

BIOPHOTONICS

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Response of vegetable organisms to quasi-monochromatic light of different duration, intensity and wavelength

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Abstract. **By the example of vegetable organisms differing in structure and functional properties it is shown that their response to the action of quasi-monochromatic light from laser sources does not obey the Bunsen–Roscoe dose law. The dependence of biological effect on the irradiation time has the multimodal (multiextremal) form with alternating maxima and minima of the stimulating effect. Such a property manifests itself in the spectral ranges, corresponding to photoinduced conversion of chromoproteins of photocontrol systems and is probably related to the cyclic variations of metabolic activity in vegetable cells.**

Keywords: *laser radiation, vegetable organisms, duration and intensity of irradiation, photocontrol system, response, multimodality.*

1. Introduction

The presence of light is a necessary condition of life activity and evolution of vegetable organisms. By means of light the synthesis, regulatory, destructive, reparation, adaptation and other processes are implemented. Optical radiation controls the most important cell functions, including the gene expression [1]. While the photosynthesis is studied well enough, the photocontrol mechanisms are still not obvious. It remains unclear how individual light quanta are able to trigger the fast and obvious transformations of the morphological condition of plants, how the transformation of the optical signal into a chemical one and its amplification occur, and what biological role is played by the own radiation of living organisms. From a large number of discussable questions the two most controversial ones can be selected, namely, the relation between the response and the dose of absorbed laser light and the ability of cells to react to the statistical ordering (coherence) of electromagnetic waves. The first problem will be considered in the present paper and the second problem in the forthcoming one, which will be the continuation of this paper.

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One of the first attempts of a complex study was made in a series of papers under the supervision of Karu in early 1980s. By the example of HELA cells, the biological action of low-intensity visible light was analysed as a function of "…coherence, dose, wavelength and irradiation regime" [2–4]. The methodological approaches presented in these publications became very popular and were used by many authors in application to different biological objects [2–7]. Despite the large number of such papers, they could not resolve the existing controversies because of very disputable grounds.

Typically, the photocontrol effect of quasi-monochromatic, e.g., laser radiation is described in the 'dose-effect' coordinates [2, 3, 8–11], apparently, in analogy with the ionising radiation. Neither theoretical, nor experimental confirmations of the energy nature of the effect are usually presented. The observed reactions are considered as dose-dependent basing only on the fact that under the action of different doses the magnitude of the biological effect could be different. Here the following methodical problem arises. The dose (dose density) is defined by the product of power (power density) of the action by its duration. Each of the factors will equivalently contribute to the observed effect only if the interchangeability Bunsen–Roscoe law is valid. Such a reaction type is characteristic for some radiobiological effects, photosynthesis and photodestruction processes. There are reasons to suppose that the action of low-intensity coherent radiation (LICR) does not obey this law. It follows from the data, described in the referred papers. For example, "the power density was 1.5×10^{-4} and 3×10^{-5} W m^{-2}, the dose was acquired by irradiating the cells for between 50 sec to 4 min" ([2], page 1136). Similarly, in other papers the power density remained constant or took a few fixed values, and the dose variation was implemented by changing the exposure duration within sufficiently wide limits [8–10, 12–15]. As a result, the authors of these papers obtained the experimental dependences on the irradiation time, but referred them to as dose dependences.

An attempt was made to determine the "…influence of irradiation time for a given dose…" ([3], page 1170). The reported dependence of the DNA synthesis rate on the intensity of the red ($\lambda = 633$ nm) light had nonlinear character with an expressed maximum. But in this case, naturally, the irradiation duration was also varied, so that both components of the dose, the power density and the irradiation duration, appeared to be variable quantities. This organisation of the experiment predetermined the ambiguous conclusion that "… the DNA synthesis stimulation was very sensitive to the irradiation time and to the intensity of light when the dose was 100 J m^{-2}" ([3], page 1170). A similar result was obtained in the study [10], performed in Escherichia coli bacteria using the same technique, i.e., with the fixed dose. However, in a

later publication by one of the authors it was pointed out that the dose law can be invalid [16]. The manifestation of doubts about the validity of using the dose as a universal indicator can be seen in the fact that the authors additionally indicate the dose components, too [17, 18]. There is a direct indication of the necessity to record the power density and irradiation time, rather than the total amount of energy, acting on the living organism [19]. With such controversial assessments the question of whether the photocontrol effect of quasi-monochromatic light is purely dose-dependent remains open. This fact stimulates the use of alternative methodological approaches in order to solve the problem.

