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Abstract

Luminous marine bacteria are widely used as a bioassay with luminescence intensity being a physiological parameter tested. The purpose of the study was to determine whether bacterial genetic alteration is responsible for bioluminescence kinetics change under low-dose radiation exposure. Alpha-emitting radionuclide 241Am and beta-emitting radionuclide 3H were used as sources of low-dose ionizing radiation. Changes of bioluminescence kinetics of Photobacterium Phosphoreum in solutions of 241Am(NO3)3, 7 kBq/L, and tritiated water, 100 MBq/L, were studied; bioluminescence kinetics stages (absence of effect, activation, and inhibition) were determined. Bacterial suspension was sampled at different stages of the bioluminescent kinetics; the doses accumulated by the samples did not exceed 1 Gy, being close to a tentative limit of a low-dose interval. Sequence analysis of 16S ribosomal RNA gene did not reveal a mutagenic effect of low-dose alpha and beta radiation. Previous results on bacterial DNA exposed to low-dose gamma radiation (0.25 Gy) were analyzed and compared to those for alpha and beta irradiation. A conclusion was made that DNA mutations are not associated with bacterial bioluminescence activation and inhibition under the applied conditions of low-dose alpha, beta, and gamma radioactive exposure.

Keywords	low-dose radiation; luminous marine bacteria; bioassay; DNA; mutations
Taxonomy	Environmental Monitoring, Environmental Assessment, Aquatic Ecology
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ABSTRACT

Luminous marine bacteria are widely used as a bioassay with luminescence intensity being a physiological parameter tested. The purpose of the study was to determine whether bacterial genetic alteration is responsible for bioluminescence kinetics change under low-dose radiation exposure. Alpha-emitting radionuclide ^{241}Am and beta-emitting radionuclide ^{3}H were used as sources of low-dose ionizing radiation. Changes of bioluminescence kinetics of *Photobacterium Phosphoreum* in solutions of $^{241}Am(NO_3)_3$, 7 kBq/L, and tritiated water, 100 MBq/L, were studied; bioluminescence kinetics stages (absence of effect, activation, and inhibition) were determined. Bacterial suspension was sampled at different stages of the bioluminescent kinetics; the doses accumulated by the samples did not exceed 1 Gy, being close to a tentative limit of a low-dose interval. Sequence analysis of 16S ribosomal RNA gene did not reveal a mutagenic effect of low-dose alpha and beta radiation. Previous results on bacterial DNA exposed to low-dose gamma radiation (0.25 Gy) were analyzed and compared to those for alpha and beta irradiation. A conclusion was made that DNA mutations are not associated with bacterial bioluminescence activation and inhibition under the applied conditions of low-dose alpha, beta, and gamma radioactive exposure.

Keywords: low-dose radiation, luminous marine bacteria, bioassay, DNA, mutations

Abbreviations:
ROS - Reactive Oxygen Species
HTO – tritiated water

1. Introduction

Recent years have seen a growing interest to low-dose radiation impact on environment related to escalating use of radioactive elements and concern about the increase of background radiation. Moreover, there has been a change in the radiobiological approach: investigations have become primarily targeted at the biota as a whole with a human included as part of it. It explains the attention paid to microorganisms which are essential part of the biosphere. Particularly, their physiological responses to external exposures are widely used for monitoring ecological toxicity including radiation toxicity. This is evident in the case of luminous marine bacteria used as a convenient tool in radiobiological and radioecological investigations. Bioluminescence intensity of the bacteria is the major parameter tested which can be easily measured with simple physics devices. The simplicity of the registration procedure is beneficial because it enables researchers to conduct a large number of experiments under comparable conditions ensuring adequate statistical treatment of the results. For the last decades, bioluminescent bacteria-based assays have been widely applied for toxicity monitoring in water media including the effects of low-dose radiation (Roda et al., 2009; Girotti et al., 2008; Kudryasheva and Tarasova, 2015, Kudryasheva and Rozhko, 2015).

