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Quantitative Variability in Wheat Following Irradiation, EMS, and Hybridization

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Summary. The effects of gamma irradiation and EMS seed treatment on the genetic properties of pure line and hybrid wheat populations were measured. Two hundred lines were derived from each mutagenic treatment of each genetic source and, together with their control materials, were assayed for heading date, plant height, spike length, and kernel weight in a replicated field experiment.

Both mutagens induced significant genetic variability for the four traits in either 'Giza 150' or 'Sonora 64', two pure cultivars, but neither was effective in increasing the genetic variation in their hybrid background. The relative magnitude of induced variation compared with that from hybridization depended on the particular mutagen and attribute and averaged less than 50% of that from hybridization. Heritabilities and expected genetic gains were not much lower in mutagenic populations than in hybrid populations. The relative distributions of the variance components among families and within families, and the estimates of the genetic correlations in the various populations, indicated that induced mutations were somewhat similar in nature to the variation released from hybridization. The induced variation was not accompanied by any shift in the population mean and, in most cases, variation was equally distributed around the population mean.

Introduction

During the past ten years symposia and regional and international meetings have been held to evaluate the use of induced mutations in applied plant breeding programs and in basic research. Meanwhile many papers have been published on this subject; only literature pertinent to the present work will be reviewed here.

Recently several workers, including Abrams and Frey (1964), Borojevic (1966), Mertens and Burdick (1956), Oka et al. (1958), Williams and Hanway (1961), have shown that irradiation and chemical mutagens induce quantitative variability in various crop plants similar in phenotypic expression to that released through hybridization. The increase in this genetic variability was accompanied in many cases by negative shifts in the population means, and, in a few cases, by positive shifts. On the other hand, Khadr (1970) reported no change in the population means for kernel traits of wheat following mutagen treatments. Gregory (1965) presented data suggesting that the numbers of plus and minus mutations in the polygene system are nearly equal, and that it is the magnitude of the phenotypic effect of a mutation which gives 'minus' effects and not its unidirectional character. He further postulated that the direction of the shift in the mean is related to the ecological nature of the character. The mean decreased for the fitness traits, but was not changed for nonfitness traits.

Krull and Frey (1961) estimated that the genetic variation from oat irradiation was approximately 50% of that from hybridization. Furthermore, Khadr and Frey (1965) using oats and Ramirez et al. (1969) using wheat proved that the induced variability was as heritable and useful in either a direct selection or crossing program as variability from hybridization. Gaul et al. (1969) were able to select micromutations in barley having a yield potential 10% higher than that of the mother cultivar.

The studies of Gregory (1961) in peanuts, Khadr and Frey (1965) in oats, and Khadr (1970) in wheat, indicated that a hybrid genetic background somewhat depressed the production and/or the expression of irradiation-induced variability. Gaul (1958) pointed out that mutations in quantitative traits are apt to be buffered by non-mutated genes affecting the same traits.

This study measures: (1) the magnitude and direction of variation in quantitative traits of wheat induced by gamma irradiation and EMS compared with that from hybridization; and (2) the expected use of this induced variability in wheat plant breeding.

Material and Methods

A brief description of the origin of the wheat populations (*Triticum aestivum* L. em. Thell.) will be presented here; for details of sampling through generations of increasing the progenies of these populations see Khadr (1970). Nine populations were produced by treating the seeds of each of 3 genetic sources with 3 different mutagenic treatments. The genetic sources were 'Giza 150', 'Sonora 64' and their hybrid F_2-seeds. The treatments were control, gamma irradiation at a dose of 25 kr., and an EMS solution 0.12 M. Each population consisted of 100 families (a family is traced back to an M_1, F_2 or M_1 F_2 plant) each represented by two lines (a line is the progeny of one M_2, F_3 or M_2 F_3 plant).

In 1968, a field experiment was conducted to estimate the effects of irradiation and EMS on the means and variances of different quantitative traits. The experiment was arranged in a split-split-plot design with 3 replicates. Populations occupied main plots, families subplots, and lines within families sub-subplots. Therefore the experiment contained 1800 entries and 5400 subplots. A sub-plot was a hill planted with 25 seeds. Hills were spaced 30 cm apart.

