



Jakub Oliwa*, Alina Amelina

Institute of Biology and Earth Sciences, University of the National Education Commission, Krakow,
Podchorążych 2 St., 30-084 Kraków, Poland

*jakub.oliwa@uken.krakow.pl

Exposure to blue light during morphogenesis enhances high-light tolerance in *Platycerium bifurcatum* sporophytes

Abstract

The spectral composition of light during early plant development may influence the functional organisation of the photosynthetic apparatus and plant tolerance to environmental stress. However, these mechanisms remain poorly understood in ferns. The aim of this study was to determine whether exposure to blue light during early sporophyte development affects the subsequent tolerance of the photosynthetic apparatus to high-light stress in *Platycerium bifurcatum*. Spores, gametophytes, and young sporophytes were cultivated for nine weeks under either blue or white light. Subsequently, all plants were grown for nine months under identical environmental conditions. One-year-old sporophytes were then exposed to high-light (PPFD = 800 $\mu\text{mol m}^{-2} \text{s}^{-1}$) for seven days. Photosynthetic performance was assessed using fast chlorophyll *a* fluorescence kinetics and OJIP analysis.

Plants that developed initially under blue light exhibited greater tolerance to high-light stress, maintaining higher photosynthetic performance indices and showing less pronounced impairment of photosynthetic electron transport following exposure to excessive high-light. These findings demonstrate that the spectral composition of light during morphogenesis influences the acclimation capacity of the photosynthetic apparatus. Appropriate manipulation of light quality using LED technology may therefore provide an effective strategy for improving the physiological quality of commercially propagated ornamental ferns.

Keywords: chlorophyll *a* fluorescence, OJIP, photosystem II, ornamental ferns, abiotic stress

Received: [2026.07.22]

Accepted: [2026.09.14]

Introduction

Platycerium bifurcatum (Cav.) C. Chr. is one of the most widely cultivated epiphytic fern species worldwide. Owing to its distinctive leaf morphology and high ornamental value, this species is propagated extensively using both conventional horticultural techniques and *in vitro* culture methods (Jones, Goudey, 1981; Camloh, Gogala, 1992; Liao, Wu, 2011). Recent

advances in controlled-environment horticulture have created new opportunities to manipulate plant morphology and physiology through precise regulation of environmental factors, particularly light quality.

Light serves not only as the primary energy source driving photosynthesis but also as a crucial environmental signal regulating plant morphogenesis and the physiological processes underlying photosynthetic acclimation to changing environmental conditions. The spectral composition of light influences chloroplast biogenesis, the expression of photosynthesis-related genes, pigment accumulation, and the development of photoprotective mechanisms throughout plant ontogeny (Fankhauser, 2001; Folta, Maruhnich, 2007). Increasing evidence indicates that light conditions experienced during the earliest developmental stages may induce persistent modifications in the structure and function of the photosynthetic apparatus, thereby determining its acclimation capacity later in plant development. This phenomenon has attracted considerable interest because of its potential application in modern horticultural production systems (Hogewoning et al., 2010; Hernández, Kubota, 2016).

Manipulation of light spectra using LED technology has therefore become an increasingly common strategy to improve crop performance by modifying plant morphology, photosynthetic efficiency, and tolerance to abiotic stresses (Morrow, 2008; Ouzounis et al., 2015; Bantis et al., 2018). Such approaches are particularly valuable in ornamental horticulture, where commercial quality and post-production performance depend largely on the physiological condition of plants.

High-light stress represents one of the major environmental factors limiting the quality of ornamental plants during both cultivation and post-production handling. Sudden increases or fluctuations in light intensity may impair photosystem II (PSII) function and induce photoinhibition, particularly in shade-adapted species (Demmig-Adams, Adams, 1996; Brestic, Živčák, 2013; Demmig-Adams, 2018). Consequently, increasing high-light tolerance through appropriate manipulation of developmental conditions has emerged as a promising strategy for improving the physiological quality of commercially produced ferns.

Among the different spectral components, blue light plays a particularly important role in regulating chloroplast differentiation, stomatal function, photosynthetic performance, and photoprotective responses. Blue-light-dependent signalling pathways have been shown to influence photosynthetic response and acclimation capacity in numerous angiosperm species (Folta, Maruhnich, 2007; Hogewoning et al., 2010; Hernández, Kubota, 2016). However, the developmental effects of blue light on the photosynthetic apparatus remain poorly understood in seed-free vascular plants.

Ferns exhibit photomorphogenetic responses that differ substantially from those of seed plants owing to differences in phytochrome signalling and the presence of chimeric photoreceptors that combine characteristics of phytochromes and phototropins (Briggs, Olney, 2001; Kawai et al., 2003). Previous studies demonstrated that light spectral composition affects sporophyte development, photosynthetic performance, and pigment accumulation in *P. bifurcatum* (Oliwa et al., 2016; Oliwa, Skoczowski, 2019). Nevertheless, it remains unknown whether light conditions experienced during gametophyte development and the earliest stages of sporophyte ontogeny exert long-term effects on the photosynthetic apparatus and its subsequent tolerance to environmental stresses, particularly high-light.

