ACCUMULATION OF GENETIC EFFECTS AND RETURN TO A HOMEOSTATIC POPULATION IN SUCCESSIVE GENERATIONS OF IRRADIATED *SORGHUM BICOLOR* (L.) MOENCH SEED

by

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ABSTRACT

Two strains, a normal inbred diploid and doubled haploid of Sorghum bicolor (L.) Moench, cultivar 'Tx 403', were irradiated for this study. Gamma ray radiations of 2.5-5.0-7.5 Kr from a cobalt-60 source were applied in 38 treatment combinations. The major portion of the experiment was conducted during 1969 and 1970 using appropriate statistical designs to evaluate a) treatment effects of radiation, b) sensitivity to radiation between strains, c) effects on sensitivity caused by recurrent irradiation, and d) return of an irradiated population in subsequent generations to a homeostatic state equal to that of a nonirradiated population.

The results indicate that a) radiation levels produced a disruption in an immediate generation and not all variables responded similarly, b) strains responded differently, c) sensitivity of effects seemed to be altered by recurrent irradiation, and d) the return to gene equilibrium begins immediately and is achieved by the second generation following irradiation.

CHAPTER 1

INTRODUCTION

For several decades, irradiation studies have been conducted on individual plants and plant populations. An irradiated population is normally screened and those plants not showing abnormalities are usually discarded. Only the mutant plants are retained for study or to develop a new population. The mutants, if allowed to remain and increase in the original population, should cause a shift in the adapted mean for that population and alter its range. The tendency, however, for the population to return to the original mean after several generations may be great enough to bring the population back to a state of gene equilibrium equivalent to that of the original. The equilibrium, or homeostatic state for a population consisting of inbred (homozygous) plants is a result of a particular genotype or genotypes which function as a buffer against fluctuations in the environment, such that the population can maintain an adaptive mean for any character. If radiation changes the buffering genotype, as would be indicated by a shift in the adaptive mean, then the homeostatic state for the treated population, when compared to that of the non-treated population, would also be changed. If the mean for the treated population after subsequent generations returns to the same level as that for the non-treated, it would indicate (especially if controlled by a small number of genes) a return to the same

genotype as expressed in the non-treated population. The treated and non-treated populations should, therefore, once again be in the state of equilibrium and would be expected to function similarly for the character measured in any environment.

The questions that may be considered are: if radiation is applied to successive generations of a population, are the mean and range in variation resulting from each radiation treatment maintained at the new level, or are they shifted and altered even more, or do they immediately start to return to a homeostatic state equivalent to that of the non-irradiated?

To facilitate distinguishing mutants in an irradiated population from normal segregates, a homozygous non-segregating population produced by several generations of selfing is normally used for radiation studies; however, according to the Hardy-Weinburg law, 100 percent homozygosity can never actually be attained by selfing. If the chromosome number of a haploid is doubled, the resulting progeny will theoretically be 100 percent homozygous. In addition to studying shifts in means for various factors, another question to be answered is whether the homozygous diploid population derived by selfing versus the doubled haploid population will respond differently when exposed to identical irradiation dosages?

This study was therefore designed, using Sorghum bicolor (L.) Moench as the test material with the following objectives:

1. Investigate the possible effects of irradiation on the means and ranges of both the inbred diploid and doubled haploid populations.

2. Explore the possibility and rate of return of irradiated populations to a homeostatic state equal to that of the non-irradiated population.

3. Determine how the population sensitivity to radiation is effected by radiation in successive generations.

CHAPTER 2

REVIEW OF LITERATURE

Numerous studies have been reported regarding the effects of ionizing radiation on plants since the classic paper by Muller (1927). Sparrow, Binnington and Pond (1958) summarized the radiation research conducted from 1896 to 1955 and listed 2,580 references relative to the ionizing radiation effects on higher plants. The summary did not even include the vast number of references concerning the effect of ultraviolet radiation on plants. There is a plethora of information relative to irradiation of plants, such as, techniques, dosages, and effects on different species, but little has been published relevant to the return of an irradiated population of higher plants to a homeostatic state equal to that of the original or to the sensitivity of a population to recurrent irradiation.

Harris, Burton, and Johnson (1965) published one of the most recent and comprehensive studies on the effects of gamma radiation on Sorghum bicolor. They studied the radiation effects in the X_1, X_2, X_3, and X_4 generations for two cultivars, Shallu and Redbine 60, in which dormant seed had been treated with 0, 10, 20, 30, 40, 50 Kr of gamma radiation. They found that in the X_1 generation, all irradiation levels produced observable effects on the population for the characters studied. In the X_2 generation, those effects had decreased substantially. In a

grain yield trial conducted with X_3 and X_4 populations, no significant differences were attributed to any previous irradiation treatment irregardless of the dosage level.

During the X_1 generation, Harris et al. (1965) observed a significant increase in growth rate for shallu seedlings up to 10 days following the planting of seed that had received radiation at low dosage levels, but at higher dosage levels the growth rate was decreased. The height of mature plants originating from irradiated seed was reported to be reduced significantly as compared to the check for all treatment levels. This observation agrees with that of Sax (1955) who noted that mature plant height was inversely related to dosage and that the response was in approximately the same proportion as a change in dosage.

Harris et al. (1965) also found in the X_1 generation that head length for Redbine 60 was reduced significantly as compared to the check, but in an inverse relationship to the radiation level; whereas, Shallu did not exhibit this variation. He recorded that regardless of treatment neither variety reflected a change in the number of days required to reach mid-anthesis. The number of tillers per plant were found to increase directly as an effect of dosage levels. This increase in tiller number was probably a secondary growth response directly related to an increase in sterility associated with increased radiation dosages. Sterility as used by Harris et al. (1965) was defined as the total weight of all the seed per linear inch of head; therefore, a sterility percentage indirectly reflects the number of seed set on the head. A low weight of seed indicates low fertility and vice versa. Similarly, Kaukis and Webster

(1956) reported a 19.8 percent sterility for an X_1 population as estimated by the number of florets setting seed, which measures the same character as reported by Harris et al. (1965) but by a different technique.

Harris et al. (1965) reported that the grain yield for an X_1 generation, as measured by weight of seed per head, was inversely related to the radiation dosage. He also found that the weight of 100 seed (seed index) increased with larger dosages which was probably due to an increase in sterility and the subsequent storage of metabolic products in fewer seed thereby resulting in heavier individual seed.

