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Correlation Between Resistance to UV Irradiation and the Taxonomic Position of Microorganisms

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UV irradiation is known to cause harmful effects on microorganisms. As a result, microorganisms have developed protection against exposure to harmful UV irradiation. We suggested that resistance to UV might be a specific characteristic of certain genera of microorganisms. So, the aim of the work is to assess whether there is a correlation between UV resistance and the taxonomic position of microorganisms or it is the adaptation of cells to extreme conditions. The study involved 67 strains from extreme ecosystems (phytocenoses and ornithogenic soil of the Antarctic, hypersaline ecosystems of the Crimea and the Dead Sea, the lake Baikal). The sequence of 16S rRNA genes, phylogenetic analysis and UV resistance were performed according to standard procedures. Phylogenetic analysis revealed live representatives of the following genera: *Pseudomonas*, *Serratia*, *Rheinheimera*, *Aeromonas*, *Buttiauxella*, *Brevundimonas*, *Sphingomonas*, *Sphingopyxis*, *Dermacoccus*, *Frondihabitans*, *Microbacterium*, *Rhodococcus*, *Janthinobacterium*, *Arthrobacter*, *Micrococcus*, *Kocuria*, *Sphingobacterium*, *Flavobacterium*, *Chryseobacterium*, *Bacillus*, *Staphylococcus*, *Paenibacillus*, and *Sporosarcina*. Gram-positive bacteria were significantly more resistant to UV irradiation ($LD_{99.99}$ 750–1400 J/m^2). Gram-negative had lower resistance ($LD_{99.99}$ 35–150 J/m^2). Most pigmented strains were more resistant to UV than non-pigmented ones. According to the values of lethal doses of UV irradiation we suggest that investigated microorganisms have effective mechanisms to repair DNA damages. Resistance of microorganisms to UV was not found to be related to the ecological features of their habitat. Thus, there is a correlation between the resistance of microorganisms to UV irradiation and their taxonomic position, which allows considering UV resistance as a diagnostic feature at the genus level.

Keywords: UV irradiation, resistance, phylogenetic analysis, taxonomic position.

Introduction

The investigation of ultraviolet radiation influence on microorganisms is becoming an increasingly relevant topic of research today. It is related with the growing anthropogenic impact on the atmosphere. It leads to the destruction of the ozone layer protecting the Earth from the harmful effects of ultraviolet. Ultraviolet radiation on the Earth's surface is noted to be increased from about 5% to 20% (depending on latitude) by the end of the 21st century (Zepp et al., 2011). Such intensity may affect a significant part of living organisms having a great ecological importance in biochemical cycles.

It is known that UV radiation is one of the most harmful abiotic factors. UV rays cause various physiological effects depending on the spectrum and dose of radiation. They adversely affect all living organisms, including bacteria, damaging such vital biomolecules as proteins, lipids and DNA (Ayala et al., 2014; Gabani, et al., 2013; Santos et al., 2013; Wynn-Williams et al., 2002). Therefore, microorganisms, especially from extreme ecosystems, have developed various mechanisms of protection against damage caused by UV radiation. Protection of bacteria from UV irradiation includes UV protective pigments (Dieser et al., 2010; Fernandez et al., 2006), effective reparation mechanisms to recover DNA damage induced by UV rapidly (Arrieta et al., 2000), and active protection against UV-induced oxidative stress (Chen et al., 2009). The ability of microorganisms to survive at high levels of UV irradiation is associated with the stability of their genome (Goosen et al., 2008; Singh et al., 2011). Bacteria resistant to UV radiation have been reported (Singh et al., 2011; Gabani et al., 2014) to be capable to produce the metabolites of the primary and secondary metabolism for their protection. According to the literature (Sinha et al., 1998), cyanobacteria have developed mechanisms for counteraction to UV radiation.

Some bacteria are adapted to survive under the pressure of UV irradiation. The molecular mechanisms helping microorganisms to adapt in the natural environment are not discovered yet. However, the so-called hypothetical mechanism has been proposed to provide the survival of radiation-sensitive extremophiles (Singh et al., 2011).

