



## Radiation Resilience in Bacteria: Mechanism and Bioremediation Applications

*Oladapo, Olukunle Olaonipekun<sup>1</sup>, Aguda, Opeyemi Nifemi<sup>2</sup>, Solomon, Oluwadamilola Omotunde<sup>3</sup>*

<sup>1</sup>Department of Science Laboratory Technology, Ladoke Akintola University of Technology, Ogbomoso, Nigeria.

<sup>2</sup>Department of Biological Sciences, Kings University, Ode-Omu, Osun State, Nigeria.

<sup>3</sup>Applied Biotechnology, School of Life Science, University of Westminster, United Kingdom

Email: [opeagda@gmail.com](mailto:opeagda@gmail.com)

Doi : <https://doi.org/10.55248/gengpi.5.0924.2521>

### ABSTRACT

The ability of certain bacteria to withstand and adapt to ionizing radiation (IR) has significantly advanced our understanding of cellular resistance mechanisms and their potential biotechnological applications. This review examines the bio-physical properties of radioresistant bacteria, focusing on the molecular mechanisms that underpin their varied responses to radiation. Bacteria such as *Deinococcus radiodurans* are exemplary models, showcasing robust DNA repair pathways, protein protection strategies, and powerful antioxidant defenses that collectively contribute to their extraordinary resilience. Beyond their survival mechanisms, the ecological roles of these bacteria in extreme environments are explored, highlighting the evolutionary advantages conferred by their radioresistance. The review also discusses the potential applications of these microorganisms in bioremediation, where they could be utilized to detoxify environments contaminated with radioactive materials, and in radiation therapy, where their unique properties might inspire new treatment strategies. By delving into the bio-physical interactions that enable microbial survival in high-radiation habitats, this work provides comprehensive insights into the resilience of these bacteria, offering promising avenues for innovative applications in both scientific research and industrial processes

### 1.0 INTRODUCTION

The remarkable ability of certain bacteria to withstand high levels of ionizing radiation has drawn considerable attention due to its potential benefits in both ecological restoration and biotechnological innovations. These bacteria, known for their radiation resilience, possess complex biological mechanisms that enable them to endure environments with extreme radiation, such as those found in nuclear waste sites, outer space, and other naturally high-radiation areas like hot springs (Slade & Radman, 2011; Daly, 2012).

Understanding these organisms offers valuable insights into their unique DNA repair pathways, antioxidant defenses, and cellular adaptations that protect them from radiation damage (Gupta & Kushwaha, 2016). These insights are not only of academic interest but also have practical applications, particularly in the bioremediation of environments contaminated with radioactive substances. By investigating the molecular and cellular strategies employed by these bacteria, we can better understand their role in ecosystem recovery and explore their potential use in cleaning up radioactive pollutants (Sharma et al., 2020).

On Earth, there are many places where life coexists and thrives in perfect harmony, but there are also habitats where life flourishes in spite of harsh environmental conditions like high salinity, high pressure, high or low pH, high or low temperature cycles, desiccation, and intense UV or high-level ionising radiation (Kumar et al., 2022). The most outstanding category of extremophiles (organisms that live and thrive in hostile environments) are the radiation-resistant species, which include bacteria and archaea that can withstand extremely high doses of ionising radiation (IR) (Kumar et al., 2022).

In recent years, there has been an increase in interest in the research of radioresistant bacteria and their potential use in bioremediation and biotechnology (Nayak et al., 2021), in contrast to alternative methods for bioremediation that have been tested and confirmed. Some bacteria offer potential for use in bioremediation because of their rapid growth rates, capacity to metabolise waste chemicals, and resilience to high radiation doses (Shukla et al., 2017). The response of microorganisms to IR has become more important in a number of biophysical fields. Since the proposal and presentation of a unique bio-concept known as "The Primacy of Proteome over Genome" (de Toledo Arruda-Neto et al., 2023); this has increased the significance of studying organisms exposed to radiation.

Radioresistant bacteria, and their potential applications in bioremediation is still considered a relatively young area of research (Shukla et al., 2017). Although a few researchers first noticed the existence of radioresistant microorganisms in the 1950s (Bruckbauer and Cox, 2021); however, it was nearly two decades later that the first microorganism with these characteristics was discovered. A number of radiation-resistant bacteria, including *Deinococcus*, *Acinetobacter*, *Chroococciopsis*, *Hymenobacter*, *Kineococcus*, and *Methylobacterium*, have been described (Arjomandi et al., 2018). In

addition, *hyperthermophilic euryarchaeota* species such as *Thermococcus* and *Pyrococcus* contain radiation-resistant strains; these strains are less resistant in comparison with *Deinococcus* and *Rubrobacter* (Kumar *et al.*, 2022).

Research on radioresistant bacteria and their potential uses in bioremediation is still in its infancy (Shukla *et al.*, 2017). The first microorganism with these traits was found over two decades after a few researchers originally noted the existence of radioresistant bacteria in the 1950s (Bruckbauer and Cox, 2021). Several bacteria that are resistant to radiation have been identified, such as *Deinococcus*, *Acinetobacter*, *Chroococcidiopsis*, *Hymenobacter*, *Kineococcus*, and *Methylobacterium* (Arjomandi *et al.*, 2018). Furthermore, radiation-resistant strains have been identified in *hyperthermophilic euryarchaeota* species as *Thermococcus* and *Pyrococcus*, however these strains are not as resistant as the strains found in *Deinococcus* and *Rubrobacter* (Kumar *et al.*, 2022). Certain bacteria, like *Bacillus* sp., exhibit intrinsic resistance IR by producing spores, and their methods for resisting radiation differ from those of other radiation-resistant bacteria that do not generate spores (Vlašić *et al.*, 2014). According to Rettberg *et al.* (2019), *Deinococcus radiodurans* is the most radiation-resistant bacterium. It can withstand more than 20 kGy of gamma radiation and 1000 Jm<sup>2</sup> UV light. Most vertebrates are killed by 10 Gy of radiation.

Radiation is one of the most potent chemicals that can damage DNA, yet bacteria that are resistant to radiation have a number of excellent defence mechanisms against it (Chatterjee and Walker, 2017). The investigation and study of these bacteria have shown a promising, yet unexplored, area of biotechnology and bioremediation. Understanding the molecular and genetic pathways driving their radiation reaction is the main task (Averbeck *et al.*, 2020). Once this is done, creative solutions for environmental cleanup and biotechnological breakthroughs may become possible. This review work's objective is to compile and evaluate studies on radioresistant bacteria in order to clarify the underlying genetic and molecular processes of resistance. Furthermore, it delves into the possible uses of these organisms in bioremediation, emphasising their ability to tackle environmental issues and propel biotechnological progress (Reyes *et al.*, 2021).

---

## 2.0 RADIATION AND ITS TYPES

According to Oladapo *et al.* (2020a), radiation is the emission and propagation of energy over space as waves or particles in a material medium. It influences everything from the energy of the sun to the atomic structure of matter, making it a basic phenomenon in the cosmos (Karmaker *et al.*, 2021). Radiation units like Sieverts (Sv) are used to assess biological effects, and Becquerels (Bq) are used to monitor the rate of radioactive decay. Other commonly utilised units for absorbed dosage are "rad" (for absorbed dose in earlier systems) and Gray (Gy). Depending on the dose and length of exposure, IR can have a variety of negative health impacts (Oladapo *et al.*, 2020b). Acute radiation syndrome (ACS) is a condition marked by symptoms such as nausea, vomiting, exhaustion, and hair loss that develops after a brief period of intense radiation exposure. Long-term exposure raises the possibility of developing cancer (Oladapo *et al.*, 2020c). Radiation exposure can cause changes in DNA that could be inherited by subsequent generations (Alimba *et al.*, 2021).

