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ORIGINAL ARTICLE

Temperature and LED lightning affect the regeneration of somatic embryo-derived sporophytes on the internode explants of the tree fern *Cyathea delgadii* Sternb.

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Abstract

The influence of the temperature and different light qualities emitted by light-emitting diodes (LEDs) and fluorescent lamps (Fl) on the micropropagation of the tree fern *Cyathea delgadii* was evaluated. The most efficient somatic embryo production was obtained on internode explants at 22 °C. The optimal temperature range for obtaining well-developed plants was 24–28 °C. This stimulated the elongation and development of the first leaf and the formation of the next leaf and roots primordia. Temperatures lower than 24 °C and higher than 28 °C inhibited the formation of young sporophyte organs and delayed their development. The RBUV (35% red, 15% blue, and 50% UV) and B (100% blue) lights and Fl light were beneficial for the sporophyte production on internode explants. However, plants obtained under RBUV light were undeveloped. The white LED light stimulated the number of explants capable of gametophyte production and development. The RB light (70% red and 30% blue) enhanced the number of roots of newly-formed plants. Most of the LED lights tested had a good impact on root elongation compared to Fl light and constant darkness. The R light (100% red) benefits leaf development and elongation. Research shows that temperature and LED lightning play a significant role in the process of morphogenesis in *C. delgadii*, significantly affecting the embryogenic competence of somatic cells and the development of sporophytes.

Key message

A wide range of temperatures and light qualities have been investigated for optimizing the efficiency of in vitro morphogenesis of the tree fern *Cyathea delgadii*.

Keywords Micropropagation · In vitro culture · Light-emitting diode · Somatic embryo · Temperature

Małgorzata Grzyb and Wojciech Tomaszewicz contributed equally to the work and share first authorship.

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Introduction

Temperature and light are important factors that influence plant propagation and development processes, including ferns (Gauer Medeiros et al. 2017). In the case of somatic embryogenesis (SE), the majority of the studies on the effect of temperature on the process are mainly restricted to the short-term use of low or high temperatures as a trigger for stress-related cell reprogramming (Pescitelli et al. 1990; Afele et al. 1992; Touraev et al. 1996; Kiviharju and Pehu 1998; Tenhola-Roininen et al. 2005; Fu et al. 2008). This heat shock treatment is well documented for microspore cultures in which a shift in temperature interrupts the developmental program of pollen and initiates microspore embryogenesis (Shariatpanahi et al. 2006). Other studies indicate that varying the temperature can significantly affect the type of morphogenesis (Decout et al. 1994), the frequency of shoot regeneration (Sengar et al. 2011), as well as somatic embryo production (Li and Wolyn 1996; Almeida et al. 2014; García-Mendiguren et al. 2016) and their development (Li and Wolyn 1996; García-Mendiguren et al. 2016). Currently, this factor is usually not taken into account, and tissue cultures are most often maintained at constant temperatures between 24 and 26 °C (Pierik 1997). Ferns are no exception, although the temperature in their lives has a decisive impact on the proper development of both gametophytes and sporophytes (Hvoslef-Eide 1991).

The second factor i.e. light, being the energy source in photosynthesis, is the fundamental signal that regulates growth and developmental processes. Controlling light quality, irradiances and photoperiod enables the production of plants with desired characteristics (Cavallaro et al. 2022). The changes in light quality are perceived in plants by different types of photoreceptors, such as cryptochromes and phytochromes (Su et al. 2017). Plant photoreceptors are known to be primarily stimulated by red and blue regions of the light spectrum, thus, most of the studies evaluated the impact of monochromatic red, blue, and combined red with blue lights. Scarce is the information available on the effects of the green, yellow, and far-red regions of the spectrum (Cavallaro et al. 2022). The literature is rich with works confirming that light-emitting diodes (LEDs) have several advantages compared to fluorescent lamps that are typically used as light sources in micropropagation, including long lifespan, low energy consumption, and low heat emissions (Bula et al. 1991; Gupta and Jatothou 2013; Yeh et al. 2009). Moreover, the wavelength specificity of LEDs allows adjustment of the spectra that fulfill plant needs (Cavallaro et al. 2022). Taking into account that the plant responses to light spectra generated by LEDs vary according to species (Miler et al. 2019), genotype (Ouzounis et al. 2016), varieties (Lupo et al. 2022) and explant type (Santos Lazzarini et al. 2018), in vitro cultures of different plant materials require continuous improvement in this area. Further, lighting conditions provided during the in vitro stage can modify the morphogenetic response of fern explants by stimulating the development of gametophytes via apospory (Mikuła et al. 2015a; Tomaszewicz et al. 2022), as well as they may greatly affect the plant vigor after transferring to nonsterile conditions (Kulus and Woźny 2020). Although plant tissue cultures depend entirely upon artificial light sources, research on the influence of LEDs on fern growth and morphology is limited only to a few recent papers (Yu et al. 2021; Tomaszewicz et al. 2022).