The UV irradiation is known to be able to act as an independent factor as well as in the combination with other environmental factors. Extreme ecosystems that we studied are characterized by a combination of abiotic factors. Thus, the Antarctic is recognized as the extreme geographically isolated region with low temperature, multiple freezing and thawing and wet-dry cycles, low nutrient levels, dehydration and high levels of solar UV radiation caused as the result of the destruction of the ozone layer in the atmosphere of the region (Adlam et al., 2010, Arrieta et al., 2000; Wynn-Williams et al., 1990). Hypersaline ponds occurring in all climatic zones on different continents also belong to the extreme regions on the planet (Grant et al., 2004). Hypersaline ecosystems of the Dead Sea and the Crimea are primarily characterized by high temperature, saltiness and high levels of UV radiation.

So, it is necessary to investigate the diversity of ultraviolet radiation resistant microorganisms from such environments in order to study in future the physiological mechanisms providing survival of microorganisms under the pressure of ultraviolet radiation (Gabani et al., 2014). We did not find data on the UV resistance of microorganisms of investigated ecosystems in the literature available for us. Moreover, there was no information about the correlation between the UV resistance and the taxonomic position of the microorganisms of any biotopes.

So, the aim of the work is to assess whether UV resistance of microorganisms correlates with their taxonomic position or it is the adaptation of cells to extreme conditions.

Previously, the investigation of resistance (or sensitivity) to UV radiation of microorganisms isolated from different extreme regions showed that this factor was not always associated with the level of solar (or other short-wave) radiation in their natural habitats (Romanovskaya et al., 2013; Romanovskaya et al., 2014; Vasileva-Tonkova et al., 2014). We have suggested the UV radiation resistance to be the characteristic of certain genera of microorganisms (or taxa of another level). Previously we have studied UV resistance of microorganisms from various extreme ecosystems and regions (phytocenoses and ornithogenic soil of the Antarctic) (Romanovskaya et al., 2014; Vasileva-Tonkova et al., 2014), hypersaline basins of the Crimea and biotopes of the Dead Sea (Romanovskaya et al., 2013), phytocenoses and soil of the 10-km zone of the Chernobyl nuclear power plant contaminated by radiation after the disaster in 1986 (Romanovskaya et al., 1999). So, the current work continues our research in the field of microbial UV-resistance.

Methods

Aerobic chemoorganotrophic microorganisms described earlier (Romanovskaya et al., 2013; Romanovskaya et al., 2014; Vasileva-Tonkova et al., 2014) were investigated. They were isolated at 1–5°C or 30°C from phytocenoses and ornithogenic soil of the Western Antarctic, the hypersaline ecosystems of the Dead Sea and the therapeutic mineralized mud lakes of the Crimea (isolated at 42ºC). Also, some part of strains was presented to us by our colleagues from the Limnological Institute of the Siberian Branch of the Russian Academy of Sciences. These strains were isolated from the low-temperature region of shallow water biofilms formed on the plates of rocks and from deep (500–1400 m) ecosystems of the lake Baikal. The investigated strains are stored in the collection of the department of biology of extremophilic microorganisms of the Zabolotny Institute of Microbiology and Virology of the National Academy of Sciences of Ukraine.

Strains isolated from the Antarctic and hypersaline ecosystems were cultivated on Nutrient Agar (NA) medium (HiMedia Laboratories Pvt. Ltd.) or meat-peptone agar medium (MPA) and glucose-potato agar medium (GPA). The standard agarized medium R-2A (agar Fluka Analytical, code: 17209) was used for cultivation of the Baikal strains. To suppress the growth of filamentous fungi, nystatin was added to the media at the concentration 50 mg/L. Psychrotolerant microorganisms were cultivated at the temperature of 18–20°C, mesophilic microorganisms at 30°C, and thermotolerant microorganisms at 42°C.

