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GENETIC VARIABILITY IN QUANTITATIVE CHAR-
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TREATMENT OF DIPLOID, TETRAPLOID AND
HEXAPLOID OAT SEEDS.

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GENETIC VARIABILITY IN QUANTITATIVE CHARACTERS
INDUCED BY THERMAL NEUTRON TREATMENT OF DIPLOID,
TETRAPLOID AND HEXAPLOID OAT SEEDS

by

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INTRODUCTION

Genetic variability, which is the raw product for evolution in plant species, is replenished by spontaneous mutations. Plant breeding, which is controlled evolution, in its beginning was dependent upon genetic variability from natural sources. In 1928, when Stadler (1929) discovered that mutations could be induced artificially in plants by X-ray treatment, it appeared that plant breeders possessed a new tool with which to create genetic variability at will. Researchers, including Stadler (1929, 1930), questioned the practicability of using artificially induced mutations, especially in polyploidy species. Certainly a lack of knowledge about the nature of induced mutations and the factors which govern the radiosensitivity of plants has delayed the progress in this field.

Mutations induced by irradiation can be classified into two categories: (a) chromosomal aberrations, and (b) genic or point mutation. The first type refers to rearrangements, losses or gains of chromosomes or chromosome parts, whereas the second type refers to chemical rearrangement within the gene. The nature of mutations which are observed in progenies of irradiated plants or seeds is dependent upon a number of factors, but two very important ones are the specific mutagen used and the degree of polyploidy of the specie. Types of mutations which can be tolerated by species at any ploidy level are point mutations and chromosomal aberrations of the

translocation, inversion and small deletion type. The polyploid species can tolerate additional chromosomal aberrations of the gross deletion type, as evidenced by the fact that loss of a whole chromosome is not lethal in hexaploid wheat and oats (Sears, 1954 and O'Mara, 1961).

Because the type of mutations induced by irradiation can be significant in determining the way that a plant breeder uses genetic variability obtained from this source, it is necessary to define the degree to which observed variability is due to certain types of chromosomal aberrations or to point mutations, especially in the polyploid species. It is likely that spontaneous mutations also include both chromosomal aberrations and point mutations, but the mutations which produce deleterious effects on viability characteristics are eliminated through natural selection processes. In mutation breeding there are two important aspects: (1) to understand the types of mutations which are responsible for induced genetic variability, and (2) to formulate and test breeding procedures which optimize the usefulness of induced variability. The specific objectives of this study were:

1. To study the nature of the mutations induced by thermal neutron irradiation of Avena sp. from different ploidy levels.
2. To compare the relative magnitude of induced variability for quantitative characters in diploid, tetraploid and hexaploid oats.

REVIEW OF LITERATURE

Irradiation mutagens can be classified in two categories:

(a) non-ionizing, such as ultra violet rays, and (b) ionizing, such as X-, gamma, beta, and alpha rays. Sparrow (1961) classified ionizing irradiation into two types: (1) electromagnetic, which includes X- and gamma rays, and (2) particulate, which includes alpha and beta rays, protons, deuterons, etc.

The principal difference between ionizing and non-ionizing irradiations is that the former produces ionization and can transfer energy by excitation, while the latter transmits energy by excitation but does not produce ionization. Neutrons are considered as ionizing irradiation, but ionization occurs indirectly through nuclear reactions after the absorption of the atomic nuclei. Chemical mutagens have also been used to induce genetic changes.

Artificially induced mutations in plants were first reported by Stadler (1930, 1931a, 1931b) who obtained chlorophyll mutants from treating corn and barley with X-rays. He noted frequent chromosome rearrangements and losses after X-ray treatment.

Konzak (1957), Prakken (1959), Gustafsson and von Wettstein (1956), and MacKey (1954b) classified irradiation-induced mutations into several categories:

1. Gene or point mutation--no apparent cytological alteration in the chromosomes.
2. Chromosome alteration--deletions, duplications, inversions and translocations.
3. Changes in chromosome number--aneuploids and polyploids.
4. Cytoplasmic mutations--maternally inherited.

According to Sax and Swanson (1941), X-radiation produces two types of responses: (a) a temporary cessation of mitosis and clumping of metaphase and anaphase chromosomes as a result of physiological changes, and (b) chromosome breaks which result in deletions and other chromosome alterations.

Gustafsson (1947) pointed out that for induced mutations to be useful to a plant breeder, it was necessary to produce a high proportion of vital to lethal mutants.

Sparrow (1961) suggested that growth inhibition following irradiation of seeds or plants is associated with cytogenetic damage and a drop in auxin level. Gelin (1941) found that sterility following irradiation closely reflects the degree of chromosomal disturbance. Caldecott et al. (1954) concluded that thermal neutrons induced more chromosomal aberrations and mutations but less killing than did X-rays. Bora et al. (1961) observed a linear relationship between irradiation dose and frequency of aberrant and sterile plants.

Nishiyama and Ichikawa (1962a) using gamma irradiation on wheat seeds, obtained many morphological and physiological

but no chlorophyll mutants. They assumed that most of the mutants were due to chromosomal aberrations since many abnormal meiotic configurations were observed. Evans (1961) found the aberration frequency per chromosome to be the same in diploids and tetraploids. The intrachromosome aberrations were distributed at random among nuclei, while interchromosome aberrations were not. Conger and Johnston (1956) working with Tradescantia found that diploid cells had twice as many aberrations as haploid cells, so aberration frequency per chromosome was the same for haploids and diploids.

Ehrenberg et al. (1961) found that all ionizing irradiation sources produced chromosomal rearrangement as well as gene mutations, whereas among the chemical mutagens, some produced only gene mutations and others produced both chromosomal and gene mutations. Diethylsulphate used on barley induced a higher mutation frequency, but fewer chromosome aberrations than did irradiation mutations (Konzak, et al., 1961b). Stadler (1946) reported fewer structural changes in ultraviolet-treated than in X-ray-treated corn. In fact, the mutations induced by X-rays were usually deletions.

Larter and Elliot (1956) working with wheat, found that increasing dosages of X-rays caused a decrease in chromosome interchange frequency, whereas increasing dosages of thermal neutrons caused an increase. Since the percentage of survival in neutron-treated and check materials were equal, the thermal

neutrons were more practical for mutation breeding. From a review of the literature, Nilan (1956) observed that neutron irradiations of cereal seeds gave more uniform seedling height, higher survival and fertility of M_1 plants and a higher frequency of chromosome aberrations and genetic mutations than did X- or gamma rays. MacKey (1952) and Nilan (1956) concluded that thermal neutrons affected the genetic apparatus only, whereas X-rays affected both the genetic and non-genetic systems. Konzak and Singleton (1952) reported that M_1 seedlings of oat, barley and rye were more uniform after thermal neutron than after X-ray treatment of the seeds.

The efficiency of different mutagens for inducing genetic variability has been investigated extensively. Singleton et al. (1956) found that the frequency of corn endosperm mutations increased more sharply than the irradiation doses from Co^{60} . He also stated that neutrons were more efficient than other mutagens, since their effect was uniform regardless of the physiological condition of seeds. Ehrenberg and Nybom (1954) also stated that the sensitivity of seeds to thermal neutrons was independent of water content and the neutrons gave a higher total yield of mutations than did X-rays.

Ehrenberg et al. (1961) found that neutron and X-ray treatment of barley produced a mutation rate of 8-10 per cent whereas some chemical mutagens produced 60 per cent.

Abrams (1963) comparing variability induced by three mutagens, reported that thermal neutron and ethyl methanesul-

phonate (EMS) seed treatment produced greater variability for heading date, plant height and weight per 100 seeds of oats than did P³². According to Prakken (1959), the order of preference for ionizing radiation for mutation breeding was X-rays, neutrons, gamma rays, and electrons (P³² and S³⁵).

Not only do many factors cause mutagens to produce a differential germination of M₁ seeds, survival of M₁ plants, chromosomal disturbances and sterility, but they also may influence the efficacy of mutagens for inducing mutations. Physical factors which influence the efficiency of mutagens are the type of mutagen (Ehrenberg et al. 1953, Sparrow and Evans 1961), the oxygen content and the temperature of the treatment atmosphere (Ehrenberg et al. 1953, Ehrenberg and Nybom 1954, Konzak et al. 1961a, Sparrow et al. 1961, Caldecott 1956) and the conditions of storage (Konzak et al. 1961a, Nilan 1960, Matsumura 1960). Factors associated with the plant materials being treated are moisture content and age of the seed (Ehrenberg et al. 1953, Caldecott 1955, Abrams 1956, Konzak 1954b, Konzak et al. 1961a, Natarajan 1958, Palenzona 1961), chromosome size, nuclear volume and DNA content of the cells (Gustafsson and Tedin 1954, Sparrow et al. 1961, Sparrow and Evans 1961), genotype and degrees of polyploidy (Muntzing 1942, Froier et al. 1942, Gustafsson and Tedin 1954, Abrams 1956, Konzak et al. 1961a, Sparrow and Evans 1961, Swaminathan 1961), length and stage of the nuclear division

(Konzak et al. 1961a, Nilan 1960, Sparrow and Evans 1961), and seed size and covering (Gonzalez 1957).

There is some evidence of mutagenic specificity in higher plants. Smith (1961) proposed that irradiations are non-specific in causing breakage within chromosomes, whereas chemical mutagens break chromosomes preferentially. The preferential chromosome breakage by chemicals was related to particular heterochromatic regions.

Gustafsson and MacKey (1948) reported that mutation spectra resulting from chemical mutagens differed from those obtained from irradiation. Hagberg et al. (1958) found that the barley locus at which an erectoid mutant occurred was related to the mutagen used and the genotype of the material being treated. Similar results were reported by Lundquist and von Wettstein (1962) for the eceriferum (waxless) mutants in barley.

The relationship of polyploidy to mutation expression has been a matter of controversy since Stadler (1929, 1930, 1932) reported the decrease from many chlorophyll mutations in diploids to few in the polyploids. These results caused skepticism about the use of mutation breeding in polyploid crops. Meanwhile, Goodspeed and Olson (1928) reported about 20 per cent mutant plants in irradiated tetraploid Nicotiana species, and Horlacher and Killough (1933) obtained two progressive mutations from X-radiation of tetraploid cotton. Later, MacKey (1952, 1954a, 1954c) reported a high mutation

frequency in irradiated hexaploid wheat.

Gustafsson et al. (1960) concluded that the ability of polyploids to tolerate structural changes might prove useful in mutation breeding. Froier et al. (1941) reported that ploidy level affected the curves between increasing doses of irradiation and chromosomal damage. Marshak and Bradley (1944) found that the meiotic survival after irradiation treatment was directly proportional to the degree of polyploidy in the cells.

Smith (1946) and Konzak and Singleton (1952) observed that polyploid species showed a greater tolerance to X-radiation than did diploid species. The later authors found that auto-tetraploid rye, barley and maize were more resistant than their diploid counterparts to thermal neutron irradiation, but natural tetraploid oats was more resistant than either diploid or hexaploid oat species. MacKey (1954a, 1958) explained a higher mutation frequency in hexaploid wheat than in diploid einkorn and barley by the fact that polyploids had better tolerance to chromosome disturbances. Much of the irradiation induced variability in oats observed by MacKey (1956) was due to gross chromosomal aberrations (deletions, duplications). Wolff (1961) found that extra sets of chromosomes buffer aberrations resulting in a greater viability of gametophytic cells.

MacKey (1958) reported a higher survival and fertility

percentage in the M_1 generation of irradiated wheat as the ploidy level increased. Palenzona (1961) reported that irradiation effects on seeds depend on the ploidy of the species and the nature of the character under study.

Sparrow and Schairer (1958) reported getting a positive straight line relationship between radiosensitivity and chromosome number in Sedum. According to Natarajan et al. (1958), the sensitivities per unit of wheat chromosome length were identical for all ploidy levels when X-rays were the mutagen source, but with fast neutrons, polyploid species exhibited more breaks per unit chromosome length than did diploids.

Matsumura and Nezu (1961) found that T. monococcum was less resistant to fast and thermal neutrons than was T. durum, but no significant difference was observed between T. durum and T. vulgare. Nishiyama et al. (1962b) found that germination of irradiated seeds was less affected in hexaploid than in diploid wheat.

In recent years, much research has been conducted on mutations which affect quantitative characters. Gaul (1958) pointed out that micromutations should occur more frequently than macromutations, and furthermore, that micromutations would be of most importance to plant breeders. MacKey (1954a, 1954b, 1954c) also suggested that "subtle" mutations were of greater practical value than drastic mutations in a breeding program.

Gregory (1955, 1956b, 1957) isolated several X-radiation induced mutant peanut strains which produced yields superior to the checks. The frequency of superior yielding peanut mutants was 1 in 500-5000 M₂ peanut plants. Mertens and Burdick (1957) produced two tomato lines with increased earliness and plant size by treating with X-rays and thermal neutrons.

Rawlings et al. (1958) reported that X-ray and thermal neutron treatment of two soybean varieties increased genetic variability for plant height, maturity, yield and seed weight by as much as 500 per cent.

Oka et al. (1958) working with rice, found that X-ray treatments increased the genetic variability for plant height and heading date, while the mean values of the populations remained unchanged, and Gustafsson and MacKey (1948) reported barley mutants from irradiation which were 1 to 3 days earlier than the check.

Kao et al. (1960) in a theoretical study showed that the fixable genetic variability in the M₂ and M₃ generations was 1/8 and 3/8, respectively, of the total variability, suggesting that selection should be delayed until the M₃ generation.

Krull (1960) and Krull and Frey (1961) reported that thermal neutron irradiation of hexaploid oats shifted the population means toward heavier seed weight, later heading date and taller plant height. There were neither consistent

positive or negative changes in skewness in any of the characters, indicating that the induced mutations occurred equally in both directions from the population means. The genetic variabilities from irradiation and hybridization were equally heritable. Murphy (1961) found similar results for the characters, groat weight, length and width. Abrams (1963) increased the genetic variability of oats with all mutagens for all characters studied. He reported a greater genetic variability in M_3 than in the M_2 generation.

Papa et al. (1961) found that irradiated soybeans increased variability for most of the characters studied but selection was more efficient for highly heritable characters. In the same materials, Williams and Hanway (1961) reported significant variation for oil and protein content.

Matsuo and Onozawa (1961) reported that in rice genetic variances for stem length and grain weight were increased by irradiation. Early maturing mutants with yield comparable to the original varieties were found by Li et al. (1961).

Brock and Latter (1961) increased the genetic variance for flowering time in clover by treating with X-rays and thermal neutrons.

