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Variation and Covariation of Seed Weight and its Components in Wheat Following Irradiation, EMS, and Hybridization

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Summary. Seeds from two hexaploid wheat varieties, 'Giza 150' and 'Sonora 64', and the F_2 seeds of their hybrid were given two mutagenic treatments, gamma irradiation and ethyl methanesulfonate (EMS), to study the type of variation and covariation in seed weight, width, and length induced by irradiation, EMS, and hybridization. Measurements of seed weight and its components were taken on 30 replicated lines derived from each treated and non-treated material.

Both irradiation and EMS produced significant variability in seed weight and its components in the pure genetic background. The hybrid genetic background somewhat depressed the expression of irradiation-induced variability. The variations resulting from EMS and hybridization were to a great extent independent and cumulative.

Neither EMS nor irradiation caused any significant shift in the means of seed weight, width, and length. The positive association between inheritance of width and length in irradiation-derived materials did not increase the mean seed weight compared with the control.

The magnitude of the genetic correlations in irradiation varieties was double that obtained from hybrid- or EMS-derived materials. It is suggested that EMS mainly produced mutations of genes and/or minute chromosomal aberrations, whereas the genetic variation produced by gamma irradiation was accompanied by the loss and/or gain of large segments of the chromosomes.

Introduction

The pioneer work of Muller (1927) with *Drosophila* and of Stadler (1930) with the higher plants, which revealed that X-irradiation induced mutations, stimulated many researchers to investigate the genetic effects of mutagens on crop plants. Until recently, most investigations were designed to study artificially induced mutations for the qualitative characters only. Since techniques and methods for estimating quantitative parameters have been refined, many researchers (Abrams and Frey 1964, Gregory 1961, Khadr and Frey 1965, Krull and Frey 1961, Mertens and Burdick 1956, Oka et al. 1958, Rawlings et al. 1958, Williams and Hanway 1961) have shown that different types of radiation and chemical can be used to induce quantitative variability. The increase in the genetic variability was in some cases accompanied by positive or negative shifts in the means of the populations (Abrams and Frey 1964, Krull and Frey 1961, Mertens and Burdick 1956, Oka et al. 1958, Okabe et al. 1963, Rawlings et al. 1958, Williams and Hanway 1961).

The usefulness of artificial mutations in plant breeding is still in debate. However, the frequency of superior mutants isolated from artificially induced mutations (Gregory 1957, Gustafsson 1954) appears to be about equal to the frequency of superior segregates reported from hybridization (Vettel 1957, Williams 1959).

Grafius (1956) and Frey (1959) suggested that the compound attributes of higher plants, such as grain yield and seed weight, can be expressed as geometric products of several components. Murphy and Frey (1962) postulated that oat groat weight varies as a function of length, width, and density, as expressed in the formula:

$$\text{Groat weight} = L\,(W/2)^2\,\pi\,DK$$

where L, W, and D stand for groat length, width, and density, respectively, $\pi = 3.14$, and K is a factor which corrects for the fact that groats are not cylindrical. They found that the density was constant with a value of 1.36. The differences between the expected (calculated from the above formula) and actual means for groat weight of irradiated hexaploid oat populations were interpreted by Okabe et al. (1963) as being caused by the deletion of large chromosomal segments, resulting in negative or positive genetic correlations between groat width and length. Thus the associated inheritance of the two components of groat weight caused a shift in the population mean.

The object of the present work was to study: (a) the nature of the genetic variation and covariation for seed weight, width, and length following gamma irradiation, EMS treatment, and hybridization in hexaploid wheat; (b) the effect of covariation between seed width and length upon the mean seed weight of the population.

