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Ultraviolet Irradiation of Maize (*Zea Mays* L.) Pollen Grains
II. Pollen Genotype Effects on Plant Characteristics

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Summary. Mature pollen grains from two single cross (F_1) hybrids, Wf9 × H55 and K64 × K55, were exposed to eleven levels (0 to 6.80 erg/cm^2 × 10^5 at 0.68 intervals) of ultraviolet irradiation and then were used to pollinate their source. Height and kernel characteristics (kernel weight, weight /100 kernels, kernel number) of individual F_2 plants produced by the normal F_2 kernels obtained from these pollinations were measured within each level and population. Highly significant exposure × population interactions were found for all characters, indicating that the effect of irradiation depended on the genetic source of the pollen grains. Increasing exposure increased or did not change the mean of Wf9 × H55 and decreased the mean in K64 × K55 for all characters. For coefficient of variation values, the interaction, exposure × population, was not significant for any character measured, indicating that irradiation-induced variability was unrelated to pollen source. The results indicate that pollen source strongly influenced the effect of ultraviolet irradiation on plant means but had no influence on variability.

Key words: Maize - Pollen - Irradiation - Plant Characteristics - Variability

Introduction

Ultraviolet irradiation has many unique properties as a mutagenic agent. In contrast to those produced by ionizing irradiation, the changes induced by ultraviolet have been classified as true point mutations because of their size, reverse mutation capabilities, viability and transmission characteristics in the gametophytic generation, lack of recessive lethality and effect on crossing over (Fujui 1969, Ikenaga and Mabuchi 1966, Nuffer 1957, Stadler 1941, Stadler and Roman 1943, Stadler and Sprague 1936, Stadler and Sprague 1937). Therefore, ultraviolet irradiation may represent one of the most desirable methods to artificially produce new allelic forms and thereby increase genetic variation.

In higher plants, the induction of transmissible genetic changes by ultraviolet is limited to pollen treatment because of its low penetrance. Pollen irradiation is known to produce kernel abortion expressed as a decrease in the percent of normal kernels (Pfahler and Linskens 1976). However, pollen treatment with any mutagenic agent has distinct advantages because only one genome in the resulting kernels is exposed to irradiation, the embryos contain no chimeras and the extreme lethal effects produced by irradiation are eliminated by kernel abortion (Brewbaker and Emery 1962).

No information is available regarding the effect of irradiation on plants produced by the normal kernels obtained from pollination with irradiated pollen grains. This study was designed to measure this effect on a number of quantitative characters (plant height, kernel weight, weight/100 kernels, kernel number) in maize. Pollen from two single cross hybrids was exposed to irradiation to determine if pollen source was a contributing factor.

Material and Methods

The single cross hybrids, collection and irradiation procedures and pollination methods are presented in a related paper (Pfahler and Linskens 1976). In brief, pollen grains from two single cross (F_1) hybrids, Wf9 ×H55(W) and K64×K55(K), were exposed to eleven levels (0 to 6.80 erg/cm^2 × 10^5 at 0.68 intervals) of ultraviolet. After irradiation, the pollen grains from each level were used to pollinate their genetic source.

The normal (embryo and endosperm normal in appearance and size) F_2 kernels obtained from these pollinations were field-planted in replicated and bordered plots in each of two years, 1973 and 1975. In each year, the plant height, kernel weight, weight/ 100 kernels and kernel number from each of 100 F_2 plants in each level and population were measured.

Appropriate variance and regression analyses were performed on each character measured. Be-

Table 1. Mean squares from the variance analyses associated with the means of each character

Source of variation	Degrees of freedom	Plant height	Kernel weight	Weight/ 100 kernels	Kernel number
Population (P)	1	360100**	200097.2**	25.4	4277709**
Exposure (E)	10	9287**	8589.2**	119.6**	50031**
E × P	10	19248**	13383.1**	195.7**	84331**
Year (Y)	1	309340**	2274.9	807.6**	1181425**
Y × P	1	25195**	23899.3**	121.8*	342621**
Y × E	10	2658**	2068.5	47.5*	4604
Y × E × P	10	979	5021.8**	50.0*	21806
Error	4356	572	1597.3	23.8	19227

*, ** F values significant at the 5 and 1% level respectively

fore analysis, inverse sine transformations were applied to the percent data associated with the coefficient of variation values. The minimum differences for significance were obtained by means of the revised Duncan's ranges using for p only the maximum number of means to be compared (Harter 1960).

