Plant & Fungal Research (2026) 9 (1): 23-31
https://doi.org/10.30546/2664-5297.2026.9.01.031

ISSN 2617-8001 (print), ISSN 2664-5297 (online)

The role of natural saponins in protecting the thylakoid membrane of wheat under low-temperature stress

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Abstract: Low temperatures alter the structural and functional properties of chloroplast membranes and negatively affect photosynthetic activity. In the present study, *Triticum aestivum* seedlings were incubated at 4˚C to evaluate the protective effects of triterpene saponins isolated from *Glycyrrhiza glabra* roots and steroidal saponins isolated from *Yucca aloifolia* roots, which differ in their chemical structure. The DPPH assay demonstrated free radical scavenging activity of triterpene saponins (IC_{50} = 1.26 µg/ml) and steroid saponins (IC_{50} = 7.3 µg/ml). Analysis of fluorescence and absorption spectral characteristics showed that the studied saponins contributed to the restoration of photosystem II activity under low-temperature stress, including partial recovery of electron transport processes at the $P680^+ –Q_A–Q_B$ site and stabilization of chlorophyll a_{680} and chlorophyll b_{645} absorption in the chloroplast antenna complex. In addition, treatment with saponins was associated with a reduction in PNRSV viral load in Gizella 6 cherry rootstock, as determined by ELISA. The obtained results suggest that triterpene and steroidal saponins may contribute to the maintenance of photosynthetic membrane functions under cold stress conditions through their antiradical and membranotropic properties.

Keywords: *cold stress, Glycyrrhiza glabra* L., *photosystem II, saponins, Triticum aestivum* L., *Yucca aloifolia* L.

INTRODUCTION

Photosynthesis is a sequence of redox reactions involving the absorption of photon energy by light-harvesting chlorophyll-protein complexes of the thylakoid membrane and its transfer to photosynthetic reaction centers [Baker, 2008]. One of the major causes of photosynthetic impairment under stress conditions is damage to chloroplast membrane systems [Zhang et al., 2019; Jafarova et al., 2021; Shanker et al., 2022].

Low-temperature stress induces a series of physiological and biochemical changes in plants, including the accumulation of reactive oxygen species and a decline in photosynthetic activity. Low temperatures affect the activity of photosynthetic enzymes, alter membrane fluidity, and modify the ratio of unsaturated to saturated fatty acids, leading to disturbances in membrane permeability, ion transport, and electron transport processes in chloroplasts and mitochondria [Yang et al., 2017; Bychkov et al., 2020; Kurepin et al., 2013; Bártolo et al., 2023]. These changes negatively affect energy metabolism and the functional integrity of photosynthetic membranes. Plant secondary metabolites play an important role in regulating oxidative processes and protecting plants against stress-induced damage [Cui et al., 2020; Gill, Tuteja, 2010; Ganiyeva et al., 2021].

Among plant secondary metabolites, saponins have attracted considerable attention because of their biological activity and their interaction with biological membranes. Depending on plant species and physiological conditions, both the content and biosynthesis of saponins may vary substantially, suggesting an important role in plant metabolism and adaptation [Pastorino et al., 2018; Ganiyeva et al., 2024]. Due to their amphipathic structure, saponins can interact with membrane lipid components and influence membrane properties. Their antiradical activity has also been associated with protection against oxidative stress [Akinpelu et al., 2014].

Glycyrrhiza glabra L. is an important source of triterpene saponins, whereas *Yucca aloifolia* L. contains steroidal saponins differing in chemical structure [Pastorino et al., 2018; Jiménez et al., 2021; Kato et al., 2022; Chuyen, 2023]. Several *Glycyrrhiza* species

Received: 15.01.2026; Received in revised form: 17.02.2026; Accepted: 29.05.2026

Citation: Dadashova, S. B., Babayeva, G. Kh., Askerova, A. J., Huseynova, N. B., Hummatova, S. T., & Ganiyeva, R. A. (2026). The role of natural saponins in protecting the thylakoid membrane of wheat under low-temperature stress. *Plant & Fungal Research*, *9*(1), 23-31.

occur in the Republic of Azerbaijan and differ in their morphological and phytochemical characteristics [Amirova, 1993; Ibadullayeva, Alakbarov, 2013; Askerov, 2016]. Because triterpene and steroidal saponins differ structurally, comparison of their biological effects may provide useful information regarding their potential protective roles under stress conditions. In addition, steroidal saponins have been associated with a variety of biological activities, including antioxidant and antiviral effects [Cui et al., 2024].

