Photosynthesis and productivity

UDC 635.1/.7:581.524

doi: 10.15389/agrobiology.2016.5.680rus

doi: 10.15389/agrobiology.2016.5.680eng

PHOTOSYNTHETIC APPARATUS OF POTATO PLANTS (*Solanum tuberosum* L.) GROWN *in vitro* AS INFLUENCED BY DIFFERENT SPECTRAL COMPOSITION OF LED RADIATION

**Yu.Ts. MARTIROSYAN^{1, 3}, T.A. DILOVAROVA¹, V.V. MARTIROSYAN¹,
V.D. KRESLAVSKI², A.A. KOSOBRYUKHOV^{1, 2}**

¹All-Russian Research Institute of Agricultural Biotechnology, Federal Agency of Scientific Organizations, 42, ul. Timiryazevskaya, Moscow, 127550 Russia, e-mail yumart@yandex.ru;

²Institute of Basic Biological Problems, Federal Agency of Scientific Organizations, 2, ul. Institutskaya, Pushchino, Moscow Province, 142290 Russia, e-mail kosobr@rambler.ru;

³N.M. Emanuel Institute of Biochemical Physics of RAS, Federal Agency of Scientific Organizations, 4, ul. Kosygina, Moscow, 119991 Russia

Acknowledgements:

Supported in part by the grant from Russian Foundation for Basic Research 15-04-01199a

Received April 6, 2016

Abstract

In vitro reproduction is an important stage in seed potato propagation. Various radiation spectra can be used to regulate *in vitro* the growth and morphogenesis of potato seedlings (*Solanum tuberosum* L.). We studied the effect of light emitting diodes (LEDs) light sources, which differ in the spectral composition of the radiation, on the growth processes and functional parameters of the photosynthetic apparatus in potato plants (variety Agria) grown *in vitro*. The red LEDs with $\lambda_m = 635$ nm and the half-width of the emission band (HW) of 45 nm, blue LEDs with $\lambda_m = 463$ nm (HW = 23 nm), green LEDs with $\lambda_m = 521$ nm (HW = 38 nm), and white LEDs (400-730 nm) with an intensity of light equal to 60-65 micromol photons $\cdot$ m⁻² $\cdot$ s⁻¹ at plant level, and white fluorescent lamps (OSRAM AG, Germany) of the same light intensity were used. On day 28 the growth parameters, CO₂ gas exchange rate and parameters of variable chlorophyll fluorescence were measured. The highest biomass accumulation was observed during irradiation of plants with fluorescent lamps. A smaller plant biomass accumulation was observed when plants were irradiated with white LEDs. Blue LEDs was shown to reduce the accumulation of plant biomass by 49.5 % compared to the white LEDs. Irradiation with green and red LEDs led to decrease biomass accumulation by 75.6 and 67.5 %, respectively. The observed changes in the accumulation of dry plant biomass for different spectral ranges are associated with a higher activity of the photosynthetic apparatus of the plants grown under irradiation with blue and white LEDs. The rate of photosynthesis (per unit of the leaf surface) in these plants was higher than in those grown under green or red LEDs. The effective quantum yield of PS 2 in all studied plants had small changes in the range of 0.47 to 0.53, but higher values were observed in the plants grown under fluorescent lamps and white and green LEDs. Electron transport rate (ETR) and non-photochemical quenching (NPQ) were changed in similar manner under different growth conditions. Curve analysis showed that in the conditions when the input of CO₂ was not limited the rate of photosynthesis decreased depending on lighters as follows: fluorescent lamps > white LEDs > red LEDs > blue LEDs > green LEDs. Maximal rate of carboxylation and greater efficiency of the reaction were observed when plants were exposed to fluorescent light and white LEDs. The irradiation of plants with blue, red and, especially, the green LEDs led to a decrease in carboxylation rate to 77.9, 67.9 and 11.1 % of the maximum values. Efficiency of carboxylation in plants grown under red and green LEDs sharply decreased to 37.5 % and 6.7 % of the maximum values. Electron transport rate when using fluorescent lamps, white, red, blue and green LEDs was equal to 100, 97.3, 75.1, 68.0 and 20.8 %, respectively. At the same time there has been a decrease in the utilization rate of triosphosphates to a value of 88.9, 48.7, 28.2 and 9.4 %, respectively, compared to 100 % under fluorescent lamps. Thus, at low levels of light intensity we did not observe significant changes in the activity of both light and dark photosynthetic reactions and the accumulation of plant dry matter. These results allow us to understand the role of separate regions of visible light on the functioning of the photosynthetic apparatus, and more effectively to use LEDs for plant cultivation.

