Plant sulfolipid. III. Role in adaptation

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The quality and/or relative content of plant sulfoquinovosyl diacylglycerol (SQDG) change in response to a stress action. Various types of stress action induce two types of response – more general to the oxidative stress and specific – to a concrete stress factor. Besides, two types of reaction take place in photosynthesizing and non-photosynthesizing tissues. SQDG molecules take part in the adaptation reaction being cytochrome oxidase, CF_1, F_1, ATPase regulators, protectors and stabilizing agents for D_1/D_2 dimers and LHC II. This compound in non-photosynthesising tissues could be connected with negative charge domination required for lipoprotein complex stabilisation. SQDG quantitative changes and acyl composition shifts take place at both abiotic and biotic factors impact.

Keywords: sulfolipid, sulfoquinovosyl diacylglycerol, stress.

In response to environmental stresses, living organisms acquired the capability of recognizing such stresses and adapting themselves to various types of stress during evolution. Stress affects many physiological processes including protein and lipid metabolism and enzyme activity [1–5]. Since lipids are major components of membranes and are influenced considerably by environmental factors [6, 7] overall plant growth and development will be affected by significant changes in lipid metabolism. The results of studies devoted to lipid involvement in adaptation processes show that both sulfoquinovosyl diacylglycerol (SQDG) quantitative changes and fatty acid composition shifts take place.

Oxidative stress. The questions of specificity of plant adaptive reaction to the environment unfavorable factor action are bound mainly with the oxidation stress. Abiotic and biotic stresses can cause in plants secondary oxidation stress. Plenty of oxygen and highly power reactions of electron transfer associated with the thylacoid membranes are the main source of highly active oxygen intermediators in photosynthesizing tissues of plants. Anion of superoxide of O_2^- or a free oxygen radical is generated when electrons of PS II are accepted by O_2 instead of feredoxine and is transformed with participation of SOD usually in H_2O_2 or sometimes in highly toxic free radical $^.OH$ via Fe-catalyzed Haber-Weiss reaction [8]. Action of abiotic and biotic stresses causes growth of maintenance of highly active oxygen derivates. Superoxides are the charged molecules and can not pass via biological membranes.

Therefore subcellular compartmentation of protective mechanisms is critical for elimination of superoxide ions in the places of their origin in cells [9]. Oxygen radical action upon isolated membranes caused an inccrease in their viscosity and permeability, in temperature of lipid phase transition, lipid phosphorus liberation and piling up free fatty acids

[10]. In general the mechanism of attack of free radicals is known to include the oxidation of acyl chains [11], but it is not excluded, that free radicals can cause the reactions of de-etherification of polar lipids and liberation of fat acids which can be easily oxidized [12]. Bearing in mind that the oxidative stress accompanies many other stresses of plants, any changes in the lipid composition caused under such circumstances are of special significance.

A few data available evidence that oxidative processes induced by a high concentration of ozone run in two phases. During the first phase (8 hours) a loss of pigments and lipids (mainly MGDG with some DGDG) was observed. The loss in chloroplast lipids is accompanied by a small increase in the malondialdehyde (MDA), TAG and DAG content. The second phase of oxidative injury is characterized by a massive destruction of pigments and begins with a drastic fall in MGDG and a smaller decrease in DGDG and PC contents which are accompanied by significant increases in TAG, DAG and MDA [13]. However, the anionic lipid (SQDG and PI) 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 (depending on a species) [14, 15]. Interesting results were obtained with a sulfoglycolipidic fraction isolated from the red microalga *Porphyridium cruentum*. It was demonstrated that sulfolipid contained large amounts of palmitic acid (26.1 %), arachidonic acid (C20:4n-6, 36.8 %), eicosapentaenoic (C20:5n-3, 16.6 %) acids and 16:1n-9 fatty acid (10.5 %) and strongly inhibited the production of superoxide anion generated by peritoneal leukocytes [16]. Our experiments with the induced oxidative stress showed that hydrogen peroxide affect pigment and glycolipid composition with increasing lipid peroxidation activity in dose and time dependent manner. The treatment with various hydrogen peroxide concentration caused significant SQDG content increase in all variants. The results of field experiments showed a drastic fall of SQDG level in 24 hours (h) with a subsequent significant lipid accumulation. This compound

