

The Distribution of Gene Frequencies.—A formula for the distribution of gene frequencies in populations subject to evolutionary pressure Δq and sampling variance $\sigma_{\Delta q}^2$ was reached in a previous paper.⁸

$$\varphi(q) = (C/\sigma_{\Delta q}^2) e^{2\int (\Delta q/\sigma_{\Delta q}^2) dq} \quad (21)$$

The approximate formula for the distribution of q in $2k$ -ploids is thus as follows, letting $\Delta q = v(1 - q) - uq + \frac{q(1 - q)}{2k\bar{W}} \frac{d\bar{W}}{dq}$ from combination of (1) and (4) and letting $\sigma_{\Delta q}^2 = q(1 - q)/2Nk$.

$$\varphi(q) = C\bar{W}^{2n} q^{4nkv - 1} (1 - q)^{4nku - 1} \quad (22)$$

The joint distribution for a system of multiple genes can be written as follows, letting \bar{W} here be the mean selective value of the population in terms of all gene frequencies as variables.

$$\varphi(q_1 \dots q_n) = C\bar{W}^{2n} \Pi [q_i^{4nki v_i - 1} (1 - q_i)^{4nki u_i - 1}] \quad (23)$$

It is to be noted that this applies to aneuploids (k variable) as well as to euploids (k constant).

¹ Wright S., *Genetics*, **6**, 111-178 (1921).

² Wright S., *Proc. Nat. Acad. Sci.*, **23**, 307-320 (1937).

³ Haldane, J. B. S., *Jour. Genetics*, **22**, 359-372 (1930).

⁴ Wright, S., *Proc. Nat. Acad. Sci.*, **19**, 411-420 (1933).

⁵ Wright, S., *Ann. Math. Stat.*, **5**, 161-215 (1934).

⁶ Muller, H. J., *Amer. Nat.*, **48**, 508-512 (1914).

⁷ Bartlett, M. S., and J. B. S. Haldane, *Jour. Gen.*, **29**, 175-180 (1934).

⁸ Wright, S., *Proc. Nat. Acad. Sci.*, **24**, 253-259 (1938).

THE MECHANISM OF DELAYED KILLING OF MAIZE SEEDS WITH X-RADIATION

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Biological response to x-rays has often been interpreted on the basis of the quantum theory of radiation absorption and the so-called hit theory¹ involving the concept of a particular sensitive volume within the material. For the death of single-celled individuals it is frequently found that survival-dosage curves show a simple exponential relationship indicating the presence of one sensitive volume which requires only one hit or penetration by an electron in order to produce death. When multi-cellular systems

are studied it is usually found that the survival curves are no longer exponential but have a sigmoid shape. The hit theory in this case has two indistinguishable alternatives; either death occurs from a number of hits within one sensitive volume or a different number of hits within two or more sensitive volumes.

Certain tests of this theory will be described for the x-ray treatment of corn seeds. In this instance the seed embryos under investigation are large enough for scanning experiments designed for the purpose of searching for the position of a possible single sensitive volume. Killing in this case comes at a particular stage in the growth of the seedlings as a result of irradiation of the dry seeds with dosages ranging from 50,000 to 100,000 "r" units. Within approximately one week after the emergence of the plumule elongation ceases and usually a thick crumpled first leaf will show. After elongation has stopped the seedling remains green for about another week before dying. The maximum height obtained is about 1 to 2 cm. This type of death has been called delayed killing² and figure 1 illustrates the manner in which it occurs. A continuous band of radiation is used with a maximum intensity at 0.50 Å and a short wave-length limit of 0.26 Å. Dosage values are given to within 5 per cent as determined by an open air ionization chamber.³

Experimental survival ratio-dosage relationships are shown in figure 2 where a sigmoid-shaped curve is obtained. Interpretation of these results can be made from a consideration of the hit theory which is formulated in the following manner:¹ Given Z_0 seeds each with one sensitive volume v (cm.³) which requires n successive hits or penetrations by primary electrons in order to produce delayed killing, then the number Z which survive a dosage of q ("r" units) will be given by the following Poisson series:

$$\frac{Z}{Z_0} = e^{-\alpha q} \left(1 + \alpha q + \frac{(\alpha q)^2}{2!} + \frac{(\alpha q)^3}{3!} + \dots + \frac{(\alpha q)^{n-1}}{(n-1)!} \right) \quad (1)$$