Keywords: potato plants, *Solanum tuberosum* L., growth, photosynthesis, light-emitting diodes, LED, photoreceptors.

In vitro reproduction is an important stage in producing revitalized potato planting material. Available data indicate that the different radiation spectrum can be used to regulate in vitro the growth and morphogenesis in potato seedlings (*Solanum tuberosum* L.) [1-4]. For example, when irradiated with fluorescent lamps (red light, maximum at $\lambda = 660$ nm), seedlings had small leaves and weak sprouts [2]. When illuminated with blue light from fluorescent lamps (maximum at $\lambda = 480$ nm), the plants produced well-developed leaves. Red-enriched light led to an increase in leaf surface [5]. The combination of red and blue light emitting diodes (LEDs) contributed to the growth and development of potato seedlings in a laboratory assessment [6].

It should be noted that known works devoted to this subject mostly dealt with the study of a combined effect of red and blue light spectra on the growth and metabolic processes in leaves [7-9]. Certain addition of other spectral bands, in particular in the green (GSB) region, increases the effectiveness of the sources of exposure being used [7, 10]. The positive effect on the photosynthetic apparatus and production process was also shown when using additional irradiation of plants with a light at a maximum around $\lambda = 630$ nm [11, 12]. In this case, the proportion of the active form of phytochrome B in the pool of phytochromes is changing, which may lead to increased photosynthetic activity in plants [13, 14].

Despite the identified patterns of the LED irradiation influence on the growth processes and photosynthetic apparatus [15-17], the impact of certain regions of the spectrum on the activity of light and dark reactions in photosynthesis in intact leaves still remain poorly investigated.

In this paper, we studied for the first time the association between light and dark phases of photosynthesis and in vitro growth in potato seedlings when exposed to mono- and polychromatic light.

The aim of the study was to investigate the effect of the spectral composition of light on plant development and functional characteristics of the photosynthetic apparatus during in vitro reproduction of potato plants.

Technique. In a laminar box, the upper parts of potato plants (Agria variety) were cut and planted in sterile test tubes containing the Murashige and Skoog medium (Murashige T., Skoog F., 1962) for rooting to produce in vitro culture. The tubes were then placed in a phytotron, where they remained under strictly controlled conditions (18-20 °C, 16-hour photoperiod).

LEDs (OOO Focus, Russia) of red (RS, $\lambda = 635$ nm) with a half-width of the emission band (HW) 45 nm, blue (BS, $\lambda = 463$ nm, HW 23 nm), green (GS, $\lambda = 521$ nm, HW 38 nm) and white light (WS, $\lambda = 400-730$ nm), with a light intensity equal to 60-65 micromol photons $\cdot$ m⁻² $\cdot$ s⁻¹ at plant level, were used for illumination. Some of the plants were placed under white fluorescent lamps (OSRAM AG, Germany) at the same light intensity.

The leaf area and plant height were measured at day 28. To account for the dry biomass, 6-8 plants were sampled in each test option, then the above-ground and underground parts were separated, fixed at 105 °C, dried at 70 °C, and weighed.

The CO₂ gas exchange rate was determined using a portable infrared gas analyzer LCPro + (ADC BioScientific Ltd, UK). The curves of CO₂ gas exchange in leaves depending on the light intensity and carbon dioxide concentration in the air were obtained and analyzed as described [15].

The chlorophyll fluorescence was measured on the leaves from 2-3 upper tiers, using a pulse-amplitude modulated fluorometer (JUNIOR-PAM, Heinz Walz GmbH, Germany). Fluorescence parameters were recorded after 20 minutes of dark adaptation. The effective quantum yield of the PS II (photosys-

tem II), the relative electron transport rate (ETR), and non-photochemical quenching (NPQ) were determined [18].

