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Review

ANTARCTIC ALGAE – A MODEL SYSTEM FOR OXIDATIVE STRESS RESISTANCE

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Summary. A considerable reduction in stratospheric ozone concentration above different latitudes due to the increased ultraviolet-B radiation has been reported by NASA experts. The enhanced ultraviolet radiation affects major metabolic processes in living organisms and causes damages to many organic molecules including DNA. Deep understanding of ultraviolet-B rays impact on plants and animals, is a matter of topical significance and is considered to be a wide field for biodiversity and environmental protection investigations. The resistance of algae is connected with the efficiency of their repair system and the stability of cell antioxidant defense. Such kinds of studies are of great significance because of the fact that man and environment plants are forced to live under deteriorating anthropogenic pressure. Many harmful effects accumulate genomic and cell defence system changes that have to be predicted. Much more significant are the growing questions concerning the elucidation of mechanisms underlying resistance to UV, oxidative, light and temperature stresses. Some algae remain vital even at highest UV levels, and for that reason their adaptation is expected to adjust easily to higher radiations that may occur in the future. In this aspect, the use of Antarctic algae as a model system for creation of survival strategies is appropriate due to their ability to survive settling in various ecological niches and thus to become extremely resistant to severe ecological factors impact.

Key words: Antarctic algae; biochemical and molecular markers; oxidative stress; review.

INTRODUCTION

A considerable reduction in stratospheric ozone concentration above different latitudes and especially over the Antarctic has been reported by NASA experts. According to scientific forecasts the ozone level that absorbs the most part of harmful ultraviolet (UV) rays, will continue to deplete during the next two decades. In addition, an enlargement in ozone holes is observed and the future status of atmospheric ozone remains uncertain. The penetration of solar UV-B radiation into Earth's surface puts at a risk its flora and fauna and becomes a global problem. A lot of investigations show dramatic effects of UV radiation

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on plant molecular and morphological structures, as well as on the most important biochemical and physiological processes (Viñegla et al., 2006; Lesser, 2008). The UV-B radiation is known to induce deleterious photochemical reactions in various biomolecules (pigments, proteins, structural changes in DNA molecules, etc.), and to damage photosynthesis, respiration and other cell metabolic processes. Moreover, UV radiation, like ionising radiation, could induce "genome" stress.

From an ecological and agricultural perspective the modified environmental situation could induce new recombination and mutation events, which may affect the genetic variability in populations. "Genome stress" could result in reduced productivity of cultivars, poor quality of production, genome degradation of cultivars and of the dominant species in plant populations. On the other hand, it could be considered as a main cause for increased genetic diversity because the genotype resistance to stress is an important regulating factor for genetic diversity (Hoffmann and Parsons, 1991; Lupu et al., 2006).

Eco-toxicological defence mechanisms operate at a number of levels. In order to understand defence strategies that operate in living cells/organisms it is useful to have multiple model systems for contrast and comparison. Because it is well known that many toxicological defence strategies, which operate in unicellular organisms operate also in higher organisms, the study of simple organized organisms can give important information regarding cell-mediated processes, which have been conserved during the evolution. In unicellular organisms cellular barriers can minimize exposure if damage has occurred. Reproductive potential may be normalized by stress-protein responses, DNA repair mechanisms, and cell-cycle checkpoints or by biochemical/physiological changes that lead to long-term adaptation. Deep understanding of UV-B radiation impact on living organisms and on plants, in particular, is a matter of topical significance and is considered a wide field for biodiversity and environmental protection investigations.

The sensitivity of two Antarctic isolates of the green alga *Ulva* to UV radiation was shown to be influenced by the environmental temperature (Rautenberger and Bischof, 2006). Temperature stress has a devastating effect on plant metabolism, cellular homeostasis, and uncoupling physiological processes (Suzuki and Mittler, 2006). In contrast, based on quantum efficiency measurements on PSII at different temperatures and UV-B radiation Huiskes et al. (2001) have suggested that temperature screens the UV effect on PSII and concluded that such approach application is useless.

The degree of damages caused by UV radiation can also be affected by the amount of photosynthetically active radiation (PAR) used for the pretreatment of algae. Studies on Antarctic terrestrial and planktonic algae showed that the negative effect of UV radiation on their major biochemical and physiological processes can be reduced by previous exposure of algae to visible light, and it depends on the UV-radiation/PAR ratio (Bouchard et al., 2005; Hughes, 2006; Viñegla et al., 2006; Martinez, 2007). On the other hand, exposure of filamentous green algae *Cladophora* and *Enteromorpha* to high intensity PAR provokes oxidative stress, while low temperature in combination with high irradiance creates less oxidative damages (Choo et al., 2004). The lack of consentience on the impact of the UV stress-caused damages when combined with other kinds of stress justifies a wide range of future investigations.

