ISSN 0026-2617, Microbiology, 2006, Vol. 75, No. 5, pp. 568–574. © Pleiades Publishing, Inc., 2006.
Original Russian Text © O.K. Davydova, D.G. Deryabin, G. I. El'-Registan, 2006, published in Mikrobiologiya, 2006, Vol. 75, No. 5, pp. 654–621.

EXPERIMENTAL ARTICLES

Influence of Chemical Analogues of Microbial Autoregulators on the Sensitivity of DNA to UV Radiation

O. K. Davydova[a], D. G. Deryabin[a,1], and G. I. El'-Registan[b]

[a] *Orenburg State University, pr. Pobedy 13, Orenburg, 460018 Russia*
[b] *Winogradsky Institute of Microbiology, Russian Academy of Sciences, pr. 60-letiya Oktyabrya 7, k. 2, Moscow, 117312 Russia*

Received December 12, 2005

Abstract—We established that chemical analogues of alkylhydroxybenzenes (AHB), belonging to alkylresorcinols and functioning as microbial autoregulatory d_1 factors, enhance the UV resistance of various DNA molecules of different origin and conformation. These include the linear DNA of the λ phage, bovine spleen DNA, and the DNA of the pUC19 plasmid that is composed of a number of annular (supercoiled and relaxed) and linearized molecules. Irradiating DNA with UV light (λ = 254 nm) in the presence of methylresorcinol (MR) or hexylresorcinol (HR) results in comparatively insignificant DNA destruction as evidenced by our data on the electrophoretic mobility pattern in agarose gel. Using the linear *Hin*dIII restricts of the λ phage DNA, we revealed that the protective effect of AHB varies depending on their chemical structure (it is more manifest with HR than MR) and the concentration. Importantly, the effect of HR on bovine spleen DNA was based on its protective activity and manifested itself after a long incubation period. Studies using the pUC19 plasmid demonstrated that AHB, apart from increasing the resistance of linearized DNA molecules to UV irradiation, prevented both the supercoiled annular–supercoiled relaxed and the supercoiled relaxed–linearized transitions. The possible mechanisms of the UV-protective effect of AHB on DNA and their contributions to the resistance of dormant microbial forms to environmental factors are discussed.

DOI: 10.1134/S0026261706050067

Key words: DNA, DNA stabilization, microbial d_1 factors, alkylhydroxybenzenes, UV irradiation, dormant microbial forms.

Ultraviolet (UV) light is of particular importance in terms of microbial ecology because it causes a number of mutagenic and lethal effects in microbial cells [1]. These effects predominantly result from the UV impact on DNA that is characterized by intense absorption within the 240–300 nm range with a maximum at 254 nm. Irradiation causes various kinds of DNA damage. The earliest—and the most widespread—event in UV-irradiated DNA is the formation of pyrimidine dimers from adjacent thymine and cytosine residues [2]. Although the formation of such dimers accounts for 70–80% of the total effect of UV on DNA, they are efficiently removed by the enzyme systems of bacterial cells [3]. Additional UV-dependent DNA damage that is also partially repaired includes photohydration of pyrimidine rings (which only occurs in single-stranded DNA) and the formation of pyrimidine adducts, covalent DNA–protein bonds, and cross-links between contacting DNA duplexes [4]. Increasing UV intensity results in an increased percentage of serious irreparable damage such as the rupture of one or both DNA strand(s). This is accompanied by severe DNA destruction and ultimately causes bacterial cell death.

Dividing vegetative microbial cells are particularly sensitive to UV irradiation, whereas stationary phase and especially anabiotic dormant forms are usually characterized by enhanced photoresistance. High stress resistance is typical of *Bacillus* endospores, although it was also revealed in other kinds of dormant cells including cystlike refractile cells [5, 6]. Since microbial autoregulatory d_1 factors (identified as alkylhydroxybenzenes, AHB in a number of bacteria) significantly contribute to the formation of anabiotic cystlike cells, it is of particular interest to investigate the function of these low molecular weight ligands in the modification of DNA sensitivity to UV irradiation. An additional reason for this study was provided by our earlier in vitro data on direct AHB–DNA interactions resulting in changes in the physical and chemical properties of DNA and its resistance to a number of deleterious factors, including thermal denaturation [7]. We also revealed that some AHB belonging to alkylresorcinols protect enzyme proteins against photodestruction [8]

[1] Corresponding author; e-mail: dgderyabin@yandex.ru

and, at the cell level, protect bacteria and yeasts against temperature shock and photooxidation [9–11].

In the light of the above considerations, the goals of this work were (i) to assess the results of the UV impact on linear and annular DNA molecules, placing special emphasis on detecting severe irreversible damage of these biopolymers and (ii) to resolve the question of whether alkylhydroxybenzenes, chemical analogues of microbial autoregulators can be used as protectors increasing the UV resistance of DNA.