Radiation is a natural phenomenon, with sources including cosmic rays from space, radioactive materials in the earth's crust, and even natural elements within the human body. However, human activities, such as nuclear power generation, medical imaging, and industrial applications, have significantly increased exposure to both ionizing and non-ionizing radiation (UNSCEAR, 2021). Understanding the effects of radiation on biological systems is crucial for developing protective measures, particularly in medical, environmental, and occupational settings. The study of radiation also plays a vital role in fields like radiotherapy, where controlled doses of ionizing radiation are used to treat cancer by damaging the DNA of cancerous cells, thereby inhibiting their ability to replicate (Hall & Giaccia, 2022)

Particle and electromagnetic radiation are two types of radiation (Kontomaris *et al.*, 2019). Electromagnetic radiation, which includes radio waves, microwaves, infrared radiation, visible light, ultraviolet radiation, X-rays, and gamma rays, is made up of energy waves that travel at the speed of light without mass or charge. On the other hand, mass-carrying particles like neutrons, beta particles, and alpha particles are part of particle radiation. In the meanwhile, radiation can come from both natural and artificial sources, including solar radiation, nuclear power plants, medical imaging, industrial processes, and consumer goods like jewellery (Jha *et al.*, 2024). Natural sources of radiation include cosmic rays, solar radiation, and earth's radioactive minerals. According to Samarth *et al.* (2020), radiation can be further divided into two categories: ionising and non-ionizing. Ionising radiation has the ability to take electrons from atoms, which can cause damage to cells and DNA. Non-ionizing radiation does not have this energy, although it can still have effects like heating.

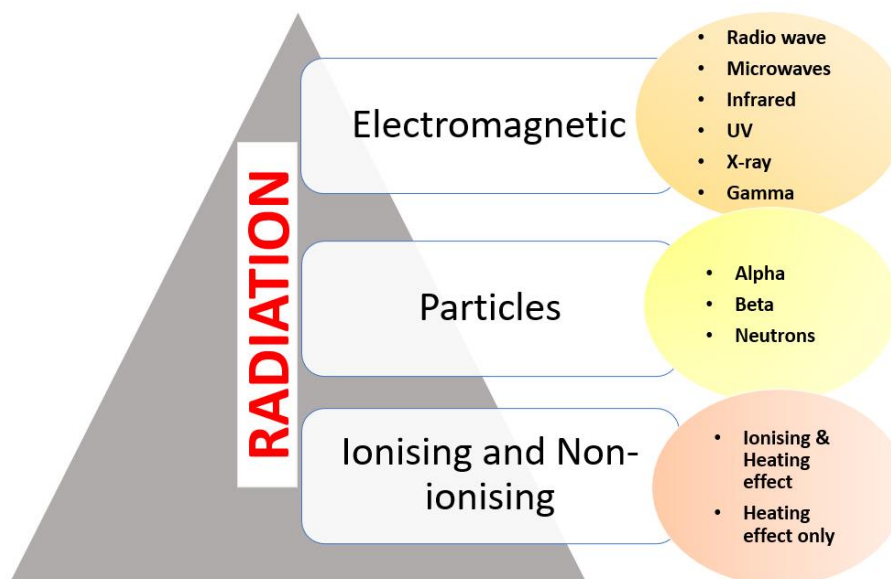


Figure 1: Categories of Radiation and their examples

### 3.0 METHODS OF STUDY OF RADIORESISTANT BACTERIA

#### 3.1 Radiation Exposure

Due to the remarkable resistance to ionising radiation, which normally damages DNA in most organisms, radioresistant bacteria have drawn a lot of attention (Nayak *et al.*, 2021). Certain bacteria, such as *Rhodobacter radiotolerans* and *D. radiodurans*, have been found to develop complex defence systems to shield their cellular constituents and effectively repair DNA damage caused by radiation (Pal *et al.*, 2024). Through carefully regulated radiation exposure technique, these bacteria are studied in order to shed light on their molecular survival strategies and to better understand important biological processes including protein stabilisation, oxidative stress management, and DNA repair.

Radiation resilience in bacteria is a fascinating area of study, particularly as it reveals the extraordinary capabilities of certain microorganisms to survive and thrive in environments saturated with ionizing radiation. Bacteria such as *Deinococcus radiodurans* have evolved highly effective mechanisms to repair extensive DNA damage caused by radiation, including efficient DNA repair systems, protein protection strategies, and powerful antioxidant defenses (Slade & Radman, 2011; Daly, 2012). These mechanisms not only prevent radiation-induced cell death but also enable these bacteria to maintain cellular functions under extreme stress conditions. The ability of these bacteria to withstand radiation has significant implications for biotechnology, especially in the field of bioremediation, where radioresistant bacteria can be employed to detoxify environments contaminated with radioactive materials (Sharma *et al.*, 2020). Additionally, ongoing research into these organisms may uncover new strategies for enhancing radiation resistance in other biological systems, potentially leading to advances in medical treatments for radiation exposure and the development of new materials for radiation shielding (Reyes *et al.*, 2021).

Researchers can generate and track cellular responses in these bacteria, such as the activation of repair enzymes, the production of stress-related proteins, and metabolic alterations, by exposing them to radiation (Wang *et al.*, 2019). Controlled radiation exposure experiments can also aid in the discovery of novel biomolecules and pathways that may find use in biotechnology, radiation therapy, and bioremediation by replicating the extreme conditions that these organisms face in their natural habitats. As a result, these investigations not only broaden our knowledge of microbial resistance but also provide hope for the creation of novel methods to lessen the effects of radiation on other biological systems.

Yazdani *et al.* (2009) identified thirty clean colonies with a range of colours and shapes from water and mud samples taken from the high-radiation Abe-Siah hot springs in Ramsar, North Iran. Only one colony survived the 22 KGy radiations that were used to irradiate it. Promising features were displayed by the survived bacteria, which grew best at 30 to 37 °C, pH 6 to 7, and at least 5% salt concentration.

In Vlašić *et al.* (2014) study, 200 µl of *Bacillus subtilis* spores that had been purified were placed in PCR tubes, and they were exposed to room temperature X-rays (200 kV/15 mA) produced by an X-ray tube. Plotting the logarithm of the survival percentage against the applied X-ray radiation dose yielded the survival curves. The data reported are average values with standard deviations, and each X-ray irradiation experiment was performed at least three times. Furthermore, the expression for spore resistance following X-ray radiation was found to be the  $D_{10}$ -value, denoting the X-ray dose at which spore survival is reduced to 10%.

The National Collection of Industrial and Marine Bacteria (NCIMB) provided the strains of *Methylobacterium extorquens* and *M. radiotolerans*, which subsequently underwent radiation exposure method (Nogueira *et al.*, 1998; Consiglieri *et al.*, 2020). After being separated from the initial bioburden of ophthalmic cotton dressings, a 1.47 kGy.h<sup>-1</sup> dose of gamma radiation was applied to the wild strain. Test pieces and bacterial samples in phosphate

buffer were exposed to radiation at room temperature concurrently in dosage ranges of 3 kGy to 21 kGy, with intervals of 3 kGy. Dosimeters were used to measure the absorbed dosages. Viable cells were identified following radiation after a prolonged incubation period of 14 days.

In order to compare the metabolites produced by the irradiated isolates of *Pantoea* sp to those of the control (non-irradiated isolates) using mass spectrometry, molecular networking, and chemometric analysis, Oliveira et al. (2024), determined the effect of irradiation on bacterial growth. Notably, bacterial cells of *Pantoea* sp. showed a noteworthy 6-log increase in comparison to non-irradiated cells following a 48-hour radiation exposure. Pyridindolol, 1-hydroxy-4-methylcarbostyryl, N-alkyl, and N-2-alkoxyethyl diethanolamine are the only compounds produced by non-irradiated cells; on the other hand, 5'-methylthioadenosine was only found in irradiated cells. These results imply that *Pantoea* sp.'s metabolic profile stayed mostly unchanged. The study's findings demonstrate the potential of the bacteria in radiation protection and radionuclide bioremediation.

### 3.2 Omics Technologies

The molecules that comprise a cell, tissue, or organism are viewed holistically by omics technologies (Vailati-Riboni *et al.*, 2017). With the ability to analyse radiation-induced changes at the genetic, transcriptase, protein, and metabolite levels, omics technologies (genomics, transcriptomics, proteomics, and metabolomics) offer a multifaceted understanding of how radioresistant bacteria withstand extreme stress. They are largely focused on the non-targeted and non-biased universal detection of genes (genomics), mRNA (transcriptomics), proteins (proteomics), and metabolites (metabolomics) in a particular biological sample (Vailati-Riboni *et al.*, 2017). Omics techniques often referred to as Systems biology is the term used to describe the integration of various methodologies; this is also known as high-dimensional biology (Yan *et al.*, 2018). It is crucial to understand that omics research encompasses more subfields than the four previously listed ones, including lipidomics, phenomics, interactomics, epigenomics, and glycomics.