Cyatheaceae is the largest group of tree ferns including about 640 species of which many are of economic importance as construction material, animal food, source of medicinal substances, and ornamental value (Simpson 2019). They are important members of plant communities in tropical and sub-tropical environments, but increasing evidence suggests that their survival in some global regions is under threat (Anderson 2021). To preserve biodiversity, it is recommended to include tree ferns in tropical forest restoration programs and ex situ plant protection programs including storage of their gametophytes in cryobanks (Barnicoat et al. 2011; Mikuła et al. 2022b; Zimnoch-Guzowska et al. 2022). The enhancement of in vitro production of these plants is needed on this account. The present work pertains to *Cyathea delgadii* Sternb., a species of evergreen tree fern (10 m tall) native to the forests of the Caribbean, Central, and South America (Tomiczak et al. 2018). It is currently one of two fern species for which somatic embryogenesis (SE) was described (Mikuła et al. 2015a, b; Tomiczak et al. 2023). The way of propagation of ferns may become a very interesting model to gain insight into the evolution of higher plants as well as an effective way of sporophyte production (Mikuła et al. 2022a). Somatic embryogenesis in ferns is induced independently of plant growth regulators. Our studies conducted so far indicate that the efficiency of the process can be regulated by several chemical and physical factors that affect both the type of morphogenetic responses and sporophyte development. The present study aimed to evaluate the influence of a wide range of temperatures and light quality on the regeneration of sporophytes and gametophytes on internode explants of *C. delgadii*.

Materials and methods

Plant material and culture conditions

The source of plant material was 5-month-old etiolated sporophytes of *C. delgadii* with 3 or 4 developed leaves obtained as described previously (Mikuła et al. 2015b).

They were cultured on the hormone-free Murashige and Skoog (Murashige and Skoog 1962) medium containing half-strength salts and full composition of vitamins (0.5MS). The medium was supplemented with 2% (*w/v*) sucrose and 0.7% (*w/v*) agar. The pH was adjusted to 5.8 before autoclaving at 121 °C for 20 min. Donor sporophytes culture was carried out in the glass jars of 150 ml containing 40 ml of medium in the dark phytotron under temperature 24 ± 1 °C. The internode explants approximately 1.5 mm in length, which were excised from the stems between the first (the youngest) leaf of donor sporophytes and the second one, were used in the study.

Temperature conditions

To investigate the effect of temperature on the embryogenic potential of internodes, the cultures were maintained in the climatic chambers (Termometal, Poland) under the following temperature regimes: 20 °C, 22 °C, 24 °C, 26 °C, 28 °C, and 30 °C. The climatic chambers were 94 l in volume. The temperature was uniform throughout the chamber and tested during the experiment. The explants were cultured on the 0.5MS medium supplemented with 1% (*w/v*) sucrose in the dark for 30 days.

Light conditions

To optimize light conditions, internode explants were cultured on the 0.5MS medium supplemented with 1% (*w/v*) sucrose for 4 days in the dark, and after that, they were treated with an aqueous solution of 0.4 M sucrose for 45 min and rinsed three times with sterile water as described previously (Tomaszewicz et al. 2024). The sucrose-treated explants were cultured in darkness for the first 3 weeks and then under 16/8 h light/dark for the next 9 weeks. A fluorescent lamp (Philips TK-D 36 W/54) and the specially designed and constructed LED panels (PXM, Poland) were used to ensure photoperiod conditions (Table 1, Pałka et al. 2023). The temperature in the climatic chamber was 24 ± 1 °C. The explants cultured for 12 weeks in darkness (further marked as Dark in this paper) were used as a control.

