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**Regulation of morphogenetic reactions of *Glycine max* (L.) Merr.
by selective light *in vivo* and *in vitro***
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The work is devoted to the study of photomorphogenic reactions of plants to monochromatic irradiation *in vivo* and *in vitro*. The aim of the work was to investigate the effect of red (660 nm) and blue (450 nm) light irradiation on the photomorphogenesis of seedlings and callus culture of the soybean (*Glycine max* (L.) Merr.) under *in vivo* and *in vitro* conditions. The studies were conducted on 10-day-old seedlings and primary callus culture of soybean (*Glycine max* (L.) Merr.) of the short-day variety Clark. Seed germination and infection, as well as growth processes of experimental seedlings under *in vivo* conditions, were analysed by determining linear dimensions and biomass. In callus culture under *in vitro* conditions, the growth rate, absolute growth, and such indicators of morphogenetic reactions as callusogenesis, chlorophyllogenesis, rhizogenesis, and necrosis were determined. It was shown that red and blue light irradiation stimulates seed germination, while blue light irradiation contributes to a decrease in seedling infection. Under *in vivo* conditions, red light irradiation inhibits the elongation of the studied seedlings, while blue light irradiation stimulates the linear growth of seedlings. Irradiation with selective light of both studied spectra promotes biomass accumulation in seedlings. At the same time, organ-specific reactions are observed: RL irradiation promotes an increase in the biomass of the above-ground part, while BL irradiation mainly promotes an increase in the root part. Under *in vitro* culture conditions, the growth of primary callus tissue is inhibited during irradiation with red and blue light. The prolonged effect of red and blue light is expressed in the inhibition of callus tissue growth by RL and the absence of BL influence on the growth index compared to the control. BL irradiation also stimulates the manifestation of various pathways of callus culture morphogenesis in *in vitro* conditions. The uniformity of the reactions of seedlings and callus culture of the short-day line of soybean in *in vivo* and *in vitro* culture conditions is observed.

Key words: photobiotechnology, *in vitro* photomorphogenesis, photoreceptors, selective light, *Glycine max* (L.) Merr., seedlings, callus

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Introduction

Photobiotechnology is an emerging field focused on the interaction between light and biological systems and its application in regulating physiological and developmental processes in plants (Ganesan et al., 2017). One area of research is photomorphogenesis, the process of plant life and development under the influence of various light parameters, such as wavelength range (spectrum), intensity, integral daily radiation, photoperiod, and light flux direction (Liu, H. et al., 2020; Izzo L. G. et al., 2020). Different light wavelengths uniquely influence morphogenetic and biosynthetic processes, and this effect depends individually on the species, variety, and ecological group of plants (González et al., 2023; Zhao et al., 2024).

With the growing demand for sustainable agricultural and biotechnological products, research into one of the main environmental factors, namely light, on plant morphogenesis is relevant. This has led to the development of photobiotechnology and the emergence of light culture technology, in which the required level of irradiation, both with daylight and other spectra, is provided by the use of various light sources (Paradiso, Proietti, 2022). A revolutionary stage in the development of photobiotechnology and

light culture was the emergence of new lamps – light-emitting diodes (LEDs), which provide radiation of a certain wavelength of monochromatic (selective) light and a combination of light wavelengths. Unlike traditional light sources used in photobiotechnology, which generate radiant heat, the use of LEDs in LED matrices reduces the thermal impact on plants and allows the intensity of lighting and duration of exposure to be regulated. This, in turn, makes it possible to study the effect of a specific light spectrum on plant growth and morphogenesis and to ensure optimal conditions for their cultivation (Paradiso, Proietti, 2022; Kusuma et al., 2020).