where α represents the number of times the sensitive volume v is hit by primary electrons per "r" unit measured. It has been shown by Glocker¹ that when the range of the primary electrons is taken into account

$$\alpha = N_0 \cdot \frac{R + a}{a} \cdot v \quad (2)$$

N_0 being the number of primary electrons formed per cm.³ per "r" unit measured, R the range of the primary electrons in the biological material and a the average path traversed by the primary electrons in a spherical sensitive volume of radius r when $R \gg a$, thus $a = \frac{4}{3}r$. Equation 1 can be evaluated by means of the incomplete gamma-functions from tables

prepared by Karl Pearson. A theoretical survival curve which approximately fits the experimental curve is shown in figure 2. In this case α

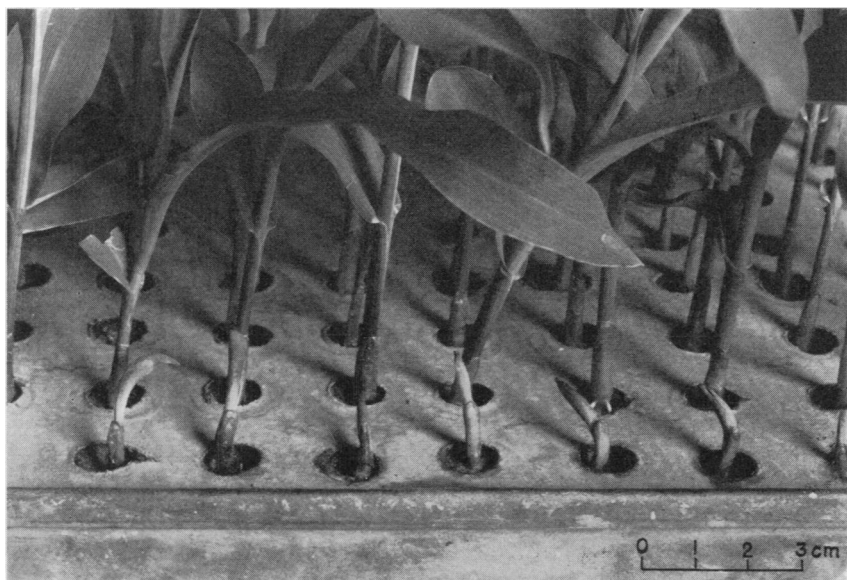


FIGURE 1

Photograph of delayed killed corn plants shown in the first row as compared with normal seedlings.

was taken equal to 4.5×10^{-4} ("r" units) $^{-1}$ which established the relationship between α and q . A value of $n = 14$ was obtained by selecting

TABLE 1
SUMMARY OF RESULTS OBTAINED WITH $\frac{1}{2}$ MM. SLIT WIDTH

ZONE NUMBER IRRADIATED	DOSAGE "r" UNITS	NUMBER OF SEEDS GERMINATED	PERCENTAGE SHOWING DELAYED KILLING	MEAN HEIGHT OF DEAD PLANTS (CM.)
6	50,000	83	none
7	50,000	45	none
8	50,000	125	none
9	50,000	42	none
10	50,000	274	none
11	50,000	42	none
12	50,000	123	none
13	50,000	42	none
14	50,000	122	none
16	50,000	81	none
10	100,000	60	none
10	300,000	248	43.0	6.6 \pm 0.8*

* Standard error of mean

the proper slope for the theoretical curve. The spherical sensitive volume required by equation 2 is approximately 1×10^{-15} cm.³ assuming the primary electrons to be the effective particles. This calculation was made on the basis of monochromatic radiation of wave-length 0.50 Å which is close to the average wave-length used.