Material and Methods

The materials used were selfed seeds from two typical individuals of 'Sonora 64' (P_1) and 'Giza 150' (P_2), two hexaploid wheat cultivars (*Triticum aestivum* L. em. Thell.), and the progeny seeds of two F_1 plants from the cross $P_1 \times P_2$. The seeds from each of these three genetic sources were divided into three random lots each of 1000 seeds. Three seed lots, representing P_1, P_2, and $P_1 \times P_2$, were used as control material. Similar seed lots were either exposed to gamma radiation of dose 25 kr., or immersed in a .12 M solution of EMS (1000 cc per 250 seeds) for 6 hours at room temperature followed by a rinse with tap water. In autumn 1966, seeds from each of the three controls and the six treatments were planted in the field. Strips 5 meters wide were grown with barley among the control, irradiation, and EMS populations to prevent natural crossing among plants from different mutagen treatments. In 1967, the seeds from each individual plant of the previous season were planted in a progeny row in the field. Plants from the same treatment were planted in blocks of rows to minimize natural crossing. At maturity, the M_2, M_2F_3, and control plants were harvested and threshed individually. In 1968, for each population a sample 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 from one M_2, F_3 or M_2 F_3 plant) was tested in a split experiment of 3 replicates at the Sakha Agricultural Experiment Station. Populations occupied the main plots, families within populations the subplots, and lines within families the sub-sub plots. A sample of 25 seeds from each line was planted in a randomly allocated hill in each replicate. Hill plots were spaced one foot apart in perpendicular directions. When the plants matured, the plots were harvested and threshed individually.

A random sample of 30 replicated lines from each of the above described nine populations was chosen for the present study. Weight per 100 seeds was recorded for the 3 plots of each line. A random subsample of 20 seeds from each plot was measured for seed dimensions each seed was measured individually for length and width to the nearest 0.1 mm. Means of seed width and length for these 20 seeds per plot were used in the statistical analyses.

Table 1. *Mean squares from the analyses of variance of seed weights, widths, and lengths of wheat lines derived from the control, irradiation, and EMS treatments*

Source of variation	Degrees of freedom	Mean squares		
		Weight	Width	Length
		Lines within Giza 150		
Control	29	0.1228	0.0099	0.0189
Gamma irradiation	29	0.4959**	0.0398**	0.0886**
EMS	29	0.2455**	0.0207*	0.0940**
Error	174	0.1019	0.0097	0.0190
		Lines within Sonora 64		
Control	29	0.0624	0.0120	0.0094
Gamma irradiation	29	0.3034**	0.0221**	0.947**
EMS	29	0.3362**	0.0368**	0.0695**
Error	174	0.0537	0.0076	0.0120
		Lines within Giza 150 × Sonora 64		
Control	29	0.4417**	0.0735**	0.1554**
Gamma irradiation	29	0.4852**	0.0523**	0.2303**
EMS	29	0.5417**	0.0931**	0.2188**
Error	174	0.0640	0.0108	0.0170

* Exceeds the 5% level of significance
** Exceeds the 1% level of significance

Results

The intrapopulation variability for seed weight, width, and length in the Giza 150- and Sonora 64-derived materials was not significant (Table 1). This proves that the original seed samples of these two varieties were genetically pure for the attributes studied. Both irradiation and EMS produced significant variability for seed weight and its components in Giza 150 and Sonora 64 varieties. Also mean squares for all the measured attributes were highly significant in the hybrid-derived material.

In the hybrid genetic background, irradiation and EMS slightly increased the variability of seed weight. For seed width, it was decreased by irradiation but increased by EMS. Variability in seed length was increased by approximately 50 percent by either irradiation or EMS.

Except for the seed weight of irradiated Giza 150, the magnitude of variability for all attributes produced by exposing seeds of each pure parent to irradiation or EMS was, in general, half of that released by hybridization. Krull and Frey (1961) reported that thermal neutron irradiation expanded the variability for seed weight in oats by 50 per cent of that from hybridization. Irradiation and EMS increased the variability to a similar extent in Sonora 64, but Giza 150 responded more to irradiation than to EMS.

Gregory (1956) postulated that the variation induced by irradiation might be cumulative with that of hybridization. The actual variances for seed weigth, width, and length shown in Table 2 represent the genetic variances of irradiated- and EMS-hybrid populations. The comparable predicted values were calculated from the following formula proposed by Khadr and Frey (1965):

$$\text{Predicted } O^{\bar{2}}_{NH} = {}^{1}/_{2}\,[(O^{\bar{2}}_{NP_1} - O^{\bar{2}}_{P_1}) + (O^{\bar{2}}_{NP_2} - O^{\bar{2}}_{P_2})] + O^{\bar{2}}_{H}$$

The subscript, *N* refers to irradiation or EMS and P_1, P_2, and *H* refer to the origin of the treated seeds,

Table 2. *Mean actual and expected variance components and ratios between them for attributes of irradiation- and EMS-hybrid materials*

Seed attributes	Variance component					
	Actual	Expected	$\frac{\text{Act.} \times 100}{\text{Expect.}}$	Actual	Expected	$\frac{\text{Act.} \times 100}{\text{Expect.}}$
	Irradiation			EMS		
Weight	0.1404	0.2282	62	0.1592	0.1919	83
Width	0.0145	0.0275	53	0.0253	0.0274	93
Length	0.0699	0.0711	98	0.0665	0.0673	99
Mean	0.0753	0.1085	71	0.0846	0.0945	91

i. e., parent one and two and their hybrid, respectively.

