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RESPONSE REACTION OF *DESCHAMPSIA ANTARCTICA* DESV. PLANTS TO UV-B IRRADIATION AND OXIDATIVE STRESS

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Abstract. The effect of stress factors – ultraviolet radiation (UV-B) and hydrogen peroxide (H2O2) upon two species of *Deschampsia* plants – *D. antarctica* and *D. caespitosa* were studied. Investigations performed with *D. Antarctica* plant samples delivered of Antarctic and *D. caespitosa* from Carpathian Mountains showed that UV-B radiation caused changes mainly pigment composition - chlorophyll *a* and almost all (except violaxanthin) carotenoids. Lipid composition was characterized by accumulation of triacylglicerols, sulphoquinovosyl diacylglycerol and phopsphatydylcholine while monogalactosyldiacylglycerol quantity decreased. H_2O_2 treatment cause increase chlorophyll *a* content in both species and carotenoids in *D. antarctica* plants. Concerning glycolipid composition one could see monogalactosyldiacylglycerol content decrease in *D. caespitosa* whereas only insignificant SQDG enlargement was noted in *D. antarctica* leaves.
Key words: *Deschampsia,* glycolipids, sulfolipid, sulfoquinovosyldiacylglycerol, SQDG.

Реферат. Досліджувався вплив стресових факторів – ультрафіолетового випромінювання (UV-B) та пероксиду водню (H_2O_2) на представників двох видів роду *Deschampsia – D. antarctica* і *D. caespitosa*. Встановлено, що UV-B випромінюванняя викликало зміни у вмісті пігментів – хлорофілів і каротиноїдів (крім віолоксантину). Склад ліпідів характеризувся накопиченням триацилгліцеролів, сульфохіновадилдіацилгліцеролу, фосфатидилхоліну та деструкцією вмісту моногалактозилдіацилгліцеролу. Вплив H_2O_2 спричиняв акумуляцію хлорофілу *a* в рослинах обох видів і каротиноїдів у рослинах *D. antarctica*. Дослідження складу гліколіпідів встановило зменшення вмісту моногалактозилдіацилгліцеролу в листках *D. caespitosa* та незначне накопичення сульфохіновадилдіацилгліцеролу в рослинах *D. antarctica*.
Ключові слова*: Deschampsia,* гліколіпіди, сульфоліпід, сульфохіновазилдіацилгліцерол, СХДГ.

Реферат. Исследовалось влияние стрессовых факторов – ультрафиолетового излучения (UV-B) и перекиси водорода (H_2O_2) на представителей двух видов рода *Deschampsia – D. antarctica* и *D. caespitosa*. Установлено, что UV-B излучение вызвало изменения в содержании пигментов – хлорофиллов и каротиноидов (кроме виолоксантина). Состав липидов характеризовался накоплением триацилглицеролов, сульфохиновазилдиацилглицерола, фосфатидилхолина и деструкцией моногалактозилдиацилглицерола. Влияние H_2O_2 вызывало аккумуляцию хлорофилла *a* в растениях обоих видов и каротиноидов в растениях *D. antarctica*. Исследование состава гликолипидов установило уменьшение содержания моногалактозилдиацилглицерола в листьях *D. caespitosa* и незначительное накопление сульфохиновадилдиацилглицерола в растениях *D. Antarctica*.
Ключевые слова*: Deschampsia,* гликолипиды, сульфолипд, сульфохиновазилдиацилглицерол, СХДГ.

Introduction

Declines in global concentrations of stratospheric ozone over the past 15 years led to increase in levels of ultraviolet-B radiation (UV-B; 280–315 nm) reaching the earth's surface (Madronich et al., 1998) which is most pronounced in Antarctica and reach a double UV-B levels (UNEP, 1998; Xiong, Day, 2001). High-intensity light and low temperatures in their turn can damage the photosynthetic