Table 1 Light qualities generated by lamps used in the experiments

Type of lamps	Abbreviation	Parameters
Fluorescent	Fl	Philips TK-D 36 W/54
Light Emitting Diodes (LEDs)	B	100% blue (430 nm)
	R	100% red (670 nm)
	RB	70% red, 30% blue
	RBfR	35% red, 15% blue, 50% far-red (730 nm)
	RBY	35% red, 15% blue, 50% yellow (600 nm)
	RBUV	35% red, 15% blue, 50% UV (400 nm)
	RBG	35% red, 15% blue, 50% green (528 nm)
	Wh	white (1:1:1 2700 K:4500 K:5700 K)

The light intensity and quality were set using an LI-250 A light meter with a Q 50,604 sensor (LI-COR, Lincoln, NE, USA) and a BTS256 spectrometer (Gigahertz-Optik, Türkenfeld, Germany). The photosynthetic photon flux density (PPFD) was adjusted at 40 µmol m^{-2} s^{-1} in all treatments (excluding the period of darkness).

Evaluation of regeneration ability and plant development

In the temperature experiment, the efficiency of SE was calculated as the percentage of responding explants [calculated as follows: (number of explants that formed somatic embryos/total number of explants) × 100%] and the number of somatic embryos per responding explant following 1 month of culture.

In the light experiment, the efficiency of somatic embryo-derived sporophyte formation, and the ability of gametophyte production, as well as of four parameters of sporophyte development were assessed after 12 weeks of culture on 0.5MS, without subculturing the plant material at that time. The **ratio of explants with sporophytes/gametophytes** was defined as the number of explants with regenerated sporophytes/gametophytes divided by the total number of explants used for culture initiation. **Number of sporophytes** was calculated as the total number of obtained sporophytes divided by the sum of cultured explants. The **ratio of explants with mass produced gametophytes** was assessed as the number of explants that produced gametophytes with a total surface equal to or higher than 4 mm^2, per total number of explants used for culture initiation. The **ratio of sporophytes with a developed leaf** was determined as the number of sporophytes with at least 1 leaf at crosier stadium or older, per sum of all sporophytes (including those with only a leaf primordium). The **length of the longest leaf** was calculated as the sum of the length of the longest leaf from each sporophyte per the sum of obtained leaves. **Number of the roots** was defined as the sum of roots divided by the total number of sporophytes. The **length of the roots** was defined as the sum of root length divided by the total number of roots.

Somatic embryos and their development were observed and counted under a stereo microscope (Olympus SZH, Tokyo, Japan) and images were acquired with Olympus SC30 camera (Tokyo, Japan) using Olympus cellSens Standard software.

Statistical analysis

Data were analyzed statistically using Statistica version 13 and PQStat software. Analysis of variance (ANOVA) was performed followed by Duncan's post hoc multiple range test (at $p \leq 0.05$) when data fulfilled the assumptions of normality and homoscedasticity. When data were not normally distributed, a Kruskal–Wallis test was performed followed by Conover-Imann post hoc test to identify significant differences (at $p \leq 0.05$). The experiments were repeated 3 times, each repetition consisting of one Petri dish with 20 explants.

Results

Effect of temperature on SE efficiency and embryo development

Temperature was found to have a significant effect on the efficiency of SE (Table 2). The most effective parameters of somatic embryo formation were achieved at 22 °C. This temperature induced the greatest percentage of explants to produce somatic embryos (98.8%) and the greatest number of somatic embryos per explant (3.0). Lowering the temperature to 20 °C and raising it to 30 °C strongly reduced the efficiency of SE.

Studies showed that the development of somatic embryos into sporophytes was greatly affected by temperature (Fig. 1). Temperatures as high as 24–28 °C promoted them. Under optimal temperature conditions, somatic embryos formed on internode explants grew very fast, and well-developed juvenile sporophytes were obtained following 1 month of culture (Fig. 1C, D). These developed the first leaf and shoot apex, as well as the primordia of both the second leaf and root. Therefore, a temperature of 24 °C was chosen for further experiments. Whereas lower (i.e. 20 and 22 °C) and higher temperatures (i.e. 30 °C) inhibited their growth and development.

Table 2 Effect of temperature on the efficiency of SE on internode explants cultured for 30 days in the dark

Temperature [°C]	% of explants with somatic embryos	Number of somatic embryos /responding explant
20	71.7 ± 5.8 c	1.9 ± 1.6 ab
22	98.8 ± 2.5 a	3 ± 1.9 a
24	91.3 ± 11.1 b	2.5 ± 1.5 a
26	88.8 ± 8.5 b	2.6 ± 1.8 a
28	90 ± 8.2 b	2.7 ± 1.8 a
30	76.3 ± 8.5 c	1.6 ± 1.4 b

Mean ± standard deviations marked by different letters are significantly different ($p \leq 0.05$) following Duncan's multiple range test

Effect of light quality on the sporophyte and gametophyte production

The quality of light under which the cultures of the *C. delgadii* internode explants were initiated did not affect the ratio of explants with sporophytes (Fig. 2A). Its stimulating effect on the number of sporophytes was revealed for seven of the nine light qualities tested compared to constant darkness. The number of sporophytes per explant was about 1.8 and 2.2 times greater under RBUV light in comparison to the constant darkness and RBfR light, respectively (Fig. 2B).