The degree of agreement between actual and predicted variances appeared to be related to the kind of attribute and to the type of mutagenic agent used. For seed length, with either irradiation or EMS, the actual variances were very close to the predicted ones.

For the EMS treatment, the mean ratio of actual to predicted variances over the three attributes was 91 per cent, whereas the comparable ratio for gamma irradiation was 71 per cent. It appears that the variabilities (as measured by genetic variance) resulting from treating wheat seeds with EMS and released following hybridization are to a great extent independent and cumulative when the hybrid seeds are used as material for EMS treatment. In contrast, irradiation-induced variation was not cumulative with that of hybridization. It is perhaps an accidental but nevertheless interesting fact that the mean ratio of actual to predicted variances for their radiated hybrid population was 71 per cent and that Gregory (1961) and Khadr and Frey (1965) reported very similar values of 77 and 74 per cent for peanut seed yield, and three quantitative characters of oats, respectively.

Although the sample size used to measure seed weight (100 seeds) was five times that used for measuring width and length (20 seeds), the coefficients of variability (Table 3) were 6.8, 2.9, and 2.1 per cent for seed weight, width, and length, respectively. Apparently seed width and length were measured more precisely than was seed weight.

Table 3. *Coefficients of variability for seed weight, width, and length in the Giza 150-, Sonora 64-, and Hybrid-derived materials*

Material	Seed character		
	Weight	Width	Length
Giza 150	8.2	3,1	2.2
Sonora 64	5.8	2.5	1.8
Hybrid	6.5	3.1	2.2
Mean	6.8	2.9	2.1

Seeds of Giza 150 were 29 mm. longer and .29 mm. narrower than the seeds of Sonora 64 (Table 4), but both varieties had a similar seed weight, partly because width and length compensate for one another in each variety. Since seed width contributes to weight in a squared manner, it was expected that the seeds of Sonora 64 would be heavier than those of Giza 150. However, the seeds of Giza 150 fit more closely the cylinder shape than do those of Sonora 64 (Table 5).

In general, the irradiation and EMS treatments caused slight reductions in seed weight, but this was not significant in all cases (Table 4). In the Giza 150 materials, irradiation decreased the mean seed weight, and also seed width and length, but not significantly. EMS slightly but not significantly lowered the mean seed weight, but neither width nor length were changed. The means of all attributes in the Sonora 64 variety and in the hybrid material were not shifted significantly either in the plus or the minus direction following irradiation or EMS treatment.

Table 4. *Mean① seed weight, width, and length for nine wheat populations derived from the control, irradiation, and EMS treatments*

Treatment	Wt. per 100 seeds g	Width mm	Length mm
	Giza 150		
Control	4.06	3.24	6.16
Gamma irradiation	3.76	3.15	6.13
EMS	3.89	3.22	6.18
	Sonora 64		
Control	4.05	3.52	5.87
Gamma irradiation	4.03	3.47	6.02
EMS	3.99	3.49	6.01
	Giza 150 × Sonora 64		
Control	3.94	3.34	6.04
Gamma irradiation	3.9	3.30	6.04
EMS	3.92	3.30	6.04

① Means of attributes within either the two varieties or their hybrid were not significantly different at the 5% level.

Table 5. *Values of K (a correcting factor for seed shape) estimated from control populations*

Populations	K value
Giza 150	0.592
Sonora 64	0.522
Hybrid	0.548

The formula proposed by Murphy and Frey (1962) for oats: groat weight $= L\,(W/2)^2\,\pi\,DK$ (for definition of symbols see the review of literature), was used to predict the mean seed weight of the irradiation and EMS populations. The density value (D) was found to be a constant of 1.36 and the K values were cal-

Table 6. *Actual and expected mean weights per 100 seeds for irradiation- and EMS-derived populations*

Material		Seed treatment	
		EMS	Irradiation
Giza 150	Actual	3.89	3.76
	Expected	4.04	3.84
Sonora 64	Actual	3.99	4.03
	Expected	4.08	4.04
Hybrid	Actual	3.92	3.91
	Expected	3.85	3.85

culated from the control populations (Table 5). The actual and expected means for seed weight (Table 6) were similar, with overall actual and expected means of 3.92 and 3.95 gms., respectively.