The present study investigated whether exposure to blue light during the earliest stages of ontogeny—including spore germination, gametophyte development, and early sporophyte formation – modifies the organisation and function of the photosynthetic apparatus and influences the subsequent response of PSII to high-light stress in *P. bifurcatum*. We hypothesized that blue light applied during early development would initially induce a transient reduction in photosynthetic performance but would subsequently enhance the acclimation capacity of PSII through developmental priming, thereby increasing tolerance to high-light stress in mature sporophytes.

Materials and Methods

Plant material and growth under different light spectra

Fresh spores of *Platycerium bifurcatum* were collected from 13-year-old sporulating parent plants maintained in the living collection of the University of the National Education Commission, Kraków, Poland. Mature spores were obtained from acrostichoid sori located at the apical regions of fertile sporotrophophylls that had ceased their assimilatory function. The spores were gently scraped from the fronds using a sterile scalpel and cleaned of scales by gentle shaking. Spores were sown onto sterile Petri dishes containing agar-solidified Menon and Lal medium, which is commonly used for fern and moss cultures (Menon, Lal, 1974). The spores were evenly distributed over the surface of the solidified medium using a sterile fine brush.

Plants were cultivated in a controlled-environment growth chamber (Angelantoni EKOCHL700, Angelantoni, Italy) equipped with white fluorescent lamps supplemented with far-red radiation. Four Petri dishes were maintained under white light at a photosynthetic photon flux density (PPFD) of $150 \pm 10 \mu\text{mol m}^{-2} \text{s}^{-1}$, with a 16 h light /8 h dark photoperiod, day/night temperatures of 24/16°C, and 60% relative humidity. A second set of four Petri dishes was

cultivated under monochromatic blue LED light (peak wavelength 450 nm) at the same PPFD ($150 \pm 10 \mu\text{mol m}^{-2} \text{s}^{-1}$) and identical environmental conditions. The emission spectra of both light treatments are presented in fig. 1.

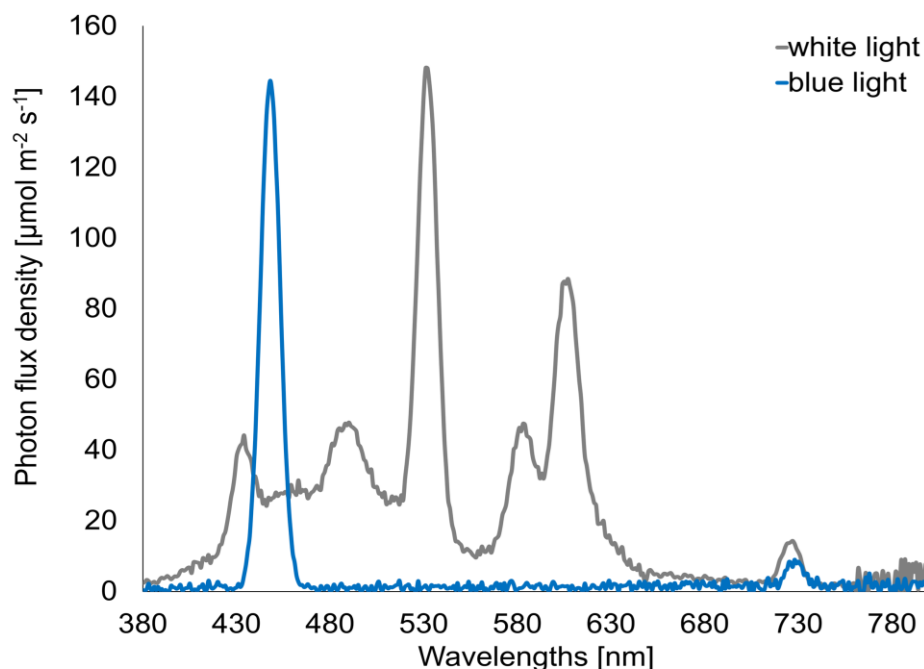


Fig. 1. The dependence of light intensity on wavelength in the spectrum used in the phytotron chamber

Developing gametophytes were misted with distilled water twice weekly. After 30 days of culture on agar, gametophytes from both light treatments were transferred to containers filled with a commercial peat-based substrate (*Compo Universal*). Following the initiation of sporophyte development and degeneration of the prothalli, individual young sporophytes were transplanted into plastic pots containing the same substrate (one sporophyte per pot). Thirty sporophytes originating from each light treatment were established.

Plants remained under their respective light conditions for an additional nine weeks, maintaining the same photoperiod and environmental conditions as during spore germination and gametophyte development. Plants were irrigated weekly with equal volumes of distilled water. After this period, the ten most vigorous young sporophytes from each treatment were selected for chlorophyll fluorescence measurements. Subsequently, all plants were transferred to identical environmental conditions and cultivated for an additional nine months under white light at $150 \mu\text{mol m}^{-2} \text{s}^{-1}$, with a 16 h light/8 h dark photoperiod, day/night temperatures of 24/16°C, and 60% relative humidity. Following this common cultivation period, the high-light stress experiment was initiated.