The link between light signalling and plant photomorphogenesis is the photoreceptor system, which consists of specialised light-sensitive proteins that participate in triggering cascade reactions for the genetic regulation of plant life processes. To date, five classes of photoreceptors have been identified: phytochromes – receptors of red (660 nm) and far-red light (730 nm), cryptochromes, phototropins and F-box proteins – receptors of blue light and ultraviolet A, and the UVR8 protein – a receptor of ultraviolet B (Paik, Huq, 2019; Oka, Yamamoto, 2019). Active forms of photoreceptors are capable of interacting in one way or another with the main large regulatory modules: the photomorphogenesis activator HY5 (ELONGATED HYPOCOTYL 5), the systemic integrators PIFs (PHYTOCHROME-INTERACTING FACTORS) and COP1 (CONSTITUTIVE PHOTOMORPHOGENIC 1, substrate receptor of E3 ubiquitin ligase CUL4), on which the switching of many genetic programmes depends, including photomorphogenesis, circadian rhythms and other plant development processes (Gangappa, Botto, 2016; Wang et al., 2022). Thanks to this, photoreceptors influence other regulatory mechanisms in plants – phytohormonal and trophic signalling, plant antioxidant systems, etc. (Wang et al., 2019; Wang et al., 2022). It is known that one of the characteristics of plants that affects the response to light irradiation of various parameters is the ecological group, for example, the photoperiodic response. Based on their photoperiodic response, plants are divided into photoperiod-sensitive plants: long-day (LDP) and short-day (SDP), and photoperiod-insensitive (neutral-day – NDP) (Vonk, Shackelford, 2020). Since it is the cryptochrome and phytochrome systems that are involved in the perception of the photoperiodic response (Goto, 2022; Fantini, Facella, 2020), we can assume that photoperiod-sensitive plants may have a more pronounced response to the activation of these photoreceptor systems by selective light irradiation.

In vitro culture is a modern model system for studying plant growth and development processes. Cells of callus tissue of higher plants in *in vitro* culture, along with acquiring new specific properties, are able to retain properties characteristic of plants *in vivo* (Pasternak, Steinmacher, 2024). Therefore, the question of the difference in photomorphogenic reactions of plants of the same species and variety in different cultures: *in vivo* and *in vitro*, remains relevant.

Soybean (*Glycine max* (L.) Merr.) belongs to the *Fabaceae* family and is a leading agricultural crop in the world and in Ukraine. This plant, among whose varieties there are short-day and neutral-day representatives, is also a classic model object for studying the photoperiodic response of plants (Anderson et al., 2019). Currently, *in vitro* models are widely used for studying this important crop (Begum et al., 2019). However, there are few studies on the effect of LED irradiation as a regulatory factor in *in vitro* morphogenesis of soybeans.

Therefore, the aim of our work was to study the processes of photomorphogenesis of seedlings and callus culture of a short-day soybean cultivar *in vivo* and *in vitro* under the action of monochromatic red (RL 660 nm) and blue (BL 450 nm) light spectra.

Materials and Methods

Plant material. The plant material used in this study was seedlings and callus culture of soybean (*Glycine max* (L.) Merr.) of the Clark variety, which is characterised by a short-day photoperiodic response.

In vivo studies were conducted on etiolated 10-day-old seedlings. Pre-sterilised seeds were germinated in Petri dishes on filter paper with the addition of 5 ml of water in the dark at a temperature of 22°C in a TSO-80 MICROmed thermostat, 10 seeds per dish for 3 days. After that, the photoreceptor systems of the studied seedlings were activated by irradiation with monochromatic (selective) light of different spectra. Etiolated seedlings in an isolated box in the dark were irradiated daily for 7 days for 30 minutes using LED matrices with red (660 nm) and blue (450 nm) light with an illumination intensity of 120 mW/m² and a photon distribution of 0.45-0.65 μmol/(m²·s). Control plants were cultivated in darkness at a temperature of 22°C without irradiation. On the 7th day of the experiment, the germination (in %) and seed infection (in %) were analysed (Ostrenko, et al., 2011). On the 10th day of the experiment, growth processes were analysed by determining the linear dimensions and biomass of the obtained seedlings.

