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DYNAMIC REGULATION OF PHOTOSYNTHETIC PROCESSES UNDER VARIABLE SPECTRAL LED IRRADIATION OF PLANTS

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Abstract

In natural conditions of plant growth, along with changes in the intensity of light during different periods of time, there is a change in the spectral composition of the incident radiation. The ratio between the blue and red spectral regions changes from ≈ 0.50 for direct radiation of the sun, to ≈ 0.95 for diffuse solar radiation, depending on the height of the sun and the time of day. The work investigated the effect of light of different spectral composition on the functional characteristics of the photosynthetic apparatus of potato plants (*Solanum tuberosum* L.) of the Zhukovsky Early variety, grown by aeroponics in two vegetation chambers of a phytotron using LEDs sources with preferential irradiation of plants with blue light (LEDs BL, $\lambda_{max} = 470$ nm) or red light (LEDs RL, $\lambda_{max} = 660$ nm) of the spectral range of photosynthetically active radiation (PAR). With a total PAR intensity of 400±28 μmol · m^{-2} · s^{-1}, the proportion of blue light was 293.6 μmol · m^{-2} · s^{-1} (chamber 1), and of red light it was 262.0 μmol · m^{-2} · s^{-1} (chamber 2). As a result, the ratio BL/RL (when comparing the intensities of radiation in the two chambers of the phytotron) was about 0.7. The measurements were carried out on plants grown for a long time under irradiation in the PAR rang with the predominant blue (PAR + BL) or red light (PAR + RL). The dynamics of photosynthetic indexes were investigated 0, 1, 2, and 3 hours after the light regime changed from PAR + RL to PAR + BL or from PAR + BL to PAR + RL. When plants were irradiated with a larger share of the red light PAR spectrum (PAR + RL), a lower rate of photosynthesis was observed compared to plants grown with PAR + BL, both at 400 μmol · m^{-2} · s^{-1} and at saturating light intensity (1200 μmol · m^{-2} · s^{-1}). A change in the PAR + RL spectral mode for PAR + BL resulted in an increase in the rate of photosynthesis, a slight increase in the effective quantum yield and non-photochemical quenching. When the light mode changed from PAR + BL to PAR + RL, photosynthesis rate, electron transport speed, non-photochemical quenching decreased compared to plants irradiated with PAR + BL, but no change was observed in the maximum and effective quantum yield. The specific effects of blue and red light on the activity of light reactions in photosynthesis and the rate of photosynthesis in changing spectral composition after long-term plant exposure to environmental factors, which we detected for the first time in this work, make it possible to better understand the nature of plant adaptation in natural growth conditions. In plant growing with LED lighting, this allows directional use of LED emitters of different spectral composition, given the duration of predominantly blue or red irradiation.

Keywords: spectral regime, photosynthetic apparatus, rate of photosynthesis, electron transport, non-photochemical quenching, light-emitting diodes, *Solanum tuberosum* L., potato

Intensity and spectral composition of light are important for regulating activity of photosynthetic apparatus, and plant growth [1, 2]. In natural conditions of plant growth, along with changes in the intensity of light in different periods of time, there is a change in the spectral composition of the incident radiation. In this manner energy in blue (BL, λ = 400-500 nm) and red (RL, λ = 600-700 nm) spectral regions is distributed in 1:3 ratio in daytime [3]. Proportion of red and far red component as compared to the blue one is increasing in morning and evening hours making BL/RL value as 0.74. According to some papers [4-6], the ratio between energy of the blue and red spectral regions is changing from ≈ 0.50 (direct radiation) to ≈ 0.95 (diffuse radiation), depending on the solar altitude.

Light regimes affecting photosynthetic activity are major elements of artificial lighting technologies and controlled plant growing in phytotrons, with LED-based sources being actively used therewith. White LEDs [7] together with red and red-blue ones [8, 9], as well as with various combinations of blue, red and other spectral regions [10-12] are widely spread. Depending on plant variety, the reaction thereof to RL and BL ratio may differ [2]. RL/BL ratio in ontogenesis to be changed is also worth noting [13].

Nowadays one of main approaches in studying ever-changing environmental plant adaptation is comparison of dynamic features of adaptive processes [14, 15], with major attention being paid to effect or aftereffect of various factors in time intervals [16, 17]. Such approach enables to assess response of photosynthetic apparatus over time similar to natural environmental change within several hours. It should be noted that mechanisms of plant light adaptation are complicated and to be further analyzed for appropriate usage of LED sources of various spectral composition in plant growing.