Gametophyte production was completely inhibited in the cultures in constant darkness (Fig. 2C, D). The R light had a positive influence on their mass production; however, gametophytes obtained under this light had only residual form (Fig. 2E). They did not develop normally and did not reach maturity. The Wh light promoted both the production of gametophytes and their development (Fig. 2C, D, F). The gametophytes attained maturity and were able to reproduce sexually.

Effect of light quality on the sporophyte development

The quality of light affected the development of the *C. delgadii* sporophytes (Fig. 3). The RB light spectrum increased the number of roots. In contrast, constant darkness and RBUV light completely inhibited the root formation (Fig. 3A). The mean length of the roots was enhanced by six of the eight LEDs (i.e. B, R, RBfR, RBY, RBG, Wh) compared to Fl light. The roots reached an average length of 0.7 and 1.4 mm under Fl and RBY light, respectively (Fig. 3B).

The RBUV light and constant darkness negatively affected the ratio of sporophytes with a developed leaf and the length of the longest leaf (Fig. 3C-E). On the other hand, the R light promoted these parameters (Fig. 3C, D, F). Under R light, the mean length of the longest leaf was equal to 3.0 mm, which was about 2.7 times greater than in the RBUV light (Fig. 3D).

Discussion

Effect of temperature on SE

Although most plant tissue cultures grow successfully at around 25 °C (Pierik 1997), the optimum temperature for in vitro morphogenetic responses and plantlet development varies from species to species. It has been reported that temperatures of less than 20 °C are appropriate for the induction of bulb organogenesis, in vitro growth, and plant development in certain bulbous species, such as crocus and tulip (Ahouran 2014; Maślanka and Bach 2014). By contrast,