quantity was stable after the second treatment when light MGDG decrease was noted and DGDG level was stable during the whole experiment [17]. Concerning the meaning of these changes the idea seems acceptable that this lipid may also provide a source of cysteine under the conditions of oxidative stress [18]. It functions as a component in the sulfur cycle in plants and is rapidly metabolized for protein production under the conditions of sulfur depletion [19]. Thus the additionary quantity of thiol group needed at oxidative agent action can be supplied.

Irradiation level. The quantity of the light in natural environments can vary over several orders of magnitude and on a time scale that ranges from seconds to seasons. Plant acclimation to light intensity depends upon the structure and function of the photosynthetic apparatus. The photosystems and their subcomplexes (LHCs, D_1, D_2) are anchored within the thylakoid membrane through the lipids. This close connection between lipids and photosystem subcomplexes indicate an interdependence between both, which supports the concept of photosynthesis regulation by changes in the thylakoid membrane structure or the entire chloroplast [20]. Besides, it was said earlier that the cells of *Chlamydomonas* SQDG-deficient mutant tended to suffer from photoinhibition [21]. The data available indicate that the red alga *Tichocarpus crinitus* exposed to low light (10 % of the incident photosynthetically active radiation) conditions accumulated the only SQDG content characterized by palmitooleic (hexadecenoic, 16:1) acid 20-fold increase with small content deviation of the other FA residues [22]. But Antarctic sea ice diatoms (the algal composition in the culture was 66 ± 11 % of *Navicula gelida* var. *antarctica*, 20 ± 7 % of *Fragilariopsis curta* and 14 ± 9 % of *Nitzschia medioconstricta*) did not show any difference in SQDG content at two different photon flux densities – 15.0 ± 5.0 mol photons $m^{-2}s^{-1}$ and photon flux density of 2.0 ± 1.0 mol photons $m^{-2}s^{-1}$. The main difference was palmitic residue decrease accompanied by stearic (18:0) and eicosapentaenoic acid (20:5n-3) twice increase [20]. The authors considered the increase in photon trapping and an increase in electron transport velocity at PS II under 2 mol photons $m^{-2}s^{-1}$ between bound Q_A and Q_B as a consequence of increasing FA desaturation of typical chloroplast lipids (MGDG,

SQDG, PG), particular by increasing 20:5 n-3 of MGDG and SQDG. It supports the Q_A and Q_B interactions and thus the velocity of electron flow.

Thermoresistance. Many studies on the lipid changes caused by temperature have been made with cyanobacteria because these prokaryotic organisms are homogeneous in culture and respond very quickly to the temperature shifts. The experiments performed showed that a temperature decrease caused an increase in the SQDG content or did not affected it. For example, in *Anacystis nidulans* an increase in MGDG and SQDG and a decrease in DGDG were observed. Almost all of the palmitate at the *sn*-1 position of SQDG was converted to palmitoleate at low growth temperatures [23–25]. In the cyanobacterium *Spirulina platensis* cultivated at 35, 30 and 27 C the low temperatures caused the SQDG content increase accompanied by the desaturation of palmitate at the *sn*-2 position of SQDG [26]. On the other hand, for *Anabaena variabilis* growing at low temperatures, the level of SQDG was stable with only a small conversion of palmitate to palmitoleate [23–25]. Low temperatures also induced similar effect in the higher plant lipid compositions. Our earlier investigations showed that, during autumn hardening, SQDG accumulation took place in one-year-old apple shoot bark and wood (!) and was especially striking for a hardy apple specie (*Malus boccata* Borh) [27]. Oquist [28] found a 2-fold increase in the SQDG content in pine thylakoid preparations during the autumn which remained high during the winter and then lowered in spring. SQDG from pine in the winter was enriched in linoleate whereas palmitate was dominant in the summer.

