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June 1993

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Experimental and Theoretical Cross Sections for *Escherichia coli* Mutants B, B/r, and B_{s-1} after Heavy-Ion Irradiation

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Abstract

Data for the inactivation of three *Escherichia coli* mutants by energetic heavy ions are fitted by the track theory of a one-hit detector in an extended target mode. The respective E_0 's are 46, 36.5, and 12.6 Gy for *E. coli* B, B/r, and B_{s-1}, and a_0 , the assumed target radius, is 0.5 μm for all three. The parameter E_0 , the D_{37} with γ rays, is measured directly, while a_0 is fitted to the data. It is significant that neither a point target model nor calculations with $a_0 = 0.2$ and 1.0 μm fit the data. Our fitted target radius, a_0 , approximates the size of the bacterium. These results raise questions as to why the *E. coli* mutants are one-hit detectors, and concerning the differences in the E_0 's in relation to a mechanistic interpretation of cell killing.

Introduction

According to the theory of Butts and Katz (1) and the radial distribution of dose calculated by Waligorski *et al.* (2), we have calculated cross sections for heavy-ion bombardments of *Escherichia coli* B which are consistent with the data obtained by Grigoriev *et al.* (3), and also for heavy-ion bombardment of *E. coli* B/r and B_{s-1} which are consistent with data of Haynes (4).

Theory

In the studies of radiation effects, the medium is both a source of the secondary particles which are largely responsible for the observed effects, and the container of the affected targets. We must consider the irradiated medium as an assemblage of targets and that the action cross section represents the probability that the interaction of an incident projectile with the target ultimately results in the measured end point.

Our model is based on the assumption that the effects produced by secondary electrons from γ rays and those from the secondary electrons from heavy ions (δ rays) are comparable at the same dose.

When we speak of the dose of δ rays surrounding a heavy ion's path, we imagine that we study the energy deposited in nests of coaxial cylindrical shells surrounding many ions. Thus the dose of δ rays within a shell is an average quantity over a synthetic large volume made up of equivalent shells about many ions. We use the effect produced in a macroscopic volume by a given dose of γ rays to estimate the effect produced in the shell about our typical averaged ion. That effect is the probability of activating a target as a function of macroscopic dose. This probability is also an average quantity.

The inactivation probability P at a given radial distance (t) is

$$P(t) = 1 - e^{-\bar{D}(t)/D_{37}} \quad (1)$$

where D_{37} is the γ -ray dose for 37% survival and $\bar{D}(t)$ is the average dose at the target, whose center is at a distance t from the ion's path.

Even at large distances from an ion's path, where there are very few δ rays penetrating a shell, we estimate the effect on the basis of a similarly low dose of γ rays where there also are few secondary elec-

trons. Our track model is said to be "amorphous," so chosen as to make it possible to use the "amorphous" γ -ray dose-response relationship as a transfer function to evaluate heavy-ion response.

This procedure is "operational" in the sense that each of the several steps is accessible to experiment. Thus the survival data obtained from an X- or γ -ray irradiation are folded into the radial dose distribution to yield a radial distribution of inactivation probability whose radial integral is the cross section.

In other words, the above equation can then be integrated around the ion's path to the maximum radial penetration T of δ rays to produce a radial integral for the cross section, σ :

$$\sigma = 2\pi \int_0^T (1 - e^{-\bar{D}(t)/D_{37}}) t dt. \quad (2)$$

This perspective implies that we can neglect any differences in the initial electron energy spectra, as the response to a dose of electrons, photons, or δ rays is nearly independent, say within 10%, of the initial electron energy spectrum. We also neglect the "dose-rate effect," the temporal differences between the duration of a γ -ray exposure and the extremely short pulse of a δ -ray exposure which irradiates a target as the ion passes.

In these calculations, target size is of consequence. Typically we have represented the target as a short cylinder of radius a_0 whose axis is parallel to the ion's path, and consider that the dose experienced by the cylinder is averaged over the target volume. This is because the dose falls off radially inversely with the square of the radial distance, so that the dose gradient may be large close to the ion's path, but becomes negligible at larger distances. $\bar{D}(t)$ is then taken to be the average dose delivered to targets whose axis is at a radial distance t from the ion's path.