For an X_2 generation, Harris et al. (1965) reports no significant difference between treatment levels for seedling emergence, days to mid-anthesis, mature plant height, uniformity of head length, or head length which might suggest that potential seed set should have been approximately the same on each head. The total weight of seed per head, however, was significantly reduced with higher dosages; whereas, the weight of 100 seed was increased as in the X_1 generation, which again suggests that the fewer seed on each head were individually larger but collectively weighed less since there were less of them. In the X_2 generation sterility was most evident at the 50 Kr level.

Kaukis and Webster (1956) exposed original parental seed to 50 Kr of X-ray radiation and observed 19.8 and 8.3 percent sterility in the X_1 and X_2 generations respectively. Fertility was improving and this character was apparently returning to a homeostatic state in the population.

In an X_3 yield test, Harris et al. (1965) found no significant differences for treatment levels. Likewise, an X_4 yield test grown from samples of seed collected from the X_3 test was reported to exhibit the same results for all treatment levels. Their research would suggest that by the X_3 generation the character had returned to a homeostatic state for the population similar to the findings reported by Kaukis and Webster (1956).

Abrams (1956) records the sensitivity of six different oat varieties to recurrent X-ray irradiation of dormant seed for consecutive generations. He considered recurrent irradiation could be applied in three sequences: 1) irradiation of the seed from each generation for three consecutive generations, 2) irradiation of the seed from each generation for two consecutive generations, or 3) irradiation of the seed from an X_2 population.

Abrams (1956) concluded that recurrent irradiation cause the sensitivity (as described in sequence 1 and 2) of a population, as measured by germination percentage and seedling height, to increase directly with the number of successive generations exposed to radiation. He further observed that irradiating X_3 seed from an X_2 population and irradiation seed with no previous irradiation history produced populations exhibiting similar effects for germination percentages and seedling height. This observation suggests that sensitivity due to radiation was essentially lost in two generations of selfing and that the population had returned to a homeostatic state equivalent to that expressed in the non-irradiated population. Sensitivity, as used here, describes the condition of a plant

by successive treatments such that the effects produced becomes somewhat additive to the plant. To describe sensitivity differently, an initial irradiation of a population may require a given Kr level to produce a measurable or observable effect; however, successive dosages at lower levels might produce the same or greater expression of effects. It could be assumed, therefore, that the population had become more sensitive to irradiation because after receiving the first dosage any additional irradiation may result in greater observable effect even if all the dosages are the same.

There is no question that irradiation of seed causes a disruptive effect on the genetic architecture of a plant, but to what extent the alteration will effect subsequent generations of plants, particularly Sorghum bicolor, is not fully known. A survey of literature indicates that the return towards a homeostatic state or genetic equilibrium starts immediately. Apparently an equilibrium is reached by the X_3 or X_4 generations for the characters reported; however, in oats, if the population is irradiated for consecutive generations, the effect of the disruption in the genotypic balance may be maintained. The research reported in the present study is designed to verify previous work and eluciate additional irradiation treatments in X_3 and X_4 populations as well as make comparisons with the X_1 and X_2 generations.

CHAPTER 3

MATERIALS AND METHODS

Two strains, inbred diploid and doubled haploid of sorghum cultivar 'Tx 403', were used in this study. In June 1967, a small seed lot of each of these two strains was received from Dr. K. F. Schertz, USDA-ARS, College Station, Texas. To obtain enough seed to conduct this study, the original seed lots were increased at The University of Arizona Campbell Avenue Farm, Tucson, during the summer of 1967. Parental seed will designate the seed obtained from this particular seed increase.

All radiation treatments were applied to dormant seed in a cobalt-60 gamma ray device by the personnel of the Nuclear Engineering Department of The University of Arizona. Seed lots were removed from the unit at predetermined time intervals designed to provide the prescribed radiation dosages chosen.

Recurrent irradiation as referred to in this study will be considered as being of the following types: 1) irradiation for three successive generations, 2) irradiation for two successive generations, or 3) irradiation of seed from the X_2 generation. An explanation of the symbols that will be used in the text to represent the various population types is given in table 1.

Table 1. Symbols used in representing irradiated and nonirradiated plant populations

Symbol	Explanation
X_0	Seed advanced one generation with no irradiation history
X_1	First irradiated generation
X_2	Second generation after irradiation
X_3	Third generation after irradiation
X_4	Fourth generation after irradiation
X_2X_1	Irradiated X_2 seed
X_3X_2	Progeny from X_2X_1 population
X_4X_3	Progeny from X_3X_2 population
X_3X_1	Irradiated X_3 seed
X_4X_2	Progeny from X_3X_1 population
$X_3X_2X_1$	Irradiated X_2X_1 seed
$X_4X_3X_2$	Progeny from the $X_3X_2X_1$ population

In the winter of 1967-1968, seed of the two parental strains, normal diploid and doubled haploid, were divided into 19 lots each making a total of 38 lots. Eight lots from each strain were exposed to the gamma radiation dosages shown in table 2. The 16 treated (eight normal diploid and eight doubled haploid) lots and one non-irradiated lot from each strain were planted in the greenhouse. The heads from these plants were bagged prior to anthesis to ensure self-fertilization, and the resulting seed were bulked separately by dosage level. The ten remaining seed samples listed in table 2 and not used in 1967-1968 were saved for subsequent plantings.

In the summer of 1968, five more of the parental seed lots from each of the two strains were exposed to gamma radiation at the dosage levels shown in table 2. These X_1 seed and a nonirradiated parental lot from each strain were planted with the X_2 seed, the recurrent irradiated X_2X_1 seed, and the seed from the nonirradiated populations which had been grown in the greenhouse during the winter 1967-1968. This 1968 summer planting was grown in a block at the Campbell Avenue Farm of The University of Arizona. Just before these plants began to bloom, their heads were bagged. Equal numbers of seed from each head produced in 1968 were bulked according to irradiation dosages and grown in 1969.