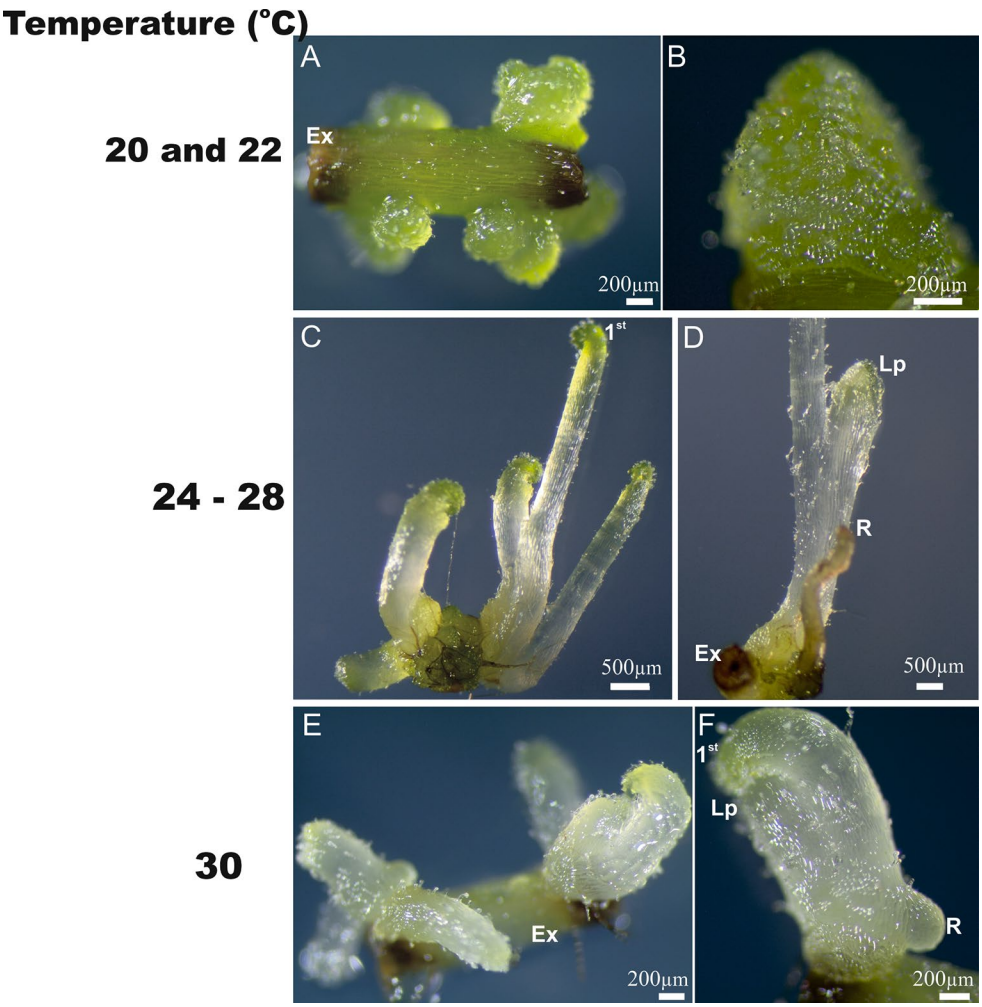


Fig. 1 Effect of temperature on the development of somatic embryos on internode explants cultured for 30 days in the dark. (**A**, **B**) Somatic embryos without sporophyte organs visible. (**C**, **D**) Well-developed plants with elongated first leaf, next leaf primordium, and root. (**E**, **F**) Somatic embryos with visible next leaf and root primordium. Ex – explant; Lp – leaf primordium; R - root; 1st - first leaf

some tropical species usually require higher growth room temperatures that oscillate between 27 °C and 30 °C (Fonnesbech and Fonnesbech 1980; Sengar et al. 2011). *Cyathea delgadii* grows in forests extending from North-eastern to Southern Brazil, with average temperatures of 12.9 °C and 25.1 °C for the coldest and warmest months, respectively (Schmitt and Windisch 2007). The optimum temperature for this tree fern in vitro growth of embryogenic cultures showed in this study was 24–28 °C.

Since Decout et al. (1994) demonstrated that the type of morphogenetic response during in vitro culture is temperature-dependent, it is clear that greater attention should be paid to this factor. Their studies showed that the temperature change by 5 °C resulted in the formation of callus tissue and shoots, direct SE, or all forms of morphogenesis. In the cultures of internode explants of *C. delgadii*, the temperature had a noticeable effect on the frequency of somatic embryo regeneration and the number of responding explants but did not change the pathway of their origin. Temperature affected the capacity of direct (Almeida et al. 2014) and indirect SE (Li and Wolyn 1996; García-Mendiguren et al. 2016) in other plant species. In three genotypes of *Coffea arabica* L., a temperature of 30 °C significantly favored the formation of somatic embryos compared with 25 °C (Almeida et al. 2014). Whereas our findings showed that the temperatures of 30 °C significantly reduced the embryogenic response of *C. delgadii* explants. Data presented by Li and Wolyn (1996) showed that optimal culture conditions are restricted to a very short range of temperatures. The calli of three responsive genotypes of *Asparagus officinalis* L. produced the most and the least numbers of total, bipolar, and globular embryos when incubated at 27 °C and 24 °C, respectively (Li and Wolyn 1996). Our study revealed that the range of temperature at which SE can be induced in *C. delgadii* is very wide as it ranges from 20 °C to 30 °C. However, below 24 °C and above 28 °C, the sporophyte development was inhibited. Temperature had also a completely different effect on the culture of *Pinus radiata* D. Don. Explants cultured at the lowest temperature (18 °C) showed the greatest initiation rates compared to those cultured at 28 °C and 23 °C (García-Mendiguren et al. 2016). Regardless of different induction conditions, the authors agree that the lower