machinery of plants. Thus, increased solar UV-B irradiation together with high light and low temperatures are the main abiotic factors which cause the formation of reactive oxygen species (ROS) inducing oxidative stress and damaging photosynthetic apparatus. It is known, that dominant ROS in UV-irradiated plant leaves was O_2^-, while $^1O_2$ was minor (Hideg et al., 2002)**.** These species react with lipids, proteins, pigments, and nucleic acids and cause lipid peroxidation, membrane damage, inactivation of enzymes, thus affecting cell viability. Therefore, an efficient mechanism of ROS scavenging would contribute to support photosynthetic activity and plant survival in is a hostile for plant growth environment of the Antarctic geobotanical zone. There are some ways to defend photosynthesis mechanism from ROS action – to scavenge them with the help of enzymes and to protect with the help of carotenoids. The antioxidative system of plants comprises several enzymes and low molecular weight (ascorbate, glutathione) quenchers that are principally constitutive and vary in plants at cellular and subcellular levels. Superoxide radicals generated in plant cells are converted to H_2O_2 by the action of superoxide dismutase (SOD). The accumulation of H_2O_2, a strong oxidant, is prevented in the cell either by catalase (CAT) or by the ascorbate-glutathione cycle where ascorbate peroxidase (APX) reduces it to H_2O. Thus, these compounds interrupt the cascades of uncontrolled oxidation in some organelles (Noctor, Foyer, 1998).

Carotenoids react with free radicals directly (Palozza, Krinsky, 1992), forming a carotenoid radical. It could be regenerated by interaction with tocopherols and ascorbate in the lipid phase of the membrane (Edge *et al*., 1997). Carotenoids of the xanthophyll cycle cycle (violaxanthin and zeaxanthin) are closely related to the control of ROS production by chlorophylls when the photosynthetic electron chain is saturated (Foyer *et al*., 1994). It is shown that zeaxanthin is a very efficient ROS scavenger (Lim *et al*., 1992; Sielewiesiuk, Matula, Gruszecki, 1997).

It is well-known, that lipids are integral components of thylakoid membranes and are substantial for their photosynthetic activity. The plant thylakoid membranes contain mainly nonphosphorous glycolipids such as the nonbilayer lipid monogalactosyldiacylglycerol (MGDG) and the bilayer lipid digalactosyldiacylglycerol (DGDG) (Webb, Green, 1991; Lee, 2000), which contribute to thylakoid aggregation and stacking (Menikh, Fragata, 1993; Hincha, 2003). Besides, there is an anionic sulpholipid – sulphoquinovosyl diacylglycerol (SQDG) with a sulfonic acid derivative of glucose. About 50–60% of polar lipids in photosynthetic tissue are represented by MGDG and 20–25% are DGDG. The third glycolipid – SQDG-comprises between 8 and 24% of the four major chloroplast lipids and contains a substantial quantity of high melting point fatty acids (Kenrick, Bishop 1986; Murata, Siegenthaler, 1998; Joyard *et al*., 1998). The glycosyl moiety of it is characterized by carbon being directly bonded to sulfur as $C\text{-}SO_3^-$. Sulfonic acid of this type is chemically stable and strong acid in wide pH range (Barber, Gounaris, 1986).

The study of the core peptide D1 showed that in it MGDG, PG and SQDG molecules are bound in the molar ratio 1:3:17. The isolated LHCP-complex contained in bound form 3 MGDG molecules, 1 molecule of DGDG, 1 molecule of PG and 1 molecule of lutein. Less than 1 molecule of SQDG, β-carotene, neoxanthin and violaxanthin are found. In contrast to the lipids of the thylakoid membrane, the lipids bound to proteins/peptides are characterized by a strongly saturated character (Gasser, Raddatz, Radunz, Schmid, 1999). Besides, for activity of violoxanthine de-epoxidase (VDE) – a water-soluble enzyme located in the thylakoid lumen (Hager, Holocher, 1994) specifically requires the major thylakoid lipid, MGDG (Siefermann, Yamamoto, 1975; Yamamoto, Higashi, 1978). It is four times more efficient in precipitating VDE compared to the DGDG, and up to 38 times more efficient than other thylakoid lipids (Rockholm, Yamamoto, 1996).

Deschampsia antarctica Desv. (Poaceae) is the only native Gramineae found in the Antarctic, where it is restricted to the Antarctic Peninsula and its offshore islands. It was found that, *D. antarctica* exhibited high levels of SOD and APX activity compared with other plants. Pigment analyses show that the xanthophyll cycle is operative in this plant. It was proposed that photochemical quenching and particularly the high level of antioxidants help *D. antarctica* to resist photoinhibitory conditions. The

relatively high antioxidant capacity of *D. antarctica* may be a determinant for its survival in the harsh Antarctic environment (Pérez-Torres et al., 2004).