MATERIALS AND METHODS

This study used a number of DNA preparations including λ phage DNA (Sibenzyme, Russia) cut with endonuclease *Hin*dIII into linear fragments with a length of 23130, 9416, 6557, 4361, 2322, 2027, 564, and 125 nucleotide pairs. Another preparation was that of highly polymeric linear DNA isolated from bovine spleen and containing a pool of irregular fragments with lengths from 200 to 25000 bp. The third preparation under study was the DNA of the pUC19 plasmid with a size of 2686 bp (Sibenzyme, Russia) including a group of annular supercoiled, annular relaxed, and linearized molecules.

Methylresorcinol (MR, molecular weight 124) and hexylresorcinol (HR, molecular weight 194) with a purity degree of 99.9% were used as chemical analogues of autoregulatory d_1 factors. Aqueous solutions of individual DNA molecules added at the same concentrations and incubated under the same conditions were used as controls.

In our studies concerning UV irradiation effects, DNA and DNA + AHB samples with a volume of 100 μl were placed in flat-bottomed polystyrene wells and irradiated with a broad-band UV lamp (Osram) at a distance of 5 cm through a 254 nm light filter. The irradiation time was 60, 120, and 180 min.

The DNA and DNA + AHB samples were electrophoretically separated in 0.8% agarose gel in the presence of 0.5 μg/ml ethidium bromide at a current of 100 mA and electrical field strength of 5 V/cm. DNA migration after 2 h of electrophoresis was monitored with a transluminator (Vilber Lourmat, France), and the digital pictures obtained were processed using the ImageJ software package. In total, we conducted three series of studies with three repeats each. The statistical analysis of the data was based on standard mathematical methods and performed using the SPSS for Windows software package.

RESULTS

The electrophoresis of *Hin*dIII restricts of λ phage DNA in agarose gel yielded seven clear-cut bands. Each band contained fragments with fixed molecular weights ranging from 23130 to 564 bp (under the conditions applied, the smallest fragment of 125 bp was located outside of the electrophoretic field) (Fig. 1). Against this background, UV irradiation of this DNA type caused a gradual decrease in the intensity of each of the bands, which gradually become substituted by a single "track" composed of fragments with different molecular weights that displayed an enhanced electrophoretic mobility. Only the "track" without any of the typical bands (Fig.1, trace *2*) was revealed after 3 h of UV irradiation. The immediate cause of this effect was the rupture of both DNA strands at several points, resulting in the separation of each of the molecules into two or more irregular fragments.

Incubating DNA with AHB caused no changes in its electrophoretic mobility, but the sensitivity of the macromolecule to UV irradiation altered even after a short interaction time (during the first incubation week). The effects we revealed attest to the formation of DNA + AHB complexes whose UV resistance varies depending on the concentrations and chemical peculiarities of the AHB involved. Using MR at a concentration of 10^{-4} M failed to produce a protective effect. Increasing its content in irradiated samples to 10^{-3} M (Fig. 1, lane *4*) enabled us to retain, against the background of the merged "track," some of the fragments with molecular weights typical of *Hin*dIII λ phage DNA restricts prior to irradiation. Based on our calculations, up to 62.3 ± 3.0% of the original linear DNA fragments were retained in the presence of 10^{-3} M methylresorcinol after irradiation of phage DNA restricts with UV light for 3 h. DNA complexes with hexylresorcinol that contains a longer alkyl radical were characterized by a more significant resistance to UV irradiation. A considerable protective effect already occurred with 10^{-4} M HR, and using 10^{-3} M HR enabled us to retain up to 82.1 ± 4.7% of the original DNA fragments (Fig. 1, lane *5* and *6*).

In studies with linear bovine spleen DNA, it initially formed a single "track" that consisted of fragments with irregular molecular weights on the electrophoregram. UV irradiation of DNA of this type resulted in a gradual increase in the average electrophoretic mobility of the fragments, which was accompanied by a decrease in the total amount of electrophoretically detectable DNA (Fig. 2). After irradiating the control sample for 60 min, 74.7 ± 3.2% of the original DNA amount in the sample was revealed on the electrophoregram. The DNA content decreased to 56.1 ± 2.2% and 42.2 ± 2.7% after 2 and 3 h of irradiation, respectively. Apart from the separation of the initial DNA fragments into a large number of smaller fragments, this effect could result from complete DNA denaturation caused by UV irradiation.