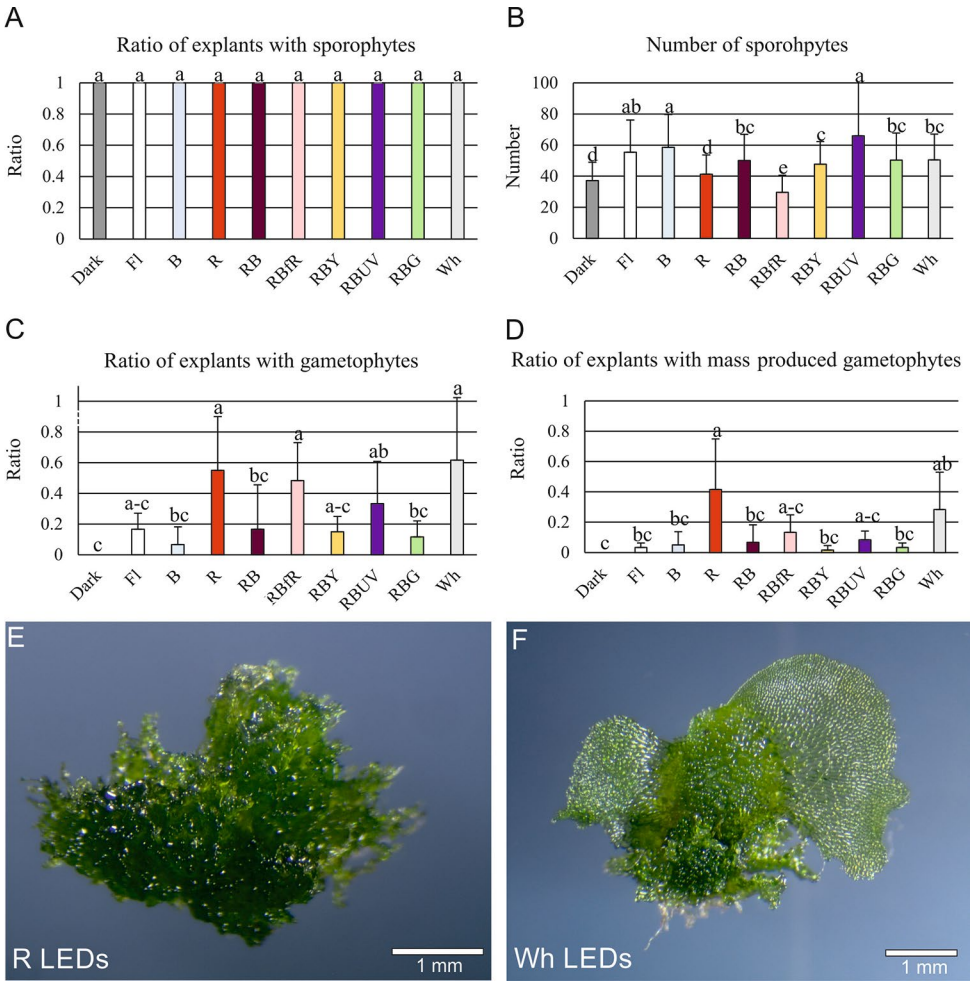


Fig. 2 The influence of light quality on the efficiency of sporophytogenesis and gametophytogenesis in *Cyathea delgadii* after 12-week-long-culture of internode explants treated with 0.4 M sucrose solution on the fourth day after excision. (**A**) The ratio of explants with sporophytes. (**B**) The number of sporophytes. (**C**) The ratio of explants with gametophytes and (**D**) mass-produced gametophytes. (**E**) The picture of residual form gametophyte obtained under R LED light. (**F**) Developed gametophyte after culture under Wh LED light. Fl—control light: fluorescence Philips TL-D 36 W/54 lamps; B—100% blue LED light (430 nm); R—100% red LED light (670 nm); RB – combination of red (70%) and blue (30%) LED lights; RBfR—combination of red, blue, and far-red (730 nm) LED lights (35%/15%/50%); RBY—combination of red, blue, and yellow (600 nm) LED lights (35%/15%/50%); RBUV—combination of red, blue, and UV (400 nm) LED lights (35%/15%/50%); RBG—combination of red, blue, and green (528 nm) LED lights (35%/15%/50%); Wh—white LED (1:1:1 2700 K:4500 K:5700 K); Mean ± standard deviations marked by different letters are significantly different ($p \leq 0.05$) following Conover-Imann post hoc test

temperatures significantly affected the transition of somatic embryos to plantlets (Li and Wolyn 1996; García-Mendiguren et al. 2016).

Effect of light conditions on gametophyte production

Gametophyte is a delicate and potentially fragile cellular monolayer structure in the fern life cycle, particularly subjected to environmental pressures (Anderson 2021). In nature, its life starts as a result of spore germination. Etiolated explants of *C. delgadii* are also capable of producing gametophytes (Mikuła et al. 2015a, b), but it does not happen in the dark. It is in line with the results showing that light is a determining factor for fern gametophyte formation from spores (Pérez-García et al. 2007; González de León et al. 2021). Cooke et al. (1995) found that monochromatic red light effectively induced the germination of spores in *Adiantum capillus-veneris*, *Ceratopteris richardii*, and *Onoclea sensibilis*. In addition, white light promoted this process in *Cyathea divergens* (Riaño Ospina et al. 2015). It has been previously shown that light quality affected the development of gametophytes in ferns *Lygodium japonicum* and *Anemia phyllitidis* (Swami and Raghavan 1980; Grill 1987). Our results are consistent with those of other authors. We indicated that R and Wh light has stimulated both the