Experiments in systems biology or omics deviate from traditional research, which is primarily hypothesis driven (Karahalil, 2016). Systems biology studies, on the other hand, generate hypotheses through the use of holistic methods; no predetermined or known hypothesis is used; instead, all data are gathered and examined in order to develop a hypothesis that may be investigated further. Bacteria under selective pressure may be identified using full-genome DNA resequencing when it is discovered in a radioactively polluted environment.

Following *D. radiodurans*' exposure to vacuum and UVC irradiation, space-related situations, to ascertain their molecular response, Ott et al. (2017) comprehensive proteome and metabolomic investigation identified multiple molecular changes in the bacterium's metabolic and stress response pathways. In reaction to the stressful environment created by UVC irradiation in vacuum, *D. radiodurans*' molecular key processes, such as the tricarboxylic acid cycle, DNA damage response systems, ROS scavenging systems, and transcriptional regulators, reacted. His work's findings demonstrated how useful the integrative proteometabolomic method is for molecularly analysing the microbial stress response brought on by space-related factors.

In order to identify the changed proteins in *D. radiodurans* that were rapidly sensitive to IR, Gao et al. (2022) carried out a proteomics profile on the species immediately following the heavy ion irradiation treatment. Unlike *Escherichia coli* strains, *D. radiodurans* demonstrated remarkable resistance to  $^{12}\text{C}^{6+}$  heavy ion irradiation, according to the study. The kinetics of proteome alterations caused by varying dosages of  $^{12}\text{C}^{6+}$  heavy ion irradiation were mapped using iTRAQ (Isobaric Tags for Relative and Absolute Quantitation)-based quantitative mass spectrometry analysis. The work's findings showed that 452 proteins had differential expression in response to heavy ion irradiation, with most of the proteins showing upregulation. This suggests that functional categories of translation, the TCA cycle (tricarboxylic acid cycle), and antioxidation regulation were all upregulated.

## 4.0 MECHANISM OF RESISTANCE IN RADIORESISTANT BACTERIA

In a cell, ionising radiation causes extensive molecular damage that impacts proteins, lipids, DNA, and RNA. Therefore, a multitude of elements need to be considered in order to clarify the method by which radioresistant bacteria are able to withstand exposure to high levels of radiation. According to Munteanu et al. (2015), the main mechanisms put forth indicate that radioresistant bacteria have special DNA repair mechanisms that are far more effective than those of other organisms. They also use antioxidant systems that are both enzymatic and nonenzymatic, and they have an extremely effective cellular cleansing system that exports damaged nucleotides out of the cell.

Given to nucleotide excision repair, these bacteria are resistant to extremely high radiation doses and DNA cross-linking agents (Nayak *et al.*, 2021). One method of repairing DNA is nucleotide excision repair. Chemicals, radiation, and other mutagens constantly cause damage to DNA; nevertheless, there are three excision repair mechanisms that can be used to repair damaged DNA: base excision repair, nucleotide excision repair, and DNA mismatch repair (Chatterjee and Walker, 2017). Hundreds of small DNA fragments are produced when DNA experiences single-strand breaks (SSBs) and double-strand breaks (DSBs) due to extreme desiccation and ionising radiation exposure. However, certain kinds of extremely effective DNA repair proteins or enzymes found in radioresistant bacteria like *D. radiodurans* enable them to fix hundreds of DSBs as well as SSBs.

Some radioresistant bacteria consist of transcriptional repressors called LexA<sub>1</sub> and LexA<sub>2</sub>, which are involved in the 'SOS'- (save our souls) response, a defence mechanism against DNA damage (Appukuttan *et al.*, 2015; Meyer *et al.*, 2018). These two repressors are present in *D. radiodurans* (Meyer *et al.*, 2018). The pleiotropic protein promoting DNA Repair A (pprA promoter) is activated when the LexA<sub>2</sub> is disrupted by UV light or any other type of radiation. The pprA gene's promoter region is crucial in boosting the bacteria's capacity to repair damaged DNA, which in turn adds to their extraordinary resilience. Furthermore, bacterial proteins like RadA and RadB are engaged in recombination and DNA repairs. RadA is an ATPase that forms nucleoprotein filaments to aid in DNA strand exchange and repair (Wardell *et al.*, 2017). By stabilising RadA's association with single-stranded

DNA and increasing its recombination activity, RadB helps RadA. Both proteins fix DNA breaks and stop recombination activities, which contribute to the genomic stability of the radioresistant bacteria.

Numerous studies have shown that *D. radiodurans* contains a chain of proteins called UvrA, UvrB, UvrC, and UvrD; these proteins are in charge of eliminating large DNA lesions brought on by UV light, shielding the bacteria from UV-induced damage (Timmins and Moe, 2016). Recombination repair of single and/or double-strand DNA damage is also aided by proteins including recA, recF, recJ, recO, and ruvB (Singh *et al.*, 2016). According to Torres-Barceló *et al.* (2013), superoxide dismutase and catalase offer defence against oxidative stress, whereas the mutS protein aids in mismatch repair. This clearly reveals the operation of the three excision repairs pathways for DNA repair (DNA mismatch repair, base excision repair, and nucleotide excision repair) in *D. radiodurans*. The synergistic effect of these proteins and processes provides compelling evidence for the possibility that *D. radiodurans* possesses its exceptional ability to survive radiation-induced stress (Nayak *et al.*, 2021).

According to Nayak *et al.* (2021), bacteria capacity to produce protective primary and secondary metabolic products (extremozymes and extremolytes) contributed to their resistance to the effects of radiation. Many frequent extremolytes, such as scytonemin, phlorotannin, Porphyrin-334, shinorine, mycosporine-like amino acids, palythine, biopterin, and so on, provide "harsh" surviving bacteria the capacity to absorb a broad variety of radiations and associated effector molecules. Extremolytes are highly popular in the biotechnology industry and have a wide range of commercial uses, such as sunscreens, antioxidant formulations, anticancer treatments, and nanoparticle production.

Cho *et al.* (2023) characterised underlying biological pathways relevant to radiation-resistance in *Spirosoma montaniterrae* and inferred regulatory network using six computational biology methods. He specifically determined the primary regulators of radiation-resistance and deduced the gene regulatory network (GRN) and operons of the radiation-resistant bacteria *Spirosoma montaniterrae* DY<sup>10</sup>. The findings demonstrated that the cAMP receptor protein (CRP)/fumarate and nitrate reduction regulatory protein (FNR) family transcriptional regulator functions as a master regulatory transcription factor in the early response to radiation, and that DNA repair and Reactive Oxygen Species (ROS) scavenging mechanisms are important processes. The N-terminal ligand-binding domain for small molecules (such as cAMP, NO, or O<sub>2</sub>) and the C-terminal DNA-binding domain are the two conserved domains of CRP/FNR-type transcription factors, which belong to a well-characterized across the globe TF family in bacteria (Filipek *et al.*, 2024).

According to Kanekar and Kanekar (2022), radioresistant bacteria have a remarkable resistance to the deadly and mutagenic effects of ionising radiation. A bacterium species known as *D. radiodurans* is extremely resistant to radiation, with a maximum radiation tolerance of 15 kGy for acute ionising radiation and 60 Gyh<sup>-1</sup> for chronic radiation (where Gy stands for grayscale and 1 Gy for 100 rad, or radiation absorbed dose). The organism can be found in oceans, hot springs, deserts, and radiation-contaminated areas. In addition, the organism shows resistance to oxidation, hypertonic stress, and desiccation. Self-repairing DNA damage, effective cellular damage clearance mechanisms such as hydrolysing damaged proteins, overexpressing repair proteins, and efficient removal of reactive oxygen species are some of the very efficient radiation-protection systems. The aforementioned information explains why *D. radiodurans* is regarded as one of the most radiation-resistant organisms and has earned the moniker "the toughest bacterium in the world" (Liu *et al.*, 2023).