High-light stress treatment

One-year-old sporophytes originating from the two developmental light treatments (white and blue light) were subjected to high-light stress. Five plants from each developmental treatment were exposed to high irradiance produced by high-pressure sodium lamps (Philips SON-T AGRO 400 W), resulting in a PPFD of $800 \mu\text{mol m}^{-2} \text{s}^{-1}$ under a 16 h light/8 h dark photoperiod for seven days. An additional five plants from each developmental treatment were maintained under standard growth chamber conditions ($150 \mu\text{mol m}^{-2} \text{s}^{-1}$) and served as controls. Immediately after the stress treatment, chlorophyll *a* fluorescence measurements were performed.

Chlorophyll a fluorescence measurements

Fast chlorophyll *a* fluorescence transients were measured using a portable Handy PEA fluorimeter (Hansatech Instruments Ltd., King's Lynn, UK) according to the methodology described by Strasser et al. (2000). Measurements were performed non-destructively on fully developed sporophyte leaves at an ambient temperature of approximately 22°C. Before each measurement, leaves were dark-adapted for 25 min using the manufacturer's leaf clips to ensure complete oxidation of the photosynthetic electron transport chain. Fluorescence induction was initiated using a saturating red light pulse with an intensity of $1500 \mu\text{mol photons m}^{-2} \text{s}^{-1}$. Fluorescence transients were analysed using PEA Plus software (Hansatech Instruments). The following fluorescence parameters were evaluated: F_o (minimal fluorescence), F_m (maximal fluorescence), F_v/F_m (maximum quantum efficiency of PSII photochemistry), F_v/F_o (ratio of variable to initial fluorescence), TR_o/RC (trapped energy flux per active reaction centre), ET_o/RC (electron transport flux per reaction centre), RE_o/RC (electron flux reducing PSI end acceptors per reaction centre), DIO/RC (energy dissipation per reaction centre).

The OJIP transients were analysed using fluorescence intensities recorded at the characteristic O, J, I, and P steps (20 μs , 2 ms, 30 ms, and the fluorescence maximum, respectively). Fluorescence induction curves were normalised between the O and P values before further analysis.

Statistical analysis

Experimental data were analysed using one-way or two-way ANOVA, depending on the experimental design, followed by Duncan's multiple range test at $p \leq 0.05$. Statistical analyses were performed using Statistica 13 (TIBCO Software Inc., USA) and Microsoft Excel.

Photosynthetic performance of young sporophytes developed under blue and white light

Analysis of chlorophyll *a* fluorescence parameters and OJIP transients revealed that the spectral composition of light during the earliest stages of ontogeny markedly affected the photosynthetic performance of young *Platycerium bifurcatum* sporophytes. Plants that developed from spore germination under monochromatic blue light exhibited significantly lower photosynthetic efficiency than those grown under white light (Tab. 1).

Tab. 1. Selected chlorophyll *a* fluorescence parameters of young *Platycerium bifurcatum* (Cav.) C. Chr. sporophytes grown from spore germination to week 13 under white or blue light in a growth chamber. Values followed by the same letter within a column do not differ significantly according to Duncan's multiple range test ($p \leq 0.05$, $n = 10$ biological replicates)

Light spectrum	Fo	Fm	Fv/Fm	Fv/Fo	DIo/RC	TRo/RC	ETo/RC	REo/RC	PI total
blue	318a ±28	1538b ±114	0.748b ±0.015	2.954b ±0.210	0.584a ±0.071	0.171b ±0.022	0.646b ±0.024	0.187b ±0.009	0.364b ±0.059
white	325a ±16	1960a ±153	0.840a ±0.010	5.317a ±0.301	0.388a ±0.030	0.270a ±0.014	0.848a ±0.021	0.260a ±0.011	0.740a ±0.087

No significant difference was observed in minimal fluorescence (Fo), indicating that the number of active PSII reaction centres remained comparable between both developmental light treatments. In contrast, plants developed under blue light exhibited significantly lower maximal fluorescence (Fm) and a reduced maximum quantum efficiency of PSII (Fv/Fm), which was approximately 11% lower than in white-light-grown plants. Likewise, Fv/Fo, reflecting the functional integrity of the oxygen-evolving complex (OEC), was almost twofold lower in blue-light-grown sporophytes (Tab. 1).

More pronounced differences were detected in JIP-test parameters describing energy fluxes within the photosynthetic electron transport chain. Compared with plants developed under white light, blue-light-grown sporophytes exhibited reductions of approximately 37%, 24%, and 28% in TRo/RC, ETo/RC, and REo/RC, respectively. These changes indicate lower trapping efficiency and reduced electron transport both beyond Q_A and towards the terminal electron acceptors of PSI. In parallel, DIo/RC tended to increase, suggesting enhanced dissipation of absorbed excitation energy. Consequently, the total performance index (PI_{total}) which integrates the efficiency of energy absorption, trapping, and electron transport throughout the entire photosynthetic electron transport chain, was reduced by more than twofold in plants developed under blue light (Tab. 1). OJIP fluorescence transients supported these observations (Fig. 2A). Blue-light-grown plants displayed a slight depression of the J–I

phase accompanied by a relatively elevated I–P phase compared with white-light-grown sporophytes. These changes indicate slower reduction of the plastoquinone pool and lower electron transport efficiency between PSII and PSI. In contrast, the O–J phase remained nearly identical in both treatments, suggesting that blue light did not substantially affect the initial closure of PSII reaction centres but primarily influenced the subsequent stages of electron transport.

