AGRICULTURAL BIOLOGY,
2019, V. 54, № 1, pp. 121-129
(SEL'SKOKHOZYAISTVENNAYA BIOLOGIYA)

ISSN 2412-0324 (English ed. Online)
ISSN 0131-6397 (Russian ed. Print)
ISSN 2313-4836 (Russian ed. Online)

LEDs for plant lighting

UDC 635.92:631.543.1:581.14:631.588.5

doi: 10.15389/agrobiology.2019.1.121eng
doi: 10.15389/agrobiology.2019.1.121rus

THE SPECTRAL LIGHT INFLUENCE ON YOUNG ORNAMENTAL PLANTS' RESISTANCE TO SHORT-TERM COLD STRESS

V.V. KONDRATIEVA, T.V. VORONKOVA, L.S. OLEKHNOVICH, G.F. BIDYUKOVA, O.L. ENINA, O.V. SHELEPOVA

Tsitsin Main Botanical Garden RAS, 4, Botanicheskaya ul., Moscow, 127276 Russia, e-mail lab-physiol@mail.ru (✉ corresponding author), winterness@yandex.ru, shelepova-olga@mail.ru
ORCID:
Kondratieva V.V. orcid.org/0000-0003-3934-9288
Voronkova T.V. orcid.org/0000-0002-6112-271X
Olekhnovich L.S. orcid.org/0000-0002-3230-0038
Bidyukova G.F. orcid.org/0000-0002-0740-947X
Enina O.L. orcid.org/0000-0002-8971-6384
Shelepova O.V. orcid.org/0000-0003-2011-6054
The authors declare no conflict of interests
Received July 10, 2018

Abstract

LED light sources allow for variations in the spectral composition which makes it possible to evaluate the effect of light with narrow spectral width on plants performance. The combination of such lighting with natural lighting can significantly change the direction and intensity of metabolic processes in plants to adapt to changing environmental conditions. In the present paper, we showed for the first time that additional illumination with narrow-spectrum light allows the seedlings of ornamental plants to successfully adapt to cold stress. The aim of our work was to estimate the effect of red light (600 nm) and blue light (400 nm) from LED panels on adaptation of tagetes (*Tagetis panula* L.) cultivar Karmen, snapdragon (*Antirrhinum majus nanum* L.) cultivar Flora shower white and petunias (*Petunia hybrida* L.) cultivar Mambo blue seedlings to spring frosts when transplanting to open ground. These plants are often used in landscaping settlements and are exposed to low positive and zero temperatures, especially in the first days after transplanting to open ground. The experiment was carried out in a greenhouse (18 °C, humidity 85%). During thirty days, one third of the plants were additionally red lightened (RL), and one third ones were blue lightened (BL) using Focus MC2 (JCC-12) LED panels (Russia) for 12 hours after the end of daylight hours. A third of the plants were grown under natural light only (C). After the end of the LED illumination period, a half of the plants in each variant were placed in the chamber with 2 °C for 24 hours. The second half plants were control without cooling. The effectiveness of lighting was assessed by the decorative state of plants, the change in the selective permeability of membranes, the content of salicylic and abscisic acids, the triggers of the cascade of protector reactions in the leaf tissues, and the survival of plants transplanted to the open ground. Our experiments showed that additional lightening with blue and red light contributes to seedling resistance to low positive temperatures. In RL- and BL-exposed plants, the leaf turgor was quickly restored, the habitus of plants was preserved, and budding began. In these variants, the cell membrane stabilization was noted, i.e. i.e. an increase in the outlet of potassium ions was two times lower than in the control. The changes of cell membranes was estimated by output of electrolytes from the 0.25 g leaves measured potentiometrically (ITAN, OOO SPE Tom'analit, Russia) with an ion-selective electrode (Elit-031, OOO NIKO ANALIT, Russia). Abscisic acid (ABA) and salicylic acid (SA), the important triggers and tuners of cascade responses to abiotic stress, were determined in a single sample, at the final stage, by isocratic HPLC method (Stayer system, ZAO Aquilon, Russia), with column PR-18 (250/4.6 mm) (Phenomenex, Inc., USA). ABA concentration in leaves of RL-exposed tagetes plants increased 4.4-fold and the SA 3.3-fold compared to the control, and in BL-exposed tagetes only SA content increased 1.4-fold ($p \le 0.05$). After cold exposure, the RL plants restored turgor, while in BL the restoration was slower and the leaf infiltration began. Similar changes were in control. In snapdragons and petunias, blue light also caused a 1.5-fild increase in the SA level in leaves, while red light led to insignificant changes. After cold stress, the RL- and SS-exposed plants of these species quickly recovered, their habitus was almost as in unaffected plants. The control plants recovered more slowly, and their decorativeness was worse. The survival rate of RL plants replanted to open ground was 100 % for tagetes and petunias, and 85-90% ($p \le 0.05$) for snapdragons. In BL-exposed plants, these indicators were 70% ($p \le 0.05$) for tagetes and 85-90 % ($p \le 0.05$) for petunias. The rooting of the control plants not exposed to RL or BL and subjected to the cold stress reached 60-70% ($p \le 0.05$). The physiological