The results available in literature indicate that superoptimal temperatures cause an increase of SQDG content in most plants studied. For example, *Atriplex lentiformis* plants grown in coastal and desert regions accumulated SQDG (by 260 % and 64 % respectively) at high growth temperatures [1]. When *Nerium oleander* was grown at 45 C rather than 20 C the main changes in molecular species were an increase in the proportion of dipalmitoyl-SQDG from 12 up to 20 % and a decrease in that of linolenoyl-palmitoyl SQDG from 40 to 30 % at the higher growth temperature. At the same time the phase transition temperature increased from 19 ± 3 C to 24 ± 3 C. Taking into ac-

count the fact that dipalmitoyl-SQDG undergoes a transition at 42 C, it was suggested that this molecular species could be a major lipid component involved in a phase transitions in the thylakoid polar lipids [29]. Our data showed that growth at high temperature induced sulfolipid accumulation but only in the wheat leaves and chloroplasts of drought resistant varieties. In contrast, in the only sensitive species (Myronivska 808) there was a decrease in the SQDG content. The heating at temperatures 40, 45 and 50 C caused the SQDG content changes in chloroplasts described by curve with one apex at 45 C with following drop at 50 C in all resistant plants [30].

The exploration of physical properties of the SQDG showed that only in sponge cucumber did phase separation begin at 15 C for SQDG. Nevertheless, SQDG from the chilling sensitive species contained up to three times more stearic acid than resistant plants [31]. Furthermore, Kenrick and Bishop [32] concluded that if the primary event in chilling sensitivity of higher plants is a phase transition in bulk chloroplast membrane lipids, then not only PG, but also SQDG might be involved. In particular, the main difference between *Carica papaya* (tropical origin) and *C. pubescens* (adapted to temperate climates) was in their SQDG species (57 % and 36 % saturated, respectively), and not in PG. Their results showed that linolenic acid residue was abundant in SQDG from the chilling-tolerant species whereas palmitate was a major component in the temperature-sensitive plants.

Water deficit. Water deficit affected the SQDG amounts in wheat depending upon wheat variety drought resistance. Our data showed that water deficit induced some SQDG accumulation in drought resistant wheat plants and the drastic decrease of it content in sensitive plants [33]. Similar results were presented by Quartacci et al. [2]. So, thylakoids of tolerant wheat variety were characterized by SQDG accumulation whereas sensitive varieties loosed it. Palmitic residue content increased while palmitooleic and linolenic ones decreased in tolerant plant SQDG whereas palmitic residue level diminished and linolenic enlarged in soft one. Thus, the SQDG accumulation in tolerant plants with a parallel rise in saturation was observed while changes in sensitive plants were exactly the opposite. Field experiments with artificial irriga-

tion (conferred as «control») during drought showed an increase in SQDG at two stages of development (the stage of stooling and the stage of milk ripeness) for wheat exposed to drought (by 73.7 and 51.1 % respectively) [34]. Similar data were obtained by Pancratova and Karimova [35] when they exposed rye to drought. Combine action of heat and water deficit induced the SQDG accumulation in the almost all resistant plant chloroplasts, whereas the SQDG content decreased in sensitive variety more drastically than in the cases of single factor action [36]. Thus the shifts observed at the heat are similar to those under the water deficit action and their combine effect induced the SQDG accumulation sometimes much more significant than when single factor action. The importance of SQDG was also indicated from experiments on rehydration of air-dried cells of the desiccation-tolerant filamentous cyanobacterium *Nostoc commune*. The radiolabeled pool sizes of PG and SQDG reached steady-state within several minutes, whereas the two abundant membrane glycolipids, MGDG and DGDG, achieved uniform labeling only within 2 h [37]. This rapid response may be connected with the ability of this cyanobacterium to tolerate desiccation.