In vitro studies. Primary callus of soybean was obtained through the stage of aseptic seedlings cultivated on a hormone-free Schenk and Hildebrandt medium (Phillips, G. C., & Garda, M., 2019), after which the explants were transferred to medium for callus induction by Murashige and Skoog (MS) with the addition of 5 mg/l 2,4-D. Primary callus was cultivated for 2 weeks in a TSO-80 MICROmed thermostat at a temperature of 26°C. During this period, callus tissues were irradiated daily with red (RL) and blue light (BL) for 15 minutes per day using LED matrices, while simultaneously analysing callus growth indicators – area, growth rate and increment. Callus area was measured using the ImageJ 1.52k computer program.

The growth rate of callus tissues (V) was determined by the formula:

$$V = (S_2 - S_1)/t, \text{ where}$$

S₁ – callus area on the first day of measurement, cm²

S₂ – callus area on the last day of measurement, cm²

t – experiment time, days

Callus growth (ΔS) was determined by the formula:

$$\Delta S = S_2/S_1 \times 100 \%, \text{ where}$$

S₁ – callus area on the first day of measurement, cm²

S₂ – callus area on the last day of measurement, cm²

After this period, the callus tissues were transferred to Murashige-Skoog regeneration medium (Phillips, Garda, 2019), with the addition of 0.5 mg/l indoleacetic acid (IAA) and 0.5 mg/l benzylaminopurine (BAP) phytohormones and cultivated in a luminostat with a light flux of 2–3 kLx for 4 weeks, analysing the expression of morphogenic potential of the control and experimental callus. Four variants were distinguished: control (Dark) – callus that were not irradiated and were cultivated in darkness throughout the experiment, WL (white light) – callus that were not irradiated with selective light before cultivation in white light, RL – callus that were photoinduced with red light (660 nm) in the preliminary stage before cultivation in white light, and BL – callus that were photoinduced with blue light (450 nm) before cultivation in white light.

Among the indicators of morphogenetic reactions, the following were studied: callusogenesis, chlorophyllogenesis, rhizogenesis, necrosis (Avksentieva, Chumakova, 2021). These characteristics were calculated as the ratio of callus tissues exhibiting certain reactions to the total number of calluses cultivated.

The results of the experiments were statistically processed using ANOVA dispersion analysis with Microsoft Office Excel 2019 software and the Statistica 5.0 software package. The significance of differences between variants was determined using Student's t-test (Mishra, et al., 2019). All experiments were repeated three times, when studying the results of *in vivo* research, 30–35 seedlings were analysed, and *in vitro* 15–17 calluses were analysed. The tables and graphs show the mean values and their standard errors.

Results and Discussion

The results of the study of the effect of RL and BL irradiation on the germination of the Clark variety of soybean seed showed that the germination energy of seeds is 75.6% (Fig. 1). At the same time, irradiation with red light (RL 660 nm) and blue light (BL 450 nm) stimulates seed germination by 14.9% and 24.3%, respectively. BL irradiation contributes to a 5.2 % reduction in infection, which may be due to its bactericidal effect, while RL irradiation not only increases seed infection by 10 %, but also stimulates the occurrence of developmental abnormalities in seedlings, such as root bifurcation and the formation of short or underdeveloped roots. According to the literature, it is known that RL irradiation stimulates seed germination, which is controlled by the plant's phytochrome system (Paik, Huq, 2019; Lazzarin et al., 2021). The appearance of various anomalies in the development of the root system of the studied seedlings under RL irradiation may be associated with a violation of geotropic reactions or root cell growth (Yun et al., 2023). It is known that plant morphogenesis is accompanied by changes in the cytoskeleton, which is constantly being restructured in response to signals related to development and environmental influences. Such remodelling of the cytoskeleton regulates cell growth, in particular, it ensures the transport and exocytosis of membrane and cell wall components during their expansion, and also contributes to the formation of morphological structures in response to light conditions. External and internal signals lead to changes in the activity of proteins associated with the cytoskeleton, microtubule-associated proteins (MAPs), and actin-binding proteins (ABPs) through the influence of the photomorphogenesis regressor COP1 (CONSTITUTIVE PHOTOMORPHOGENIC1) (Lian et al., 2021; Yuan et al., 2023).