Results

Mean squares from the variance analyses are presented in Table 1. The main effect, exposure, and the interaction, exposure × population, were significant at the 1% level for all characters. The main effect, population, was significant at the 1% level for all characters except weight/100 kernels. The effect of year and its interactions with other main effects was quite inconsistent and depended on the character involved.

The means associated with the variance analyses are presented in Table 2. In general, increasing irra-

Table 2. Means of the various characters. Each value represents the mean of 100 plants

Character	Population	Year	Exposure ($erg/cm^2 \times 10^5$)										
			0	0.68	1.36	2.04	2.72	3.40	4.08	4.76	5.44	6.12	6.80
Plant height(cm)[a]	W	1973	172	169	171	183	176	185	177	194	181	182	180
		1975	191	184	190	203	204	220	202	221	205	201	194
	K	1973	182	160	176	169	172	157	157	159	168	160	163
		1975	188	171	185	186	186	175	171	172	177	172	172
Kernel weight(g)[b]	W	1973	117.1	117.4	120.6	124.1	129.6	132.8	127.1	133.1	129.6	126.5	128.0
		1975	132.1	123.0	131.7	132.2	134.6	144.3	135.9	133.5	139.6	140.2	132.1
	K	1973	138.4	118.0	125.3	122.9	120.1	109.1	109.9	109.2	116.3	112.0	107.1
		1975	127.9	110.6	116.0	115.5	128.9	108.2	103.1	108.0	112.5	111.6	110.8
Weight(g)/ 100 kernels[c]	W	1973	24.9	25.9	25.4	24.3	26.4	25.6	26.6	26.2	26.7	25.8	26.3
		1975	28.5	25.3	26.8	27.0	26.5	25.9	26.0	25.0	27.1	25.3	25.7
	K	1973	25.0	23.8	23.6	23.6	25.5	26.3	25.8	25.0	27.0	26.3	26.4
		1975	26.3	24.1	26.1	25.7	26.5	26.1	23.7	24.4	24.4	24.3	25.5
Kernel number[d]	W	1973	473	454	475	515	490	523	486	514	482	482	492
		1975	538	520	557	564	533	563	529	550	529	543	515
	K	1973	488	462	467	459	453	420	426	433	429	443	416
		1975	486	468	451	478	488	428	441	450	470	463	439

[a] Minimum differences between any two height means for significance are 9 and 11 at the 5 and 1% level respectively

[b] Minimum differences between any two kernel weight means for significance are 14.3 and 18.7 at the 5 and 1% respectively

[c] Minimum differences between any two weight/100 kernel means for significance are 1.7 and 2.3 at the 5 and 1% level respectively

[d] Minimum differences between any two kernel number means for significance are 50 and 65 at the 5 and 1% level respectively

