

Ph.D Thesis

The role of the lipids in the cold acclimation in winter barely

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Introduction

According to the KSH data for 2019, winter wheat was grown on 954,943 hectares, spring wheat on 16,804 hectares, our second most important cereal crop, winter barley, on 161,711 hectares, and spring barley on 101,235 hectares. The data series faithfully reflects the fact that crop growers prefer winter cereals over spring ones due to their higher productivity and thus higher yields. With this decision, of course, they take the risk of overwintering. Winter barley grown in Hungary has been tested at the Táplánszentkereszt research station for years in a sowing time experiment. Based on this, the multi-year data clearly confirm mid-October sowing as the most appropriate. While in the case of sowing in mid-October there is only an extinction of around 10%, in the sowing seasons of mid-September and November this rate is above 50%. Premature sowing often also causes viral damage, which is facilitated by settling vectors and can lead to further extinction (<http://web.archive.org/web/20160807064318/https://www.agronaplo.hu/szakgáloirat/2006/08/santofold/ossi-arpa-cultivator-keychildren>). It is considered optimal if the germinated plants reach the three-leaf developmental stage by the arrival of frosts in late November and early December. However, if we also examine the daily temperature fluctuation, we are confronted with the fact that the number of days below $-4\text{ }^{\circ}\text{C}$ in October of the last twenty years (1981-2010) was sixteen. Plants need to endure frosty nights through the field. Genetically determined frost resistance is achieved by cereals during cold hardening in several weeks. At this early stage, the seedlings are at the beginning of the hardening process. In the temperate zone of the Earth, day length, temperature, intensity and spectrum of sunlight have been changing cyclically for millions of years, depending on the seasons and time of day. Thus, it can be assumed that plants perceive these changes and react to them in a similar way regardless of their evolutionary classification. During the day, for example, the red/far-red light ratio is constant and independent of the presence of clouds but decreases significantly at dusk, when the Sun is less than 10° above the horizon. In the spectrum of the incident light, the ratio of the far-red light increases as we move away from the equator. This is mainly observed in the temperate and boreal (subarctic) zones of the northern hemisphere. The sun is low from November onwards, and it typically takes a long time for the red/far-red light ratio of the spectrum of sunlight to decrease, which can be followed by frost at night. For this reason, it seems reasonable to hypothesize that plants may use a decrease in the red/far-red ratio of light as a kind of signal that initiates cold acclimatization processes at relatively high, climatic temperatures, resulting in increased frost resistance. This hypothesis was first experimentally confirmed by Franklin and Whitelam (2007) in *Arabidopsis* model plant. Later, colleagues from Martonvásár confirmed this hypothesis on winter cereals (Novak et al., 2016). Under artificial conditions the frost resistance of winter cereals (wheat and barley) increased when the spectrum of white light used for illumination was amended with far-red light. This regulation has also been shown to involve phy A and B light receptors.

It has also been reported that blue light has an effect on the development of cold resistance in *Arabidopsis* via the cryptochrome signaling pathway (Imai, Kawamura, Nagatani, & Uemura, 2021). Based on previous research by my colleagues, it was clarified that monochromatic blue light induces the expression of the *C-repeat binding factor 14* (*CBF14*) gene involved in frost resistance in cereals (Novak et al., 2017). Previous research has shown that cold treatment

induces changes in lipid composition, as well (Chao et al., 2011; Chen, Markham, & Cahoon, 2012; Chen, Markham, Dietrich, Jaworski, & Cahoon, 2008; Falcone, Ogas, & Somerville, 2004; Markham et al., 2011; Saucedo-Garcia et al., 2011; Wang et al., 2008). However, the question of what metabolomic changes are induced by supplementing the spectrum of white light with far-red in the leaves of plants resulting in increased frost tolerance remains unanswered. It was also not known whether the addition of blue light modulates the effect of the far-red light treatment. We challenged these questions in our research.

Aims

It is well known that during cold hardening, the lipid composition of the cell membrane changes, thereby reducing its viscosity, which prevents membrane damage caused by frost. However, when setting up the experiments detailed in this work, no information was available on the lipidome change caused by the addition of far-red or blue light to the white light used to illuminate the plants. Therefore, the experiments described here aimed at the comparison of membrane lipid changes induced by cold and modulated light spectrum.