The development of some superior commercial varieties on field crops by mutation breeding disproves the early belief that induced mutations are always deleterious. Summaries of useful mutations induced by radiation has been presented by Aronoff and Frey (1958), Gaul (1958), Gustafsson and

Wettstein (1956), Ehrenberg et al. (1956), Konzak (1957), MacKey (1956), Singleton (1956), Singleton et al. (1956) and Smith (1958).

Andersson and Olsson (1954) released a white mustard variety, Primex, and Gelin (1954) described the Stralart (Ray pea) pea variety, both developed via mutation breeding. Stralart variety yielded 5 per cent more than the mother strain. Gregory (1960) released an induced mutant peanut variety, NCX₄.

Down and Andersen (1956) developed a bush type navy bean from irradiated Michelite variety (Phaseolus vulgaris) and released it under the name Sanilac. Pallas barley, an erectoides mutant type, was released from Svalof (Borg et al. 1958), and Florad (Chapman et al. 1961) and Alamo-X (Atkins, 1962) oat varieties were released in Florida and Texas, respectively. All three of these small grain varieties were developed via mutation breeding. A number of strains of wheat, barley, peas and lupines isolated from irradiation-derived population have been placed in the official Swedish yield state trials (Ehrenberg et al. 1956).

Gaul (1961) stated, "The induction of mutations offers a new tool which is potentially able to make progress in plant breeding similar to that obtained with conventional methods". And MacKey (1956) concluded, "all types of plants are suitable to mutation breeding: diploids, polyploids, self and cross pollinated, sexuals and asexuals".

In addition to being useful for the development of commercial crop varieties, mutation breeding has other practical values. Aronoff and Frey (1958) mentioned three areas where mutation breeding has been useful: (a) in asexually reproduced crops, (b) for transferring chromosomal segments in species and genera crosses, and (c) in inducing useful heritable variation in sexual reproduced crop plants.

Stadler (1930) first proposed using induced somatic mutations in asexually propagated crops. A number of desirable mutants were described by Singleton et al. (1956) in the asexually propagated plants, dogwood, apples, and carnations.

Sears (1956) used X-radiation to transfer a small chromosome segment which carried a leaf rust resistance gene from Aegilop umbellulata germplasm to a wheat chromosome. Similar work was reported by Elliott (1957) who induced a translocation of an Agropyron elongatum chromosome segment which carried a stem rust resistance gene to wheat.

A number of useful mutations which could be used in a hybridization program have been reported. Frey (1954, 1955) induced mutations in oats for shortened straw, earliness and field resistance to crown and stem rust, and Konzak (1954a, 1956a, 1956b) found mutants which were resistant to Victoria blight and oat stem rust. Cooper and Gregory (1960) obtained induced mutations for resistance to peanut leaf spot.

Froier (1954) published a report of 100 promising barley mutants induced by radiation in Sweden, and Shebeski and

Lawrence (1954) obtained induced mutations for stiff straw, early maturity and dense spike in barley.

Borg et al. (1958) considering the importance of mutation breeding in crop improvement stated, "since there is no fundamental difference in structure between spontaneous and induced mutations, we can safely presume that if mutations appearing spontaneously can improve a variety, this will happen by means of induced mutations".

MATERIALS AND METHODS

The oat species and varieties used in this study were Avena strigosa var. Saia, A. abyssinica, var. P.I. 193958, and A. sativa vars, Andrew (C.I. 4170) Burnett (C.I. 6537) and Pusa (C.I. 3442). A lot of 500 seeds containing 8 per cent moisture from each variety was treated with thermal neutrons to a total dosage of 1.89×10^{13} neutrons¹ per cm² \pm 15 per cent over a period of $7\frac{1}{2}$ hours. Irradiated seeds were planted 5 seeds per 4-inch pot in the greenhouse in the fall of 1961. Non-irradiated seeds from each variety were planted at the same time. To avoid intervarietal crossing, each variety was grown in a separate greenhouse room, with the exception of Burnett, which was sown at a later date, so it would not pollinate at the same time as the other varieties.

When mature, the panicle on the primary culm of each plant was harvested and threshed individually. Seeds from a panicle were space planted in a progeny row in the field in 1962. The progeny rows were 12 feet long and spaced 3 feet apart to facilitate mechanical cultivation and minimize the opportunity for inter-progeny crossing. Ranges of progeny rows were separated by 5-foot alleys. When the M₂ and check plants were mature, 80 rows in each population were randomly

¹Radiation was performed and dosage calculated under the direction of Dr. Seymour Shapiro of the Department of Biology, Brookhaven National Laboratory, Upton, L.I., New York.

chosen and two plants were harvested from each row. Each selected plant was threshed and stored in a properly labelled envelope. Subsequently 40 lines were chosen to represent each population in 1963 experiment. These lines were chosen so that one was selected from each of 40 M_2 progenies.

In 1963, the experiment designed to determine the nature and degree of genetic variability induced by thermal neutrons was grown at Ames, Iowa. The experimental design was a split-split-plot with 3 replications. The main plots consisted of varieties, the subplots consisted of the treatments (radiated and non-radiated), and the sub-subplots consisted of 40 lines¹ from a treatment within a variety. The experiment contained 400 entries and a total of 1200 plots. A plot consisted of a hill planted with 25 seeds and the hills were spaced one foot apart in perpendicular directions. In order to prevent a rust epiphytotic that could confound the genetic expression of certain agronomic characters, the experiment was sprayed with a fungicide (active ingredients--Nabam² and zinc sulphate) at weekly intervals from anthesis to maturity.

The plant attributes measured were heading date, plant height, number of branches per panicle, length of flag leaf, weight per 100 seeds, groat length and groat width.

¹A line was the progeny from one M_2 plant.

²Nabam is a short name applied to disodium ethylene bisdithiocarbamate. The Rohm and Haas Co's. brand Dithane D-14 was used as source of Nabam.

Heading dates were recorded on a plot basis when 50 per cent of the panicles were completely emerged from the boot. Plant height was recorded on a plot as the number of inches from the ground surface to the panicle tips. Number of branches per panicle was determined by counting all of the branches emerging from the main axis of 5 panicles per plot, and flag leaf length was measured on five culms per plot. At maturity, but before harvest, the tip spikelets from 10 panicles were harvested from each plot. This stratified sample of spikelets was taken in order to prevent the introduction of variability associated with the position of the seed on the panicle. Next, the panicles in each plot were harvested, threshed and the weight was taken on a 100-seed sample.

The samples of tip spikelets were threshed by hand and 7 primary seeds from each plot were dehulled. The groats were singed to remove pubescence and the length and width of each groat was measured to 0.1 millimeter by projecting its shadow, at 10x magnification, onto a sheet of "millimeter graph paper" with a Master Vu Graph.

The degree of sterility present in the M_3 generation and in the checks was estimated on 25 per cent of the lines in each population. Two panicles were harvested from each plot of the selected lines, and the number of sterile and fertile florets were counted on each panicle. Per cent sterility was calculated as the ratio of sterile to total florets.

All data were transferred to punch cards for derandomization and the computations necessary for variance, covariance, skewness and kurtosis (Snedecor, 1956) analyses.

EXPERIMENTAL RESULTS

The relative precision of measurement of 6 of the attributes measured (except heading date) can be judged from the coefficients of variation (Table 1). The C.V.'s ranged from 2.2 per cent for groat width to 9.7 per cent for flag leaf length. Coefficients of variation were not calculated for heading date, since this character was recorded with June 1 as the arbitrary zero point. It appears that all of the attributes were measured precisely. Even measurements with C.V.'s of 9.5 and 9.7 per cent are considered satisfactory.

Table 1. Coefficients of variation for six attributes measured in diploid, tetraploid and hexaploid oat varieties

Attribute	C.V.
Plant height	4.0
Number of branches per panicle	9.5
Flag leaf length	9.7
Weight per 100 seeds	5.4
Groat width	2.2
Groat length	2.5

The mean squares from the analyses of variance for heading date, plant height, number of branches per panicle, flag leaf length, weight per 100 seeds and groat length and width are presented in Tables 2, 3 and 4. As expected the variety means differed significantly for every attribute measured. The wide genetic and phenotypic differences among the varieties chosen for the study dictated that significant differences would exist among varieties.

Because there was significant genetic variation among lines within check populations for some characters, the significance of the variation induced by irradiation was measured by using the mean squares within check populations to test the mean squares within irradiation derived populations (Table 6).

In a number of cases the population means were shifted by irradiation treatment. The mean heading date was shifted significantly in Pusa (Table 5 and Figure 5). Abrams (1963) and Krull and Frey (1961) reported that mutagen-derived populations were later than the check when Clintland oat variety was used as the source material. One line in each of the irradiated-derived populations of the tetraploid and Burnett was earlier than any 'check' line (Figures 2 and 4). The variability among lines within populations was increased by irradiation in each variety except Pusa, but only in the tetraploid and diploid was it increased significantly (Table 6).

Table 2. Mean squares from the analyses of variance of heading dates and plant heights of oat lines derived from diploid, tetraploid and hexaploid irradiated and non-irradiated seeds^a

Source of variation	Degrees of freedom	Mean squares	
		Heading date	Plant height
Total	1199	48.16	27.39
Replications	2	15.53	46.84
Among varieties	4	13799.20**	7221.99**
Error (a)	8	15.64	38.34
Treatments	1	20.28**	336.02**
Treatments x varieties	4	13.45**	7.70
Error (b)	10	2.73	9.07
Lines w/populations/treatments	390	2.94**	3.77**
Lines w/diploid			22
Irradiated	39	1.99	7.29**
Non-irradiated	39	1.18	3.06*
Lines w/tetraploid			
Irradiated	39	6.96**	5.84**
Non-irradiated	39	2.63**	2.44
Lines w/hexaploid			
Andrew			
Irradiated	39	2.39**	4.33**
Non-irradiated	39	2.09*	1.59
Burnett			
Irradiated	39	5.38**	3.78**
Non-irradiated	39	3.24**	3.96**

^aHereinafter * and ** will denote significance at the 5 and 1 per cent levels, respectively.

Table 2. (Continued)

Source of variation	Degrees of freedom	Mean squares	
		Heading date	Plant height
Pusa			
Irradiated	39	1.43	4.57**
Non-irradiated	39	2.12*	0.83
Error (c)	780	1.47	2.09

Table 3. Mean squares from the analyses of variance of number of branches per panicle and flag leaf length of oat lines derived from diploid, tetraploid and hexaploid irradiated and non-irradiated seeds

Source of variation	Degrees of freedom	Mean Squares	
		Number of branches	Flag leaf length
Total	1199	1339.19	652.78
Replications	2	12232.11	1195.05
Among varieties	4	339207.58**	168669.38**
Error (a)	8	6414.99	675.76
Treatments	1	5668.05*	311.61
Treatments x varieties	4	2123.74	176.79
Error (b)	10	655.32	164.51
Lines w/populations w/treatments	390	147.39*	116.67**
Lines w/diploid			
Irradiated	39	194.08*	28.83
Non-irradiated	39	256.34**	22.67
Lines w/tetraploid			
Irradiated	39	141.43	67.36
Non-irradiated	39	122.70	62.75
Lines w/hexaploid			
Andrew			
Irradiated	39	117.02	186.78**
Non-irradiated	39	86.39	202.75**
Burnett			
Irradiated	39	186.54*	215.85**
Non-irradiated	39	145.16	296.80**
Pusa			
Irradiated	39	154.60	48.84
Non-irradiated	39	69.63	34.10
Error (c)	780	121.64	66.72

Table 4. Mean squares from the analyses of variance of weight per 100 seeds, groat length and groat width of oat lines derived from diploid, tetraploid and hexaploid irradiated and non-irradiated seeds

Source of variation	Degrees of freedom	Mean Squares		
		Weight per 100 seeds	Groat length	Groat width
Total	1199	.4760	9.39	13.24
Replications	2	.1804	57.13	4.06
Among varieties	4	131.2825**	1959.90**	3883.22**
Error (a)	8	.1065	34.87	3.27
Treatments	1	.3012	3.23	1.24
Treatments x varieties	4	.1976	6.81	2.89
Error (b)	10	.1080	18.74	1.35
Lines w/populations w/treatments	390	.0396**	3.78**	0.37**
Lines w/diploid				
Irradiated	39	.0373**	3.24**	0.26*
Non-irradiated	39	.0172	1.48	0.09
Lines w/tetraploid				
Irradiated	39	.0121	2.84**	0.30**
Non-irradiated	39	.0096	2.02	0.16
Lines w/hexaploid				
Andrew				
Irradiated	39	.0749**	5.25	0.51**
Non-irradiated	39	.0481**	2.73*	0.30**
Burnett				
Irradiated	39	.0589**	5.17**	0.33**
Non-irradiated	39	.0518**	2.36	0.13
Pusa				
Irradiated	39	.0636**	11.91**	1.37**
Non-irradiated	39	.0226	0.83	0.26
Error (c)	780	.0205	1.71	0.18

Table 5. Means of seven attributes measured on oat lines derived from diploid, tetraploid and hexaploid irradiated and non-irradiated seeds

Populations	Attributes						
	Heading date	Plant height	Number of branches	Flag leaf length	Weight per 100 seeds	Groat length	Groat width
Diploid							
Irradiated	18.9	43.6	34.0	9.6	1.97	8.28	1.77
Non-irradiated	18.4	44.8	36.8	9.7	1.96	8.29	1.74
Tetraploid							
Irradiated	22.9	35.6	25.2	16.3	1.79	8.16	1.87
Non-irradiated	23.0	36.3	25.9	16.6	1.76	8.11	1.85
Hexaploid							
Andrew							
Irradiated	9.2	35.3	18.6	22.7	2.79	8.81	2.51
Non-irradiated	9.3	36.8	19.3	22.8	2.86	8.81	2.54
Burnett							
Irradiated	10.2	36.8	18.8	21.1	3.26	8.79	2.70
Non-irradiated	10.1	37.4	19.0	20.9	3.28	8.85	2.73
Pusa							
Irradiated	4.7	28.1	17.5	13.6	3.30	7.88	3.09
Non-irradiated	3.8	29.5	17.0	14.4	3.44	7.94	3.13

Table 6. Ratios (F values) of mean squares from irradiated to check populations for and hexaploid oats and the level of significance of the ratios.