During the summer of 1969, three of the remaining parental lots from each strain were radiated at the dosage levels shown in table 2. These X_1 seed and the two remaining parental seed lots were planted together with the seed harvested from the plants grown

Table 2. Gamma radiation levels (Kr) applied to both normal diploid and doubled haploid seed in given years

Treatment Number	Winter 1967-68	1968	1969	1970
1	0 X_0	0 X_0	0 X_0	0 X_0
2	2.5 X_1	2.5 X_2X_1	2.5 $X_3X_2X_1$	0 $X_4X_3X_2$
3	2.5 X_1	2.5 X_2X_1	0 X_3X_2	0 X_4X_3
4	2.5 X_1	0 X_2	2.5 X_3X_1	0 X_4X_2
5	2.5 X_1	0 X_2	0 X_3	0 X_4
6	5.0 X_1	0 X_2	0 X_3	0 X_4
7	5.0 X_1	2.5 X_2X_1	0 X_3X_2	0 X_4X_1
8	5.0 X_1	0 X_2	2.5 X_3X_1	0 X_4X_2
9	7.5 X_1	0 X_2	0 X_3	0 X_4
10	*	0 X_0	0 X_0	0 X_0
11	*	2.5 X_1	2.5 X_2X_1	0 X_3X_2
12	*	2.5 X_1	0 X_2	0 X_3
13	*	5.0 X_1	0 X_2	0 X_3
14	*	5.0 X_1	2.5 X_2X_1	0 X_3X_2
15	*	7.5 X_1	0 X_2	0 X_3
16	*	**	0 X_0	0 X_0
17	*	**	2.5 X_1	0 X_2
18	*	**	5.0 X_1	0 X_2
19	*	**	7.5 X_1	0 X_2

* Seed not irradiated or grown in Winter 1967-68
** Seed not irradiated or grown in 1968
Kr = Kiloroentgen

in 1968. This 1969 planting consisted of 38 entries each was grown in two replications at the Campbell Avenue Farm. Each entry was planted in a single row 3.75 meters long. To ensure obtaining a representative sample of the population 25 plants from each entry of each replication were used for tabulating data. Each of the 25 plants per entry were observed daily and when approximately 50 percent of the florets on the main head of each plant had opened the bloom date was recorded. Simultaneously at the 50 percent anthesis, the head was bagged for self-pollination of the remainder of the head

At maturity, each bagged head was cut at the top of the flag leaf sheath and the remainder of the plant was measured for height data. The portion of the peduncle from the lowest floret branch to where it was cut from the plant was excised from the head portion and measured for length which will be referred to hereafter as head exsertion. The head was measured for length and weighed.

Since the heads were not covered with bags until they had reached 50 percent anthesis, there was a possibility of having cross-pollinated seed in the top portion; therefore, the head was cut in half to ensure obtaining a supply of self-pollinated seed from the lower half. The top and bottom portions of each were threshed individually and the seed were weighed. Three hundred seed from the lower half of the head were weighed to provide a seed index for the head. These three hundred seed plus the remaining seed from the lower half were then bulked according to treatment to obtain seed to plant in a yield trial.

In 1970, all 19 treatments for each strain were planted in a replicated yield trial at the Arizona Agriculture Experimental Farm located at Marana, Arizona, in dry soil on May 14 and irrigated on May 26. The trial contained 38 entries planted in eight replications using a randomized split plot design. The treatment levels served as main plots, and the diploid and doubled haploid strains within each treatment served as paired subplots. Each subplot consisted of two 8.5 X 1 meter rows with 0.61 meter alleys and were seeded at a rate of 728 seed per subplot.

Originally, for the 1970 experiment, a number of agronomic characters were to have been studied depending on the extent to which they expressed variation among treatments; however, the only agronomic character showing visible variation in the field among treatments was the date of 50 percent anthesis. For this reason, bloom date, yield and percent crude protein were the only characters for which data were collected. When the plots reached maturity, each subplot was harvested with a plot combine and the grain weighed. From two replications, approximately one kilogram of seed was retained from each entry to be used for determining the percentage of protein. The protein analyses were performed by the personnel of the Poultry Science Department of The University of Arizona.

Analysis of Data

Values for several characteristics for each of the 24 plants per entry grown in 1969 were obtained by using values from the seven measured variables (date of 50 percent bloom, height to top of flag

leaf sheath, head exsertion, head length, total head weight, total seed weight per plant, and weight of 300 seed) from which to calculate them. Days to 50 percent anthesis was derived from the 50 percent bloom date. Height to top of flag leaf sheath, head exsertion, and head length measurements were summed to obtain a value for total plant height. Total seed weight per head and total weight per head values were used to calculate a threshing percentage. The values for total seed weight, weight of 300 seed, and total head weight were used to calculate the total number of seed per linear centimeter of head.

The above ten variables, assuming days to 50 percent anthesis to be a synonymous measurement for date of 50 percent bloom, were evaluated for each of the plants observed in the 1969 planting. A mean value for each of these variables within each treatment was calculated. These means were used as individual observations in making a randomized complete block analysis as described by Steel and Torrie (1960). By this procedure the error due to location was removed even though the treatments were arranged in identical order in each replication. Treatment means were compared using the Duncan's new multiple-range test.

For the 1970 data, the date of 50 percent bloom was reported as days to 50 percent anthesis (the two descriptions being synonymous). The yield weight per subplot, percent protein, and days to 50 percent anthesis were statistically compared by using the split plot analysis. Specific means were compared by using the least significant difference test.

CHAPTER 4

RESULTS AND DISCUSSION

1969 Experiment

In 1969, ten variables were evaluated in Sorghum bicolor populations derived from normal diploid or doubled haploid seed sources. Seed of these two strains had been treated with various levels and in various generations with cobalt-60 gamma ray radiation. The study was so designed that each variable was measured for 38 different treatment populations. A summary of the data tabulated for each treatment within each strain is given in appendix tables A-1 and A-2.