All the genetic correlations among seed weight, length, and width were positive (Table 7). The correlations showed that seed width contributed more to seed weight than did length with the exception of one case EMS Giza 150. Of course, variation in seed width has more influence on weight than does a proportional variation in length because width is used as a squared function in the seed volume. In fact, both seed length and width were similar in their relative genetic variability. The mean genetic coefficient of variability over irradiation and EMS populations was 3.2 per cent for either seed weight or length (Table 8).

The genetic correlation between width and length in the hybrid population was low with a value of .21. This means that genes for width and length are mostly randomly located on the chromosome sets of the two hexaploid wheat varieties used in the present work. Therefore, genes for width should be to a large extent inherited independently of genes for length.

The correlation between seed width and length in irradiation Giza 150 or irradiation Sonora 64 was double that for the hybrid population. This suggests that irradiation might have caused loss or duplication of large chromosomal segments that carry some genes for length and width. In contrast, the magnitude of the genetic correlation between width and length in EMS-derived materials was very similar to that obtained from the hybrid population. This may indicate that the type of variation induced by the EMS treatment was more likely to be point mutations which segregated through the generations in a similar way to the Mendelian variation encountered in the hybrid population.

Since the hybrid genetic background reduced the genetic variance of the irradiation population to 71 per cent of the expected value (Table 2), it was expected that covariation between seed width and length would not be changed to the same extent as in the irradiated pure varieties. In fact, irradiation did not change the magnitude of the genetic covariation between width and length in the hybrid material.

The reduction in genetic correlation between seed width and length which resulted from the treatment of the hybrid seeds with EMS may confirm the previous suggestion that EMS might have caused genetic changes of the point mutations type. If EMS randomly affected the genes for the different attributes, it would reduce the genetic covariation between width and length in the hybrid material; in fact, the genetic correlation between width and length was reduced from .21 in the hybrid population to .15 in the EMS hybrid population. However this change in the correlation was not subjected to a statistical test of significance, so no definite conclusion could be drawn from the estimates of the genetic correlations.

Table 7. *Genotypic correlations of seed weight, width, and length in irradiation- and EMS-derived populations*

Population	Correlated attributes		
	Weight and width	Weight and length	Width and length
Irradiation Giza 150	0.92	0.72	0.50
EMS Giza 150	0.27	0.48	0.17
Irradiation Sonora 64	0.89	0.79	0.42
EMS Sonora 64	0.92	0,56	0.24
Hybrid	0.85	0.68	0.21
Irradiation hybrid	0.78	0.67	0.17
EMS hybrid	0.93	0.56	0.15
Mean	0.78	0.64	0.27

Table 8. *Genetic coefficients of variability for seed weight, width, and length in irradiated and EMS populations*

Treatment	Seed character		
	Weight	Width	Length
		Giza 150	
Gamma irradiation	9.6	3.2	2.5
EMS	5.6	1.9	2.6
		Sonora 64	
Gamma irradiation	7.2	2.0	2.8
EMS	7.7	2.8	2.3
		Giza 150 × Sonora 64	
Control	9.0	4.3	3.5
Gamma irradiation	9.6	3.6	4.4
EMS	10.3	5.0	4.3
Mean	8.4	3.2	3.2

Discussion

Several investigators (Abrams and Frey 1964, Edwards and Williams 1966, Ehrenberg et al. 1961, MacKey 1954 and 1956, Okabe et al. 1963, Stadler 1932, Stadler and Roman 1948) have discussed the types of mutations (whether genic or chromosomal) produced by the treatment of plant material with mutagens. Mackey (1954) believes that chromosome mutations of the gross deletion type account for a considerable amount of the irradiation-induced variability in hexaploid oats and wheat. He indirectly drew this conclusion from the fact that fatuoid and speltoid mutations, which are known to be associated with chromosome deletions, were more frequent in irradiation-derived populations of hexaploid oats and wheat, respectively. Ehrenberg et al. (1961) and Edwards and Williams (1966) found that the lower rates of chlorophyll-deficient mutations induced by X-rays in comparison with EMS were accompanied by high frequencies of chromosomal aberrations in barley and durum wheat.

