expected of large populations, are very much the same for nearly every character. The standard deviations show that the selfs were scattered over a greater variety of soil conditions than the sib crosses. This parallels the results found in Part I and would be expected from the fact that the selfs comprised the larger population of the two groups.

Of chief interest to Part II are the coefficients of variation. There seems to be a common belief that the number of rows of kernels per ear is the character least influenced by environment and heterogeneity of the soil and hence is an excellent character for estimating the purity of a line. An examination of Table XI does not in-

dicate that such a belief is valid. Number of nodes with a coefficient of variation for the selfs of 2.15 ± .05, number of days from planting date to first pollen shedding date with a coefficient of variation of 4.48 ± .11, and number of days from planting date to first silk appearance date with a coefficient of variation of 4.75 ± .12, all are less variable than the number of rows of kernels per ear. Results of this experiment show that rows of kernels per ear is between four and five times as variable as number of nodes and about twice as variable as days to pollen shedding, and days to silk appearance. Of the eight characters studied number of nodes is most free from environmental effects and, therefore, probably most useful as an index of homozygosity and as a character which may best serve as a subject for analysis of genetic composition.

Maximum height is another character rather widely used by agronomists and plant breeders. From these studies it does not appear to indicate soil differences as reliably as some other characters. This probably is due to the fact that plants on fertile soil reach maturity earlier than those on poor soil. The plants on poor soil, therefore, grow for a longer period of time

and this additional period of growth tends to erase differences in maximum height so that the character does not indicate as much soil difference as really exists. Height of plants when most of the population is about three fourths grown would probably indicate soil differences better than maximum height.

CONCLUSIONS

Number of rows of kernels per ear, contrary to common belief, is not the character least affected by environment, as shown by this experiment. Number of nodes, number of days from planting to first pollen shedding and number of days from planting to first silk appearance all seem to be less influenced by environment.

Number of nodes per plant is outstanding as a character little influenced by environment. Maximum height of plants does not appear to be such an excellent character for determining soil conditions as is generally supposed. Height of plants when half to three fourths grown probably is a better character for indicating soil differences than maximum height.

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BIBLIOGRAPHY

Altenburg, Edgar.
The limit of radiation frequency effective in producing mutations. Amer. Nat. 62:540-545. 1928.

Anderson, E. G.
The constitution of primary exceptions obtained after x-ray treatment of Drosophila. Gen. 16:386-396. 1931.

Avery, A. G. and Blakeslee, A. F.
Radium experiments with Datura. IV Visible gene mutations in radium treated and control material. Anat. Rec. 41:99. 1928. (abstr.)

Babcock, E. B. and Collins, J. L.
Natural ionizing radiation and the rate of mutation. Nature, 124:227-228. 1929.

_____
Does natural ionizing radiation control the rate of mutation? Proc. Nat. Acad. Sci. 15:623-628. 1929.

Barth, L. G.
The effect of x-rays on the spermatazoa of Drosophila. Anat. Rec. 41:117. 1928. (abstr.)

Blakeslee, A. F., Bergner, A. D., Satina, S., Avery, A. G., Cartledge, J. L., and Potter, J. S.
Analysis of Datura stromonium plants grown from seeds exposed to x-rays. Anat. Rec. 44:281. 1929. (abstr.)

Cartledge, J. L. and Blakeslee, A. F.
Radium experiments with Datura. II. Pollen abortion in F_1s from radium treated parents. Anat. Rec. 41:98. (abstr.)

Chalmers, Eliz. R.
Mutations and freaks from x-rayed adult males of Habrobracon. Anat. Rec. 47:294. 1930.

Cockerel, T. D. A.
Radiation and Genetics. Amer. Nat. 64:474-476. 1930.

Demerec, M. and Farrow, J. G.
Non-disjunction of the x chromosome in Drosophila virilis. Relation between the x-ray dosage and the frequency of primary non-disjunction of x chromosomes. Proc. Nat. Acad. Sci. 16:707-714. 1930.

DeVries, Hugo.
Species and varieties: their origin by mutation. Open Court Publ. Co., Chicago. 1899.

Dunning, W. F.
A study of the effect of x radiation on occurrence of abnormal individuals, mutations, viability and fertility of the parasitic wasp. Gen. 16:505-532. 1931.