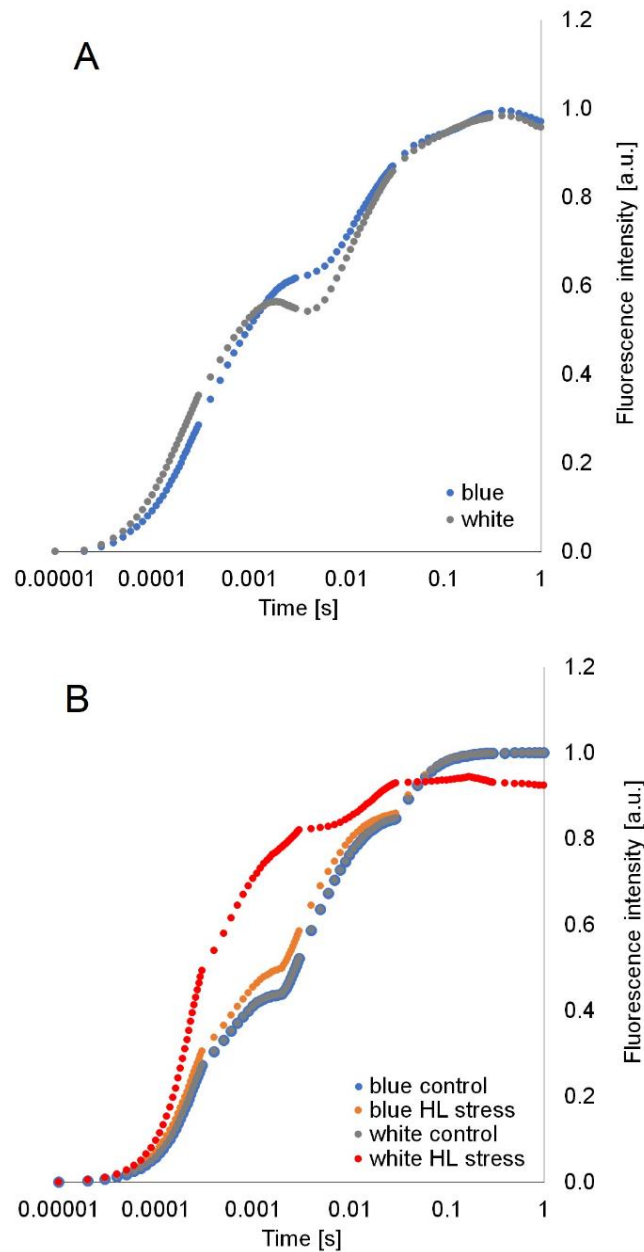


Figure 2. OJIP chlorophyll *a* fluorescence transients of young *Platyserium bifurcatum* (Cav.) C. Chr. sporophytes grown from spore germination to week 13 under white or blue light (A), and of one-year-old sporophytes after 7 days of exposure to high light (HL stress, PPFD = 800 $\mu\text{mol m}^{-2} \text{s}^{-1}$) or control conditions (PPFD = 150 $\mu\text{mol m}^{-2} \text{s}^{-1}$) (B). Values followed by the same letter within a column do not differ significantly according to Duncan's multiple range test ($p \leq 0.05$, $n = 5$ -10 biological replicates)

Response of one-year-old sporophytes to high-light stress

A markedly different response was observed after all plants had been cultivated for nine months under identical white-light conditions and subsequently exposed to high-light stress ($800 \mu\text{mol m}^{-2} \text{s}^{-1}$ for seven days). Under control conditions, no significant differences were detected between plants originating from the two developmental light environments. All fluorescence parameters exhibited similar values, indicating complete recovery of PSII photochemical performance after prolonged growth under identical environmental conditions (Tab. 2).

Tab. 2. Selected chlorophyll *a* fluorescence parameters of one-year-old *Platycerium bifurcatum* (Cav.) C. Chr. sporophytes after 7 days of exposure to high light (HL stress, PPFD = $800 \mu\text{mol m}^{-2} \text{s}^{-1}$) or control conditions (PPFD = $150 \mu\text{mol m}^{-2} \text{s}^{-1}$). Values followed by the same letter within a column do not differ significantly according to Duncan's multiple range test ($p \leq 0.05$, $n = 5$ biological replicates)