**Table 1: Mechanisms of resistance and radiation tolerance dosage of diverse bacterial species**

Bacteria	Mechanism of Resistance	Average dose	Ref.
<i>Bacillus subtilis</i>	For DNA damage tolerance in <i>B. subtilis</i> spores, which have a single non-replicating genome without a template for repair, specific repair mechanisms are essential. RecA protein and its accessory factors (RecF, RecO, RecR, and RecX) are critical for regulating radiation-induced double-strand breaks (DSBs) and are considered key processes. Additionally, spore resistance to different ionising radiations such as protons and X-rays is mostly dependent on DNA repair via abasic (AP) endonucleases and non-homologous end joining (NHEJ). Radiation sensitivity of spores lacking in base excision repair (BER) or DSB repair is significantly higher. Moreover, non-cleavable LexA proteins assist decrease sensitivity to double-strand breaks (DSBs), and spores' low core water content may help limit hydroxyl radicals produced by gamma radiation.	1 kGy (D <sub>10</sub> )	Vlašić, I <i>et al.</i> , 2014; Moeller <i>et al.</i> , 2014.
<i>Bacillus nealsonii</i>	Spores of <i>B. nealsonii</i> produce beta-galactosidase and catalase, and they are very resistant to gamma radiation. It has a similar resistance technique as <i>B. subtilis</i> .	5 kGy	Yazdani <i>et al.</i> , 2009; Zammuto <i>et al.</i> , 2018
<i>Bacillus megaterium</i>	Isolated from Iranian hot springs and subjected to ionizing radiation, <i>B. megaterium</i> spores demonstrate that manganese levels are essential for spore resistance to a variety of agents, with the exception of gamma radiation.	3-5 kGy (D <sub>10</sub> )	Ghosh <i>et al.</i> , 2011; Bratkic <i>et al.</i> , 2024
<i>Desertibacter roseus</i>	Gamma radiation at a dose of 10 kGy was applied to sand samples containing <i>Desertibacter roseus</i> . The resultant bacteria could convert nitrate to nitrite and were positive for catalase and oxidase, but they were not able to fix nitrogen.	10 kGy	Liu <i>et al.</i> , 2011; Li <i>et al.</i> , 2021
<i>Deinococcus radiodurans</i>	Antioxidant enzymes like superoxide dismutase, a high intracellular Mn/Fe concentration ratio, and the presence of low-molecular-weight (LMW) Mn (2+)-metabolite complexes work together to neutralise free radicals and shield vital proteins and enzymes from oxidative damage and carbonylation.	10 kGy (D <sub>10</sub> )	Sharma <i>et al.</i> , 2013; Krisko and Radman, 2013; Sharma <i>et al.</i> , 2017
<i>Escherichia coli</i>	<i>E. Coli</i> served as a radiosensitive control in these investigations. Nonetheless, after 20 cycles—each of which eliminated more than 99% of the population—radioresistance was attained in <i>E. Coli</i> strain K-12 through directed evolution. When the surviving cells were given the opportunity to fully recover, developed populations with a survival rate at 3 kGy radiation increased by 3–4 orders of magnitude.	0.73 kGy (D <sub>37</sub> ) - 2 kGy (D <sub>37</sub> )	Harris <i>et al.</i> , 2009; Byrne <i>et al.</i> , 2014; Bruckbauer <i>et al.</i> , 2019
<i>Gloeobacter violaceus</i>	Certain cyanobacterial cells can survive X-ray doses as high as 15 kGy. The phytoene desaturase enzyme of the cyanobacterium <i>G. violaceus</i> shares 68% amino acid sequence similarity with the <i>Deinococcus radiodurans</i> DR0861 enzyme.	15 kGy	Pavlopoulou <i>et al.</i> , 2016
<i>Geodermatophilus tziadiensis</i>	<i>G. tziadiensis</i> is extracted from dry soil following exposure to doses of radiation varying between 17 and 30 kGy. It uses the same mechanism like <i>G. violaceus</i> .	17 – 30 kGy	Liu <i>et al.</i> , 2022

<i>Geodermatophilus obscurus</i>	Significant radiotolerance ( $D_{10} = 9$ kGy) and robust resistance to $H_2O_2$ -induced oxidative stress are displayed by <i>G. obscurus</i> .	9 kGy ( $D_{10}$ )	Gtari <i>et al.</i> , 2012
<i>Hymenobacter swuensis</i>	The most well-known scavengers of reactive oxygen species in these bacteria are called carotenoids. The majority of <i>Hymenobacter</i> sp. generate unique 2'-hydroxy-carotenoids in addition to their methyl, pentosyl, and hexosyl derivatives.	5 kGy ( $D_{10}$ )	Jung <i>et al.</i> , 2014
<i>Halobacterium salinarum</i>	Upregulation of genes such as <i>rfa3</i> , <i>rfa8</i> , and <i>ral</i> promotes DNA repair in highly radioresistant mutant strains of <i>Haemophilus salinarum</i> by inducing an excess of single-stranded DNA-binding protein (RPA), which shields intermediates and speeds up repair processes. Metabolic modifications, Mn-antioxidant complexes, and a high Mn/Fe ratio are also linked to increased radioresistance. Furthermore, these mutant strains are more viable when the <i>ura3</i> gene is deleted.	8 kGy ( $D_{10}$ )	Karan <i>et al.</i> , 2014
<i>Kocuria</i> sp.	<i>Kocuria</i> sp. enzymatic antioxidant defence systems, which include catalase and peroxidase, non-enzymatic antioxidants such carotenoids, and molecular repair processes, are partially responsible for its modest resistance to gamma-radiation and other stressors.	2kGy	Asgarani <i>et al.</i> , 2012; Gholami <i>et al.</i> , 2015
<i>Kineococcus radiotolerans</i>	In contrast to other bacteria, <i>K. radiotolerans</i> exhibits an over-representation of base excision (BER) and nucleotide excision (NER) repair genes. This suggests that the NHEJ repair pathway is absent in this bacterium due to its lack of the Ku protein. Although it lacks cytochrome c peroxidase ( <i>ccpA</i> ) and superoxide reductase ( <i>sorA</i> ), it has detoxifying enzymes such as alkyl hydroperoxide reductase ( <i>AhpC</i> ), catalase ( <i>KatE</i> ), Fe/Mn superoxide dismutase ( <i>SodA</i> ), and glutathionylspermidine synthase ( <i>Gsp</i> ) that help it defend against oxidative stress. The bacterium supports radioresistance by boosting metabolism and growth during chronic irradiation, and it has a high Mn/Cu ratio, which is similar to other radioresistant bacteria's Mn/Fe ratio.	3 kGy ( $D_{20}$ )	Bagwell <i>et al.</i> , 2008; Li <i>et al.</i> , 2015
<i>Modestobacter marinus</i>	<i>M. marinus</i> possesses multiple copies of several key genes which assist it in resistance to ionizing radiations, these include <i>coxSML</i> (carbon monoxide dehydrogenase), <i>dnaJ</i> (Hsp40 chaperone), <i>kata</i> (manganese-containing catalase), <i>mcrA</i> (mitomycin radical oxidase), <i>ohrR</i> (organic hydroperoxide resistance regulator, MarR family), <i>recQ</i> (DNA helicase), <i>soxABDG</i> (sarcosine oxidase), <i>trxAB</i> (thioredoxin reductase), <i>trwC</i> (conjugative relaxase), and <i>uvrACD</i> (UV resistance).	6 kGy ( $D_{10}$ )	Normand <i>et al.</i> , 2012; Montero-Calasanz <i>et al.</i> , 2019
<i>Pyrococcus furiosus</i>	Even at 95°C, <i>Pyrococcus furiosus</i> can withstand extreme heat. Their DNA is extremely resistant to deterioration by heat. Nevertheless, radiation-induced single-strand breaks (SSBs) and double-strand breaks (DSBs) are not prevented by the DNA stabilisation mechanism. These creatures' extraordinarily effective DNA repair systems, not DNA protection mechanisms, are what allow them to demonstrate radioresistance.	2.5 kGy ( $D_{75}$ )	Williams <i>et al.</i> , 2007; Stefanska <i>et al.</i> , 2016
<i>Pyrococcus abyssi</i>	The ideal temperature for hyperthermophilic species, such as <i>Pyrococcus abyssi</i> , is 100°C. The proteins RadA and RadB, which are eukaryotic and bacterial homologs of RecA and Rad51, are involved in homologous recombination (HR). Because these proteins are hyperthermophilic, <i>Pyrococcus</i> sp. expresses	2.44 kGy ( $D_{37}$ )	Hogrel <i>et al.</i> , 2020

	them constitutively rather than as a result of DNA damage.		
<i>Rubrobacter radiotolerans</i>	An increased Mn/Fe ratio in <i>R. radiotolerans</i> is linked to a high intracellular concentration of the antioxidant disaccharide trehalose. Carotenoids and manganese superoxide dismutase (Mn-SOD) have also been found to be radioprotective agents in <i>R. radiotolerans</i> .	12 kGy (D <sub>10</sub> )	Egas <i>et al.</i> , 2014; Ranawat and Rawat, 2020
<i>Rubrobacter xylanophilus</i>	An increased Mn/Fe ratio is linked to <i>R. xylanophilus</i> high intracellular content of the antioxidant disaccharide trehalose. However, a unique glyceryl diglycoside is present in the thermophilic and extremely radioresistant <i>R. xylanophilus</i> .	10 kGy (D <sub>10</sub> )	Lamosa <i>et al.</i> , 2015
<i>Thermococcus gammatolerans</i>	Rather of being caused by a wide variety of recognised DNA repair enzymes, its great radiotolerance is probably caused by unidentified proteins. Proteins that protect anaerobic processes from oxygen inhibition are encoded by certain genes. Two peroxiredoxins and thioredoxin reductase, a glutaredoxin-like protein, also aid in the archaeon's ability to regulate oxidative stress.	30 kGy	Webb and DiRuggiero, 2012; Ranawat and Rawat, 2017