Statistical analysis was performed using Statistica 10 software (Statsoft Inc., USA). In all cases, P was calculated for a significance level of 0.05. The tables and diagrams provide arithmetic means with a standard error ($\bar{X} \pm x$).

Results. One of our study objectives was to monitor the growth processes and photosynthetic rate, as well as to analyze the activity of the light and dark reactions in the photosynthetic apparatus when rooting the potato cuttings depending on the spectral composition of the light emitting diode illuminators.

1. Dry weight (g) of organs in potato (*Solanum tuberosum* L.) Agria variety microplants in vitro at different illumination spectra ($\bar{X} \pm x$)

Lamp type, light spectral composition	Leaf	Stem	Root	Plant
White fluorescent lamps (control)	0.55±0.10	0.25±0.02	0.15±0.05	0.94±0.16
LED lamps:				
white ($\lambda = 400-730$ nm)	0.52±0.03	0.28±0.03	0.06±0.02*	0.86±0.06
blue ($\lambda = 463$ nm)	0.29±0.09*	0.21±0.03	0.02±0.01*	0.52±0.13*
green ($\lambda = 521$ nm)	0.16±0.06*	0.10±0.04*	0.04±0.02*	0.21±0.07*
red ($\lambda = 635$ nm)	0.13±0.02*	0.14±0.01*	0.02±0.00*	0.28±0.04*

Note. LED — light emitting diode. These are mean values with a standard error from 6-8 plants.

* Differences vs. control are significant ($P < 0.05$).

The spectral composition of light significantly influenced the growth and developmental processes in plants (Table 1). Thus, under fluorescent lights, the growth rate, estimated by the production of the above-ground biomass, was the highest. A somewhat lesser biomass accumulation was observed with the irradiation from white LEDs. The effect of blue light was in the reduced biomass in plants by 49.5 % vs. a test where white LEDs were used. The irradiation from GS LEDs and RS LEDs resulted in the decreased accumulation of biomass by 75.6 and 67.5 %, respectively.

2. Growth of potato (*Solanum tuberosum* L.) Agria variety microplants in vitro at different illumination spectra ($\bar{X} \pm x$)

Lamp type, light spectral composition	Stem height, cm	Biomass (roots + stems)/leaves ratio	Number of internodes
White fluorescent lamps (control)	16.30±1.83	0.72	8.20±0.55
LED lamps:			
white ($\lambda = 400-730$ nm)	13.78±0.99	0.65	9.00±0.37
blue ($\lambda = 463$ nm)	19.46±1.18	0.79	9.00±0.30
green ($\lambda = 521$ nm)	24.77±1.53*	0.88	9.30±0.33
red ($\lambda = 635$ nm)	32.79±1.52*	1.23	10.10±0.31

Note. LED — light emitting diode. These are mean values with a standard error from 6-8 plants.

* Differences vs. control are significant ($P < 0.05$).

The uneven distribution of dry biomass in plant organs depending on the type of illuminator and the spectral composition of light should also be noted (Table 2). The ratio of the weight of stems and roots to the weight of leaves showed that its high accumulation in plants under fluorescent lamps and white LEDs was due to a higher gain of dry matter in leaves vs. roots and stem. The irradiation with RS LEDs led to a greater accumulation of dry biomass in the attracting organs, i.e. the stem and the roots.

The revealed changes in the accumulation of dry matter at various spectral regimes of irradiation were associated with a higher activity of the photosynthetic apparatus when growing plants under white and blue LEDs (Table 3). The photosynthetic rate per unit of leaf area in these tests was higher than in those where green or red LEDs were used. For plants grown under fluorescent illumination as well as white LEDs, high values of stomatal conductance and transpiration rate were also observed.