Light spectrum	Treatment	Fo	Fm	Fv/Fm	Fv/Fo	DIo/RC	TRo/RC	ETo/RC	REo/RC	PI total
blue	control	322c	1666a	0.807a	4.173a	0.339c	1.793a	1.325a	0.796a	16.030a
		± 1	± 4	± 0.000	± 0.011	± 0.002	± 0.004	± 0.003	± 0.003	± 0.110
	HL stress	354b	1613b	0.780b	3.560b	0.432b	1.737b	1.224b	0.705b	11.350b
		± 1	± 2	± 0.001	± 0.015	± 0.006	± 0.003	± 0.005	± 0.004	± 0.159
white	control	323c	1667a	0.806a	4.167a	0.341c	1.796a	1.325a	0.796a	16.000a
		± 1	± 3	± 0.000	± 0.010	± 0.002	± 0.003	± 0.003	± 0.003	± 0.088
	HL stress	447a	1499c	0.702c	2.354c	0.769a	1.577c	0.902c	0.427c	3.140c
		± 2	± 3	± 0.002	± 0.020	± 0.010	± 0.005	± 0.007	± 0.005	± 0.092

However, exposure to high irradiance revealed pronounced differences that depended on the light conditions experienced during early ontogeny. Plants that had initially developed under white light exhibited a photoinhibition characterised by an increase in Fo parameter, accompanied by decreases in Fm, Fv/Fm, and Fv/Fo, indicating considerable impairment of PSII photochemical efficiency (Tab. 2).

The largest differences were observed in parameters describing energy fluxes per active PSII reaction centre. In these plants, DIo/RC more than doubled, demonstrating a pronounced increase in non-photochemical energy dissipation. Simultaneously, TRo/RC, ETo/RC, and particularly REo/RC decreased significantly, indicating severe limitations in linear electron transport towards the terminal electron acceptors of PSI. As a consequence, PI_{total} declined almost fivefold relative to the control (Tab. 2). In contrast, sporophytes originating from the blue-light treatment exhibited substantially greater tolerance to high-light stress. Exposure to excessive irradiance resulted only in a slight increase in Fo and moderate decreases in Fm, Fv/Fm, and Fv/Fo. Likewise, reductions in ETo/RC and REo/RC were considerably smaller than those observed in plants originating from white light, while the increase in DIo/RC was

more than twofold lower. Consequently, PI_{total} remained more than three times higher in blue-light-derived sporophytes than in plants that had developed under white light (Tab. 2).

The OJIP fluorescence transients fully supported these findings (Fig. 2B). In sporophytes originating from white light, high-light stress markedly altered the shape of the J–I and I–P phases, indicating impaired reduction of the plastoquinone pool and restricted electron transport towards PSI. By contrast, OJIP transients recorded from plants originating from blue light remained similar to those of the corresponding controls, indicating that the functional integrity of the photosynthetic electron transport chain was largely preserved despite exposure to high irradiance.

Discussion

The analysis of chlorophyll *a* fluorescence kinetics and OJIP transients demonstrated that exposure to blue light during the early stages of ontogeny initially reduced the photochemical performance of developing sporophytes. However, the spectral composition of light during early ontogeny may exert long-lasting effects on the functional properties of PSII in the studied fern, as evidenced by the response of older sporophytes to high-light stress, despite their subsequent nine-month cultivation under identical growth-chamber conditions.

The pattern of changes in chlorophyll *a* fluorescence parameters revealed that, despite lower values of TRo/RC , ETo/RC , REo/RC , and PI_{total} immediately after the period of exposure to blue light, no increase in F_o was observed. This suggests that the observed response was not directly associated with PSII damage or the loss of active reaction centres, but primarily involved changes in the efficiency of energy and electron transfer in the chloroplasts of developing plants. According to the assumptions of the JIP test, parameters describing energy trapping (TRo/RC), electron transport beyond the primary quinone acceptor Q_A (ETo/RC), and the reduction of terminal electron acceptors on the PSI acceptor side (REo/RC) reflect successive levels of organisation of photosynthetic electron transport and are more sensitive to functional changes than the conventional F_v/F_m ratio (Strasser et al., 2004; Tsimilli-Michael, Strasser, 2013; Stirbet, Govindjee, 2011). The overall efficiency of successive stages of energy conversion in the photosynthetic apparatus—from the abundance of active reaction centres, through the efficiency of primary photochemistry, to electron transport towards terminal acceptors on the PSI acceptor side—is effectively integrated by PI_{total} (Kalaji et al., 2017). In *Platycerium bifurcatum*, performance index values have also been shown to reflect changes in photosynthetic activity associated with leaf development and responses to high-light stress more effectively than parameters related exclusively to PSII (Oliwa, Skoczowski, 2019).

Therefore, the simultaneous reduction in all these parameters in plants developed under blue light should be interpreted as a transient reorganisation of photosynthetic electron transport rather than as evidence of PSII photoinhibition. Such a temporary decrease in electron transport efficiency in young sporophytes does not necessarily induce a persistent limitation of plant photosynthetic capacity.

Blue light is currently widely recognised as having a dual function: it serves as a source of energy and as a signal regulating chloroplast development. In angiosperms, cryptochrome activation leads to the inhibition of the COP1/SPA complex and the stabilisation of the HY5 transcription factor, which controls the expression of genes associated with chloroplast biogenesis, chlorophyll biosynthesis, thylakoid membrane organisation, and the composition of photosynthetic complexes (Gangappa, Botto, 2016). Consequently, light quality may influence the differentiation of chloroplasts rather than merely their current photosynthetic activity. Although this mechanism has been studied most extensively in model angiosperms, it currently provides the most plausible conceptual framework for explaining the long-term effects of the light environment on the development of the photosynthetic apparatus.