Therefore, the aim of the present study was to evaluate the antiradical activity of triterpene and steroidal saponin extracts and to investigate their effects on photosystem II (PSII) activity and chlorophyll spectral characteristics in *Triticum aestivum* L. seedlings exposed to low-temperature stress. Moreover, the possible effect of the studied saponins on PNRSV viral load in Gizella 6 cherry rootstock was assessed.

MATERIAL AND METHODS

Plant material and experimental conditions: The study included two experimental approaches: (i) evaluation of the antiradical activity of saponin extracts and their effects on photosynthetic membrane functions under low-temperature stress, and (ii) assessment of their effect on PNRSV infection.

The antiradical activity of crude triterpene saponin extracts obtained from the roots of *G. glabra* and crude steroidal saponin extracts obtained from the roots of *Yucca aloifolia* L. was investigated using seven-day-old wheat plants (*Triticum aestivum* L. 'Bereketli 95'). Seedlings were grown at 24˚C under a light intensity of 250 μW/cm² for seven days and subsequently transferred to media with or without saponin extracts at 4˚C.

Trolox, and 2,2-diphenyl-1-picrylhydrazyl (DPPH) were purchased from Sigma-Aldrich Pte. Ltd. (Singapore). For PNRSV detection, a BIOREBA ELISA kit was used, including extraction buffer (10×/5×), coating buffer, conjugate buffer (10×), substrate buffer (5×), wash buffer, and pNPP substrate. Ethanol was supplied by Alfa (Republic of Azerbaijan).

Experimental Design: *Extraction of total saponin extracts.* Total triterpene saponin extracts were obtained from the roots of *G. glabra* L., whereas total steroidal saponin extracts from the roots of *Y. aloifolia* L.

For each extraction, 50.0 g of plant material was mixed with 350 ml of 70% ethanol, and heated to boiling in a water bath for 1 h, followed by filtration. The residue was subsequently extracted twice with 100 ml of 70% ethanol for 40 min each.

The combined extracts were concentrated to an aqueous residue, and 10% hydrochloric acid was added dropwise until pH 3–4 was reached. The extract was then filtered through a 6-cm-thick polyamide layer on a 10-cm-diameter glass filter (POR 100).

The target fraction was eluted with 95% ethanol. The resulting ethanolic eluate was concentrated to a volume corresponding to approximately half the mass of the original plant material, mixed with acetone (1:1, v/v), and adjusted to pH 7–8 by dropwise addition of 25% ammonia solution under continuous stirring. The resulting precipitate was collected by filtration and washed with acetone and chloroform [Weng et al., 2009; Kurkin et al., 2016].

The identity of the *G. glabra* L. extract was supported by infrared (IR) spectroscopy. The corresponding spectrum is shown in Figure 1.

Determination of antiradical activity: Antiradical activity was evaluated using the DPPH radical scavenging assay according to Brand-Williams et al. [1995]. The absorbance of DPPH (2,2-diphenyl-1-picrylhydrazyl) in methanol was measured at 518 nm after 20 min using a Jenway 7305 UV-Vis spectrophotometer. Trolox (1–10 μg/ml), was used as the reference standard, and measurements were performed in cuvettes with a 10-mm optical path length. Data analysis was performed using the software provided by Perella Scientific Inc. (Amherst, MA, USA) [Molyneux, 2004].

The scavenging activity was calculated using the following equation:

IC% (inhibitory concentration 50%) = [1-(Abs_{sample}/$Abs_{control}$)] x 100.

Determination of the antiviral activity of saponins:The antiviral study was conducted using 45-day-old Gizella 6 rootstocks infected with Prunus necrotic ringspot virus (PNRSV). Plants were maintained under laboratory conditions at 26˚C at the Scientific Research Institute of Fruit Growing and Tea Growing (Guba, Republic of Azerbaijan).