The attributes measured on each hill were heading date, plant height, spike length, and weight per 100 kernels. Heading date was recorded, in days after February 4th, when 50% of the spikes of the plot were completely out of the boots. Plant height was measured in cm from the ground to the tips of the spikes, excluding the awns. At maturity, the plots were harvested separately. Length of spikes in mm was taken as the average of 5 random spikes per plot. Spikes of each plot were threshed and the weight per 100 kernels was recorded.

The variance among families (σ_f^2) within each population and the variance among lines (σ_l^2) within families were estimated from the following random model:

Source of variation	d.f.	Expected mean squares
Families	99	$\sigma_b^2 + 2\,\sigma_a^2 + 3\,\sigma_1^2 + 6\,\sigma_f^2$
Error a	198	$\sigma_b^2 + 2\,\sigma_a^2$
Lines w/families	100	$\sigma_b^2 + 3\,\sigma_1^2$
Error b	200	σ_b^2

where σ_b^2 and σ_a^2 are the error components of variance associated with the line and family plots, respectively.

The genetic covariances among attributes were measured by applying this model to the covariance analyses to obtain the genetic covariance components for family and line sources for calculating the genetic correlations.

The fertility of a random sample of 30 lines within each of the nine populations was measured. Two random spikes were collected from each of the 3 plots of an entry. The two lateral florets of the 10 central spikelets of each spike were examined and the fertile florets were recorded. Fertility percentage was calculated on a plot basis, as the ratio of fertile florets to the total number of florets, and was transformed to the square root before calculating the analysis of variance.

Results

Estimates of the means, genetic variance components, heritability and expected genetic gain, and genetic correlations for some quantitative traits were used to assay the effect of gamma irradiation and EMS seed treatment on the genetic properties of the wheat populations.

Genetic Variation

The sample size and procedure used to derive the various populations were similar for both the mutagen and the control materials, to minimize the variation in sampling error among populations. Furthermore, the variance components were used, instead of the mean squares, to measure the variability existing within each population because the variance components are independent of the magnitude of the error components associated with the mean squares.

The variability among progenies derived from nontreated seeds of 'Giza 150' or 'Sonora 64' was not significant for any attribute, except for heading date of 'Giza 150', as shown in Table 1. These results were expected because the original seed sample of each cultivar was seeds selfed for two generations from two individual plants which should have been genetically pure. 'Sonora 64' proved to be homozygous and homogeneous for the studied traits. 'Giza 150' was also genetically pure for plant height, spike length, and kernel weight, but not for heading date.

In both 'Giza 150' and 'Sonora 64', either gamma irradiation or EMS seed treatment caused significant genetic variability (Table 1) for the four quantitative traits. It was obvious that the control hybrid population showed considerable genetic variability among progenies for all traits. In general, neither irradiation nor EMS was effective in increasing the genetic variation in the hybrid background (see the bottom 3 rows of Table 1).

There is a general belief that artificial mutations occur mostly from the dominant to the recessive direction. If this is true, we would expect that the genetic variance components among lines (σ_1^2) within families should exceed those among families (σ_f^2) within populations. Our data in Table 1 did not

Table 1. *Variance components for families (σ_f^2) and lines within families (σ_1^2) for attributes measured from control, irradiation, and EMS treatments*

Treatment	Heading date		Plant height		Spike length		Kernel weight	
	σ_f^2	σ_l^2	σ_f^2	σ_l^2	σ_f^2	σ_l^2	σ_f^2	σ_l^2
				Giza 150				
Control	0.55*	0.58*	−1.31	1.51	0.0009	−0.0030	0.0088	0.0001
Irradiation	2.03*	2.31*	−2.00*	21.66*	0.1627*	0.0942*	0.0288*	0.0218*
EMS	1.75*	1.04*	3.57*	7.95*	0.1496*	0.0688*	−0.0073	0.0326*
				Sonora 64				
Control	0.16	0.03	1.32	0.47	−0.0023	0.0047	0.0059	−0.0010
Irradiation	2.06*	2.39*	6.97*	19.38*	−0.0398*	0.1897*	0.0206*	0.0382*
EMS	0.07*	3.16*	2.36*	8.70*	0.0376*	0.1274*	0.0012*	0.0594*
				Giza 150 × Sonora 64				
Control	24.22*	19.36*	55.58*	29.85*	0.0966*	0.0981*	0.0495*	0.0751*
Irradiation	24.33*	18.64*	51.04*	40.59*	0.1481*	0.2104*	0.0594*	0.0872*
EMS	28.95*	21.64*	38.30*	39.21*	0.1731*	0.1493*	0.0469*	0.0713*