We are looking for answers to the following questions and assumptions:

- 1) How does the addition of white light combined with blue light affect the frost tolerance of barley leaves at different temperatures?
- 2) To elucidate the gene expression patterns of “key genes” that determine lipid biosynthesis under elevated far-red illumination.
- 3) How does the decreased red/far-red and combined far-red + blue light generated by the applied artificial LED light sources affect the lipid composition of barley leaves at normal (15 °C) and low (5 °C) temperatures?

Materials and methods

The selected model plant was *Hordeum vulgare ssp. vulgare* “Nure” genotype of winter barley. Three days after germination in the dark (21 °C), 480 seeds were planted in 36 mm diameter Jiffy-7 feeding discs (Jiffy Group, Oslo, Norway). The seedlings were then grown in a PGV-36 (Convion PGV36, Controlled Environments Ltd., Winnipeg, MB, Canada) phytotron chamber, where the light was provided by modulated ceiling LED illumination with a 12-hour photoperiod. Plants were grown for fourteen days under white light illumination (Philips Lumileds, LXZ2-5790). The intensity of light was 250 $\mu\text{mol m}^{-2} \text{s}^{-1}$ (PAR) and the temperature was 15 °C. The plants were irrigated with ½ Hoagland's medium (Hoagland & Arnon, 1938).

When the plants reached the three-leaf stage equivalent to 13 at the Zadok scale (Zadoks, Chang, & Konzak, 1974), we started the treatments. For the treatments, we used two different temperatures (5 and 15 °C) and four different spectral light configurations (white light (Philips Lumileds, LXZ2-5790), combined white and far-red light (Edison Edixeon, 2ER101FX00000001), combined white, far-red and blue light (P-Tech, PLBT- 3535-DP UV) and monochromatic blue light (Philips Lumileds, LXZ1-PR01)). At 5 °C we did not use monochromatic blue light illumination. The modulated LED light panel was divided into four or three separate parts for light treatments at 15 and 5 °C, respectively. The total illuminance

was 250 $\mu\text{mol m}^{-2} \text{s}^{-1}$ photon flux density in all cases. The ratio of the R/FR was ~ 0.5 and the blue/red was ~ 1.8 . To simulate the average temperatures for October and November we set 15 °C for ten days. In the second stage of the treatment the cold was imitated by reducing the temperature to 5 °C under the same light conditions (but we did not use at this part the monochromatic blue light illumination) for seven days.

After the treatments, the frost resistance of the leaf segments was determined by conductance measurements according to Webb et al. (1994). Leaf samples were frozen in a liquid Grant GP-200-R4 freezer (Grant Instruments, Sepreth, UK). The freezing temperatures for plants grown at 15 °C were -5, -7, and -9 °C. For those maintained at 5 °C for one-week, freezing temperatures of -8, -10, and -12 °C were used for one hour.

We also tested the frost tolerance of barley leaves by measuring the chlorophyll-a fast fluorescence transient before and after 2 and 24 hours the following freezing protocol: 9 h 2 °C, 1 h 0 °C, 4 h -2 °C, 1 h -3 °C, 1 h -4 °C, 1 h -5 °C, 5 h -6 °C, 1 h -5 °C, 1 h -3 °C, 1 h 0 °C. The maximum (F_v/F_m) and actual efficiencies ($Y(II)$) of PSII was determined from the fluorescence transient measured by using a pulse amplitude modulated PAM-2000 fluorometer (Heinz Walz GmbH, Effeltrich, Germany).

It is well known that the lipid composition of the membrane and the cold response of organisms are strongly related and that the lipid biosynthesis is also regulated by the CBF gene family. We examined the lipid composition of the collected snap frozen leaf samples for lipid extraction. Leaves were collected separately from three plants and stored at -80 °C until processing. Lipids were extracted by Welti et al. (2002) and the dry weight of extracted leaves were determined.

Mass spectrometric analysis of the total lipid extract was performed by MS-based method in the analytical laboratory of the Kansas Lipidomics Research Center (https://www.kstate.edu/lipid/analytical_laboratory/lipid_profiling/index.html).

Determination of ESI-MS/MS lipid profile automated electrospray ionization-tandem mass spectrometry was used. Data collection, analysis, and acyl group identification were performed as described earlier (Xiao et al., 2010). The response factor of internal standards was quantified according to Welti et al. (2002).

Lipid extracts were introduced into the ESI source by continuous injection on a triple quadrupole MS/MS (API4000, ABSciex, Framingham, MA, USA). Data processing is described on the Kansas Lipidomics Research Center website:

https://www.k-state.edu/lipid/analytical_laboratory/lipid_profiling/index.html.

