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Special issue in honor of Prof. Győző Garab

EDITORIAL

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The present special issue in honour of Győző Garab celebrates the 75th birthday of the renowned Hungarian researcher who has served as an editor for Photosynthetica for decades and contributed to many aspects of the present knowledge of the structural and functional organization of the chloroplast thylakoid membrane (Fig. 1). Győző has led a tremendously fruitful research career based at the Hungarian Academy of Sciences, Biological Research Centre, Szeged, resulting in over 300 scientific publications cited more than 10,000 times. Today he is continuing his research efforts as an emeritus research professor at the now HUN-REN Biological Research Centre, Szeged. Throughout his career, Győző formed a network of hundreds of collaborators, colleagues, and friends around the globe, relentlessly spreading his ideas and passion for his favourite subjects. In this issue, Prof. G. Govindjee has shared an illuminating account of his friendship and collaboration with Győző over the years (Govindjee 2023). Some of his most significant discoveries concerning the dynamic three-dimensional macro-organization of the thylakoid membranes were made thanks to pioneering the innovative application of an arsenal of spectroscopic and microscopic techniques in photosynthesis research.

Polarized-light spectroscopy techniques, such as linear dichroism (LD) and circular dichroism (CD) spectroscopy, have been indispensable tools for extracting structural information about the organisation of the pigment–protein complexes in the thylakoid membranes (Garab and van Amerongen 2009). Using CD spectroscopy, Győző and his coworkers revealed the existence of chiral macrodomains in the granal thylakoid membranes, having long-range order of the chlorophyll and carotenoid pigments maintained across multiple protein subunits, which gives rise to large anomalous CD signal, termed 'psi-type' CD (Garab *et al.* 1988a,b; Garab and Mustárdy 1999). The psi-type CD was attributed to the ordered macro-organization of PSII and light-harvesting complex II (LHCII) with spectral features related to different protein interactions and structural units in the membrane (Garab *et al.* 1991, Kovács *et al.* 2006, Damkjær *et al.* 2009). The pigment order in the membrane macrodomains can be directly visualized by implementing differential polarization microscopy, which proved to be a highly valuable tool for studying the anisotropic organization of biological or artificial, biomimetic systems (Finzi *et al.* 1989, Steinbach *et al.* 2005, 2009). Győző and coworkers also introduced the application of anisotropic CD (ACD) spectroscopy of oriented samples (Fig. 2) for gaining further insight into the structural arrangement and excitonic interactions of pigments in the photosynthetic membranes (Miloslavina *et al.* 2012, Nielsen *et al.* 2016, Akhtar *et al.* 2019).

Fig. 1. Győző Garab at Villa Lanna in Prague on the occasion of Photosynthetica's 50th anniversary (2017).

By mainly observing the psi-type CD of native chloroplasts and thylakoid membrane models, Győző revealed a remarkable dynamic flexibility of the thylakoid membrane in response to physical and physico-chemical stimuli, especially (unsurprisingly) light (Garab *et al.* 1988c, Barzda *et al.* 1996, Szabó *et al.* 2008). Most surprisingly, the light-induced reversible changes in

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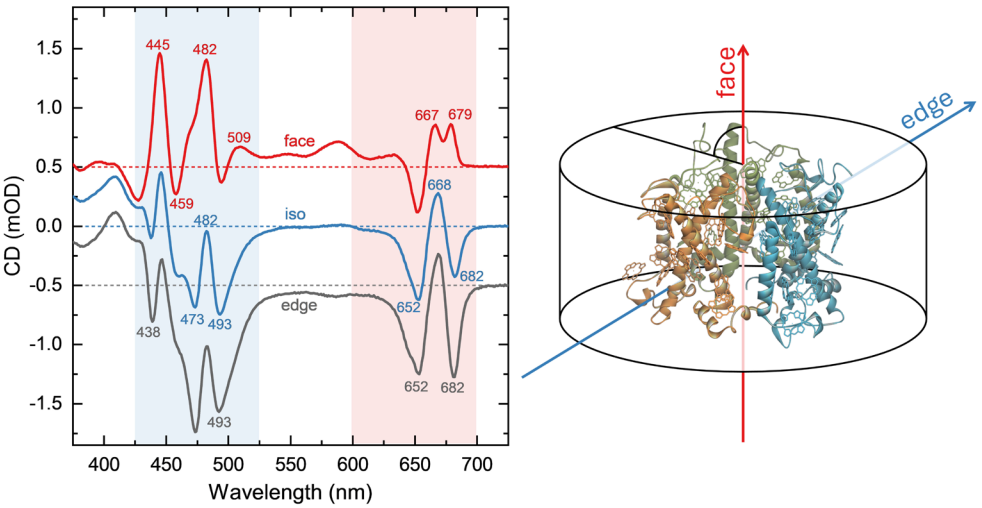