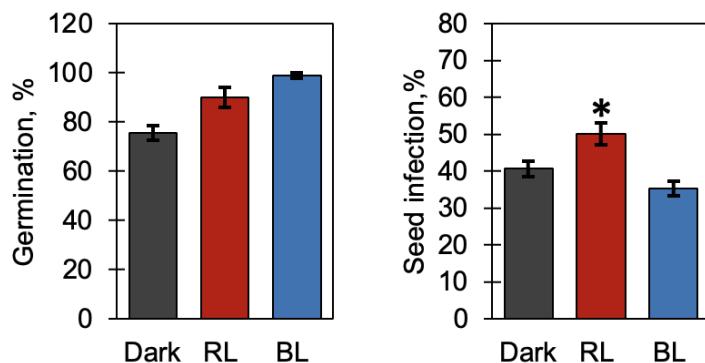


Fig. 1. Effect of photoirradiation with selective light RL (660 nm) and BL (450 nm) on the germination of Clark soybean seeds with a short-day photoperiodic response, % (M \pm s, n=30). Note * – differences compared to the control are significant at p \leq 0.05

It is known that seedlings growing in darkness develop according to the skotomorphogenesis programme and are called etiolated. Such seedlings have an elongated hypocotyl, apical hook, pale stem colour and poorly developed leaves (Josse, Halliday, 2008). Exposure of such seedlings to light leads to the suppression of the activity of COP/DET/FUS, a group of proteins that in turn suppress photomorphogenesis in darkness. This is accompanied by light-dependent accumulation of several transcription factors that promote photomorphogenesis, including HY5, HYH, HFR1, and LAF1, which promotes the transition of seedlings to photomorphogenesis, the direction of which depends on the spectrum and intensity of irradiation (Osterlund et al., 2000; Holm et al., 2002). A study of the growth response to the activation of the phytochrome and cryptochrome systems in short-day soybean seedlings showed that RL and BL irradiation have different effects (Fig. 2). RL irradiation inhibits seedling elongation – the total length of the seedling decreases, its above-ground and underground parts by 33.3% and 28.8%, respectively, compared to the control variant, which is associated with the de-etiolation of the seedling, its transition to photomorphogenesis, accompanied by thickening of the stem and cessation of its elongation. BL irradiation, on the contrary, stimulates the growth of the seedling in length, especially the root system (by 40%), compared to the above-ground part (by 17.9%). The elongation of seedlings, especially the root system, under the influence of BL may be associated with the stimulation of the process of cell vacuolisation and, accordingly, the 'stretch growth' of root cells.

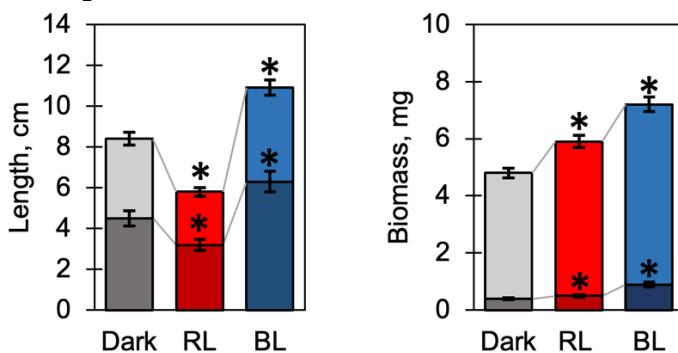


Fig. 2. Effect of photoirradiation with selective RL (660 nm) and BL (450 nm) on the growth response of the above-ground and root parts of Clark soybean seedlings with a short-day photoperiodic response (M \pm s, n=30)

■ – root part, □ – above-ground part

Note * – differences compared to the control are significant at p \leq 0.05

The study of the integral indicator of growth response – biomass increase under irradiation with RL and BL – showed that the activation of both phytochrome and cryptochrome systems stimulates biomass growth, but to a greater extent under the action of BL. Under RL irradiation, there was a 22.7% increase in the biomass of the above-ground part, and under BL irradiation there was a 125% increase in the biomass of the entire seedling, but mainly in the root part, compared to the control. Thus, the study of morphogenetic

reactions *in vivo* showed the manifestation of different pathways of photomorphogenesis under the action of different light spectra: irradiation with RL promotes de-etiolation of the seedling: inhibits seedling elongation and stimulates the accumulation of above-ground biomass, while BL irradiation promotes seedling elongation due to the root system and increases biomass.