For 1969, the ten variables on which data were tabulated for each population were as follows: 1) days to 50 percent anthesis, 2) height to top of flag leaf sheath, 3) head exsertion, 4) head length, 5) total head weight, 6) total seed weight per head, 7) threshing percent, 8) weight of 300 seed, 9) total number of seed per linear centimeter of head, and 10) total plant height. Of these variables observed only total plant height and number of seed per linear centimeter demonstrated significant differences between radiation treatments and, therefore, merit further discussion. Total plant height was statistically significant at the 0.01 level (table 3). The total number of seed per

Table 3. Significance between irradiation treatments as measured by total plant height, Tucson, Arizona, 1969

Source of Variation	D. F.	M. S.
Replication (R)	1	
Irradiation Treatments (T)	37	8.2
Error	37	3.2

linear centimeter of head, likewise responded to treatment (table 5), but at a lesser degree (0.10 level) than total plant height. Fundamental to any consideration of the return of a population to a homeostatic state or the effects on the sensitivity of the population to reccurrent irradiation treatment, the following questions must be answered: were the radiation levels used sufficient to cause a phenotypic disruption in the population? The entries for 1969 were analysed as being individual treatments to evaluate the effects of radiation disregarding the strain. This analysis detected statistically significant differences among the treatment levels. Examination of the overall analyses of factors considered would suggest that the characters responding to treatment and for which observations could be measured were probably the variables of a qualitative nature and perhaps controlled by the smallest number of genes. Total plant height is probably the least affected by environmental conditions of all the factors studied followed by total number of seed set per linear centimeter of head. The total number of seed per linear centimeter of head is the results of an interaction of the environment and the genetic factors controlling fertility in the flower (perhaps a relatively small number of genes); with the number of seed being under genetic control, but with the actual number being effected by environment. The other genetic factors not discussed here and statistically not significant are possibly more quantitative in action, or the

measurement techniques were not sophisticated enough to detect the smaller magnitude of differences.

Since there is statistical support that the basic treatments were effective and sufficient to disrupt the adapted population means, then the two strains can be compared to determine whether they differ in their sensitivity. Table 4 specifically compares total plant height means for each radiation treatment. The two strains, doubled haploid and normal diploid, appear to respond differently to irradiation as exhibited by the fact that five population means of the doubled haploid strain showed significant differences, whereas, only three population means of the normal diploid strain were different.

Using the same 38 populations as described for total plant height, table 5 reveals that irradiation treatments as measured by total number of seed per linear centimeter of head showed significant differences among them at the 0.10 level. This level of significance strongly suggests that radiation treatment did have an effect upon the entire plant population, but the effect was not of the same magnitude as that on total plant height.

Table 6 specifically compares the mean total number of seed per linear centimeter of head for the radiation treatments. As observed for total plant height the two strains appear to react differently to the treatments. For example, the means for the normal diploid range from 42 to 22 total seed per linear centimeter whereas, the doubled haploid means for the total number of seed per linear centimeter ranged from 44 to 18. This greater range in the means for the doubled haploid

Table 4. Comparison of total plant height means for irradiation treatment levels for normal diploid and doubled haploid, Tucson, Arizona, 1969

Irradiation Treatments	Generation	Normal Diploid	Doubled Haploid
0	X_0	68.1 abc	70.8 ab
0-0	X_0X_0	70.5 ab	68.7 abc
0-0-0	$X_0X_0X_0$	68.5 abc	68.3 abc
2.5	X_1	68.7 abc	70.0 abc
2.5-2.5	X_2X_1	67.5 abc	68.3 abc
2.5-2.5-2.5	$X_3X_2X_1$	66.7 bc	70.0 abc
2.5-0-0	X_3	71.5 a	69.6 abc
2.5-0	X_2	69.2 abc	67.2 abc
2.5-2.5-0	X_3X_2	68.2 abc	66.7 bc
2.5-0-2.5	X_3X_1	69.8 abc	67.6 abc
5.0	X_1	69.9 abc	68.4 abc
5.0-2.5	X_2X_1	67.3 abc	69.4 abc
5.0-2.5-0	X_3X_2	67.4 abc	71.4 a
5.0-0	X_2	68.5 abc	66.9 bc
5.0-0-0	X_3	69.7 abc	68.3 abc
7.5	X_1	69.7 abc	68.3 abc
7.5-0	X_2	71.0 ab	71.1 ab
7.5-0-0	X_3	70.1 abc	65.7 c

Table 5. Significance between irradiation treatments as measured by number of seed per linear centimeter of head, Tucson, Arizona, 1969

Source of Variation	D. F.	M. S.
Replication (R)	1	
Irradiation Treatments (T)	37	73.5+
Error	37	44.0

+ Significance at .10 level

Table 6. Comparison of the means for the total number of seed per linear centimeter of head for irradiation treatment levels for normal diploid and doubled haploid, Tucson, Arizona, 1969

Irradiation Treatments Kr	Generation	Normal Diploid	Doubled Haploid
0	X_0	35.7 abcd	40.4 ab
0-0	X_0X_0	37.4 abcd	38.2 abc
0-0-0	$X_0X_0X_0$	36.5 abcd	38.7 abc
2.5	X_1	37.7 abcd	40.4 ab
2.5-2.5	X_2X_1	31.5 abcde	30.5 abcde
2.5-2.5-2.5	$X_3X_2X_1$	27.8 abcde	36.4 abcd
2.5-0-0	X_3	42.1 ab	37.3 abcd
2.5-0	X_2	37.4 abcd	35.6 abcd
2.5-2.5-0	X_3X_2	34.3 abcd	33.5 abcde
2.5-0-2.5	X_3X_1	32.4 abcde	34.2 abcd
5.0	X_1	26.0 acde	25.7 bcde
5.0-2.5	X_2X_1	22.6 cde	35.8 abcd
5.0-2.5-0	X_3X_2	29.7 abcde	39.0 ab
5.0-0-2.5	X_3X_1	30.4 abcde	35.0 abcd
5.0-0	X_2	34.6 abcd	35.0 abcd
5.0-0-0	X_3	41.5 ab	35.8 abcd
7.5	X_1	21.7 de	17.7 e
7.5-0	X_2	32.6 abcde	43.5 a
7.5-0-0	X_3	26.4 abcde	26.9 abcde

strain may indicate a greater sensitivity to radiation for that strain; furthermore, the number of means exhibiting significant differences within the doubled haploid strain is greater than is the number in inbred diploid.

To evaluate the data collected in this study to determine if an irradiated population did return to a homeostatic state equivalent to that of the original, several criteria must be considered. First, were the nonirradiated check populations for all generations homogeneous? This would demonstrate that the original population was stable for the duration of the experiment. Second, did the radiation exposure cause a disruption in the adapted mean for the X_1 or X_2 generation as compared to its nonirradiated check? Thirdly, after this disruption did the mean for the irradiated population return to the mean level of the corresponding nonirradiated check population? To have the preceding criteria valid one assumption must be made, when the X_2, X_3, or X_4 populations were at the X_1 or X_2 generation, they reacted to radiation as did the X_1 and X_2 populations which were actually tested. These considerations were met with the mean for the total number of seed per linear centimeter of head and the appropriate mean comparisons are exhibited in the appendix tables, A-3 and A-4.