Fig. 2. Anisotropic CD spectra of reconstituted LHCII membranes. *Left*: Isotropic CD (*blue*) and face-aligned ACD (*red*) spectra recorded from dehydrated reconstituted LHCII membrane patches and edge-aligned ACD (*grey*) calculated as $(3CD_{iso} - ACD_{face})/2$. *Right*: Schematic illustration of the direction of the measuring beam with respect to the LHCII trimer structure for face-aligned and edge-aligned ACD. Reproduced from Akhtar *et al.* (2019).

the membrane macro-organization detected by CD were not only pertinent to whole thylakoid membranes and chloroplasts but also to isolated macroaggregates containing only LHCII and lipids and a certain multilamellar order (Barzda *et al.* 1996, Simidjiev *et al.* 1998, 2011). Several additional observations, such as the independence of the reorganizations on the photoinduced electron transport and their light and temperature dependence characteristics led to the proposal of a novel thermo-optic mechanism of light sensing and structural regulation in the chloroplast thylakoid membranes (Istokovics *et al.* 1997, Cseh *et al.* 2005, Holm *et al.* 2005). Győző and coworkers demonstrated that dynamic reversible reorganizations can be followed by other independent techniques as well, such as electron microscopy (Hind *et al.* 2014) and especially small-angle neutron scattering (Fig. 3), which can be applied not only to isolated systems but also to monitor dynamic membrane reorganizations in the whole algal cells and plant leaves (Nagy *et al.* 2011, 2012; Posselt *et al.* 2012, Ünnep *et al.* 2014, 2017, 2020; Nagy and Garab 2021).

Lipids are an essential structural component of all biological membranes and their role in the dynamic macro-organization and function of the thylakoid membranes has been a main focus of Győző Garab's research (Simidjiev *et al.* 1998, 2000; Garab *et al.* 2000, Páli *et al.* 2003). Thylakoid membranes have a unique lipid composition containing primarily galactolipids and substantial amounts of the non-bilayer forming monogalactosyldiacylglycerol (MGDG). The physiological significance of non-bilayer lipids in the thylakoid and, in fact, all energy-converting membranes, has remained enigmatic. Győző and coworkers, using different spectroscopic tools, especially ^{31}P-NMR, have shown the dynamic lipid polymorphism in the chloroplast thylakoid membranes with the co-existence of lamellar and non-lamellar, or non-bilayer phases and their response to external environmental factors (Krumova *et al.* 2008, Garab *et al.* 2016, 2017; Kotakis *et al.* 2018, Dlouhý *et al.* 2020, 2022a). A dynamic exchange model (DEM) was proposed, according to which non-bilayer phases play key roles in the lipid exchange between membrane compartments and several enzymatic processes not only in photosynthesis but also in respiration (Garab *et al.* 2017, 2022; Gasanoff *et al.* 2021, Dlouhý *et al.* 2022b).

Light induces rearrangements on fundamentally different structural levels of the photosynthetic apparatus – from molecular vibrations to chloroplast and leaf movements. In the photosystems, the absorbed light energy induces electron and proton motions creating large transient electric fields. The charge separation in PSII, specifically the reduction of the primary quinone acceptor Q_A has been associated with the variable fluorescence of PSII that is a staple tool in photosynthesis research (Papageorgiou and Govindjee 2004). Győző and coworkers have accumulated evidence (Fig. 4) that the Q_A model of PSII fluorescence is incomplete and that successive charge separation events driving structural rearrangements in the PSII reaction centre are a key component of the fluorescence induction phenomenon (Schansker *et al.* 2014, Magyar *et al.* 2018, 2022, 2023; Sipka *et al.* 2019, 2021). This sets the chlorophyll fluorescence induction on new grounds, necessitating a re-evaluation of the variable fluorescence as a measure of photochemical quantum efficiency and the significance of structural dynamics of PSII during the transition from dark to light-adapted state.