* Comparable mean squares significant at the 0.01 probability level.

support this hypothesis. In some cases (σ_l^2) exceeded (σ_f^2), but in others the situation was reversed or both components were very similar.

The magnitude of the genetic variability induced by irradiation or EMS treatment was expressed as a percentage of the values for the hybrid control population (Table 2). The relative magnitude of variance from mutagen treatment compared with hybridization was related to the kind of attribute and the type of mutagen. For heading date, which might be controlled by a lower number of loci than the other three traits, both irradiation and EMS were very much less efficient than hybridization in producing variability. For this trait, the average ratios of the variance components were consistent among cultivars and averaged 0.10 and 0.07 for irradiation and EMS, respectively. In contrast, both mutagens were equally as effective as hybridization in creating genetic variability for spike length. For kernel weight, the genetic variability from irradiation was close to 50% of that from hybridization and the comparable value for EMS was 27%. The average ratios for plant height were 36 and 16% for irradiation and EMS, respectively. It is very interesting to compare the relative magnitude of these ratios for families with those from lines within families. The average ratio of variance components from either irradiation or EMS in 'Giza 150' to those from the control hybrid was very similar for families and lines. For irradiation, it was 0.57 for families vs. 0.52 for lines, and for EMS, 0.38 vs. 0.36. The results were different for 'Sonora 64' where the average ratios were higher for lines than for families. The genetic significance of these ratio comparisons is that the genetic variability among lines within families (σ_l^2) in mutagenic-derived materials was equal to or higher than that among families (σ_f^2) when expressed in terms of the variability from hybridization. The variability among lines within families from mutagen treatment probably originated from segregation at loci which had become heterozygous after gamma irradiation or EMS seed treatment of the pure genotypes and was similar to that released from hybridization.

Table 2. *Ratio of families and lines variance components from irradiated and EMS populations to control hybrid population*

Attribute	Giza 150		Sonora 64		Mean
	Families	Lines	Families	Lines	
	Irradiation				
Heading date	0.08	0.12	0.09	0.12	0.10
Plant height	−0.04	0.72	0.13	0.65	0.36
Spike length	1.68	0.96	−0.41	1.93	1.04
Weight per 100 kernels	0.58	0.29	0.42	0.51	0.45
Mean	0.57	0.52	0.05	0.80	0.48
	EMS				
Heading date	0.07	0.05	0.00	0.16	0.07
Plant height	0.06	0.27	0.04	0.29	0.16
Spike length	1.54	0.70	0.39	1.29	0.98
Weight per 100 kernels	−0.15	0.43	0.02	0.79	0.27
Mean	0.38	0.36	0.11	0.63	0.37

Means and Ranges

The means of attributes from the populations derived from each of the three genetic sources are presented in Table 3. Only in one case out of 24 different comparisons did the mean of the mutagen-derived population deviate significantly from its control. This special case was 'Sonora 64' where EMS treatment shifted the population mean for heading to a date approximately two days later than the control. On the whole, the results indicate that the two mutagens did not cause significant changes in the population means either in the plus or minus directions.