The evaluation of the photosynthetic apparatus function demonstrated

that the effective quantum yield of PS II in the studied plants varied only slightly (ranging from 0.47 to 0.53), while higher values were observed in the test with fluorescent lamps and white and green LEDs. The electron transport rate (ETR) and non-photochemical quenching (NPQ) were changed in a similar way, depending on the plant growth conditions. As a result, at low light intensity the low photosynthetic rate in case of RS LEDs and GS LEDs is primarily related to the activity of the dark reactions in photosynthesis and poor stomatal conductance.

3. Parameters of the photosynthetic function and transpiration in potato (*Solanum tuberosum* L.) Agria variety microplants in vitro at different illumination spectra ($X \pm x$)

Parameter	Spectral regime				
	FS	WS LED	BS LED	RS LED	GS LED
Photosynthetic rate, $\mu\text{mol CO}_2 \cdot \text{m}^{-2} \cdot \text{s}^{-1}$	9.6 $\pm$ 0.8	9.0 $\pm$ 0.8	7.8 $\pm$ 0.7	5.7 $\pm$ 0.5*	4.7 $\pm$ 0.5*
Transpiration rate, $\mu\text{mol H}_2\text{O} \cdot \text{m}^{-2} \cdot \text{s}^{-1}$	4.9 $\pm$ 0.2	4.7 $\pm$ 0.2	4.6 $\pm$ 0.2	2.6 $\pm$ 0.1*	3.1 $\pm$ 0.2*
Water-use efficiency, $\mu\text{mol CO}_2/\text{mmol H}_2\text{O}$	2.0 $\pm$ 0.1	1.9 $\pm$ 0.2	2.2 $\pm$ 0.1	2.2 $\pm$ 0.1	1.5 $\pm$ 0.1*
Stomatal conductance, $\text{mol H}_2\text{O} \cdot \text{m}^{-2}$	0.41 $\pm$ 0.02	0.38 $\pm$ 0.02	0.36 $\pm$ 0.03	0.14 $\pm$ 0.02*	0.17 $\pm$ 0.02*
Y (II)	0.51 $\pm$ 0.03	0.53 $\pm$ 0.02	0.49 $\pm$ 0.03	0.47 $\pm$ 0.02	0.53 $\pm$ 0.02
NPQ	0.51 $\pm$ 0.03	0.53 $\pm$ 0.03	0.49 $\pm$ 0.02	0.47 $\pm$ 0.02	0.53 $\pm$ 0.03
ETR	61.2 $\pm$ 1.6	63.2 $\pm$ 2.1	58.2 $\pm$ 1.2	56.3 $\pm$ 1.7	63.3 $\pm$ 2.0

Note. FS — fluorescent lamps (control); LED — light-emitting diode lamps (WS LED — white light, $\lambda = 400\text{--}730$ nm; BS LED — blue light, $\lambda = 463$ nm; RS LED — red light, $\lambda = 635$ nm; GS LED — green light, $\lambda = 521$ nm); Y (II) — the effective quantum yield of photosystem II, RU; NPQ — non-photochemical quenching, RU; ETR — relative electron transport rate. These are mean values with a standard error from 6–8 plants.

* Differences vs. control are significant ($P < 0.05$).

Rates of light and dark reactions of photosynthesis in potato (*Solanum tuberosum* L.) Agria variety microplants in vitro at different illumination spectra. FS — fluorescent lamps, WS — white light-emitting diode lamps (LED) ($\lambda = 400\text{--}730$ nm), BS — blue LED ($\lambda = 463$ nm), RS — red LED ($\lambda = 635$ nm), GS — green LED ($\lambda = 521$ nm). A model of G.D. Farquhar et al. (1980) was used for approximation of carbon dioxide curves of CO₂-exchange.

To determine the potential activity of light and dark reactions of photosynthesis, carbon dioxide curves were constructed. Their analysis using a biochemical model [19] showed that when the photosynthetic rate is not limited by CO₂ level, the absorption of carbon dioxide by leaves decreases in a row of fluorescent lamps > white LEDs > red LEDs > blue LEDs > green LEDs (Fig.).