In this special issue honouring Győző Garab, we have collected personal and historical accounts, as well as review articles and new research articles that related to these aspects of the structure and function of the thylakoid membranes – from the three-dimensional organization of the photosynthetic complexes and visualizing membrane

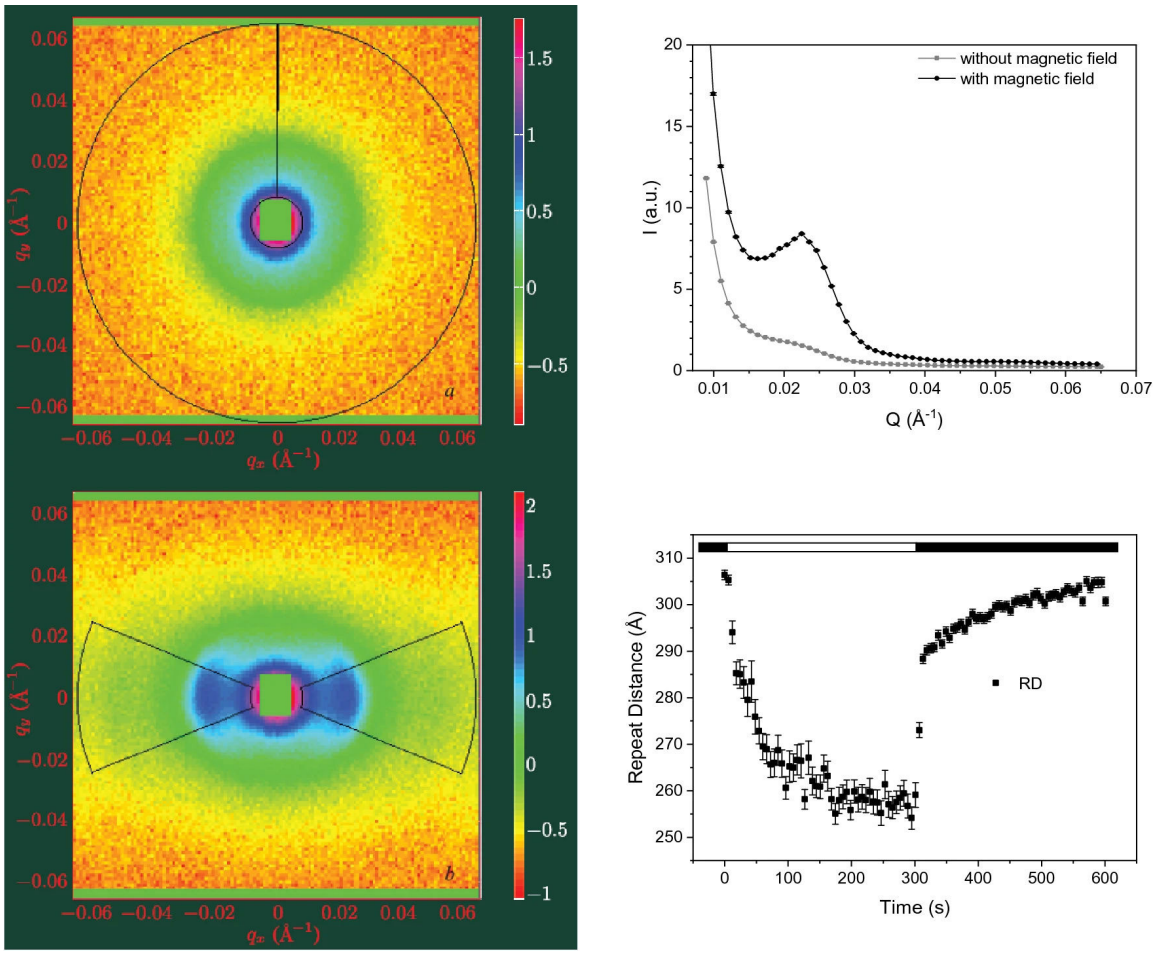

Fig. 3. Dynamic reorganizations in thylakoid membranes revealed by small-angle neutron scattering. *Left*: 2-D scattering profiles of isolated spinach thylakoid membranes in the absence and presence of 1.5 T magnetic field (*upper and lower panels*, respectively); black sectors represent the area of radial averaging; colour codes represent the differential scattering cross-section values in a logarithmic scale in arbitrary units. *Right*: radially averaged SANS profiles (*top*) and light-induced changes in the membrane repeat distance calculated from the peak position of the SANS profile (*bottom*). The figure is reproduced from Nagy and Garab (2021), published by Springer.

microdomains, the role of lipid and protein interactions and dynamics to novel uses of chlorophyll fluorescence.