The different molecular species were identified based on the particular head group fragment and its mass. Quantities were calculated in mol%. An average value was used to compare the peaks in the sample and the peaks in the internal standards. 1 signal unit are equivalent to 1 nmol of internal standard from the same lipid group (usually by correction for variance based on m/z) (https://www.k-state.edu/lipid/analytical_laboratory/protocols_and_methodology/lipid_extraction_arabidopsis_leaves/index.html). Production scanning can be used to

determine the head group or other fragments formed and to identify fatty acid groups, especially for polar lipid species.

The unsaturation index of each lipid molecule was determined according to the following formula: $DBI = [\sum (\% \text{ normalized signal intensity} / \text{dry weight of lipid type} \times \text{number of double bonds})] / 100$ (Falcone et al., 2004).

The gene expression examination has been made by the following. Total RNA was isolated from the collected leaf samples using the Directzol® RNA MiniPrep kit (Zymo Research Corp., Irvine, CA, USA) according to the manufacturer's protocol. Subsequently, cDNA libraries were prepared using eighteen primers of Moloney Murine Leukemia Virus (M-MLV) reverse transcriptase and oligo (dT) (Promega Corporation, Madison, WI, USA). Relative expression levels were determined using the KAPA SYBR® FAST, Master Mix (2X), Universal qPCR kit (Kapa Biosystems, Inc., Wilmington, MA, USA), CFX96 Touch™ real-time PCR detection system (Bio-Rad Hungary Ltd., Budapest), Hungary). PCR primers were designed using NCBI-Primer Design Tool (National Biotechnology Information Center, Bethesda, MD, USA) software. Relative expression levels were calculated by the $\Delta\Delta C_t$ method using cyclophilin as a reference gene (Livak & Schmittgen, 2001). After evaluating the data, we focused primarily on the genes of the major enzymes involved in lipid metabolism.

The results presented are the means \pm SEM calculated from the measurements of at least three independent experiments in each case. For statistical analysis one-way ANOVA was performed with Dunnett's posthoc test using one-day samples grown in white light at 15 °C as controls. In some cases, t-test was used.

Summary

The development of genetically determined frost tolerance in plants requires a long acclimatization process (cold hardening), which is mainly determined by the ambient temperature and light conditions. As plants adapt to the cold, the composition of the lipid membranes of their cells changes dynamically. We also sought an answer to the question of how the addition of white light combined with far-red and blue light affects the membrane lipid composition of barley leaves at different temperatures. Within the scope of this question, we primarily examined the expression pattern of the major genes involved in lipid biosynthesis, lipid composition, and double-bond content of lipid acyl chains in barley leaves.

Based on our results, we can draw the following conclusions:

1. *Based on the conductivity and chlorophyll-a fast fluorescence transient measurements used to determine frost tolerance, it can be stated that the enrichment of white light in far-red and blue light increases the frost tolerance of barley.* The addition of blue light at 15 °C helps maintain the integrity of the membranes. Lipid metabolism is affected by blue and far-red light signal.
2. *Far-red light affects the expression of some key genes involved in lipid metabolism.* Far-red illumination multiplies the expression of *DGDI* at 15 °C regardless of the length of the illumination. At low temperatures (5 °C), far-red light had less effect, and even one-day

treatment inhibited the expression of these genes. However, the amounts of MGDG and DGDG did not correlate with the expression of the *MGD2* and *DGD1* genes, as their total transcript levels were not affected by far-red light treatment.

The expression of the *NC* gene changed in parallel with the expression of *DGD1*. This change demonstrates that ceramides as signaling lipids may play an important role in the light regulation of cold acclimatization.

Elevated ratio of far-red/red illumination transiently reduced *PLD α 3* expression after one day of 5 °C treatment. Although gene expression was still lower compared to control samples kept at 15 °C, it was higher than that of control samples grown at 5 °C illuminated with white light. This phenomenon suggests that far-red supplementation has the opposite effect in this respect compared to cold treatment.

The relative expression of *LOC* may be under the control of elevated rates of far-red illumination in a temperature-dependent manner, as at 5 °C, the expression of *LOC* mRNA was decreased by the use of far-red supplemental light. From this, it can be concluded that the lipid-degrading processes of the plant are inhibited by the increased proportion of far-red illumination. It can be assumed that in this way the far-red light contributes to the increase of frost tolerance.

