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THE SURVIVAL ABILITIES OF DEINOCOCCUS RADIODURANS BACTERIUM

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Abstract

The aim of this review is to highlight the survival abilities of the Deinococcus radiodurans bacterium after it suffers degradation caused by exposure to high levels of ionizing radiation. Ionizing radiation is a type of energy either in wavelength or particle form, able to produce ions by removal of electrons and breaking of chemical bonds and with harmful potential leading to DNA strand breaks and cell death. Deinococcus radiodurans has built up a strong resilience to factors like dehydration and oxidative stress, the imbalance between reactive oxygen species and antioxidants. It relies on a complex defence system comprising of several mechanisms such as: catalase and superoxide dismutase, enzymes capable of breaking down the harmful free radicals; nonenzymatic antioxidants like manganese and carotenoids complexes, among which deinoxanthin is a pigment produced solely by this particular bacterium and transcriptional regulatory proteins - PpRM, IrrE, DdrA-.
This ability to withstand the oxidative stress of the ionizing radiation led to the discovery of a wide range of practical applications such as usage in the medical field, in environmental protection like cleaning toxic and radioactive waste and even prospective use in areas with high levels of radiation like the surface of planet Mars.

Key words*: Deinococcus radiodurans, ionizing radiation, oxidative stress, survival abilities*.

INTRODUCTION

Deinococcus radiodurans is a non-sporulating, non-pathogenic bacterium, with a characteristic pink orange colour and a well-known resistance to ionizing radiation (IR), dehydration and oxidising molecules (Murray, 1986; Murray, 1992; Munteanu et al., 2015). Its optimum growth temperature is 30°C, but it can continue to show increased growth up to 37°C. The development stops at a minimum of 4°C and a maximum temperature of 45°C (Battista, 1997). *Deinococcus radiodurans* was first isolated in 1956 by Arthur (Andy) Anderson and his colleagues at the Oregon Experimental Agricultural Station in Corvallis, Oregon, USA after signs of contamination appeared in a meat can which had been previously subjected to radiation treatment.

IR represents high-energy radiation that produces ions by breaking molecular bonds and by displacement of electrons from atoms, a fact which generates alterations in living cells with both beneficial and harmful effects. Examples include gamma rays and X-rays on the upper end of the electromagnetic spectrum and subatomic particles, like alpha and beta particles. IR can produce reactive oxygen species (ROS) through water radiolysis. These can be classified in 3 groups: hydroxyl radical (OH), hydrogen peroxide (H2O2), and superoxide (O2•-) (Ghosal, 2005). As a main cause of oxidative stress, ROS can either be the results of the metabolic processes or can be produced by exposure to physical or chemical agents like IR, dehydration, ultraviolet radiations, hydrogen peroxide and mitomycin (Ghosal et al., 2005; Potts, 1994; Jurkiewicz and Buettner, 1994; Imlay, 2003; Lown et al., 1978). The free oxygen radicals can cause degradation of DNA, RNA and proteins (Zeng and Ma, 2017).

IR-based sterilization techniques represent a key component in a wide range of sectors of activity, since most bacteria do not survive a 500 Gy irradiation (Daly, 2011; Thornley, 1963). While most bacteria can sustain between 1 and 5 IR-induced double-strand DNA breaks on the haploid genome, *Deinococcus radiodurans* can

survive up to almost 200 such ruptures (Daly and Minton, 1995; Lin et al., 1999).
Additionally, *Deinococcus radiodurans* presents a high resistance to dehydration, exhibiting the ability to survive up to 6 years in a desiccator with a 10% viability (Murray, 1992). Studies showed a connection between the IR resistance and the dehydration resistance, proving that during dehydration, *Deinococcus radiodurans* suffers double-strand DNA breaks (Mattimore and Battista, 1995). Thus, it seems feasible to consider that the special ability to resist IR is an effect of its adaptability to withstand dehydration (Battista, 1997).
This paper gives a brief overview of the possible survival mechanisms, as well as the potential applications of this unique feature that *Deinococcus radiodurans* possesses.

MATERIALS AND METHODS

The present paper represents a scientific literature review from the public domain. The relevant websites consulted were Science direct, Google Scholar, PubMed and Mendeley. In this study, only the research articles from the last few years were consulted. For this review more than 150 papers were accessed, the most relevant to the subject being selected.