The available results may indicate some organ specificity of photoreceptor activity and the presence of a response to irradiation with light of a certain spectrum: RL receptors – phytochromes, mainly regulate the reactions of the above-ground part, while BL receptors – cryptochromes and phototropins, participate in the regulation of the response to irradiation in the root system.

The next stage of the work was related to the study of photomorphogenic reactions *in vitro*. We introduced soybean into an *in vitro* culture and obtained primary soybean calluses. When cultivated in the dark, primary calluses are typical callus tissue: yellowish in colour, amorphous, highly hydrated, and fast-growing.

During the period of photoinduction by RL and BL, the growth response of callus tissue was determined by measuring its area (Fig. 3). The results of the studies showed that the growth and growth rate of primary callus tissues under the influence of RL and BL irradiation are inhibited. RL irradiation contributes to a decrease in the absolute growth and growth rate of callus tissue by 20% and 13%, respectively, while BL irradiation contributes to a decrease in these indicators by 17.2% and 4.6%, respectively. Morphologically, callus tissues after 2 weeks of irradiation are practically indistinguishable – typical, waterlogged, amorphous, heterogeneous masses. Only with BL irradiation is the development of foci of mixotrophic areas of callus tissue observed, which may indicate high activity of blue light receptors – cryptochromes – in callus cells.

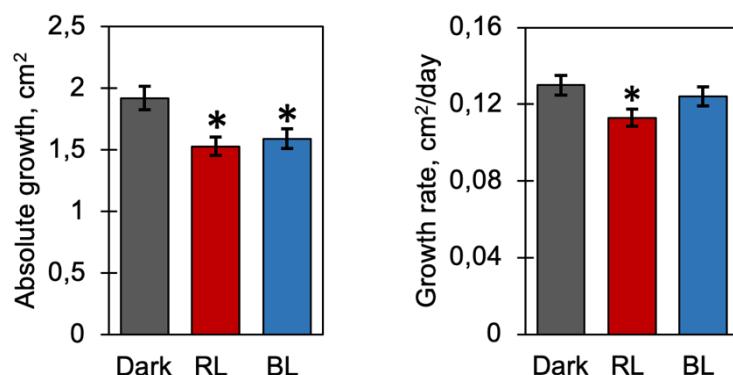


Fig. 3. Effect of photoirradiation with selective RL (660 nm) and BL (450 nm) on the growth response of primary callus of soybean Clark variety with short-day photoperiodic response (M±s, n=15) (culture medium – MS+0.5 mg/l 2,4 D). Note * – differences compared to the control are significant at $p \leq 0.05$

The study of the long-term effects of irradiation continued with the transplantation of callus tissues into a regenerative culture medium. According to the results of the study, the transplantation of callus tissues under white light irradiation inhibits their absolute growth and growth rate compared to tissues cultured in the dark. At the same time, the previous photoinduction with RL and BL affects the further development of callus tissues during further cultivation under white light conditions. The analysis of growth parameters showed that previous photoinduction with RL inhibits the growth of callus tissues by 42% and the growth rate by 60% compared to the dark control, and by 17% and 33%, respectively, compared to callus tissues that did not have preliminary irradiation with RL and BL. This may be due to the inhibition of cell division and vacuolisation and their growth by 'stretching'. BL irradiation, in turn, ensures the growth of callus tissues at the same rate as during cultivation under white light conditions (Fig. 4), although it is 40% less compared to the dark control.

Similar reactions were observed when seedlings were grown *in vivo*. Thus, the photomorphogenetic effects of soybean seedlings under *in vivo* conditions show a co-directed effect with the manifestation of the prolonged effect of irradiation with RL and BL under *in vitro* conditions.