Table 3. *Population means of attributes measured from the control, irradiation, and EMS treatments*

Treatment	Heading date+ (days)	Plant height (cm)	Spike length (cm)	Kernel weight (gm/100 kernel)
	Giza 150			
Control	25.2	127	8.12	3.99
Irradiation	26.3	123	8.10	3.73
EMS	25.3	127	8.05	3.87
	Sonora 64			
Control	10.8 a++	102	9.23	4.09
Irradiation	12.9 ab	104	9.34	4.02
EMS	13.6 b	105	9.21	4.01
	Giza 150 × Sonora 64			
Control	18.7	124	8.84	4.03
Irradiation	18.2	117	8.88	3.92
EMS	19.6	120	8.65	4.01

+ Heading date recorded in days after February 4*th*.

++ Only mean of heading date of EMS-'Sonora 64' was significantly later than the control.

The extension of the variation in the plus and minus directions following mutagenic treatment was dependent to some extent on the nature of the genetic background. In general, EMS and irradiation did not extend the range of the hybrid population beyond that of the control. 'Giza 150' is an intermediate cultivar for heading date and plant height, whereas 'Sonora 64' is an early, short cultivar. Both mutagens extended the range of plant height in 'Giza 150' more to the shorter side, but in 'Sonora 64' more to the taller side. The frequency distributions (Figures 1, 2, and 3) for kernel weight of the control and mutagen-derived populations illustrate this differential genotypic response to mutagens. It is obvious that both EMS and irradiation extended the variability for kernel weight in both the plus and minus directions in 'Sonora 64', but the change was mostly in the minus direction in 'Giza 150'. The distribution

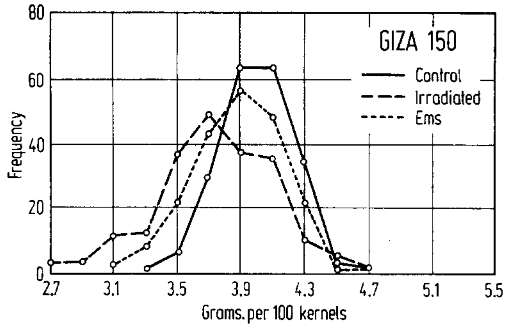

Fig. 1. Frequency distributions of kernel weights for wheat lines derived from 'Giza 150'

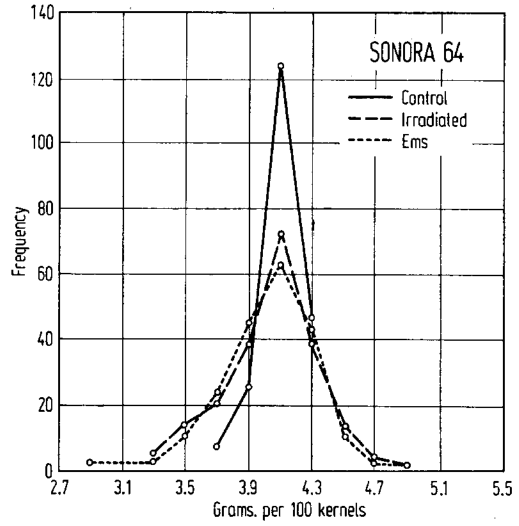

Fig. 2. Frequency distributions of kernel weights for wheat lines derived from 'Sonora 64'

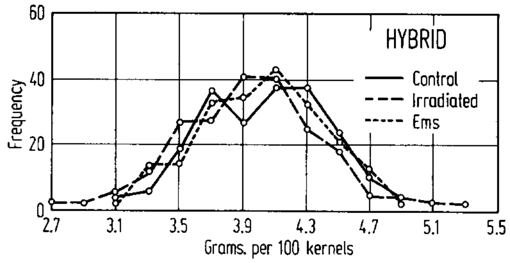

Fig. 3. Frequency distributions of kernel weights for wheat lines derived from 'Giza 150 × Sonora 64'

for the hybrid population (Figure 3) was not much changed by either irradiation or EMS treatment.