The maximum carboxylation rate and a greater efficiency of the reaction were observed when the plants were exposed to fluorescent light and white LED light. In the tests with BS LED, RS LED and especially GS LED, the carboxylation rate decreased down to values constituting 77.9, 67.9 and 11.1 % of that obtained under the fluorescent lights. The carboxylation efficiency sharply decreased after exposure to RS LEDs and GS LEDs, such as down to 37.5 % and 6.7 % of the maximum values, respectively. The electron transport rate under irradiation with fluorescent lights was the greatest, and it amounted to 97.3; 75.1; 68.0 and 20.8 % of this parameter in tests with WS LED, RS LED, BS LED and GS LED, respectively. There was a concurrent decrease in the rate of triose phosphate utilization, such as to 88.9; 48.7; 28.2 and 9.4 %, respectively, of the value observed under fluorescent lighting (100 %).

The results obtained indicate that different spectral compositions of light may differently affect the activity of the light and dark stages in photosynthesis. In natural CO₂ concentrations, under irradiation from LEDs, emitting in different spectral regions, the rate of initial photosynthetic processes varied insignificantly. At that, the plants modified functional activity of their photosynthetic apparatus. With elevated CO₂ concentrations, when the restriction of the photosynthetic rate due to activity of the dark processes is reduced, the maximum carboxylation rate and efficiency changed only slightly under irradiation with fluorescent lamps, white and blue LEDs, but decreased significantly with RS LEDs and GS LEDs. As a result, the data, obtained using the model, support the conclusion about the contribution of reduced stomatal conductance to decreases in the photosynthetic rate when the plants are exposed to RS LED and, especially, to GS LED, which is due to inhibition of the CO₂ flow to the centers of carboxylation (Table 3). Along with the rate of light and dark reactions of photosynthesis, the respiration was also affected by the spectral composition of the irradiation. The highest respiration rate was observed when plants were illuminated by BS LEDs vs. other test options. The exposure to RS LED led to a decrease in the intensity of gas exchange.

Our data on the effect of different sources of illumination on the plants during in vitro propagation, indicate that the activity of light reactions of photosynthesis does not significantly change at a low light intensity, irrespective of spectral composition and type of illuminator (fluorescent lamps or LEDs), and the differences observed in the accumulation of dry matter by plants are mediated by the processes associated with the activity of the dark phase reactions of photosynthesis (the rate and efficiency of carboxylation, the rate of triose phosphate utilization), as well as with a decrease in stomatal conductance. Moreover, there were significant differences in gas exchange, resulting in a modified relation between respiration rate and photosynthesis.

The changes in the activity of the photosynthetic apparatus are not the only plant response to different spectral composition of light [20-22]. The literature suggests an important role of photoreceptors in the regulation of plant growth and morphogenesis, as well as in the activity of the photosynthetic apparatus [23-25]. Regulatory photoreceptors in different light bandwidths play a major role in the manifestation of the light effects [26-28]. The spectral composition of light had no significant effect on the initial growth processes, however, the red light contributed to the intensive development of axial organs, probably, by means of stimulating the red light photoreceptor, i.e. phytochrome. In contrast, in case of exposure to blue light, the plant growth was inhibited, which could be due to the effect of cryptochrome. The effect of light is also manifested in the changed hormonal status of plants (the content and ratio of gibberellins and auxins) and in the regulation of the activity of physiological processes [22].

Therefore, the study of the photosynthetic function and growth in vitro in potato revealed the complexity of the changes in the activity of the individual processes of light and dark stages in photosynthesis depending on the type of illuminator and the spectral composition of light. At low intensity of the luminous flux of various spectral compositions, the changes in the dry matter accumulation by plants are related to different activity of reactions in the dark phase of photosynthesis. Our results allow to approach to the clarification of the role of individual monochromatic LED illuminators in the photosynthetic apparatus functioning, so that to specifically use LED illuminators when growing plants.