The energy effect on a cell can be described by such independent parameters, as the irradiation time, power density and wavelength. In the present paper we estimate the influence of each of these parameters on the magnitude of the photo-induced reaction in different biological systems subjected to high-coherence (laser) radiation.

2. Experimental results

In order to clarify the most general properties of the response we used the biological models, strongly differing from each other in structure and functional properties, namely, barley seeds, berry pollen and blackberry explants (microsprouts) cultivated *in vitro*.

The barley seeds of the selection form D-101 (hybrid of Dvoran breed) were irradiated under the air-dry conditions and then couched in Petri dishes on wet filtering paper at the temperature 22 °C. The number of repetitions was 5. In each repetition of each version of the experiment 50 seeds were used. On the third day the germination energy (the fraction of germinated seeds) and on the seventh day the length of the first leave was determined. Taking the high germination energy of the D-101 form (greater than 90%) into account, the caryopses were preliminarily processed with the ionising radiation (γ ^{60}Co) with the dose 8 kGy. The artificial decrease (to 51%) in the germination energy allowed using this characteristic for the assessment of laser simulation.

In the experiments with the pollen of Pennsylvania cherry we used special cytological preparations. The surface of microscope slides was coated with a thin layer of a nutritive substrate, containing 0.8% of agar, 15% of sucrose and 0.001% of boric acid. On the solidified substrate the pollen was seeded with the mean density of 20 grains per square millimetre. After the exposure to quasi-monochromatic light from a laser source the preparations were placed in Petri dishes with wet filtering paper, where they were kept at the temperature 28 °C during 24 hours. The pollen was inactivated with chloroform and the number of germinated pollen grains was determined according to the standard technique [20]. The number of repetitions was 6.

The blackberry explants were cultivated on agar-based nutritive media, prepared according to the prescription MS [21] in two modifications. The generation substrate contained sucrose (30 g L^{-1}), 6-benzylaminopurine (1.0 mg L^{-1}) and gibberellic acid (1.0 mg L^{-1}). The rootage substrate contained 1/2 of MS macrosalts, full MS microsalts and vitamins, sucrose (15 g L^{-1}), and β-indolyl-3-butyric acid (1.0 mg L^{-1}). In every version of the experiment 30–40 plants were used. The cultivation was carried out at the temperature 25 °C, illuminance 2500–3000 lx and the light day duration 16 hours. In the generation substrate we determined the total length of sprouts from one explant. In the rootage substrate we measured the number and the mean length of roots per one explant. The revisions were executed 4 times with the interval of 10 days.

The control objects were subjected to similar procedures under the similar conditions as the experimental ones, except the irradiation with laser light. They were also protected from the scattered coherent radiation. In the process of cultivation the objects of study were isolated using opaque shields in order to prevent their interaction via the biochemiluminescence [22, 23].

As high-coherence light sources, we used LG-113, LGN-222 and LGN-303 helium–neon lasers (Russia), operating in the oscillation regime with a single transverse TEM_{00} mode with the wavelength 632.8 nm. The light flux with the given intensity was formed using a tunable objective with a Fourier filter. The latter was necessary to remove the higher-order spatial harmonics, arising in the optical path because of the diffraction noises. As a result of the undertaken measures, the radiation possessed high spatio-temporal coherence (the coherence length and the correlation radius exceeding 1000 μm) and had a Gaussian profile of the beam cross section. We also used MDI 635-4 (Russia), HLDPM12-655-10HJ (Japan) and LP-532/50 (China) semiconductor lasers generating radiation at the wavelengths 641, 655 and 532 nm, respectively, as well as LS-1-N-660/50 (λ = 660 nm), LS-1-N-532/50 (λ = 532 nm) and LS-1-N-473/50 (λ = 473 nm) (China) solid-state lasers. They had a smaller coherence length of 300–500 μm.

The power and the power density of radiation were measured with a VEGA Ophir laser radiation meter (Israel) and an IMO-2N calorimetric meter ('Etalon', Russia). To determine the spectral composition of incident radiation we used a SOLAR F150-2-36-48USB analyser (Belarus). The particular exposure parameters will be indicated below in the description of each experiment. In all figures and tables the standard experimental errors are presented.