All of the comparisons tested to determine a return to the original homeostatic state as measured by the total number of seed per linear centimeter of head for the inbred diploid population proved to be homogeneous. This indicates that the X_1 population did not

exhibit a significant difference from the nonirradiated checks which makes it impossible to detect a return to a homeostatic state equivalent to that of the original since, by definition it was never out of equilibrium.

For the doubled haploid strain, the means for the total number of seed per linear centimeter for the X_0, X_0X_0, and $X_0X_0X_0$ checks were all homogeneous with each other when compared in all possible combinations, indicating that the original population was stable.

In the X_1 (2.5 Kr) population, the mean for the total number of seed per linear centimeter was statistically the same as the X_0 check suggesting that the 2.5 Kr level of radiation in one dosage did not disrupt the population mean and may be eliminated in any further comparisons for determining a return to equilibrium. The means for the X_1 generations 5.0 Kr and 7.5 Kr exhibited a significant difference from the corresponding X_0 check which indicates that these two levels of radiation disrupted the original stable mean for the total number of seed per linear centimeter of head.

When the means for the total number of seed per linear centimeter of head for the X_2 populations for 5.0 Kr and 7.5 Kr were compared with the X_0X_0 nonirradiated check mean there were no differences. The means for the X_3 populations for 5.0 Kr and 7.5 Kr were, likewise, in complete agreement with the mean for the $X_0X_0X_0$ check. The X_2 and X_3 generations were, therefore, assumed to have exhibited a significant response to radiation when they were X_1 populations. As a result, it follows that

in one generation the disrupted mean for the total number of seed per linear centimeter of head had returned to the same level of equilibrium as its nonirradiated check.

This immediate return to the original homeostatic state for the total number of seed per linear centimeter may be expected because this measurement is an indication of the number of fertile florets on the head. The factors favoring fertility are naturally selected and the ones causing sterility are lost which results in higher fertility in the next generation.

Sensitivity as defined earlier describes the conditioning of a plant by successive treatments such that the measured effect is somewhat additive in the plant. To help establish whether sensitivity is altered by recurrent irradiation, several specific considerations must be made. First, does the mean of the recurrently irradiated population vary significantly from its corresponding nonirradiated population mean and secondly, to what extent does the accumulative effect from recurrent irradiation in successive generations agree with the effect caused by the same total amount of radiation applied in one generation. To evaluate the effects on sensitivity, the means of the total number of seed per linear centimeter were tested for these two considerations. For the normal diploid and doubled haploid, the means from the recurrent irradiated population all revealed statistical agreement (appendix tables A-3, A-4) with their corresponding nonirradiated population means. Because this first comparison is critical in detecting effects on sensitivity, nothing can be said concerning it even though the doubled haploid mean

comparison for X_1 (7.5 Kr) treatment versus the $X_3X_2X_1$ (2.5-2.5-2.5 Kr), X_2X_1 (5.0-2.5 Kr), and X_3X_1 (5.0-0-2.5 Kr) were significantly varied. This was most likely caused by the low mean value for the X_1 (7.5 Kr) treatment.

1970 Experiment

The 1969 data was based on two replications for each treatment and the populations were relatively small. The comparisons, therefore, were less precise than desired, but considered reliable because in 1970, enough seed had been produced from the 1969 experiment to preform a statistical test of the populations using a split plot design with eight replications and the results did not differ. In this test, three variables grain yield, days to 50 percent anthesis, and percent crude protein were tabulated. Because protein analysis is very time consuming, and the percent of protein is a rather stable factor in a cultivar, data was collected for two replications rather than eight.

Due to the greater number of replication used in the 1970 portion of the study, it could be considered a more accurate test of the true treatment differences.

Table 7, summarizes an analysis for grain yield per subplot data which gives statistical support to what was observed as being significant in 1969 - treatments were sufficiently high, strains differed, and interaction between strains occurred. The radiation treatments were different at the 0.05 percent level, and the response between strains was significantly different at 0.01 level which gives

Table 7. Significance between irradiation treatments as measured by grain yield, Marana, Arizona, 1970

Source of Variation	D. F.	M. S.
Replication (R)	7	12.85
Irradiation Treatments (A)	18	2.59
Error (a)	126	1.53
Strains (B)	1	14.50
Interaction (AB)	18	1.96
Error (b)	133	0.76

statistical support to what could only be implied from the 1969 data. The highly significant interaction could be explained as being due to different reactions to radiation treatments between strains.

The same criteria and comparisons as were used to determine a return to the original homeostatic state and to determine the effect on sensitivity by recurrent irradiation on a population for the 1969 data were used again for the 1970 data evaluation. The one difference from the 1969 evaluation being that all the populations had advanced one generation.

For the normal diploid, the treatment mean comparisons for grain yield designed to determine a return to the original homeostatic state were all non-significant (appendix table A-5) indication that a disruption in the equilibrium had not taken place.

The normal diploid X_3X_2 (2.5-2.5 Kr) population as measured by grain yield agreed with the criteria for indicating an effect on sensitivity to radiation as a result of recurrent irradiation. The mean for the X_3X_2 (2.5-2.5 Kr) population was significantly different from its corresponding nonirradiated $X_0X_0X_0$ population mean and from the population mean which had received the same total amount of irradiation, but in one generation (appendix table A-5). This particular results would indicate that there may be some conditioning by the first treatment such that the following treatment had a greater effect. If this is the case, then the $X_4X_3X_2$ (2.5-2.5-2.5 Kr) population mean should have exhibited a difference from the nonirradiated check mean,

but it did not. As a result, the indication of increased sensitivity for the X_3X_2 (2.5-2.5 Kr) population may be questionable.

The doubled haploid X_2 (5.0 Kr) population is the one that most clearly illustrates a return to the original homeostatic state for grain yield. The X_2 (5.0 Kr) treatment mean showed a significant difference from the nonirradiated check mean, and the appropriate X_3 (5.0 Kr) and X_4 (5.0 Kr) population means agreed with their corresponding check population means (appendix table A-6).

The yield data indicated that recurrent irradiation produced some effect on the sensitivity for two doubled haploid populations. Both the X_4X_2 (2.5-2.5 Kr) and X_4X_2 (5.0-2.5 Kr) population means demonstrated statistical differences from the nonirradiated $X_0X_0X_0X_0$ population means. They also exhibited differences from the means for the populations which had received the same total amount of radiation, but in one generation (appendix table A-6). Interestingly, these two treatments had one generation of nonirradiation between irradiation treatments. If this character does return to a homeostatic state equivalent to that of the nonirradiated as indicated, then the new level of sensitivity must in some way be maintained within the plant but without showing phenotypic expression which also makes the effect on the sensitivity of the population questionable.