Phylogenetic affiliation of bacterial isolates was determined by 16S rRNA gene sequence analyses. Purification and sequencing of rDNA PCR products were performed by Macrogen Inc. (South Korea). The small-subunit rRNA gene was amplified from the extracted DNA using universal bacterial primers specific to 16S rRNA gene 27L (5´–3´: AGAGTTTGATCATGGCTCAG) and 1542R (5´–3´: CAKAAAGGAGGTGATCC) (Belkova, 2009) as described previously (Romanovskaya et al., 2014; Romanovskaya et al., 2014a; Vasileva-Tonkova et al., 2014). Obtained sequences of bacterial isolates were compared with sequences deposited in GenBank database at [http://blast.ncbi.nlm.nih.gov/Blast.cgi] using BLAST search analysis to determine their closest relatives and phylogenetic affiliation. Phylogenetic position was determined by construction of the tree showing the taxonomic position of the studied strains among closely related and typical species (program ClustalX 2.1, Mega v. 6.00). Phylogenetic analyses of gene sequence data were conducted using the neighbor-joining (NJ) method. The reliability of internal branches was assessed from 1000 bootstrap pseudoreplicates.

The UV-resistance (UV-*C*) of microorganisms was determined as described previously (Romanovskaya et al., 2013; Romanovskaya et al., 2014a). UV irradiation of microorganisms was carried out using BUF-15 lamp, λ = 254 nm. The exposure time was from 1 to 40 min (40–1600 J/m^2). The dose of irradiation (J/m^2) was determined using a DAU-81 dosimeter. To quantify microbial UV-resistance the lethal dose of UV was calculated. The UV dose that causes the death of 99,99% cells (LD$_{99.99}$) was calculated.

The experiments were carried out in triplicate. The obtained data were processed statistically applying Microsoft Office Excel software package. The reliability of the results of the studies was assessed according to the Student's t-test, taking the differences as statistically significant at the level of $p \leq 0.05$.

Results and Discussion

Phylogenetic analysis based on 16S rRNA gene sequencing revealed the affiliation of bacterial isolates from the extreme regions to the following family: *Micrococcaceae, Nocardiaceae, Dermacoccaceae, Microbacteriaceae, Pseudomonadaceae, Xanthomonadaceae, Enterobacteriaceae, Chromatiaceae, Aeromonadaceae, Caulobacteraceae, Sphingomonadaceae, Alcaligenaceae, Oxalobacteraceae, Sphingobacteriaceae, Flavobacteriaceae, Bacillaceae, Staphylococcaceae, Paenibacillaceae, Planococcaceae.*

The taxonomic position of bacterial isolates was established by phylogenetic analysis using the 16S rRNA gene sequence. Pigmented and/or spore-forming strains were identified among the isolated bacteria.

Table 1 shows the results regarding the sensitivity of bacteria from extreme biotopes (the Antarctic, hypersaline ecosystems of the Crimea and the Dead Sea, the lake Baikal) to UV as well as their determined taxonomic position. UV resistance inherent to isolates from extreme biotopes with enhanced insolation, etc. was not also excluded. It helped to determine whether there is a correlation between the resistance of microorganisms to UV radiation and their taxonomic position (Table 1).

Table 1. *Bacteria isolated from extreme biotopes and their resistance to UV ($LD_{99.99}$)*