2.1. Effect of irradiation time

The barley seeds were irradiated with the helium–neon laser (λ = 632.8 nm), operating in the regime of single transverse mode generation. The mean power density in the working zone amounted to 0.25 W m^{-2}.The duration of light action was 0.05, 0.5, 1, 2, 4, 6, 8, 12, 16, 24, 32, 48, 64, 120 and 240 seconds. The dependence of seed germination energy on the irradiation time has several extrema, i.e., a multimodal form (Fig. 1). The differences between the maxima and minima of the representative indicator were well expressed and statistically significant (the probability of zero hypothesis $\alpha < 0.01$). The response had a nonlinear character. With the power density being fixed, the similar magnitude of the photo-induced effect could be obtained at the irradiation durations, differing by tens or hundreds of times. For example, the seed germination energy achieved 66%–67% at the irradiation times of 0.5, 6, 12, 64 and 240 s, non-monotonically varying at intermediate duration values.

This type of response was observed in many vegetable organisms in a very wide temporal interval. Stimulation maxima of root and sprout regeneration were recorded at the irradiation times up to tens (40–70) of minutes. The intensity of growth processes in blackberry cultivated *in vitro* multiply changed within the range from 0.07 to 960 s, achieving the twofold swing. Only for the irradiation time of 0.04 s the difference compared to the control object were not observed,

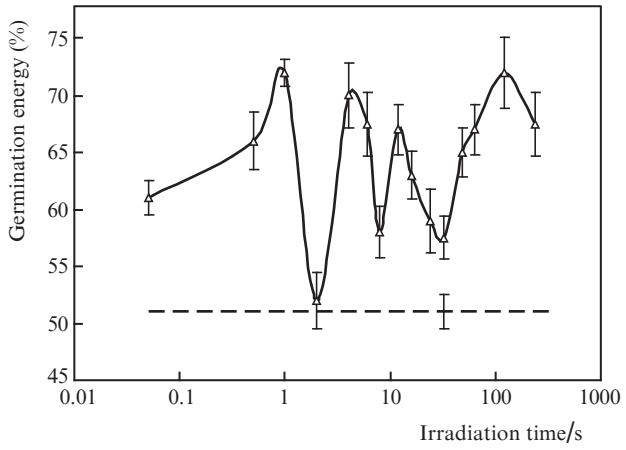

Figure 1. Dependence of the germination energy of barley seeds on the irradiation time of a laser ($\lambda = 632.8$ nm) with a power density 0.25 W m^{-2}. The dashed line shows the results for control objects.

which is probably due to the finite relaxation time of the phytochrome photocontrol system.

The multimodal character of the response does not vanish in the process of growth and development of the irradiated organisms; on the contrary, it becomes more and more apparent. In particular, in blackberry in 10 days after irradiation only one stimulation peak could be seen in the temporal dependence of the number of sprouts (Fig. 2). In 10 more days there were already two peaks, and they remained to be seen during all the observed vegetation period.

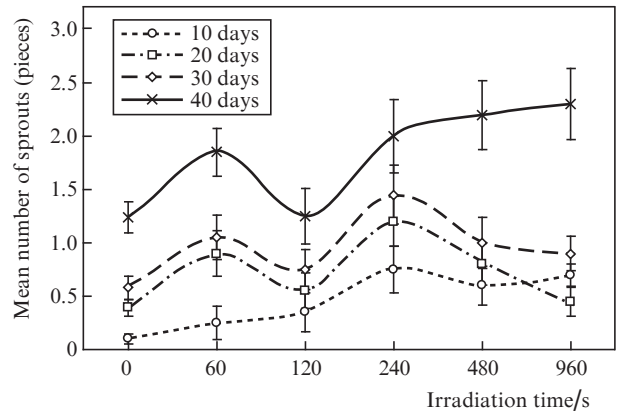

Figure 2. Dependence of the number of blackberry sprouts *in vitro* on the laser irradiation time ($\lambda = 632.8$ nm) of explants. The terms of cultivation are 10, 20, 30 and 40 days after irradiation, the power density is 6 W m^{-2}. Here and in Figs 3, 5–8 the x axis scale is nonlinear.