Gager, C. S. and Blakeslee, A. F.
Chromosome and gene mutations in Datura following exposure to radium rays. Proc. Nat. Acad. Sci. 13:75-79. 1927.

Goodsell, S. F.
The relation between x-ray intensity and the frequency of deficiency in the maize endosperm. Anat. Rec. 47:381. 1930. (abstr.)

Goodspeed, T. H.
The effects of x-rays and radium on species of the genus nicotiana. Jour. Hered. 20:243-259. 1929.

———
Cytological and other features of variant plants produced from x-rayed sex cells of nicotiana tabacum. Bot. Gaz. 87:563-582. 1929.

Goodspeed, T. H. and Olson, A. R.
The production of variation in nicotiana species by x-ray treatment of sex cells. Proc. Nat. Acad. Sci. 14:66-69. 1928. (abstr.)

———
Progenies from x-rayed sex cells of Tobacco. Sci. 67:46. 1928. (abstr.)

Hance, R. T.
The reaction of homozygous and heterozygous adult characters under the influence of x-rays. Anat. Rec. 37:170. 1928. (abstr.)

_____ Altering a matured genetic character. Jour. Hered. 18:377-380. 1928.

Hanson, Frank Blair.
The effects of x-rays on productivity and the sex ratio in Drosophila. Amer. Nat. 62:352-362. 1928.

_____ The effect of x-rays in producing return gene mutations. Sci. 67:562-563. 1928.

_____ An analysis of the effects of different rays of radium in the production of lethal mutations in Drosophila. Anat. Rec. 41:99. 1928. (abstr.)

Hanson, Frank Blair and Heys, Florence.
The effect of radium in producing lethal mutations in Drosophila. Sci. 68:115-116. 1928.

_____ Duration of the effects of x-rays on male germ cells in Drosophila. Amer. Nat. 63:511-516. 1929a.

_____ The effect of natural (earth) radiations in producing lethal mutations in Drosophila. Anat. Rec. 44:293. 1929. (abstr.)

_____ Effects of different rays of radium in producing lethal mutations in Drosophila. Amer. Nat. 63:201-213. 1929.

_____ A possible relation between natural (earth) radiation and gene mutations. Sci. 71:43-44. 1930.

Hanson, Frank Blair, Heys, Florence, and Stanton, Eliz.
The effects of increasing x-ray voltages on the production of lethal mutations in Drosophila melanogaster. Amer. Nat. 65:134-142. 1931.

Hanson, Frank Blair and Winkleman, Elvene.
Visible mutations following radium irradiation in Drosophila. Jour. Hered. 20:277-286. 1929.

Harris, B. B.
The effects of aging of x-rayed males upon mutation frequency in Drosophila. Jour. Hered. 20:299-302. 1929.

Harrison, J. W. H. and Garrett, F. C.
The induction of melanism in the Lepidoptera and its subsequent inheritance. Proc. Royal Soc. 99B: 241-263. 1926.

Hersch, A. H.; Karrer, E.; and Loomis, A.
An attempt to induce mutations in Drosophila by means of supersonic vibrations. Amer. Nat. 64:552-559. 1930.

Horlacher, W. R. and Killough, D. T.
Radiation induced variation in cotton. Jour. Hered. 22:253-262. 1931.

Jenkins, Merle T.
Heritable characters in maize. XXXIV. Rootless. Jour. Hered. 21:79. 1930.

Johannesen, W.
Ueber Erblichkeit in Populationen und in reinen Linien. G. Fischer, Jena. 68 pp. 1903.

Johnson, Edna L.
Effect of x radiation on growth and reproduction of tomato. Plant Physiol. 6:685-694. 1931.

Jones, D. F.
Attainment of homozygosity in inbred strains of maize. Gen. 9:405-418. 1924.

Lindstrom, E. W.
Hereditary radium induced variations in the tomato. Jour. Hered. 24:128-137. 1933.

Mavor, J. W.
An effect of x-rays on crossing over in Drosophila. Proc. Soc. Exp. Biol. & Med. 20:335-338. 1923.

———— An effect of x-rays on the linkage of Mendelian characters in the first chromosome of Drosophila. Gen. 8:355-366. 1923.