Győző's most successful research direction is the biophysical aspects of the organization of photosynthetic membranes. A review paper focusing on the molecular organization of the light-harvesting complex of PSII demonstrates the importance of this topic. Besides Rubisco, LHCII is one the most abundant protein on the Earth. A review paper by Janik-Zabrotowicz and Gruszecki, highlighting the latest results, demonstrates the multiple roles of LHCII (Janik-Zabrotowicz and Gruszecki 2023). Under low light conditions, it is beneficial if the system can use the available light energy with as much efficiency as possible. They demonstrate the strategies related to LHCII, with the help of which the system is optimized for the most efficient use of light. Among others, these include the recycling of energy released from LHCII as heat and utilized to power the linear electron transfer between PSII and PSI; the monomerization of LHCII trimers; and the involvement of the xanthophyll cycle. On the other side, the apparatus must also be protected from extreme light conditions, so the LHCII-related light protection mechanisms have also been discussed.

The lipid composition of thylakoid membranes significantly determines its structure and functions. In contrast to vascular plants, diatom thylakoids can usually be characterised by high sulfoquinovosyl diacylglycerol (SQDG) contents. Liebisch and co-workers hypothesised that this relates to their special thylakoid structure, where they are organized in bands of three thylakoids each, forming from six membranes. To test this hypothesis, they examined the influence of a reduced SQDG content in the knock-down *sqd1* mutants of *Thalassiosira pseudonana* cells. This mutant grew slower than the wild type, however, it had a high chlorophyll content per cell. The approx. 20% decrease in SQDG content did not affect the organization of thylakoid bands of three, which remained almost unchanged. They found that reduced SQDG also led to the reduction of other lipid classes, leading to a stable ratio between the different lipid classes. Furthermore, enhanced chlorophyll content led to tighter packing of pigments in the mutants, which was balanced