## 5.0 RADIORESISTANT BACTERIA IN BIOREMEDIATION

Bioremediation is the process of eliminating environmental contaminants, especially heavy metals, from soil, water, air, and industrial effluents. This can be done in both natural and artificial environments, using any type of biological resource such as fungi, bacteria, algae, and even dead plants to remove these pollutants. Researchers have been using biological systems to clean contaminated environments in recent years due to the organisms' capacity to absorb, collect, and degrade both common and emergent contaminants (Jin *et al.*, 2019; Lopez and Fernandez *et al.*, 2020).

Using a variety of techniques, bacteria are essential to the bioremediation of radioactive pollutants, helping to remove them from the environment. According to Banerjee *et al.* (2024), there are three processes utilised in this bioremediation process that can be broadly classified into three strategies:

1. Precipitation and enrichment beyond cells
2. Conversion via precipitation or intracellular adsorption
3. Transformation through precipitation or adsorption on the cell surface.

Bacteria aid in the cleanup and restoration of damaged environments by reducing and immobilising radioactive pollutants through these mechanisms.

Considering *Deinococcus* sp. has a high tolerance for absorbing radionuclide ions and the ability to degrade them, it appears to be more effective than other microbes at cleaning up radioactive pollution. According to Chauhan *et al.* (2017), a *Deinococcus*DR1 strain that was isolated from freshwater shown resistance to radiation and arsenic. It possesses genes for *arsB*, *arsR*, and arsenate reductase in addition to heavy metal translocation P-type ATPase, heavy metal transport/detoxification proteins, and heavy metal-related domain proteins. These all support its proactive defence against radiation and arsenic. Furthermore, the research of Orellana *et al.* (2018), showed that *D. radiodurans* was genetically modified to perform bioremediation of heavy metals and persistent organic pollutants. It was found that strains of *Deinococcus perariditoris* isolated from arid desert soil in the northern region of Antofagasta (Chile), exhibited a stronger resistance to IR than strain R1, a model *Deinococcus radiodurans* strain. *Deinococcus* sp. were recognised for bioremediation of radioactive wastes and ecosystems because of their inherent resilience to high radiation levels (Orellana *et al.*, 2018).

A unique Gram-negative bacterium from the dry Taklamakan desert was found by Luo *et al.* (2014); it has a strong resistance to radiation and the heavy metal lead (Pb). This bacterial strain was named *Microvirga aerilata* LM (=CCTCC AB 208311) after phylogenetic and phenotypic studies revealed that it was closely related to *Microvirga aerilata*. It was discovered that *M. aerilata* LM could efficiently accumulate Pb and create intracellular precipitates. Also, it maintains a comparable capacity to eliminate Pb<sup>2+</sup> in radioactive stress. According to the data, *M. aerilata* LM could provide a safe, efficient, and *in situ* method for removing soluble lead pollutants from radioactive waste.

It was also reported that to remove trace cobalt from spent decontamination solutions of nuclear power reactors using bioremoval, Gogada *et al.* (2015) genetically modified *D. radiodurans* R1 with NiCoT genes. Because of its long half-life and strong gamma-energy values, radioactive cobalt (<sup>60</sup>Co) is recognised to be a key contributor to person-sievert budgetary in his work. It has been shown that certain bacterial Ni/Co transporter (NiCoT) genes have a preference for absorbing cobalt. The *groESL* promoter was used in the study to clone the NiCoT genes *nxIA* and *nvoA* from *Novosphingobium aromaticivorans* F-199 (NA) and *Rhodospseudomonas palustris* CGA009 (RP), respectively. Because *D. radiodurans* has a higher radiation resistance than other bacterial strains, several genes were expressed in it. The study demonstrated that cobalt and nickel stimulated the expression of NiCoT-RP and NiCoT-NA using qualitative real-time PCR. In the presence of >10 mM Fe, Cr, and Ni, the functional expression of genes in bioengineered *D. radiodurans* R1 strains led to >60% removal of <sup>60</sup>Co (≥5.1 nM) after 90 min from simulated wasted decontamination solution containing 8.5 nM of Co. In comparison to recombinant *E. coli* (ARY023) expressing NiCoT-RP and NA, *D. radiodurans* R1 (DR-RP and DR-NA) demonstrated improved survival and efficiency in co-remediation up to 6.4 kGy.

Recombinant *D. radiodurans* was employed by Manobala *et al.* (2019) for the bioremediation of radioactive wastes that include uranium. *D. radiodurans* has been modified to increase the effectiveness of its uranium removal, demonstrating its promise for the cleanup of radioactive waste. The effectiveness of a recombinant *D. radiodurans* (DR1-bf<sup>+</sup>) strain that can form biofilm for uranium cleanup was examined in this study. The uranium concentration was estimated using the modified Arsenazo III dye technique. Aqueous uranyl nitrate solution was produced during reprocessing nuclear fuel. The uranyl ion removal capacity of the *D. radiodurans* biofilm (DR1-bf<sup>+</sup>) cultivated in the presence of 20 mM Ca<sup>2+</sup> was impressive. Thirty minutes after treatment, the DR1-bf<sup>+</sup> (+Ca<sup>2+</sup>) biofilm extracted about 75±2% of the 1000 mg/L of uranium from the uranyl nitrate aqueous solution.

Furthermore, it has been discovered that the c-type cytochrome-producing bacteria *Geobacter sulfurreducens* converts soluble uranium radioisotopes into insoluble ones (Nayak *et al.*, 2021). However, Marques, 2018 found that successful *in situ*-based bioremediation was achieved due to the increase in *Geobacter* sp. activity brought about by bio-stimulation with acetate enrichment, which also shown enhancement in

uranium reduction. Likewise, Shukla et al. (2019) discovered two novel bacteria from radionuclide-containing soil: *Providencia vermicola* AM3 and *Ochrobactrum* sp. AM7. These bacteria have been found to have potential use in bioremediation of radionuclide-containing waste seeing that they are also radioresistant.

---

## 6.0 CONCLUSION

This study has explored the multifaceted nature of radiation, a phenomenon that plays a critical role across a wide spectrum of contexts, from biological systems to cosmic phenomena. Radiation, classified into particle and electromagnetic types, exerts a profound influence on living organisms and the environment, with ionizing radiation posing significant risks, including DNA damage, acute radiation sickness, and elevated cancer risk.

The exceptional resilience of radioresistant bacteria, particularly *Deinococcus radiodurans*, has been highlighted as a key area of interest in understanding cellular defense mechanisms against ionizing radiation. These bacteria exhibit sophisticated DNA repair systems, robust antioxidant defenses, and effective cellular damage management strategies, enabling them to withstand and recover from substantial molecular damage induced by radiation. This study has underscored the potential of these microorganisms in various biotechnological applications, including bioremediation, where their ability to detoxify environments contaminated with radioactive substances could be harnessed for environmental cleanup. Furthermore, their unique properties make them valuable in the field of radiation therapy, where insights from these bacteria could inspire new approaches to managing radiation exposure and improving treatment outcomes.

The findings of this research contribute to a deeper understanding of microbial resilience to extreme conditions, expanding our knowledge of radiation biology and offering promising avenues for innovative applications in environmental science, biotechnology, and medical research. The remarkable ability of radioresistant bacteria to survive and thrive in high-radiation environments not only enhances our comprehension of life in extreme conditions but also opens up new possibilities for leveraging their properties in addressing some of the most pressing challenges associated with radiation exposure and contamination.