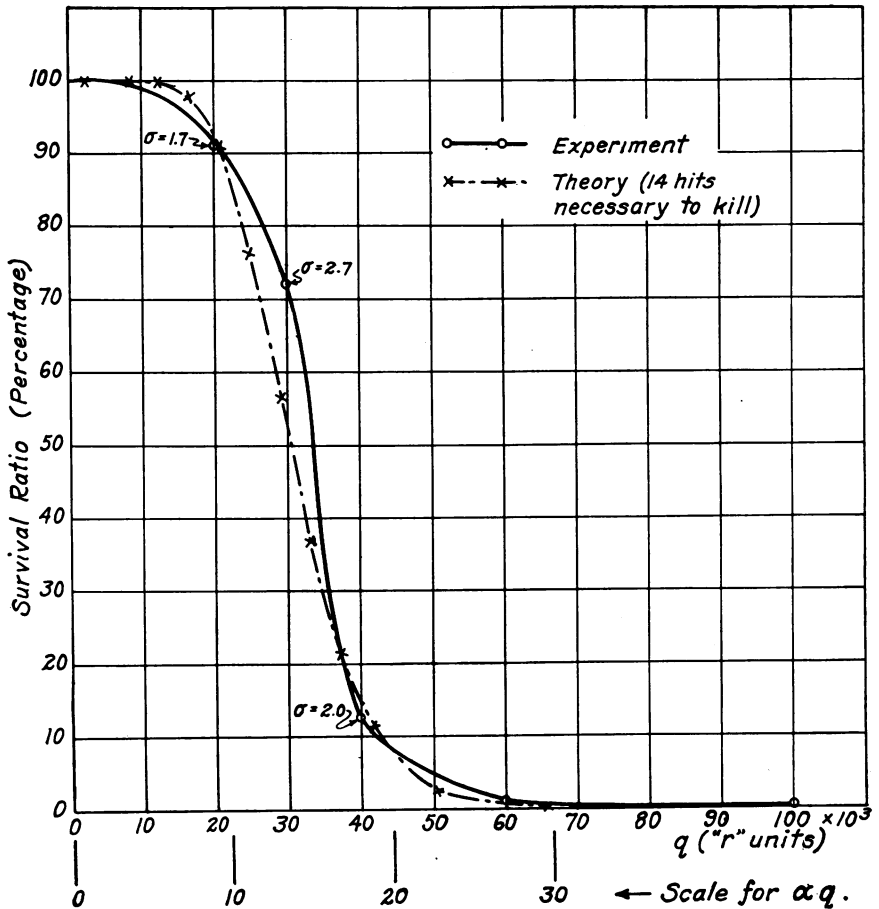


FIGURE 2

Survival ratio curves for the delayed killing of corn seeds. Values for the standard deviation (σ) are given for the experimental points.

A search for this sensitive volume was made by irradiating various assigned zones laid out crosswise of the seed as indicated in figure 3, while figure 4 shows the seed rack with lead slits used for the scanning experiments. Photographic films placed in the position occupied by the seed embryos provided a test for the actual width of the irradiated area ob-

tained. In table 1 are given the results of treatment taken over the length of the embryos with an irradiation area $\frac{1}{2}$ mm. in width. On the basis of a single sensitive volume contained within the embryo (which is about 7 mm. long) it is expected on the average that at least one out of every fourteen seeds or not less than 7% of the seeds should be killed. However, it is seen from table 1 that no delayed killing is observed for dosages of 100,000 "r" units or less involving treatment of more than 1000 seeds. The probability that this failure to kill could be the result of random sampling is so remote as to *eliminate the possibility of the existence of a single "sensitive volume" as defined by the hit theory.* At 300,000 "r" units a large

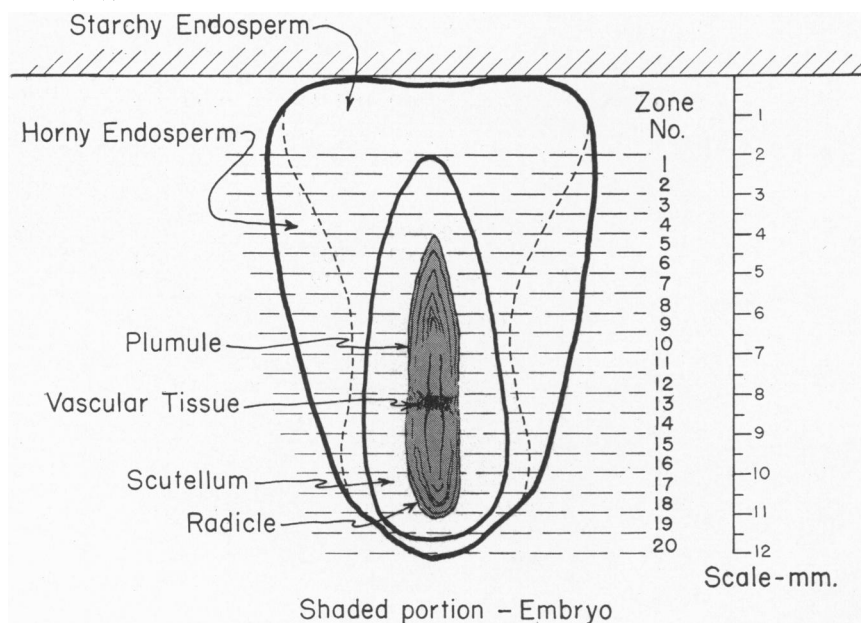


FIGURE 3

Drawing of a typical corn seed showing various zones used for irradiation.

number of the plants were killed but at a later stage in growth, indicating a different type of response.