Monitoring the UV sensitivity of linear DNA + AHB complexes after a short incubation time (four weeks or less) did not reveal any differences between these samples and control systems. However, if the incubation time was increased to more than five weeks, the electrophoretic mobility of DNA + HR complexes

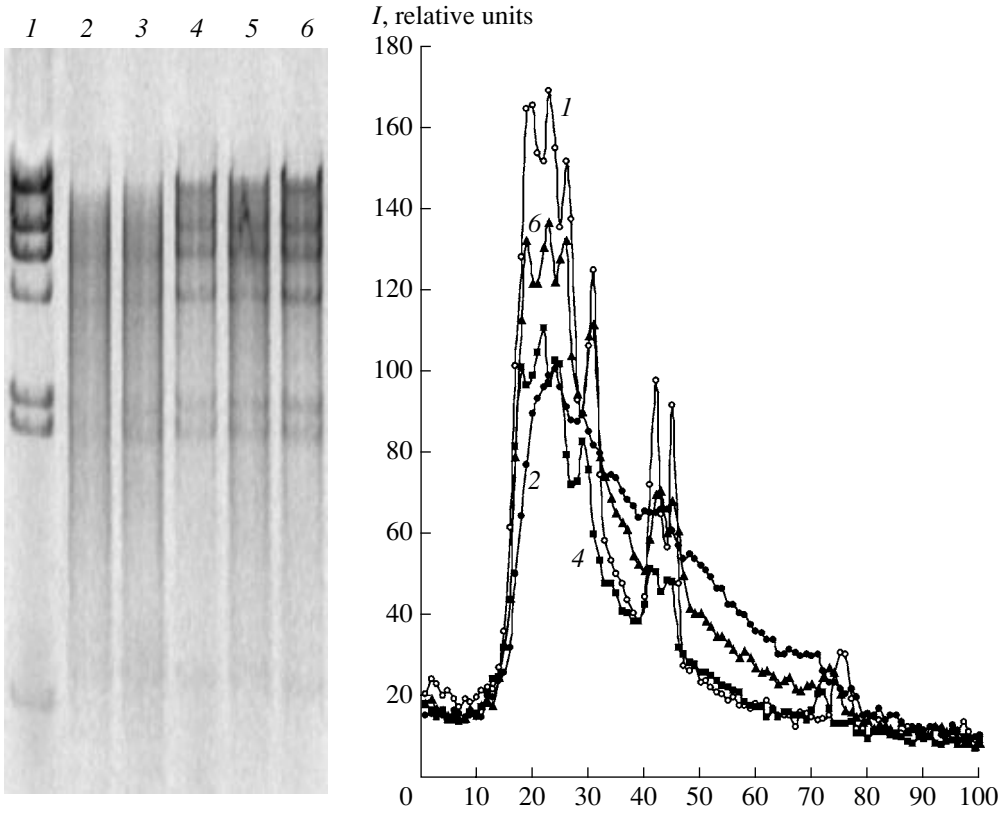

Fig. 1. Electrophoretic mobility of *Hin*dIII restricts of the λ phage DNA after UV irradiation. Left, results of electrophoresis: *1*, control, before irradiation; *2–6*, after 3 h of irradiation; 2, control, after irradiation; *3*, with 10^{-4} M MR; *4*, with 10^{-3} M MR; *5*, with 10^{-4} M HR; *6*, with 10^{-3} M HR. Right, electrophoretic mobility profiles; horizontal axis, distance from the start; vertical axis, band intensity (*I*), relative units.

changed significantly. This manifested itself in a decrease in the distance they covered in the agarose gel during electrophoresis (Fig. 2, lanes *5* and *7*). In addition to DNA stabilization upon complexation with AHB, this phenomenon may be due to the formation of supermolecular structures from AHB molecules on the surface of DNA strands (cf. [7]). These structures may screen the charged groups in the carbohydrate–phosphate structure of the DNA and, therefore, decrease its electrophoretic mobility. The change in the electrophoretic behavior of DNA + HR complexes was accompanied by an increase in their UV resistance: up to 52.8 ± 3.0% of the original DNA amount was retained after irradiation of DNA + HR solutions with an HR concentration of 10^{-4} M for 3 h. Raising the HR concentration to 10^{-3} M (Fig. 2, lane *8*) resulted in an increase in the share of the DNA retained to 61.3 ± 2.7%. Importantly, in our studies with linear DNA from bovine spleen, the decrease in the electrophoretic mobility of DNA + AHB complexes in conjunction with an increase in their UV resistance only occurred in the samples to which hexylresorcinol, not methylresorcinol, was added.

The next series of studies used a pUC19 plasmid DNA preparation that contained three conformationally different DNA variants. They significantly differed in their electrophoretic mobility (Fig. 3, lane *1*) [12]. The variant characterized by the maximum migration distance in agarose gel (band I) was a supercoiled DNA form that accounted for up to 56% of the absolute DNA content in the tested preparation. Annual relaxed DNA molecules were located at the minimum distance from the start (band III). The intermediate band II corresponded to the linearized form with a molecular weight of 2686 bp.