and biochemical changes that we identified in the leaves of the seedlings of ornamental plants suggest that spectral light facilitates the modulation of plant metabolism and activates non-specific protective mechanisms aimed at preserving the ionic and redox cell homeostasis. An exposure of growing seedlings of ornamental plants to light with narrow spectral width, in addition to natural light, can be very effective to reduce the loss of re-planted plants from spring frosts.

Keywords: *Tagetis panula* L., tagetes *cv*. Karmen*, Antirrhinum majus nanum* L., snapdragon cv. Flora shower white, *Petunia hybrida* L., petunias cv. Mambo blue, narrow spectral light, cold stress, cell membranes, water soluble carbohydrates, salicylic acid, abscisic acid, ABA

Adaptation of plants to changes in the environmental temperature is often accompanied by stress. This is a complex multi-stage process, discovering the mechanisms of which is important for research and application.

Narrow-spectrum LED light combined with natural lighting may significantly alter the intensity and direction of plant metabolism [1, 2]. Using LED lamps and panels in new protected cultivation technologies becomes a trendy orangery technology [3]. However, the physiology and biochemistry of adaptation remain understudied. Light intensity, duration, and wavelength may trigger the expression of certain genes and the synthesis of a number of new substances affecting the generative organs of plants [4, 5]. One assumption is that the effects of narrow-spectrum light are related to the activation of COR genes that initiate the synthesis of cold shock proteins [6, 7]. This cascade of interrelated transformations involves multiple light-dependent responses, which causes significant readjustments in plant metabolism, as it alters the hormonal and carbohydrate status of cells and their membrane permeability, while also activating or inhibiting some enzymes [8-10]. Improved resistance of plants to hypothermia is associated with the suppression of oxidative stress due to binding the reactive oxygen species (ROS) and free radicals; this binding is enabled by antioxidant enzymes and the accumulation of low molecular weight organic antioxidants [11, 12]. When adapting to cold shocks, plants accumulate stress defensive agents, such as amino acids, soluble sugars, sugar alcohols, and sundry metabolites.

Some believe that COR genes are activated by exposure to red (λ = 660 nm) or blue (λ = 400 nm) light, i.e. the regulation of COR gene expression involves the phytochrome and cryptochrome light receptors [13, 14]. It is suggested that there exist primary elicitor signals of various nature; the suggestion is backed by the data on the stabilizing effects red and blue light has on gene expression regulation under stress. Low-temperature adaptation is modeled by a number of interrelated processes that enable plants to adjust their cellular and metabolic homeostasis [15]. Salicylic acid (SA) and abscisic acid (ABA) are important for the functioning of such cascade mechanisms. SA is one of the metabolites that initiate the expression of genes responsible for the synthesis of antioxidative enzymes, which helps control the ROC, preserve the integrity of cellular membranes, as well as the redox status of plant cells [16-18]. The accumulation of ABA in tissues triggers an ABA signaling cascade that culminates in the expression of COR genes, which in their turn determine the cold tolerance of the species [19].