## REFERENCES

- Alimba, C. G., Adewumi, O. O., Binuyo, O. M., and Odeigah, P. G. (2021). Wild black rats (*Rattus rattus* Linnaeus, 1758) as zoomonitor of genotoxicity and systemic toxicity induced by hazardous emissions from Abule Egba unsanitary landfill, Lagos, Nigeria. *Environmental Science and Pollution Research*, 28, 10603-10621.
- Appukkuttan, D., Seo, H. S., Jeong, S., Im, S., Joe, M., Song, D., and Lim, S. (2015). Expression and mutational analysis of DinB-like protein DR0053 in *Deinococcus radiodurans*. *PLoS One*, 10(2), e0118275.
- Arjomandi, Z., Salehzadeh, A., and Mirzaie, A. (2018). Isolation and characterization of two novel radiation-resistant bacteria from a radioactive site in Iran. *Iranian Journal of Science and Technology, Transactions A: Science*, 42, 1007-1013.
- Asgarani, E., Soudi, M. R., Borzooee, F., and Dabbagh, R. (2012). Radio-resistance in psychrotrophic *Kocuria* sp. ASB 107 isolated from Ab-e-Siah radioactive spring. *Journal of environmental radioactivity*, 113, 171-176.
- Averbeck, D., Candéias, S., Chandna, S., Foray, N., Friedl, A. A., Haghdoost, S., and Sabatier, L. (2020). Establishing mechanisms affecting the individual response to ionizing radiation. *International Journal of Radiation Biology*, 96(3), 297-323.
- Bagwell, C. E., Bhat, S., Hawkins, G. M., Smith, B. W., Biswas, T., Hoover, T. R., and Shimkets, L. J. (2008). Survival in nuclear waste, extreme resistance, and potential applications gleaned from the genome sequence of *Kineococcus radiotolerans* SRS30216. *PloS one*, 3(12), e3878.
- Banerjee, S., Gupta, N., Pramanik, K., Gope, M., GhoshThakur, R., Karmakar, A., and Balachandran, S. (2024). Microbes and microbial strategies in carcinogenic polycyclic aromatic hydrocarbons remediation: a systematic review. *Environmental Science and Pollution Research*, 31(2), 1811-1840.
- Bratkic, A., Jazbec, A., Toplak, N., Koren, S., Lojen, S., Tinta, T., and Snoj, L. (2024). The colonization of an irradiated environment: the case of microbial biofilm in a nuclear reactor. *International journal of radiation biology*, 100(1), 108-121.
- Bruckbauer, S. T., and Cox, M. M. (2021). Experimental evolution of extremophile resistance to ionizing radiation. *Trends in Genetics*, 37(9), 830-845.
- Bruckbauer, S. T., Trimarco, J. D., Martin, J., Bushnell, B., Senn, K. A., Schackwitz, W., and Cox, M. M. (2019). Experimental evolution of extreme resistance to ionizing radiation in *Escherichia coli* after 50 cycles of selection. *Journal of bacteriology*, 201(8), 10-1128.

- Byrne, R. T., Klingele, A. J., Cabot, E. L., Schackwitz, W. S., Martin, J. A., Martin, J., and Cox, M. M. (2014). Evolution of extreme resistance to ionizing radiation via genetic adaptation of DNA repair. *Elife*, 3, e01322.
- Chatterjee, N., and Walker, G. C. (2017). Mechanisms of DNA damage, repair, and mutagenesis. *Environmental and molecular mutagenesis*, 58(5), 235-263.
- Chauhan, D., Srivastava, P. A., Yennamalli, R. M., and Priyadarshini, R. (2017). Draft genome sequence of *Deinococcus indicus* DR1, a novel strain isolated from a freshwater wetland. *Genome Announcements*, 5(31), 10-1128.
- Cho, C., Lee, D., Jeong, D., Kim, S., Kim, M. K., and Srinivasan, S. (2023). Characterization of radiation-resistance mechanism in *Spirosoma montaniterrae* DY10 T in terms of transcriptional regulatory system. *Scientific Reports*, 13(1), 4739.
- Consigliari, E., Xu, Q. Z., Zhao, K. H., Gärtner, W., and Losi, A. (2020). The first molecular characterisation of blue- and red-light photoreceptors from *Methylobacterium radiotolerans*. *Physical Chemistry Chemical Physics*, 22(22), 12434-12446.
- Egas, C., Barroso, C., Froufe, H. J. C., Pacheco, J., Albuquerque, L., and da Costa, M. S. (2014). Complete genome sequence of the radiation-resistant bacterium *Rubrobacter radiotolerans* RSPS-4. *Standards in Genomic Sciences*, 9, 1062-1075.
- Filipek, J., Chalaskiewicz, K., Kosmider, A., Nielipinski, M., Michalak, A., Bednarkiewicz, M., and Pietrzyk-Brzezinska, A. J. (2024). Comprehensive structural overview of the C-terminal ligand-binding domains of the TetR family regulators. *Journal of Structural Biology*, 108071.
- Gao, Y., Li, N., Zhou, Y., Zhang, Z., Zhang, Y., Fan, P., and Xu, P. (2022). iTRAQ-based proteomic analysis of *Deinococcus radiodurans* in response to 12C6+ heavy ion irradiation. *BMC microbiology*, 22(1), 264.
- Gholami, M., Etemadifar, Z., and Bouzari, M. (2015). Isolation a new strain of *Kocuria rosea* capable of tolerating extreme conditions. *Journal of environmental radioactivity*, 144, 113-119.
- Ghosh, S., Ramirez-Peralta, A., Gaidamakova, E., Zhang, P., Li, Y. Q., Daly, M. J., and Setlow, P. (2011). Effects of Mn levels on resistance of *Bacillus megaterium* spores to heat, radiation and hydrogen peroxide. *Journal of Applied Microbiology*, 111(3), 663-670.
- Gogada, R., Singh, S. S., Lunavat, S. K., Pamarthi, M. M., Rodrigue, A., Vadivelu, B., and Apte, S. K. (2015). Engineered *Deinococcus radiodurans* R1 with NiCoT genes for bioremoval of trace cobalt from spent decontamination solutions of nuclear power reactors. *Applied microbiology and biotechnology*, 99, 9203-9213.
- Gtari, M., Essoussi, I., Maaoui, R., Sghaier, H., Boujmil, R., Gury, J., and Normand, P. (2012). Contrasted resistance of stone-dwelling Geodermatophilaceae species to stresses known to give rise to reactive oxygen species. *FEMS Microbiology Ecology*, 80(3), 566-577.
- Gupta, P., & Kushwaha, R. (2016). Radiation resistance in bacteria: A paradigm shift towards understanding extreme resistance. *Journal of Bacteriology & Mycology*, 3(2), 108-112.
- Hall, E. J., & Giaccia, A. J. (2022). *Radiobiology for the Radiologist* (8th ed.). Lippincott Williams & Wilkins
- Harris, D. R., Pollock, S. V., Wood, E. A., Goiffon, R. J., Klingele, A. J., Cabot, E. L., and Battista, J. R. (2009). Directed evolution of ionizing radiation resistance in *Escherichia coli*. *Journal of bacteriology*, 191(16), 5240-5252.
- Hogrel, G., Lu, Y., Alexandre, N., Bossé, A., Dulermo, R., Ishino, S., and Flament, D. (2020). Role of RadA and DNA polymerases in recombination-associated DNA synthesis in hyperthermophilic archaea. *Biomolecules*, 10(7), 1045.
- Jha, S. K., Patra, A. C., Verma, G. P., Iyer, I. S., and Aswal, D. K. (2024). Natural Radiation and Environment. In *Handbook on Radiation Environment, Volume 1: Sources, Applications and Policies* (pp. 27-72). Singapore: Springer Nature Singapore.
- Jin, M., Xiao, A., Zhu, L., Zhang, Z., Huang, H., Jiang, L., 2019. The diversity and commonalities of the radiation-resistance mechanisms of *Deinococcus* and its up-to-date applications. *Amb. Express*. <https://doi.org/10.1186/s13568-019-0862-x>.
- Jung, J. H., Yang, H. Y., Jeong, S., Joe, M. H., Cho, Y. J., Kim, M. K., and Lim, S. (2014). Complete genome sequence of *Hymenobacter swuensis*, an ionizing-radiation resistant bacterium isolated from mountain soil. *Journal of Biotechnology*, 178, 65-66.
- Kanekar, P. P., and Kanekar, S. P. (2022). Radiophilic, radioresistant, and radiotolerant microorganisms. In *Diversity and biotechnology of extremophilic microorganisms from India* (pp. 251-267). Singapore: Springer Nature Singapore.
- Karahalil, B. (2016). Overview of systems biology and omics technologies. *Current medicinal chemistry*, 23(37), 4221-4230.