3. *The total lipid content of "Nure" winter barley leaf membranes changed under different spectral compositions.* It is likely that the increase in MGDG concentration in the chloroplast membrane induced by far-red and blue light supplementation may have contributed to the increase in frost tolerance of barley leaves.

It is hypothesized that the transiently higher PG content induced by the light treatments may have facilitated the proper functioning of the thylakoid membrane at 5 °C.

The amount of PC was significantly increased by blue light treatment regardless of temperature while it was not affected by far-red light.

Although the added far-red treatment did not change the PA level, the blue light and blue light combined with far-red decreased it. This trend was independent of temperature. The change in the amount of PA maybe related to the fact that PA is one of the most important precursors of lipid biosynthesis.

4. *Light spectral compositions have an effect on the DGDG/MGDG ratio of the membrane.* According to our experimental results, the DGDG/MGDG ratio decreased for light treatment. Blue light illumination reduced this ratio more strongly than the far-red supplement and this change may have contributed significantly to the increase in frost tolerance.

5. *The level of phospholipids that make up the cell membrane varies under different spectral compositions.* The amount of phospholipids is slightly increased due to the higher ratio of far-red illumination, which may improve cold tolerance. *With far-red supplementation, the amount of both PC and PE increases, but the PC/PE ratio does not change. However, the blue light treatment combined with far-red changes the amount of PC and PE in the opposite direction resulting in an increase in the PC/PE ratio.* This change is most likely one of the main

reasons why adding blue light to the white and far-red light combination further increases frost resistance. PC is known to be a component of the bilayer membrane while PE is not. An increase in the PC/PE ratio can stabilize the membrane under stress conditions.

6. *The double bond content of the fatty acid chains of the membrane forming lipids was also influenced by different light spectral compositions.* Previous findings suggest that changes in the unsaturation of the PE lipid family are associated with an increase in the frost tolerance of cereals. Our results are consistent with this statement. As well as the elevated ratio of far-red, blue light combined with far-red and monochromatic blue light increased the cold acclimatization level of “Nure” frost tolerant winter barley at 15 °C by changing the PE. As a result of the increase in the number of double bonds, the value of the double bond index of the membrane lipids also increased under different spectral compositions. Already at 15 °C, the total double bond index of the examined winter barley leaves increased due to the addition of light.

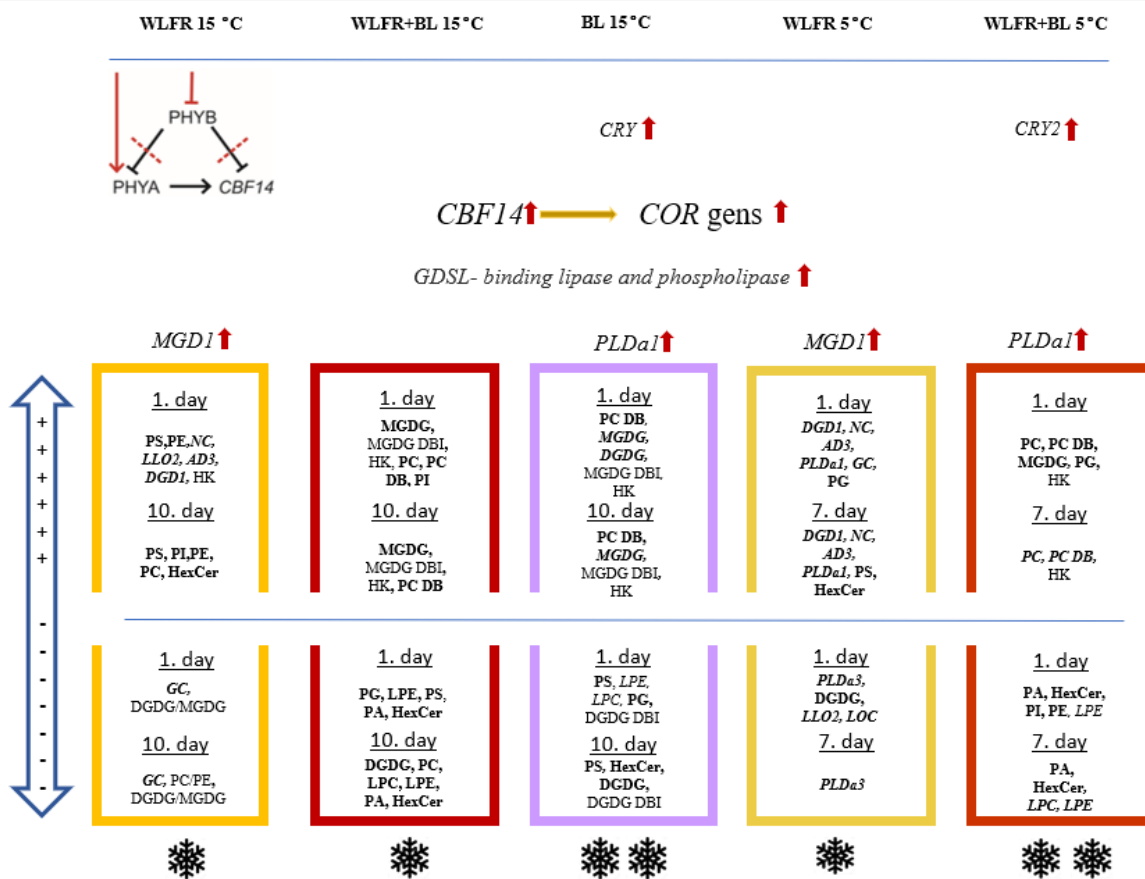
The increase in the PG double bond index under the influence of blue light should be highlighted, which may promote the balanced function of the protein complexes performing the photosynthetic electron transport chain located in the thylakoid membrane.