REFERENCES

1. Aksenova N.P., Konstantinova T.N., Chailakhyan M.Kh. Morphogenetic effects of blue and red light during exposure of overground and underground organs of potato in culture in vitro. *Doklady Botanical Sciences*, 1989, 305: 508-512.
2. Aksenova N.P., Konstantinova T.N., Sergeeva L.I., Machackova I., Golyanovskaya S.A. Morphogenesis of potato plants in vitro. I. Effect of light quality and hormones. *J. Plant Growth Reg.*, 1994, 13: 143-146 (doi: 10.1007/BF00196378).
3. Seabrook J.E.A., Douglass L.K. Prevention of stem growth inhibition and alleviation of intumescence formation in potato plantlets in vitro by yellow filters. *Am. J. Potato Res.*, 1998, 75: 219-224 (doi: 10.1007/BF02854216).
4. Seabrook J.E.A. Light effects on the growth and morphogenesis of potato (*Solanum tuberosum* L.) in vitro: a review. *Am. J. Potato Res.*, 2005, 82: 353-367 (doi: 10.1007/BF02871966).
5. Charles G., Rossignol L., Rossignol M. Environmental effects on potato plants in vitro. *J. Plant Physiol.*, 1992, 139: 708-713 (doi: 0.1016/S0176-1617(11)81715-3).
6. Jao R.C., Fang W. Growth of potato plantlets in vitro is different when provided concurrent versus alternating blue and red light photoperiods. *Hort. Sci.*, 2004, 39: 380-382.
7. Kim S.J., Hahn E.J., Heo J.W., Paek K.Y. Effects of LEDs on net photosynthetic rate, growth and leaf stomata of chrysanthemum plantlets in vitro. *Hort. Sci.*, 2004, 101: 143-151.
8. Ohashi-Kaneko K., Takase M., Kon N., Fujiwara K., Kurata K. Effect of light quality on growth and vegetable quality in leaf lettuce, spinach and komatsuna. *Environ. Control Biol.*, 2007, 45: 189-198 (doi: 10.2525/ecb.45.189).
9. Yorio N.C., Goins G.D., Kagie H.R., Wheeler R.M., Sager J.C. Improving spinach, radish, and lettuce growth under red light-emitting diodes (LEDs) with blue light supplementation. *Hort. Sci.*, 2001, 36: 380-383.
10. Kim H.H., Goins G.D., Wheeler R.M., Sager J.C. Green-light supplementation for enhanced lettuce growth under red- and blue-light-emitting diodes. *Hort. Sci.*, 2004, 39: 1617-1622.
11. Kosobryukhov A.A., Kreslavski V.D., Khramov R.N., Bratkova L.R., Shchelokov R.N. Influence of additional low intensity luminescent radiation on growth and photosynthesis of plants. *Biotronics*, 2000, 29: 23-31.
12. Tarakanov I.G., Yakovleva O.S. V sbornike: *Fiziologo-biokhimicheskie osnovy produktsionnogo protsessa u kul'tiviruemykh rastenii* [In: Physiology and biochemistry of crops yield formation]. Saratov, 2010: 95-97 (in Russ.).
13. Kreslavski V.D., Lyubimov V.Y., Shirshikova G.N., Shmarev A.N., Kosobryukhov A.A., Schmitt F.J., Friedrich T., Allakhverdiev S.I. Preillumination of lettuce seedlings with red light enhances the resistance of photosynthetic apparatus to UV-A. *J. Photochem. Photobiol. B Biol.*, 2013, 122: 1-6 (doi: 10.1016/j.jphotobiol.2013.02.016).
14. Kreslavskii V.D., Lyubimov V.Yu., Shabnova N.I., Shirshikova G.N., Shmarev A.N., Kosobryukhov A.A. *Doklady RASKHN*, 2014, 1: 20-23 (in Russ.).
15. Martirosyan Yu.Ts., Polyakova M.N., Dilovarova T.A., Kosobryukhov A.A. Photosynthesis and productivity of potato plants in the conditions of different spectral irradiation. *Agricultural Biology*, 2013, 1: 107-112 (doi: 10.15389/agrobiol.2013.1.107eng) (in Engl.).
16. Avercheva O.V., Berkovich Yu.A., Erokhin A.N., Zhigalova T.V., Pogoyan S.I., Smolyanina S.O. *Fiziologiya rastenii*, 2009, 56: 17-26 (in Russ.).
17. Johkan M., Shoji K., Goto F., Hashida S., Yoshihara T. Blue light-emitting diode light irradiation of seedlings improves seedling quality and growth after transplanting in red leaf lettuce. *Hort. Sci.*, 2010, 45: 1809-1814.
18. Gol'tsev V.N., Kaladzhi Kh.M., Kuzmanova M.A., Allakhverdiev S.I. *Peremennaya i zamedlennaya fluorestsentsiya khlorofilla a — teoreticheskie osnovy i prakticheskoe prilozhenie v issledovanii rastenii* [Variable and delayed fluorescence of chlorophyll a — theoretical foundations and practical application in plant research]. Izhevsk-Moscow, 2014 (in Russ.).
19. Farquhar G.D., von Caemmerer S., Berry J.A. A biochemical model of photosynthetic CO₂ assimilation in leaves of C3 plants. *Planta*, 1980, 149(1): 78-90 (doi: 10.1007/BF00386231).