Population	Heading date		Plant height		Number of branches		Flag leaf length	
	Ratio	Sig.	Ratio	Sig.	Ratio	Sig.	Ratio	Sig.
Diploid:								
Irradiated vs. Non-irradiated	1.70	5%	2.38	1%	0.76	N.S.	1.27	N.
Tetraploid:								
Irradiated vs. Non-irradiated	2.64	1%	2.39	1%	1.15	N.S.	1.07	N.
Hexaploid:								
Andrew								
Irradiated vs. Non-irradiated	1.14	N.S.	2.72	1%	1.36	N.S.	0.96	N.
Burnett								
Irradiated vs. Non-irradiated	1.66	10%	0.95	N.S.	1.29	N.S.	0.73	N.
Pusa								
Irradiated vs. Non-irradiated	0.67	N.S.	5.5	1%	2.21	1%	1.43	N.

Figure 1. Frequency distributions of heading dates of oat lines derived from diploid irradiated and non-irradiated seeds

Figure 2. Frequency distributions of heading dates of oat lines derived from tetraploid irradiated and non-irradiated seeds

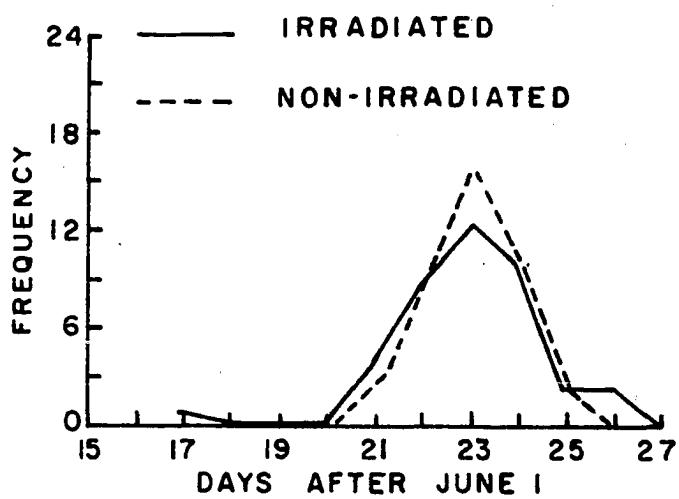
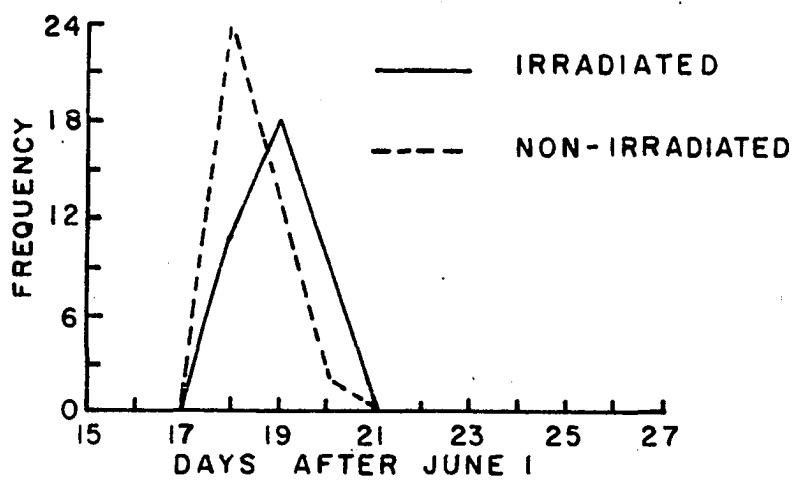
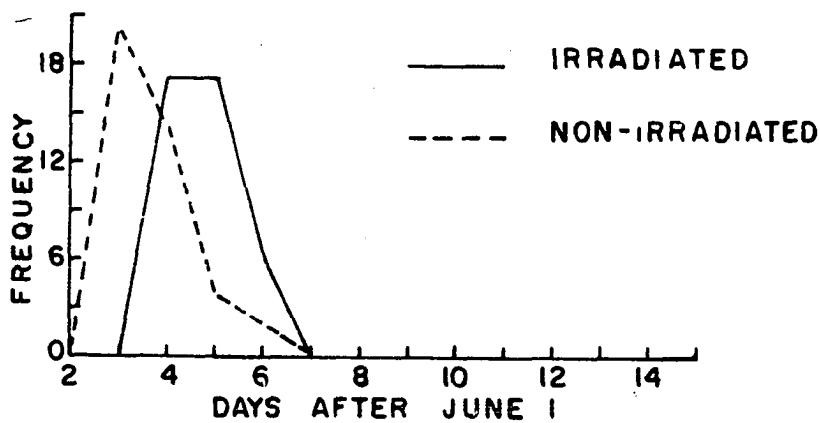
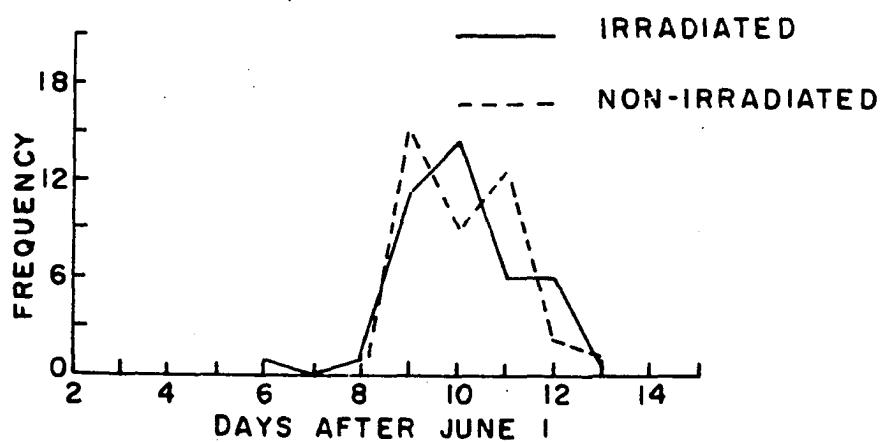
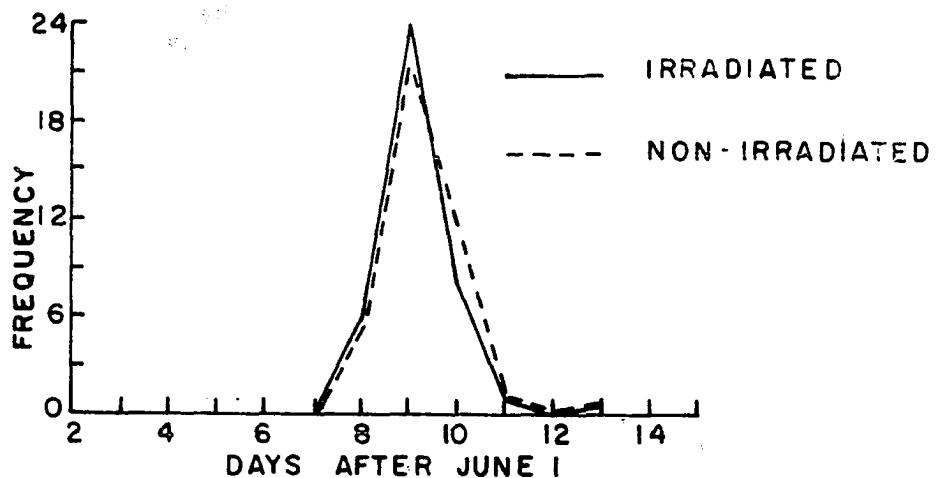


Figure 3. Frequency distributions of heading dates of oat lines derived from Andrew irradiated and non-irradiated seeds

Figure 4. Frequency distributions of heading dates of oat lines derived from Burnett irradiated and non-irradiated seeds

Figure 5. Frequency distributions of heading dates of oat lines derived from Pusa irradiated and non-irradiated seeds



The mean plant heights of the irradiation-derived populations were consistently shorter than the means of the corresponding check populations, ranging from 0.6 inch shorter in Burnett to 1.3 inches in Andrew and Pusa (Table 5). In all cases except Burnett, the variability among lines in the irradiation-derived population was significantly greater than in the check population (Table 6 and Figures 6-10). In the diploid, nine irradiation-derived lines were shorter than the shortest check line. In each of the tetraploid and hexaploid varieties the irradiation-derived populations contained several lines shorter but none taller than the ranges of the checks (Figures 7-10).

The mean number of branches per panicle was decreased by the irradiation treatment in all varieties except Pusa. The decrease ranged from 0.2 branch in Burnett to 2.8 branches in Saia. In Pusa the mean branch number was increased 0.5 (Table 5). This attribute was especially interesting in that Pusa was the only variety in which the variability was significantly increased by irradiation (Table 7 and Figures 11-15). In the case of Saia the variability was actually decreased (Table 3). Only in Pusa was the mean flag leaf length changed materially by the irradiation treatment (Table 5).

The mean weight per 100 seeds was not significantly changed by thermal neutron irradiation in any of the varieties

Figure 6. Frequency distributions of plant heights of oat lines derived from diploid irradiated and non-irradiated seeds

Figure 7. Frequency distributions of plant heights of oat lines derived from tetraploid irradiated and non-irradiated seeds

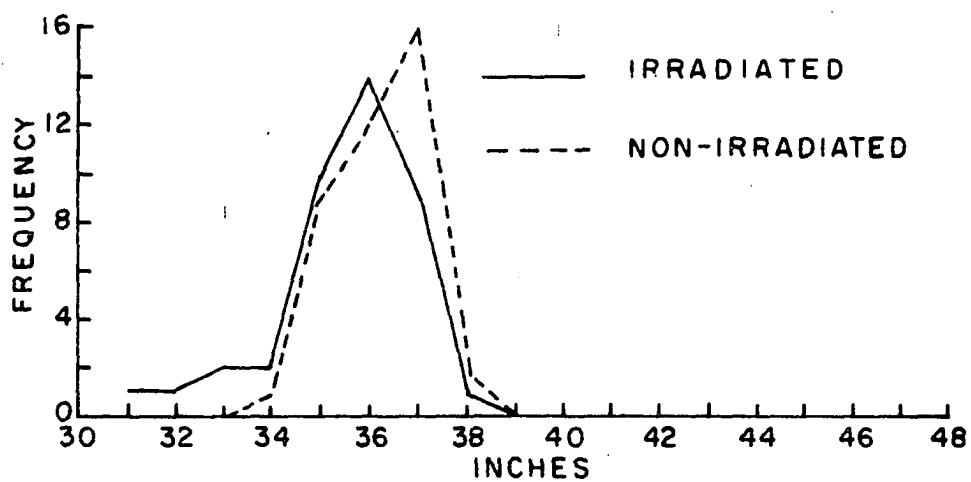
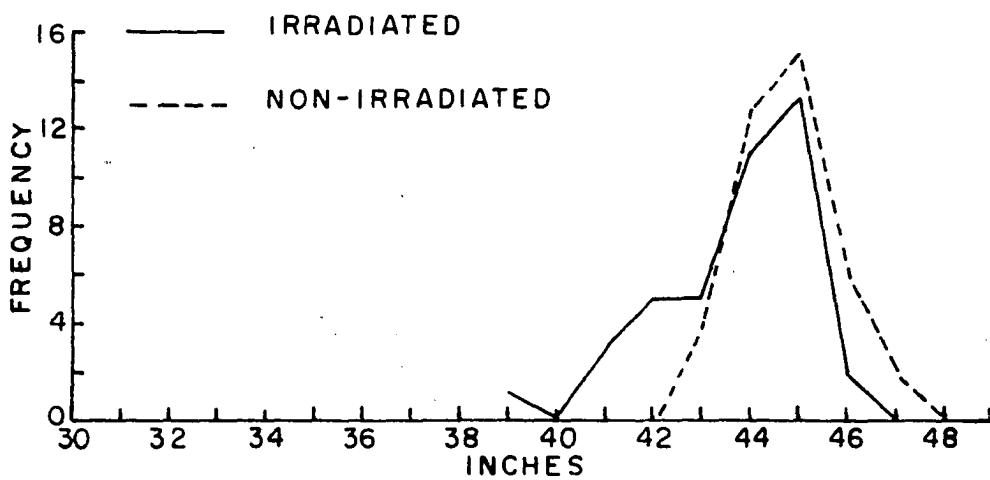


Figure 8. Frequency distributions of plant heights of oat lines derived from Andrew irradiated and non-irradiated seeds

Figure 9. Frequency distributions of plant heights of oat lines derived from Burnett irradiated and non-irradiated seeds

Figure 10. Frequency distributions of plant heights of oat lines derived from Pusa irradiated and non-irradiated seeds