This paper is the first to demonstrate that exposure to narrow-spectrum light enables the seedlings of ornamental plants to successfully adapt to cold shock.

The research objective is to find whether preliminary supplementary red or blue lighting will affect the resistance of seedlings to short-term low positive temperatures during spring frosts.

Techniques. The following plant species were selected: snapdragon (*Antirrhinum majus nanum* L.) short-stem cultivar Flora shower white; tagetes (*Tagetis panula* L.) short-stem cultivar Karmen; and petunia (*Petunia hybrida* L.) cultivar Mambo blue; all of those are popular ornamental plants used in open ground in

urban gardening. At the fifth-to-seventh leaf development stage, the plants were planted in pots with sand, 5 plants per pot, 15 pots per group. The plants were growing in a semi-controlled environment: the natural light was supplemented with red light (max $\lambda = 600$ nm), group 1, RL, or blue light (max $\lambda = 400$ nm), group 2, BL. The intensity for RL and BL was 2.58×10^{18} and 6.04×10^{18} photons/($m^2 \cdot s$), respectively. Extra light came from Focus MC2 (JCC-12) LED lamps (Russia). Supplementary lighting was on for 12 hours daily; the control group (group 3, or C) comprised plants exposed to natural light only. Seedlings were watered with distilled water daily, fed once a week with 150 ml of Knop's solution (0.25 mg potassium phosphate, 0.25 magnesium sulfate, 1 g calcium nitrate, and 0.125 g potassium chloride per 1 l of distilled water). After the supplementary lighting experiment was over, half of the plants from each group (RL, BL, and C) were placed for 24 hours in a chamber with a temperature of 2 °C; the remainders (the controls) were left non-cooled.

Samples for biochemical tests were taken on day 35 (when the experiment was over) and on day 37 (after 2 days of exposure to cold shock). To determine the functional status of cellular membranes, 0.3 g of leaves was placed in a bidistillate, kept for 24 hours in a thermostat at 26 °C; the conductivity of the eluate was measured, and the content of K^+ was quantitated by potentiometry using ion-selective electrodes (ITAN pH meter/ionometer, OOO NPP Tomanalit, Russia; Elit-031 ion-selective electrode, OOO NIKO Analit, Russia) according to earlier published guidelines [20].

The content of monosaccharides was found spectrophotometrically (Specol 1300, Analytik Jega AG, Germany) in terms of picric acid [21]. The concentration of salicylic acid (SA) and abscisic acid (ABA) was analyzed from a single sample: 2 g of fresh leaves were extracted by ethanol (80%); the extract was evaporated to an aqueous phase, which was divided into two parts of equal volume. To extract SA and ABA, the extract was purified using the laboratory-modified method [22]. At the final stage, the research team used isocratic high-performance liquid chromatography (a Stayer isocratic chromatograph, ZAO Aquilon, Russia) with an RP-18 (250/4.6 mm) column (Phenomenex, Inc., United States).

The data was processed statistically with Excel 2010 and Past v3.0 software [23]. The means of the analyzed values (M), standard errors of the mean ($\pm$SEM), and confidence intervals at 95% confidence level ($t_{0.05} \times$SEM) were calculated. The significance of differences between the groups was evaluated by non-parametric statistic (paired Shapiro-Wilcoxon test). The inter-group difference was deemed significant at $p \leq 0.05$.

Results. Diurnal temperature swings in spring and fall often damage or even kill plants. The temperature that was used to simulate cold shock (2 °C) is not lethal for the plants under analysis; however, it can significantly damage their leaves [24].

Supplementary red and blue lighting did not cause any significant habitus or morphology difference in tagetes between the groups, see Figure 1, A. Both experimental plants and controls had good leaf turgor; almost 30% began budding. In snapdragons and petunias, supplementary red lighting caused the aerial biomass of the plants to become 1.5 times and 2.4 times larger, while the root biomass became 1.6 times and 1.8 times larger, respectively, see Figure 1, B. Experimental plants did not differ from the controls in terms of flowering onset; however, the flowering performance was 19% to 23% better in the former. In May, when replanting the plants in open ground (at 10 to 12 °C in daytime and 2 to 5 °C in nighttime), the survival rate of RL- and BL-exposed plants varied from 100% for tagetes and petunias to 80% for snapdragons; the survival rate of

the controls was only about 60% to 70%.