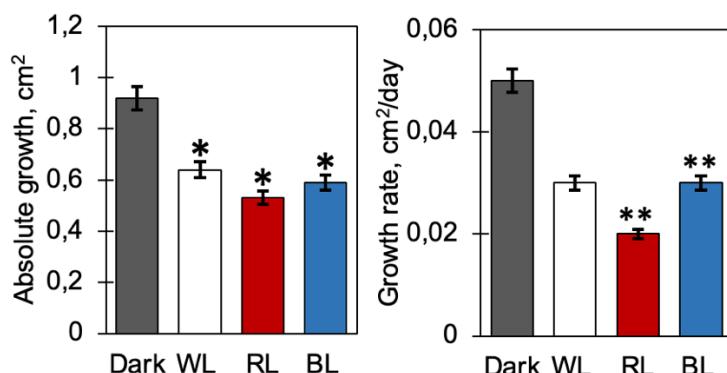


Fig. 4. Prolonged effect of selective light irradiation with RL (660 nm) and BL (450 nm) on the growth response of Clark soybean callus with a short-day photoperiodic response when cultivated on a morphogenic medium of MS + 0.5 mg/l IAA + 0.5 mg/l BAP (M \pm s, n=15);

Dark – no irradiation, cultivation in darkness

WL (white light) – no irradiation, cultivation in white light (full spectrum)

Note * – differences compared to the control are significant at $p \leq 0.05$

** – differences compared to the control are significant at $p \leq 0.001$

When studying the effect of RL and BL irradiation on the manifestation of the morphogenetic potential of callus tissues, we noted such characteristics of callus as colour, the appearance of necrotic spots, callus formation, the development of morphogenic structures and rhizogenesis (Fig. 5). When cultivating callus tissues of soybean in the light, we observed the formation of mixotrophic callus capable of partial autotrophic nutrition (Fig. 6 A-D).

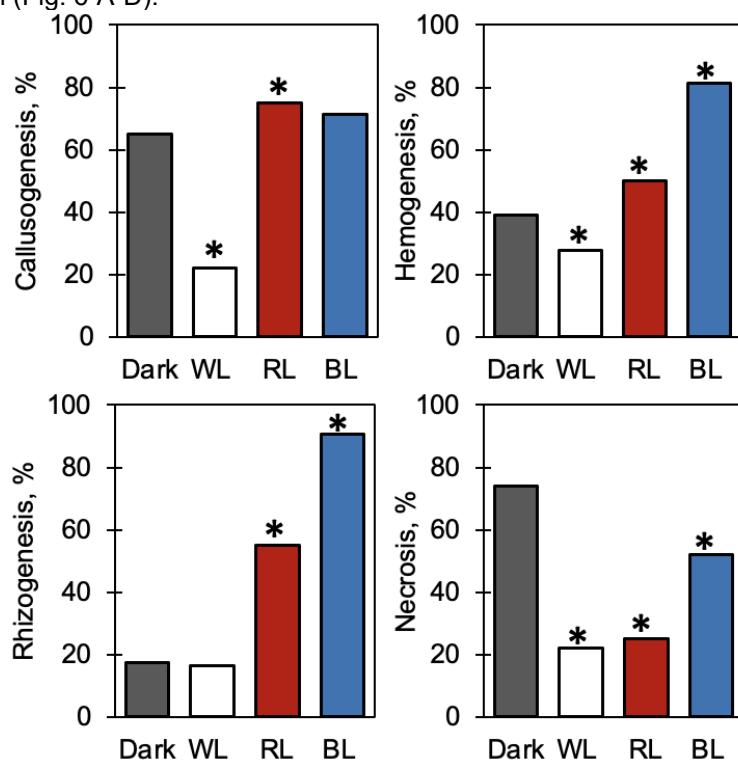


Fig. 5. Prolonged effect of photoirradiation with selective RL (660 nm) and BL (450 nm) on morphogenic reactions of Clark soybean callus with a short-day photoperiodic reaction when cultivated on a morphogenic medium MS + 0.5 mg/l IAA + 0.5 mg/l BAP (M \pm s, n=15);