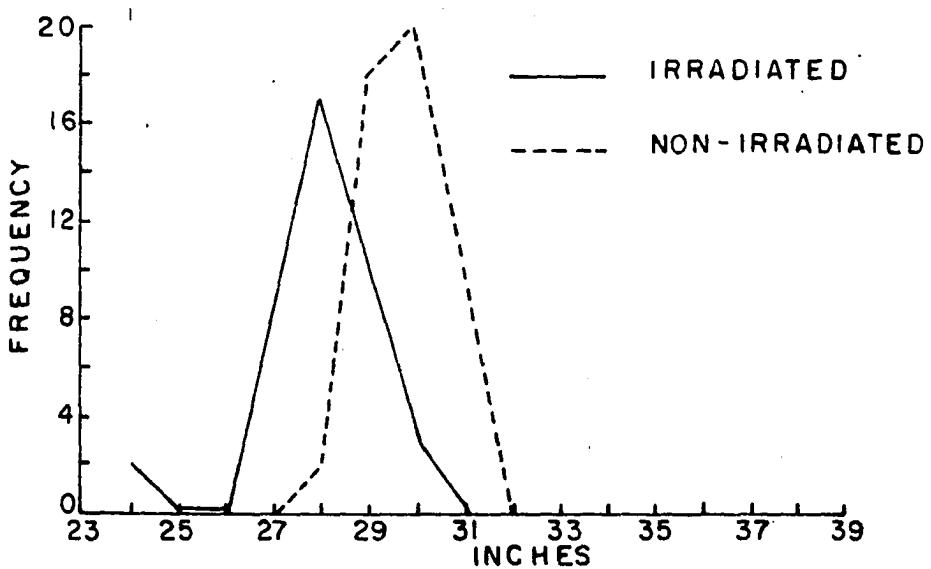
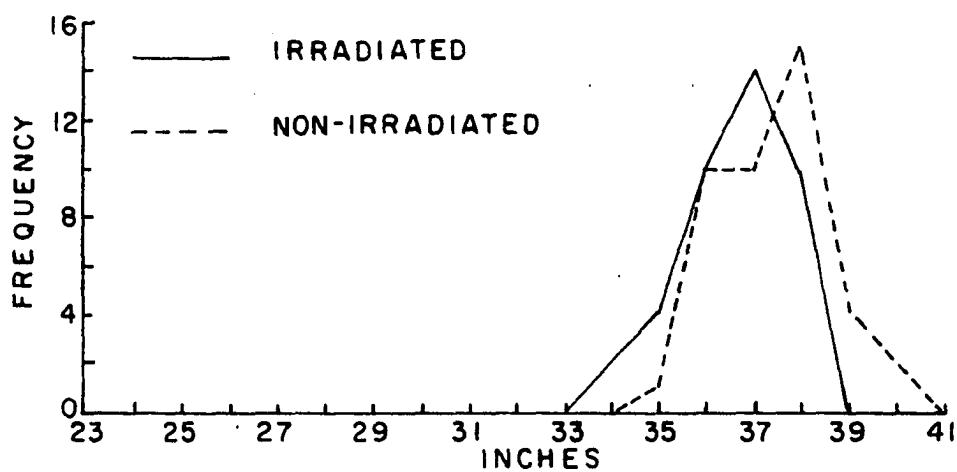
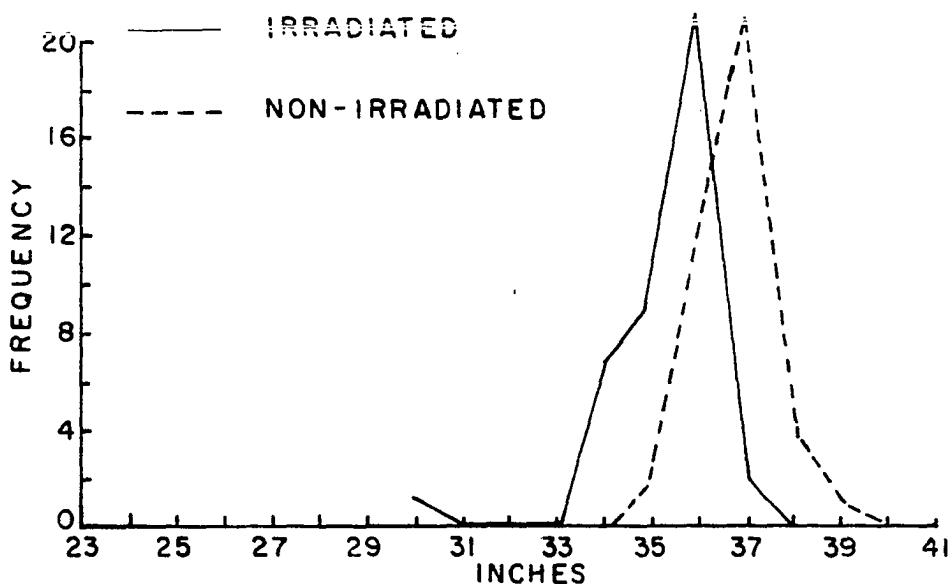


Figure 11. Frequency distributions of numbers of branches per panicle of oat lines derived from diploid irradiated and non-irradiated seeds

Figure 12. Frequency distributions of numbers of branches per panicle of oat lines derived from tetraploid irradiated and non-irradiated seeds

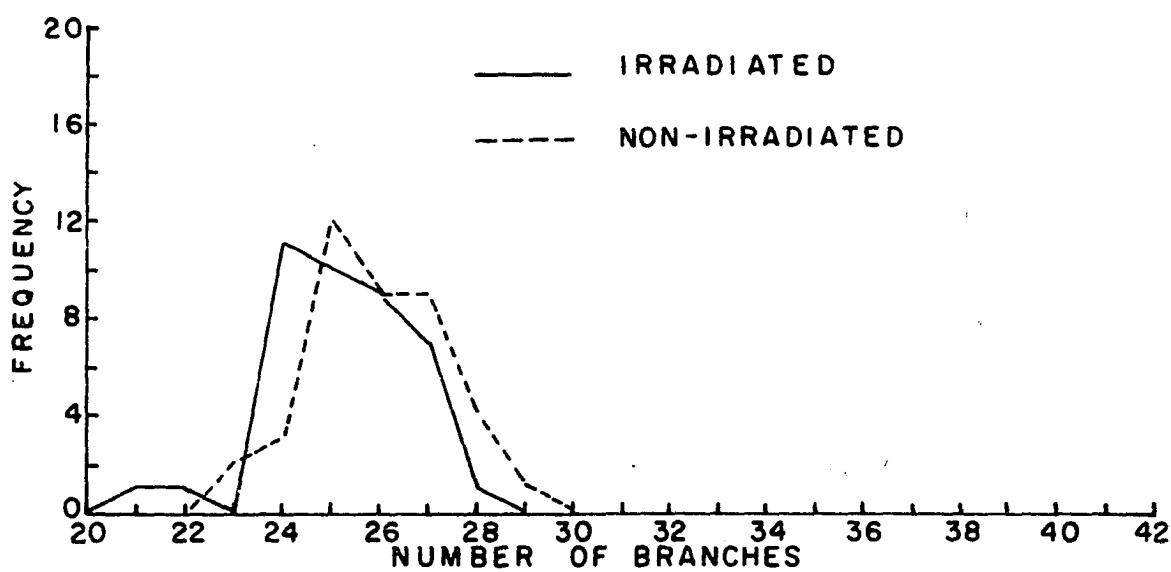
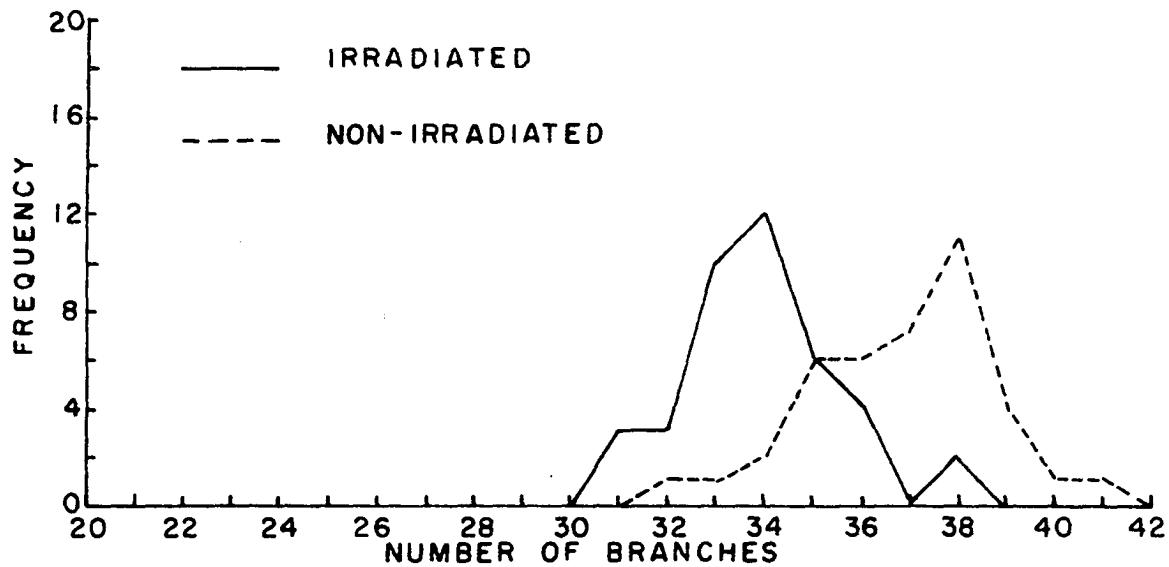


Figure 13. Frequency distributions of numbers of branches per panicle of oat lines derived from Andrew irradiated and non-irradiated seeds

Figure 14. Frequency distributions of numbers of branches per panicle of oat lines derived from Burnett irradiated and non-irradiated seeds

Figure 15. Frequency distributions of numbers of branches per panicle of oat lines derived from Pusa irradiated and non-irradiated seeds

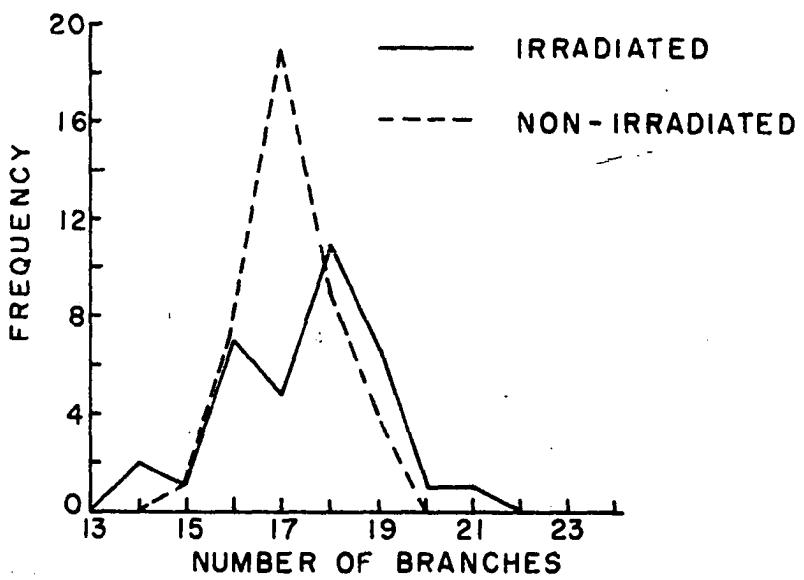
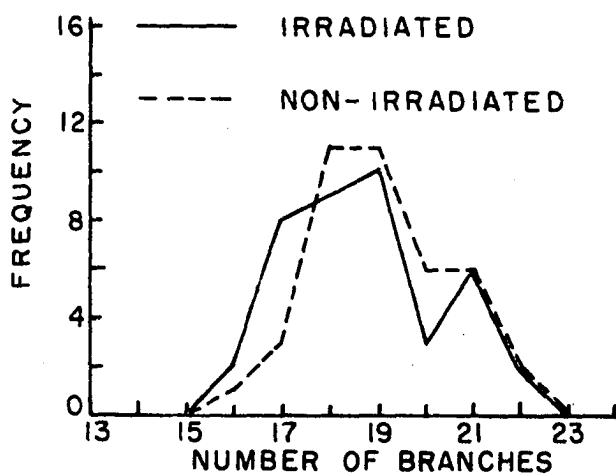
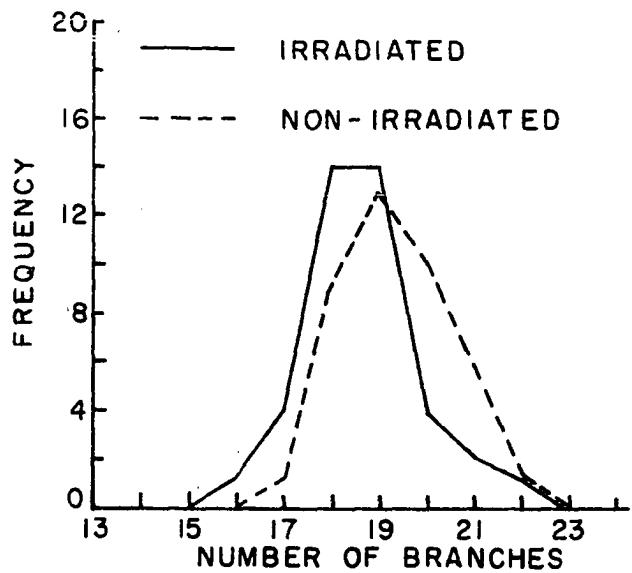


Table 7. Ratios of mean square for irradiated and non-irradiated populations at different ploidy level for seven attributes and the mean ratios of characters and ploidy levels

Ploidy level	Heading date	Plant height	Number of branches	Flag leaf length	Weight per 100 seeds	Groat length	Groat width	Mean
Diploid	1.7	2.4	0.8	1.2	2.2	2.2	2.7	1.9
Tetraploid	1.3	2.4	1.2	1.0	1.2	1.4	1.9	1.5
Hexaploid	1.2	2.0	1.5	0.8	1.6	3.8	3.2	2.0
Mean	1.4	2.3	1.2	1.0	1.7	2.5	2.6	

(Table 5). However, it is interesting that the mean seed weight was increased slightly in the diploid and tetraploid varieties, but decreased in all three hexaploid varieties (Table 5 and Figures 21-25). The variability among lines was increased by irradiation in every variety, but the only significant increases were in Saia, the diploid, and Pusa, the hexaploid (Table 6). The irradiation-derived populations of Saia, Burnett and Pusa had lower mean groat lengths than the check population, whereas the mean groat length of P.I. 193958 was increased by irradiation (Table 5 and Figures 26-30). Thermal neutron irradiation increased the groat length variability among lines significantly in all varieties except P.I. 193958, the tetraploid (Table 6).

The mean groat width was increased by the irradiated treatment in Saia and P.I. 193958, but it was decreased in each of the hexaploid varieties (Table 5 and Figures 31-35). The irradiation treatment increased the variability significantly in all five varieties (Table 6). In Saia and Pusa, both wider and narrower groat lines were obtained (Figures 26 and 30).