RESULTS AND DISCUSSIONS

1. HYPOTHESES ON SURVIVAL MECHANISMS

DNA Protection

Given the critical functions of DNA, one could consider that a robust repair system would play a major role in the IR resistance of *Deinococcus radiodurans* (Qi et al., 2020). However, the ability of *Deinococcus radiodurans* to survive in IR, compared to sensitive organisms, cannot be explained either by unusual methods of DNA protection or by a special protein dedicated to repairing DNA, neither by the large number of genomes or by their alignment and structure (Daly et al., 2009). No specific protein has been identified that would confer *Deinococcus radiodurans* a special ability to survive compared to IR-sensitive bacteria like *Shewanella oneidensis* and *Escherichia coli* and there is no evidence of increased activity of DNA repair proteins such as RecA and PolA in *Deinococcus radiodurans* (Daly et al., 2009; Krisko and Radman, 2010; Slade and Radman, 2011).
It seems that a major factor in the radiation protection of the bacterium is represented by a high capability to neutralize reactive oxygen species generated after irradiation (Daly et al., 2007).
The genome of the bacterium *Deinococcus radiodurans* is not special in terms of resistance to IR. Numerous studies have shown that it is as sensitive to IR as other species (Gerard et al., 2001). Instead, its proteins are better protected against oxidative stress caused by ROS compared to radiation-sensitive species (Daly et al., 2007).

Protein Protection

Walter Dale (1940; 1942; 1943) together with his team were the first to study the effects of IR on vitro purified enzymes in the year 1940. They observed that the enzymes deactivate at a dose smaller than 20 Gy. In addition to this, Dale proved that by adding substrates or other smaller organic compounds like sugars, amino acids or nucleotides to these purified enzymes, their capacity to resist IR grows significantly.
In 2007, Daly and his team emphasized that the level of protein oxidation was different in IR resistant bacteria in comparison to IR sensitive ones. Not only that, their survival was correlated with this level of oxidation.
Following those studies, Daly et al. (2010) pointed out that the oxidation of proteins in radiated cells is not a consequence of the cell's death, but rather it could be the reason behind it.
In a study made in 2020 by Gao et al. concerning the level of *Deinococcus radiodurans* protein overexpression after oxidative stress, it was observed that ribosomal proteins were overexpressed by up to 242(rpsl), 232(rpsR) and 193(rpsT) times than normal. This suggests that a large number of proteins must be resynthesized to replace the essential proteins affected by IR. These discoveries are consistent with other studies highlighting the fact that transcription and translation were induced as a response to cell irradiation, a necessity for the rapid synthesis of proteins and thus, for the replacement of the affected protein. This, in turn, leads to the repair of the cells'

macromolecules (lipids, DNA, etc) (Lipton et al., 2002; Liu et al., 2003; Zhang et al., 2005).
Studies were done that suggest the fact that the whole protein complex of the *Deinococcus radiodurans* bacterium is well protected by the antioxidant system after IR exposure (Agapov and Kulbachinskiy, 2015; Munteanu et al., 2015).

Cellular Wall

Also following the study made by Gao et al. (2020), the transmission electron microscopy results showed that the integrity of the cellular wall suffered because of the oxidative stress caused by exposure of the *Deinococcus radiodurans* bacteria to a concentration of 80 mM H2O2 for 30 minutes.
Other studies indicated that exposure to thermal stress affects the cellular wall in *E. coli* as well as in *Deinococcus radiodurans* (Ji, 2010; Carbonneau et al., 1989; Xue et al., 2019). Following these results, it has been proven that external stress destroys the cellular wall first, after which it affects the physiological activities of the bacteria (Gao et al., 2020).