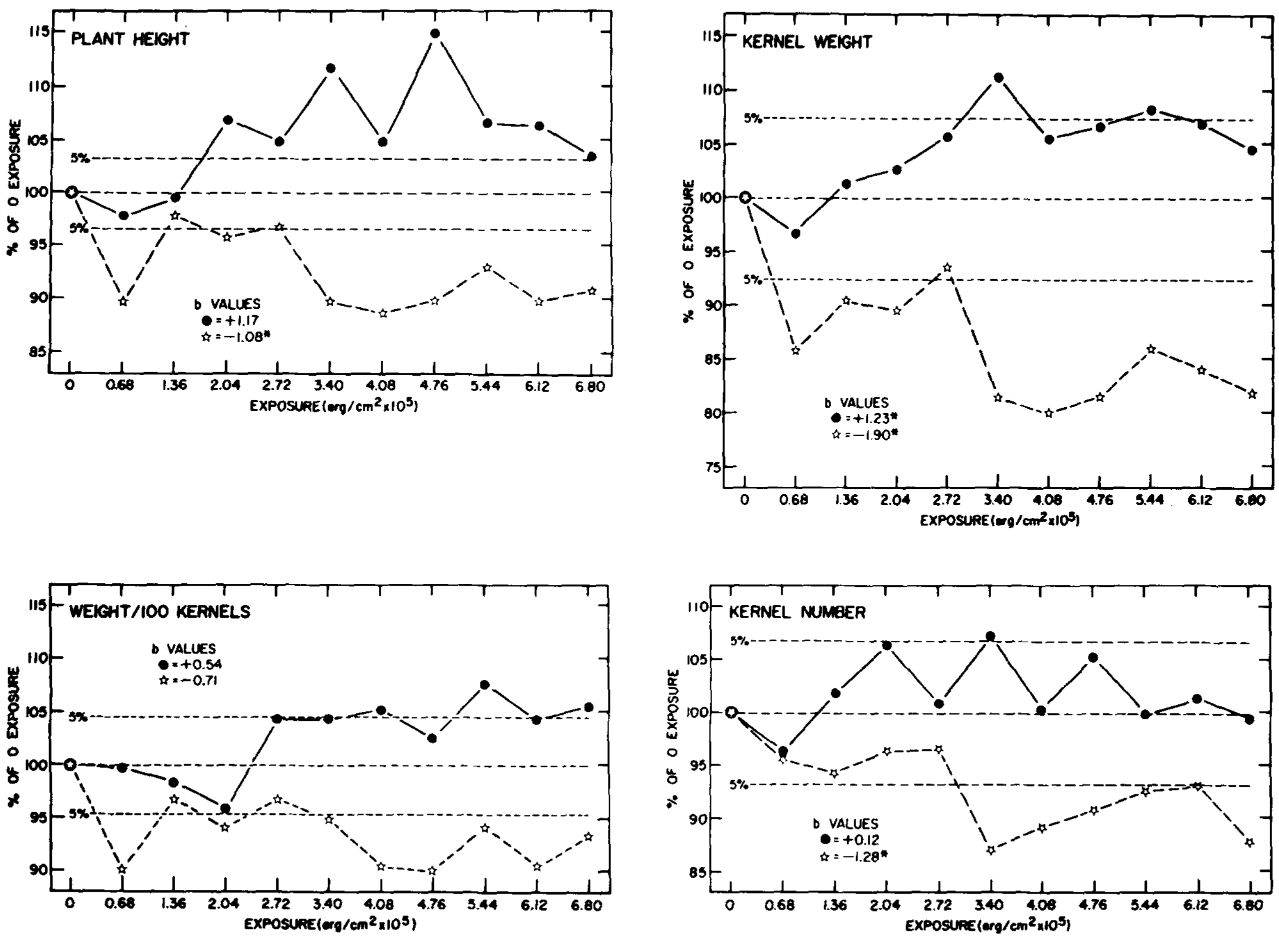

Fig.1. The effect (in % of 0 exposure) of various exposure levels on the characters measured in the two populations. The 5% significance range from 0 exposure level is indicated by the horizontal lines equidistant above and below 100%. Circles = W; stars = K

diation increased or did not change the means in W but decreased them in K in each year for all characters. This pattern is shown graphically in Fig.1 where the population means over both years are plotted as a % of 0 exposure. For plant height, the intermediate and higher exposure levels significantly increased the means in W in comparison with the 0 exposure level. With K, these levels resulted in a significant decrease in plant height in relation to the 0 exposure level. For kernel weight, weight/100 kernels, and kernel number, increasing exposure slightly increased or did not change the means in W, but significantly decreased them in K expecially at the higher levels.