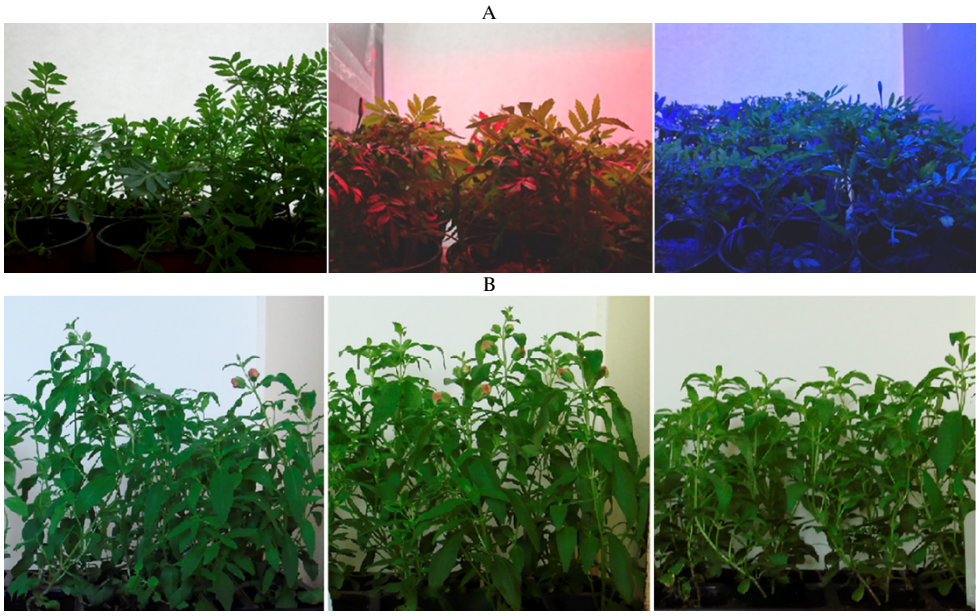

Fig. 1. Tagetes (*Tagetis panula* L., cultivar Karmen) (A) **and snapdragon (*Antirrhinum majus nanum* L., cultivar Flora shower white)** (B) **after 35 days of supplementary lighting for 12 hours a day:** left-to-right — controls (natural light only), red light (max λ = 600 nm) and blue light (max λ = 400 nm); Focus MC2 (JCC-12) LEDs (Russia).

Physiological parameters of cold-shocked ornamental plants as a function of supplementary narrow-spectrum lighting (pot experiment, 5-fold repetition)

Indicator	C (control)		RL				BL			
	1	2	1		2		1		2	
	abs. units	abs. units	abs. units	%	abs. units	%	abs. units	%	abs. units	%
Tagetes (*Tagetis panula* L.), cultivar Karmen										
A	41.0±1.8	45.3±2.1	27.4±1.3	67*	37.3±1.7	82*	40.6±1.5	99	39.6±1.7	88*
B	9.8±0.4	10.8±0.5	3.7±0.2	38*	6.8±0.3	63*	1.6±0.1	16*	1.2±0.1	11*
C	0.48±0.02	0.65±0.04	1.07±0.10	223*	0.46±0.09	71*	0.50±0.03	104	0.25±0.02	39*
Snapdragon (*Antirrhinum majus nanum* L.), cultivar Flora shower white										
A	58.7±2.4	82.4±4.1	63.1±3.5	108	74.6±3.9	91	85.2±4.1	143*	51.9±2.1	63*
B	10.0±0.5	16.3±0.6	7.1±0.3	71*	3.3±0.2	20*	8.5±0.4	85*	4.5±0.3	28*
C	2.33±0.15	1.19±0.13	2.57±0.16	110*	1.17±0.11	98	3.31±0.21	142*	1.32±0.12	111*
D	6.46±0.42	10.20±0.20	5.83±0.37	91	11.60±0.30	114*	6.50±0.44	101	12.30±0.30	121*
Petunia (*Petunia hybrida* L.), cultivar Mambo blue										
A	22.1±0.7	55.3±2.3	24.3±1.3	110	26.3±1.2	48*	32.4±1.5	147*	26.9±1.3	49*
B	9.2±0.4	14.0±0.5	5.3±0.2	58*	5.9±0.3	42*	4.7±0.3	51*	4.5±0.2	32*
C	1.23±0.12	1.39±0.13	1.52±0.16	124*	1.07±0.11	77*	1.49±0.13	121*	0.95±0.08	68*
D	3.05±0.19	3.24±0.16	2.88±0.14	95	3.53±0.21	109	2.93±0.16	96	4.43±0.24	137*