The increased variability due to thermal neutron treatment was significant in only 18 of 35 variety-attribute combinations measured. However, the ratio of mean squares from irradiation-derived to check populations was greater than 1.0 in all except five cases, heading date for Pusa, plant height for Burnett, flag leaf length for Andrew and Burnett and

Figure 16. Frequency distributions of flag leaf length of oat lines derived from diploid irradiated and non-irradiated seeds

Figure 17. Frequency distributions of flag leaf length of oat lines derived from tetraploid irradiated and non-irradiated seeds

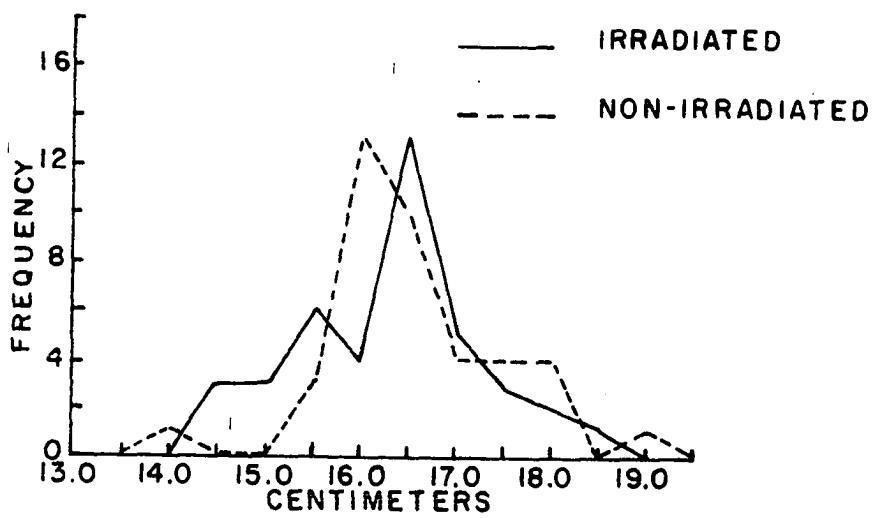
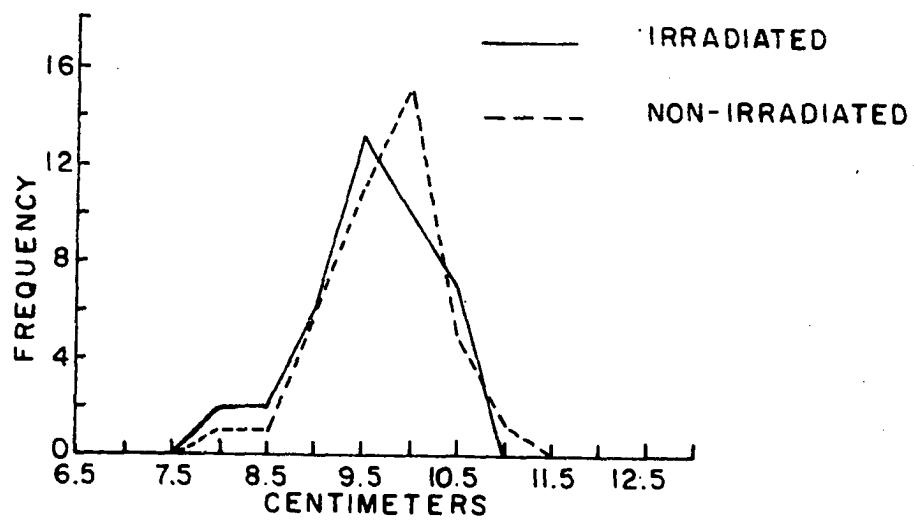


Figure 18. Frequency distributions of flag leaf lengths of oat lines derived from Andrew irradiated and non-irradiated seeds

Figure 19. Frequency distributions of flag leaf lengths of oat lines derived from Burnett irradiated and non-irradiated seeds

Figure 20. Frequency distributions of flag leaf lengths of oat lines derived from Pusa irradiated and non-irradiated seeds

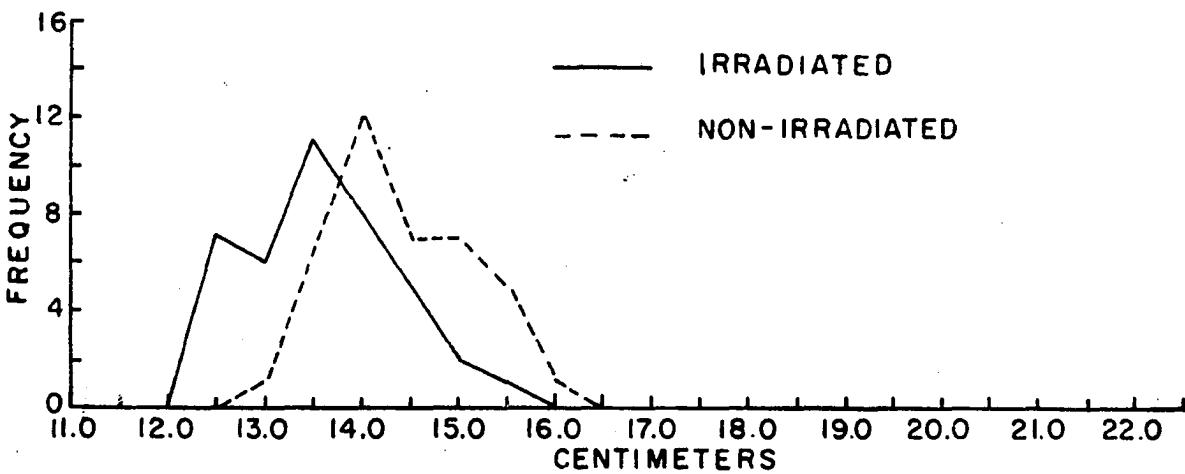
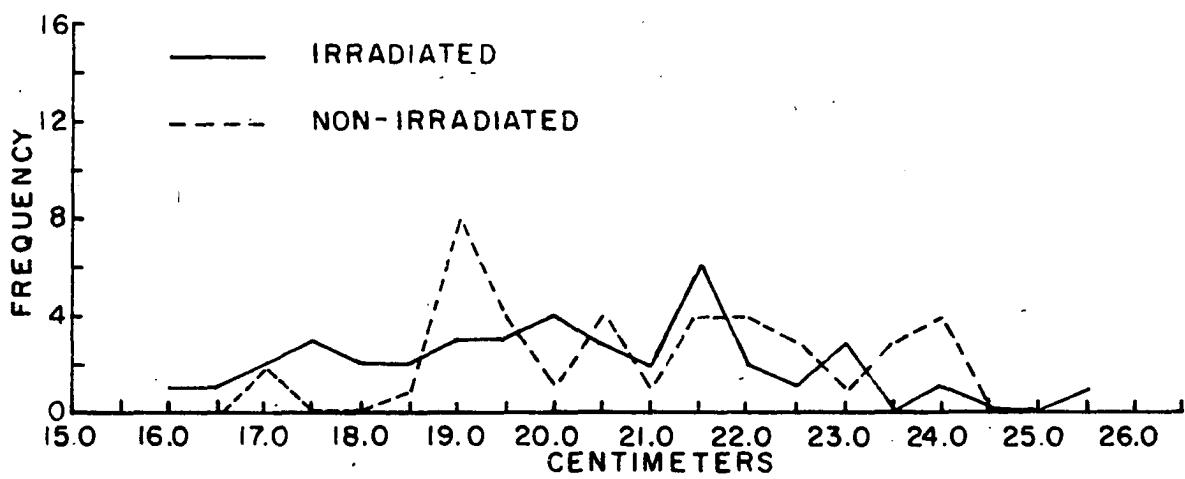
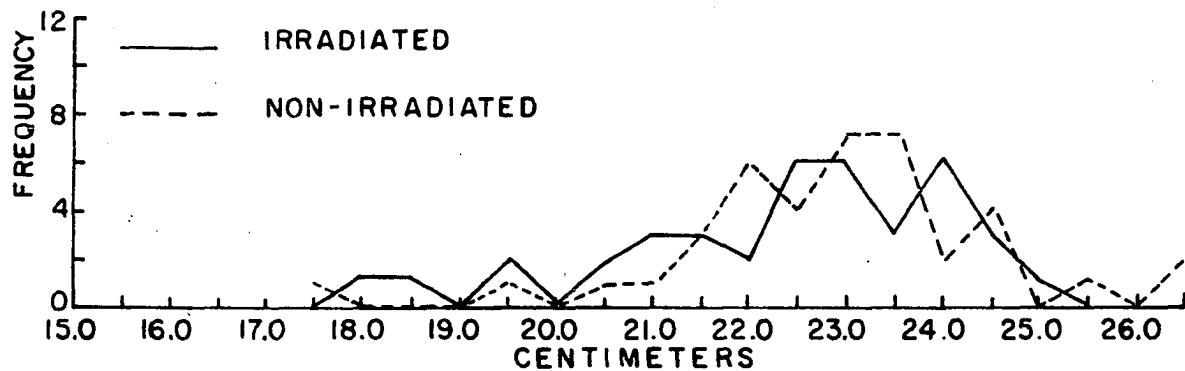


Figure 21. Frequency distributions of weights per 100 seeds of oat lines derived from diploid irradiated and non-irradiated seeds

Figure 22. Frequency distributions of weights per 100 seeds of oat lines derived from tetraploid irradiated and non-irradiated seeds

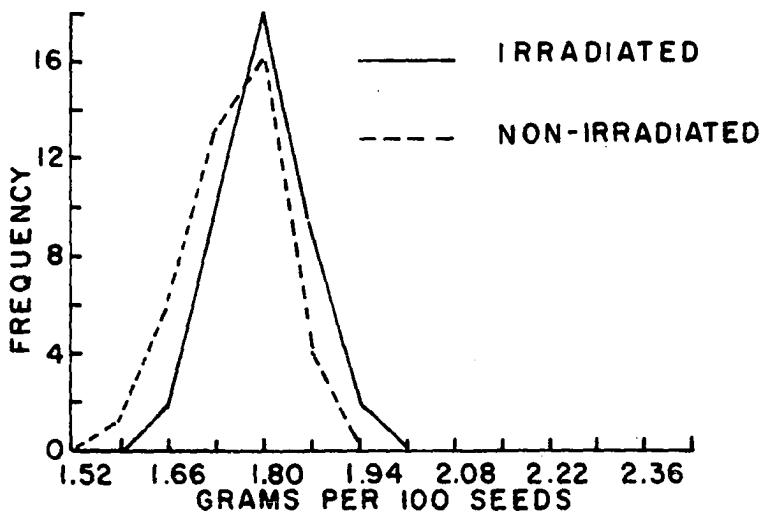
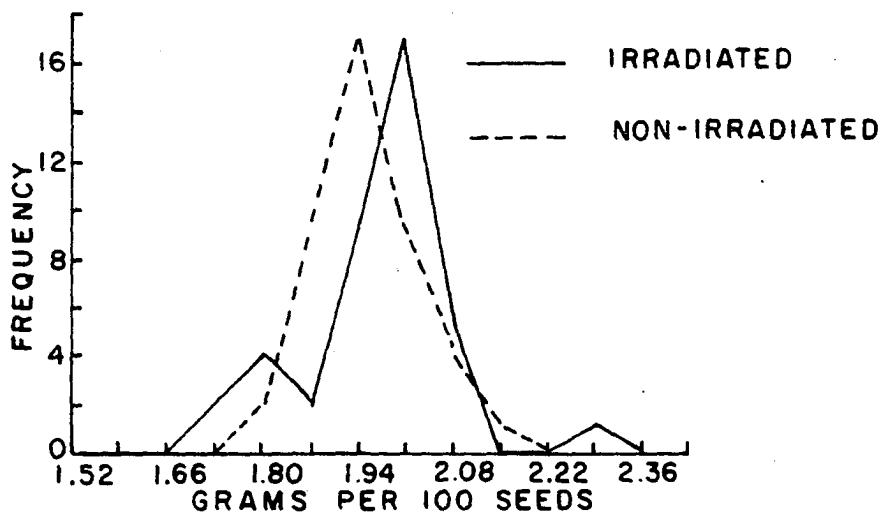


Figure 23. Frequency distributions of weights per 100 seeds of oat lines derived from Andrew irradiated and non-irradiated seeds

Figure 24. Frequency distributions of weights per 100 seeds of oat lines derived from Burnett irradiated and non-irradiated seeds

Figure 25. Frequency distributions of weights per 100 seeds of oat lines derived from Pusa irradiated and non-irradiated seeds

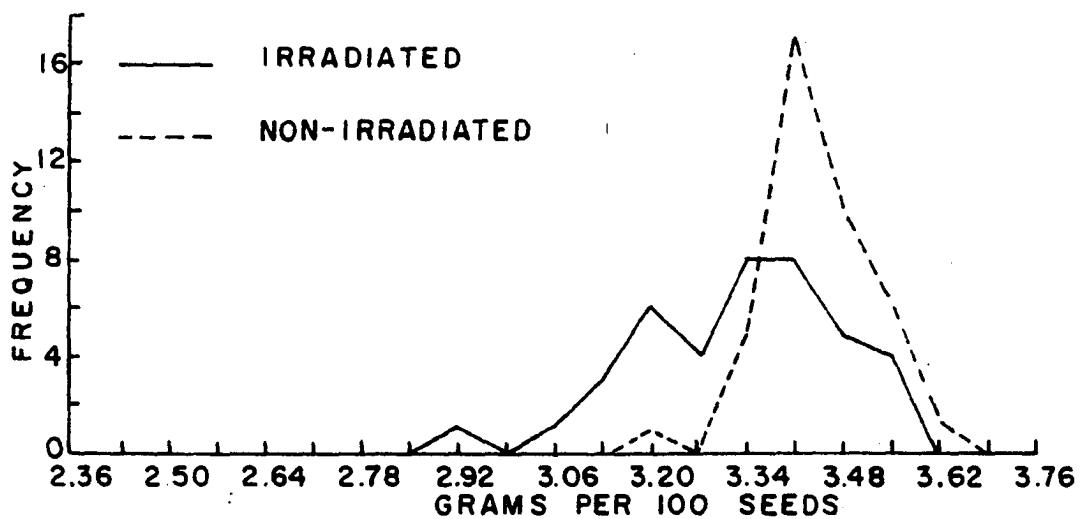
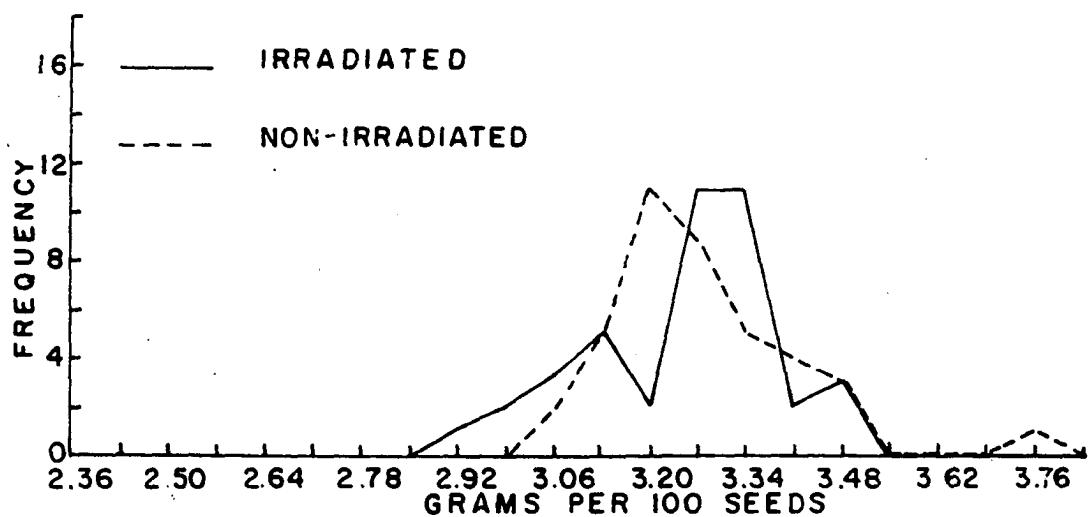
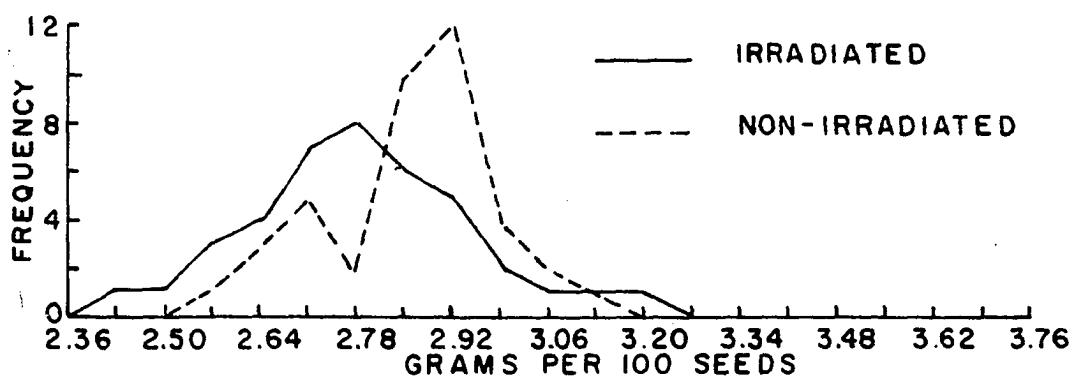