Prolong effect of monochromatic spectral irradiation sources influencing potato plants grown in vitro [18] has been analyzed by us earlier, and we have found out that no significant differences in activity of light reactions of photosynthesis are seen under low light. Changes in accumulation of dry substance by plants therewith were stipulated by stomatal conductance, as well as by light-independent reaction processes in photosynthesis, as efficiency of carboxylation reaction, rate of triose phosphate utilization.

The special effect of blue and red spectral regions under plant irradiation with all spectral range of photosynthetically active radiation (PAR) originally presented by us in this analysis is that change of red light to blue light is increasing photosynthesis rate, quantum efficiency and non-photochemical quenching, while under changing of blue to red light we observe converse effects.

The paper investigated the activity of photosynthetic apparatus of potato leaves exposed for a long time to various spectral compositions, as well as under changing of radiation spectrum with prevailing red or blue area.

Techniques. Potato plants (*Solanum tuberosum* L.) of Zhukovsky Early variety were grown by aeroponics in two environmentally-controlled phytotron chambers. The plants were cultivated by apical meristem method and tested for viruses and potato viroid by RT-PCR applying appropriate kits (OOO NPK Sintol, Russia). Each chamber contained 15 plants, with vegetation period thereof being 60 days, and 12 h photoperiod.

Radiation intensity in chamber 1 was increased by blue LEDs (BL LEDs, λ_{max} = 470 nm), with red LEDs being switched off, thereby under total intensity of 400±28 $\mu mol \cdot m^{-2} \cdot s^{-1}$ the proportion of BL was 293.6 $\mu mol \cdot m^{-2} \cdot s^{-1}$. Radiation intensity in chamber 2 was increased by red light (RL LEDs, λ_{max} = 660 nm), with blue LEDs being switched off, thereby under total intensity of 400±28 $\mu mol \cdot m^{-2} \cdot s^{-1}$ the proportion of RL was 262.0 $\mu mol \cdot m^{-2} \cdot s^{-1}$. BL/RL value (if radiation intensity in two phytotron chambers is compared) is within 0.7-09. Other microclimatic conditions inside the chambers remained constant (CO_2 concentration is 395 ±12 $\mu mol\ CO_2 \cdot mol^{-1}$, air humidity is 60-80 %, temperature is 24 ±1 °C).

The analyzed values (0, 1, 2, 3 hours) were measured with plants in two variations: under stationary light mode with prevailing blue light (PAR+BL) or red one (PAR+RL) and after changing the light mode from PAR+RL to

PAR+BL or from PAR+BL to PAR+RL.

Rate of photosynthesis in leaves was registered in the morning (at 10 AM) under light intensity of 400 and 1200 $\mu mol \cdot m^{-2} \cdot s^{-1}$. Dependence between the process rate and light intensity was being found within PAR range of 0-1200 $\mu mol \cdot m^{-2} \cdot s^{-1}$ at natural CO_2 concentration in the air of 395 ±12 $\mu mol\ CO_2 \cdot mol^{-1}$. Values of variable fluorescence of chlorophyll *a* characterizing activity of photosystem II (PS II) were being assessed therewith [19].

Rate of photosynthesis was measured by portable gas analyzer LCPro+ (ADC BioScientific, Ltd, Great Britain), variable fluorescence — by fluorometer PAM-Junior (Heinz Walz GmbH, Germany). Spectral values inside phytotron chambers were controlled by spectrometers ASENSEtek, PG100N, UPRtek (Taiwan). Light curve was approached to by J.L. Prioul & P. Chartier model [20].

The experiments were made with 4-5-fold analytical and 3-fold biological replication. Calculations were made by one biological experiment data. Statistical data were processed by Statistica 10 application (StatSoft, Inc., USA). Arithmetic mean values (*M*) with standard error (±SEM) are given in the figures. Statistical significance of differences was found by Student *t*-test at P = 0.95.

Results. Plant growing under full PAR spectrum with prevailing either red or blue radiation (Fig. 1) resulted in morphological values changing. Under PAR+BL the plants were characterized by shortened internodes and differentiated root system, while under PAR+RL the plants were higher with less differentiated root system. Growth values observed are due to functional activity of photosynthetic apparatus.