UV irradiation exerted a considerable influence on the electrophoretic properties of the pUC19 plasmid DNA, which manifested itself in the disappearance of the typical bands or a change in their relative intensity and in the appearance of bands characterized by abnormal electrophoretic mobility (Fig. 3, lanes *2–4*). The following effects were revealed. After 1–2 h of irradiation, the typical band I disappeared, with a concomitant (temporary) increase in band III intensity, which resulted from the transition of the supercoiled plasmid DNA form to the relaxed form. Another effect was due to a gradual increase in band II intensity. This was presumably caused by the transition of annular plasmid DNA molecules to the linearized form, owing to the rupture of both DNA strands at one site. In addition, a

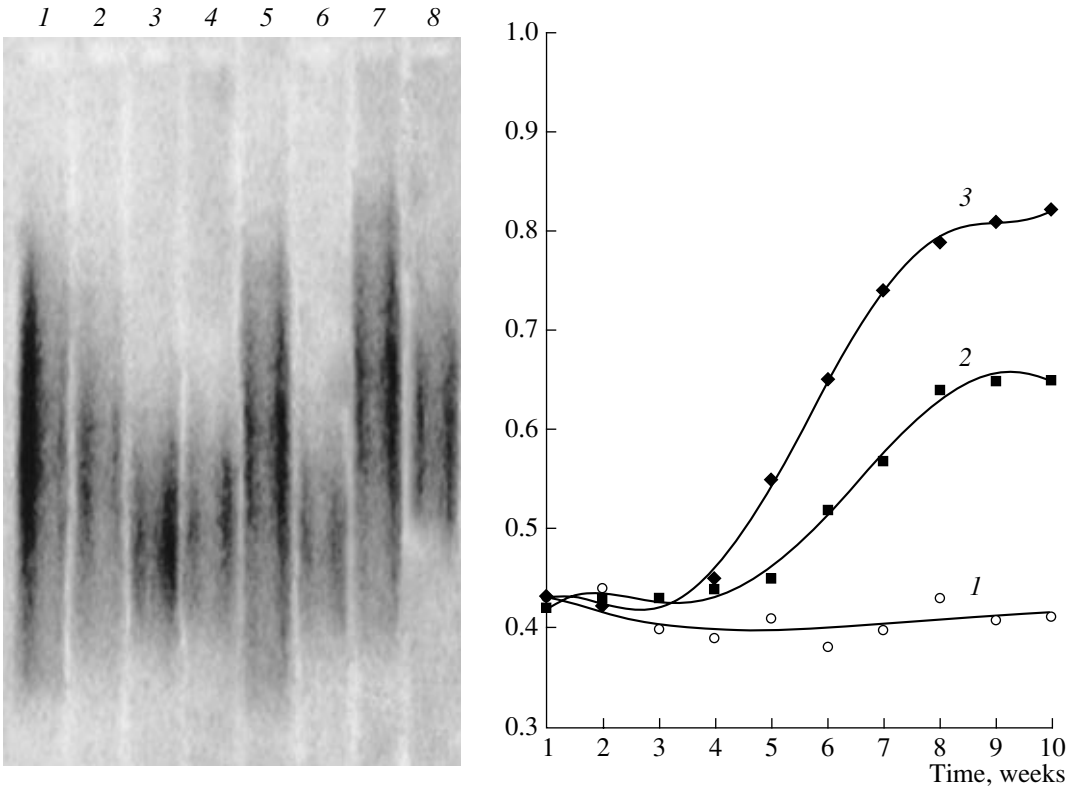

Fig. 2. Electrophoretic mobility of bovine spleen DNA after UV irradiation. Left, results of electrophoresis: *1*, control, before irradiation; *2*, control, after 1 h of UV irradiation; *3*, control, after 2 h of UV irradiation; *4*, control, after 3 h of UV irradiation; *5*, DNA + 10^{-3} M HR, one week of incubation; *6*, the same, after 3 h of irradiation; *7*, DNA + 10^{-3} M HR, six weeks of incubation; *8*, the same, after 3 h of irradiation. Right, the UV resistance level of DNA+HR complexes plotted vs. incubation time. Horizontal axis, incubation time, weeks; vertical axis, relative DNA amount retained after 3 h of irradiation (the original DNA amount corresponded to 1.0 on this scale). (*1*), control DNA samples; (*2*), DNA + 10^{-4} M HR; (*3*), DNA + 10^{-3} M HR.

new band (band IV) with an abnormally low electrophoretic mobility appeared. Presumably, this was due to the formation of cross-links between separate linear DNA duplexes caused by UV irradiation [4]. Evidence for this suggestion was provided by the fact that the calculated size of the DNA that formed band IV was twice the size of the original linearized pUC19 plasmid form (about 5400 bp.). A further increase in UV dose (the irradiation time 3 h) caused serious DNA degradation that manifested itself in the disappearance of bands I, III, and IV and the formation of a single "track" including linear fragments with variable molecular weights; band II was retained (Fig. 3, lane *4*). After 3 h of UV irradiation, the total amount of electrophoretically detectable DNA was 39.9 ± 4.1% of its original content in the sample. Thus, annular DNA forms were characterized by maximum photosensitivity.