Family of microorganisms	Species, strain	Region of isolation	UV, $LD_{99.99}$ J/m^2
Phylum *Actinobacteria*			
Micrococcaceae	*Arthrobacter scleromae* 28r5g	Antarctic	240
	Micrococcus luteus O-1		220
	Rothia sp. O-11		300
	Kocuria sp. 3A	Lake Baikal, shallow water	600
	Micrococcus sp. 3, 11		200–280
Nocardiaceae	*Rhodococcus fascians* 181n3	Antarctic	280
	Rhodococcus sp. 3, 16	Lake Baikal, 500 m	180–280
Dermacoccaceae	*Dermacoccus profundi* U9	Antarctic	600
Microbacteriaceae	*Frondihabitans* sp. 4r5, 5r5, 40r5, U11	Antarctic	110–120
	Microbacterium trichothecenolyticum O-3		165
	Microbacterium foliorum O-6		320
	Microbacterium sp. 10	Lake Baikal, 500 m	180
Phylum *Proteobacteria* (class *Gammaproteobacteria*)			
Pseudomonadaceae	*Pseudomonas mandelii* U1	Antarctic	80
	Pseudomonas fluorescens R3, R5		115–130
	Pseudomonas sp. 4, 6A	Lake Baikal, shallow water	50–80
	Pseudomonas sp. 38	Lake Baikal, 500 m	70
Xanthomonadaceae	*Stenotrophomonas rhizophila* U10	Antarctic	190
Enterobacteriaceae	*Serratia* sp. 6r1g	Antarctic	70
	Serratia sp. 1A, 10	Lake Baikal, shallow water	35–50
	Serratia sp. 9	Lake Baikal, 500 m	135
	Buttiauxella sp. 21m		65
Chromatiaceae	*Rheinheimera* sp. 61		110
Aeromonadaceae	*Aeromonas* sp. 15m		40
Phylum *Proteobacteria* (class *Alphaproteobacteria*)			
Caulobacteraceae	*Brevundimonas vesicularis* O-8	Antarctic	200
	Brevundimonas sp. 37, 43, 47	Lake Baikal, 500 m	100–140
Sphingomonadaceae	*Sphingomonas* sp. 21		120
	Sphingopyxis sp. 45		90
Phylum *Proteobacteria* (class *Betaproteobacteria*)			
Alcaligenaceae	*Achromobacter* sp. 49	Lake Baikal, 500 m	160
Oxalobacteraceae	*Janthinobacterium* sp. 33m		70
Phyla *Bacteroidetes*			
Sphingobacteriaceae	*Sphingobacterium anhuiense* U3	Antarctic	260

Family of microorganisms	Species, strain	Region of isolation	UV, $LD_{99.99}$ J/m^2
Flavobacteriaceae	*Flavobacterium* sp. 38m	Lake Baikal, 500 m	280
	Chryseobacterium sp. 61m		80
Phylum *Firmicutes*			
Bacillaceae	*Bacillus licheniformis* 7t1	Hypersaline environments of the Crimea and the Dead Sea	1500
	B. subtilis subsp. *subtilis* 7t3		1100
	B. subtilis subsp. *spizizenii* R1		1300
	Bacillus simplex 1t4, 3s2		800–1400
	Bacillus mojavensis R6		1200
	Bacillus sp. 1t2, 1t5, 6t2		1200–1250
	Bacillus sp. 2A, 2B, 3B, 5B, 2C, 8, 9,12A	Lake Baikal, shallow water	420–1000
	Bacillus sp. 44	Lake Baikal, 500 m	800
Staphylococcaceae	*Staphylococcus* sp. 6t1	Dead Sea	400
	Staphylococcus sp. O-10	Antarctic	300
Paenibacillaceae	*Paenibacillus* sp. 5A, 7, 12B	Lake Baikal, shallow water	400–720
Planococcaceae	*Sporosarcina aquimarina* O-7, O-9	Antarctic	480–540

Note. $p \leq 0.05$

The majority of bacteria of Antarctic phytocoenoses and soils were resistant to UV. The results showed that the lethal dose of UV ($LD_{99.99}$) for most bacterial strains was in the range ~200–500 J/m^2. The exception was bacteria *Pseudomonas mandelii* U1, *P. fluorescens* R3 and R5, *Serratia* sp. 6r1g, *Frondihabitans* sp. U11, 4r5, 5r5, 40r5. Apparently, it is due to the fact that classical representatives of *Pseudomonas*, as well as other proteobacteria, are sensitive to UV ($LD_{99.99}$ usually is in the range 40–100 J/m^2) (Romanovskaya et al., 2011). The strains isolated from the black moss on the southern side of the vertical cliffs (rocks), *Sporosarcina aquimarina* O-7 and O-9, were the most resistant to UV among the Antarctic bacteria (480–540 J/m^2) (Belkova, 2009).

Since the ecosystems of the Dead Sea and the Crimea are almost always open to the Sun, the UV resistant bacteria are to be present there. All studied bacteria showed resistance to UV radiation (Romanovskaya et al., 2002). The lethal dose of UV ($LD_{99.99}$) for strains of the spore-forming genus *Bacillus* was 750–1500 J/m^2; for *Staphylococcus* sp. 6t1 (does not form spores) – 400 J/m^2.

