



Influence of far-red light coherence on the functional state of plants

A. V. Budagovsky ^{1,2,*}, N. V. Solovykh,² O. N. Budagovskaya ^{1,2} and I. A. Budagovsky ^{3,†}

¹Michurinsk State Agrarian University, ulitsa Internationalnaya, 101, 393760 Michurinsk, Tambov Region, Russia

²Michurin Federal Research Center, ulitsa Michurina 30, 393774 Michurinsk, Tambov Region, Russia

³P. N. Lebedev Physics Institute, Leninsky prospekt 53, 119991 Moscow, Russia



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The influence of the coherence of far-red (730 nm) light on the functional activity of plants was studied. Blackberry explants cultivated *in vitro* on an artificial nutrient medium served as a biological model. The explants were irradiated with light beams with different spatial and temporal coherence. The average cell size D was taken as the discrimination threshold for the coherence length L_{coh} and the correlation radius r_{cor} . The results of irradiation were judged by the length and number of shoots formed on each explant. The greatest photoinduced effect was observed when the conditions $L_{\text{coh}}, r_{\text{cor}} > D$ were fulfilled, i.e., when the cell fit completely in the coherence volume of the light wave field. Significant differences in growth parameters were also observed in the variants of the experiment with a constant frequency spectrum of radiation (fixed L_{coh}), but different r_{cor} . It is concluded that the correlation properties of radiation affect photoregulatory processes.

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I. INTRODUCTION

In biology, the interest in coherent processes arose more than half a century ago. One of the stimuli was the work of Dicke, which showed the possibility and conditions for the generation of correlated radiation by gas molecules [1]. In the 1970s, Fröhlich established that coherent electromagnetic oscillations occur in biomembranes in the millimeter wavelength range [2,3]. They appear due to excess metabolic energy and perform an important function of intra- and intercellular regulation. The theory of coherent excitations developed by Fröhlich [4,5] explained the mechanism of a strong reaction of biosystems to weak disturbances. This happens due to the cooperative behavior of individual elements of a system, which begin to behave as a single whole (Fröhlich condensation), nonlinearly enhancing the effect.

In recent years, attention to this topic has increased significantly. The processes of photosynthesis [6–8], selective permeability of biomembranes [9], exciton migration in reaction centers [10], and nonchemical intra- and intercellular communication [11–15] are considered from the standpoint of quantum coherence. It has been suggested that a living cell can generate coherent light quanta [16–18], which were called biophotons. It is believed that, in contrast to spontaneous biochemiluminescence, caused, for example, by lipid peroxidation, they have a higher statistical ordering than natural light [17,19]. However, the methods for assessing the coherence of biophotons are currently reasonably criticized, and the mechanism of their generation continues to be the subject of discussion [20].

According to Refs. [17,19], the excited states of biopolymers can relax, causing the generation of coherent photons. Their fluxes have a very low intensity—units and tens of quanta per second from the cell surface, and the radiation spectrum lies in the visible and adjacent regions [17,21,22]. In the opinion of Popp, exciplexes of DNA are most suitable for the role of a source of biophotons [22]. The biomembranes are also being considered [23]. It is considered that biophotons can perform informational and regulatory functions [21,24,25] and, in particular, control the growth and differentiation of cells [22]. Despite the large number of works devoted to biophotons, the question of the mechanism of their reception remains open.

For the generation of coherent photons to have a biological meaning, cells must have a structure with the properties of a phase detector. The existence of such a mechanism is indicated by the ability of living organisms to distinguish the correlation properties of illuminating radiation [26]. Notably, both the temporal and spatial coherence of the light beam are important. The highest photoinduced response is observed when the cells are completely placed in the coherence volume of the light wave field: $L_{\text{coh}}, r_{\text{cor}} > D$, where D is the cell size, L_{coh} is the coherence length, and r_{cor} is the correlation radius. This effect is manifested in the cells of plants, fungi, bacteria, as well as in the cenotic interactions of organisms with different cell sizes [26–28].

A necessary condition for the operation of a biological phase detector is the absorption of light quanta by photoreceptors. In the visible and near UV regions of the spectrum, light is absorbed by special chromoproteins: phytochromes, cryptochromes, BLUF (blue light sensing using FAD) and LOV (light, oxygen, voltage) domains, which are primary in photoregulatory reactions [29,30]. Excitation of their chromophore centers initiates chemical signaling cascades that control various metabolic and epigenetic processes in the