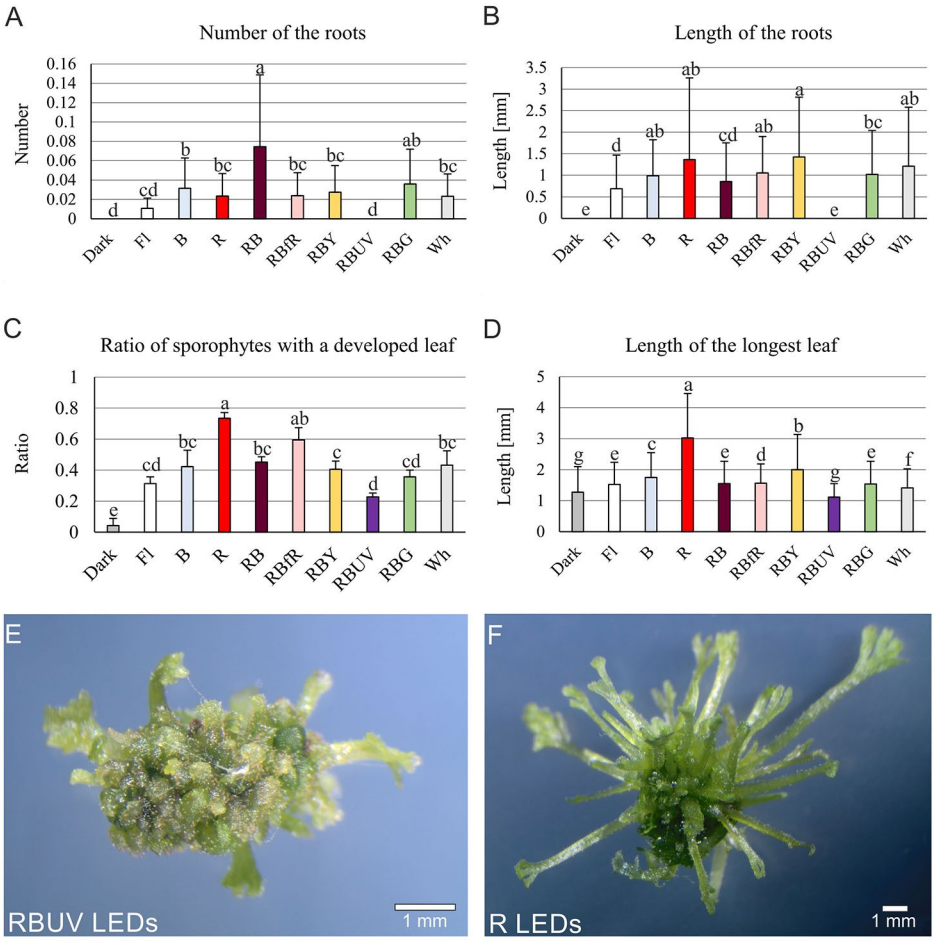


Fig. 3 The influence of light quality on the sporophyte development of *Cyathea delgadii* after a 12-week-long culture of internode explants treated with 0.4 M sucrose solution on the fourth day after excision. (**A**) Root production. (**B**) Length of the roots. (**C**) The ratio of sporophytes with a developed leaf. (**D**) Length of the longest leaf. Somatic embryo-derived sporophytes obtained under (**E**) RBUV LED light and (**F**) R LED light. Fl—control light: fluorescence Philips TL-D 36 W/54 lamps; B—100% blue LED light (430 nm); R—100% red LED light (670 nm); RB—combination of red (70%) and blue (30%) LED light; RBfR—combination of red, blue, and far-red (730 nm) LED lights (35%/15%/50%); RBY—combination of red, blue, and yellow (600 nm) LED lights (35%/15%/50%); RBUV—combination of red, blue and UV (400 nm) LED lights (35%/15%/50%); RBG—combination of red, blue, and green (528 nm) LED lights (35%/15%/50%); Wh—white LED (1:1:1 2700 K:4500 K:5700 K); Mean ± standard deviations marked by different letters are significantly different ($p \leq 0.05$) following Conover-Imann post hoc test

mass production of gametophytes on internodes of *C. delgadii* and their development.