Taking into account that oxidative stress is a main effect of UV-B irradiation we consider it to be expedient to study antioxidant indexes and glycolipid composition of *Deschampsia* plans caused by H_2O_2 action also. With this purpose we introduced *Deschampsia antarctica* plants delivered from Antarctic in conditions of temperate climate of Europe and investigated plant reaction against UV-B irradiation and oxidation stress induced by spraying leaves with H_2O_2 solution. In order to compare reactions we use also *Deschampsia caespitosa* plants growing in Carpathian Mountains (typical representative of Ukrainian Carpathian ecosystems).

Materials and Methods

Plants of *D. antarctica* plants delivered from Antarctica and *D. caespitosa* (30 days old) were used. The control plants were grown under the lamps of daily illumination at a 16-hour photoperiod. The plants of experimental variant were grown under the lamps of daily illumination (photoperiod – 16 h) and were irradiated by UV-B for 20 hours by 5-times exposition (4h on light period). The UV-B lamp with absorption filter (TL 20Вт/12RS (Philips)) was used for illumination of the plants. The biologically effective UV-B radiation (UV-BBE) was 6.17 kJ m^{-2} d^{-1}. Distance to the source of illumination was 10 cm. Oxidative stress was induced by spraying plants with H_2O_2 (500 μM for 4 hours).

The pigment content in leaves was determined with generally accepted method (Arnon, 1949). The separate carotenoid content was determined using TLC method (Merzlyak, 1978) in our modification. Polar lipids were isolated according to L. Zill and E.Harmon (Zill, Harmon, 1962) in modification of G. Yakovenko and A. Mihno (Yakovenko, Mihno, 1971). Glycolipids were separated with the help of TLC and then MGDG and DGDG were determined by densitometring TLC plates against standards (Yamamoto, 1980). SQDG was registered according to E. Kean (Kean, 1968).

Results and Discussion

Our investigations performed with *D. Antarctica* plant samples delivered from Antarctic showed that UV-B radiation action caused changes mainly pigment composition – chlorophyll *a* most and almost all (except violaxanthin) carotenoids (Fig. 1). Chlorophyll *a* quantity enlarged by 30,6%, while chlorophyll *b* by 24,4 and carotenoid content by 20%. β -carotene increment was most significant (by 82%) amidst other carotenoids. Information presented in literature showed that UV-B radiation caused a reduction in total chlorophyll in *Sinapis alba, Capsicum frutescens, Phaseolus vulgaris* and *Spinacia oleracea*. The size of the reduction varied from 24% to a 40% loss in S. oleracea. But five cultivars of L. sativa showed an increase in chlorophyll content displaying levels almost double those of controls. Plants which showed a decrease in chlorophyll content altered their chlorophyll a:b ratio, with four of the five species displaying reduced ratio. None of the species with increased chlorophyll content showed such a shift (Smith, Burritt, Bannister, 2000). Similar data were got with Soybean (*Glycine max*) irradiated by UV-B – chlorophyll a and carotenoids increase was noted at one of two cultivars (Middleton, Teramura, 1993). The total carotenoid content of mature vine leaves was found to be less in vines grown under a UV screen (Steel1, Keller, 2000). Thus, our data are not in contradiction with information available.

Lipid composition was characterized by accumulation of triacylglicerols (TAG) but it intensity decreased on the reparation stage (Fig. 2*a*). Monoacylglicerols (MAG) and diacylglicerols (DAG) content changed according to the changes of amount of TAG (as intermediate products of synthesis of TAG). Sterol content accumulated only in 24 hours after insignificant fall after irradiation (by 70,1% comparing to the meaning after exposure). Concerning glycolipids we can notice only slight SQDG accumulation (Fig. 2*b*).

H_2O_2 treatment cause insignificant decrease in SOD activity of both species (Taran, Batsmanova, Okanenko, 2007). Pigment composition was characterised by increase chlorophyll *a* content in both species and carotenoids in *D.antarctica* plants (Fig. 3*a, b*). Concerning glycolipid

composition (Fig. 4*a*) one could see stable galactolipid content and insignificant SQDG enlargement in *D. antarctica* whereas only MGDG quantity decrease was noted in *D. caespitosa* leaves (Fig.4*b*).