———— X-rays and mutations. Sci. 69:500-501. 1929.

———— The effect on crossing over and non-disjunction of x-raying the anterior and posteria halves of Drosophila pupae. Gen. 14:129-159. 1929.

Mavor, J. W. and Svenson, H. K.
An effect of x-rays on the linkage of Mendelian characters in the chromosomes of Drosophila melanogaster. Gen. 9:70-89. 1923.

———— X-rays and crossing over. Sci. 58:124-126. 1923.

———— A comparison of the effects of x-rays and temperature on linkage and fertility in Drosophila. Gen. 9: 588-608. 1924.

———— Crossing over in the second chromosome of Drosophila melanogaster in the F_1 generation of x-rayed females. Amer. Nat. 58:311-315. 1924.

Muller, H. J.
Artificial transmutation of the gene. Sci. 66: 84-87. 1927.

———— The effects of x radiation on genes and chromosomes. Sci. 67:82. 1928.

———— The production of mutations by x-rays. Proc. Nat. Acad. Sci. 14:714-726. 1928.

———— The problem of genic modification. Zeitschr. Indukt. Abstam. Vererb. Suppl. 1:234-260. 1928.

———. The production of mutations in some cells of Drosophila melanogaster by means of x-rays. Jour. Exp. Zool. 53:327-372. 1929.

———. The method of evolution. Sci. Mo. 29:481-505. 1929b.

———. Types of visible variations produced by x-rays in Drosophila. Jour. Gen. 22:299-334. 1930.

———. Effect of radiation on morphology of chromosomes and point mutations. Amer. Nat. 64:220-251. 1930.

Muller, H. J. and Altenburg, E.
Chromosome translocation produced by x-rays in Drosophila. Anat. Rec. 41:100. 1928. (abstr.)

———. The frequency of translocation produced by x-rays in Drosophila. Gen. 15:283-311. 1930.

Muller, H. J. and Mott-Smith, L. M.
Evidence that natural radioactivity is inadequate to explain the frequency of natural mutations. Proc. Nat. Acad. Sci. 16:277-285. 1930.

Muller, H. J. and Painter, T. S.
The cytological expression of changes in gene alignment produced by x-rays in Drosophila. Amer. Nat. 63:194-200. 1929.

McKay, J. W. and Goodspeed, T. H.
The effects of x radiation on cotton. Sci. 71:644. 1930.

Nabours, Robert K. and Robertson, W. R. B.
An x-ray induced chromosomal translocation in Appotettix eurycephalus Hancock (grouse locusts). Proc. Nat. Acad. Sci. 19:234-239. 1933.

Navashin, M.
A preliminary report on some chromosome alterations by x-rays in Crepis. Amer. Nat. 65:243. 1931.

Oliver, C. P.
The effect of varying the duration of x-ray treatment upon frequency of mutation. Sci. 71:44-46. 1930.

_____
Complex gene rearrangements induced by x-rays. Anat. Rec. 47:385. 1930. (abstr.)

Olson, A. R. and Lewis, G. N.
Natural radioactivity and the origin of species. Nature, 121:673-674. 1928.

Painter, T. S. and Muller, H. J.
The parallel cytology and genetics of induced translocations and deletions in Drosophila. Jour. Hered. 20:287-298. 1929.

Patterson, J. T.
The effect of x-rays in producing mutations in somatic cells of Drosophila melanogaster. Sci. 68:41-43. 1927.

_____
X-rays and somatic mutations. Jour. Hered. 20: 260-267. 1928.

_____
The production of mutations in the somatic cells of Drosophila by means of x-rays. Jour. Expt. Zool. 53:329-372. 1929.

_____
Proof that the entire chromosome is not eliminated in the production of somatic variations by x-rays in Drosophila. Gen. 15:141-149. 1930.

_____
The production of mosaics in Drosophila by x-rays. Anat. Rec. 47:394. 1930.

_____
Gynaudromorphs by x-rays. Jour. Expt. Zool. 60: 173-203. 1931.

_____
Continuous versus interrupted irradiation and the rate of mutation in Drosophila. Biol. Bul. 61:133-138. 1931.

Patterson, J. T. and Muller, H. J.
Are progressive mutations produced by x-rays? Gen. 15:495-577. 1930.