The data for days to 50 percent anthesis are evaluated in table 8. Differences among treatments were significant at 0.01 level which adds support to the hypothesis that the radiation treatments were

Table 8. Significance between irradiation treatments as measured by days to 50% anthesis, Marana, Arizona, 1970

Source of Variation	D. F.	M. S.
Replication (R)	7	
Irradiation Treatments (A)	18	3.14
Error (a)	126	1.46
Strains (B)	1	5.20
Interaction (AB)	18	1.09
Error (b)	133	1.35

disruptive to the population, but there was no difference in strain response.

For the doubled haploid mean comparisons (appendix table A-7), the X_2 (2.5 Kr) and X_2 (5.0 Kr) population means for days to 50 percent anthesis were significantly different from the mean for the X_0X_0 population. The X_3 (2.5 Kr) and X_4 (2.5 Kr) population means expressed agreement with their respective nonirradiated $X_0X_0X_0$ and $X_0X_0X_0X_0$ population means. This evaluation indicates that the disrupted mean for this character had returned to equilibrium by the X_3 generation.

The date for percent crude protein are summarized in table 9. There were no significant differences for irradiation treatments, between strains or interaction.

Table 9. Comparison of irradiation treatments as measured by percentage crude protein, Marana, Arizona, 1970

Source of Variation	D. F.	M. S.
Replication (R)	1	
Irradiation Treatments (A)	18	0.44
Error (a)	18	0.31
Strains (B)	1	0.81
Interaction (AB)	18	0.09
Error (b)	19	0.07

CHAPTER 5

SUMMARY, CONCLUSIONS, AND SUGGESTIONS

The data presented for this research report was used to evaluate the original hypothesis of: 1) is it possible to disrupt the adapted mean for a sorghum population through radiation, and do the inbred diploid and doubled haploid strains respond differently, 2) is the sensitivity of a strain to radiation effected by radiation, and 3) how soon does the disrupted population mean return to equilibrium?

By subjecting Sorghum bicolor populations of inbred diploid and doubled haploid seed to radiation treatments of 0-2.5-5.0-7.5 Kr in various combinations over several generations, the following conclusions are made:

1. Radiation treatments will produce a disruption in an immediate generation that can be measured by agronomic charaters.

2. Inbred diploid and doubled haploid strains exhibit different responses to treatments and at least the theoritically more homozygous the strain the more evident the effect.

3. The total plant height, total number of seed per linear centimeter of head, grain yield, and days to 50 percent anthesis are factors that best evaluate treatment effects.

4. Variables that show very small effects from radiation or are only a component of some other factor, such as head exsertion, threshing percentage do not make good criteria for treatment evaluation with the techniques used in this study.

5. A return to the equilibrium defined in this thesis and as measured by treatment means is achieved in the second generation after treatment.

6. It appears that recurrent irradiation is more disruptive to the population mean than is the same amount of radiation in one dosage; however, some of the results are questionable.

Suggestions

1. Increase the amount of seed radiated so that data may be accumulated relative to radiation levels that are sufficiently high to include lethality in the test populations.

2. Include an X_1 population and X_0 population in all comparisons especially for determining a return to equilibrium.

3. Radiate dry seed, and seed immediately after germination for comparison of effects.

4. Accumulate enough parental seed so that the early irradiated populations may be sufficiently replicated, and data collected from them for comparison over years.

APPENDIX A

VARIABLE MEANS AND SPECIFIC TREATMENT MEAN COMPARISONS

Table A-1. Means of pariables observed for the normal diploid strain at various irradiation levels, Tucson, Arizona, 1969

Treatment	Population	Days to 50% Anthesis	Height to top of flag leaf sheath (cm)	Head Exsertion (cm)	Head Length (cm)	Total Head Weight (gm)	Total Seed Weight (gm)	Threshing Percent	Weight of 300 seed (gm)	Total number of seed per linear centimeter of head	Total plant height (cm)
0	X_0	51	35.2	16.5	16.3	21.6	14.8	63.2	6.7	35.7	68.1
0-0	X_0X_0	50	35.2	18.3	16.9	20.6	13.9	65.2	6.9	37.4	70.5
0-0-0	$X_0X_0X_0$	51	35.5	16.2	16.8	20.8	13.8	62.5	7.4	36.5	68.5
2.5	X_1	50	35.3	17.0	16.4	22.0	15.3	66.0	7.3	37.7	68.7
2.5-2.5	X_2X_1	52	35.7	15.0	16.6	21.5	14.7	61.1	7.3	31.5	67.5
2.5-2.5-2.5	$X_3X_2X_1$	52	35.2	15.3	16.2	17.7	11.9	64.0	8.1	27.8	66.7
2.5-0-0	X_3	50	37.0	16.6	17.9	26.6	18.3	68.0	7.5	42.1	71.5
2.5-0	X_2	50	35.0	17.2	17.0	22.6	15.7	63.1	6.8	37.4	69.2
2.5-2.5-0	X_3X_2	51	34.8	16.2	17.1	20.3	14.5	61.1	7.0	34.3	68.2
2.5-0-2.5	X_3X_1	50	35.4	17.7	16.7	19.2	13.1	66.2	7.4	32.4	69.8
5.0	X_1	50	35.1	18.1	16.8	17.5	11.9	59.1	8.3	26.0	69.9
5.0-2.5	X_2X_1	54	35.0	15.4	16.9	17.4	10.8	50.3	7.4	22.6	67.3
5.0-2.5-0	X_3X_2	52	34.5	16.6	16.3	15.2	9.6	56.5	5.5	29.7	67.4
5.0-0-2.5	X_3X_1	52	34.3	15.9	16.7	18.2	11.8	55.3	6.5	30.4	66.9
5.0-0	X_2	51	35.5	16.1	16.9	20.0	13.2	62.5	7.0	34.6	68.5
5.0-0-0	X_3	50	35.4	19.0	17.0	23.5	16.8	69.4	7.6	41.5	69.7
7.5	X_1	51	35.8	16.8	17.1	16.8	10.8	51.6	7.8	21.7	69.7
7.5-0	X_2	51	35.8	17.9	17.4	21.5	14.4	61.1	7.4	32.6	71.0
7.5-0-0	X_3	51	27.2	15.1	17.8	17.8	11.7	57.2	7.5	26.4	70.1