2.2. Effect of radiation power density

With the nonlinear character of the biological system response taken into account, the influence of the power density was studied at different irradiation times of the laser ($\lambda = 632.8$ nm). The most convenient object with a fast (a few hours) response is the pollen. For irradiation we used the matrix of regimes, containing 11 grades of power density (0.5, 1.2, 3, 4, 5, 6, 7, 8, 9 and 10 W m^{-2}) and 9 grades of irradiation time (0.5, 1, 2, 4, 6, 8, 12, 16 and 24 min). Thus, the value of each indicator was changed by no less than twenty times, and the total number of exposure regimes was 99. The monitored indicator was the fraction of germinated pollen grains. This criterion is accepted for use for assessing the functional activity of male gametophyte in plants [24].

The dependence of pollen grain germination on the irradiation times also possesses multimodal (multiextremal) form, which was almost unchangeable in the studied range of power densities (Fig. 3). With the growth of the light flux intensity, a slight shift of the extrema towards the smaller irradiation times was observed.

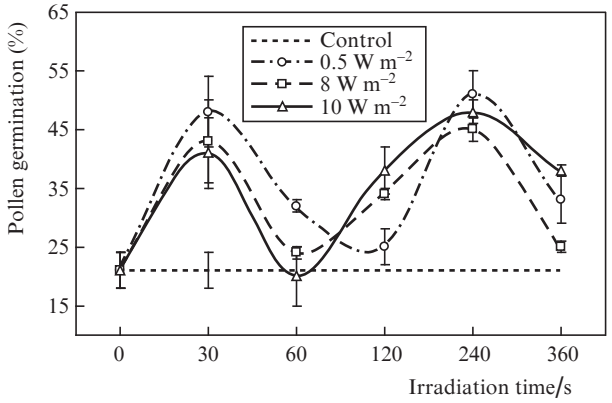

Figure 3. Dependence of cherry pollen germination on the laser irradiation time at different power densities.

For the fixed irradiation time even a 20-fold increase in the power density had a minor effect on the change in the resultant indicator. This is most clearly shown by approximating experimental data with the multiple regression equation. At the response surface in 3D coordinates the folds are distinctly expressed along the time axis and insignificant deformation along the power density axis can be seen (Fig. 4).

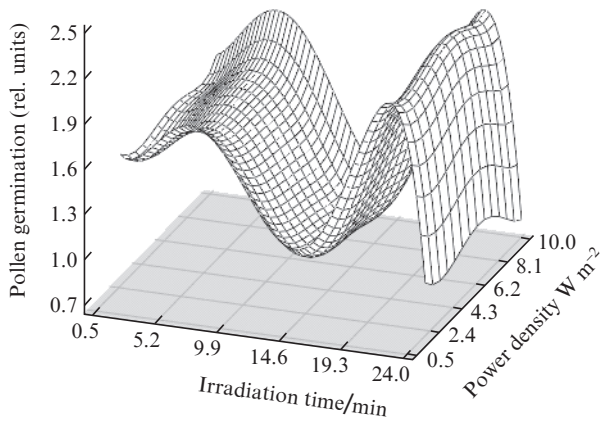

Figure 4. Dependence of the cherry pollen germination on the laser irradiation time and power density (approximation of experimental data by the multiple regression equation).

It is important to note that similar changes in the irradiation time and the power density introduce different contributions to the magnitude of the stimulating effect (Table 1). Therefore, the latter cannot be described by the product of

Table 1. Effect of laser irradiation on the pollen germination.

Irradiation time/min	Power density/ W m^{-2}	Dose density/ kJ m^{-2}	Pollen germination (%)
4	8	1.9	45±2
8	4	1.9	34±2
16	2	1.9	22±3
8	1	0.5	37±5
8	5	2.5	34±2
8	10	5	34±3
Control experiment			21±1

these quantities, i.e., the irradiation dose density. The invalidity of the Bunsen–Roscoe law was observed also in other biological models, e.g., seeds, fruits and vegetating plants. Similarly to the case of irradiating the pollen, several different values of the function, describing the resultant indicator, could correspond to one value of the dose argument, depending on the method using which the latter was obtained.