Thus, as UV-B irradiation so and H_2O_2 treatment caused similar changes in *D.antarctica* pigment content, whereas chlorophyll *b* increase was significant and carotenoid content was stable in *D. caespitosa* leaves. Glycolipid changes were very close in *D.antarctica* and MGDG content decrease was more meaningful in *D. caespitosa* plants.

Our data match partly with results of Musil C.F. with colleagues (Musil, Chimphango, Dakora, 2007). According their results chlorophyll *a*, *b* and carotenoid content change at UV-B action depending upon species. The main trend was chlorophylls decrease in experiment, but some plants reveal their accumulation, e.g. *Leucadendron Iaureolum* (chlorophyll *a* – by 17,8%, chlorophyll *b* –

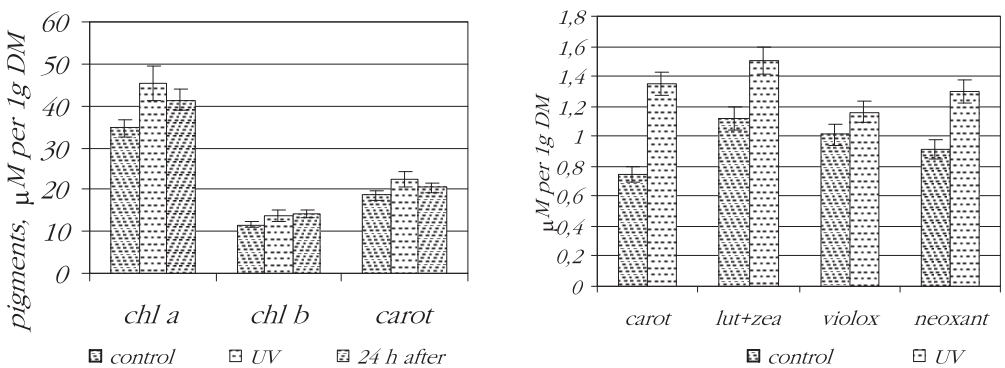

Fig. 1. Pigment content in *D. antarctica* leaves under UV-B irradiation (chl – chlorophyll, carot –carotenoids, carot – β -carotene, lut+zea – lutein+zeaxanthin, violox – violoxanthin, neoxant –neoxanthin).

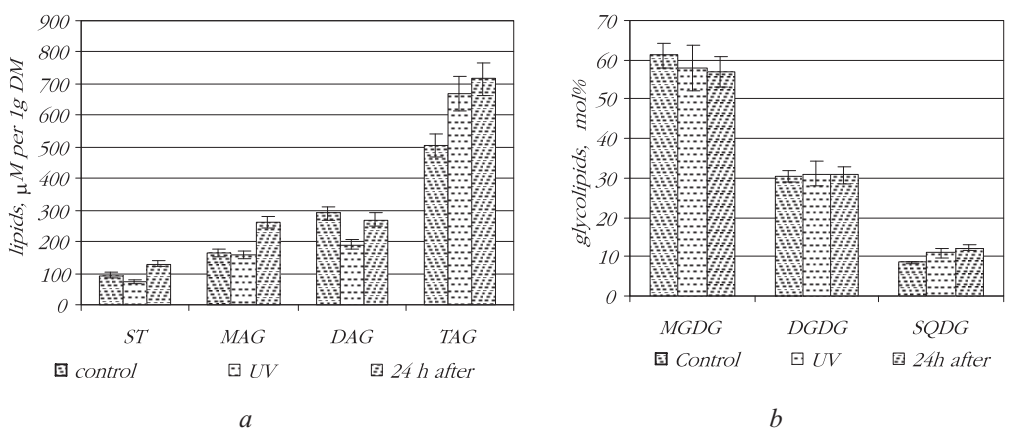

Fig. 2. Neutral (*a*) and polar (*b*) lipid composition of *D. antarctica* leaves under UV-B irradiation.