Note. A is the release of electrolytes (in terms of electrical conductivity), μS; B is the potassium ion concentration, μg/ml of solution; C is the salicylic acid content, μg/g of wet substance; D is the total free monosaccharides, μg/mg of dry substance; 1 is for day 35 (narrow-spectrum lighting experiment complete); 2 is for day 37 (after a 2-day cold shock). The control indicators were 100%. The confidence intervals $M \pm (t_{0.05} \times \text{SEM})$ did not exceed ±5% ($p \le 0.05$). Statistical processing used a nonparametric Shapiro-Wilcoxon test (pairwise comparison of each group against its respective control).

* Differences for pairwise comparisons (C1 и RL1, C1 и BL1; C2 и RL2, C2 и BL2) were deemed statistically significant at $p \le 0.05$.

Leaf cell membrane system status is an important indicator of plant stress tolerance. Preserving the selective permeability of plasmalemma to certain ions and water molecules helps sustain the cellular homeostasis [25]. To preserve it, a cell must accumulate sodium ions in its vacuole and maintain the physiological concentration of potassium ions and a high K^+/Na^+ ratio in the cytoplasm [26], i.e. the increase in the potassium ion release indicated negative changes in the cell internals. After the supplementary lighting experiment, tagetes leaf tissues

had the selective permeability of membranes decreased in the RL group, although the same indicator was within the control parameters for the BL group; on the other hand, exposure to RL increased the release of electrolytes in snapdragons and petunias insignificantly compared to the control and significantly compared to the BL group ($p \leq 0.05$), see Table. The release of potassium ions dropped significantly ($p \leq 0.05$) in both experimental groups compared to the controls, which preserved the high K^+/Na^+ ratio in the cytoplasm of the plants exposed to supplementary lighting.

Exposure to low positive temperatures deteriorated the membrane semipermeability in all plants, but it was the controls that displayed maximum deterioration. RL- and BL-exposed petunias had the best resistance to short cold shock: their leaf tissue electrolyte release was 51% to 52% lower than in the controls ($p \leq 0.05$). In tagetes, the reduction was 12% to 18%; in snapdragons, 9% to 37% ($p \leq 0.05$). Potassium ion release was significantly ($p \leq 0.05$) lower in all plants exposed to RL, even more so in the BL group. Notably, supplementary narrow-spectrum lighting accelerated the post-shock recovery of plants, especially in the RL group, whereas the controls recovered more slowly, and their decorativeness was worse, see Figure 2.

Fig. 2. Supplementary lightened tagetes (*Tagetis panula* L., cultivar Karmen) (A) **and snapdragons (*Antirrhinum majus nanum* L., cultivar Flora shower white)** (B) **after a cold shock (day 37):** left-to-right — controls (natural light only), red light (max λ = 600 nm) and blue light (max λ = 400 nm); Focus MC2 (JCC-12) LEDs (Russia).

Supplementary narrow-spectrum lighting did not affect the content of water-soluble carbohydrates in leaf tissue, see Table. Cold shock increased the monosaccharide content in snapdragons and petunias in both RL and BL groups as compared to the controls; the increase in water-soluble carbohydrates (21% for snapdragons and 37% for petunias) was most significant in the BL-exposed plants. It is known that monosaccharides are not merely a source of energy; they are also an important defensive agent that helps preserve cellular homeostasis under stress [27]. In this experiment, these agents might have contributed to a specific response that helped the plants survive hypothermic stress.