Gizella 6 is a hybrid cross between *Prunus cerasus* and *Prunus canescens* used as a rootstock for sweet cherry. Five groups of five Gizella 6 rootstocks were initially infected with PNRSV. Sampling was carried out weekly for six weeks to assess the dynamics of viral infection. The infected material was treated with two groups of saponins: group 1 – steroids, group 2 – triterpenes, for six weeks. The soil was irrigated with saponins once a week at a concentration of 5 μg/mL. Infected material was confirmed for the presence of PNRSV by ELISA using the Bioreba diagnostic kit. Infected leaves were crushed,

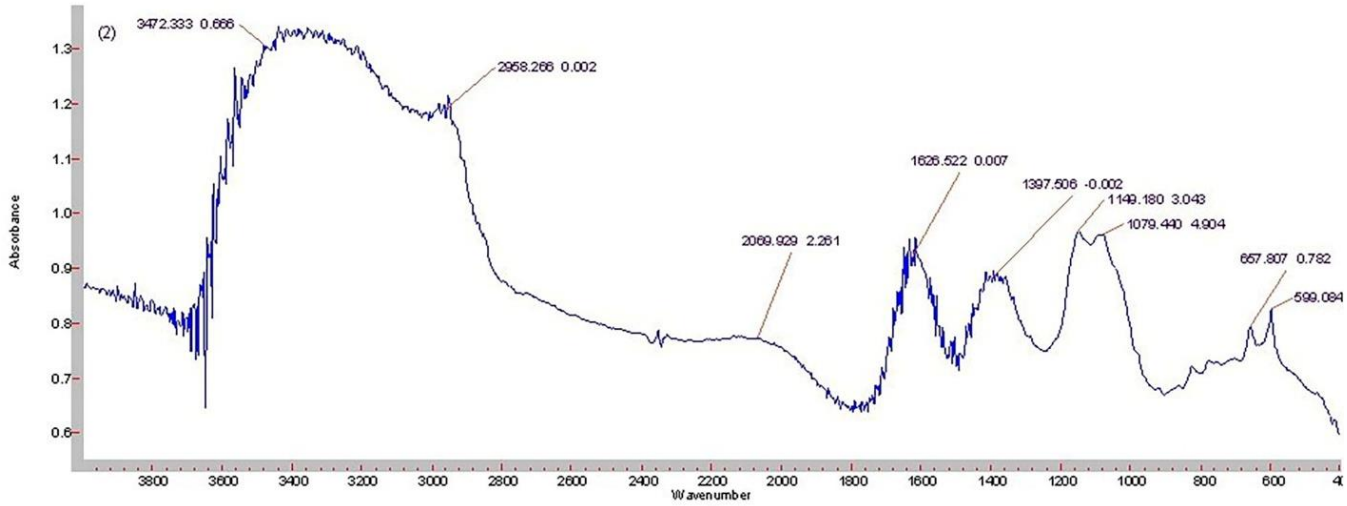

Figure 1. Infrared (IR) spectrum of the *Glycyrrhiza glabra* L. extract. The spectrum was used to support the characterization of the extract used in the biological assays.

processed to the desired consistency with buffers and the required reagents, and placed into microplates using a BioTek Epoch 2 Microplate Reader [Mekuria et al., 2003]. Optical absorbance (OD) values were determined at 405-492 nm. The dynamics of viral infection were analyzed at each time point using appropriate parametric tests. Statistical significance was accepted at $p < 0.05$.

Fluorescent and spectral characteristics: The functional activity of PS II in the thylakoid membrane was assessed by analyzing induction transitions in the kinetic curves of millisecond delayed chlorophyll α fluorescence (msDF Chlα). Measurements were performed with a fluorimeter equipped with a phosphoroscope, using a delay time of 1.25 ms between excitation and fluorescence detection [Goltsev et al., 2009; Gasanov et al., 2015] (Fig. 2).

Chlorophyll absorption spectra in the range from 400 to 750 nm were recorded on a Fourier Cary 50 Scan Varian spectrophotometer at room temperature. The homogenate obtained from 2 g of fresh weight wheat seedling leaves was centrifuged for 2 minutes at 1200 rpm. The resulting supernatant was used to obtain the absorption spectrum. A one-way analysis of variance was performed to compare the three groups (control, stress, and stress + saponins). Optical parameters of the samples are presented in the figures as relative units. Differences in parameters in the text are presented as percentages.