Radiosensitivity of organisms is usually evaluated as a dose-effect relationship, but there is a considerable uncertainty concerning low-dose exposures. Three models exist describing this relationship: linear, threshold, and hormesis models (Kudryasheva and Rozhko, 2015; Burlakova et al., 2004; Calabrese, 2014; Baldwin and Grantham, 2015). The hormesis hypothesis suggests that low-dose radiation can be favorable for living organisms. Probably, the hormesis model could be accepted as the basic one (Shi et al., 2016), while the other two (threshold and linear models) could be considered as simplified derivatives from the former coming into being under certain conditions.

The review by Kudryasheva and Rozhko (2015) summarizes the results of the exposure of luminous marine bacteria to chronic low-intensive ionizing radiation of alpha and beta types. The effects of model solutions of americium-241, uranium-235+238, and tritium were analyzed, nonlinear dose-response dependencies were demonstrated and attributed to the hormesis phenomenon. Three successive stages in bioluminescence response to ionizing radiation were demonstrated: (1) absence of effect (stress recognition), (2) activation (adaptive response), and (3) inhibition (suppression of the physiological function or radiation toxicity). The effects of alpha and beta emitting radionuclides were compared in (Selivanova et al., 2014); different effects were explained with the differences in the Reactive Oxygen Species (ROS) concentration and the efficiency of biochemical redox processes (Alexandrova et al., 2011; Selivanova et al., 2013). Low-dose effects of gamma radiation on luminous bacteria were studied in (Kudryasheva et al., 2017). Gamma-radiation effects differed from the effects of ionizing radiation of alpha and beta types: bacteria demonstrated time/response dependence of threshold type and did not show bioluminescence activation. This peculiarity was explained with lower ionization ability and higher penetrability of electromagnetic gamma radiation. A number of research findings indicate that low-intensive gamma irradiation might induce a mutagenic effect in different organisms (Bolsunovsky et al., 2016; Sykes et al., 2006; Hussain and Ehrenberg, 1979); however, estimated probability of direct interaction of gamma-rays with bacterial cells is very low (Lampe et al., 2016).

The mechanism of bacterial bioluminescence response to low-dose radiation of different types might be related to mutations in bacterial DNA triggered by a series of events, such as water radiolysis, ROS formation, and penetration of elementary particles (electrons, protons, and neutrons) and gamma-quanta into cells. The ability of ROS to interact with DNA directly leading to DNA alteration has been shown in (Kohen and Nyska, 2002). Similar effects are known to be caused by reactive nitrogen (Pauly et al., 2006) and chlorine (Mishra et al., 2016) species.

Alternatively, the results of low-dose exposures might be explained in terms of the novel “exposome” concept, where ‘exposome complements the genome and encompasses the totality of environmental non-genetic exposures’

(Rappaport and Smith, 2010; Wild, 2012). It has been discussed earlier that not only genetic mechanisms but membrane processes can be responsible for radiation induced changes of cellular functions in bacteria (Kudryasheva and Rozhko, 2015). Rozhko et al. (2016) made a conclusion on a 'non-genomic' mechanism of bioluminescence activation by tritium. It was supposed that tritium effects were caused by ionization of aqueous media followed by intensification of cellular membrane processes. Hydrated electrons and ROS were considered to behave as biologically active particles in aerated water solutions.

The paper continues a series of investigations on effects of low-dose radiation of different types on luminous marine bacteria. Alpha and beta emitting radionuclides (americium-241 and tritium, respectively) were used as model radioactive sources. Bacterial bioluminescence kinetics was studied under the conditions of chronic irradiation. To evaluate probability of nonspecific DNA damage in irradiated bacteria, sequence analysis was performed for 16S ribosomal RNA gene responsible for vital functions of bacterial cells (Clarridge, 2004). DNA was isolated from irradiated and control samples of bacteria collected at the stages of bioluminescence activation and inhibition. The findings were compared to the results obtained earlier under similar conditions with low-dose gamma radiation. A conclusion was made on a role of DNA mutations in examined low-dose radiation effects on luminous bacteria.