In this context, our results are consistent with the hypothesis that blue light acting during early ontogeny initiates a process leading to the reorganisation of the functional properties of PSII, the first manifestation of which is a transient decrease in electron transport efficiency. However, it should be emphasized that the present study does not allow the observed effect to be attributed to a specific molecular mechanism or confirm the involvement of the CRY–COP1–HY5 pathway in *P. bifurcatum*. It may only be concluded that the pattern of changes in the JIP-test parameters is consistent with a model involving the functional reorganisation of chloroplasts during sporophyte development. Identification of the mechanisms responsible for the persistence of this effect will require further studies, including analyses of regulatory gene expression, chloroplast ultrastructure, and photoprotective processes.

The persistent nature of the changes described above was demonstrated by the photosynthetic response of one-year-old sporophytes to high-light stress. Despite the prolonged cultivation of all plants under identical light conditions, earlier exposure to blue light clearly affected the functioning of PSII during subsequent stress. We therefore suggest that blue light modified the functional stability of PSII, which became apparent later under conditions of excess excitation energy. This interpretation is supported by the pattern of changes in JIP-test parameters, particularly the higher ETo/RC, REo/RC, and PI_{total} values compared with plants whose early developmental stages occurred under white light. During high-light stress, plants originating from the blue-light treatment also showed a markedly smaller decrease in Fv/Fm. However, this parameter reflects the maximum photochemical efficiency of PSII after dark

adaptation, whereas the parameters listed above provide a more comprehensive description of the efficiency of the photosynthetic electron transport chain, including both PSII activity and the efficiency of electron transfer towards acceptors on the PSI side (Strasser et al., 2004; Tsimilli-Michael, Strasser, 2013; Stirbet, Govindjee, 2011). The maintenance of higher REo/RC values in plants originating from the blue-light treatment reflects their ability to sustain electron flow through the entire photosynthetic electron transport chain and to preserve the balance between electron supply from PSII and electron utilisation on the PSI acceptor side. Maintaining this balance is essential for chloroplast redox homeostasis. Its disruption leads to over-reduction of electron transport chain components, thereby increasing the probability of reactive oxygen species formation and photoinhibition (Foyer et al., 2012). Although the present study did not include measurements of reactive oxygen species or redox-related parameters, the maintenance of higher REo/RC values is consistent with a model assuming greater functional stability of photosynthetic electron transport under excessive irradiance. It should nevertheless be emphasized that the greater stability of electron transport may also have resulted from changes in thylakoid membrane organisation, remodelling of photosynthetic complexes, more efficient non-photochemical energy dissipation, improved regulation of redox homeostasis, or altered activity of chloroplast signalling pathways. All these processes contribute to plant responses to excess light.

Blue-light photoreceptors interact with a regulatory network controlling chloroplast development and the expression of genes associated with photosynthetic function, whereas signals generated within chloroplasts—including redox-dependent signals—participate in the regulation of nuclear gene expression through retrograde signalling mechanisms (Chan et al., 2016). These mechanisms enable the coordination of chloroplast development with the light conditions prevailing during ontogeny. Although they have been characterized most extensively in angiosperms, they provide a possible interpretation for the phenomenon observed here, which has not previously been described in ferns.

Previous studies on *P. bifurcatum* demonstrated a strong influence of light quality on morphogenesis, leaf anatomy, and current photosynthetic properties (Oliwa et al., 2016), indicating substantial phenotypic plasticity in this species. In *P. bifurcatum* sporophytes exposed to high irradiance, parameters describing electron transport, including ETo/RC and REo/RC, as well as the photosynthetic performance index PI_{total} , responded substantially earlier than Fv/Fm, reflecting progressively increasing functional limitations of the entire electron transport chain (Oliwa, Skoczowski, 2019). The present study suggests that chlorophyll *a* fluorescence parameters may reveal not only the immediate effects of high-light stress but also

more persistent consequences of environmental conditions, particularly those experienced during early ontogeny, for the functional tolerance of PSII.

In conclusion, we suggest that the light environment during ontogeny shapes the functional plasticity of the photosynthetic apparatus in *P. bifurcatum*. In the present experiment, exposure to blue light was associated with a transient reduction in the efficiency of photosynthetic electron transport in young sporophytes, whereas at later stages of development the plants showed greater stability of this process under high-light conditions. In epiphytic ferns, this observation extends the current understanding of the mechanisms of photosynthetic acclimation and suggests that light quality during the earliest stages of development may play an important role in shaping the subsequent functional plasticity of PSII and the tolerance of the light-dependent reactions of photosynthesis to stress.

Conflict of interest

The authors declare no conflict of interest related to this article.