Although the photoinduced reaction depended stronger on the irradiation time, the effect of the power density could not be neglected, particularly when its change was significant. In the pollen this became visible, when the irradiation intensity increased by 16 times (Fig. 3). Wider variation of this indicator lead not only to the shift of stimulation peaks along the time axis, but also to the appearance of new extrema. The laser (λ = 632.8 nm) irradiation with the power density 0.06 W m^{-2} caused the maximal increase in the blackberry sprout length in the case of long-term irradiation during 240 s (Fig. 5). At the power density 0.6 W m^{-2} the maximum of the growth reaction was shifted to the duration 120 s, and at 6 W m^{-2} to 60 s. Besides, a negative extremum at the duration 120 s and a new maximum at 240 s appeared. Thus, the number of stimulation peaks and their position at the time axis depended also on the power density of the incident light. In the present experiment the twofold change in the irradiation time caused a similar shift of the growth reaction maximum as in the case of the tenfold change in the power density. Therefore, the dose law did not hold.

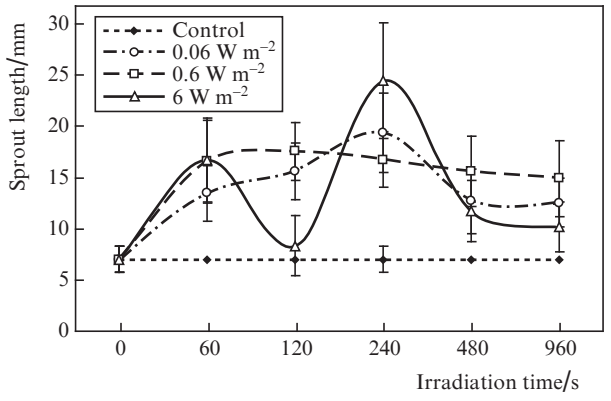

Figure 5. Length of blackberry sprouts grown in vitro at different times and power densities of (λ = 632.8 nm) laser irradiation of explants. The vegetation duration is 30 days.

2.3. Effect of radiation wavelength

The photocontrol action of light in plants is implemented by means of specific chromoproteins, as a rule, attached to biological membranes or cell organelles. In the red spectral range the phytochromes (PCs), the photomorphogenesis receptors, are absorbing [1, 25]. They possess the ability of reversible cis–trans-isomerisation under the action of light of different spectral composition: $PC_{660} \underset{\lambda = 730}{\overset{\lambda = 660}{\rightleftharpoons}} PC_{730}$. The photoconversion of PCs affects many of the metabolic processes, e.g., protein, lipid, hydrocarbon and energy ones [1, 25–27]. The form, stimulating the physiological activity of plants, is PC_{730}. Its high concentration is maintained by the radiation in the spectral range 600–690 nm [1, 27]. The action of the far red light (700–780 nm) shifts the equilibrium towards PC_{660}, which leads to the deceleration of cell metabolism. Thus, the light controls the most important cell functions, up to the gene expression. Apart from PCs, there are other photoreceptors, e.g., cryptochromes and phototropins, absorbing in the blue spectral region. The photocontrolling chromoproteins have different modifications (the phytochrome has no less than 5 of them [28]), differing in the excitation wavelengths and the kinetics of the associated reactions. Practically, the entire visible region more or less possesses physiological activity that, in particular, is confirmed by the spectrum of the optical radiation action on the bioelectric potential of plants [29].

Above we considered the regularities of the response of a few biological models to the red (λ = 632.8 nm) light that induces the transition of PCs into the active conformation state. A question arises, whether such regularities will be observed in other spectral ranges, or they are characteristic only of the phytochrome photocontrol system. To answer this question, a series of experiments were carried out using the lasers generating radiation of different wavelengths.

The reaction of vegetable organisms to the red (λ = 660 nm), green (λ = 532 nm) and blue (λ = 473 nm) light of solid-state lasers was nonlinear and multimodal. In all three cases in the time dependence one could clearly see maxima and minima of the photoinduced effect (Fig. 6). They do not coincide in phase, which apparently is due to the independent action of different forms of chromoproteins. The stimulation effect of the red light was expressed stronger than that of the green light. This fact is in good agreement with the phytochrome concept. According to the data of Ref. [27], the ratio of the amount of phytochrome PC_{730} in the active form to its total amount will equal 0.8 under the action of light with the wavelength 660 nm and less than 0.5 for λ = 530 nm.