Data Analysis: All experiments were performed in three independent biological replicates (n = 3), and data are presented as mean ± standard deviation (SD). Statistical analysis was performed using Student's t-test or one-

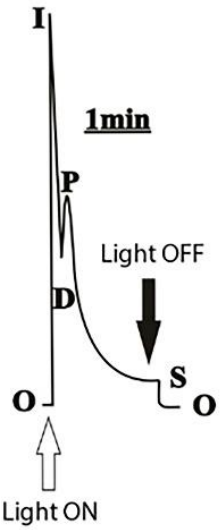

Figure 2. Standard induction curves of millisecond delayed chlorophyll a fluorescence (msDF Chlα) recorded *in vivo* in plant leaves and characterizing the electron transport chain of photosystem II: O-I, fast phase (f.ph); D-P, slow phase (sl.ph); S-O, steady state (st.s). Changes in ms DF Chl a components were evaluated using the ratio f.ph/st.ph and sl.ph/st.ph.

way analysis of variance (ANOVA), as appropriate. Post hoc comparisons were performed using Tukey's test. Statistical significance was set at $p < 0.05$.

RESULTS

The antiradical activity of steroidal and triterpene saponin extracts was evaluated using the DPPH radical scavenging assay. Based on the Trolox standard curve

(IC_{50} = 19.1 ± 0.1 µg/ml), triterpene saponins exhibited stronger radical scavenging activity (IC_{50} = 1.26 ± 0.1 µg/ml) than steroidal saponins (IC_{50} = 7.3 ± 0.2 µg/ml) (Fig. 3). These results indicate a higher antiradical capacity of the triterpene saponin extract under the experimental conditions used.

A reduction in PNRSV infection severity was observed in Gizella 6 rootstocks treated with triterpene saponin extract from the first week of treatment. Continued application was associated with a decrease in the viral load from 2.120 to 0.125 and the appearance of healthy leaves, whose number increased from the third week onward and remained stable until the end of the experiment. In plants treated with steroid saponin extract, viral load decreased from 2.000 to 0.032. Healthy leaves also appeared from the third week and remained stable throughout the experimental period (Fig.4).

The effects of saponin extracts on chlorophyll absorption under low-temperature stress were evaluated by absorption spectroscopy.

Analysis of the absorption spectra showed that, after 24 h of cold stress, the absorption of $Chl\alpha_{680}$ and Chl

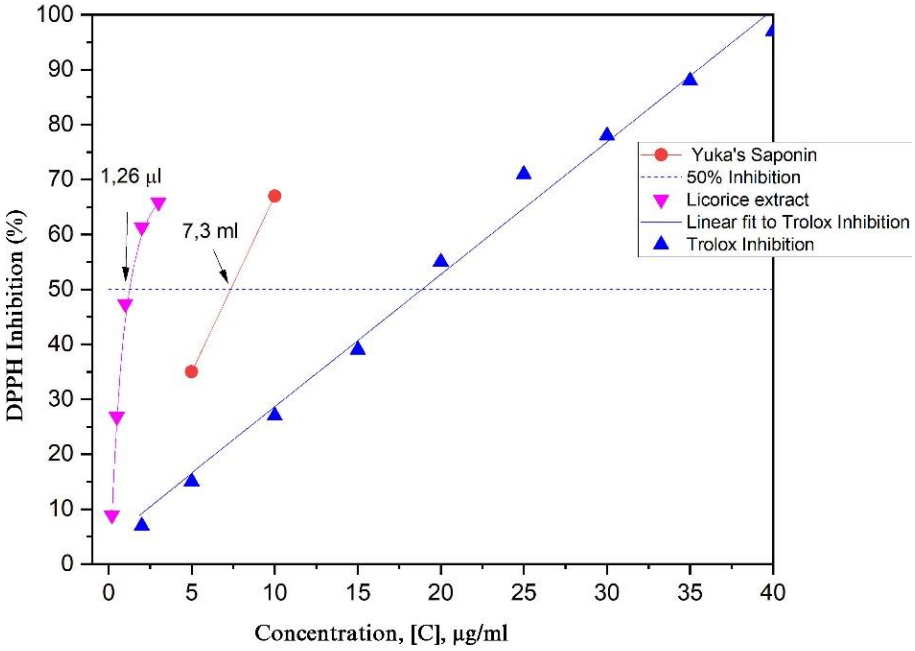

Figure 3. Antiradical activity of steroidal saponin extract obtained from *Yucca aloifolia* L. roots and triterpene saponin extract from *Glycyrrhiza glabra* L. roots, determined by the DPPH radical scavenging assay.