It was established that enhanced UV radiation reduces PS, the quantum yield of PSII fluorescence, and the content of pigments in Antarctic green algae and cyanobacteria (He et al., 2002; Xue et al., 2005; Rautenberger and Bischof, 2006; Lesser, 2008). It was also proved that the maximum photosynthetic activity, the quantum yield, and the pigment content depended on the duration of visible light exposure of the endemic Antarctic alga of genus *Palmaria* (Lüder et al., 2001). At the same time, after exposure of macrophytes from the genera *Ulva* and *Fucus* to visible light only, the PS intensity decreased. However, increased photosynthesis of the same algae was observed under artificial UV-A radiation. It was proposed that the UV/PAR ratio acted as an environmental signal involved in the control of UV photosynthetic inhibition (Viñegla et al., 2006). According to many authors the effects of both UV radiation and the UV/PAR ratio are species-specific, but not identical **(**Choo et al., 2004; Castenholz, 2004; Wong et al., 2007; Zacher et al., 2007a).

The physiological responses of algae subjected to UV radiation are not clarified yet. Besides the harmful effects of UV on PS, respiration, protein and DNA synthesis, and other cell metabolic functions (He et al., 2002; Martinez, 2007; Singh et al., 2009; Gao et al., 2009), there are also data showing an increase in growth, chlorophyll *a* content, carbohydrates and proteins in Antarctic planctonic algae under UV-B radiation conditions. Detailed SDS protein profile confirmed that UV-B radiation led to overproduction of 84-37 kDa proteins, but inhibited the synthesis of 20 and 22 kDa proteins (Rath and Adhikary, 2007). The protein content of Antarctic microalgae from different taxa increased with decreasing temperature of the natural habitat (Teoh et al., 2004)

At present, data are available showing that HSPs can protect cells, tissues and organisms against the damaging action of a wide range of stressful stimuli (Xiao et al., 2002). It has been established that HSPs are molecular chaperons that assist intracellular folding of newly synthesized proteins (Seo et al., 2006). The HSP70 plays a major role in the re-naturation of non-native proteins accumulating under stress conditions and takes part in the regulation of the cellular stress response (Schroda, 2004). HSPs90 participates also in the regulation of the stress response.

Lesser (2008) has proved that UV radiation, and especially UV-B radiation can affect PS in *Anabaena sp.* directly or indirectly through the production of ROS. It was also established that moderate radiation provoked oxidative stress by UV-B induced ROS production (He et al., 2002). ROS play a key role in mediating important signal transduction events in cells subjected to stress. Recent investigations showed the universality of ROS production during different forms of stress (He et al., 2002; Suzuki and Mittler, 2006). The main feature of all types of ROS is to cause oxidative damage of proteins, lipids, photosynthetic pigments and structures in algae under different stress conditions (He et al., 2002; Pitzschke et al., 2006; Breusegem and Dat, 2006).

Recently, special attention has been drawn to UV-induced photo oxidation impairment of DNA structures (Castenholz, 2004; Zacher et al., 2007b; Martinez, 2007; Singh et al., 2009). It was also established that UV-A and UV-B could induce a wide range of oxidative DNA damages, as well as inhibition in DNA replication (He et al., 2002). ROS induce multiple DNA lesions including base damage, single-strand and double-strand breaks (SSB, DSB), DNA-DNA and DNA-protein cross-links (Goldberg and Lehnert, 2002; Marnett et al., 2003; Asad et al., 2004). ROS could damage the cellular proteins and lipids via reactive intermediates, which could also potentially damage DNA (Halliwell and Gutteridge, 2007; Marnett et al., 2003)

According to some researchers ROS, traditionally considered to be toxic, act as signaling molecules to control various physiological processes inducing defence mechanisms (Mittler, 2002; Edreva, 2005; Suzuki and Mittler; 2006; Pitzschke et al., 2006). Their signaling function has been illustrated by data proving the induction of APX-glutathione cycle genes and acclimation phenomena mediated by H_2O_2 production. A third point of view combining the above described is that ROS are primary damage inducers, and in the same time they play a protective role by acting as signaling molecules. In this context, the equilibrium between ROS production and scavenging is extremely important. Particular attention is paid to both the chloroplasts, producing ROS in PSI and PSII centers, and to the ROS – scavenging enzymatic and non-enzymatic antioxidants (Edreva, 2005).