Table A-2. Means of Variables observed for the doubled haploid strain at various irradiation levels, Tucson, Arizona, 1969

Treatment	Population	Days to 50% Anthesis	Height to top of flag leaf sheath (cm)	Head Exsertion (cm)	Head Length (cm)	Total Head Weight (gm)	Total Seed Weight (gm)	Threshing Percent	Weight of 300 seed (gm)	Total number of seed per linear centimeter of head	Total plant height (cm)
0	X_0	50	35.3	18.9	16.5	20.9	14.1	61.8	5.8	40.4	70.8
0-0	X_0X_0	51	35.3	16.7	16.6	18.6	12.3	62.4	7.4	38.2	68.7
0-0-0	$X_0X_0X_0$	50	35.0	16.4	16.9	18.9	12.5	63.0	5.9	38.7	68.3
2.5	X_1	50	36.4	16.3	17.2	24.7	16.9	66.2	7.7	40.4	70.0
2.5-2.5	X_2X_1	51	34.7	17.3	16.3	17.7	11.8	65.0	7.3	30.5	68.3
2.5-2.5-2.5	$X_3X_2X_1$	51	36.7	15.1	18.1	25.5	17.1	61.4	7.5	36.4	70.0
2.5-0-0	X_3	50	34.3	18.5	16.8	20.0	13.5	63.1	6.0	37.3	69.0
2.5-0	X_2	52	33.7	16.8	16.8	17.9	11.4	55.5	6.0	35.6	67.2
2.5-2.5-0	X_3X_2	51	36.5	12.7	17.5	21.2	13.2	53.5	6.1	33.5	66.7
2.5-0-2.5	X_3X_1	52	35.9	15.1	16.6	22.1	14.4	60.0	8.2	34.2	67.6
5.0	X_1	51	34.9	16.3	17.3	19.6	13.5	53.9	8.3	25.7	68.4
5.0-2.5	X_2X_1	50	36.0	15.8	17.5	23.6	15.9	60.6	7.3	35.8	69.4
5.0-2.5-0	X_3X_2	50	35.2	18.9	17.3	20.3	13.1	62.2	6.0	39.0	71.5
5.0-0-2.5	X_3X_1	51	34.7	17.0	17.1	21.6	13.9	57.0	6.2	35.0	68.9
5.0-0	X_2	51	34.2	14.7	18.1	25.5	18.4	53.5	7.0	35.0	66.9
5.0-0-0	X_3	50	35.1	16.7	16.8	20.8	15.5	63.1	7.4	35.8	68.3
7.5	X_1	53	34.8	16.4	17.0	15.7	9.2	44.5	7.5	17.7	68.3
7.5-0	X_2	50	36.3	17.7	17.1	23.8	16.2	64.4	6.4	43.5	71.1
7.5-0-0	X_3	52	33.6	14.9	17.8	20.3	13.4	56.7	9.1	26.9	65.7

Table A-3. Comparisons of the check treatments versus the test treatments for the number of seed per linear centimeter of head for the normal diploid strain, Tucson, Arizona, 1969

Checks		Test Treatments					
Generation Treatment Levels Kr	$\bar{x}$	Generation Treatment Levels Kr	$\bar{x}$	Generation Treatment Levels Kr	$\bar{x}$	Generation Treatment Levels Kr	$\bar{x}$
X_0 0	37.5	X_0X_0 0-0	37.4	$X_0X_0X_0$ 0-0-0	36.5		
X_0X_0 0-0	37.4	$X_0X_0X_0$ 0-0-0	36.5				
X_0 0	37.5	X_1 2.5	37.7	X_1 5.0	26.0	X_1 7.5	21.7
X_0X_0 0-0	37.4	X_2 2.5-0	37.4	X_2 5.0-0	34.6	X_2 7.5-0	32.6
$X_0X_0X_0$ 0-0-0	36.5	X_3 2.5-0-0	42.1	X_3 5.0-0-0	41.5	X_3 7.5-0-0	26.4
$X_0X_0X_0$ 0-0-0	36.5	$X_3X_2X_1$ 2.5-2.5-2.5	27.8	X_3X_1 2.5-0-2.5	32.4	X_3X_1 5.0-0-2.5	30.4
X_1 21.7		$X_3X_2X_1$	27.8	X_2X_1	22.6	X_3X_1	30.4
X_0X_0 0-0	37.4	X_2X_1 5.0-2.5	22.6	X_2X_1 2.5-2.5	31.5		
X_1 5.0	26.0	X_2X_1 2.5-2.5	31.5	X_3X_1 2.5-0-2.5	32.4		
$X_0X_0X_0$ 0-0-0	36.5	X_3X_2 5.0-2.5-0	29.7	X_3X_2 2.5-2.5-0	34.3		

Table A-4. Comparisons of the check treatments versus the test treatments for the number of seed per linear centimeter of head for the doubled haploid strain, Tucson, Arizona, 1969

Checks		Test Treatments					
Generation Treatment Levels Kr	$\bar{x}$	Generation Treatment Levels Kr	$\bar{x}$	Generation Treatment Levels Kr	$\bar{x}$	Generation Treatment Levels Kr	$\bar{x}$
X_0 0	40.4	X_0X_0 0-0	38.2	$X_0X_0X_0$ 0-0-0	38.7		
X_0X_0 0-0	38.2	$X_0X_0X_0$ 0-0-0	38.7				
X_0 0	40.4	X_1 5.0	25.7*	X_1 7.5	17.7*	X_1 2.5	40.4
X_0X_0 0-0	38.2	X_2 2.5-0	35.6	X_2 5.0-0	35.0	X_2 7.5-0	43.5
$X_0X_0X_0$ 0-0-	38.7	X_3 2.5-0-0	37.3	X_3 5.0-0-0	35.8	X_3 7.5-0-0	26.9
$X_0X_0X_0$ 0-0-0	38.7	$X_3X_2X_1$ 2.5-2.5-2.5	36.4	X_3X_1 2.5-0-2.5	34.2	X_3X_1 5.0-0-2.5	35.0
X_1 7.5	17.7	$X_3X_2X_1$ 2.5-2.5-2.5	36.4*	X_2X_1 5.0-2.5	35.8*	X_3X_1 5.0-0-2.5	35.0*
X_0X_0 0-0	38.2	X_2X_1 5.0-2.5	35.8	X_2X_1 2.5-2.5	30.5		
X_1 5.0	25.7	X_2X_1 2.5-2.5	25.7	X_3X_1 2.5-0-2.5	34.2		
$X_0X_0X_0$ 0-0-0	38.7	X_3X_2 5.0-2.5-0	39.0	X_3X_2 2.5-2.5-0	33.5		