Table 2 shows the results obtained for various wider slit widths and for exposures taken through the central portion of the seed embryos. It is seen that death occurs at the lower dosages and that, in general, a larger percentage of deaths will take place as the slit width is increased. However, in no case does complete killing exist even at the higher dosages. *The percentage death approaches a saturation value thus indicating that it is not proportional to the total amount of energy absorbed in a restricted region of the seed.* From table 2 it is also noticed that the plants die at earlier

stages as the slit width is increased, approaching for a 3 mm. slit width the average height of 1 to 2 cm. found for delayed death when the entire seed is exposed.

TABLE 2
SUMMARY OF RESULTS OBTAINED WITH 1.0 MM., 1.5 MM., 2.0 MM. AND 3.0 MM. SLIT WIDTHS

SLIT WIDTH	ZONE NUMBER IRRADIATED	DOSAGE "F" UNITS	NUMBER OF SEEDS GERMINATED	PERCENTAGE SHOWING DELAYED KILLING	MEAN HEIGHT OF DEAD PLANTS (CM.)
1.0 mm.	9, 10	20,000	44	36.4	2.1
	9, 10	29,200	176	16.9
	9, 10	30,000	45	48.9	6.6
	9, 10	40,000	44	52.3	7.5
	9, 10	50,000	393	33.6
	9, 10	52,000	134	30.5
	9, 10	60,000	45	48.9	9.8
	9, 10	70,000	247	47.0	6.8
	9, 10	80,000	43	51.2	6.8
	9, 10	90,000	44	50.0	7.0
	9, 10	95,000	88	63.6	4.4
	9, 10	100,000	332	38.6	6.0
	9, 10	150,000	112	36.6	4.8
1.5 mm.	LH* 9, 10, 11, UH 12	31,600	177	10.7
	8, 9, 10	40,000	34	2.9	1.2
	LH 9, 10, 11, UH 12	43,500	32	69.0	3.8 ± 0.9
	LH 9, 10, 11, UH 12	54,500	129	44.4
	8, 9, 10	80,000	71	49.5	3.4
	8, 9, 10	120,000	65	57.0	2.2
	8, 9, 10	160,000	36	50.0	1.2 ± 0.5
	LH 9, 10, 11, UH 12	200,000	21	67.0	0.8 ± 0.9
	LH 9, 10, 11, UH 12	300,000	18	56.0	3.0 ± 1.2
2.0 mm.	9, 10, 11, 12	100,000	79	64.1	3.3 ± 0.75
3.0 mm.	8, 9, 10, 11, 12, 13	20,000	36	none
	8, 9, 10, 11, 12, 13	33,200	178	23.6
	8, 9, 10, 11, 12, 13	40,000	69	50	2.2
	8, 9, 10, 11, 12, 13	58,000	132	70
	8, 9, 10, 11, 12, 13	60,000	69	72	1.7 ± 0.28
	8, 9, 10, 11, 12, 13	100,000	33	87	1.4
	8, 9, 10, 11, 12, 13	150,000	30	87	2.0
	8, 9, 10, 11, 12, 13	300,000	21	95	1.6

* LH means lower half. UH means upper half.

Variations given represent standard error of mean.

Probing experiments taken over the entire length of the seed with a 2 mm. slit width are summarized in table 3. It is seen that there is a wide distribution of positions on the seed in which death occurs, with the most sensitive region located at the approximate center of the embryo. One

hundred seeds were dissected and measurements taken of the variation in position of the seed embryos. It was found that the position of the center of the embryo will have a standard deviation of approximately 0.5 mm. This fluctuation may account in part for the wide distribution of susceptible volumes. However, these sensitive volumes are many magnitudes larger than expected on the pure formal hit theory as described above.