Antioxidants

Deinococcus radiodurans contains several mechanisms which offer its strong resistance, including sRNA (small RNA), neutralization enzymes of ROS (like the catalase and superoxide dismutase), a system formed from nonenzymatic antioxidants like manganese and carotenoids complexes and also transcriptional regulators like PprM, IrrE, DdrA (Chen et al., 2019).
In 1990, Chou alongside Tan emphasized that resistance against radiation and the oxidative stress of *Deinococcus radiodurans* is due to a high level of catalase (CAT) activity and superoxide dismutase (SOD).
A study compared the activity of SOD and CAT between *Deinococcus radiodurans* and *E. coli*. The result was that SOD presented an activity 6 times bigger and CAT 30 times bigger in *Deinococcus radiodurans* (Wang and Schellhorn, 1995).
In *Deinococcus radiodurans*, three catalases were highlighted: DR1998 (KatE1), DRA0259 (KatE2) and DRA0146. The first two (DR1998 and DRA0259) are expressed continuously in normal conditions (Lipton et al., 2002; Jeong et al., 2016). In *Deinococcus radiodurans*, KetE1 is the most important catalase, having the largest activity of 68.800 U/mg and demonstrating increased efficiency neutralizing the hydrogen peroxide compared to KatE2 and DRA0146 (Jeong et al., 2016; Kobayashi et al., 2006). In the study Gao et al. (2020) made, after exposure to hydrogen peroxide, it was shown that DR1998 was overexpressed by 2.29 times in oxidative stress conditions, suggesting that it would be resistant against oxidative stress in the bacteria. Alongside KerE1, other proteins such as Dps, DdrI and IrrE were also overexpressed. The same study indicated that the rate of survival of *Deinococcus radiodurans* decreased in proportion to the time of exposure. As a result of exposing, it for 30 minutes to the treatment, the rate of survival of the bacteria dropped at 68% compared to the control group.
Depending on the structure of the protein and the metal that can be bound, SOD is cataloged in 3 groups: CuZnSOD (can be bound both to copper and zinc), FeSOD / MnSOD (binds either to iron or manganese) and NiSODO (binds to nickel) (Perry et al., 2010). *Deinococcus radiodurans* contains 2 periplasmic CuZnSOD (DR1546 and DRA0202) and 1 cytoplasmic MnSOD (DR1279). This MnSOD neutralizes superoxides more efficiently compared to the ones from the *E. coli* bacteria because of protonation and the faster release of H2O2 (Abreu et al., 2008). Some studies discovered that MnSOD from *E. coli* and *Deinococcus radiodurans* presents some characteristics which allow latching onto the DNA. This latching could protect the DNA from the effects of oxidative stress and radiation (Dennis et al., 2006; Smolik et al., 2014).
Owing to the fact that superoxides are not capable of traversing the cellular membrane, since they are negatively charged, it is assumed that CuZnSOD (DR1546 and DRA0202) neutralises the superoxides situated at the edge of the cell, thus protecting the bacterium from oxidative stress (Qi et al., 2020).
Regarding the role of carotenoids, deinoxanthin is a carotenoid which exists only in *Deinococcus* (Tian et al., 2009).
A study investigated the sensitivity of a mutant strain, without pigment, of the *Deinococcus radiodurans* bacterium to treatment with H2O2 at a concentration of 50 mM. It was observed

that the mutant bacteria's sensitivity to hydrogen peroxide was 100 times bigger (Carbonneau et al., 1989). Deinoxanthin held a higher rate of hydrogen peroxide elimination compared to xanthophylls and in vitro carotenes (Tian et al., 2009).

The following genes, CrtI (DR0861), CrtB (DR0862) and CrtO (DR0093), were discovered as the main genes that influence the biosynthesis of deinoxanthin's pigment. By eliminating them, the bacteria displayed a higher sensitivity to oxidative stress and became colorless (Zhang et al., 2007). Another study done by Gao et al. (2020) also managed to highlight the fact that CrtI (DR0861) and CrtE (DR1395) were overexpressed by 2.91 and respectively 1.79 times after *Deinococcus radiodurans* bacteria's exposure to H2O2 treatment, suggesting that these play a role in the high resistance to oxidative stress.

PprM protein is a protein that responds to oxidative stress (Jeong et al., 2016). It's elimination in *Deinococcus radiodurans* leads to a higher sensitivity of the bacteria to UV (Jeong et al., 2016). This protein seems to also be responsible for catalase KatE1 regulation in *Deinococcus radiodurans* (Jeong et al., 2016).

In a study made by Zeng and Ma (2017), a mutant variant of *Deinococcus radiodurans*, without the gene responsible for PprM protein's synthesis, was created. This variant was less colored than the wild one. In the experiment, the mutant variant had a smaller light absorption rate compared to the wild strain. This proves that the elimination of the gene responsible for PprM leads to a reduction in the biosynthesis of the deinoxanthin's pigment in *Deinococcus radiodurans*. It was also observed that in the mutant variant the genes responsible for the biosynthesis of the deinoxanthin's pigment CrtI (DR0861), CrtB (DR0862) and CrtO (DR0093), were under-expressed. CrtI (DR0861) had a 0.5 times lower transcription and both CrtB (DR0862) and CrtO (DR0093) 0.4 times lower, compared to the wild variant. Besides these, a gene with a connection in the concentration ratio Mn / Fe, DPS-2 (DRB0092) was also under-expressed, decreasing 0.5 times (Zeng and Ma, 2017; Reon et al., 2012). Exposure to dehydration emphasized the fact that the mutant variant had a lower rate of survival compared to the wild one (Zeng and Ma, 2017). Fluorescence detection showed that the mutant variant suffered ROS accumulation 2 times more than the wild strain (Zeng and Ma, 2017). After exposure to 2.000 Gy radiation, this difference of accumulated ROS increased by 4 times compared to the wild variant (Zeng and Ma, 2017). All these results suggest that PprM may influence the antioxidant abilities of *Deinococcus radiodurans* through the synthesis adjustment of deinoxantin's carotenoid and through metal ions ratio concentration adjustment (Zeng and Ma, 2017).