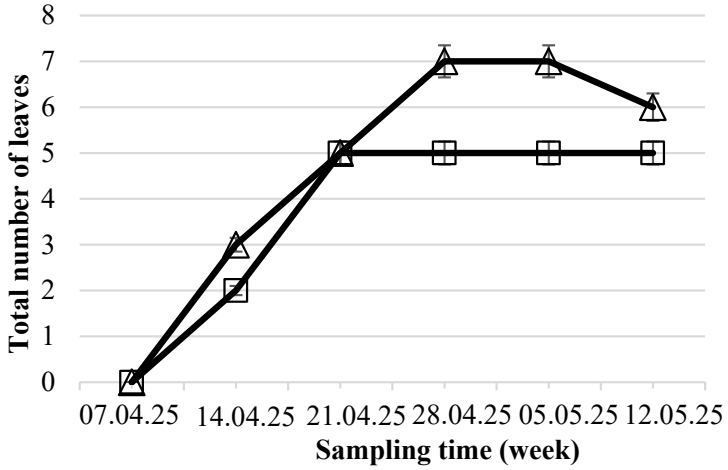

Figure 4. Effect of steroidal saponin extract from *Yucca aloifolia* L. (△) and triterpene saponin extract from *Glycyrrhiza glabra* L. (▫) on PNRSV infection in soil-grown Gizella 6 cherry rootstocks during six weeks of treatment.

β_{645} in *T. aestivum* leaves decreased by 75% and 64%, respectively, compared with the control. In the presence of triterpene saponin extract, the absorption of Chl α_{680} and Chl β_{645} increased by 67% and 62%, respectively, relative to the cold-stress treatment (Fig. 5A). Treatment with steroidal saponin extract resulted in a 38% increase in Chl α_{680} absorption and a 50% increase in Chl β_{645} absorption compared with the cold-stress treatment (Fig. 5B). The triterpene saponin extract showed a stronger effect on the restoration of chlorophyll absorption under low-temperature stress than the steroidal saponin extract (Fig. 5 A, B).

The functional activity of PS II was evaluated by analyzing changes in the fast (f.ph/st.ph) and slow (sl. ph/st.ph) phases of millisecond delayed chlorophyll α fluorescence (ms DF of Chl α) (Fig. 6 A, B). Cold stress impaired electron transport on both the donor and acceptor sides of the PS II electron transport chain. The activities of the slow and fast phases decreased by 49% and 73%, respectively, compared with the control. Treatment with steroidal saponin extract partially restored electron transport activity under cold stress. The slow phase increased by 27%, whereas the fast phase increased by 25% relative to the cold-stress treatment.

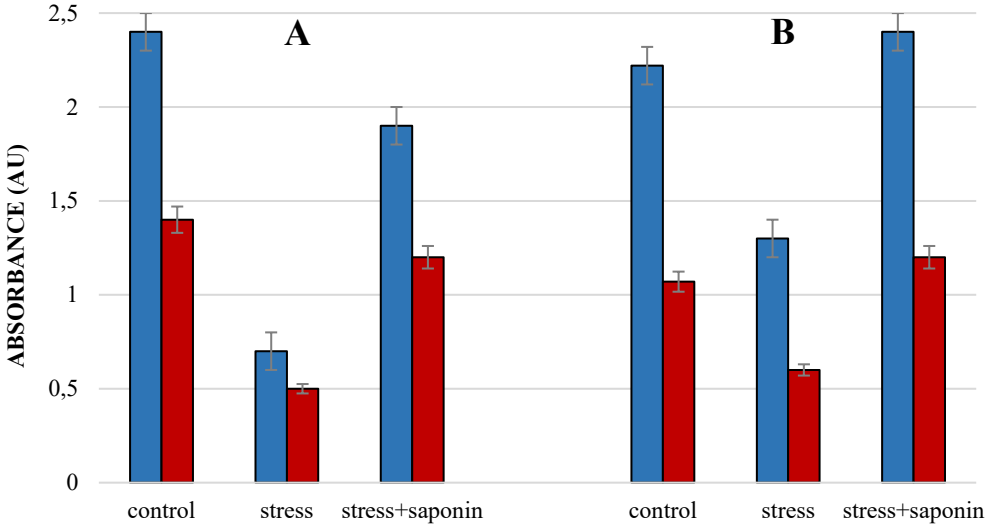

Figure 5. Effects of steroidal saponin extract from *Yucca aloifolia* L. (A) and triterpene saponin extract from *Glycyrrhiza glabra* L. (B) on the absorption of Chl α_{680} (▪) and Chl β_{645} (▪) in *Triticum aestivum* L. seedlings exposed to low temperature (4˚C) for 24 h. Control, cold-stress, and cold-stress plus saponin **e**xtract treatments are shown.