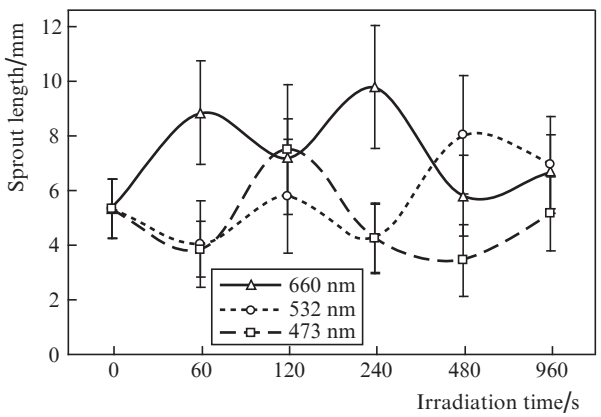

Figure 6. Length of blackberry sprouts cultivated *in vitro* vs. the irradiation time of solid-state lasers, generating red (λ = 660 nm), green (λ = 532 nm) and blue (λ = 473 nm) quasi-monochromatic light. The power density is 6 W m^{-2}, the duration of vegetation is 20 days.

A similar result was obtained using semiconductor lasers. The regeneration of roots in the *in vitro* culture occurred much better under the irradiation with red light as compared with green light, but in both cases the stimulation maxima were well expressed, i.e., a nonlinear effect took place (Fig. 7). The smaller number of maxima (only 1) than in Fig. 5 is, probably, due to a lower power density of irradiation. This agrees with the data, presented in Fig. 5. At the same time, a contradiction with the phytochrome concept arose in the comparison of the effect produced by red quasi-monochromatic light from a semiconductor and a helium–neon laser. Theoretically, the maximal stimulation is expected under the action of the radiation with $\lambda = 650–660$ nm, corresponding to the maximal quantum yield of phytochrome photoconversion into the active form $PC_{660} \xrightarrow{\lambda \approx 660\ \text{nm}} PC_{730}$ [1]. However, the radiation of the helium–neon laser with a shorter wavelength ($\lambda = 632.8$ nm) appeared to be more efficient (Fig.7).

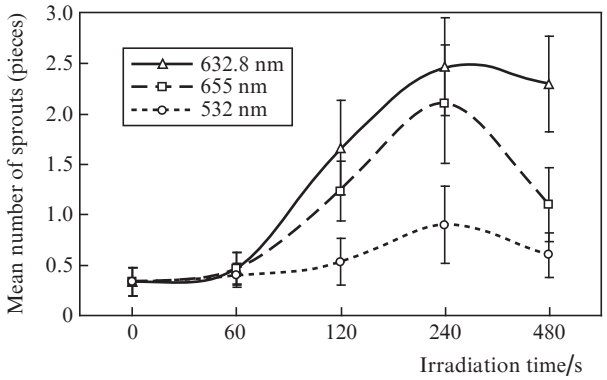

Figure 7. Dependence of blackberry risogenesis (root formation) *in vitro* on the time of irradiation with quasi-monochromatic light having different wavelengths. The power density is 1 W m^{-2}, the vegetation duration is 30 days.

The reproducibility of this contradiction was tested also in blackberry explants, but cultivated on the generation substrate. In this experiment we compared the biological effect of radiation from the helium–neon laser with that of two semiconductor lasers ($\lambda = 641$ and 655 nm). As in the previous experiment, the best result was obtained using the helium–neon laser (Fig. 8). The stimulation peaks, caused by the light of semiconductor lasers, appeared to be by two times lower. Since the intensities and durations of the light action were similar, the resolution of the controversy should be sought for in the statistical parameters of irradiation rather than in the energy ones. Indeed, the coherence of the field generated by the helium–neon laser is higher than that of the semiconductor lasers used. There are reasons to suppose that this property determined the different reaction of vegetable organisms to the action of red light with similar energy parameters, but different statistical parameters [23, 30, 31].