Cell defence mechanisms are directed towards scavenging of oxygen radicals released during UV, oxidative and temperature stresses. One of the main components of ROS protection are the pigments – carotenoids (for green algae and plants) and phycobiliproteins - phycocyanin and phycoerythrin (in cyanobacteria and red algae), acting as non-enzymatic antioxidants, and the antioxidant enzymes superoxidismutase (SOD), catalase (CAT), and peroxidase (PO). It has been proposed that the UV resistance of Antarctic planktonic algae is due most probably to the protective role of algal phycoerythrin (Martinez, 2007) and phycocyanin (Wynn-Williams et al., 2002). The same authors point out that photosynthetic microorganisms of surface planetary habitats have developed survival strategy to cope with existing high UV radiation by changes in their primary (chlorophyll) and accessory (phycocyanin) photosynthetic pigments, and that these pigments are typical biomarkers in the UV screening. Phycobilisomes as structures where phycobiliproteins are synthesized play an important role in photoprotection against UV-B radiation. They are considered to funnel radiant energy preferentially to PSII at wavelengths where chlorophyll *a* does not absorb (Xue et al., 2005; Quesada et al., 2009; Zeeshan et al., 2009). A progressive increase in carotenoid content in the cells of *Lyngbia estuarii* exposed to increased UV radiation was registered as an expression of defence and as a form of a cell repair mechanism (Rath and Adhikary, 2007). UV-B induced stimulation of the synthesis of pigments, α-tocopherol, and the antioxidative potential of methanolic soluble components of *Synechocystis* depending on the mode of irradiation was also found (Marxen et al., 2010). The protection achieved was due to the screening functions of the pigments that scavenge free radicals (Tang and Vincent, 1999; Marxen et al., 2010). Other stress and ROS defence mechanisms are involved via increasing the levels of antioxidant enzymes – SOD, CAT, and PO (Morsy et al., 2007; Martinez, 2007; Singh et al., 2009). These enzymes maintain the membrane integrity in higher plants (Morsy et al, 2007) and increase cell H_2O_2 scavenging activities in algae (Obinger et al., 1998; Choo et al., 2004). On the other hand, the significant increase in SOD activity of *Anabaena sp.* could be a marker for increasing the oxidative stress level in algal cells exposed to UV radiation (Lesser, 2008). According to Rautenberger and Bischof (2006) higher SOD activity is an indication of a higher degree of cold adaptation resulting in higher UV tolerance at 0°C of the green alga *Ulva*. In contrast, studies on the cyanobacterium *Synechococcus sp.* Have shown that FeSOD does not provide protection against severe chilling stress (Thomas et al., 1999). However, further research is necessary to elucidate the role of SOD in plants under stress conditions. It is generally accepted that various stress conditions could activate similar defence mechanisms and the differences in the response result mainly from the different genotype resistance of cells/organisms (Boreham and Mitchel, 1991; Marples and Joiner, 1993; Joiner, 1994; Wolff, 1998; Schlade-Bartusiak et al., 2002; Marples et al., 2004; Tapio and Jacob, 2007). Genotype resistance could be considered as a consequence of a multitude of factors including error-free DSB DNA rejoining, enhanced antioxidant enzyme activities, high content of SH-groups and some pigments – carotenoids and chlorophyll *a*, intact ultra structural cellular components, mitochondrial functions, chromatin structure, cell cycle control, altered DNA damage response, deficient apoptosis, induced damage to proteins and lipids, etc. (Halliwell and Gutteridge, 1989; Chankova et al., 2000; Goldberg and Lehnert, 2002; Marnett et al., 2003; Ramotar and Wang, 2003; Schaue and McBride, 2005; Bao et al., 2006; Chalmers, 2007). The different DNA repair capacity could be considered as a possible mechanism underlying cell resistance to different DNA damaging agents (Núñez et al., 1996; Ramotar and Wang, 2003; Serafin et al., 2003; Hyun et al., 2008; Singh et al., 2009).

New conceptions reveal the mechanisms of plant responses to UV-B radiation. UV-B radiation results in activation of still unknown receptor molecules. These primary events engage signal metabolic pathways causing changes in gene expression. UV-B exposure induces UV-B specific and UV-B common signals activated by different environmental factors. This is important information to understand the common plant UV-B stress responses such as reduced growth and acclimation to increased UV-B radiation.

A better understanding of the mechanisms underlying cell genotype resistance to stress and mutagens is relevant to ecological genetics and falls within the scope of the national programs for protection of the gene pool of cultivars and biodiversity preservation (Operating program “Environment 2007–2013”).

Bearing in mind the discussed data and regarding the enlargement of the ozone hole above the Southern Hemisphere and the following heat impact, there is much greater risk of chronic UV stress and photoinhibition of autotrophic organisms. From this point of view and due to the existence of controversial opinions, the investigations on the changes in antioxidant activity, DNA structures, and parameters characterising the intensity of photosynthesis in selected Antarctic algae, as well as the studies on the protective effect of abscisic acid pretreatment have been provoking considerable interest. It is also worth studying the changes occurring in the concentration of biotechnologically valuable antioxidant pigments (phycocyanin and β-carotene) in stress-exposed algal cells.

The development of plant-based biomarker test systems is topical on a global and national scale because it is directly relevant to the strategies for protection of gene pool of cultivars, biodiversity preservation, and genome stability of plant populations (natural and agricultural). In this aspect, the use of Antarctic algae as a model system for creation of survival strategies is appropriate due to their ability to survive settling in various ecological niches and thus to become extremely resistant to severe ecological factors impact.

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