Salicylic acid is one of the signaling pathway triggers. Its role in triggering and regulating the adaptation mechanism is rather ambiguous [16]. Lack or excess of SA might amplify the stress effect, as the SA and ABA amounts correlate, while the SA level is associated with initiating the cascade of defensive responses [28] which is light-dependent and acts in conjunction with other defense mechanisms [29]. After the supplementary lighting experiment was over, the SA content was found to have risen in all plants as compared to the controls; the increase was the most significant in RL-exposed tagetes (223% higher than in the controls), see Table. Apparently, such exposure altered the hormonal balance of leaf tissue, causing plant-wide metabolism readjustments. On post-shock day 2, the SA content was lower in tagetes in both groups compared to the controls (29% to 61% lower) as well as to the pre-shock values (2.3 times lower in RL-exposed plants and 2.0 times lower in their BL counterparts). In snapdragons and petunias, exposure to RL and BL did not significantly alter the SA content compared to the controls. SA levels rose by 9% and 14% ($p \leq 0.05$) in RL-exposed plants, and by 21% and 37% ($p \leq 0.05$) in BL-exposed plants (supplementary lightened snapdragon and petunia, respectively) after cold shock.

Note that cold shock caused a quick loss of turgor in BL-exposed tagetes whose leaf edges were damaged. In this group, plants took a long time to recover and bloomed later; a third of plants did not survive, see Figure 2, A. Signs of damage were less pronounced in control plants; these survived cold better, but their decorativeness was worse (weak branching, small buds). RL-exposed plants had good leaf turgor, buds opened well. Perhaps, the RL-induced changes in the hormonal status of tagetes tissue helped trigger the defensive response cascade, which neutralized the negative effects of cold. BL-induced changes in the hormone ratio did not have any positive effects. Snapdragons (see Fig. 2, B) and petunias recovered quickly after shock in both RL and BL groups; their turgor, aerial biomass, and habitus were barely affected. In the control group, post-shock recovery of snapdragons and petunias was slow; the aerial organs were 15% lighter, and the underground organs were 10% lighter; the decorativeness of non-controls was worse than in case of supplementary lighting.

The initiation of cascade responses that form the response to abiotic stress also involves abscisic acid [19]. This hormone was only detected in tagetes tissue. After the supplementary lighting experiment was over, the ABA content rose in plants exposed to RL (to 0.191 ± 0.02 μg/g) and dropped slightly (to 0.037 ± 0.005 μg/g) in their BL counterparts as compared to the controls (0.043 ± 0.003 μg/g). The post-shock ABA content in leaf tissue was significantly greater in the BL group compared to the baseline (0.066 ± 0.008 μg/g), barely changed in the controls (0.048 ± 0.004 μg/g), and became 5 times lower (dropped to 0.038 ± 0.004 μg/g) in the RL group. This proves the hypothesis that the hormonal balance of tagetes leaves is affected by supplementary lighting, which therefore restructures plant-wide metabolism.

Perhaps the lights of different spectra triggered different defensive mechanisms activation pathways. Both SA and ABA can be such triggers, and their signaling pathways partially overlap. There emerges an information network that contains antagonistic and synergistic links [27]. In the case of BL, salicylic acid might have contributed to a faster transition of metabolic processes to an adaptive mode, whereas in RL-exposed plants, this mechanism might have been triggered after an ABA release, whereby salicylic acid was not involved in the expression of defense genes.

Therefore, the combination of physiological and biochemical changes in the leaf tissue of ornamental plants (habitus, morphology, biomass accumulation, electrolyte release, potassium ion content, salicylic and abscisic acid content,

total of free monosaccharides (glucose and fructose) gives rise to a suggestion that supplementary spectral lighting restructures the metabolic processes and the activation of nonspecific defense mechanisms that preserve the ionic and redox homeostasis of cells. This research is the first to show that supplementary narrow-spectrum lighting helps such plants successfully adapt to cold shocks. When re-planted in open ground (at 2 to 5 °C at night), their survival rate is 80% to 100% if exposed to supplementary lighting; cf. 60% to 70% in the controls. Therefore, supplementing natural lighting with narrow-spectrum light from LED panels while cultivating ornamental plants will help boost their survivability in a drastic change of habitat when used for landscaping.