Results

A target radius of 0.5 μm yielded the best fit to these data. It is of interest that this approximates the size of the bacterium. For the data of Grigoriev *et al.* (3), our calculated cross sections use a D_{37} for γ rays measured by these investigations. Haynes did not report any D_{37} values. For *E. coli* B/

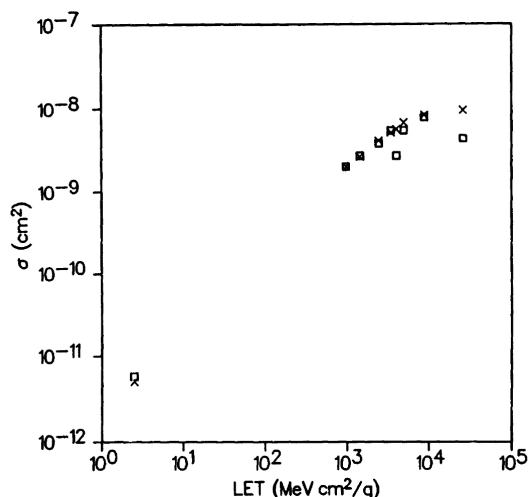


Figure 1. A comparison between the experimental and theoretical cross sections for *E. coli* B, with $E_0 = 46$ Gy and $a_0 = 0.5$ μm . From the theory of Butts and Katz (1), in the extended target model, modified by use of the radial dose distribution of Waligorski *et al.* (2). (\square) Grigoriev *et al.* (3), (\times) calculated points.

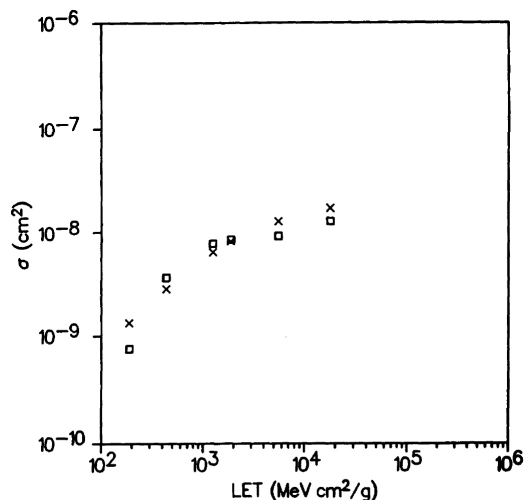


Figure 3. A comparison between the experimental and theoretical cross sections for *E. coli* B_{s-1}, with $E_0 = 12.6$ Gy and $a_0 = 0.5$ μm . From the theory of Butts and Katz (1), in the extended target model,

r and B_{s-1}, we used D_{37} doses as measured and reported by Takahashi *et al.* (5). No other parameters are needed for our calculations.

We reproduce the experimental data of Grigoriev *et al.* (3) in Figure 1 and the data of Haynes (4) (recalculated as cross sections) in Figures 2 and 3. In all of these figures, we have superimposed our calculated values for the respective cross sections. We have chosen this method to exhibit graphically the nature of the agreement between theory and experiment. We also exhibit Tables I–III, showing experimental values of

the cross sections and the calculated values based on the experimental D_{37} for γ rays and postulated target size, a_0 .

Grigoriev *et al.* (3) provide LET, experimental cross sections, and error bars for each bombarding ion. Several points measured at the lowest speeds do not fit our calculations. These lie in the thindown region where small inconsistencies in particle speed between measured and calculated values may create large discrepancies in the cross section. Except for ^{11}B and ^{40}Ar at $0.057c$ (c = velocity of light in vacuum), the calculated cross sections lie within 25% of the experi-