Concerning lipid behaviour a few data available evidence that oxidative processes induced by high concentration of ozone caused a loss of pigments and lipids (mainly MGDG with some DGDG). It was accompanied by a small increase of malondialdehyde (MDA) content and in TAG and DAG (Sakaki, 1998). However, the anionic lipid (SQDG and phosphatydylinositol) content was stable for the period of ozone exposure (in spinach leaves, at least). Similar lipid changes were also observed in several plant species, and in broad bean leaves, a relative increase in SQDG took place. Because both galactolipids were significantly destroyed during ozone exposure, the SQDG content expressed as mol% of the total glycolipids increased up to 45 mol% (depending upon species) (Sakaki et al., 1985, 1994).

Considering these changes it is worth to mention that SQDG molecules in photosynthesising tissues stabilize F-ATPase, protect and stabilise D1/D2 dimers and LHCII (Livn and Racker 1969, Pick et al., 1985). SQDG and the Rieske protein interaction in the cyt *b6f* structures is also very important (De Vitry et al., 2004). This suggests that the region delimited by the endogenous sulfolipid, the Rieske protein, and the cyt *f* helix plays a specific role in the assembly-mediated control of cyt *f* synthesis.

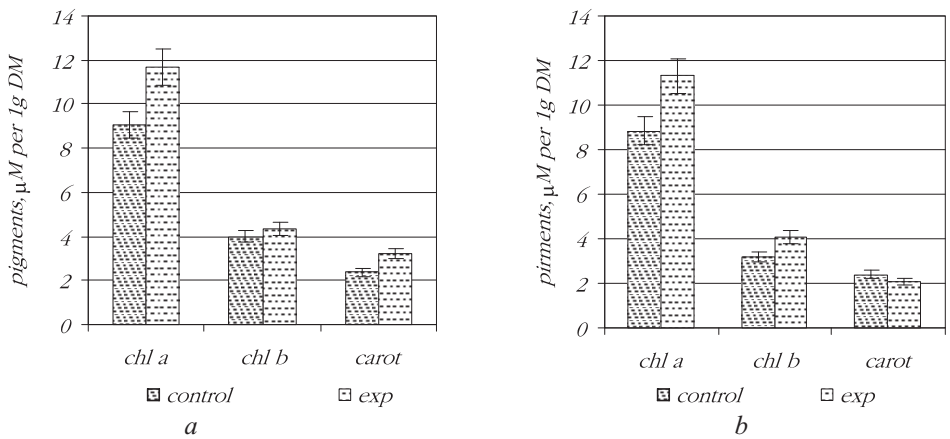

Fig. 3. Pigment content in *D. antarctica* (*a*) and *D. caespitosa* (*b*) leaves after H_2O_2 treatment.

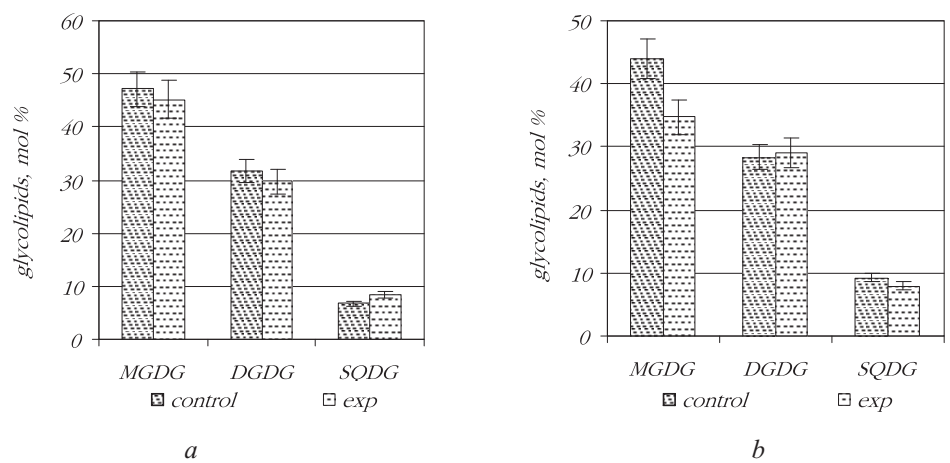

Fig. 4. Polar lipid composition of *D. antarctica* (***a***) and *D.caespitosa* (***b***) leaves after H_2O_2 treatment.