Incubating the pUC19 plasmid with AHB did not significantly influence the pattern of changes in the electrophoretic behavior of DNA after 3 h of irradiation. We observed the disappearance of band I and the formation of band IV with an anomalous electrophoretic mobility (Fig. 4, lanes *3–6*). However, the UV resistance of plasmid DNA significantly increased starting from the first week of DNA + AHB complexation. The effects observed after irradiating the complexes for three hours equaled those of 1 h DNA irradiation in control samples (Fig. 3, lane *2*). Importantly, no serious DNA degradation occurred. Using 10^{-4} M AHB after 3 h of UV irradiation enabled us to selectively retain the linearized form located in bands II and IV, where its total content was 1.38 and 1.53 times (for MR and HR, respectively) higher (Fig. 4, lanes *3* and *5*) than in UV-treated samples of unprotected intact DNA.

Increase in the operating AHB concentrations to 10^{-3} M allowed us to retain a certain amount of the annular forms of the pUC19 plasmid (Fig. 4, lanes *4* and *6*) that initially predominated in the control samples. The minimum amount of supercoiled DNA was in band I. The content of electrophoretically detectable DNA in band I after 3 h of UV irradiation was 5.4 ± 1.1% and 10.0 ± 1.7% of its original content with MR and HR, respectively. The share of the relaxed annular DNA form in band III became 1.41 and 1.66 times higher with MR and HR, respectively, than in the control samples prior to irradiation. This may be due to the protective influence of AHB on annular DNA that prevents the rupture of its two strands during UV irradia-

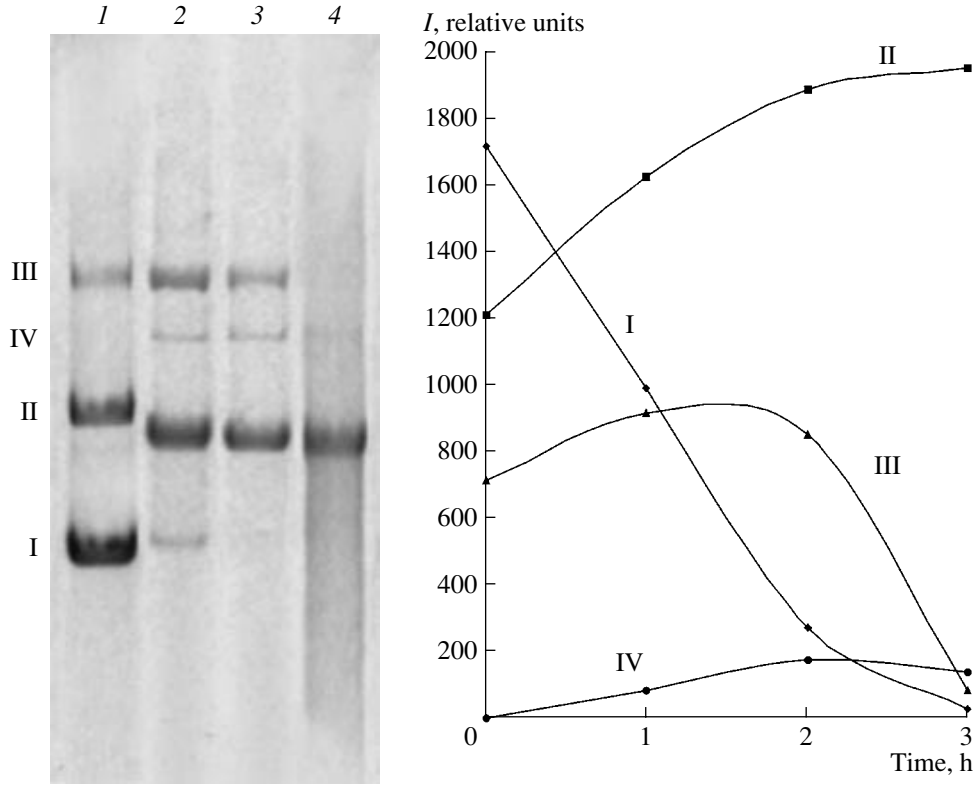

Fig. 3. Changes in the electrophoretic mobility of pUC19 plasmid DNA after UV irradiation. Left, electrophoretic mobility of various plasmid DNA conformers: *1*, control, before irradiation; *2*, after 1 h of irradiation; *3*, after 2 h of irradiation; *4*, after 3 h of irradiation. The make-up of bands I–IV is described in the text. Right, changes in the relative DNA amount in bands I–IV plotted vs. UV irradiation time. Horizontal axis, incubation time; vertical axis, DNA content, relative units.