REFERENCES

1. Olle M., Viršilė A. The effect of light emmiting diode lighting on greenhouse plant grows and quality. *Agricultural and Food Science*, 2013, 22(2): 223-234 (doi: 10.23986/afsci.7897).
2. Avercheva O.V., Berkovich Yu.A., Erokhin A.N., Zhigalova T.V., Pogosyan S.I., Smolyana S.O. *Fiziologiya rastenii*, 2009, 56(1): 17-16 (in Russ.).
3. Vanninen I., Pinto D.M., Nissinen A.I., Johansen N.S., Shipp L. In the light of new greenhouse technologies: 1. Plant-mediated effects of artificial lighting on arthropods and tritrophic interactions. *Annals of Applied Biology*, 2010, 157(3): 393-414 (doi: 10.1111/j.1744-7348.2010.00438).
4. Colquhoun T.A., Schwieterman M.L., Gilbert J.L., Joworski E.A., Langer K.M., Jones C.R., Rushing G.V., Hunter T.M., Olmsted J., Clark D.G., Folta K.M. Light modulation of volatile organic compounds from petunia flowers and select fruits. *Postharvest Biology and Technology*, 2013, 86: 37-44 (doi: 10.1016/j.postharvbio.2013.06.013).
5. Causin H.F., Jauregui R.N., Barneix A.J. The effect of light spectral quality on leaf senescence and oxidative stress in wheat. *Plant Sci.*, 2006, 171(1): 24-33 (doi: 10.1016/j.plantsci.2006.02.009).
6. Chinnusamy V., Zhu J., Zhu J.-K. Gene regulation during cold acclimation in plants. *Physiologia Plantarum*, 2006, 126(1): 52-61 (doi: 10.1111/j.1399-3054.2006.00596.x).
7. Crosatti C., Rizza F., Badeck F.W., Mazzucotelli E., Cattivelli L. Harden the chloroplast to protect the plant. *Physiologia Plantarum*, 2013, 147(1): 55-63 (doi: 10.1111/j.1399-3054.2012.01689.x).
8. van Gelderen K., Kang C., Pierik R. Light signaling, root development, and plasticity. *Plant Physiol.*, 2018, 176(2): 1049-1060 (doi: 10.1104/pp.17.01079).
9. Kreslavskii V.D., Karpentier R., Klimov V.V., Murata N., Allakhverdiev S.I. *Biologicheskie membrany*, 2007, 24(3): 195-217 (in Russ.).
10. Trotta A., Rahikainen M., Konert G., Finazzi G., Kangasjärvi S. Signalling crosstalk in light stress and immune reactions in plants. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 2014, 369(1640): 20130235 (doi: 10.1098/rstb.2013.0235).
11. Pennycooke J.C., Cox S., Stushnoff C. Relationship of cold acclimation, total phenolic content and antioxidant capacity with chilling tolerance in petunia (*Petunia* × *hybrida*). *Environ. Exp. Bot.*, 2005, 53(2): 225-232 (doi: 10.1016/j.envexpbot.2004.04.002).
12. Patton A.J., Cunningham S.M., Jolenec J.J., Reicher Z.J. Difference in freeze tolerance of zoysiagrasses. II. Carbohydrate and proline accumulation. *Crop Sci.*, 2007, 47(5): 2170-2181 (doi: 10.2135/cropsci2006.12.0784).
13. Crossatti C., Polverino de Laureto P., Bassi R., Cattivelli L. The interaction between cold and light control the expression of the cold regulated barley gene *cor14b* and the accumulation of the corresponding protein. *Plant Physiol.*, 1999, 199: 571-599 (doi: 10.1104/pp.119.2.671).
14. Zhao Y., Zhou J., Xing D. Phytochrome B-mediated activation of lipoxygenase modulates an excess red light-induced defense response in Arabidopsis. *J. Exp. Bot.*, 2014, 65(17): 4907-4918 (doi: 10.1093/jxb/eru247).
15. Rejeb I.B., Pastor V., Mauch-Mani B. Plant responses to simultaneous biotic and abiotic stress: molecular mechanisms. *Plants*, 2014, 3(4): 458-475 (doi: 10.3390/plants3040458).
16. Yuan S., Lin H.-H. Role of salicylic acid in plant abiotic stress. *Zeitschrift fur Naturforschung C*, 63(5-6): 313-320 (doi: 10.1515/znc-2008-5-601).
17. Janda T., Horváth E., Szalai G., Páldi E. Role of salicylic acid in the induction of abiotic stress tolerance. In: *Salicylic acid: a plant hormone*. S. Hayat, A. Ahmad (eds.). Springer, 2007: 91-150 (doi: 10.1007/1-4020-5184-0_5).
18. Makhdavian K., Kalantari Kh.M., Gorbanli M. *Fiziologiya rastenii*, 2008, 55(4): 620-623 (in Russ.).