Heritability and Expected Genetic Gain

Heritability percentages (on a plot basis) in M_3, F_4, or $M_3 F_4$ generation for heading date, plant height, spike length and kernel weight are presented in Table 4. The genetic portion of the variation is $\sigma_1^2 + \sigma_{f/2}^2$, whereas the mean phenotypic value is $\sigma_1^2 + \sigma_{f/2}^2 + \sigma_{a/6}^2 + \sigma_{b/3}^2$ (for symbol designations see the statistical model in the materials and methods section). In general, the heritability percentages were relatively high for most populations when compared with the values reported in the literature for these traits in hexaploid wheat. Their magnitude depended on the genetic and error components of variance. In general, heading date has the highest heritability because it has the lowest associated error variance components. The hybrid-derived populations tended to have higher values for heading date (95%) than the mutagen-derived cultivars (about 70%) because the genetic variability induced by mutagens was limited in comparison with that released from hybridization. But for spike length, hybridization and mutagens were almost equally potent for creating heritable variability. Again, irradiation and EMS did not expand the heritable portions of the variability in the hybrid background.

The expected genetic gain (G_s) from selection (assuming selection intensity of 5%) was calculated from the following formula proposed by Johnson et al. (1955):

$$G_s = 2.06\left(\frac{\sigma_1^2 + \sigma_{f/2}^2}{\bar{x}}\right)\cdot\sqrt{H}\,,$$

where σ_1^2 and σ_f^2 are as defined earlier in the text, $\bar{x}$ is the population mean and H is the heritability.

The expected genetic gains for heading date were expressed in days because the data for this character were coded in days after February 4. The 'G_s' for heading date (Table 4) was only 2 to 3 days in the mutagenic-variety populations compared with 11 to 12 days for the hybrid populations. Here, the low

Table 4. *Heritability percentages (H) and expected genetic advance (G_s) (% of population mean) from selection in the treated populations*

Treatment	Heading date		Plant height		Spike length		Kernel weight	
	H	G_s	H	G_s	H	G_s	H	G_s
				Giza 150				
Irradiation	70	3	64	6.2	64	8.5	39	6.6
EMS	68	2	45	3.4	57	7.4	42	6.2
				Sonora 64				
Irradiation	72	3	80	8.5	59	7.4	67	9.2
EMS	74	3	68	5.1	62	6.7	75	10.8
				Giza 150 × Sonora 64				
Control	96	11	85	11.6	72	7.5	80	14.5
Irradiation	95	11	85	13.2	66	10.1	85	16.6
EMS	95	12	86	12.1	66	9.4	81	14.2

values of the genetic variation for this trait in treated cultivars have set a genetic ceiling on the expected success from selection.

The genetic variability for plant height and kernel weight was less than 50% of the values from hybridization (Table 2). Furthermore, heritability of these two traits was higher in hybrid populations than in treated cultivars. For these two reasons the 'G_s' values for hybrid populations were nearly double those for irradiated or EMS cultivars. For spike length, both hybrid and varietal populations were expected to respond equally to selection.

Genetic Correlations

The genetic correlations among attributes for families and lines within families in the various populations are shown in Table 5. The genetic correlations were not calculated for the controls of 'Giza 150' and 'Sonora 64' since the genetic variabilities in these two populations were estimated to zero (see Table 1). The genetic correlation coefficients ranged from −1.77 to 1.12. Except for a few cases, there was no indication that the genetic correlations were consistently different in sign or magnitude among mutagens, genetic sources, or generations.

Table 5. *Genetic correlations among attributes for families and lines within families from irradiated and EMS derived populations*

Treatment		D & H⁺	D & L	D & Wt	H & L	H & Wt	L & Wt
			Giza 150				
Irrad.	Fams.	—	0.92	0.62	—	—	0.59
	Lines/Fams.	−0.50	−0.01	−0.21	0.20	−0.54	0.43
EMS	Fams.	−0.05	0.60	—	−0.31	—	—
	Lines/Fams.	−0.58	−0.03	−0.68	0.98	0.95	0.52
			Sonora 64				
Irrad.	Fams.	0.12	—	−0.25	—	0.53	—
	Lines/Fams.	−0.06	−0.46	−0.31	0.11	0.32	0.39
EMS	Fams.	−1.77	−1.74	−1.01	0.18	−0.08	1.12
	Lines/Fams.	0.18	0.18	−0.04	0.68	0.48	0.37
			Giza 150 × Sonora 64				
Control	Fams.	0.21	0.10	−0.49	0.25	0.24	0.27
	Lines/Fams.	0.28	0.03	−0.37	0.29	0.87	0.16
Irrad.	Fams.	0.61	0.40	−0.39	0.54	0.14	0.27
	Lines/Fams.	0.19	0.03	−0.40	0.22	0.16	0.09
EMS	Fams.	0.24	0.09	−0.07	0.20	−0.04	0.16
	Lines/Fams.	0.14	0.03	−0.79	0.61	0.36	0.31

⁺ D = Heading date, H = Plant height, L = Spike length, Wt = Weight per 100 kernels.