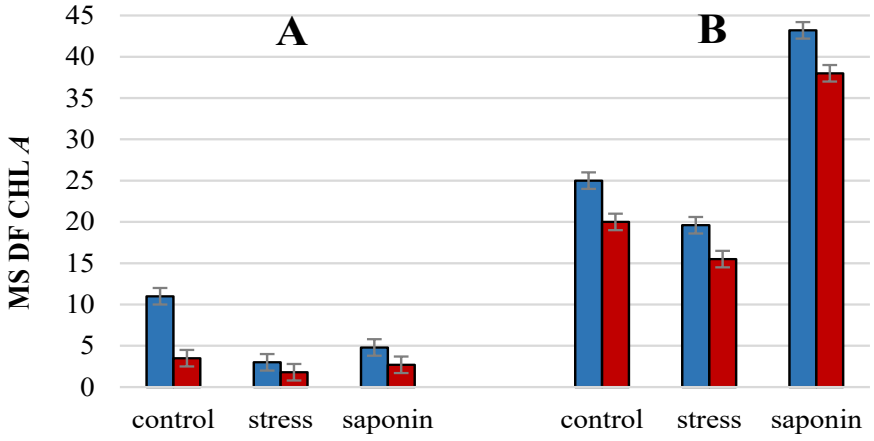

Figure 6. Effects of steroidal saponin extract from *Yucca aloifolia* L. (A) and triterpene saponin extract from *Glycyrrhiza glabra* L. (B) on PSII electron transport activity in *Triticum aestivum* L. seedlings exposed to low temperature (4˚C) for 24 hours under control, cold-stress, and cold-stress plus saponin extract conditions. Activity was evaluated from changes in the fast (f.ph/st.ph-▪) and slow (sl.ph/st.ph-▪) phases of millisecond delayed chlorophyll a fluorescence (ms DF Chl α).

Treatment with triterpene saponin extract resulted in a stronger recovery, increasing fast-phase activity by 57% and slow-phase activity by 58% compared with the cold-stress treatment.

DISCUSSION

Low-temperature stress is known to impair photosynthetic performance by altering membrane fluidity, disrupting electron transport processes, and promoting the accumulation of reactive oxygen species (ROS) [Iqbal et al., 2023; Banerjee, Roychoudhury, 2019; Muzi et al., 2016]. These alterations affect the structural and functional integrity of the thylakoid membrane and may lead to destabilization of pigment-protein complexes and reduced photosynthetic efficiency [Elfman et al., 1984; Rochaix, Bassi, 2019].

In the present study, both steroidal and triterpene saponin extracts exhibited antiradical activity in the DPPH assay, indicating their capacity to scavenge free radicals. However, triterpene saponins showed stronger activity than steroidal saponins, as reflected by their lower IC_{50} value. This higher antiradical activity was associated with a more pronounced restoration of chlorophyll absorption and photosystem II electron transport under cold-stress conditions.

Exposure of wheat seedlings to low temperature resulted in a marked decrease in the absorption of Chl α_{680} and Chl β_{645}, indicating disruption of the photosynthetic antenna system. Treatment with saponin extracts partially restored chlorophyll absorption, with triterpene saponins producing a stronger effect than steroidal saponins. These observations are consistent with previous reports showing that stabilization of pigment-protein interactions is an important component of plant adaptation to environmental stress [Elfman et al., 1984; Rochaix, Bassi, 2019].

Analysis of delayed chlorophyll fluorescence further demonstrated that cold stress impaired electron transport processes in PSII. Both saponin extracts improved the activity of the electron transport chain, although the effect was more pronounced for triterpene saponins. The observed recovery may be related to the antiradical and membranotropic properties of saponins, which could contribute to the maintenance of membrane integrity and redox balance under stress conditions [Porte et al., 2022].

In addition to their effects on photosynthetic functions, both saponin extracts were associated with a reduction in PNRSV infection in Gizella 6 rootstocks. Although the mechanisms responsible for this effect were not investigated in the present study, the results support previous reports describing antiviral properties of plant-derived saponins.

Overall, the obtained results suggest that both steroidal and triterpene saponins contribute to the protection of photosynthetic membranes under low-temperature stress, with triterpene saponins showing the stronger biological activity in the experimental systems investigated.