7. *Different spectral compositions can induce changes in species composition of various lipid families that make up the thylakoid membrane.* The amount of shorter lipid chains and their unsaturation increased. The levels of the most abundant lipid species of the thylakoid membrane forming lipid families, such as 36:6, 36:5, 36:4, 36:2, 34:3, and 34:1, help to increase the fluidity of chloroplast lipid membranes.

8. *The Lysol content of the examined leaves decreased due to the blue monochromatic illumination and the blue light supplementation combined with the far-red light treatment.* This can be explained by the increase in the amount of total lipid induced by the applied light treatment and the stimulation of the lipid biosynthetic processes.

9. *Changes in the HexCer content of the leaves were detected under different spectral compositions.* Some HexCer species were significantly elevated using white light combined with far-red light. These species may play a role in signal transduction.

Based on the results described above, we can claim that pre-hardening processes induced by modulated light composition is an important part of the frost tolerance. Overall, the change in lipidome induced by alteration of illumination correlates well with cold acclimatization. Our observations are summarized in figure 1.



1. figure Summary of the effect on cold treatment and different lighting. Samples were illuminated with far-red supplemented white light (WLFR), combined far-red + blue light (WLFR + BL), and monochromatic blue light (BL, 410 nm, only 15 °C). In addition to light treatment, two types of growth temperatures (5 and 15 °C) were used. Samples were taken on the first (day 1) and last day of treatment, which was ten days (10. day) for 15 °C and seven (7. day) for 5 °C. In each case, the leaf samples were excised from the middle of the third leaf level. The results are grouped by treatment and by change in values, gene expression, lipid families, and calculated values. During each treatment, we present the knowledge discovered so far. As well, the increased rate of far-red light supplementation inhibits phy B transcription, thereby releasing phy A transcription from inhibition and stimulating transcription of the CBF14 gene family. 410 nm illumination activates CRY at both 15 °C and 5 °C. Activation of CBF14 also triggers COR genes, a process that affects the activity of GDSL-binding lipases and phospholipases. Furthermore, it is known that the amount of the MGD1 enzyme increases regardless of temperature when exposed to the red light. Under blue light, the amount of PLDα1 enzyme also increases regardless of temperature. Statistical analysis was performed using a one-way ANOVA and Dunnett's post-hoc test using white-illuminated (WL) samples as controls. The statistical test was performed on 3-9 independent biological replicates. The figure shows the parameters that differ from the control (WL) samples by at least 0.1 significance value.

Abbreviations: alkaline ceramidase 1 (ACER1); alcohol dehydrogenase 3 (AD3); NADPH-dependent aldehyde reductase binding protein, chloroplast (ARL); digalactosyldiacyl glycerol synthase 1 (DGD); digalactosyl diacylglycerol (DGDG); non-lysosomal glucosylceramidase (GC); ceramide (HexCer); the distribution of the length and number of double bonds (HK) of the lipids forming the thylakoid membrane; linolate 9S-lipoxygenase 2 (LLO 2); lipoxygenase 2.3, chloroplast (LOC); monogalactosyl diacylglycerol synthase 2 (MGD2); monogalactosyldiacylglycerol (MGDG); mono-galactosyldiacylglycerol / di-galactosyldiacylglycerol ratio (MGDG / DGDG); neutral ceramidase (NC); phosphatidylcholine (PC); phosphatidylcholine / phosphatidylethanolamine ratio (PC / PE); phosphatidylethanolamine (PE); phosphatidylglycerol (PG); phosphatidylinositol (PI); phospholipase D-alpha 1 (PLDα1); phospholipase-D alpha 2 (PLDα2); phospholipase D alpha 3 (PLDα3); phosphatidylserine (PS)