Purity % 70.73
CRI Ra 0.0
λd nm 463
R2 0.0
λp nm 456
λpV mWm-2nm-1 1923
PPFD μmol/(m²*s)
PPFD 400-700nm 408.6
PFD-B 400-500nm 293.6
PFD-G 500-600nm 66.86
PFD-R 600-700nm 48.19
PFD μmol/(m²*s)
PFD 380-780nm 441.3
PFD-UV 380-400nm 26.10
PFD-FR 700-780nm 6.596

Purity % 46.65
CRI Ra 89.5
λd nm 590
R2 96.8
λp nm 660
λpV mWm-2nm-1 1194
PPFD μmol/(m²*s)
PPFD 400-700nm 407.0
PFD-B 400-500nm 35.97
PFD-G 500-600nm 109.0
PFD-R 600-700nm 262.0
PFD μmol/(m²*s)
PFD 380-780nm 445.8
PFD-UV 380-400nm 27.11
PFD-FR 700-780nm 11.77

Fig. 1. Spectral characteristics of phytotron chambers. PAR+BL (blue light, above): total photon flux is

408.6 $\mu mol \cdot m^{-2} \cdot s^{-1}$, blue and red spectral regions are 293.6 and 48.19 $\mu mol \cdot m^{-2} \cdot s^{-1}$, accordingly; PAR + RL (red light, below): total flux is 407.0, red and blue spectral regions are 262.0 and 35.97 $\mu mol \cdot m^{-2} \cdot s^{-1}$, accordingly. PAR — photosynthetically active radiation.

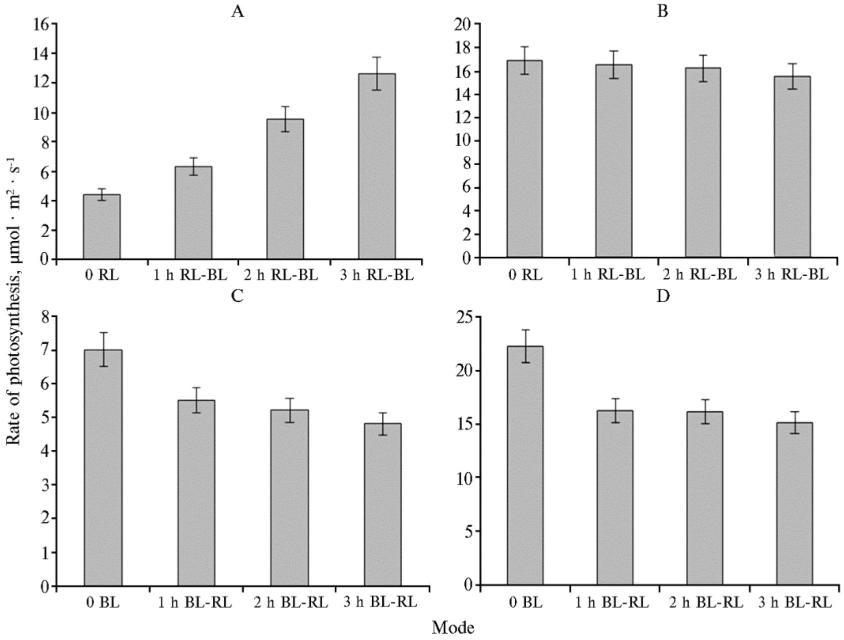

Fig. 2. Dynamics in CO_2-gas exchange in leaves of potato (*Solanum tuberosum* L.) Zhukovsky Early variety grown aeroponically at light intensity of 400 $\mu mol \cdot m^{-2} \cdot s^{-1}$, with prevailing red (RL, PAR+RL) **or blue** (BL, PAR+BL) **light after changing of prevailing light from one to another**: A, C — with no changing in light intensity (400 $\mu mol \cdot m^{-2} \cdot s^{-1}$), B, D —increase of light intensity to 1200 μmo l$\cdot m^{-2} \cdot s^{-1}$; PAR — photosynthetically active radiation.

Under PAR+RL as compared to PAR+BL the rate of photosynthesis was lower both at 400 $\mu mol \cdot m^{-2} \cdot s^{-1}$ and 1200 $\mu mol \cdot m^{-2} \cdot s^{-1}$ (Fig. 2). Mode changing from PAR+RL to PAR+BL resulted in increase in the photosynthesis rate at 400 $\mu mol \cdot m^{-2} \cdot s^{-1}$ and in some increase at 1200 $\mu mol \cdot m^{-2} \cdot s^{-1}$. If light mode was changed from PAR+BL to PAR+RL at 400 $\mu mol \cdot m^{-2} \cdot s^{-1}$ this value decreased ($p \leq 0.05$).