- Karan, R., DasSarma, P., Balcer-Kubiczek, E., Weng, R. R., Liao, C. C., Goodlett, D. R., and DasSarma, S. (2014). Bioengineering radioresistance by overproduction of RPA, a mammalian-type single-stranded DNA-binding protein, in a halophilic archaeon. *Applied microbiology and biotechnology*, 98, 1737-1747.
- Karmaker, N., Maraz, K. M., Islam, F., Haque, M. M., Razzak, M., Mollah, M. Z. I., and Khan, R. A. (2021). Fundamental characteristics and application of radiation. *GSC Advanced Research and Reviews*, 7(1), 064-072.
- Kontomaris, S. V., Malamou, A., Balogiannis, G., and Antonopoulou, N. (2019). A simplified approach for presenting the differences between ionising and non-ionising electromagnetic radiation. *Physics Education*, 55(2), 025007.
- Krisko, A., and Radman, M. (2013). Biology of extreme radiation resistance: the way of *Deinococcus radiodurans*. *Cold Spring Harbor perspectives in biology*, 5(7), a012765.
- Kumar, R., Merugu, R., Mohapatra, S., and Sharma, S. (2022). Extremophiles life of microorganisms in extreme environments. In *Extremophiles* (pp. 43-66). CRC Press.
- Lamosa, P., Lourenço, E. C., d'Avó, F., Nobre, A., Bandeiras, T. M., Da Costa, M. S., and Santos, H. (2015). A unique glyceryl diglycoside identified in the thermophilic, radiation-resistant bacterium *Rubrobacter xylanophilus*. *Extremophiles*, 19, 373-382.
- Launay, A. (2016). *Study of the emergence of the diversity of Escherichia coli in vivo by whole genome sequencing* (Doctoral dissertation, Université Pierre et Marie Curie-Paris VI).
- Li, L., Chen, Z., Ding, X., Shan, Z., Liu, L., and Guo, J. (2015). Deep sequencing analysis of the *Kineococcus radiotolerans* transcriptome in response to ionizing radiation. *Microbiological Research*, 170, 248-254.
- Li, S., Shi, L., Lian, W. H., Lin, Z. L., Lu, C. Y., Xu, L., and Li, W. J. (2021). *Arenibaculum pallidiluteum* gen. nov., sp. nov., a novel bacterium in the family *Azospirillaceae*, isolated from desert soil, and reclassification of *Skermanella xinjiangensis* to a new genus *Deserticella* as *Deserticella xinjiangensis* comb. nov., and transfer of the genera *Indioceanicola* and *Oleisolibacter* from the family *Rhodospirillaceae* to the family *Azospirillaceae*. *International Journal of Systematic and Evolutionary Microbiology*, 71(7), 004874.
- Liu, F., Li, N., and Zhang, Y. (2023). The radioresistant and survival mechanisms of *Deinococcus radiodurans*. *Radiation Medicine and Protection*, 4(02), 70-79.
- Liu, M., Dai, J., Liu, Y., Cai, F., Wang, Y., Rahman, E., and Fang, C. (2011). *Desertibacter roseus* gen. nov., sp. nov., a gamma radiation-resistant bacterium in the family *Rhodospirillaceae*, isolated from desert sand. *International journal of systematic and evolutionary microbiology*, 61(5), 1109-1113.
- Liu, Y., Chen, T., Li, J., Wu, M., Liu, G., Zhang, W., and Zhang, G. (2022). High proportions of radiation-resistant strains in Culturable bacteria from the Taklimakan Desert. *Biology*, 11(4), 501.
- Lopez-Fernandez, M., Jroundi, F., Ruiz-Fresneda, M. A., Merroun, M. L., 2020. Minireview Microbial Interaction with and Tolerance of Radionuclides: Underlying Mechanisms and Biotechnological Applications. Wiley Online Libr. <https://doi.org/10.1111/1751-7915.13718>.
- Luo, X., Zeng, X. C., He, Z., Lu, X., Yuan, J., Shi, J., and Wang, Y. X. (2014). Isolation and characterization of a radiation-resistant bacterium from Taklamakan Desert showing potent ability to accumulate Lead (II) and considerable potential for bioremediation of radioactive wastes. *Ecotoxicology*, 23, 1915-1921.
- Manobala, T., Shukla, S. K., Subba Rao, T., and Dharmendra Kumar, M. (2019). A new uranium bioremediation approach using radio-tolerant *Deinococcus radiodurans* biofilm. *Journal of biosciences*, 44, 1-9.
- Marques, C. R. (2018). Extremophilic microfactories: applications in metal and radionuclide bioremediation. *Frontiers in microbiology*, 9, 1191.
- Meyer, L., Coste, G., Sommer, S., Oberto, J., Confalonieri, F., Servant, P., and Pasternak, C. (2018). DdrI, a cAMP receptor protein family member, acts as a major regulator for adaptation of *Deinococcus radiodurans* to various stresses. *Journal of bacteriology*, 200(13), 10-1128.
- Moeller, R., Raguse, M., Reitz, G., Okayasu, R., Li, Z., Klein, S., and Nicholson, W. L. (2014). Resistance of *Bacillus subtilis* spore DNA to lethal ionizing radiation damage relies primarily on spore core components and DNA repair, with minor effects of oxygen radical detoxification. *Applied and Environmental Microbiology*, 80(1), 104-109.
- Montero-Calasanz, M. D. C., Yaramis, A., Nouioui, I., Igual, J. M., Spröer, C., Castro, J. F., and Urzi, C. (2019). *Modestobacter italicus* sp. nov., isolated from Carrara marble quarry and emended descriptions of the genus *Modestobacter* and the species *Modestobacter marinus*, *Modestobacter multiseptatus*, *Modestobacter roseus* and *Modestobacter versicolor*. *International Journal of Systematic and Evolutionary Microbiology*, 69(6), 1537-1545.