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List of publications

MTMT ID: 10073240

The mandatory publication for the doctoral procedure:

Kovács T, Ahres M, Pálmai T, Kovács L, Uemura M, Crosatti C, Galiba G. (2020) Decreased R:FR Ratio in Incident White Light Affects the Composition of Barley Leaf Lipidome and Freezing Tolerance in a Temperature – Dependent Manner – *Int. J. Mol. Sci.*, Issue 21, Vol. 7557, DOI: <https://doi.org/10.3390/ijms21207557>

IF: 5,92

Other Scientific publications:

The effect of white light supplemented with decreased red/far red light ratio on the lipid composition and frost tolerance of barley leaves, (2021), MNBT, ISBN 978 – 615 – 01 – 2350 – 9

Kovacs T, Szalontai B, Kłodawska K, Vladkova R, Malec P, Gombos Z, Laczko – Dobos H. (2019) Photosystem I oligomerization affects lipid composition in *Synechocystis* sp. PCC 6803. *BBA – Molecular and Cell Biology of Lipids*, Vol. 1864, Issue 10, Pages 1384 – 1395, DOI: <https://doi.org/10.1016/j.bbalip.2019.06.013>

IF: 4,52

Sindhujaa V, Laczko – Dobos H, Petrova N, Herman É, Kovács T, Zakar T, Todinova S, Taneva S, Kovács L, Gombos Z, Tóth T and Krumova S. (2020) Phycobilisome integrity and functionality in lipid unsaturation and xanthophyll mutants in *Synechocystis*. *Photosynthesis Research*, Vol. 145, Pages 179–188, DOI: 10.1007/s11120 – 020 – 00776 – 170 – 5

IF: 3,57

Cumulative IF: 14,016

Conference presentations/posters related to the Ph.D dissertation:

How the membrane lipid composition changes on the effect of distant red and white light as well as cold stress, (2019), International Symposium on Plant Photobiology

Increased far – red light ratio in white light and temperature dependent changes in the composition of membrane lipids, (2019), Plant Biology CS

Increased proportion of far – red in the incident white light modifies membrane lipid composition by temperature dependent manner in winter barley, (2019), CBB5 – Budapest

The effect of white light supplemented with decreased red/far-red light ratio on the lipid composition and frost tolerance of barley leaves, (2021), MNBT, ISBN 978 – 615 – 01 – 2350

Other conference presentations/posters

The structural roles of carotenoids and lipids in cyanobacterial photosynthetic complexes characterized by CD spectroscopy, (2018), Straub Days

The structural roles of carotenoids and lipids in cyanobacterial photosynthetic complexes characterized by CD spectroscopy, (2018), FECPR, ePS – 1

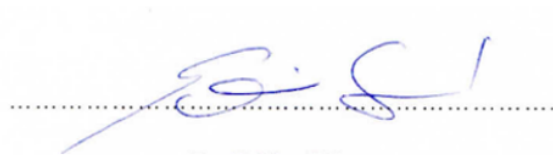
Red – light and cold stress – induced changes in the composition of membrane lipids, (2019), Straub Napok

A *synechocystis* sp. PCC6803 cytb/6f komplexénekének PetD fehérjéjének az állapot átmenetekben betöltött szerepének feltérképezése, (2020), XXIII. Tavasz Szél Konferencia

Conflict of Interest

I, myself as corresponding author of the following publication declare that authors have no conflict of interest and Terézia Kovács Ph.D. candidate had a great contribution to the published results. Results discussed in her thesis are regarded as outcomes of her own scientific work.

Kovács T, Ahres M, Pálmai T, Kovács L, Uemura M, Crosatti C, Galiba G. (2020) Decreased R:FR Ratio in Incident White Light Affects the Composition of Barley Leaf Lipidome and Freezing Tolerance in a Temperature – Dependent Manner – Int. J. Mol. Sci., Issue 21, Vol. 7557, DOI: <https://doi.org/10.3390/ijms21207557>



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