Light curves of plants photosynthesis at changing the spectral mode of irradiation were plotted together with analysis of prolonged exposure of PAR+RL and PAR+BL to photosynthetic apparatus activity. Change of mode from PAR+RL to PAR+BL resulted in increase in the rate of photosynthesis in the plateau of the light curve, increase of breathing rate and quantum yield, therewith saturation of light curve of photosynthesis being achieved at higher light intensity. On the contrary, when mode sequence was PAR+RL → PAR+BL, rate of photosynthesis and breathing and quantum yield were decreasing, while saturation of light curve took place at lower light intensity (Fig. 3).

Variations of photosynthesis rate observed are in particular due to different activity response in light stage thereof. According to analysis of variable fluorescence values the change of prevailing red light to blue one made no effect on the value of max quantum yield of photosystem II, but enabled to increase the rate of non-photochemical quenching and quantum efficiency ($p \leq 0.05$) (Fig. 4). The opposite reaction of photosynthetic apparatus (decrease in rate of electron transport and non-photochemical quenching) was noted at mode changing from PAR+BL to PAR+RL. Values of max and efficient quantum yields as compared to the ones in plants irradiated by blue LEDs remained the same (see Fig. 4).

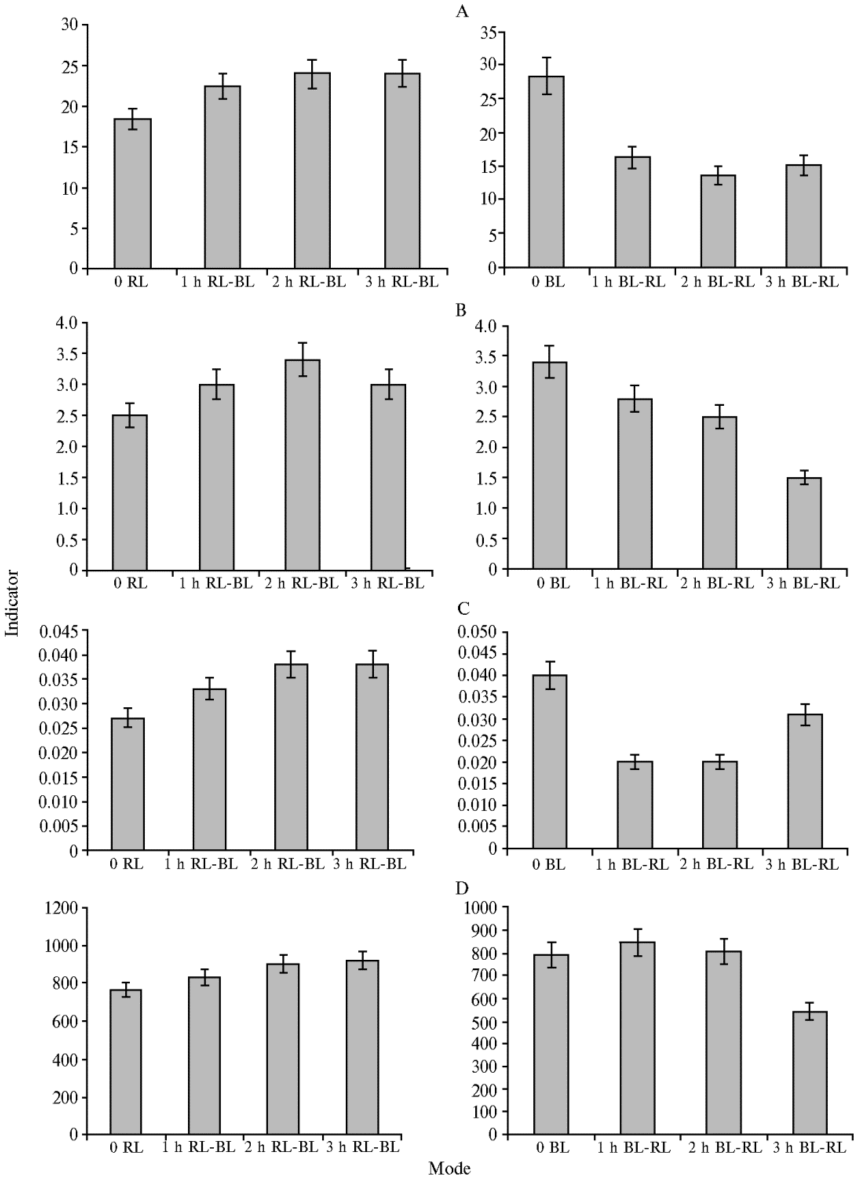

Fig. 3. Dynamics in CO_2 absorption rate, μmol · m^{-2} · s^{-1}, (A), **breathing rate, μmol · m^{-2} · s^{-1},** (B), **quantum photosynthetic efficiency, r.u.** (C) **and light intensity in the plateau of light curve, μmol · m^{-2} · s^{-1}** (D) **in potato (*Solanum tuberosum* L.) plants of Zhukovsky Early variety grown aeroponically at light intensity of 400 μmol · m^{-2} · s^{-1}, with prevailing red** (RL, PAR+RL) **or blue** (BL, PAR+BL) **light after changing of prevailing light from one to another** (RL-BL or BL-RL; PAR — photosynthetically active radiation).

PAR+RL and PAR+BL affecting the rate of photosynthesis observed in our experiments may be compared to data on photosynthetic apparatus decreased activity if plants are irradiated by monochromatic RL [21, 22]. Expansion of red or blue component in PAR spectrum noted by us resulted in no changes of max (see Fig. 3, A) and efficient (see Fig. 4, B) quantum yield of photosynthesis, electron transport rate (see Fig. 4, C), and rate of non-photochemical quenching (see Fig. 4, D). In this case the lower photosynthesis rate if irradiated by PAR+RL may be explained by lower activity of RuBisCO carboxylase enzyme, see paper by A.A. Tikhomirov et al. [2] and our study of monochromatic irradiation effect on potato plants [18].