Dark – no irradiation, cultivation in darkness

WL (white light) – no irradiation, cultivation in white light (full spectrum)

Note * – differences compared to the control are significant at $p \leq 0.05$

When calluses are cultivated under the action of WL without prior irradiation, a decrease in all studied indicators of morphogenetic reactions is observed compared to the dark control. At the same time, the prolonged action of BL stimulates the development of various types of morphogenesis, such as hemogenesis and rhizogenesis, to the maximum extent, not only compared to the dark control, but also compared to calluses cultivated only under WL. BL irradiation also activates all morphogenetic processes in callus tissues, in particular, it significantly contributes to the enhancement of callus formation.

At the same time, the activation of the cryptochrome system, which is known to control the stages of chlorophyll synthesis, stimulates the formation of bright green callus (Fig. 6D). According to the literature, BL irradiation stimulates chlorophyll synthesis in callus tissues under *in vitro* conditions, as well as in plants and under *in vivo* conditions (Liu, Van Iersel, 2021; Xiaoying et al., 2022), indicating the similarity of plant reactions *in vivo* and *in vitro*.

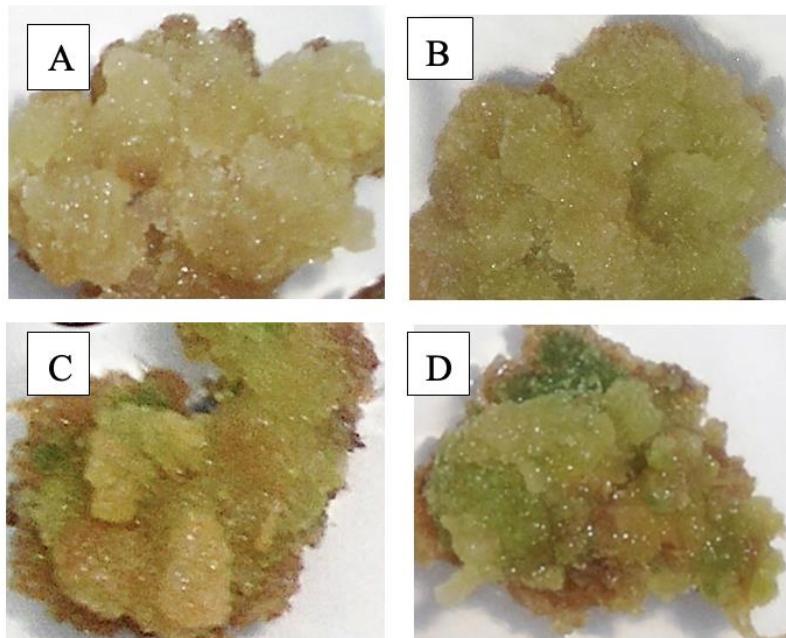


Fig. 6. Callus of *Glycine max* (L.) Merr. variety Clark after 30 days of cultivation on regeneration medium MS + 0.5 mg/l IAA + 0.5 mg/l BAP under the following light conditions: A – darkness, B – white light (WL, full spectrum), C – red light (RL 660 nm), D – blue light (BL 450 nm).

The prolonged action of RL promotes callus greening, although to a lesser extent than the action of BL (Fig. 6C). It is known that one of the reactions of de-etiolation is the synthesis of chlorophyll, which is regulated by the phytochrome system (Banaś et al., 2024). The available results may serve as confirmation of the similarity of plant reactions *in vivo* and *in vitro* to selective light irradiation, which increases the significance of the callus model for photobiological studies.

Conclusions

Thus, the results of the study show that the activation of the phytochrome and cryptochrome systems by RL and BL irradiation stimulates seed germination in a short-day soybean line. At the same time, BL irradiation has a bactericidal effect and reduces seed infection.