Effect of light conditions on the regeneration of the somatic embryo-derived sporophytes

It has been already shown that sucrose treatment and three-week-long initial culture in darkness are beneficial for the efficiency of somatic embryogenesis in *C. delgadii* (Tomaszewicz et al. 2022; Tomaszewicz et al. 2024). Here, we tried to control the sporophyte production by using different light spectra generated by LEDs, but our study showed that each *C. delgadii* internode explant can produce somatic embryos regardless of the light quality. However, RBUV had a positive influence on the number of sporophytes obtained. In contrast, this light combination had the strongest inhibitory effect among all light qualities tested when the stipe explants of *C. delgadii* were used for the initiation of culture (Tomaszewicz et al. 2022). This indicates that the response to the quality of light in in vitro culture is strongly dependent on the type of explant. Furthermore, the number of somatic embryo-derived sporophytes on the *C. delgadii* internode explants was also promoted by B light. This spectrum of light also stimulated SE in *Dianthus caryophyllus* (Aalifar et al. 2019) as well as on stipe explants of *C. delgadii* (Tomaszewicz et al. 2022).

There have been many studies concerning the effect of LEDs on the development of spermatophytes (Batista et al.

2018), while research on their influence on the development of non-seed plants is still lacking. The present paper demonstrates that light quality affects the formation of roots and leaves in the tree fern *C. delgadii*. Sun et al. (2005) reported that light signals from aboveground directly contribute to the regulation of the growth and development of roots via an internal light-conducting system from the stem to the roots. In our experiment, we showed that RB light was more effective for root production when compared with R and B lights used separately. A similar effect of this combination was observed in *Oncidium* 'Gower Ramsey' (Chung et al. 2010) and *Calanthe* hybrids 'Bukduseong' x 'Hyesung' (Abdullahil Baque et al. 2011). By contrast, longer roots in *Protea cynaroides* were obtained under monochromatic red light (Wu and Lin 2012). Data obtained in *C. delgadii* confirmed that RBY light is beneficial for the elongation of roots. Similarly, Li et al. (2018) demonstrated that roots in potato plantlets were longer under the combination of red, blue, and yellow spectra as compared to red and blue lights combined with green light. Conversely, the negative effect of yellow light on this parameter was observed in cucumber seedlings (Su et al. 2014). Moreover, we observed here that there was no statistical difference between root length in plants cultured under R and B lights. In contrast, previous research showed that these lights alone can be effective, depending on plant species (Manivannan et al. 2015; Silva et al. 2017). It has been shown that blue LED light enhances growth of *Rehmannia glutinosa* while red LED lights had a stimulating effect on the development of *Plectranthus amboinicus*.

We demonstrated here that R light was the most beneficial for the elongation of leaves. This is in accordance with the experimental result of Yu et al. 2021; which found that red light promoted the petiole elongation in fern *Pteris aspericaulis* var. *tricolor*. OuYang et al. (2015) concluded that red light promoted stem growth in *Picea abies* by regulating the biosynthesis of gibberellic acids. In the study by Li et al. (2017), red light notably promoted the expression of the auxin inhibitor protein gene, suggesting that the auxin concentrations are low in red light-treated plants, which is a condition suitable for stem length growth. Other studies have shown that red LEDs could increase plant growth by promoting the accumulation of carbohydrates (Zhang et al. 2018). The R light had a positive influence on leaf development in *C. delgadii* plants. This light emits a narrow spectrum of light close to the maximum absorbance for chlorophyll and has great potential to drive photosynthesis (Goins et al. 1997).

Summary

Results obtained for the internode explants of the tree fern *C. delgadii* clearly show that temperature is an important factor during in vitro culture, in that it affects SE efficiency and the development of young plantlets. Our study also confirmed that LED lights have an important effect on the growth and development of ferns. Based on the results obtained here, RBUV, B, and Fl lights can be recommended to enhance the efficiency of sporophyte production. However, plants obtained under RBUV light were undeveloped, so there is a need to change the light quality at some point in the culture. During the development of somatic embryo-derived sporophytes, RB light is the best choice for enhancement of the number of roots, but B, R, RBfR, RBY, and Wh are better for their elongation. Furthermore, Wh light can be appropriate for gametophyte production since it positively affects the number of explants able to produce gametophytes and their development.

Author contributions MG, WT, and AM designed the experiments. WT and MG were involved in experimental works, conducted the data analysis, and prepared the draft of the manuscript; BP and MC gave expert advice; AM supervised the project. All authors have read and agreed to the final version of the manuscript.

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Data availability The datasets generated during and/or analyzed during the current study are available from the corresponding author upon reasonable request.

Declarations

Competing interests The authors have no relevant financial or nonfinancial interests to disclose.

Ethical approval This article does not contain any studies with human participants or animals performed by any of the authors.

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