20. Bukhov N.G., Drozdova I.S., Bondar V.V., Mokronosov A.T. Blue, red and blue plus red light control of chlorophyll content and CO₂ Gas exchange in barley leaves: quantitative description of the effects of light quality and fluence rate. *Physiologia Plantarum*, 1992, 85: 632-638 (doi: 10.1111/j.1399-3054.1992.tb04765.x).
21. Matevosyan G.L., Buren' V.M., Baranova R.K., Volkova R.I., Sergeeva L.S. V sbornike: *Regulyatsiya rosta i razvitiya kartofelya* [In: Regulation of growth and development of potato plants]. Moscow, 1990: 83-87 (in Russ.).
22. Voskresenskaya N.P., Drozdova I.S., Aksenova N.P., Konstantinova T.I., Bondar V.V., Perfil'eva S.D., Chailakhyan M.Kh. V sbornike: *Regulyatsiya rosta i razvitiya kartofelya* [In: Regulation of growth and development of potato plants]. Moscow, 1990: 20-29 (in Russ.).
23. Kreslavskii V.D., Kosobryukhov A.A., Shmarev A.N., Aksenova N.P., Konstantinova T.N., Golyanovskaya S.A., Romanov G.A. *Fiziologiya rastenii*, 2015, 62(2): 222-229 (in Russ.).
24. Shin K.S., Mrthy H.N., Heo J.W., Hahn E.J., Paek K.Y. The effect of light quality on the growth and development of in vitro cultured *Doritaenopsis* plants. *Acta Physiol. Plant.*, 2008, 30: 339-343 (doi: 10.1007/s11738-007-0128-0).
25. Kreslavski V.D., Schmitt F.-J., Keuer C., Fridrich T., Shirshikova G.N., Zharmukhamedov S.K., Kosobryukhov A.A., Allakhverdiev S.I. Response of the photosynthetic apparatus to UV-A and red light in the phytochrome B-deficient *Arabidopsis thaliana* L. *hy3* mutant. *Photosynthetica*, 2016, 54(3): 321-330 (doi: 10.1007/s11099-016-0212-z).
26. Terashima I., Fujita T., Inoue T., Chow W.S., Oguchi R. Green light drives leaf photosynthesis more efficiently than red light in strong white light: revisiting the enigmatic question of why leaves are green. *Plant Cell Physiol.*, 2009, 50: 684-697 (doi: 10.1093/pcp/pcp034).
27. Kosobryukhov A.A., Lyubimov V.Yu., Kreslavski V.D. Adaptive mechanisms of photosynthetic apparatus to UV radiation. In: *Stress response in plants*. B.N. Tripathi, M. Müller (eds.). Springer International Publishing Switzerland, 2015, chapter 3: 59-78 (doi: 10.1007/978-3-319-13368-3_3).
28. Hogewoning S.W., Trouwborst G., Maljaars H., Poorter H., van Ieperen W., Harbinson J. Blue light dose—responses of leaf photosynthesis, morphology, and chemical composition of *Cucumis sativus* grown under different combinations of red and blue light. *J. Exp. Bot.*, 2010, 6: 3107-3117 (doi: 10.1093/jxb/erq132).