19. Shi Y., Yang S. ABA regulation of cold stress response in plants. In: *Abscisic acid: metabolism, transport and signaling*. D.P. Zhang (ed.). Springer, 2014: 337-363 (doi: 10.1007/978-94-017-9424-4_17).
20. Voronkova T.V., Shelepova O.V. *Sposob opredeleniya soderzhaniya vodorastvorimykh uglevodov i krakhmala iz odnoi naveski. Patent 2406293 RU MPK A01G 7/00 2006/01* [The method of determining the content of water-soluble carbohydrates and starch from a single sample. Patent 2406293 RU MPK A01G 7/00 2006/01] (in Russ.).
21. Kondrat'eva V.V., Semenova M.V., Voronkova T.V., Shelepova O.V. *Nauchnye vedomosti Belgorodskogo gosudarstvennogo universiteta (Estestvennye nauki)*, 2011, 3(98), vypusk 14/1: 339-345 (in Russ.).
22. Shelepova O.V., Kondrat'eva V.V., Voronkova T.V, Olekhnovich L.S., Enina O.L. *Byulleten' Glavnogo botanicheskogo sada*, 2012, 2: 68-73 (in Russ.).
23. Hammer O., Harper D.A.T., Ryan P.D. PAST: Palaeontological Statistics software package for education and data analysis. *Palaeontologia Electronica*, 2001, 4(1): art. 4, 9 pp.
24. Petrovskaya-Baranova T.P. *Fiziologiya adaptatsii i introduktsiya rastenii* [Physiology of plant adaptation and introduction]. Moscow, 1983 (in Russ.).
25. Tarchevskii I.A. *Metabolizm rastenii pri stresse* [Plant metabolism under stress]. Kazan', 2001 (in Russ.).
26. Munns R., Tester M. Mechanisms of salinity tolerance. *Annu. Rev. Plant Boil.*, 2008, 59: 651-681 (doi: 10.1146/annurev.arplant.59.032607.092911).
27. Trunova T.I. *Rastenie i nizkotemperaturnyi stress. 64-e ezhegodnye Timiryazevskie chteniya* [Plant and low temperature stress. 64th Annual Timiryazev Readings]. Moscow, 2005 (in Russ.).
28. Mateo A., Frunk D., Mühlenbock P., Kular B., Mullineaux P.M., Karpisnki S. Controlled levels of salicylic acid and required for optimal photosynthesis and redox homeostasis. *J. Exp. Bot.*, 2006, 57(8): 1795-1807 (doi: 10.1093/jxb/erj196).
29. Beshtold U., Karpinski S., Mullineaux P. The influence of the light environment and photosynthesis on oxidative signaling responses in plant-biotrophic pathogen interaction. *Plant Cell & Environment*, 2005, 28: 1046-1055 (doi: 10.1111/j.1365-3040.2005.01340.x).