Analyzing the effect of UV irradiation on the survival of spore-forming bacteria we suggested that the damage minimization under UV radiation could be provided by spore formation. For instance, spores of *Bacillus subtilus* are protected by a thin protein layer from the damaging effect of UV-B and UV-C and solar UV. Layer-free mutants were very sensitive to these factors (Romanovskaya et al., 2014b). Spores of *Bacillus subtilus* contain DNA-bound protein protecting spore DNA from the brakes induced by UV or desiccation (Riesenmann et al., 2000).

Microbial spores are shown to be highly resistant to a wide variety of physical stresses such as: wet and dry heat, UV and gamma radiation, oxidizing agents, chemicals, and extremes of both vacuum and ultrahigh hydrostatic pressure (Nicholson et al., 2002). According to the results of biochemical, genetic and molecular biological studies, molecular models have been developed that describe the spores of bacteria and vegetative *B. subtilis* cells resistant to action of bactericidal agents such as ultraviolet radiation, heat, and oxidative damage (Gerhardt et al., 1989; Nicholson et al., 2000).

Under natural conditions, the Baikal strains are not exposed to solar radiation due to the peculiarities of their habitats. Therefore, these isolates could be assumed to be sensitive to UV radiation. However, comparing the lethal UV doses for the Baikal strains isolated from biofilms formed on rocks, most of them turned out to be resistant to high UV doses. First of all, there were the strains of genera: *Bacillus* and *Paenibacillus* ($LD_{99.99}$ was 400–1000 J/m^2), able to form spores in ungodly conditions. Representatives of *Actinobacteria* (strains *Kocuria* and *Micrococcus*) were also resistant to UV ($LD_{99.99}$ was 200–600 J/m^2). Gram-negative bacteria *Serratia* sp. and *Pseudomonas* sp. were sensitive to UV irradiation. The $LD_{99.99}$ was 35–80 J/m^2 for them.

It was suggested that gram-positive bacteria are better suited to ultraviolet irradiation, since their cell walls swallow a significant portion of UV radiation (Jagger, 1985), which coincides with our results.

Also, the influence of UV on the survival of bacteria from the deep (500–1400 m) ecosystems of the lake Baikal (water, sediments and cochlea *Gastropoda*) was studied. Investigated strains are not exposed to UV radiation in natural conditions due to the deep location in the lake Baikal. Therefore, these strains could be assumed to be sensitive to UV radiation. However, when determining the lethal doses of UV for the studied strains, some of them were shown to be resistant to high doses of UV. The bacterial strain *Bacillus* sp. 44 was highly resistant to UV irradiation. It is consistent with the general trend of bacilli to UV resistance as it was previously shown for bacilli isolated from biofilms formed on rocks plates. Also, *Flavobacterium* sp. and *Rhodococcus* sp. were resistant to UV. The $LD_{99.99}$ for them was 280 J/m^2. Gram-negative bacteria of genera *Brevundimonas*, *Achromobacter*, *Rheinheimera* (phylum *Proteobacteria*) were sensitive to UV. $LD_{99.99}$ UV for them varied within 100–160 J/m^2. No differences relative to UV resistance were found between the strains isolated at different depths of water (from 500 m to 1400 m).

What mechanism of UV resistance is realized by microorganisms isolated from the deep zones of the lake Baikal and from biofilms formed on plates of rocks? There are several mechanisms of UV resistance inherent in all organisms: the presence of pigments that minimize cell damage, sporulation, photoreparation and mechanisms of dark reparation of DNA damages (Arrieta et al., 2000; Dieser et al., 2010; Fernandez et al., 2006). Isolated Baikal strains that differ in the level of UV resistance (genera: *Serratia*, *Pseudomonas*, *Kocuria*, *Bacillus* and *Paenibacillus*) are unpigmented and, therefore, they have no mechanisms to minimize cell damage due to pigments (melanines, carotenoides, etc.). We eliminated the photoreparation process, since UV irradiation and further incubation of irradiated microorganisms were carried out in the darkness. The presence of effective systems of dark reparation of DNA damage in cells is the most important to repair DNA damages occurring due to various types of radiation, including solar short-wave UV radiation. The high UV resistance of some Baikal isolates suggests them to have active systems of dark reparation of DNA damages. Considering that Baikal microorganisms are constantly under stress in natural environment, their high adaptive potential allows them to actively launch various mechanisms to survive, expressed in effective DNA reparation as well as in the ability to quickly launch sporulation processes.