Changes in genetic associations can give an indirect indication of the type of induced mutation, whether point or chromosomal aberrations. If gross deletions of large segments of chromosomes had been tolerated and transmitted to the M_3 progenies, they would cause the loss of some blocks of genes and would tend to induce genetic covariability among quantitatively inherited attributes. But our results indicated that irradiation did not, in general, increase the genetic associations between traits beyond the values encountered for either EMS or hybrid-derived populations. Furthermore, in the hybrid source, the genetic correlations were very similar in the control, irradiation, and EMS treatments.

In populations derived from hybrid or variety sources, heading date was, in general, negatively correlated with kernel weight; spike length and kernel weight were positively correlated and their coefficients ranged from 0.09 to 1.12 and were generally higher in variety than in hybrid populations.

Discussion

The results indicated that both gamma irradiation and EMS seed treatment of a pure genetic background were effective in inducing variability in quantitative attributes of wheat. This induced variability was, in general, equally distributed around the population mean. But in a hybrid genetic background, both mutagens were mainly ineffective in expanding the genetic variation beyond the amount released from segregation. There might be an alternative genetic mechanism, or a combination of two, which could account for this failure in the hybrid background: (1) The genes governing these traits might be combined in balanced polygenic systems, as indicated by Mather (1943), providing the two wheat cultivars with potential concealed variation which would be released upon hybridization. In such a widely variable population any gene mutation might cause a minute genetic change which would not gain any distinct chance of phenotypic expression beyond the limits of the population. In other words, the phenotypic values of the plus and minus mutants were only within the range of the population. (2) The genetic heterogeneity of the hybrid population may have furnished protection against irradiation or EMS causing genetical changes. The work of Gregory

(1961) in peanuts, Khadr and Frey (1965) in oats and Khadr (1970) in wheat also indicated that a heterogeneous and/or heterozygous genetic background depressed the production or expression of irradiation induced variability. Gaul (1958) pointed out that mutations in quantitative traits are masked by other buffering genes.

Although the induced variabilities in 'Sonora 64' and 'Giza 150' after irradiation and EMS treatments were, in most cases, highly significant, the average variance for heading date, plant height, and kernel weight was less than 50% of that from hybridization. For these three quantitative attributes, irradiation or EMS had no obvious effect on the genetic variability of the hybrid population. But for spike length, irradiation or EMS caused variation equal to that from hybridization. For this trait, the hybrid population responded to irradiation or EMS and gave additional variability beyond the limits of the hybrid segregation. In fact, irradiation extended the range of spike length by 1.4 cm in the plus direction and 0.4 cm to the minus direction in the hybrid material.

Frey (1962) showed that when some spikelets were removed from an oat panicle, the seeds in the remaining spikelets increased in weight. Therefore, differences in seed fertility among lines derived from mutagen treatments might be a significant factor contributing to the variability of kernel weight. Although our mutagenic-derived wheat populations were lower in seed fertility than their comparable control populations (Table 6), neither irradiation nor EMS affected the mean fertility percentage to a significant extent. But, in 'Sonora 64' and the hybrid materials the variability for fertility among lines within populations was significant. In these populations, the intrapopulation correlation between fertility and kernel weight was calculated to determine whether the induced genetic variability for kernel weight was an artifact of sterility variation. None of the correlation coefficients presented in the last column of Table 6 was significant. Consequently, variation in kernel weights in these populations was not confounded by variation in fertility percentages.