Table A-5. Comparisons of the check treatments versus the test treatments for yield means from the normal diploid strain, Marana, Arizona, 1970

Check		Test Treatment					
Generation Treatment Levels Kr	$\bar{x}$	Generation Treatment Levels Kr	$\bar{x}$	Generation Treatment Levels Kr	$\bar{x}$	Generation Treatment Levels Kr	$\bar{x}$
X_0X_0 0-0	7.5	$X_0X_0X_0$ 0-0-0	7.3	$X_0X_0X_0X_0$ 0-0-0-0	7.4		
$X_0X_0X_0$ 0-0-0	7.3	$X_0X_0X_0X_0$ 0-0-0-0	7.4				
X_0X_0 0-0	7.5	X_2 2.5	7.6	X_2 5.0	7.3	X_2 7.5	7.3
$X_0X_0X_0$ 0-0-0	7.3	X_3 2.5	7.0	X_3 5.0	7.3	X_3 7.5	7.3
$X_0X_0X_0X_0$ 0-0-0-0	7.4	X_4 2.5	7.4	X_4 5.0	7.2	X_4 7.5	7.0
$X_0X_0X_0X_0$ 0-0-0-0	7.4	$X_4X_3X_2$ 2.5-2.5-2.5	7.5	X_4X_2 2.5-2.5	7.1	X_4X_2 5.0-2.5	7.0
X_2 7.5	7.3	$X_4X_3X_2$ 2.5-2.5-2.5	7.5	X_3X_2 5.0-2.5	7.4	X_4X_2 5.0-2.5	7.0
$X_0X_0X_0$ 0-0-0	7.3	X_3X_2 5.0-2.5	7.4	X_3X_2 2.5-2.5	6.7*		
X_2 5.0	7.3	X_3X_2 2.5-2.5	6.7*	X_4X_2 2.5-2.5	7.1		
$X_0X_0X_0X_0$ 0-0-0-0	7.4	X_4X_3 5.0-2.5	6.9	X_4X_3 2.5-2.5	7.3		

Table A-6. Comparisons of the check treatments versus the test treatments for yield means from the doubled haploid strain, Marana, Arizona, 1970

Check		Test Treatments					
Generation Treatment Levels Kr	$\bar{x}$	Generation Treatment Levels Kr	$\bar{x}$	Generation Treatment Levels Kr	$\bar{x}$	Generation Treatment Levels Kr	$\bar{x}$
X_0X_0 0-0	7.0	$X_0X_0X_0$ 0-0-0	7.2	$X_0X_0X_0X_0$ 0-0-0-0	6.8		
$X_0X_0X_0$ 0-0-0	7.2	$X_0X_0X_0X_0$ 0-0-0-0	6.8				
X_0X_0 0-0	7.0	X_2 2.5	7.3	X_2 5.0	7.5*	X_2 7.5	7.3
$X_0X_0X_0$ 0-0-0	7.2	X_3 2.5	7.0	X_3 5.0	7.1	X_3 5.0	6.8
$X_0X_0X_0X_0$ 0-0-0-0	6.8	X_4 2.5	6.7	X_4 5.0	7.2	X_4 7.5	7.1
$X_0X_0X_0X_0$ 0-0-0-0	7.4	$X_4X_3X_2$ 2.5-2.5-2.5	7.5	X_4X_2 2.5-2.5	6.9	X_4X_2 5.0-2.5	6.8*
X_2 7.5	7.3	$X_4X_3X_2$ 2.5-2.5-2.5	7.0	X_3X_2 5.0-2.5	7.1	X_4X_2 5.0-2.5	6.8*
$X_0X_0X_0$ 0-0-0	7.2	X_3X_2 5.0-2.5	7.1	X_3X_2 2.5-2.5	7.3		
X_2 5.0	7.5	X_3X_2 2.5-2.5	7.3	X_4X_2 2.5-2.5	6.9*		
$X_0X_0X_0X_0$ 0 0 0 0	6.8	X_3X_4 5.0-2.5	6.3	X_4X_3 2.5-2.5	7.1		

Table A-7. Comparisons of the check treatments versus the test treatments of days to 50 percent anthesis means for the doubled haploid strain, Marana, Arizona, 1970

Check		Test Treatments					
Generation Treatment Levels Kr	$\bar{x}$	Generation Treatment Levels Kr	$\bar{x}$	Generation Treatment Levels Kr	$\bar{x}$	Generation Treatment Levels Kr	$\bar{x}$
X_0X_0 0-0	62	$X_0X_0X_0$ 0-0-0	62	$X_0X_0X_0X_0$ 0-0-0-0	61		
$X_0X_0X_0$	62	$X_0X_0X_0X_0$	61				
X_0X_0 0-0	62	X_2 2.5	60*	X_2 5.0	60*	X_2 7.5	61
$X_0X_0X_0$ 0-0-0	62	X_3 2.5	61	X_3 5.0	61	X_3 7.5	61
$X_0X_0X_0X_0$ 0-0-0-0	61	X_4 2.5	61	X_4 5.0	60	X_4 7.5	60
$X_0X_0X_0X_0$ 0-0-0-0	61	$X_4X_3X_2$ 2.5-2.5-2.5	61	X_4X_2 2.5-2.5	62	X_4X_2 5.0-2.5	60
X_2 7.5	60	$X_4X_3X_2$ 2.5-2.5-2.5	61	X_3X_2 5.0-2.5	60	X_4X_2 5.0-2.5	60
$X_0X_0X_0$ 0-0-0	62	X_3X_2 5.0-2.5	60*	X_3X_2 2.5-2.5	61		
X_2 5.0	60	X_3X_2 2.5-2.5	61	X_4X_2 2.5-2.5	62*		
$X_0X_0X_0X_0$ 0-0-0-0	61	X_4X_3 5.0-2.5	61	X_4X_3 2.5-2.5	61		

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