Plough, H. H.
Radium radiations and crossing over. Amer. Nat. 58:85-87. 1924.

Promptov, A. N.
The effect of short ultraviolet rays in the appearance of hereditary variations in Drosophila melanogaster. Jour. Gen. 26:59-74. 1932.

Sapehin, A. A.
Rontgen mutations in wheat. Zuchter, 2:257-259. 1930.

Serebuovsky, A. S. and Dubinin, N. P.
X-ray experiments with Drosophila. Jour. Hered. 21:259-265. 1930.

Stadler, L. J.
The frequency of mutation in maize. Quoted on p. 33 in Breeding Crop Plants, by Heys, Herbert Kendall and Garber, Ralph John. Second Edition. McGraw-Hill, N. Y. 1927.

_____
Mutations in barley induced by x-rays and radium. Sci. 68:186-187. 1928a.

_____
Genetic effects of x-rays in maize. Proc. Nat. Acad. Sci. 14:69-75. 1928.

_____
Genetic effects of x-rays in maize and barley. Anat. Rec. 37:176. 1928.

_____
The rate of induced mutation in relation to dormancy, temperature and dosage. Anat. Rec. 41:97. 1928. (abstr.)

_____
Some genetic effects of x-rays in plants. Jour. Hered. 21:3-19. 1930a.

———. The frequency of mutation of specific genes in maize. Anat. Rec. 47:381. 1930. (abstr.)

———. The experimental modification of heredity in crop plants. Sci. Agr. 11:557-572. 1931.

Stadler, L. J., Kirkpatrick, R. T., and Tascher, W. R. The effects of x-ray treatment on corn. Mo. Sta. Bul. 300. 1931.

Stadler, L. J.
On the Genetic Nature of Induced Mutations in Plants. Proc. Sixth Int. Congress Plt. Gen. 1:274-294. 1932.

———. On the Genetic Nature of Induced Mutations in Plants. II A Haplo-Viable Deficiency in Maize. Univ. of Mo. Res. Bul. 204. 29 p. 1933.

Student.
Evolution by selection. Eugenics Rev. 24:293-296. 1933.

Svenson, H. K.
On the biologic effects of x-rays. Sci. 69:361. 1929.

Timofeef-Ressovsky, H. A.
Induced gene variations in Drosophila funebris. Jour. Hered. 21:167-71. 1930.

Timofeef-Ressovsky, N. W.
The effect of x-rays in producing somatic genovariations of a definite locus in different directions in Drosophila. Amer. Nat. 63:119-124. 1929.

———. Der stand der erzengung von genovariationen durch Rontgenbestrahlung. Jour. Psych. u. neurol. 39:432-437. 1929.

———. Ruckgenovariationen und die genovariabilitat in vershiedenen Richtungen. I Somatische genovariationen der gene W, w^e und w bie Drosophila unter dem unfluss der Routgenbestrahlung. Roux. Arch. Entw mech. 15:620-635. 1929.

———. Reverse genovariations and gene mutations in different directions. II The production of reverse genovariations in Drosophila by x-ray treatment. Jour. Hered. 22:67-70. 1931.

———. Does x-ray treatment produce a genetic after effect? Jour. Hered. 22:221-223. 1931.

Weinstein, Alexander.
The production of mutations and rearrangements of genes by x-rays. Sci. 67:376-77. 1928.

———. Genetic effects of x-rays and other environmental agents. Anat. Rec. 41:100 (abstr.) 1928.

Whiting, Anna R. and Bostian, Carey H.
The effects of x-radiation of larvae of Habrobracon. Gen. 16:659-680. 1931.

Whiting, P. W.
The production of mutations by x-rays in Habrobracon. Sci. 68:59. 1928.

———. Heredity of miniature (body), an x-ray mutation in Habrobracon. Anat. Rec. 41:106. 1928. (abstr.)

———. X-rays and parasitic wasps. Jour. Hered. 20:269-76. 1929.

Whiting, P. W. and Whiting, Anna R.
The mutant types, x-ray and natural of Habrobracon. Anat. Rec. 44:285. 1929. (abstr.)