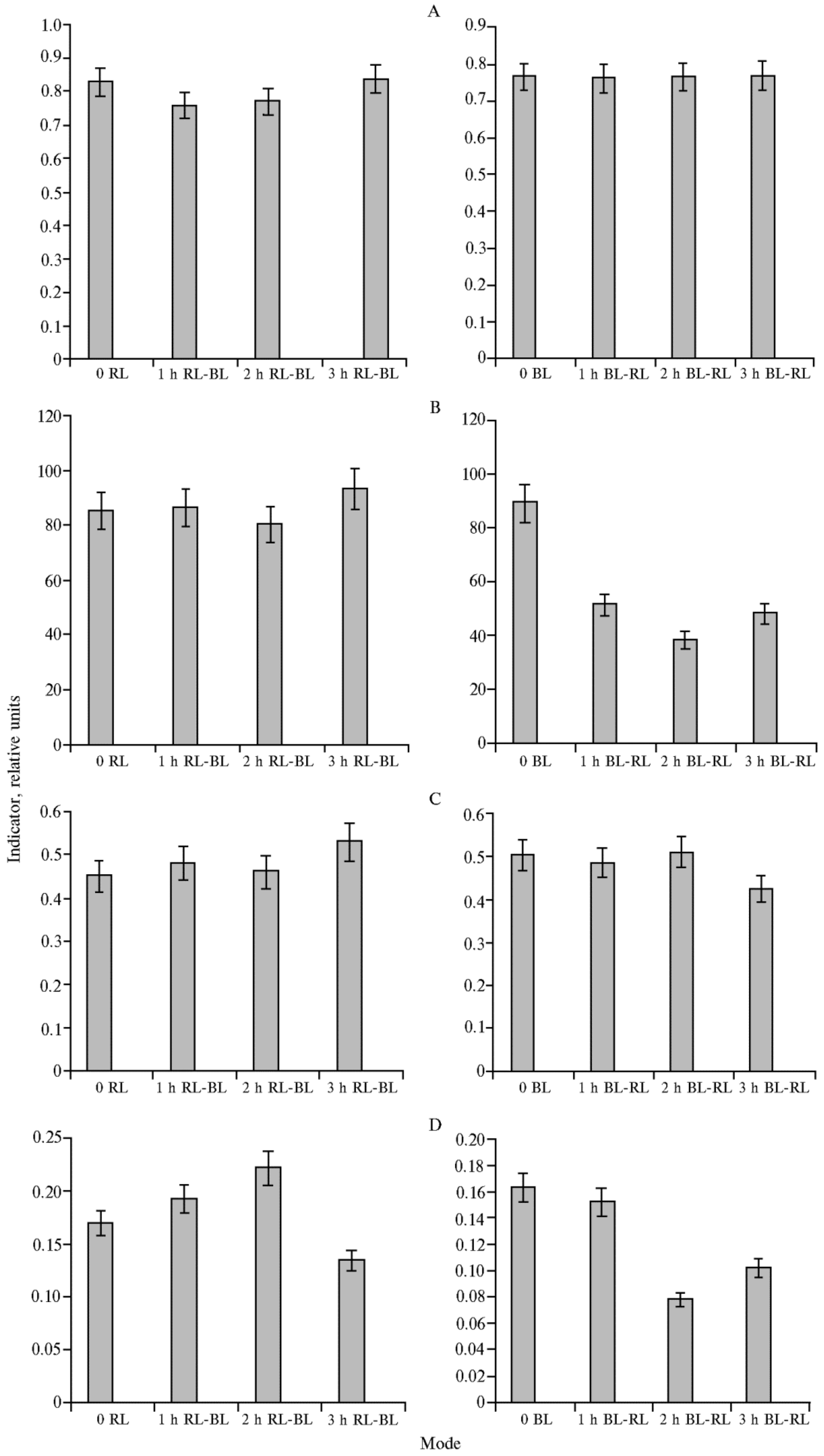

Fig. 4. Max quantum yield of photosystem II (A), **quantum photosynthetic efficiency of photosystem II** (B), **electron transport rate** (C) **and non-photochemical quenching rate** (D) **in potato (*Solanum tuberosum* L.) plants of Zhukovsky Early variety grown aeroponically at light intensity of 400 μmol · m^{-2} · s^{-1}, with prevailing red** (RL, PAR+RL) **or blue** (BL, PAR+BL) **light after changing of prevailing light from one to another** (RL-BL or BL-RL; PAR — photosynthetically active radiation).

Decrease in rate of non-photochemical fluorescence quenching (NPQ) in 3 hours after plants irradiation by PAR+BL may also indicate to increase of efficiency in using blue light in assimilation processes even at low value of BL/RL ratio. M. Kośvancová-Zitovб et al. [23] have noted high rate of photosynthesis induction at BL/RL ratio equal to 3:1. Decrease of blue ($\lambda_{max} = 455$ nm) or red ($\lambda_{max} = 625$ nm) light gave no differences in photosynthesis induction in leaves equally irradiated by BL and RL (1:1) and reducing BL in relation to RL (1:3). Significant changes in the rate of photosynthesis were found when changing the light mode of plant growing. Thus, 2-3-fold increase took place when changing PAR+RL to PAR+BL within 3 hours (see Fig. 2, A, C). Higher values of quantum yield of photosynthesis were obtained under the same conditions (see Fig. 3, C). At light saturation (1200 $\mu mol \cdot m^{-2} \cdot s^{-1}$) the rate of photosynthesis is actually remained unchanged (see Fig. 2, B, D) indicating high operational potential of photosynthetic apparatus produced by the plant irradiated mostly by red light in total flux. Therewith, one hour after changing of the light mode no significant activities of photosynthetic apparatus were seen.