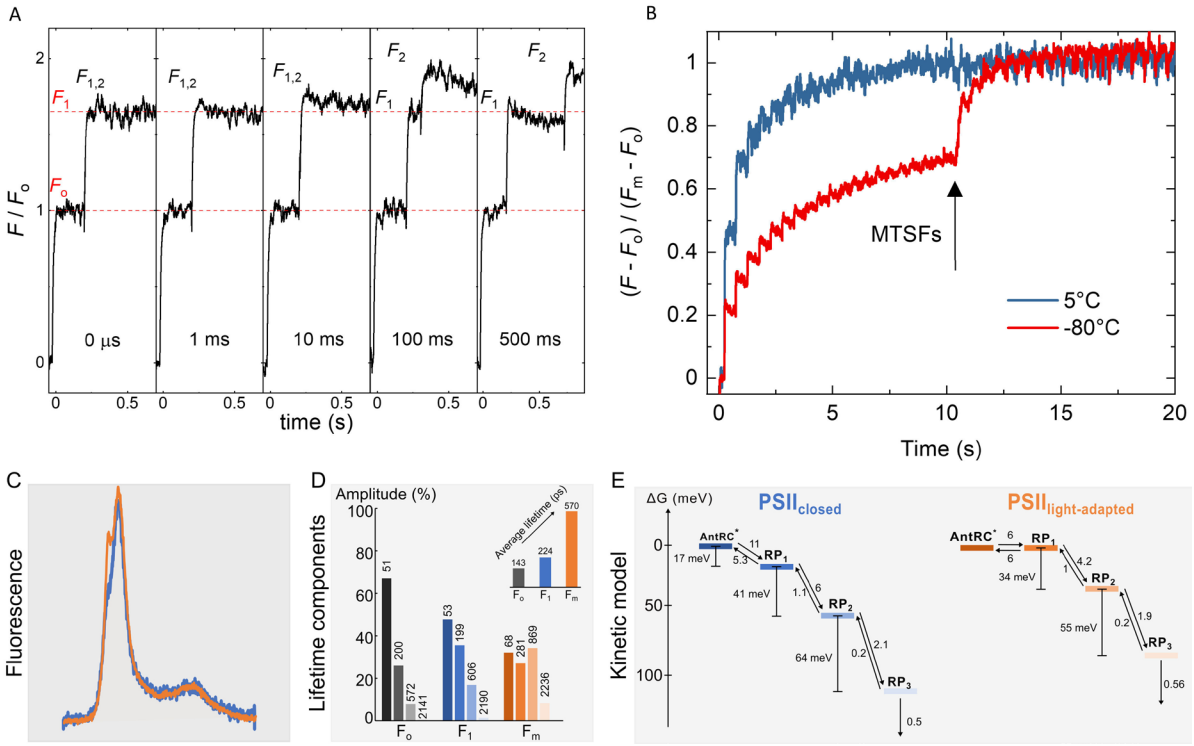

Fig. 4. Main novel features of chlorophyll fluorescence induction. Kinetic transients (*A* and *B*) induced by single-turnover saturating flashes (STSFs), 80K emission spectra (*C*), and lifetime components (*D*) of DCMU-treated PSII core complexes of *Thermosynechococcus vulcanus*, and a kinetic model (*E*) – as described by Magyar *et al.* (2023) (*A* and *B*) and Sipka *et al.* (2021) (*C–E*). Panel *A*, double-STSFs induced fluorescence increments at –80°C, with different waiting times between the two flashes, as indicated. Panel *B*, transients induced by a train of STSFs followed by multiple-turnover saturating flashes (MTSFs) (5 and –80°C). Panel *C* and *D*, respectively, normalized 80 K emission spectra, and lifetime components at 5°C, which are characteristic of F_O ($PSII_O$, *black and grey*), F_I ($PSII_C$, *blue colours*), and F_m ($PSII_L$, *red colours*) states. Reproduced from Garab *et al.* (2023).

by reduced fucoxanthin–chlorophyll protein contents and a modified PSII/PSI ratio (Liebisch *et al*. 2023).

To better understand the photosynthesis-related mechanisms within the thylakoid membranes, Fehér and co-workers investigated the effects of temperature on the biophysical properties of thylakoid lipid membranes, using the Coarse-grained molecular dynamics simulation. After visual inspection and lipid clustering, determination of density profiles of lipid and water, calculation of the deuterium order parameter, the translational diffusion coefficients of each lipid for each temperature, the compressibility modulus, which describes the resistance of the bilayer against compression, they concluded that within the range of physiologically relevant temperatures, thylakoid membranes are more fluid and water-permeable than the typical phosphatidylcholine membranes. Taking into account that besides the membrane lipids, properties of the thylakoid membranes also depend on several other factors, including among others the protein and carotenoid compositions, these results may serve as a basis for future studies to develop new models describing certain thylakoid membrane structures (Fehér *et al*. 2023).

Research aimed at increasing the photosynthetic activity of plants is particularly important from an economic point of view. One possible way to do this is to treat plants exogenously with growth-regulating substances, which can directly or indirectly affect photosynthetic efficiency, too. Krumova and co-workers demonstrated the effects of priming of pea (*Pisum sativum* L.) seeds with stabilized *Pluronic P85* nanomicelles on seedling development and certain photosynthetic processes (Krumova *et al.* 2023). Pluronics are widely available, stable, easily soluble synthetic polymers. They can penetrate cellular membranes, therefore they can be used as carriers of certain compounds, including drugs into the cells in site-specific and slow-release ways. It was shown that nanomicelles at a concentration of 0.2 g L^{-1} stimulated the root elongation of pea plants; however, at high concentrations, they impaired root length, leaf anatomy, and photoprotection. The latter statement was assumed that plants grown from seeds treated with high concentration of stabilized *Pluronic P85* micelles tried to compensate for the impaired functionality of PSII for photoprotection by increasing the number of PSII reaction centres and thus the total effective PSII quantum yield. However, at low concentrations, *Pluronic P85* can be safely used as a bio-stimulator of plant growth and development. Of course, further research is needed to reveal the exact mechanisms induced by Pluronics in the seeds to demonstrate how it can penetrate the seed coat, cell walls, and membranes; and what kind of further

short- and long-term effects it may have on the plants, including on the photosynthetic processes.