- Munteanu, A. C., Uivarosi, V., and Andries, A. (2015). Recent progress in understanding the molecular mechanisms of radioresistance in Deinococcus bacteria. *Extremophiles*, 19, 707-719.
- Nayak, T., Sengupta, I. K. and Dhal, P. 2021; A new era of radiation resistance bacteria in bioremediation and production of bioactive compounds with therapeutic potential and other aspects: An inperspective review; <https://doi.org/10.1016/j.jenvrad.2021.106696>
- Nogueira, F., Botelho, M. L., and Tenreiro, R. (1998). Radioresistance studies in Methylobacterium spp. *Radiation Physics and Chemistry*, 52(1-6), 15-19.
- Normand, P., Gury, J., Pujic, P., Chouaia, B., Crotti, E., Brusetti, L., and Gtari, M. (2012). Genome sequence of radiation-resistant Modestobacter marinus strain BC501, a representative actinobacterium that thrives on calcareous stone surfaces.
- Oladapo, O. O., Oni, O. M., Aremu, A. A., Oyero, O. P., Lawal, M. K., and Dare, O. D. (2020a). Evaluation of Power Density Radiation from Selected Mobile Base Stations in Ogbomoso, South-Western Nigeria. *International Journal of Health Science and Research*, 10(12), 157-162.
- Oladapo, O. O., Oni, O. M., Oni, E. A., Olive-Adelodun, A. O., and Aremu, A. A. (2020b). Determination of Excess Relative Risk of Radon from Residential Buildings in Some Selected Cities in Southwestern, Nigeria. *International Journal of Health Sciences and Research*, 10, 12.
- Oladapo, O. O., Amekudzi, L. K., Oni, O. M., Aremu, A. A., and Osei, M. A. (2020c). Climate Change Impact on Soil Moisture Variability: Health Effects of Radon Flux Density Within Ogbomoso, Nigeria. *African Handbook of Climate Change Adaptation*, 1-16.
- Oliveira, J. A. D. S., Polli, A. D., Ferreira, A. P., Lopes, N. B., Mangolim, C. A., Vicentini, V. E. P., and Azevedo, J. L. Radiotolerant endophytic bacteria and analysis of the effects of <sup>137</sup>Cesium on the metabolome of Pantoea sp. *Brazilian journal of microbiology: [publication of the Brazilian Society for Microbiology]*.
- Orellana, R., Macaya, C., Bravo, G., Dorochesi, F., Cumsille, A., Valencia, R., and Seeger, M. (2018). Living at the frontiers of life: extremophiles in Chile and their potential for bioremediation. *Frontiers in Microbiology*, 9, 2309.
- Oren, A. (2019). Extremophiles and their natural niches on Earth. *Handbook of astrobiology*, 635-660.
- Ott, E., Kawaguchi, Y., Kölbl, D., Chaturvedi, P., Nakagawa, K., Yamagishi, A., and Milojevic, T. (2017). Proteometabolomic response of Deinococcus radiodurans exposed to UVC and vacuum conditions: initial studies prior to the Tanpopo space mission. *PLoS One*, 12(12), e0189381.
- Pal, S., Yuvaraj, R., Krishnan, H., Venkatraman, B., Abraham, J., and Gopinathan, A. (2024). Unraveling radiation resistance strategies in two bacterial strains from the high background radiation area of Chavara-Neendakara: A comprehensive whole genome analysis. *Plos one*, 19(6), e0304810.
- Pavlopoulou, A., Savva, G. D., Louka, M., Bagos, P. G., Vorgias, C. E., Michalopoulos, I., and Georgakilas, A. G. (2016). Unraveling the mechanisms of extreme radioresistance in prokaryotes: lessons from nature. *Mutation Research/Reviews in Mutation Research*, 767, 92-107.
- Ranawat, P., and Rawat, S. (2017). Radiation resistance in thermophiles: mechanisms and applications. *World Journal of Microbiology and Biotechnology*, 33, 1-22.
- Ranawat, P., and Rawat, S. (2020). Radiation-Resistant Thermophiles: From High Temperature and Radiation to Engineered Bioremediation. In *Beneficial Microbes for Sustainable Agriculture and Environmental Management* (pp. 287-318). Apple Academic Press.
- Rettberg, P., Antunes, A., Brucato, J., Cabezas, P., Collins, G., Haddaji, A., and Treuet, J. C. (2019). Biological contamination prevention for outer solar system moons of astrobiological interest: What do we need to know?. *Astrobiology*, 19(8), 951-974.
- Reyes, M. R., Smith, M. A., & Johnson, S. S. (2021). Biotechnological potential of radiation-resistant bacteria in waste management. *Frontiers in Microbiology*, 12, 653254. <https://doi.org/10.3389/fmicb.2021.653254>
- Samarth, R., Kumar, M., Matsumoto, Y., and Manda, K. (2020). The Effects of Ionizing and Non-Ionizing Radiation on Health. *Recent Trends and Advances in Environmental Health*, 179.
- Sharma, A., Gaidamakova, E. K., Grichenko, O., Matrosova, V. Y., Hoeke, V., Klimenkova, P., and Daly, M. J. (2017). Across the tree of life, radiation resistance is governed by antioxidant Mn<sup>2+</sup>, gauged by paramagnetic resonance. *Proceedings of the National Academy of Sciences*, 114(44), E9253-E9260.
- Sharma, A., Gaidamakova, E. K., Matrosova, V. Y., Bennett, B., Daly, M. J., and Hoffman, B. M. (2013). Responses of Mn<sup>2+</sup> speciation in Deinococcus radiodurans and Escherichia coli to  $\gamma$ -radiation by advanced paramagnetic resonance methods. *Proceedings of the National Academy of Sciences*, 110(15), 5945-5950.

- Sharma, P., Salve, P. R., & Chandra, R. (2020). Radioresistant microorganisms and their role in environmental cleanup. *Journal of Environmental Management*, 261, 110271. <https://doi.org/10.1016/j.jenvman.2020.110271>
- Shukla, A., Parmar, P., and Saraf, M. (2017). Radiation, radionuclides and bacteria: An in-perspective review. *Journal of environmental radioactivity*, 180, 27-35.
- Shukla, A., Parmar, P., Saraf, M., and Patel, B. (2019). Isolation and screening of bacteria from radionuclide containing soil for bioremediation of contaminated sites. *Environmental Sustainability*, 2, 255-264.
- Singh, A., Bhagavat, R., Vijayan, M., & Chandra, N. (2016). A comparative analysis of the DNA recombination repair pathway in mycobacterial genomes. *Tuberculosis*, 99, 109-119.
- Slade, D., & Radman, M. (2011). Oxidative stress resistance in *Deinococcus radiodurans*. *Microbiology and Molecular Biology Reviews*, 75(1), 133-191. <https://doi.org/10.1128/MMBR.00015-10>
- Stefanska, A., Gaffke, L., Kaczorowska, A. K., Plotka, M., Dabrowski, S., and Kaczorowski, T. (2016). Highly thermostable RadA protein from the archaeon *Pyrococcus woesei* enhances specificity of simplex and multiplex PCR assays. *Journal of applied genetics*, 57, 239-249.
- Timmins, J., and Moe, E. (2016). A decade of biochemical and structural studies of the DNA repair machinery of *Deinococcus radiodurans*: major findings, functional and mechanistic insight and challenges. *Computational and structural biotechnology journal*, 14, 168-176.
- Torres-Barceló, C., Cabot, G., Oliver, A., Buckling, A., and MacLean, R. C. (2013). A trade-off between oxidative stress resistance and DNA repair plays a role in the evolution of elevated mutation rates in bacteria. *Proceedings of the Royal Society B: Biological Sciences*, 280(1757), 20130007.
- UNSCEAR (2021). Sources, Effects and Risks of Ionizing Radiation: UNSCEAR 2020/2021 Report to the General Assembly, with Scientific Annexes. United Nations Scientific Committee on the Effects of Atomic Radiation. Retrieved from UNSCEAR Official Website.
- Vailati-Riboni, M., Palombo, V., and Loor, J. J. (2017). What are omics sciences?. *Periparturient diseases of dairy cows: a systems biology approach*, 1-7.
- Vlašić, I., Mertens, R., Seco, E. M., Carrasco, B., Ayora, S., Reitz, G., and Moeller, R. (2014). *Bacillus subtilis* RecA and its accessory factors, RecF, RecO, RecR and RecX, are required for spore resistance to DNA double-strand break. *Nucleic acids research*, 42(4), 2295-2307.
- Wang, W., Ma, Y., He, J., Qi, H., Xiao, F., and He, S. (2019). Gene regulation for the extreme resistance to ionizing radiation of *Deinococcus radiodurans*. *Gene*, 715, 144008.
- Wardell, K., Haldenby, S., Jones, N., Liddell, S., Ngo, G. H., and Allers, T. (2017). RadB acts in homologous recombination in the archaeon *Haloferax volcanii*, consistent with a role as recombination mediator. *DNA repair*, 55, 7-16.
- Webb, K. M., and DiRuggiero, J. (2012). Role of Mn<sup>2+</sup> and compatible solutes in the radiation resistance of thermophilic bacteria and archaea. *Archaea*, 2012(1), 845756.
- Williams, E., Lowe, T. M., Savas, J., and DiRuggiero, J. (2007). Microarray analysis of the hyperthermophilic archaeon *Pyrococcus furiosus* exposed to gamma irradiation. *Extremophiles*, 11, 19-29.
- Yan, J., Risacher, S. L., Shen, L., and Saykin, A. J. (2018). Network approaches to systems biology analysis of complex disease: integrative methods for multi-omics data. *Briefings in bioinformatics*, 19(6), 1370-1381.
- Yazdani, M., Naderi-Manesh, H., Khajeh, K., Soudi, M. R., Asghari, S. M., and Sharifzadeh, M. (2009). Isolation and characterization of a novel  $\gamma$ -radiation-resistant bacterium from hot spring in Iran. *Journal of basic microbiology*, 49(1), 119-127.
- Zammuto, V., Fuchs, F. M., Fiebrandt, M., Stapelmann, K., Ulrich, N. J., Maugeri, T. L., and Moeller, R. (2018). Comparing spore resistance of *Bacillus* strains isolated from hydrothermal vents and spacecraft assembly facilities to environmental stressors and decontamination treatments. *Astrobiology*, 18(11), 1425-1434.