Salinity stress. Higher plant *Calystegia soldanella* R. Br. (*Convolvulaceae*) – a halophyte plant that can grow in some areas along the Black Sea where the soil may contain up to 700–900 mg salts in 100 g soil. The main glycolipid was SQDG (31.7 %) with almost equal content of MGDG (11.1 %) and DGDG (14.3 %). Contrary to the other halophyte plants from the same region, the content of phospholipids is relatively low [38].

Adaptation of the plant cells to high salinity involves osmotic adjustment and the compartmentation of toxic ions, whereas an increasing body of evidence suggests that high salinity also induces oxidative stress [39–43]. Several laboratories have reported that salinity impairs photosynthetic activity in a number of photosynthetic organisms [44, 45] and affect lipid composition.

Early results showed that the SQDG content was stable (relative to chlorophyll) during adaptation of barley seedlings to high concentrations of sodium chloride while the MGDG content of thylakoid membranes decreased considerably. The latter decrease meant that the relative percentage of SQDG compared to total thylakoid lipids increased by 30 % [46]. In wheat roots, increased salt levels (calcium sulfate) resulted in higher (two-fold increase) levels of SQDG, while the reverse occurred in lipids from oat roots [47]. It may be interesting to note in this connection (and in view of the possible involvement of SQDG in ATPase activity) that Ca^{2+} activation (via annexin) of the root ATPase is important in wheat [48] whereas in oat roots the ATPase activity is mainly increased by Mg^{2+}. However, treatment of sugar beet with sodium sulphate did not confirm the suggestion that SQDG was involved in salt-adaptation [49]. On the other hand, SQDG ranged from 5 in spinach to 20 molecules in the halotolerant alga *Dunaliella salina* per CF_0-CF_1 ATPase complex and this lipid could not be readily exchanged [50]. Growth of *Synechococcus* 6311 in the presence of 0.5 M NaCl is accompanied by significant changes in both thylakoid and cytoplasmic membrane lipid composition. MGDG content decreased while DGDG quantity raised. The total content of anionic lipids (PG and SQDG) was always higher in the isolated membranes and the whole cells from high salt-grown cultures. The observed changes in membrane fatty acids and lipids composition correlate with the alterations in electron and ion transport activities, and it is concluded that the rearrangement of the membrane lipid environment is an essential part of the process by which cells control membrane function and stability [51]. And it should be kept in mind that in extreme halophiles (*Halobacterium cutirubrum, Haloferax volcanii* T., *Planococcus* H8) polar lipid extracts contained near 14 % sulfated glycolipids and that lipids extracted from the crystallizer ponds of the salterns of Margherita di Savoia (Italy) and Eilat (Israel) and from cultures of representative species of the *Halobacteriaceae* showed that a sulfated diglycosyl diether was the major glycolipid detected in the biomass of both salterns [52].

Results obtained by Zhang et al. [53] showed that transgenic *Brassica napus* plants overexpressing *AtNHX1,* a vacuolar Na^+/H^+ antiport from *Arabidopsis thaliana,* were able to grow, flower, and produce seeds in the presence of 200 mM sodium chloride. The data suggest that the major structural lipids of the extraplastidic compartments (PC and PE) and of the chloroplasts (DGDG and MGDG) were unaffected by the overexpression of *AtNHX1* and by the growth of the

transgenic plants at high salinity. Some differences, however, were seen in the minor chloroplastic lipids, SQDG and PG in 200 mM NaCl. Although the 16/18C ratios were the same, there was lesser unsaturation of the 18C fatty acids in both SQDG and PG from transgenic plants grown in 200 mM NaCl. SQDG expressed as mol% of four major chloroplast lipids (MGDG, DGDG, SQDG and PG) in the case of the overexpression of *AtNHX1*, a vacuolar Na^+/H^+ antiport from *A. thaliana*, overpassed wild type (at 10 mM NaCl) by 31 % at 10 mM NaCl and by 58 % at 200 mM NaCl. This phenomenon allows us to suppose SQDG to take part in the Na^+/H^+ antiport functioning (perhaps as ATPase stabilizing agent).