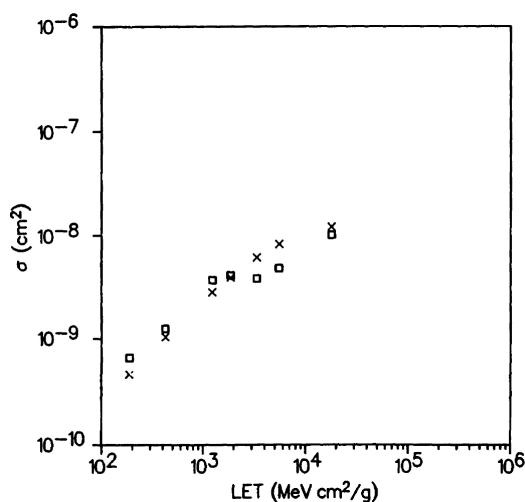


Figure 2. A comparison between the experimental and theoretical cross sections for *E. coli* B/r, with $E_0 = 36.5$ Gy and $a_0 = 0.5$ μm . From the theory of Butts and Katz (1), in the extended target model, modified by use of the radial dose distribution of Waligorski *et al.* (2). (\square) Haynes (4), (\times) calculated points.

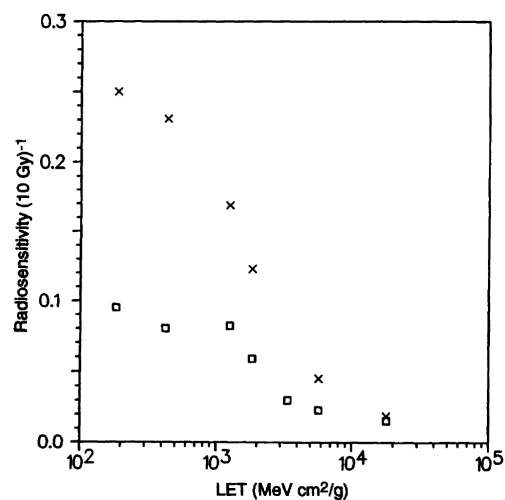


Figure 4. Radiosensitivity $(\text{LD}_{90})^{-1}$ vs LET for *E. coli* B/r (\square) and B_{s-1} (\times). Data from Haynes (4).

Table I. Numerical Values of Experimental and Theoretical Cross Sections for *E. coli* B for Each Experimental Bombardment^a

Ion	LET (MeV cm ² /g)	β (v/c)	σ expt. (cm ²)	Expt. error bars (cm ²)	σ theory (cm ²)	
¹ H	2.4	0.807	5.8×10^{-12}		6×10^{-13}	5.04×10^{-10}
⁴ He	1,150	0.046	2.0×10^{-9}		2×10^{-10}	1.99×10^{-9}
¹¹ B	1,400	0.124	2.7×10^{-9}		3×10^{-10}	2.62×10^{-9}
¹² C	2,300	0.111	3.8×10^{-9}		4×10^{-10}	4.07×10^{-9}
¹² C	3,500	0.086	5.4×10^{-9}		6×10^{-10}	5.12×10^{-9}
¹¹ B	3,900	0.057	2.7×10^{-9}		4×10^{-10}	5.61×10^{-9}
²⁰ Ne	5,000	0.133	5.4×10^{-9}		7×10^{-10}	6.76×10^{-9}
²² Ne	9,000	0.083	7.8×10^{-9}		9×10^{-10}	8.32×10^{-9}
⁴⁰ Ar	30,000	0.057	4.3×10^{-9}		7×10^{-10}	9.57×10^{-9}

Note. Also shown are the bombarding elements, LET, relative speed ($\beta = v/c$, where c is the speed of light), and experimental error bars.

^a $E_0 = 46$ Gy, $a_0 = 0.5$ μ m.

mental data, with five of the nine points within experimental errors.

Haynes (4) provides a graph of radiosensitivity (LD_{90})⁻¹ vs LET for *E. coli* B/r and B_{s-1} (Figure 4). Other experimental details relevant to these data are unavailable. Using the (LD_{90})⁻¹ and the LET, we inferred the experimental cross section for each bombardment. To calculate our theoretical cross sections, we need the atomic number Z and speed (relative to the speed of light, $\beta = v/c$) for each bombardment. Using the given LET and knowledge of existing practice at the time these experiments were performed, we inferred the identity and energy of each bombarding ion. With the exception of the ⁸O and ¹⁰Ne bombardments for *E. coli* B/r, the calculated cross sections are within 30% of the experimental values. For *E. coli* B_{s-1}, our calculations are within 39% of the experimental value, with the exception of the ²He bombardment.