tion. Apparently, DNA predominantly converts from the supercoiled form into the relaxed annular form under these conditions. On the whole, incubating the pUC19 plasmid with both AHB homologues at concentrations of 10^{-3} M after 3 h of UV irradiation made it possible to retain up to $77.2 \pm 4.6\%$ and $84.0 \pm 6.1\%$ of the original DNA content with MR and HR, respectively. This was 1.95 and 2.11 times higher than the analogous values in UV-irradiated unprotected intact DNA samples (Fig. 4).

DISCUSSION

The results obtained indicate that DNA molecules of different conformations and origins increase their UV resistance in the presence of AHB which prevent their complete degradation. The main characteristics of the protective activity of AHB are: (i) their protective effect develops with time, resulting in the formation of a stable structure of DNA + AHB complexes; (ii) the effect varies depending on the chemical properties of AHB: the homologue with a large hydrophobic alkyl radical exhibits maximum activity; and (iii) the effect is concentration-dependent.

The data obtained significantly contribute to our knowledge of autoregulatory alkylhydroxybenzene $d_1$factors that serve as adaptogens and protectors. They increase the resistance of the molecules they interact with to a wide variety of extreme environmental factors. Based on our results, the protection of DNA against the deleterious effect of UV radiation can be added to the list of known AHB effects, including an increase in the resistance of biopolymers (DNA and proteins) to high temperatures, oxidants, and other destructive factors [8–11, 13–15]. This function of AHB is of considerable importance for the long-term conservation of genetic material in dormant microbial forms. The fact that AHB are widespread not only in microorganisms, but also in plants [15] attaches special importance to their role in the adaptation of organisms to sudden environmental changes and deleterious agents.

What mechanisms may be involved in the UV-protective effect of AHB?

With regard to this question, we should emphasize that the maxima of the absorption spectra of DNA (254 nm) and AHB (277 nm for MR and 280 nm for HR) are fairly close. Due to the partial overlap between the spectra of these substances in the UV range, AHB molecules can form a sort of "optical screen" that traps light quanta moving to a DNA molecule. A secondary effect of trapping quanta is multistage oxidation of

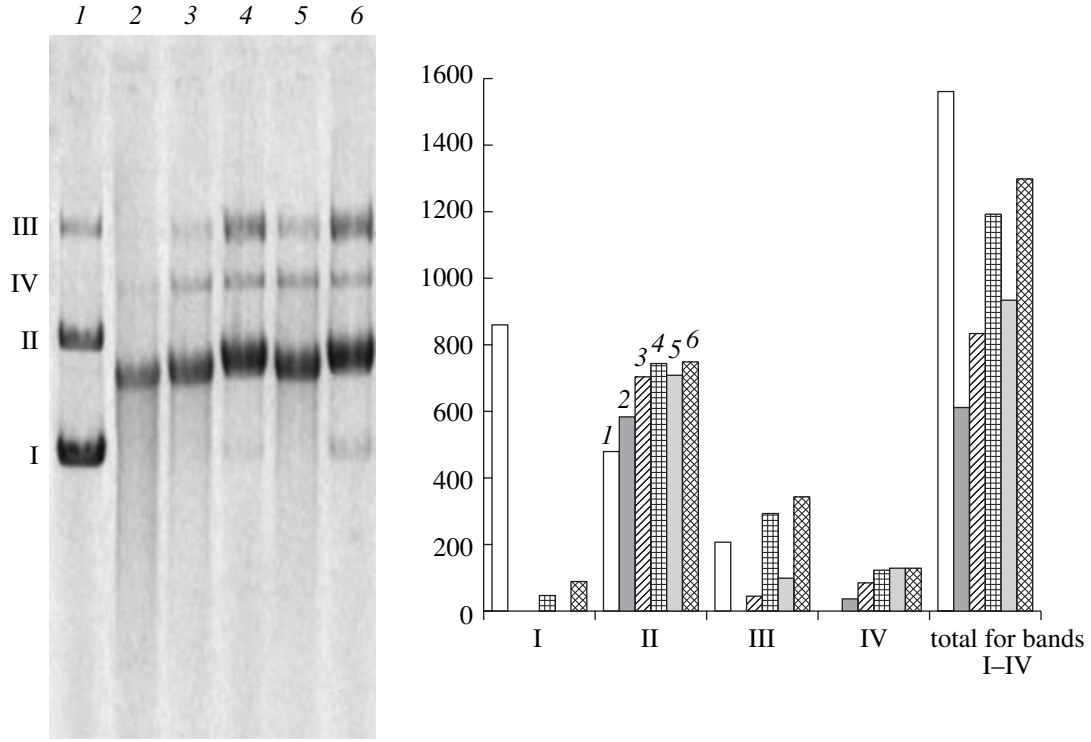

Fig. 4. Electrophoretic mobility of the pUC19 plasmid in the presence of AHB after 3 h of UV irradiation. Left, results of electrophoresis: *1*, control, before irradiation; *2*, control, after 3 h of irradiation; *3*, with 10^{-4} M MR; *4*, with 10^{-3} M MR; *5*, with 10^{-4} M HR; *6*, with 10^{-3} M HR. Right, relative amount of DNA in bands I–IV (vertical axis, relative units).