Activation of the phytochrome system (RL) initiates de-etiolation, transition to photomorphogenesis, inhibiting stem elongation and stimulating the accumulation of above-ground biomass, while BL irradiation promotes root growth through intensification of vacuolisation and cell elongation in soybean seedlings in the early stages of ontogenesis. The results also indicate the presence of organ-specific regulation of soybean seedling growth responses depending on the irradiation spectrum, which is probably due to the differentiated activity of photoreceptors in different organs.

Under *in vitro* conditions, callus tissue growth is inhibited by selective light irradiation, but a greater effect is observed under the action of RL. Visually, callus tissues remain amorphous and waterlogged, with mixotrophic areas forming only under BL, indicating the onset of chlorophyllogenesis.

When callus tissues are cultivated without prior irradiation with selective light, the main morphogenetic indicators, such as rhizogenesis, hemogenesis and callusogenesis, are reduced compared to dark control and pre-irradiated variants. The prolonged effects of RL and BL are manifested as the stimulation of various morphogenesis pathways of callus culture *in vitro*. RL irradiation stimulates callus formation but does not cause differentiation, accompanied by minimal rhizogenesis and chlorophyllogenesis, while BL irradiation stimulates rhizogenesis, chlorophyllogenesis, and the formation of morphogenic structures.

The photomorphogenic reactions of seedlings and callus tissues of the short-day soybean line in *in vivo* and *in vitro* conditions are similar, which increases the significance of the callus model for photobiological studies.

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**Регуляція селективним світлом морфогенетичних реакцій *Glycine max* (L.)
Merr. за умов *in vivo* та *in vitro***
О.О. Авксентьєва, Є.Д. Батуєва, М.О. Фесенко

Робота присвячена дослідженням фотоморфогенетичних реакцій рослин на монохроматичне опромінення в умовах *in vivo* та *in vitro*. Метою роботи було дослідити вплив опромінення червоним (660 нм) та синім (450 нм) світлом на фотоморфогенез проростків та калюсної культури лінії сої культурної (*Glycine max* (L.) Merr.) в умовах *in vivo* та *in vitro*. Дослідження проводилися на 10-добових проростках та первинній калюсній культурі сої культурної (*Glycine max* (L.) Merr.) короткоденного сорту Clark. Аналізували проростання та інфікованість насіння, проводили аналіз ростових процесів, визначаючи лінійні розміри та біомасу дослідних проростків *in vivo*, в калюсній культурі за умов *in vitro* визначали швидкість росту, приріст та показники морфогенетичних реакцій: каллюсогенез, хлорофілогенез, ризогенез та некроз. Було показано, що опромінення червоним та синім стимулює проростання насіння, а опромінення синім світлом сприяє зниженню інфікованості проростків. В умовах *in vivo* опромінення червоним світлом інгібує видовження досліджуваних проростків, у той час коли опромінення синім світлом стимулює лінійний ріст проростків. Опромінення селективним світлом обох досліджуваних спектрів сприяє накопиченню біомаси у проростках. При цьому спостерігається органоспецифічність реакцій: опромінення червоним світлом спряє збільшенню біомаси надземної частини, а

опромінення синім світлом – в основному, кореневої частини. В умовах культури *in vitro* приріст первинної калюсної тканини гальмується під час опромінення червоним і синім світлом, порівняно з калюсами, культивованими у темряві. При перенесенні досліджуваних калюсів під біле світло, досліджували пролонговані ефекти. Пролонгований ефект впливу червоного та синього світла виражається у гальмуванні червоним світлом приросту калюсної тканини і відсутності впливу синього світла на ростовий індекс, порівняно з контролем. Опромінення синім світлом також стимулює прояв різних шляхів морфогенезу калюсної культури в умовах *in vitro*. Спостерігається однотиповість реакцій проростків та калюсної культури короткоденної лінії сої культурної в умовах культури *in vivo* та *in vitro*.

Ключові слова: фотобіотехнологія, фотоморфогенез *in vitro*, фоторецептори, селективне світло, *Glycine max (L.) Merr.*, проростки, калюс

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