Materials and methods

Intact luminous marine bacteria *Photobacterium phosphoreum* 1883 IBSO (Kuznetsov et al., 1996) were used as a bioassay to monitor radiotoxicity of aquatic media. The bacteria were obtained from the collection of luminous bacteria at Institute of Biophysics SB RAS, Krasnoyarsk, Russia. Bacteria were cultivated at 22˚C, pH 7.2-7.4 on a semisynthetic nutrient medium (1 L distilled water, 30 g NaCl, 1g KH_2PO_4, 0.5 g $(NH_4)_2HPO_4$, 0.2 g $MgSO_4 \cdot 7H_2O$, 10 g $Na_2HPO_4 \cdot 12H_2O$, 3 g glycine, 5 g peptone).

Bacterial suspensions were exposed to low-dose alpha and beta radiation. A solution of $^{241}Am(NO_3)_3$, and tritiated water, HTO, were used as sources of these radiation types, respectively.

Bioluminescence kinetics of the bacterial samples was studied in 3% NaCl solutions containing $^{241}Am(NO_3)_3$ and HTO of 7 kBq/L and 100 MBq/L activity concentrations, respectively, and in control non-irradiated bacterial samples. All experiments were carried out at 20°C.

Kinetics of the bioluminescence signal of all irradiated and control bacterial samples was registered using CL3606 Biochemiluminometer (SEDD "Nauka", Russia). Bioluminescent intrensity, *I*, was averaged from three parallel experiments with five replicates for all irradiated and control bacterial suspensions. The experimental error did not exceed 3-5%. An example of bioluminescent kinetics is presented in Fig.1.

<Fig.1>

Relative bioluminescent intensity I^{rel} was calculated as

$$I^{rel} = \frac{I_{rad}}{I_{contr}},$$

where:

I_{rad} is bioluminescence intensity in an irradiated bacterial sample; I_{contr} is bioluminescence intensity in a control (non-irradiated) sample measured under similar conditions. The experimental error for I^{rel} did not exceed 10%.

Values of I^{rel} were plotted vs. time of exposure to the radiation.

To isolate the bacterial DNA for sequence analysis, the bacteria suspensions were sampled at different bioluminescence kinetics stages. The time of the exposure of the bacterial samples to radiation was as follows: 50 and

408 h for activation and inhibition stages in $^{241}Am(NO_3)_3$ solutions; 336 and 550 h for activation and inhibition stages in HTO. All bacterial samples for DNA analysis were taken in two replicates.

DNA extraction from bacteria was performed by standard procedures using AxyPrep Bacterial Genomic DNA Miniprep Kit (Rozhko et al., 2016). Possible genetic changes were analyzed in 16S ribosomal RNA gene which was subjected to PCR amplification and to direct sequencing (without cloning) using the Sanger method. Nucleotide sequences of the analyzed 16S rRNA gene obtained from experimental and control bacterial cultures were compared against each other and against the samples from the international databases to identify possible mutations.

To create full-length copies of 16S rRNA gene, a pair of primers was used: sense primer 27F (5′ AGAGTTTGATC**M**TGGCTCAG 3′) and antisense primer 1492RL (5′CCCTACGGTTACCTTGTTACGACTT3′). Primer 1492RL was elongated by adding 6 nucleotides at its 5′end to increase its melting point. The pair of primers used is universal and specific to both Archea and Bacteria. Degenerate versions of primer 27F (A or C at site 12) were synthesized separately (BIOSSET Ltd., Novosibirsk, Russia), then mixed equimolarly. PCR products were separated by electrophoresis on a 1% agarose gel with ethidium bromide (TAE buffer, 10-14 V/cm). Electrophoretograms were analyzed using Gel Doc XR gel documentation system (Bio-Rad). The target DNA fragments were purified using magnetic particles AMPure (Agencourt, Beckmann, CIIIA) (Galkiewicz and Kellogg, 2008).