References

- Bantis, F., Smirnakou, S., Ouzounis, T., Koukounaras, A., Ntagkas, N., Radoglou, K. (2018). Current status and recent achievements in the field of horticulture with the use of light-emitting diodes (LEDs). *Scientia Horticulturae*, 235, 437–451. <https://doi.org/10.1016/j.scienta.2018.02.058>.
- Barthlott, W., Schmit-Neuerburg, V., Nieder, J., Engwald, S. (2001). Diversity and abundance of vascular epiphytes: a comparison of secondary vegetation and primary montane rain forest in the Venezuelan Andes. *Plant Ecology*, 152, 145–156. <https://doi.org/10.1023/A:1011483901452>.
- Brestic, M., Živčák, M. (2013). PSII fluorescence techniques for measurement of drought and high temperature stress signal in crop plants: protocols and applications. In: Rout, G.R., Das, A.B. (eds.), *Molecular Stress Physiology of Plants*. Springer, Dordrecht, pp. 87–131. https://doi.org/10.1007/978-81-322-0807-5_4.
- Briggs, W.R., Olney, M.A. (2001). Photoreceptors in plant photomorphogenesis to date: five phytochromes, two cryptochromes, one phototropin and one superchrome. *Plant Physiology*, 125(1), 85–88. <https://doi.org/10.1104/pp.125.1.85>.
- Camloh, M., Gogala, N. (1992). In vitro culture of *Platyserium bifurcatum* gametophytes. *Scientia Horticulturae*, 51, 343–346. [https://doi.org/10.1016/0304-4238\(92\)90133-W](https://doi.org/10.1016/0304-4238(92)90133-W)
- Carvalho, S.D., Folta, K.M. (2014). Environmentally modified organisms – expanding genetic potential with light. *Critical Reviews in Plant Sciences*, 33(6), 486–508. <https://doi.org/10.1080/07352689.2014.929929>
- Chan, K.X., Phua, S.Y., Crisp, P., McQuinn, R., Pogson, B.J. (2016). Learning the languages of the chloroplast: retrograde signaling and beyond. *Annual Review of Plant Biology*, 67, 25–53. <https://doi.org/10.1146/annurev-arplant-043015-111854>
- Demmig-Adams, B. (1998). Survey of thermal energy dissipation and pigment composition in sun and shade leaves. *Plant and Cell Physiology*, 39(5), 474–482. <https://doi.org/10.1093/oxfordjournals.pcp.a029394>
- Demmig-Adams, B., Adams, W.W.III (1996). The role of xanthophyll cycle carotenoids in the protection of photosynthesis. *Trends in Plant Science*, 1(1), 21–26. [https://doi.org/10.1016/S1360-1385\(96\)80019-7](https://doi.org/10.1016/S1360-1385(96)80019-7).

- Fankhauser, C. (2001). The phytochromes, a family of red/far-red absorbing photoreceptors. *Journal of Biological Chemistry*, 276(15), 11453–11456. <https://doi.org/10.1074/jbc.R100006200>
- Folta, K.M., Maruhnich, S.A. (2007). Green light: a signal to slow down or stop. *Journal of Experimental Botany*, 58(12), 3099–3111. <https://doi.org/10.1093/jxb/erm130>.
- Force, L., Critchley, C., van Rensen, J.J.S. (2003). New fluorescence parameters for monitoring photosynthesis in plants. *Photosynthesis Research*, 78(1), 17–33. <https://doi.org/10.1023/A:1026012116709>
- Foyer, C.H., Neukermans, J., Queval, G., Noctor, G., Harbinson, J. (2012). Photosynthetic control of electron transport and the regulation of gene expression. *Journal of Experimental Botany*, 63(4), 1637–1661. <https://doi.org/10.1093/jxb/ers013>
- Gangappa, S.N., Botto, J.F. (2016). The multifaceted roles of HY5 in plant growth and development. *Molecular Plant*, 9(10), 1353–1365. <https://doi.org/10.1016/j.molp.2016.07.002>
- Hernández, R., Kubota, C. (2016). Physiological responses of cucumber seedlings under different blue and red photon flux ratios using LEDs. *Environmental and Experimental Botany*, 121, 66–74. <https://doi.org/10.1016/j.envexpbot.2015.04.001>
- Hogewoning, S.W., Trouwborst, G., Maljaars, H., Poorter, H., van Ieperen, W., Harbinson, J. (2010). Blue light dose-responses of leaf photosynthesis, morphology and chemical composition of *Cucumis sativus* grown under different combinations of red and blue light. *Journal of Experimental Botany*, 61(11), 3107–3117. <https://doi.org/10.1093/jxb/erq132>.
- Jones, D.L., Goudey, C.J. (1981). *Ferns in Australia: common, rare and exotic: origin, identification and cultivation*. Reed Books, Sydney.
- Kalaji, H M., Schansker, G., Brestic, M., Bussotti, F., Calatayud, A., Ferroni, L., Goltsev, V., et al. (2017). Frequently asked questions about chlorophyll fluorescence, the sequel. *Photosynthesis Research*, 136(1), 13–66. <https://doi.org/10.1007/s11120-016-0318-y>
- Kawai, H., Kanegae, T., Christensen, S., Kiyosue, T., Sato, Y., Imaizumi, T., Wada, M. (2003). Responses of ferns to red light are mediated by an unconventional photoreceptor. *Nature*, 421, 287–290. <https://doi.org/10.1038/nature01310>
- Liao, Y.K., Wu, M.D. (2011). *In vitro* propagation of *Platyserium bifurcatum* (Cav.) C. Chr. via green globular body initiation. *Botanical Studies*, 52(4), 455–463.
- Morrow, R.C. (2008). LED lighting in horticulture. *HortScience*, 43(7), 1947–1950. <https://doi.org/10.21273/HORTSCI.43.7.1947>.
- Oliwa, J., Kornas A., Skoczowski, A. (2016). Morphogenesis of sporotrophophyll leaves in *Platyserium bifurcatum* depends on the red/far-red ratio in the light spectrum. *Acta Physiologiae Plantarum*, 38, 247. <https://doi.org/10.1007/s11738-016-2260-1>
- Oliwa, J., Kornaś A., Skoczowski, A. (2017). A low ratio of red/far-red in the light spectrum accelerates senescence in nest leaves of *Platyserium bifurcatum*. *Acta Biologica Cracoviensia Series Botanica*, 59(2), 17–30. <https://doi.org/10.1515/abcsb-2017-0011>
- Oliwa, J., Skoczowski, A. (2019). Different response of photosynthetic apparatus to high-light stress in sporotrophophyll and nest leaves of *Platyserium bifurcatum*. *Photosynthetica*, 57(1), 147–159. <https://doi.org/10.32615/ps.2019.037>
- Ouzounis, T., Rosenqvist, E., Ottosen, C.O. (2015). Spectral effects of artificial light on plant physiology and secondary metabolism: a review. *HortScience*, 50(8), 1128–1135. <https://doi.org/10.21273/HORTSCI.50.8.1128>