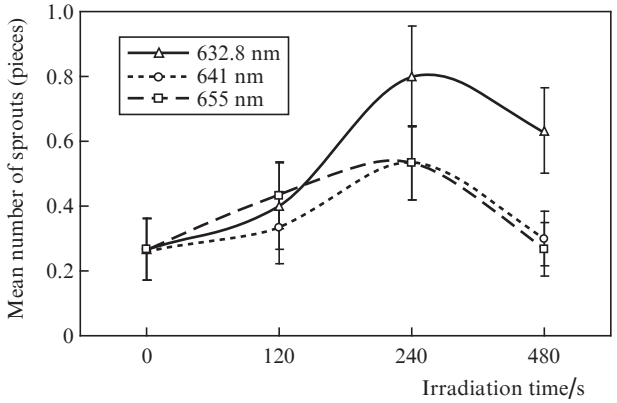

Figure 8. Effect of red quasi-monochromatic light, generated by the helium–neon ($\lambda = 632.8$ nm) and semiconductor lasers ($\lambda = 641$ and 655 nm) on the sprout-forming capacity in blackberry explants *in vitro*. The power density is 1 W m^{-2}, the vegetation duration is 30 days.

3. Conclusions

The performed studies have shown that the response of vegetable organisms to the action of quasi-monochromatic red, green and blue light is nonlinearly related to the irradiation time and does not obey the Bunsen–Roscoe dose law. Therefore, its description in terms of the 'dose–effect' concept is not possible.

The characteristic time dependence is multimodal (multiextremal) and is observed in the range of irradiation times from hundredths of a second to tens of minutes. The position of maxima (peaks) of the stimulation effect is not determinate, and they could take different positions at the time axis. Their excess over the control object dependences was, as a rule, biologically significant and statistically confident. The variation of the power density had a smaller effect on the magnitude of the response that that of the irradiation time; however, the significant power density growth, e.g., from 0.06 to 6 W m^{-2}, could lead to the shift of the position of stimulation peaks and the appearance of new extrema. Since the multimodal dependence of the response of plants on the irradiation time manifests itself in a wide spectral range, we can suppose that different photocontrol systems (phytochrome, cryptochromes) have analogous mechanisms of transforming the light signal into a chemical one and its amplification.

The violation of the Bunsen–Roscoe law in the response to LICR was observed rather long ago, both in vegetable [30, 32] and in animal [33] cells. However, the dose concepts remain rather popular and are still used in the description of photocontrol processes (see, e.g., [11, 15, 34]). Operating with the dose only, it is impossible to reproduce such experiments because of non-equivalent contribution of the duration and the power density of irradiation to the observed effect.

In some publications the presence of a maximum and the bell-like shape of the response curve were reported [35–38]. The reduction of the stimulating effect after reaching the maximal value was explained by the saturation and suppression of cell metabolism under the laser irradiation with a greater duration or dose [35, 39, 40]. Although this point of view is widespread, it cannot be considered as sufficiently justified. In many experiments variation of the dose, or, to be more precise, the dose density, was implemented by varying the irradiation time, the power density being fixed. Such curves actually reflect the dependence of the stimulating effect on the time of irradiation. At a power density 0.1–1 W m^{-2}, which is essentially smaller than the natural illuminance, the increase in light exposure by a few tens of seconds cannot lead to functional disturbances in the cell. Therefore, the bell-like shape of the curve reflects the regulatory process rather than a destructive one, and most probably is a fragment of the mul-

timodal dependence. This is confirmed by the experimental data of a number of papers, e.g., [40, 41], where the second maximum was also present, but the authors did not pay attention to it, since it was in contradiction with the common opinion.

The multimodality effect essentially complicates the understanding of the mechanism of transduction of the light signal into the chemical one. Apparently, an important role in it is played by biological rhythms. According to the concept by Zaguskin [42], the periodic variation of structure and functional parameters of a cell and the kinetics of processes occurring in it provides the stability of biological systems and their high adaptability. The laser irradiation increases the intensity of cellular processes without disturbing their oscillatory character [33].

The photostimulation effect caused by LICR was observed starting from thousandths of a second that, according to Goodwin, corresponds to the relaxation time of a cell metabolic system 10^{-1}–10^{-2} s [43]. The alternation of positive and negative extrema in the experimental time dependence indicates the presence of a feedback mechanism with a certain phase shift. In such a system the amount of regulatory metabolites will alternatingly decrease and increase. The termination of irradiation at a certain moment of time will determine their concentration in the cell cytoplasm and, therefore, the amplitude of the photoinduced reaction. Therefore, the relation between the duration of light excitation and the parameters of biological rhythms is, probably, one of the factors that determine the laser stimulation efficiency and its multimodal character.

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