3. Results and Discussion

Bacterial bioluminescence kinetics was studied under exposure to ionizing radiation in solutions of $^{241}Am(NO_3)_3$ (7 kBq/L) and in tritiated water, HTO (100 MBq/L). Bacteria were sampled for sequence analysis at different stages of the kinetics.

An example of bioluminescence kinetic curves in ^{241}Am solution is presented in Fig.2. Similar to the previous studies (Alexandrova et al., 2011; Rozhko at al., 2007), nonlinearity of bioluminescence response to ^{241}Am is evident from Fig.2; three stages of bioluminescence kinetics are observed: (1) absence of effect (stress recognition), (2) bioluminescence activation (adaptive response), and (3) suppression of the bioluminescence function of the bacteria (toxic effect). Similar responses of organisms to external exposures are usually attributed to the hormesis phenomenon (Kudryasheva and Rozhko, 2015; Burlakova et al., 2004; Calabrese, 2014; Baldwin and Grantham, 2015; Shi et al., 2016).

<Fig.2>

Bioluminescence kinetics in HTO is presented in Fig.3. Similar to alpha-emitting radionuclide ^{241}Am (Fig.1A), the response to beta-emitting radionuclide tritium is not linear too. However, in contrast to ^{241}Am, tritium induced only two stages of the bioluminescence response: absence of the effect (stress recognition) and bioluminescence activation (adaptive response). The third stage (suppression of bioluminescence, i.e. toxic effect) was not found; bioluminescence activation was more pronounced (up to 600%). A two-stage bioluminescence response and effective bioluminescence activation were found in a wide range of HTO activity concentrations from 1 to 100 kBq/L. No dependence of bioluminescent intensity on HTO activity concentration was determined.

<Fig.3>

The previous studies of tritium effects discovered that bioluminescence kinetics of lyophilized preparation of *P.Phosphoreum* was represented with a three (Selivanova et al., 2013; 2014) or two-stage curve (Rozhko et al., 2016), effective activation was reported in (Rozhko et al., 2016). No dependence between the effects of low-dose radiation on activity concentration was also revealed in (Selivanova et al., 2013; Kudryasheva and Rozhko, 2015).

Possible mutagenic effects of different radiation types on bacteria were examined using sequence analysis of 16S ribosomal RNA gene of *P.Phosphoreum*. To determine the effect of alpha radiation emitted by ^{241}Am, bacteria

were sampled at the activation and inhibition stages of the bioluminescence kinetics. The sampling times were T_1=50 hours and T_2=408 hours of incubation with $^{241}Am(NO_3)_3$ as shown in Fig. 2. The doses accumulated by bacterial samples were 0.10 and 0.85 Gy, respectively. In experiments with HTO as a source of beta radiation, samples were taken at T_1=336 hours and T_2=550 hours of exposure (Fig. 3) corresponding to accumulated doses of 0.11 and 0.18 Gy. All doses were close or a little higher than a tentative limit of a low-dose interval (0.1-0.2 Gy) (Goldberg et al., 2006; Matsumoto et al., 2007).

Samples were examined using sequence analysis of the 16S ribosomal RNA gene. Nucleotide sequences of target DNA fragments were determined and compared in bacteria exposed to ^{241}Am or HTO and control bacterial suspension not exposed to radiation. All compared gene sequences were discovered to be identical which does not indicate any occurrences of mutation events in the analyzed gene under the applied conditions of low-dose alpha and beta radiation inducing changes in bacterial luminescence.

Previously, biological effects of low-dose effects of gamma irradiation (≤ 250 mGy) on luminous marine bacteria were studied (Kudryasheva et al., 2017). These irradiation conditions were also shown to induce bioluminescence changes but not a mutagenic effect: sequence analysis of 16S ribosomal RNA gene did not reveal changes in nucleotide sequences of this gene in bacteria subjected to irradiation compared to the control.