Figure 26. Frequency distributions of groat lengths of oat lines derived from diploid irradiated and non-irradiated seeds

Figure 27. Frequency distributions of groat lengths of oat lines derived from tetraploid irradiated and non-irradiated seeds

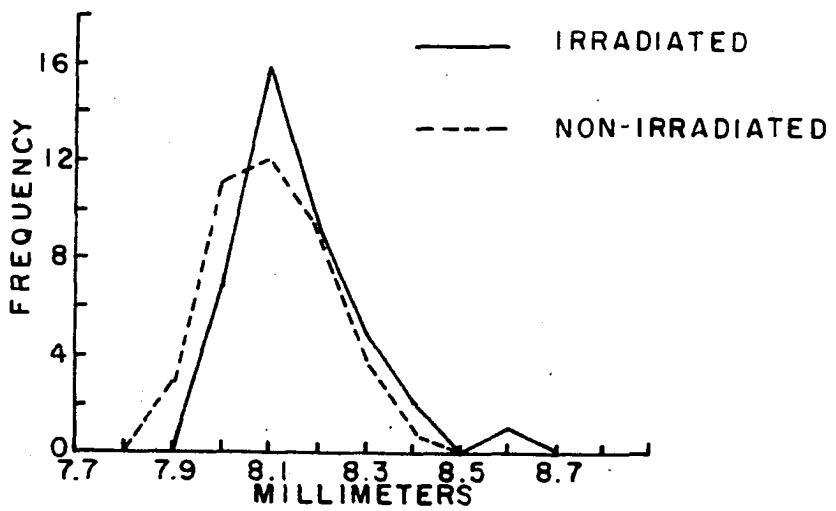
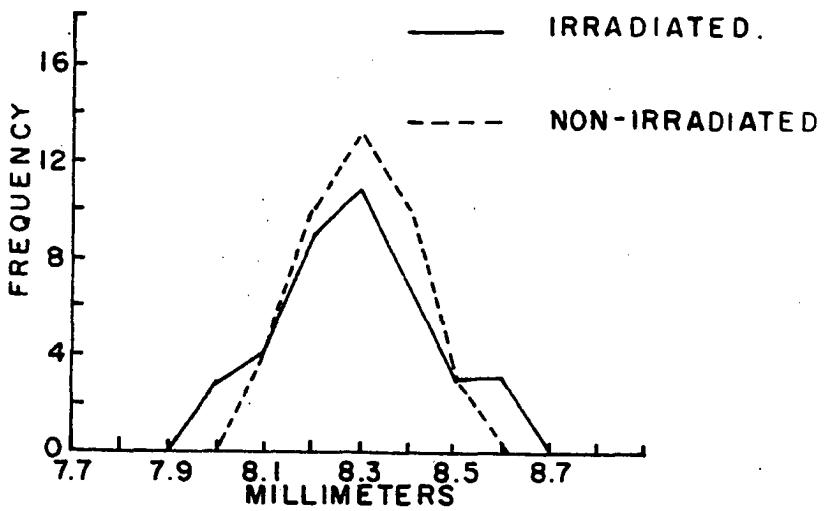


Figure 28. Frequency distributions of groat lengths of oat lines derived from Andrew irradiated and non-irradiated seeds

Figure 29. Frequency distributions of groat lengths of oat lines derived from Burnett irradiated and non-irradiated seeds

Figure 30. Frequency distributions of groat lengths of oat lines derived from Pusa irradiated and non-irradiated seeds

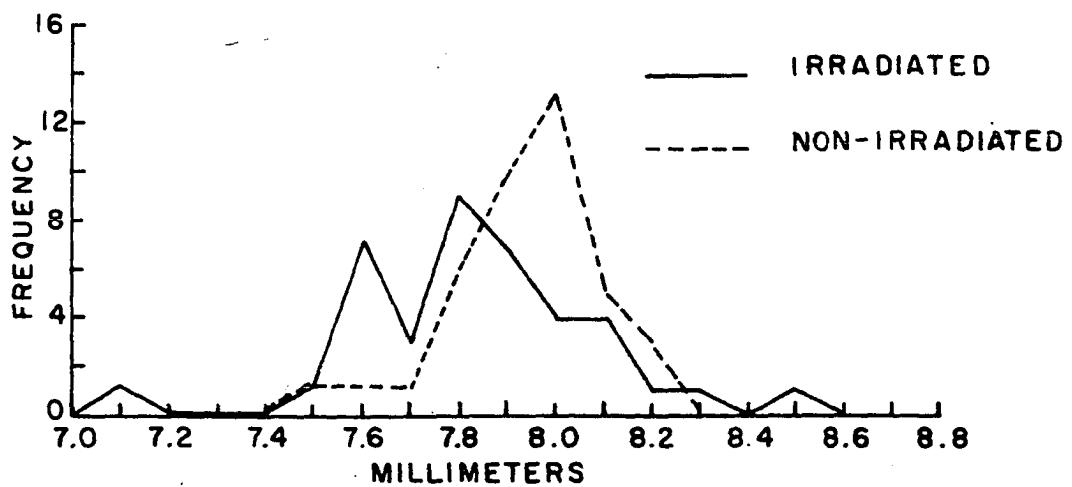
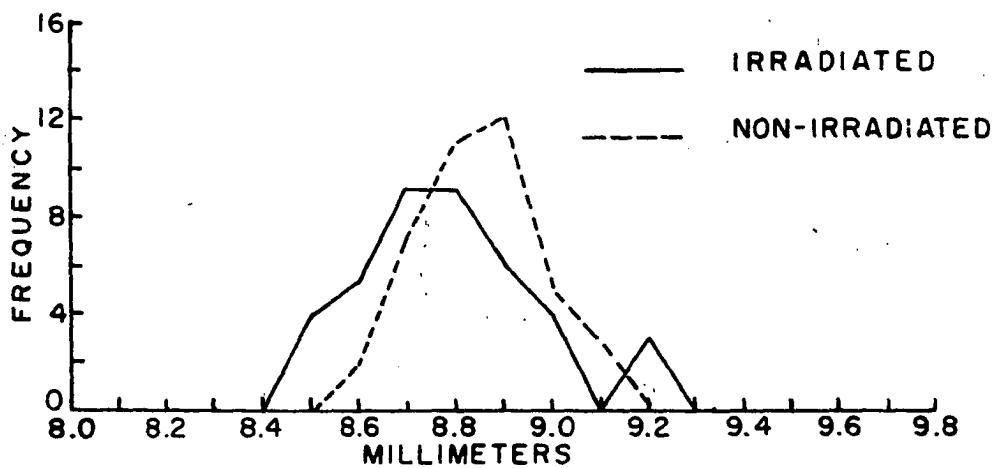
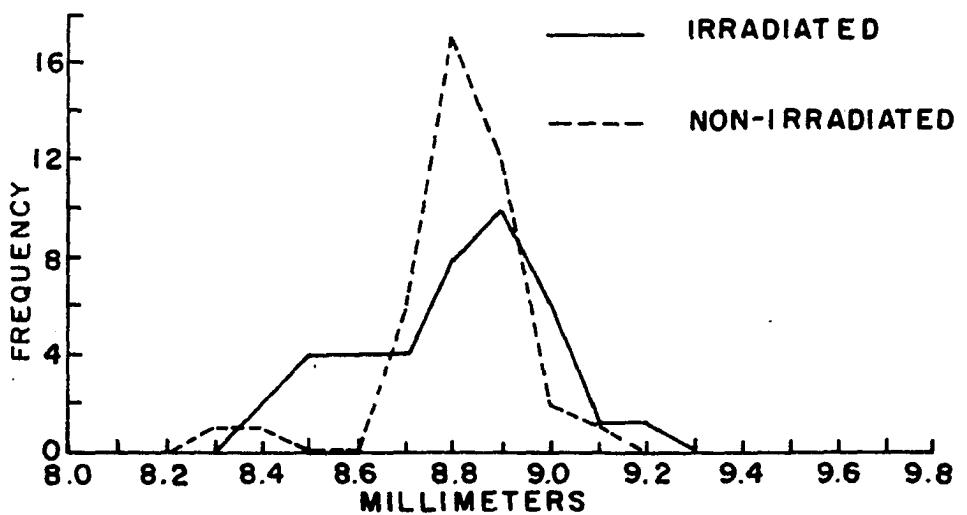


Figure 31. Frequency distributions of groat widths of oat lines derived from diploid irradiated and non-irradiated seeds

Figure 32. Frequency distributions of groat widths of oat lines derived from tetraploid irradiated and non-irradiated seeds

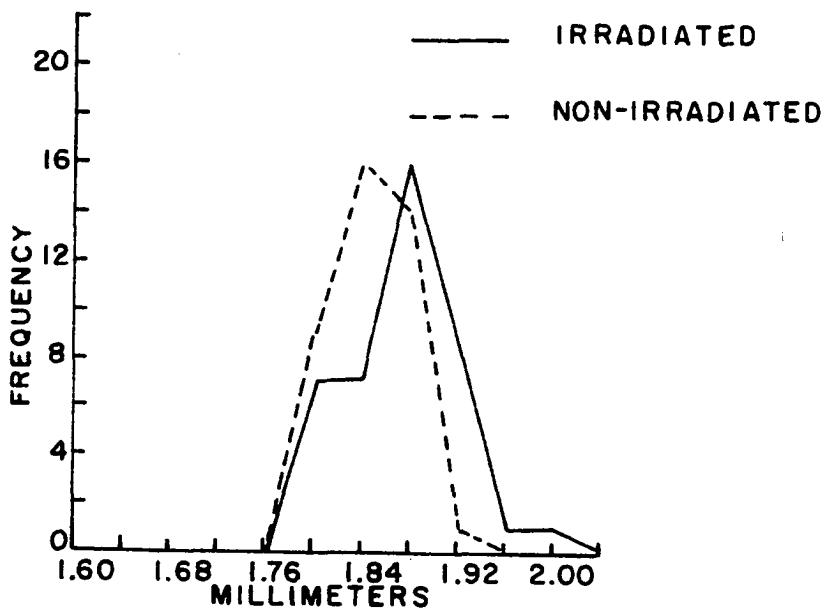
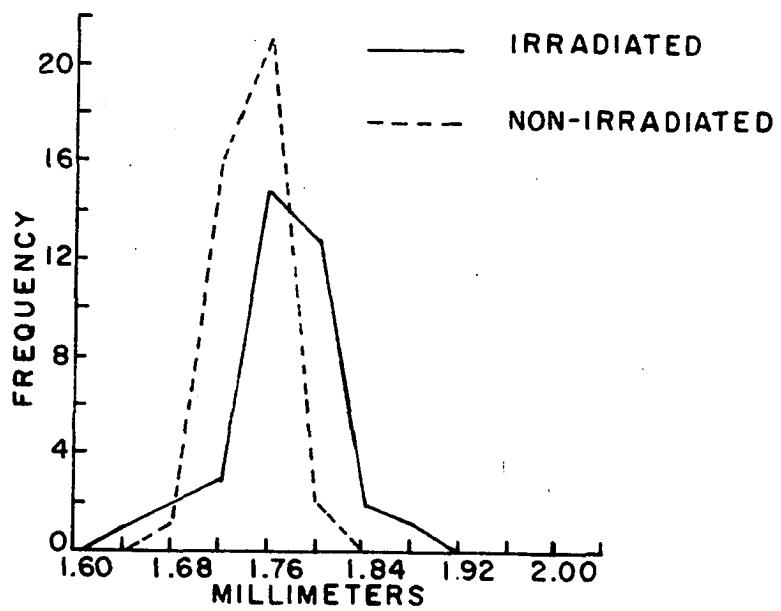
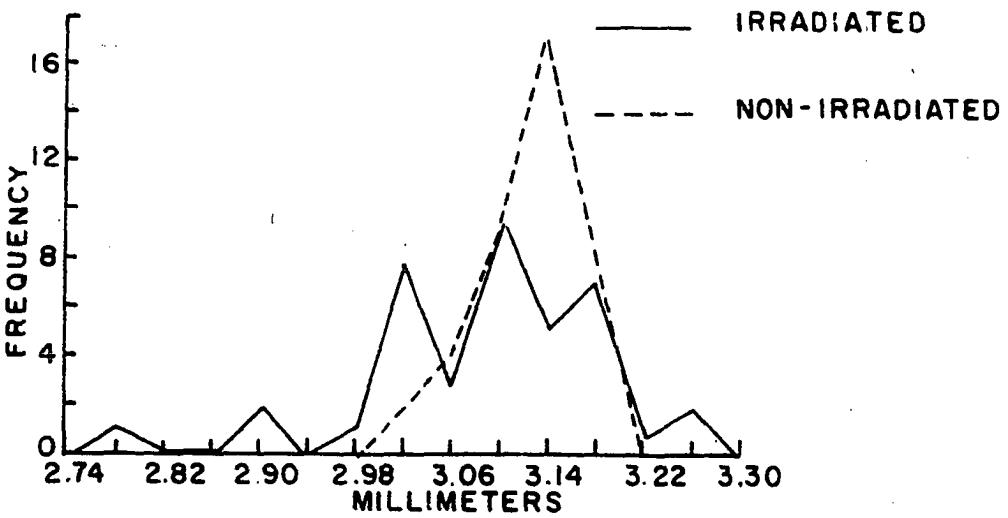
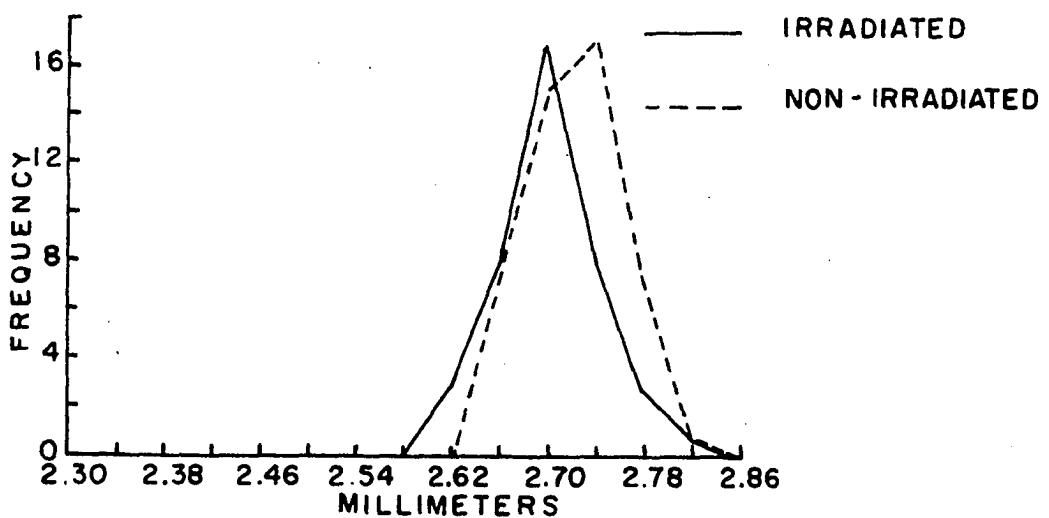
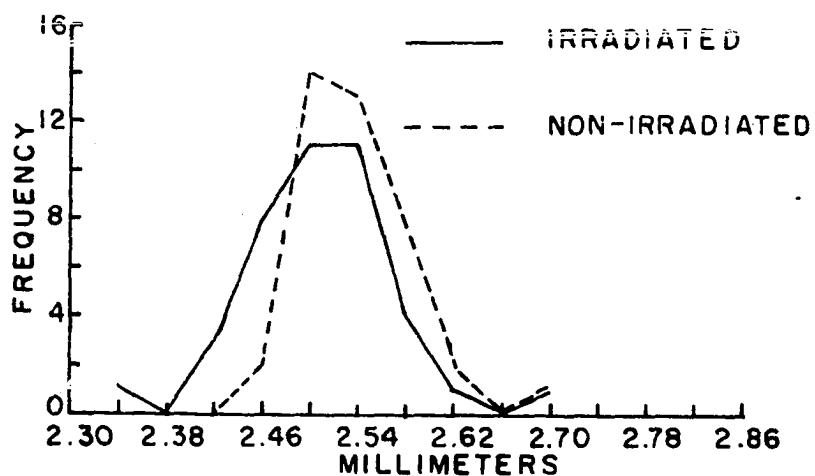