CONCLUSION

The results of this study demonstrate that both steroidal saponin extracts from *Y. aloifolia* L. and triterpene saponin extracts from *G. glabra* L. possess antiradical activity and contribute to the protection of photosynthetic functions under low-temperature stress. Treatment with saponin extracts was associated with partial restoration of chlorophyll absorption, recovery PSII electron transport activity, and reduction of PNRSV infection in Gizella 6 rootstocks. Under the experimental conditions used, triterpene saponins exhibited stronger biological activity than steroidal saponins. These findings support the potential role of natural saponins as protective agents against oxidative and cold-stress-induced damage in plants.

ACKNOWLEDGEMENT

The authors thank Nigar Aghayeva, an employee of the Institute of Botany for the technical support.

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Aşağı temperaturlu stres şəraitində buğdanın tilakoid membranının qorunmasında təbii saponinlərin rolu

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Aşağı temperatur xloroplast membranlarının struktur və funksional xüsusiyyətlərini dəyişdirir və fotosintetik aktivliyə mənfi təsir göstərir. Bu tədqiqatda kimyəvi quruluşlarına görə fərqlənən *Glycyrrhiza glabra* köklərindən təcrid olunmuş triterpen saponinlərinin və *Yucca aloifolia* köklərindən təcrid olunmuş steroid saponinlərin qoruyucu təsirlərini qiymətləndirmək üçün *Triticum aestivum* cücərtiləri 4°C-də inkubasiya edilmişdir. DPPH analizi triterpen saponinlərinin (IC_{50} = 1.26 μq/ml) və steroid saponinlərin (IC_{50} = 7.3 μq/ml) sərbəst radikalları tənzimləmə aktivliyini nümayiş etdirdi. Flüoressent və udma spektrlərinin təhlili göstərdi ki, tədqiq olunan saponinlər aşağı temperatur gərginliyi altında fotosistem II aktivliyinin bərpasına, o cümlədən $P680^+$ $–Q_A–Q_B$ yerində elektron ötürmə proseslərinin qismən bərpasına və xloroplast antenna kompleksində xlorofil a_{680} və xlorofil b_{645} udmasının sabitləşməsinə töhfə verir. ELISA metodu ilə müəyyən edildi ki, saponinlər Gizella 6 albalı kökündə PNRSV-nin virus yükünü azaldır. Bu nəticələr göstərir ki, triterpen və steroid saponinlər antiradikal və membranotrop xüsusiyyətlərinə görə soyuq stress altında fotosintetik membran funksiyasının qorunmasına kömək edə bilər.

Açar sözlər: *soyuq stres, Glycyrrhiza glabra* L., *fotosistem II, saponinlər, Triticum aestivum* L., *Yucca aloifolia* L.

Роль природных сапонинов в защите тилакоидной мембраны пшеницы в условиях низкотемпературного стресса

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Низкие температуры изменяют структурные и функциональные свойства мембран хлоропластов и негативно влияют на фотосинтетическую активность. В данном исследовании саженцы *Triticum aestivum* инкубировали при 4 ˚C для оценки защитного действия тритерпеновых сапонинов, выделенных из корней *Glycyrrhiza glabra*, и стероидных сапонинов, выделенных из корней *Yucca aloifolia* которые различаются по своей химической структуре. Метод DPPH продемонстрировал активность тритерпеновых сапонинов (IC_{50} = 1,26 мкг/мл) и стероидных сапонинов (IC_{50} = 7,3 мкг/мл) по нейтрализации свободных радикалов. Анализ флуоресцентных характеристик и спектров поглощения показал, что исследованные сапонины способствовали восстановлению активности фотосистемы II в условиях низкотемпературного стресса, включая частичное восстановление процессов переноса электронов на участке $P680^{+}$ $–Q_A–Q_B$ и стабилизации поглощения хлорофилла a_{680} и хлорофилла b_{645} в комплексе хлоропластной антенны. Кроме того, обработка сапонинами была связана со снижением вирусной нагрузки PNRSV в подвое вишни Gizella 6, как было определено методом ELISA. Полученные результаты позволяют предположить, что тритерпеновые и стероидные сапонины могут способствовать поддержанию функций фотосинтетических мембран в условиях холодового стресса благодаря своим антирадикальным и мембранотропным свойствам.

Ключевые слова: *холодовой стресс, Glycyrrhiza glabra* L., *фотосистема II, сапонины, Triticum aestivum* L., *Yucca aloifolia* L.