Hence, the conclusion could be made that mutagenicity is not responsible for the activation and inhibition effects of alpha, beta, and gamma radiation under the applied conditions of low-dose exposures.

The results of this study might be interpreted by using the novel concept of “exposome”, which complements the genome and encompasses the totality of environmental (i.e. non-genetic) exposures (Rappaport and Smith, 2010; Wild, 2012). Although this term was initially introduced for human exposures, the study of simple model organisms might provide fundamental molecular, physicochemical, biochemical, and cellular bases for human exposure science.

Conclusions

Current paper continues a series of investigations on mechanisms of cellular response to low-dose radioactive exposure, with the luminous marine bacterium as an example of a cell-based bioassay. The purpose of the study was to determine whether the bacterial response to low-dose radioactive exposures could be caused by DNA mutations. Two types of bacterial cell response were under study: activation and inhibition of bacterial luminescence, which were described in terms of hormesis phenomenon and attributed to adaptive and toxic responses, respectively. Alpha and beta emitting radionuclides (americium-241 and tritium, respectively) were applied as model sources of ionizing radiation. Bacteria were sampled at different stages of the bioluminescent kinetics, their DNA was extracted and subjected to sequence analysis. Previous results on the effect of low-dose gamma radiation exposures on bioluminescence kinetics and DNA alteration were discussed. A conclusion was made that under the applied conditions no mutations in the sequence of 16S rRNA gene were associated with biological effects of low-dose radiation of alpha, beta, and gamma types. This result stimulates additional investigation into possible changes in less conservative genes responsible for the structure of vast number of cell enzymes. Another mechanism of biological regulation to be considered is related to cell membrane processes, which can be altered noticeably by the increase of water media ionization and ROS concentration under the conditions of radioactive exposure. This provokes further interest to studying the effect of low-dose radiation on the intracellular processes, such as enzyme activity, ATP mediated energy transfer and specific gene regulation.

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Figure Captions

Fig.1. Bioluminescence intensity, *I*, of *P.phosphoreum* vs. time of exposure: 1 – control sample, (2) in $^{241}Am(NO_3)_3$ solution, 7 kBq/L.

Fig.2. Relative bioluminescence intensity, I^{rel}, of *P.phosphoreum* in $^{241}Am(NO_3)_3$ solution (7 kBq/L) vs. time of exposure. T_1 and T_2 – times of sampling bacteria for genetic sequence analysis.

Fig.3. Relative bioluminescence intensity, I^{rel}, of *P.phosphoreum* in HTO (100 MBq/L) vs. time of exposure. T_1 and T_2 – times of sampling bacteria for genetic sequence analysis.