Figure 33. Frequency distributions of groat widths of oat lines derived from Andrew irradiated and non-irradiated seeds

Figure 34. Frequency distributions of groat widths of oat lines derived from Burnett irradiated and non-irradiated seeds

Figure 35. Frequency distributions of groat widths of oat lines derived from Pusa irradiated and non-irradiated seeds



number of branches per panicle in Saia (Tables 6 and 7). In these latter five cases the ratios were less than 1.0.

One of the objectives of this study was to compare the relative variability induced at the different ploidy levels. The sampling herein is somewhat unfair because three hexaploid varieties were used, whereas only one variety was used at each of the other ploidy levels. However, the mean squares for the three hexaploid varieties were averaged and the mean square ratios for each ploidy level are given in Table 7. There does not appear to be any relation between ploidy level and the degree to which variability is increased. When averaged across all seven attributes the mean squares were 90 per cent higher in the irradiation-derived than in the check populations for the diploid, 50 per cent higher in the tetraploid, and 100 per cent higher in the hexaploid. The tetraploid level appeared to be less sensitive to variability induction than the diploid, but the diploid and hexaploid levels had nearly equal induction of relative variability. Using mean square ratios between irradiation-derived and check populations to measure the relative magnitude of induced genetic variability had certain limitations because the ratio was confounded by the magnitude of the error mean square and by natural genetic variability which existed in certain varieties. A more reliable method for comparing the relative variability induced at the various ploidy levels was through genetic coefficients of variability. The genetic standard deviations (σ_g) were obtained using the formula:

$$\sigma_g = \sqrt{\frac{M.S._{Ir} - M.S._{Ck}}{3}}, \text{ where } M.S._{Ir} \text{ and } M.S._{Ck} \text{ are the}$$

mean squares for the irradiation-derived and check populations, respectively.

Genetic coefficients of variability varied with the attribute and the variety (Table 8). Certainly, the genetic coefficients of variability are associated with the attribute measured. The mean genetic coefficients of variability across attributes in which genetic variability was induced were very similar (from 7.3 to 8.8) for the diploid, tetraploid and two hexaploid varieties, Andrew and Burnett, but for Pusa the mean genetic coefficient of variability was nearly twice as large as that of the other varieties (16.2). When the mean genetic C.V.'s were calculated only for the attributes in which genetic variability was induced in all varieties (weight per 100 seeds, groat length, and groat width), similar values were obtained to those when all attributes were included. Obviously, the relative magnitude of genetic variability induced in quantitative characters of oats by thermal neutron treatment is highly dependent upon the germplasm source used. However, the variability induced in the polyploids was equal to or greater than that induced in the diploid.

The data presented herein are contrary to the general conclusion of Stadler (1929) and others, namely, that mutation breeding would be of little value in polyploid species because the expression of induced mutations in the polyploids would

Table 8. Genetic coefficients of variation for seven attributes measured in diploid, tetraploid and hexaploid oat varieties

Ploidy level and variety	Attributes						Mean for all attributes	Mean for seed attributes
	Heading date	Plant height	Number of branches	Flag leaf length	Weight per 100 seeds	Groat length	Groat width	
Diploid	0.6	2.7	--	14.9	3.9	9.3	13.8	7.5
Tetraploid	2.5	2.9	9.9	12.3	1.7	6.5	11.7	7.9
Hexaploid								
Andrew	0.4	2.7	16.9	--	3.4	10.1	10.5	7.3
Burnett	2.1	--	19.7	--	1.7	10.9	9.8	8.8
Pusa	--	4.0	28.5	16.3	4.6	24.1	19.7	16.2

For heading date and plant height the frequency distribution characteristics of the irradiation-derived populations are similar for diploids and polyploids (Figures 1-10).

Comparisons for number of branches per panicle and flag leaf length would be inappropriate since significant variability was not induced. The frequency distributions for the groat and seed attributes (Figures 21-35) tend to show the characteristic differences expected of diploids vs. hexaploids.

The characteristics of the tetraploid curves fit more closely to the diploid than to the hexaploids. For weight per 100 seeds and groat width the peaks of diploid and tetraploid frequency curves have not been lowered much by the irradiation treatment, whereas in two of the three hexaploid varieties the peaks have been flattened out. For groat length the same is true except that all three hexaploid varieties show the flattening out of the distribution peak. In each of these attributes from one to five lines in the irradiation-derived diploid and tetraploid populations fall distinctly outside of the range of the check without any very noticeable change in the remainder of the frequency distribution curves. No greater proportion of irradiation-derived lines transcend the check in the hexaploids, but there tends to be a general reshaping of the whole frequency distributions.

In general, the characteristics of the frequency distributions of the irradiation-derived populations when compared to the checks support the conclusions that: (a) a mutation

which occurs in a diploid line will produce a more distinct expression than a mutation which occurs in a hexaploid, and (b) a larger proportion of lines in the hexaploids carry mutations which show some degree of expression. Of course, the data supporting these conclusions herein are not as definitive as desired. Examples are: (a) only certain attributes showed differential frequency distribution characteristics between the ploidy levels, and (b) the tetraploid behaved more like the diploid than the hexaploid. However, all of the data support the conclusion that mutation breeding should be as useful in polyploid as in diploid species. The magnitude and direction of genetic variability induced by thermal neutron treatment is dependent upon the attribute studied and genotype treated. For example, the thermal neutron treatment did not induce significant variability in any of the varieties for flag leaf length and only in Pusa for number of branches per panicle, whereas for groat width significant variation was induced in all varieties. The average increase in mean squares for irradiation-derived populations compared to the checks, across all varieties, ranged from zero for flag leaf length to 150 and 160 per cent for groat length and width, respectively.

In a majority of cases increased variability for an attribute was due to mutations occurring in both directions from the check mean, but in some cases the induced variability

was nearly unidirectional, e.g., number of branches per panicle in Saia variety (Figure 11). Also, among the hexaploid varieties there were sharp differences in degree of mutability for a given character. Pusa showed a significant increase in variability due to irradiation treatment in five of the seven characters measured where variability was increased significantly in only two characters in Burnett.

An important problem related to mutation breeding where thermal neutrons serve as the mutagen source is the classes of mutations induced. Of course, the most reliable method for studying the classes of mutations induced is via cytological observations, but a great limitation on this method is the small quantity of materials that can be assayed because the procedures are so laborious.

Genetic correlations can be used to give an indication about the occurrence of certain classes of chromosomal mutations. Okabe et al. (1963) explained that point mutations and certain chromosomal mutations, such as small deletions, inversions, translocations, etc. would be tolerated in diploid, tetraploid, and hexaploid species alike. However, gross chromosomal deletions, where large segments of chromosomes or whole chromosomes were missing, would be tolerated only at the higher polyploid level. Except for instances of mutations affecting loci with pleiotropic effects, the first class of mutations would cause phenotypic variability in various attributes independently. However, the gross chromosomal

deletions would cause the loss of whole blocks of genes and would give covariability among attributes. The covariability could be measured by genetic correlations.

If gross chromosomal deletions are an important source of variability in hexaploids the genetic correlations among attributes in irradiation-derived populations should be of greater (both positive and negative) magnitude in hexaploid than in diploid oats.

In order for a genetic correlation to be calculated, significant induced variability was required for both attributes being correlated. The numbers of possible genetic correlations were 10, 3, 6, 3, and 10 for Saia, P.I. 193958, Andrew, Burnett, and Pusa, respectively (Table 9). There does not appear to be any relationship between the magnitude of the genetic correlations and the ploidy level of the oats. The mean correlations, ignoring signs, were 0.43, 0.39, and 0.44 for the diploid, tetraploid, and hexaploid levels, respectively. There is certainly no indication that gross chromosomal deletions were an important source of variability in the hexaploid oats.

Almost none of the frequency distributions for the attributes studied showed significant skewness or kurtosis (Tables 10 and 11, and Figures 1 to 35). There were neither consistent positive nor negative changes in skewness nor kurtosis values for the mutagen-derived frequency distributions when compared to the checks (Table 12). Only four shifts in skewness were significant.

Table 9. Genetic correlations among different characters of mutagen-derived lines from different ploidy level

Characters	Saia	P.I. 193958	Andrew	Burnett	Pusa
Heading date and:					
Plant height	-0.52	-0.33	--	--	--
Wt./100 seeds	-0.18	--	--	--	--
Groat length	-0.15	--	--	0.46	--
Groat width	0.19	-0.51	--	0.29	--
Plant height and:					
No. of branches	--	--	--	--	0.97
Wt./100 seeds	0.69	--	1.07	--	0.37
Groat length	0.44	--	0.03	--	0.09
Groat width	0.39	0.32	1.07	--	0.24
No. of branches and:					
Wt./100 seeds	--	--	--	--	-0.06
Groat length	--	--	--	--	-0.40
Groat width	--	--	--	--	0.10
Wt./100 seeds and:					
Groat length	0.95	--	0.13	--	0.27
Groat width	0.53	--	1.50	--	0.33
Groat length and:					
Groat width	0.26	--	-0.37	-0.07	-0.49

Table 10. Skewness values for the frequency distributions of seven attributes measured on oat lines derived from mutagen-treated and nontreated seeds

Population	Heading date	Plant height	Number of branches	Flag leaf length	Weight per 100 seeds	Groat length	Groat width
Diploid							
Irradiated	0.98**	-0.10	0.47	-0.64	-0.14	0.89*	-0.71
Non-irradiated	0.72	0.28	-0.36	-0.52	0.26	-0.16	-0.17
Tetraploid							
Irradiated	-0.11	-0.12	-0.49	0.62	0.15	0.12	0.17
Non-irradiated	-0.11	-0.29	0.72	0.22	-0.35	0.66	0.29
Hexaploids							
Andrew							
Irradiated	0.19	-0.23	0.54	-0.60	0.28	-0.37	-0.38
Non-irradiated	0.17	0.19	0.23	-0.52	-0.34	-0.16	0.11
Burnett							
Irradiated	-0.26	-0.62	0.35	0.88*	-0.42	0.25	-0.50
Non-irradiated	0.54	0.26	0.20	-0.19	0.94*	0.19	0.60
Pusa							
Irradiated	0.46	-0.14	-0.39	0.29	-0.57	0.49	-0.77*
Non-irradiated	0.12	-0.56	0.16	0.31	0.17	-0.69	-0.77*

Table 11. Kurtosis values for the frequency distributions of seven attributes measured on oat lines derived from mutagen treated and nontreated populations

Population	Heading date	Plant height	Number of branches	Flag leaf length	Weight per 100 seeds	Groat length	Groat width
Diploid							
Irradiated	-0.21	0.58	0.64	0.24	0.16	-0.37	0.12
Non-irradiated	0.35	-0.16	0.17	0.76	0.20	-0.65	-0.36
Tetraploid							
Irradiated	0.42	0.19	0.84	-0.23	0.19	0.20	0.19
Non-irradiated	-0.30	-0.63	-0.29	0.13	-0.19	0.33	-0.55
Hexaploids							
Andrew							
Irradiated	0.69	0.90	0.98	0.15	0.37	-0.28	0.78
Non-irradiated	0.60	0.81	-0.52	0.23	-0.11	0.53	0.23
Burnett							
Irradiated	0.12	-0.16	-0.70	0.17	0.95	0.52	0.58
Non-irradiated	-0.36	-0.39	-0.44	-0.93	0.15	-0.39	-0.25
Pusa							
Irradiated	-0.89	0.40	-0.26	-0.42	0.19	0.24	0.13
Non-irradiated	0.83	-0.56	-0.30	-0.74	0.20	0.12	0.42

Table 12. The "t" values for differences between mutagen-derived and check population frequency distributions for skewness and kurtosis for seven attributes

Population	Heading date	Plant height	Number of branches	Flag leaf length	Weight per 100 seeds	Groat length	Groat width
Skewness							
Diploid							
Irradiated vs. check	0.20	0.00	1.56	-0.22	-0.76	1.98	-1.01
Tetraploid							
Irradiated vs. check	0.01	0.20	-2.29*	0.74	0.95	-1.03	0.24
Hexaploids							
Andrew							
Irradiated vs. check	0.04	-0.80	0.59	-0.15	1.17	-0.40	-0.92
Burnett							
Irradiated vs. check	-1.51	-1.68	0.28	2.02*	-2.57*	0.11	-2.09*
Pusa							
Irradiated vs. check	0.66	0.80	-1.05	0.04	-1.40	2.22*	-0.01
Kurtosis							
Diploid							
Irradiated vs. check	-0.54	0.71	0.45	-0.50	-0.58	0.26	0.47
Tetraploid							
Irradiated vs. check	0.68	0.42	1.09	-0.35	0.38	0.52	0.72
Hexaploids							
Andrew							
Irradiated vs. check	0.09	0.05	1.45	-0.77	0.46	-0.24	0.53
Burnett							
Irradiated vs. check	0.47	0.22	-0.25	1.06	0.76	0.88	0.81
Pusa							
Irradiated vs. check	-1.66	0.89	0.03	0.30	0.00	0.12	-0.27

Sterility Percentages

The only variety in which the irradiation treatment increased the sterility percentage significantly was Pusa (Tables 13 and 14). The variability among lines within irradiation-derived populations was significant in the tetraploid and in Andrew and Pusa varieties.