The study of different NaCl concentration effect upon halophytes and a glycophyte showed that in the halophyte *Aster tripolium* the SQDG contents increased in dose-depending manner [54]. The differences in SQDG contents between the control, 258 and 517 mM NaCl in the watering solution were already substantiated after one day and change unsignificantly for 10 days of experiment. The increase in SQDG in *Aster* treated with high salt correlated positively with the increase in chlorophyll contents. The largest differences were observed on the 7th day of the treatment. In roots of the same *Aster* plants the sulfolipid contents are about 5 lower than in *Aster* leaves and increased in roots of salt treated plants especially distinctly on the 5th day.

The sulfolipid content of the other the halophyte *Sesuvium portulacastrum* was also higher in the leaves of plants treated with NaCl when compared to the non-treated plants. SQDG contained predominantly palmitic acid and -linolenic acid, and lesser amounts of linoleic acid and common tend was -linolenic acid decrease. In *Sesuvium* after 7 days of salt treatment the 18:2 species clearly increased in comparison to the control in a similar way as in *Aster*. Main SQDG molecular species in the halophytes were palmitoyl-linolenoyl (16:0/18:3) and dilinolenoyl (18:3/18:3) forms. ATPase activity study showed that F-ATPase localized in chloroplast and mitochondria increased it correlated to NaCl concentrations in the growth medium in *Aster* and, in less extent, *Sesuvium*. This phenomenon was accompanied by significant increase of SQDG content in *Aster* and *Sesuvium*. To confirm the results similar investigation was carried out in *Thellungiella halophila*, a salt tolerant relative of *Arabidopsis* and in *Arabidopsis* itself. In *Thellungiella* SQDG content increased due to the effect of NaCl echoing the result of *Aster* and *Sesuvium*, but no significant changes could be observed in *Arabidopsis* [54–56]. These results confirmed the suggestion that sulfolipids stabilize and/or activate F-ATPases.

Thus, taking into account that plenty of metabolic processes and adaptative reactions flow engaging ATPases, one could suppose the size of SQDG involvement in these processes. Authors concerned this SQDG increase supposed that this lipid is involved in stabilization of ATPase complexes and PS II – *Aster* F-ATPase activity increased with increasing NaCl concentration in the medium of growth [55] and might also play a role in signalling processes.

Our experiments [57] revealed that SQDG accumulation in euhalophyte *Salicornia europaea* L. and crinohalophyte *Halimione pedunculata L.* was possibly connected with its ability to accumulate high concentrations of salts (NaCl) in its tissues. In contrast, SQDG levels were stable in *Artemisia arenaria* DC during changes in osmotic pressure caused by photoassimilate accumulation and decreased in *Atriplex pedunculata* during the elimination of salts from this organism. Hence, any involvement of SQDG in salt adaptation seems to be dependent upon the various mechanisms of salt tolerance used by different organisms.

Thus, SQDG role in this case should be considered in following directions: as compound closely connected with photophosphorylation coupling factor and ATPase stabilizing energy supply for antioxidative activity and Na^+/H^+ antiport functioning; as compound neutralizing cation excess and capturing extra water.