Fig.1

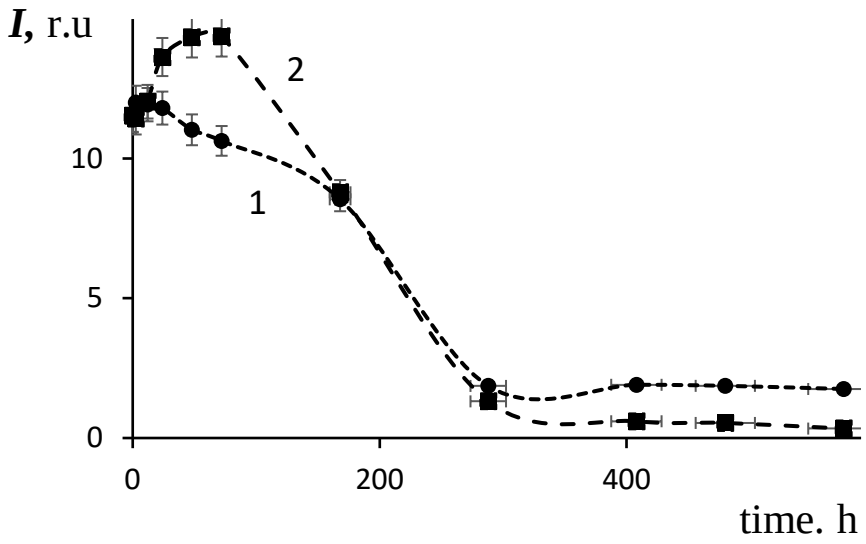


Fig.2

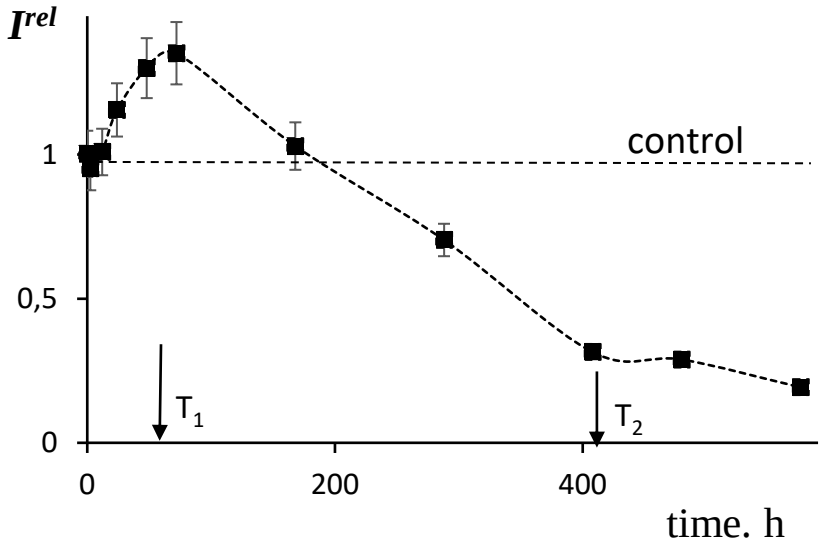
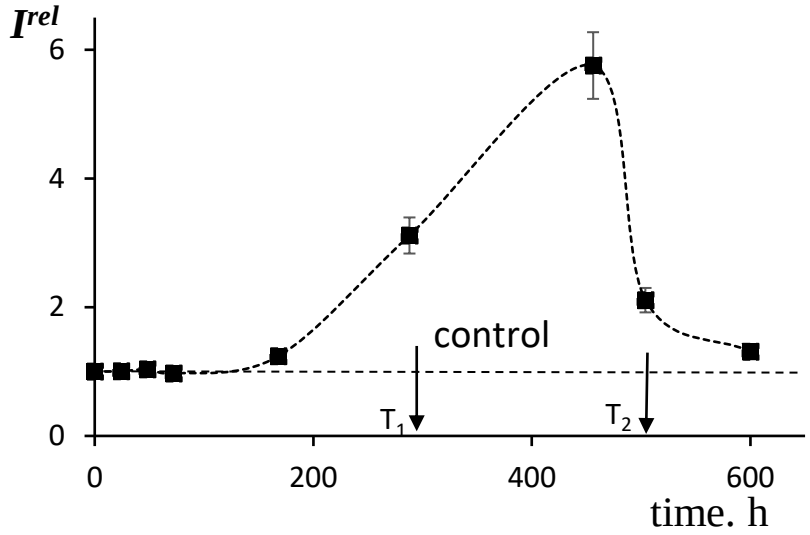


Fig.3



Luminous marine bacterium is proper tool to study mutagenicity of low-dose exposures

Bacterial response to alpha radiation includes activation and inhibition stages

Bacterial response to beta radiation includes activation and inhibition stages

Bacterial response to gamma radiation includes only luminescence inhibition stage

The bacterial low-dose responses are not due to mutations in 16S ribosomal RNA gene

Is bacterial luminescence response to low-dose radiation associated with mutagenicity?

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