Change of light mode from PAR+BL to PAR+RL resulted in decrease in the rate of photosynthesis at 400 and 1200 $\mu mol \cdot m^{-2} \cdot s^{-1}$ (see Fig. 2), as well as in decrease of dark respiration rate, the light intensity at saturation of the light curve, and quantum yield of photosynthesis (see Fig. 3). The observed changes in photosynthetic apparatus activity were due to reactions of photosynthesis light stage, i.e. delay in operation of electron-transport chain of chloroplasts (see Fig. 4, C). Decrease of electron transport rate and that of ATP synthesis [24] as a result thereof may be accompanied by RuBisCO decreased activity [25]. In this case reduction of inefficient energy loss (NPQ) may level the changing activity effect of reactions of photosynthesis primary stage.

Spectral distribution of light within irradiation sources affects the rate of photosynthesis both directly and indirectly, via imposition of effects from various parts of spectrum. A leaf is regulating the distribution balance of excitation energy between photosystems in response to relative spectral distribution of light [26]. As a result, irradiation of plants by either blue or red light with higher or lower intensity along the whole PAR area affected differently on the rate of reactions of light and dark photosynthesis stages.

Therefore, changing of red light to prevailing blue one is shown to result in increase of the rate of photosynthesis, effective quantum yield and non-photochemical quenching, while the effects are opposite when substituting blue light to red one. The found specific effects of blue and red light on the activity of light reactions in photosynthesis and the rate of photosynthesis in changing spectral composition after the plants are light-exposed for a long time, enable us to better understand the nature of plant adaptation in natural growth conditions. The obtained results may be used at programmed growing of plants in various indoor facilities.

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