It is conceivable that sterility could affect the expression of seed attributes, so that genetic variability would be under- or overestimated. Frey (1962) showed that when some spikelets were removed from an oat panicle the seeds in the remaining spikelets were increased in weight. Sterility of florets would probably have the same effect. In order to determine whether the induced genetic variability was confounded by sterility, the intrapopulation correlations between sterility and groat width were calculated for the irradiation-derived and check populations (Table 15).

The correlations ranged from -0.59 to +0.37 in the irradiated populations and from -0.44 to +0.51 for the checks. The overall correlations were -0.14 and -0.21 for irradiation-derived and check populations, respectively. None of the individual or pooled correlations was significant. Therefore, the induced genetic variability for groat width resulted from induced mutations and was not an artifact due to confounding effects of sterility.

Table 13. Mean squares from the analysis of variance for sterility percentages of oat lines derived from diploid, tetraploid and hexaploid irradiated and non-irradiated seeds

Source of variation	d.f.	M.S.
Total	299	230.632
Replications	2	251.767
Among varieties	4	9848.473**
Error (a)	8	272.627
Treatments w/varieties	5	521.128**
Diploid	1	21.421
Tetraploid	1	345.168
Andrew	1	3.89
Burnett	1	0.857
Pusa	1	2234.308**
Error (b)	10	81.19
Lines w/populations w/treatments		
Diploid:		
Irradiated	9	29.78
Non-irradiated	9	72.44
Tetraploid:		
Irradiated	9	184.76**
Non-irradiated	9	114.71
Andrew:		
Irradiated	9	138.99*
Non-irradiated	9	41.35
Burnett		
Irradiated	9	33.94
Non-irradiated	9	64.65
Pusa		
Irradiated	9	992.58**
Non-irradiated	9	22.76
Error (c)	180	64.97

Table 14. Mean sterility for irradiation-derived and checks lines of diploid, tetraploid and hexaploid oat seeds

Population	Percentage
Saia	
Irradiated	6.7
Non-irradiated	5.5
Tetraploid	
Irradiated	39.3
Non-irradiated	34.5
Andrew	
Irradiated	18.2
Non-irradiated	17.6
Burnett	
Irradiated	10.8
Non-irradiated	10.5
Pusa	
Irradiated	32.4
Non-irradiated	20.2

Table 15. Intrapopulation phenotypic correlations between sterility percentages and groat width

Variety	Populations	
	Irradiated	Non-irradiated
Saia	.50 ⁺	.08 ⁺
P.I. 193958	-.04 ⁺	-.21 ⁺
Andrew	.37 ⁺	.51 ⁺
Burnett	-.01 ⁺	-.44 ⁺
Pusa	-.59 ⁺	-.36 ⁺
Overall correlation	-.14 [*]	-.21 [†]

⁺8 degrees of freedom.

^{*}40 degrees of freedom.

DISCUSSION

Genetic variability induced by mutagen treatment could be confounded by variability from hybridization if natural outcrossing occurred upon plants derived from the mutagen treatment. It has been shown by Konzak (1959) that thermal neutron treatment of small grain seeds will increase crossability of mutagen-derived plants in the M_1 and subsequent generations. Therefore, every possible precaution was taken to minimize outcrossing as a contaminating source of genetic variability. To minimize the opportunity for interpopulation crossing, the M_1 and check populations of each variety were grown in a separate greenhouse room.

In the M_2 generation several precautions also were taken to minimize outcrossing. Plants were spaced in progeny rows and the rows were 3 feet apart in ranges separated by 5-foot alleys. Progeny rows with plants exhibiting high sterility were discarded, and furthermore, highly sterile plants would have been eliminated automatically because they would not have produced the 75 seeds required to plant the 1963 experiment.

In addition to the outcrossing hazard, sterility could modify the expression of certain attributes, especially those associated with seeds. When the number of developing caryopses per panicle is reduced, the remaining ones increase in weight (Frey 1962). Such effects, if caused by irradiation-induced

sterility, would appear as genetic variability. To determine whether sterility did contribute to the genetic variance of seed characteristics a pooled intrapopulation correlation between sterility percentage and groat width was calculated. The correlation was non-significant (-0.14), showing that sterility did not influence the induced genetic variability for this attribute. Since it was expected that sterility would confound seed characteristics more than any other attributes, and no association was shown in this case, other correlations were not run. It is concluded that the genetic variability induced by thermal neutron irradiation was due to mutations and was not an artifact of sterility.

The M_3 lines included in 1963 experiment represented a stratified random sample from the irradiation-induced population since off-type plants, such as chlorophyll deficient, dwarfs, fatuoids and partially steriles were discarded. Therefore, the variability measured did not represent the total genetic variability induced by irradiation. But from the mutation breeding standpoint, with oats, the variability carried by the discarded plants would be quite useless. The genetic variability which the discarded plants may have possessed could be released only through outcrossing and subsequent selection. Plant breeders are more interested in variability that is unconfounded with deleterious mutations. However, the results in this and other similar studies (Krull and Frey, 1961, Abrams, 1963, Gregory, 1957) indicate that

there is significant genetic variability in the "stratified random" sample of lines.

The discarding of obviously deleterious mutant lines before measuring the induced variability for quantitative characters also may have had a bearing upon the infrequency with which the means of irradiation-induced populations were significantly different from those of the checks. For example, obviously dwarfed lines were excluded from the sample measured, so the mean heights of check and irradiation-induced populations could not be expected to differ much. In most cases, the induced variability was distributed quite equally on both sides of the population means. Only five of the 35 cases tested showed a significant skewness difference between the check and irradiation-induced populations, and in no cases were the kurtosis shifts significant.

When making significance tests of variance, the existing genetic variability in a parental variety used for irradiation treatment experiments could confound the measurement of irradiation-induced genetic variation. First, existing variability may have an expanding or a depressing effect on the production of variability by the mutagen, and secondly, the denominator of the F ratio for check to irradiated populations is biased upward.

Gregory (1956b) postulated that the variation induced by irradiation should be cumulative with that from hybridization. He found that for yield of peanuts, the total genetic variance

among lines derived from irradiated hybrids was 77 per cent as great as the sum of the genetic variability induced in the irradiated parents plus the variability in the hybrids. Khadr (1964)¹ made similar comparisons and found values of 65, 88, and 87 per cent for heading date, plant height and seed weight, respectively. Therefore, it is likely that a heterogeneous background might depress the production or at least the expression of induced variability.

The effect of the overestimation of the denominator of the F ratio was circumvented herein by calculating genetic coefficients of variability to measure the relative induced variability between ploidy levels, varieties and attributes.

Through the years controversy has existed relative to the efficiency of mutation breeding in polyploid crops. Stadler (1929) and others argued that the reduplication of genes in polyploid crop species would be a handicap to the phenotypic expression of mutations. On the other hand, polyploid species because of the reduplication of genes, offer more target sites for mutations which affect a given attribute. Theoretically, a greater number of mutations would be induced in polyploids than in diploids, but the mutations occurring in polyploids could not gain expression because a majority of induced mutations are from dominant to recessive. This whole

¹Khadr, F., Agronomy Department, Iowa State University, Ames, Iowa. Data on expected genetic variability. Private communication. 1964.

argument has been built on the supposition that dominance is complete or nearly so. Newer evidence shows that, in fact, dominance is almost never complete (Sprague *et al.* 1943, Srb and Owen 1957, Sinnot, Dunn and Dobzhansky 1958). Dominance is not an intrinsic property of the gene. Its manifestation depends on a great many elements in its genetic background, its environment and possibly its own constitution. Therefore, any mutation, regardless of the extent of polyploid background in which it occurs may be expected to modify the expression of some attribute to a small degree. Furthermore, the conclusion of Stadler (1929) was based upon the relative frequencies of chlorophyll mutations, and this character tends to show nearly complete dominance. This could explain why many workers (MacKey 1952, 1954a; Gregory 1955, Krull and Frey 1961, Abrams 1963) have been successful in obtaining significant induced variability in polyploid crop species.

It can be argued that mutations which produce small "chunks" of variation are more useful than mutations which produce drastic effects. Drastic changes may upset the whole genetic systems so as to be detrimental to the phenotype. Gaul (1961) has labelled the mutations which cause small changes in phenotypic expression of an attribute as "micromutations". The greater tendency for micromutations to occur at the hexaploid level than at the diploid level is evident in a comparison of the frequency distributions for seed and grain characteristics.

In the diploid most of the lines appear to be non-mutants and the variant lines which do occur are placed distinctly beyond the limits of the check distribution. In contrast, the frequency distributions for the hexaploids tend to be flattened indicating that many mutant lines occurred, but the mutation expression in each was small. These tendencies are most evident for the seed attributes, and undoubtedly, they are also somewhat genotype-dependent.

The data herein suggest that the genetic variability for quantitative characters which can be induced in tetraploid and hexaploid species is at least as great as that which can be induced in diploids. The mean coefficients of genetic variances for all attributes were as high for hexaploids and tetraploids as for diploids. This statement is subject to some reservation since the mean genetic coefficient of variability for any ploidy level will be a function of the genotypes used in the experiments. For example, the mean genetic coefficient of variability for Pusa variety was twice as great as that for the other hexaploid varieties. Supposedly, a similar situation could occur if a different diploid variety was used. The results herein agree with MacKey (1954b) who concluded that polyploids often show a higher mutation frequency than do diploids.

Another problem which has received considerable discussion relates to the type of mutations that are produced by the treatment of higher plants with mutagens (Stadler 1946,

MacKey 1956, 1958, Krull, 1960). Mutations induced by irradiation are either genic or chromosomal. MacKey (1954b) has argued that chromosomal mutations of the gross deletion type account for a significant amount of the irradiation-induced variability in hexaploid wheat and oats. His conclusion was based on the frequency of speloid and fatuoid mutations in irradiation-derived populations of hexaploid wheat and oats, respectively. The speloid and fatuoid mutations are known to be associated with chromosome deletions (MacKey 1954c, O'Mara 1961). Okabe et al. (1963) stated that if gross chromosomal deletions represented an important source of induced genetic variability in the polyploids, it should lead to covariation among attributes because the genes would be lost in groups. They found some evidence for covariation of groat attributes in two hexaploid oat varieties. The relative importance of gross chromosomal deletions to other mutations in irradiation induced populations of hexaploid oats is subject to test by comparing the magnitude of the genetic correlations between attributes measured in oat genotypes which represent different ploidy levels.

In this study, the mean genetic correlations were similar for all ploidy levels. This indicates that gross chromosomal deletions were not an important source of induced genetic variation in the hexaploid oats. This does not necessarily refute MacKey (1954b), since his evidence was based upon fatuoid and speloid occurrence, and in this study fatuoid

and sterile plants were purposely discarded. Therefore, the plants and lines which would be expected to contain maximum chromosomal damage were not part of the sample upon which measurements were taken.

Knowledge about the types of mutations produced by irradiation is important to plant breeders. If induced-variability is due primarily to gross chromosomal aberrations, it can be used only in a direct selection program because of the cytological abnormalities that would be incurred with hybridization. In contrast, genetic variability due to point mutations would be useful in a hybridization program. Further definition on this point must await cytological investigations.

In general, the data reported herein support two important points defined in the objectives (a) thermal neutron irradiations induced genetic variability in hexaploids equal in magnitude to that in diploids, (b) the types of induced mutations measured in hexaploid and diploid species were similar.

SUMMARY

Seed lots from five oat varieties, Saia, a diploid, P.I. 193958, a tetraploid, and Andrew, Burnett and Pusa, hexaploids, were treated with thermal neutron irradiations to provide materials for comparing the magnitude of variability and the types of mutations induced at different ploidy levels. Forty lines derived from each irradiated population and a like number from check populations were grown in a replicated experiment and measured for heading date, plant height, number of branches per panicle, flag leaf length, weight per 100 seeds, groat width and groat length.

For few attributes, irradiation treatment caused a significant shift in the population means, but variability was increased for most of the attributes. In general, variability was shifted in both plus and minus directions from the population means.

The mean induced variability from all attributes as measured by genetic coefficients of variation, was as great or greater at the hexaploid level than that at the tetraploid and diploid levels.

Comparisons of the characteristics of the seed attribute frequency distributions from irradiation derived and check populations showed that: (a) mutations occurring in diploid lines produce more discrete expression than those occurring at hexaploids, and (b) a larger portion of hexaploid than

diploid lines carry mutations which show some degree of expression.

The presence and/or magnitude of genetic variability induced was influenced by the attribute being studied, and the genotype treated. No genetic variability was induced for number of branches (except in Pusa variety) and for flag leaf length, and among the hexaploid varieties, Pusa showed nearly twice as much variability as the other two varieties.

The genetic correlations indicated that the types of mutations induced by irradiation in hexaploids is similar to that induced in diploids: thus, induced genetic variability in hexaploids should be equally as heritable as that in diploids.

Thermal neutron irradiation increased sterility in two of the treated populations. However, there was no evidence that sterility contributed to the apparent induced variability. Intrapopulations correlations calculated between grain width and sterility were not significant.

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