The component analysis for seed weight has a significant bearing on the understanding of the mechanisms responsible for mutagen-induced variation. The magnitude of the genetic correlations between seed width and length may provide a clue to the types of mutations induced by irradiation and EMS treatments. The numbers of lines sampled from the mutagenic and hybrid material were equal. Therefore, the statistical estimates were subjected to a similar magnitude of sampling error. The genetic association between seed width and length in the hybrid population was low indicating that the genes for length and width (quantitative characters) are to a large extent scattered independently on the chromosomes. Thus the occurrence of gene mutations, minute deletions and/or duplications should cause independent variations in seed width and length which should give genetic covariation between length and width similar in magnitude to that obtained from hybrid segregates. On the other hand, deletions and/or duplications of whole or large segments of chromosomes would be associated with the loss or gain of both width and length genes which would, consequently, cause correlated variability. Giza 150 and Sonora 64 wheat varieties are hexaploid and could tolerate large chromosomal aberrations in their life cycle. The magnitude of the genetic correlations for the irradiated varieties was double that of the hybrid populations. In contrast the EMS did not give genetic association values different from those obtained from hybridization. These results and those of others (Abrams and Frey 1964, Edwards and Williams 1966, Ehrenberg et al. 1961) suggest that the EMS and irradiation treatments cause different types of genetic variation. The EMS mutagen produces mutations which are predominantly genic and/or due to minute chromosomal aberrations; the genetic variation produced by gamma irradiation would be accompanied by the loss and/or gain of large segments of the chromosomes which increases the genetic covariation between seed length and width.

The present study and those of Gregory (1961) in peanuts and Khadr and Frey (1965) in oats indicate that a heterogeneous and/or heterozygous genetic background somewhat depress the production and/or the expression of irradiation-induced variability. With the EMS mutagen the actual variability obtained by treatment of the hybrid material was nearly the same as that predicted by adding independent estimates of variability from the two sources. Again these results indirectly prove that the variability encountered in the EMS-derived material is of the point mutation type.

Okabe et al. (1963) postulated that "an associated inheritance between two geometric components of a character can cause a shift in the population mean without concomitant shifts in the means of the components". In their oat materials, irradiation increased significantly the mean of the seed weight, accompanied by significant increases in variance and kurtosis. In the present materials, irradiation caused a slight but not significant reduction in seed weight which was accompanied by a non-significant decrease in seed width. Although the irradiation- and EMS-induced variabilities for seed length and width were positively correlated, they did not appear to affect seed weight to a significant extent.

In fact, the calculated values for seed weight slightly exceeded the actual ones (Table 6), a result which was the reverse of what would be expected if the theory and assumptions proposed by Okabe et al. (1963) were correct. However, the deviation between the actual and expected values ranged from .25 to 4 per cent of the actual values. These deviations were similar to, or less than, the not significant differences for means of seed weight encountered between treated and non-treated populations. This shows that the positive genetic correlation between seed length and width was not expressed in seed weight, thus contradicting the conclusions of Okabe et al. (1963). Furthermore, the covariation between seed width and length did not accentuate the genetic coefficient of variability for seed weight (Table 8).

In the present work and that of Okabe et al. (1963) the K value, a constant that corrects the weight of a cylinder for the shape of the seeds, and which was used in the formula to predict the means of seed weight for the treated populations, was calculated from non-treated populations. Thus it was assumed that the seeds of the treatment-derived populations had a shape similar to that of the seeds of the original non-treated populations. But such an assumption might not be valid on the basis of the following arguments.

The variability for seed weight and its components was increased in the treated populations. Therefore, the shape of the seeds might vary among the lines derived from these populations. The K value was estimated for each line in the original and the irradiation populations for the two varieties Giza 150 and Sonora 64. In the original populations the K value was almost constant among lines and ranged from .58 to .61 for Giza 150 and from .52 to .53 for Sonora 64; in the irradiated material it fluctuated from .54 to .64 in Giza 150 and from .49 to .54 in Sonora 64. Consequently, the assumption that the K value is constant in the irradiation population is not correct. This variation in K values among lines in the irradiation populations might confound the population mean for seed weight if K and seed weight are correlated.

Furthermore, the covariation between seed width and length in the irradiation populations did not appear to accentuate the genetic coefficient of variability for seed weight (Table 8) beyond the values obtained from the EMS- or hybrid-populations.

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