Thus, SQDG seems to be involved in the turnover of cyt *f* in a similar manner like D_1 and raise the question of whether a similar mechanism underlies the role of SQDG in the assembly of both subunits (De Vitry et al., 2004). Photoinhibition arising at stressor action induces degradation and cleavage of D1 protein of RC PS II (Kettunen, Tyystjarvi, Aro, 1996). SQDG localised at the surface of the native D1/D2 heterodimer surface (Vijayan et al. 1998) might hold monomers together as dimer (de Kruijff et al., 1998) and stabilize it while unfavorauble environment changes.

A significant increase in total lipid concentration but a decrease in free sterols (FS) was registered in tobacco plants exposed to ozone. A meaningful reduction in all four major (campesterol, cholesterol, sitosterol and stigmasterol) FS occurred. But there was a greater reduction in stigmasterol concentration (by 2,8-fold) than in the concentration of the other three sterols (Trevathan, Moore, Orcutt, 1979). Decreases in free sterols (FS) and increases in sterol glycoside (SG) and acylsterol glycoside (ASG) were observed in bean leaves (Tomlinson, Rich 1971; 1973; Spotts *et al.,* 1975; Trevathan *et al.,* 1979; Whitaker *et al.,* 1990). Therefore it seems that ozone stimulates glycosylation and further acylation of sterols under acute stress. Thus, ozone enhances production of free fatty acids (FFA) from galactolipids; acylation of SG might play a scavenging role of FFA in leaf cells together with the synthesis of TG. In support, main fatty acid (FA) species increased in ASG by ozone include 18:3, a predominant FA in galactolipids (Tomlinson, Rich 1971). Results obtained in experiments with spinach (*Spinacia oleracea* L., cv New Asia) plants fumigated with ozone also showed a large reduction of galactolipids accompanied by TG increase without a corresponding effect on leaf FAs (Sakaki et al., 1985). Constituent FAs of galactolipids, especially MGDG, were largely converted to those of TG. Authors proposed that 1,2-DG liberated from MGDG is the direct precursor of TG synthesized in ozone-fumigated spinach leaves, based on the fact that 16:3, the fatty acid specific to MGDG, was recovered in 1,2-DG as well as in TG. Molecular species and FA distribution of TG accumulated in spinach (*Spinacia oleracea* L.) leaves fumigated with ozone were compared with those of MGDG. Analysis of positional distribution of the fatty acids in MGDG and the accumulated TG by the enzymatic digestion method showed that hexadecatrienoate (16:3) was restricted to *sn*-2 position of the glycerol backbone in both MGDG and TG, whereas β -linolenate (18:3) was preferentially located at *sn*-1 position in MGDG, and *sn*-1 and/or *sn*-3 positions in TG, suggesting that 1,2-diacylglycerol moieties of MGDG are the direct precursor of TG in ozone fumigated leaves. Further analysis showed that TG increased with ozone fumigation consisted of approximately an equal molar ratio of *sn*-1,3-18:3-2-16:3 and *sn*-1,2,3-18:3. Because the molecular species of MGDG in spinach leaves is composed of a similar molar ratio of *sn*-1-18:3-2-16:3 and *sn*-1,2-18:3, it was concluded that MGDG was converted to 1,2-diacylglycerol and acylated with 18:3 to TG in ozone-fumigated spinach leaves (Sakaki et al.,1990). The similar results were represented in later work (Sakaki, Tanaka, Yamada, 1994). Analysis of eight species leaf lipids after treatment with ozone revealed MGDG content decrease and TG accumulation in all plants, but the extent of the changes varied among the plant species. The FAs esterified to TG were mainly ?-linolenic acid (18:3) in 18:3 plants and hexadecatrienoic acid (16:3) and 18:3 in 16:3 plants normally esterified to MGDG in the respective plant groups. Therefore MGDG seems to have been metabolized to TG via FFA and DG in all tested plants in response to ozone.

Thus, our results correspond mainly to data available in literature and we could conclude, that UV-B and oxidative stress, caused by H_2O_2 induced similar changes. Besides, *D.caespitosa* plants revealed MGDG destruction more hard, than *D. antarctica*.

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