Table 6. *Means, ranges, and standard error of fertility percentages and correlations between fertility and kernel weight*

Treatment	Mean	Range	S.E.	Correlation with kernel weight
		Giza 150		
Control	97.6	93–100	0.18	–
Irradiation	93.3	75–100	0.35	–
EMS	95.8	83–100	0.27	–
		Sonora 64		
Control	93.6	88–100	0.23	–
Irradiation	91.6	73–100	0.28	+0.06
EMS	95.1	88–100	0.23	+0.25
		Giza 150 × Sonora 64		
Control	97.5	90–100	0.17	–0.29
Irradiation	93.3	75–100	0.31	+0.33
EMS	95.0	70–100	0.23	+0.23

It appeared that the quantitative variability induced via irradiation or EMS was heritable and might be used in selection in a similar way to the variation released from hybridization. Both Khadr and Frey (1965), in oats, and Ramirez et al. (1969), in wheat, used irradiation-induced variability in direct selection and crossing programs. However, the genetic variability in mutagen-derived populations might be of a different nature from that encountered in populations originating from hybridization. The genetic variability in a hybrid population is released by Mendelian segregation and recombination of genes, whereas the apparent variation following irradiation or EMS treatment results from gene and/or chromosomal changes that are shuffled upon selfing. The EMS and irradiation treated wheat populations in this study passed through three generations of sexual reproduction before they were tested in the M_4 generation. Thus the genotypes with large chromosomal aberrations would probably be naturally screened out of the population through the critical cycles of meiosis and self-fertilization. In fact, we observed several conspicuously abnormal phenotypes among the M_2 plants: they included completely sterile, very late, nonflowering, and stunted types. These abnormalities were not reproduced in the M_3 tested lines. Therefore, the M_3-variation measured in M_4 of the mutagen-derived populations would be expected to be mostly of the heritable type, either minute deletions and/or point mutations, similar to that released by hybridization. In spite of the relatively low amount of genetic variation in the mutagenic populations compared with the hybrid population, the heritabilities of the traits measured in the mutagenic populations were not much lower than those in the hybrid population.

Estimates of the genetic associations among traits might give indirect information about the nature of the genetic variation induced by mutagenic agents. In hexaploid wheat, the polygenes for the quantitative traits are probably scattered at random on the chromosomes of the three genome sets. If the variation encountered in the mutagen-derived population arises from large chromosome deletions, we would expect that some genes for various attributes would be lost together, resulting in genetic convariation. The sign of this induced covariability would depend on whether the lost genes were in the repulsion or coupling state. The genetic correlations among traits measured here did not deviate much in sign or magnitude from those obtained from hybrid covariation. These data indirectly support our conclusion that both irradiation and EMS caused variation of the point mutation type and/or of small deletions. Ehrenberg et al. (1961) and Abrams and Frey (1964) believed that EMS induces mutations which are predominantly genic or chromosomal with a similar effect, but that irradiation induces both chromosomal and genic mutations. However, the data presented here suggest that gamma irradiation and EMS do not differ in the genetic nature of their induced variability.

On the basis of our results, we question the assumption that induced mutations are always determinative to the population. Regardless of which direction was considered desirable for the four studied traits, there was no significant excess of individuals towards either end of the population range, except in a very few cases. Furthermore, neither EMS nor irradiation changed the population mean of any attribute, except for one case out of 24 comparisons. Sakai and Suzuki (1964) concluded that, in most cases, rice polygenes mutated unidirectionally to the minus side after X-irradiation, which caused minus shifts in population means. In the results reported here for all traits, and in those of Abrams and Frey (1964) for seed weight in oats, induced mutations were equally expressed in the plus and minus directions, contradicting the conclusion of Sakai and Suzuki.

In conclusion, EMS and gamma irradiation were equally effective for inducing genetic variation in the quantitative traits of wheat. Both agents produced approximately the same amount of heritable variability and were similar for predicted genetic gain from selection. In recent years the techniques of seed treatment with EMS have been greatly refined to give positive results for mutation programs. Besides, this chemical is easier to handle in the lab than irradiation. For these reasons, EMS seed treatment should be recommended as an alternative to irradiation in inducing genetic variability for wheat breeding purposes.

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