Table 3. Mean squares from the variance analyses associated with the transformed (inverse sine) coefficient of variation values of each character

Source of variation	Degrees of freedom	Plant height	Kernel weight	Weight/ 100 kernels	Kernel number
Population (P)	1	0.12	2.89	16.33**	7.85
Exposure (E)	10	4.41	9.32	2.59	20.92*
E × P	10	1.95	12.52	2.68	13.33
Year (Y)	1	1.79	15.21	176.68**	53.93*
Y × P	1	0.00	5.46	0.03	43.56*
Y × E	10	0.97	5.72	3.31	3.59
Y × E × P	10	2.54	9.83	3.15	7.97
Error	44	2.20	6.34	2.16	7.86

*, ** F values significant at the 5 and 1% level respectively

The variability found within the populations for each character was subjected to variance analyses which appear in Table 3. In general, no significant difference associated with the main effect, exposure, or its interactions with other main effects was obtained. For kernel number, the main effect, exposure, was significant at the 5 % level. For this character, no consistent relationship between exposure level and coefficient of variation values was obtained. The coefficient of variation (22.8 %) at 1.36 $erg/cm^2 \times 10^5$ was significantly lower than that (28.5 %) at the 0 exposure level at the 5 % level. No other level was significant from the 0 exposure level.

Discussion

In a related study (Pfahler and Linskens 1976), differences between these two hybrids were found in kernel development after pollination with ultraviolet-irradiated pollen grains. Many aspects of kernel development were altered, but in general, increasing exposure increased the weight of the normal F_2 kernels and their embryos in W and decreased or had no effect in K. The results of the study reported here indicate that the effect of pollen irradiation on the F_2 plants produced from the normal F_2 kernels was also associated with the pollen source hybrid. In general, the same pattern emerged, with increasing exposure increasing or not changing the mean of W but consistently decreasing the mean of K for all characters measured. The most obvious explanation is that the pollen grains of K are more radiosensitive or sustain more nuclear damage than those of W. However, this explanation neglects the consistent and significant increases in some characters in W with increasing exposure.

Information on the effect of ultraviolet irradiation on quantitative characters is extremely limited. Many mutagenic agents, especially ionizing irradiations, produce deletions or minute deficiencies at specific loci which appear as mutations from the dominant or active form to the recessive or inactive form (Stadler 1941, Stadler and Roman 1948). In contrast, nonionizing ultraviolet irradiation is known to produce changes which are within the limits of our definition of an allele at a specific locus and could be termed point mutations (Nuffer 1957, Stadler 1941). Also, the photoreactivation phenomenon indicates that ultraviolet-induced changes can be reversed and thus are not deletions (Fujui 1969, Ikenaga and Mabuchi 1966). Thus, ultraviolet may induce changes from the dominant or active allelic form to the recessive or inactive allelic form or vice versa.

Heterosis or hybrid vigor is associated with the expression of many quantitative characters in maize. Two theories, dominance and overdominance, have been advanced to explain this phenomenon. At this time, the general consensus is that both dominance and overdominance contribute varying amounts to hybrid vigor under specific circumstances (Crow 1952, Sprague 1955). Most, if not all, of the characters measured in this study exhibit heterosis. Thus, with our present understanding of this phenomenon, the increase found in W with increasing exposure may be related either to the increase in dominant alleles at homozygous recessive loci or the production of heterozygosity at homozygous loci. The decrease found in K is difficult to explain unless, in this hybrid, the vigor was associated with a different balance of dominant and overdominant loci. Therefore, the pollen source effect found in this study may be related to mutation interacting with the balance of dominant and overdominant loci that are associated with vigor in the specific hybrid tested.

Increased variability within the populations would be expected as a result of these mutations. In this study, no increase in variability associated with either exposure or the exposure × population interaction was found for any character except kernel number. Most quantitative characters are conditioned by a large number of loci and, in some of these complex characters, probably all the gene loci make varying contributions to the expression of the character. Therefore, the beneficial and deleterious mutations induced by irradiation are probably randomly distributed over a large number of loci in the male genome so that no change in variability was detected.

The practical significance of these results are readily apparent. Pollen irradiation with ultraviolet produced both beneficial and deleterious changes in some valuable quantitative characters depending in the hybrid. Possibly, with further research and a greater understanding in this area, the beneficial effects could be more accurately predicted and exploited.

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