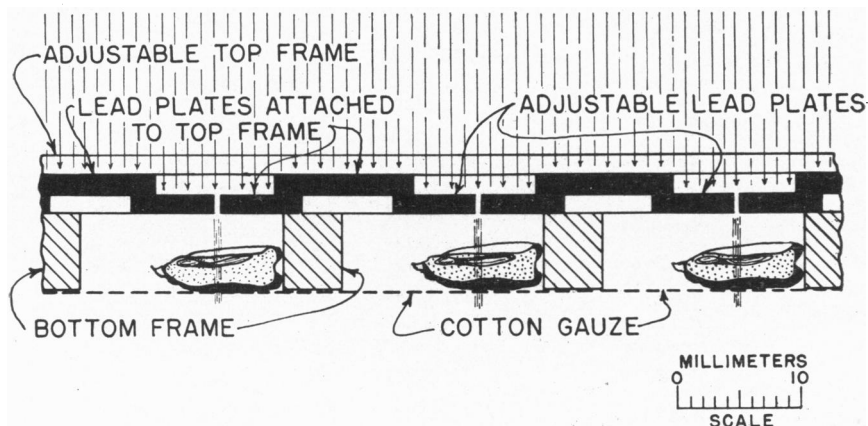


FIGURE 4

Diagram of lead slit arrangement used for irradiation.

For a multi-cellular organism such as a corn seed it is possibly not surprising that the hit theory interpretation based on the response of a single sensitive volume should fail. The alternative explanation involving a distribution of several sensitive volumes each requiring a certain number of

TABLE 3
RESULTS OBTAINED FROM SCANNING WITH 2.0 MM. SLIT WIDTH

ZONE NUMBER IRRADIATED	DOSAGE "r" UNITS	NUMBER OF SEEDS GERMINATED	PERCENTAGE SHOWING DELAYED KILLING	MEAN HEIGHT OF DEAD PLANTS (CM.)
1, 2, 3, 4	100,000	78	1.3	9.5
5, 6, 7, 8	100,000	82	32.1	2.1 \pm 0.35
9, 10, 11, 12	100,000	79	64.1	3.35 \pm 0.75
13, 14, 15, 16	100,000	81	11.1	6.51 \pm 1.10
17, 18, 19, 20	100,000	76	0.0

Variations given represent standard error of mean.

hits is not eliminated. However, on the basis of the above experiments it is safe to conclude that if multiple sensitive volumes do exist they are not contained within a spherical volume whose diameter is less than 0.5 mm.

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¹ See for instance Glocker, R., *Zeit. Phys.*, **77**, 653-675 (1932).

² Collins, G. N., and Maxwell, L. R., *Science*, **83**, 375-376 (1936); Maxwell, L. R., *Phys. Rev.*, **51**, 375 (1937).

³ For the design used see Taylor, L. S., and Singer, G., *Radiology*, **15**, 637-646 (1930).

CONTACT EFFECTS BETWEEN PLANT ROOTS AND SOIL COLLOIDS

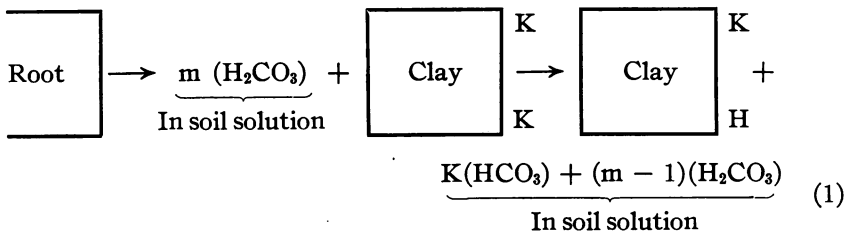
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Introduction.—The prevailing theories of mineral absorption by plants from soils are based on the concept of the *soil solution*. They postulate that a nutrient element must be an integral part of the soil solution before it can be taken up by plant roots. An ion is said to be in the soil solution when it is detached from the solid phase and can diffuse freely. It closely follows the movements of the liquid phase. Essentially, the soil solution is identified with the nutrient solution of the plant physiologist.

Equation (1) schematically illustrates the action of plant roots in soils as visualized by the soil solution theory.



The roots excrete carbonic acid into the liquid phase surrounding the soil particles. The H ions replace K from the surface of soil colloids and the resulting potassium bicarbonate is now ready for intake by roots.

In this paper an additional mechanism of mineral intake by plants from soils is proposed. It is based on the phenomenon of ion interchange existing between two surfaces which are in contact.