- Stirbet, A., Govindjee (2011). On the relation between the Kautsky effect (chlorophyll *a* fluorescence induction) and Photosystem II: basics and applications of the OJIP fluorescence transient. *Journal of Photochemistry and Photobiology B: Biology*, 104(1–2), 236–257. <https://doi.org/10.1016/j.jphotobiol.2010.12.010>
- Strasser, R.J., Tsimilli-Michael, M., Srivastava, A. (2004). Analysis of the chlorophyll *a* fluorescence transient. In: Papageorgiou, G.C., Govindjee (eds.), *Chlorophyll a fluorescence: a signature of photosynthesis*. Springer, Dordrecht, pp. 321–362. https://doi.org/10.1007/978-1-4020-3218-9_12.
- Tsimilli-Michael, M., Strasser, R.J. (2013). The energy flux theory 35 years later: formulations and applications. *Photosynthesis Research*, 117(1–3), 289–320. <https://doi.org/10.1007/s11120-013-9895-1>

Ekspozycja na światło niebieskie podczas morfogenezy zwiększa tolerancję na wysokie natężenie światła u sporofitów *Platycerium bifurcatum*

Streszczenie

Skład spektralny światła podczas wczesnych etapów rozwoju roślin może wpływać na funkcjonowanie aparatu fotosyntetycznego oraz tolerancję na stres środowiskowy. Mechanizmy te pozostają jednak słabo poznane u paproci. Celem pracy było określenie wpływu światła niebieskiego stosowanego podczas rozwoju sporofitów na późniejszą tolerancję aparatu fotosyntetycznego na stres wysokiego natężenia światła w *Platycerium bifurcatum*. Zarodniki, gametofity i młode sporofity hodowano przez dziewięć tygodni w świetle niebieskim lub białym, a następnie wszystkie rośliny uprawiano przez dziewięć miesięcy w identycznych warunkach. Jednoroczne sporofity poddano działaniu wysokiego natężenia światła (PPFD = 800 $\mu\text{mol m}^{-2} \text{s}^{-1}$) przez siedem dni. Funkcjonowanie aparatu fotosyntetycznego oceniono na podstawie szybkiej kinetyki fluorescencji chlorofilu *a* oraz analizy OJIP.

Rośliny rozwijające się początkowo w świetle niebieskim wykazywały większą tolerancję na stres świetlny, utrzymując wyższe wartości wskaźników wydajności fotosyntetycznej oraz mniejsze zaburzenia transportu elektronów po ekspozycji na wysokie natężenie światła. Uzyskane wyniki wskazują, że skład spektralny światła podczas morfogenezy wpływa na zdolności aklimatyzacyjne aparatu fotosyntetycznego. Odpowiednio dobrane warunki świetlne mogą być wykorzystane do poprawy stanu fizjologicznego paproci ozdobnych rozmnażanych z zastosowaniem technologii LED.

Słowa kluczowe: fluorescencja chlorofilu *a*, OJIP, fotosystem II, paprocie ozdobne, stres abiotyczny

Information on the authors

Jakub Oliwa <https://orcid.org/0000-0003-4341-7933>

His research interests focus on plant physiology and ecophysiology, particularly photosynthesis and fern responses to environmental factors. He investigates the effects of abiotic and biotic stresses on photosynthetic performance, using chlorophyll fluorescence techniques to evaluate the functioning of the photosynthetic apparatus.

Alina Amelina

Her research interests include plant physiological processes, with a particular focus on the responses of ornamental ferns to abiotic stress and the mechanisms underlying their stress tolerance.