IrrE protein, sometimes named PprI, was found only in the *Deinococcaceae* and *Thermaceae* bacteria. It is considered that it regulates a lot of the bacteria's reactions to stress like dehydration, IR and oxidative stress (Hua et al., 2003; Bauermeister et al., 2009; Lu et al., 2008). Gao et al. (2020) observed a rise of up to 3.77 times in the overexpression of PprI as a response to oxidative stress. The mutant variant, without PprI, showed a decrease in catalase activities as a response to IR treatment while also displaying an increase in sensitivity to these radiations (Hua et al., 2003). The overexpression in *E. coli* bacteria of the IrrE highlighted a rise in catalase activity and a higher tolerance to salt, osmosis and radiation (Gao et al., 2003; Pan et al., 2009; Zhao et al., 2015; Ma et al., 2011).

DdrI is one of the four receptor proteins of the AMP (Adenosine monophosphate) cycle synthesized by *Deinococcus radiodurans*. Under oxidative stress conditions, it was observed that this protein was overexpressed by up to 6.75 (Gao et al., 2020). A mutant variant, having their DdrI protein removed, exhibited a higher susceptibility to oxidative stress and to thermal shock. This suggests that this protein plays a role in the defensive mechanism against those external factors (Yang et al., 2016; Meyer et al., 2018). Beside this, the mutant variant had a much lower catalase activity both in normal conditions and in oxidative stress conditions (Yang et al., 2016). It was demonstrated that DdrI regulates the transcription of 8 genes: DR1998, DR0349, DR1974, DR1506, DR2531, DR1819, DRA0346 and DR1447 (Yang et al., 2016).

2. APPLICATIONS

The Cleansing Of Uranium

A study used a genetically modified variant of *Deinococcus radiodurans* bacteria (named DR1-bf + in the study) which had the ability to create biofilm, to later be used in the extraction of UO_2^{2+} from uranyl nitrate aqueous solution (Shukla and Rao, 2017; Manobala et al., 2019).
DR1-bf + bacteria, cultivated and raised in a medium enriched with 20 mM Ca2+, exhibited superior abilities of eliminating uranyl ions, having a rate of elimination of 75+-2% from 1000 mg/L uranium in the first 30 minutes of treatment (Manobala et al., 2019). It was also shown that this rate is directly proportional with the biofilm's age (Manobala et al., 2019).

Applications Outside Terrestrial Space

In a 2020 study, a team from the University of Vienna demonstrated that *Deinococcus radiodurans* survived for a long period of time in Earth's lower orbit as long as the electromagnetic radiation to which it was exposed never passed below 200 nm. The radiation spectrum on Mars exceeds the 190 nm threshold, CO2 working as a shield under this limit (Ott et al., 2020). The dehydrated cells managed to survive for one year (Ott et al., 2020).

Other Applications

In 2000, Brim et al. genetically modified a *Deinococcus radiodurans* bacterium to treat a mixture of toxic waste which contained ionic mercury.
In 2014, Misra et al. managed to precipitate uranium from radioactive areas, using a genetically modified strain of *Deinococcus radiodurans.*
In 2019, Li et al. biosynthesized gold and silver nanoparticles using *Deinococcus radiodurans*, with practical applications in the medical, industrial and environmental domains.
In 2020, Weng et al. combined the proteins from *Deinococcus radiodurans* with gold and silver nanoparticles, this mixture later being used to degrade the toxic colorant "Malachite Green".

CONCLUSIONS

This article intended to provide some information regarding the mechanisms that offer *Deinococcus radiodurans* bacterium such a strong resistance to IR and other elements such as dehydration, oxidative stress, thermic shock, mechanisms that by far do not represent the whole arsenal of *Deinococcus radiodurans*. While *Deinococcus radiodurans* does not have a specific protein to help restore or protect genetic information or lipids in its cellular wall, it uses a combination of multiple defence mechanisms to build its resilience. These abilities with practical uses in the medical fields and environmental protection offer *Deinococcus radiodurans* a vast potential, a fact highlighted by its extensive research in recent years.

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