Heavy metal action. The quantity of heavy metals in soil is often increased greatly in industrial areas and, when they are taken up by plants, they can induce both toxic and adaptive responses. There are a few studies confirms that lipid composition can be affected [58]. Cadmium exposure induced a decrease in MGDG and SQDG contents in *B. napus* leaves which was accompanied by a sharp increase in extra-chloroplastic lipids (PC and PI) [59]. Our results [60] showed that lead, supplied at various concentrations to hydroponic cul-

tures, caused a decrease in SQDG in wheat seedling leaves and roots. Thus, most heavy metals tested cause a decrease of SQDG content. Concerning the phenomenon observed we can assume, that this lipid being strong anion can create complex compound with lead atom (we observed it *in vitro* at least). It is possible competitive usage of sulfur for sulfur containing *cys*-rich peptides (phytochelatins) and protein synthesis (judging on increasing protein content) according to the suggestion that the cells utilize sulfur preferentially for the synthesis of essential metabolites, such as proteins, rather than for SQDG synthesis [61]. But information presented allows also to suggest that metabolism changes induced by lead depend upon plant species and conditions of metal action. For example, while acute exposure of the moss, *Rhytidiadelphus squarrosus*, to low levels (1–10 mM) of lead nitrate did not change the radiolabelling of SQDG significantly, populations gathered from lead-polluted soils showed more labeling of chloroplast lipids than moss from unpolluted areas. It was considered the increased metabolism of chloroplast lipids in moss from lead-polluted regions may represent an adaptive response. Thus, the membrane lipids, damaged as a result of heavy metal pollution, could be replaced and any detrimental effect on photosynthesis being minimized [62].

Mechanical injury. Plants react to wounding, either mechanical or caused by herbivore feeding, by activating the transcription of a set of genes, the function of which is mainly devoted to wound healing and the prevention of any subsequent pathogen attack. On the other hand it is known that wounding induce ROS and H_2O_2 forming [63] following by lipid composition change reactions [15]. Our data showed that wounding (cutting the leaf apex) induce increase (on 20 %) both leaf galactolipids in 4 h with returning to control in 24 h. Much more interesting were the SQDG changes both through 4 and in 24 h. In leaves this compound accumulation up to 150 % of control was observed in 4 h and changed by drastic fall (twice comparing to control) in 24 h. But most interesting was the fact (taking into account that wounding was rendered as cutting off 1 cm of leaf apex) significant SQDG content increase (twice) in roots in both 4 and 24 h. We consider this phenomenon to be an evidence of SQDG taking part in plant system response (unpublished results).

Infection. A few experiments suggest that infection can affect membrane lipids. In our experiments, a relative accumulation of SQDG in the total glycolipids in wheat plants infected by *Puccinia graminis* [34] and kidney bean plants infected by potato *x* potexvirus (PXV) or tobacco mosaic (TMV) virus was observed. The latter phenomenon was confirmed by a significant increase of the SQDG/DGDG ratio (used because DGDG was the most stable component in the experiments) [64]. These changes could be useful for the plant if the action of SQDG in inhibiting viral development (and against DNA-polymerase and reverse transcriptase activity [65, 66]), also apply to *in vivo* situations. On the other hand, it could be connected with oxidative stress accompanied the virus infection [67, 68]. But in barley stripe mosaic virus strains and poa semilatent hordeivirus losses of MGDG, PG, SQDG and chlorophyll as well as relative increases in phosphatidylcholine, phosphatidylethanolamine and phosphatidylinositol contents were observed [69]. Thus, information presented argues that quality and/or relative content of SQDG changes in response to a stressor action.

Conclusions. Thus, analyzing information presented one could conclude that SQDG functions known to date are multiple. The quality and/or relative content of SQDG changes in response to a stress action. Concerning the interpretation of the phenomena observed at various type stress action we consider to take place two type of response – more general to the oxidative stress and specific – to the concrete stress factor action. Besides, we should keep in mind the necessity of consideration of two types of reaction taking place in photosynthesizing and non-photosynthesizing tissues. In photosynthesizing tissues it seems putative to assume availability of all structural and functional SQDG molecules peculiarities known for today to supply their taking part in adaptation reaction as cytochrome oxidase, CF_1, F_1, ATPase regulators, protectors and stabilizing agents for D_1/D_2 dimers and LHC II [50, 70]. Taking into account the SQDG localization on the native heterodimer D_1/D_2 surface [71], one could assume that it might hold monomers together as dimer [72]. Therefore it is not excluded that SQDG certain molecular specie accumulation can prevent RC PS II degradation. Function of the compound in nonphotosyn-