In Figures 2 and 3, there is a consistent discrepancy in the slopes of calculated and experimental plots of cross section versus LET. For this we leave only a suggestion that the discrepancy may arise from our translation of the plotted values

of LET to Z and β . This might occur if the LET tables used by Haynes in 1966 differ from ours. We note no such discrepancy in Figure 1 or in Reference (2), where the same theory was used.

We are unable to get a consistent fit to the data of Takahashi *et al.* (5). Takahashi provided graphs of experimental cross sections vs LET for *E. coli* mutants B/r, B_{s-1}, and three K-12 mutants: AB2470(rec B), AB1157(rec +), and JC1553(rec A). For the mutants AB2470, JC1553, and B_{s-1}, we were able to obtain a reasonably good fit; our calculated cross sections were within 0.1 to 47% of the experimental values. However, for the mutants AB1157 and B/r, our calculations were within 0.4 to 70% of the given experimental values. All bombardments were of very low relative speeds. As mentioned earlier, this can lead to large discrepancies between calculated and experimental cross sections. Also, for many of the bombardments, the maximum radial distance to which δ rays penetrated do not extend beyond the postulated bacterial target size used in calculations of the cross sections.

Table II. Numerical Values of Experimental and Theoretical Cross Sections for *E. coli* B/r for Each Experimental Bombardment^a

Z	β (v/c)	LET (MeV cm ² /g)	σ expt. (cm ²)	σ theory (cm ²)
2	0.146	184	6.56×10^{-10}	4.56×10^{-10}
3	0.142	423	1.25×10^{-9}	1.05×10^{-9}
5	0.136	1,250	3.72×10^{-9}	2.83×10^{-9}
6	0.133	1,840	4.12×10^{-9}	3.92×10^{-9}
8	0.128	3,390	3.84×10^{-9}	6.16×10^{-9}
10	0.119	5,740	4.83×10^{-9}	8.28×10^{-9}
18	0.105	17,900	1.02×10^{-8}	1.22×10^{-8}

Note. Also shown are the atomic number Z of the bombarding projectiles, LET, and relative speed ($\beta = v/c$).

^a $E_0 = 36.5$ Gy, $a_0 = 0.5$ μ m.

Table III. Numerical Values of Experimental and Theoretical Cross Sections for *E. coli* B_{s-1} for Each Experimental Bombardment^a

Z	β (v/c)	LET (MeV cm ² /g)	σ expt. (cm ²)	σ theory (cm ²)
2	0.141	189	7.59×10^{-10}	1.34×10^{-9}
3	0.139	435	3.70×10^{-9}	2.86×10^{-9}
5	0.136	1,250	7.81×10^{-9}	6.45×10^{-9}
6	0.133	1,840	8.47×10^{-9}	8.18×10^{-9}
10	0.119	5,740	9.16×10^{-9}	1.27×10^{-8}
18	0.105	17,900	1.30×10^{-9}	1.74×10^{-8}

Note. Also shown are the atomic number Z of the bombarding projectiles, LET, and relative speed ($\beta = v/c$).

^a $E_0 = 12.6$ Gy, $a_0 = 0.5$ μ m.

Discussion

From a comparison of calculated and experimental values, we conclude here that *E. coli* B, B/r, and B_{s-1} are one-hit detectors with a postulated target size of 0.5 μm . This implies that a single electron passing through the bacterium is capable of inactivating it.

The bacterial chromosome is believed to be a long circle of double-stranded DNA. We have seen previously that DNA double-strand breaks in SV-40 virus in an EO buffer also respond as one-hit detectors (6). The buffer enhances the indirect effect. One might then ask if the indirect effect dominates for these *E. coli* bacteria.

Bacteria may present the best possibility for sorting out a relationship between parametric models and mechanistic understanding in radiation biophysics. One might hope that the extensive studies of bacterial DNA, and on the effects of UV irradiation for survival, mutation induction, and even repair could help explain our findings that these mutants are one-hit detectors, with different values of E_0 . We hope that our findings will stimulate radiobiologists concerned with mechanisms to examine these questions further.

Acknowledgment

This work is sponsored by the U.S. Department of Energy.

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