AHB molecules. The oxidation products have abruption maxima at ca. 500 nm and can form complexes with biopolymers [10, 11, 15, 16]. These considerations account for the dependence of the UV resistance of the DNA on the tested AHB concentration. However, no explanation is provided for the relationship between the protective effect of AHB and the chemical peculiarities of individual homologues, e.g., between the protective effect of AHB and the length of their alkyl radicals.

It seems likely that the second, and the most important cause of the emergence of UV resistance of DNA is its direct interaction with AHB, which we described earlier, based on the changes in some physical and chemical properties of DNA caused by complexation with AHB [7]. The extent of the effects we observed was proportional to the length of the alkyl radicals in the tested AHB molecules.

DNA-unbound AHB molecules, together with their oxidized forms, polymerize and aggregate on the DNA. They form supramolecular micella-like nanostructures that cover the DNA strand like a sheath [17]. As a result, the DNA is insulated from its aqueous microenvironment, which causes a decrease in its electrophoretic mobility (see above). This may potentially affect the UV sensitivity of the DNA. Presumably, DNA dehydration can result in its transition from the B form to the A form. This structural transition occurred in DNA macromolecules that were desiccated in vitro and resulted in a high UV resistance of the DNA [18]. Presumably, this DNA form occurs in bacterial endospores and provides for their enhanced resistance to environmental factors. The processes investigated in this work differ from those described in [18]: a DNA molecule surrounded by appropriately oriented AHB molecules in an aqueous solution is de facto dehydrated. This is a paradoxical example of a "desiccated polymer in an aqueous environment."

Our further research will be aimed at elucidating the molecular mechanisms of UV resistance of DNA in the presence of AHB. This research is of paramount importance in light of a recent article [19] reporting that it is feasible to use some AHB of the alkylresorcinol type as chemical UV protectors.

This work was supported by grant no. A03-12.12-437 from the Russian Ministry of Education for supporting postgraduate students' research, grant no. 04-04-49710 from the Russian Foundation for Basic Research, and the Federal Project on Science and Technology "Research and Development in Top Priority Areas of Science and Technology" (project no. 2006-RI-19.0/001/112).