thesizing tissues could be connected with negative charge domination requirement for univalent cation (Na^+ and K^+) being necessary for lipoprotein complex stabilisation. Besides, the compound can realize ATPase and PL A_2 activity regulation [73] both in photosynthetic and non-photosynthetic tissues. We assume also the possibility of the additional water amount capturing because of SQDG absorption in the space between the SQDG layers in membrane which intensity increases gradually when temperature is rising [74]. It could also inhibit the nonbilayer structure forming by means of making bilayer MGDG structure organization and takes part in the MGDG synthesis via regulation UDP-galactoso: diacylglycerol galactosyl transferase activity thus correcting MGDG/DGDG ratio in membrane [75, 76]. A certain role SQDG plays in the processes of protein synthesized transport. It is important because of the enforced synthesis of a wide set of specific proteins during a stress action. The transit peptide inserts most efficiently in monolayers of PG, SQDG and MGDG suggesting that these lipid classes are mainly responsible for insertion into the target lipid of membrane [72]. But among all functions the main seems to be energetical one. In photosynthesizing tissues SQDG molecules stabilize F-ATPase, protect and stabilize D1/D2 dimers and LHC II [50, 70]. SQDG and the Rieske protein interaction in the cyt *b6f* structures is also very important [77]. Photoinhibition arising at a stressor action induces degradation and cleavage of D1 protein of RC PS II [78]. However, SQDG localized on the surface of the native D1/D2 heterodimer might hold monomers together as a dimer [71, 72].

Thus, this lipid seems to be involved in the stress adaptation reactions and can be a unit of the adaptation mechanism chain.

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Рослинний сульфоліпід. III. Роль в адаптації

Резюме

Якісний і відносний вміст сульфохіновозилдіацилгліцеролу (СХДГ) у рослинах змінюється відповідно до дії стресора. Різні чинники індукують два види відповіді: загальну – на окислювальний стрес і специфічу – на конкретний стресовий фактор. Окрім того, два види відгуку спостерігаються у фотосинтезувальних і нефотосинтезувалиних тканинах. Молекули СХДГ беруть участь у реакції адаптації як регулятори цитохромок-

сидази, CF$_1$, F$_1$ і АТРаз та як агенти, що стабілізують димери D$_1$/D$_2$ і LHC II. Наявність цієї сполуки у нефотосинтезувальних тканинах може бути пов'язана з вимогою домінування негативного заряду одновалентного катіона (Na$^+$ або K$^+$) для стабілізації ліпопротеїнового комплексу. Кількісні зміни вмісту СХДГ та ацильного складу відбуваються при дії як абіотичних, так і біотичних стресорів.

Ключові слова: сульфоліпід, сульфохіновозилдіацилгліцерол, стрес.

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Растительный сульфолипид. III. Роль в адаптации

Резюме

Качественное и относительное содержание растительного сульфохиновозилдиацилглицерола (СХДГ) изменяется в ответ на действие стрессоров. Разные стрессоры вызывают два вида ответа: более общий – на окислительный стресс и специфический – на действие конкретного фактора. Кроме того, два вида реакции наблюдаются в фотосинтезирующих и нефотосинтезирующих тканях. Молекулы СХДГ участвуют в реакции адаптации как регуляторы цитохромоксидазы, CF$_1$, F$_1$, АТРаз и как стабилизирующие агенты димеров D$_1$/D$_2$ и LHC II. Роль этого соединения в нефотосинтезирующих тканях может быть связана с необходимостью доминирования негативного заряда одновалентного катиона (Na$^+$ или K$^+$) для стабилизации липопротеинового комплекса. Количественные изменения содержания СХДГ и ацильного состава происходят при действии как абиотических, так и биотических стрессоров.

Ключевые слова: сульфолипид, сульфохиновозилдиацилглицерол, стресс.

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