So, during the investigation, the attention was drawn to the following regularities revealed when 67 isolates from the studied biotopes were compared (Table 1):

- Gram-positive bacteria (genera: *Kocuria*, *Microbacterium*, *Arthrobacter*, *Paenibacillus* and *Bacillus*) are more resistant to UV than Gram-negative (genera: *Serratia*, *Pseudomonas*, etc.); therefore, resistance may depend on the composition of the cell wall;
- spore forms (genera *Bacillus* and *Paenibacillus*) have significantly higher UV resistance than non-sporulating ones; apparently, the survival strategy of spore-forming bacteria under the UV radiation (DNA-damaging factor) is provided both by the mechanism that minimizes DNA damages (the presence of spores) and the effective mechanisms of DNA damages reparation;
- most pigmented microorganisms (genera: *Microbacterium*, *Arthrobacter*, *Rhodococcus* and others) have higher UV resistance than unpigmented microorganisms; thus, resistance to short-wave radiation (in particular, to ultraviolet radiation) can be caused by the presence of spores or pigmentation, that is, external protection of cells from radiation and by the presence of effective mechanisms of DNA damages reparation;
- resistance of microorganisms to UV was not found to be related to the ecological features of their habitat; the exception is hypersaline reservoirs (lakes of the Crimea and the coast of the Dead Sea), where mainly spore-forming unpigmented strains of *Bacillus* were detected.

Basing on the results obtained, it can be considered that there is a correlation between the resistance of microorganisms to UV and their taxonomic position, but not their habitat. The collected data were evidenced by the several independent investigations. Thus, Agogue et al. (2005) reported that no relationship was found between the sensitivity of the isolates to solar radiation and the habitat from which they had been isolated (i.e., surface microlayer or underwater). That is, in surface microlayers and groundwater, radiation resistance is well distributed among bacteria. No correlation was found between the sample depth in the Chesapeake Bay (Bailey et al., 1983). Also, studying samples in the northern Adriatic Sea marine snow (from a 10- to 20-m depth), the top 0 to 2 mm of the sandy sediment (≈ 25-m depth) and ambient water (from a 10- to 20-m depth), no direct correlation was found between the ultraviolet sensitivity of the isolates and the isolation point (Arrieta et al., 2000). The number of UV-resistant subsurface and surface soil bacterial isolates was shown to be similar (31% and 26%, respectively) (Arrage et al., 1993). Thus, the investigated literature data and our results confirm that the resistance or sensitivity of microorganisms to UV radiation is not related to the ecological features of their habitat.

Thus, all isolates of *Proteobacteria* represented by genera *Serratia*, *Pseudomonas*, *Buttiauxella*, *Brevundimonas*, *Sphingomonas*, *Janthinobacterium* were UV-sensitive, regardless of the biotopes of their isolation. Most isolates of *Actinobacteria* were resistant to UV (genera: *Microbacterium*, *Rhodococcus*, *Arthrobacter*, *Kocuria*). At the same time, all strains of *Frondihabitans* (as well as *Actinobacteria*, *Micrococcaceae* family) were sensitive to UV. Consequently, there are both highly resistant (genus *Kocuria*) and UV-sensitive bacteria (genus *Frondihabitans*) among the one family. Both resistant (genera: *Flavobacterium*, *Sphingobacterium*) and UV-sensitive bacteria (genus *Chryseobacterium*) were detected among isolated strains of *Bacteroidetes*. Only highly resistant genera *Bacillus*, *Paenibacillus* and *Sporosarcina* were found among the *Firmicutes.*

Conclusions

Taking into account that there is a correlation between the resistance of microorganisms to UV and their affiliation to some taxon, UV resistance can be a diagnostic sign of bacteria at the level of genus and some higher taxa. Estimating the overall results, we can assume that resistance or sensitivity to UV is genetically fixed in the representatives of various taxa of microorganisms.

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