REFERENCES

1. Gromov, B.V. and Pavlenko, G.V., *Ekologiya Bakterii* (Ecology of Bacteria), Leningrad: Leningr. Univ., 1989.

2. Rubin, A.B., *Biofizika: Biofizika kletochnykh protsessov* (Biophysics: 2. Biophysics of Cell Processes), Moscow: Vysshaya Shkola, 1987.
3. Fraikin, G.Ya., Strakhovskaya, M.G., and Rubin, A.B., Light-Induced Processes of Cell Protection from Photodamage, *Biokhimiya*, 2000, vol. 65, no. 6, pp. 865–875 [*Biochemistry* (Engl. Transl., vol. 65, no. 6, pp. 737–746].
4. Pospisilova, S. and Kypr, J., UV Light-Induced Duplex-To-Duplex Crosslinking of DNA Molecules in Aqueous Ethanol Solutions, *Photochem. Photobiol.*, 1998, vol. 67, no. 4, pp. 386–390.
5. Demkina, E.V., Soina, V.S., El'-Registan, G.I., and Zvyagintsev, D.G., Reproductive Resting Forms of *Arthrobacter globiformis, Mikrobiologiya*, 2000, vol. 69, no. 3, pp. 377–382, [*Microbiology* (Engl. Transl.), vol. 69, no. 3, pp. 309–313].
6. Mulyukin, A.L, Soina, V.S, Demkina, E.V, Kozlova, A.N., Suzina, N.E, Dmitriev, V.V, Duda, V.I, and El-Registan, G.I, Formation of Resting Cells by Non-Spore-Froming Microorganisms as a Strategy of Long-Term Survival in the Environment, Hoover, R.B., Rozanov, A.Yu., and Lipps, J.H., Eds., *Proceedings of SPIE. V. 4939. Instruments, Methods, and Missions for Astrobiology VI*, Bellingham: SPIE, 2003, pp. 208–218.
7. Davydova, O.K., Deryabin, D.G., Nikiyan, A.N., and El'-Registan, G.I., Mechanisms of Interaction between DNA and Chemical Analogues of Microbial Anabiosis Autoinducers, *Mikrobiologiya*, 2005, vol. 74, no. 5, pp. 614–625 [*Microbiology* (Engl. Transl.), vol. 74, no. 5, pp. 533–541].
8. Kolpakov, A.I., Il'inskaya, O.N., Bespalov, M.M., Kupriyanova-Ashina, F.G., Gal'chenko, V.F., Kurganov, B.I., and El'-Registan, G.I., Stabilization of Enzymes by Dormancy Autoinducers as a Possible Mechanism of Resistance of Resting Microbial Forms, *Mikrobiologiya*, 2000, vol. 69, no. 2, pp. 224–230 [*Microbiology* (Engl. Transl.), vol. 69, no. 2, pp.180–185].
9. Stepanenko, I.Yu., Mulyukin, A.L., Kozlova, A.N., Nikolaev, Yu.A., and El'-Registan, G.I., The Role of Alkylhydroxybenzenes in the Adaptation of *Micrococcus luteus* to Heat Shock, 2005, vol. 74, no. 1, pp. 26–33 [*Microbiology* (Engl. Transl.), vol. 74, no. 1, pp. 20–26].
10. Stepanenko, I.Yu., Strakhovskaya, M.G., Belenikina, N.S., Nikolaev, Yu.A., Mulyukin, A.L., Kozlova, A.N., Revina, A.A., and El'-Registan, G.I., Protection of *Saccharomyces cerevisiae* against Oxidative and Radiation-Caused Damage by Alkylhydroxybenzenes, *Mikrobiologiya*, 2004, vol. 73, no. 2, pp. 204–210 [*Microbiology* (Engl. Transl.), vol. 73, no. 2, pp.163–169].
11. El-Registan, G.I., Mulyukin, A.L., Nikolaev, Yu.A., Stepanenko, I.Yu., Kozlova, A.N., Martirosova, E.I., Shanenko, E.F., Strakhovskaya, M.G., and Revina, A.A., The Role of Microbial Low-Molecular-Weight Autoregulatory Factors (Alkylhydroxybenzenes) in Resistance of Microorganisms To Radiation and Heat Shock, *J. Adv. Space Res*, 2005, vol. 36, no. 9, pp. 1718–1728.
12. Scannell, R.T., Barr, J.R., Murty, V.S., Reddy, K.S., and Hecht, S.M., DNA Strand Scission by Naturally Occurring 5-Alkylresorcinols, *J. Am. Chem. Soc.*, 1998, vol. 110, pp. 3650–3651.
13. Martirosova, E.I., Karpekina, T.A., and El'-Registan, G.I., Enzyme Modification by Natural Chemical Chaperons of Microorganisms, *Mikrobiologiya*, 2004, vol. 73, no. 5, pp. 708–715 [*Microbiology* (Engl. Transl.), vol. 73, no. 5, pp. 609–615].
14. Bespalov, M.M., Kolpakov, A.I., Loiko, N.G., Doroshenko, E.V., Mulyukin, A.L., Kozlova, A.N., Varlamova, E.A., Kurganov, B.I., and El'-Registan, G.I., The Role of Microbial Dormancy Autoinducers in Metabolism Blockade, *Mikrobiologiya*, 2000, vol. 69, no. 2, pp. 217–223 [*Microbiology* (Engl. Transl.), vol. 69, no. 2, pp.174–179].
15. Kozubek, A. and Tyman, J.H.P., Resorcinolic Lipids, the Natural Non-Isoprenoid Phenolic Amphiphiles and Their Biological Activity, *Chem. Rev.*, 1999, vol. 99, no. 1, pp. 1–31.
16. Revina, A.A., Larionov, O.G., Kochetova, M.V., Lutsik, T.K., and El'-Registan, G.I., Spectrophotometric and Chromatographic Study of the Products of Radiolysis of Aerated Alkylresorcinol Aqueous Solutions, *Izvestiya AN, Seriya Khimicheskaya*, 2003, vol. 11, pp. 2257–2263.
17. Davydova, O.K., Nikiyan, A.N., and Deryabin, D.G., Formation of Ordered Supramolecular DNA Structures in Aqueous Solutions in the Presence of alkylresorcinols, *Vestnik OGU*, 2005, no. 1, pp. 174–177.
18. Ivanov, V.I. and Minchenkova, L.E., A Form of DNA: in Search of the Biological Role, *Mol. Biol.*, 1994, vol. 28, pp. 1258–1271.
19. Vagel, A. and Roo, E., Alkylresorcinols - Rare Chemicals Available in Bulk, *Innov. Pharm. Tech*, 2004, pp. 94–95.