To get to know the photosynthetic processes even better, continuous methodological developments are also necessary. Széles and her colleagues demonstrated a single-cell microfluidic method combined with the classical chlorophyll *a* fluorescence induction technique (Széles *et al*. 2023). This newly developed set-up can trap single cells with parallel measurement of their photosynthetic activity. Determination of the lifetimes of photosynthetic subunits can be highly relevant for the bio-industry. They successfully determined the lifetime of the 33-kD oxygen-evolving complex extrinsic protein (PSBO) in *Chlamydomonas reinhardtii* cells. Their results showed that the photosynthetic activity could be better maintained in moderate light than under high light conditions, and with a limited carbon supply.

Live-cell imaging techniques may help understand the changes in the distribution of proteins within cells and reveal their role in photosynthesis. Several *in vivo* microscopic methods have been developed for this purpose; however, most of them have several limitations especially in the resolution, compared to other microscopic techniques. In a recent work, Kaňa and co-workers demonstrated the high applicability of a method using an Airyscan detector for *in vivo* imaging of certain thylakoid membrane proteins in cyanobacteria. This method may answer several open questions, for example about the mobility of phycobilisomes. The new super-resolution methods have advantages compared to the traditional techniques. For example, they have a sub-diffraction resolution in comparison to standard laser scanning confocal methods. Furthermore, dynamic protein behaviours within the grana/stroma-like membrane compartments can also be studied in living cells (Kaňa *et al.* 2023).

The photosynthetic performance of single living cells of the green alga *Haematococcus lacustris* was monitored by Szabó and coworkers using a combination of microfluidics and fluorescence imaging. *H. lacustris* is a biotechnologically important photosynthetic micro-organism due to its capacity to produce large amounts of the commercially valuable carotenoid astaxanthin. This is associated with a significant remodelling of the photosynthetic apparatus that was monitored in single cells throughout their transformation from green vegetative cells to red astaxanthin-rich cells by recording the fluorescence induction kinetics. The authors observed remarkable changes in the fluorescence kinetics during the transition from green to red state and a substantial drop in the fluorescence yield mainly due to the enhanced non-photochemical quenching sustained under high light treatment; however, the red cells retained their photosynthetic capacity. The single-cell measurements also revealed a considerable cell-to-cell heterogeneity during the transition, which is concealed in macroscopic measurements (Patil *et al.* 2023).

In another work, Vujin and co-workers characterized dried bacterial photosynthetic reaction centres/graphene composite on SiO_2/Si wafer. This was the first report to show that the dried bacterial photosynthetic reaction centres/graphene composite on SiO_2/Si performs a photochemical/-physical activity and this activity is in interaction with the graphene carrier matrix. The liquid-phase exfoliated graphene film was tested as a carrier in this configuration and the deposition of the photosynthetic reaction centre onto its surface formed of closely packed graphene nanoflakes was performed by the drop-casting method. Different techniques, such as Raman spectroscopy, scanning electron microscopy, atomic force microscopy, and electrical measurement based on light-induced change in I-source-drain/U-gate, were applied to investigate the properties of the complex after its drying. They demonstrated that films obtained using the Langmuir–Blodgett technique from liquid phase exfoliation graphene dispersion, have overlapping and edge-to-edge contact nanoflakes, providing the uniform large-area thin film suitable for the role of the carrier in the bio-hybrid complex for the optoelectronic devices. Their data provide useful information for the future direction of creating simple and efficient light-responsive low-power hybrid bio-optoelectronic organic devices. In the future, similar experiments can also be done using specifically modified reaction centres, in which the light-induced turnover rate and the spectral sensitivity can be modulated in a wide range (Vujin *et al*. 2023).

Since light can affect many other processes in plants apart from photosynthesis, independently of it or through it, it is therefore worth examining photosynthetic processes together with other metabolic changes. Common periwinkle (*Catharanthus roseus* L.), also known as bright eyes, graveyard plant, Madagascar periwinkle, old maid, pink periwinkle, rose periwinkle is a popular perennial ornamental plant, but it can also be used in the pharmaceutical industry. Some of its several alkaloids including vinblastine and vincristine, have been successfully used in cancer therapy. Using various photosynthesis and targeted and untargeted analytical techniques, Gholizadeh and co-workers determined the effects of growth light intensity on the primary and secondary metabolic processes. They demonstrated that reduced growth light caused a reduction in certain primary metabolites, including amino acids and sugars, and it also reduced the contents of many phenolic compounds. However, the effects of growth light were less pronounced on the alkaloid than on the flavonoid contents. Furthermore, besides the growth light, genotypic differences were also demonstrated (Gholizadeh *et al.* 2023).

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