*budagovsky@mail.ru

†budagovskya@mail.ru

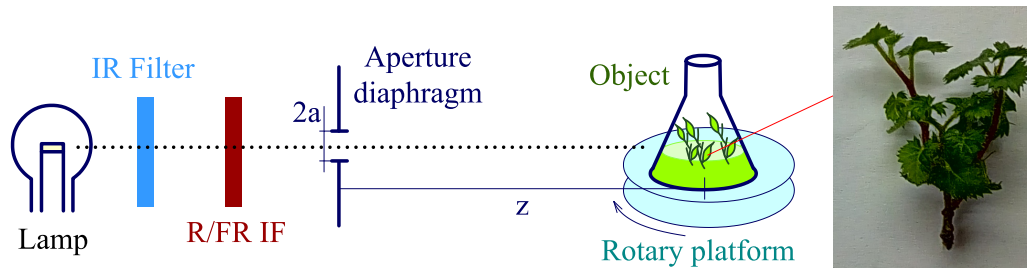


FIG. 1. Setup for the experiments with variable coherence. IR filter is infrared filter; R/FR IF is red or far-red interference filter.

cytoplasm and cell nucleus [31,32]. Considering the high sensitivity of photoregulatory reactions, the participation of biophotons in them cannot be ruled out, which is confirmed by the phenomenon of remote intercellular interaction [14].

In the red region of the spectrum, photoregulatory functions of cells are mediated by light-regulated proteins of the phytochrome group, in particular phytochrome B (*phyB*). *PhyB* is present in most cells of bacteria, fungi, and plants. The protein-bound chromophore has the property of reversible light-induced trans-cis isomerization. Under action of red light, *phyB* transitions from the Pr form (red light absorbing form) to the Pfr form (far-red light absorbing form) occur. The accumulation of the latter leads to increased functional activity of cells. Far-red light causes reverse *phyB* photoconversion, accompanied by a retardation in physiological processes [33].

In various organisms, the dependence of the response on the coherence of light was observed in the red region of the spectrum [26,28]. In this work, we consider the effect of far-red light coherence on the functional state of plants.

II. MATERIALS AND METHODS

As a biological material, we used explants (microcuttings) of the blackberry (“Black Satin”). The average cell size is $D = 18 \pm 0.3 \mu\text{m}$. The explants were grown *in vitro* (under sterile conditions in flasks) on the Murashige and Skoog artificial nutrient medium [34] with the addition of 1.0 mg/L 6-benzylaminopurine, 0.1 mg/L β -indolyl-3-butyric acid, and 0.5 mg/L gibberellic acid. In this environment, shoots propagate without the formation of roots. The cultivation was carried out with a 16-h light day at an illuminance of 2500 lx (fluorescent lamps) and a temperature of $23 \pm 2^\circ\text{C}$. Two days after planting, the explants were irradiated directly through the glass of the flasks without breaking sterility. To ensure uniformity of irradiation, the flasks were installed on platforms rotating at a speed of 2 rpm. Repetition of experiments is represented by five independent groups of seven explants each.

The quasimonochromatic light sources with high spatial coherence ($>200 \mu\text{m}$) were semiconductor LEDs ($\lambda_{\text{max}} = 660 \text{ nm}$ or $\lambda_{\text{max}} = 740 \text{ nm}$) with a spectral linewidth at a half-height $\Delta\lambda = 24 \text{ nm}$, which provided a light intensity in the area of biological samples of 2 W/m^2 . To produce a field with variable coherence, a 250-W high-temperature quartz incandescent lamp was used. In its optical path, light filters and aperture diaphragms were installed (Fig. 1), which made it possible to obtain quasimonochromatic beams with differ-

ent space-time coherence, but the same intensity of 1 W/m^2 . The radiation intensity was determined with a VEGA meter (Ophir, Israel) and an IMO-2M calorimetric meter (Russia).

Spectral measurements were carried out on an Analytik Jena Specord 250 Plus spectrophotometer (Germany) and an ASP-150T spectrometer (Russia) with an accuracy of 0.5 nm. The coherence length L_{coh} of quasimonochromatic beams was calculated using the formula $L_{\text{coh}} = \lambda_{\text{max}}^2 / \Delta\lambda$ [35]. The intensity-normalized spectra of broadband and narrow-band beams of an incandescent lamp ($\lambda_{\text{max}} = 730 \text{ nm}$) are shown in Fig. 2. Spectra were chosen to correspond to the absorption region of the phytochrome Pfr form and slightly cover the absorption region of Pr.

A circular aperture diaphragm, which determines the angular dimensions of the thermal light source, was installed behind the filters in the center of the beam. Such an optical scheme produced a quasimonochromatic spatially limited wave with a relatively uniform intensity distribution over the wave front. In this case, the magnitude of normalized transverse correlation function of the field at two points \mathbf{r}_1 , \mathbf{r}_2 can be represented as [37] $\gamma(s) = 2|J_1(kas/z)/(kas/z)|$, where $J_1(kas/z)$ is the Bessel function, $k = 2\pi/\lambda$ is the wave number, $2a$ is the source aperture, $s = |\mathbf{r}_1 - \mathbf{r}_2|$, and z is the distance from the radiation source to the sample. The function $\gamma(s)$ acquires the first zero value at $kas/z = 3.83$, and, accordingly, the correlation radius in this case is $r_{\text{cor}} = 0.61\lambda z/a$. In the experiments, we used diaphragms with an aperture of 30 or

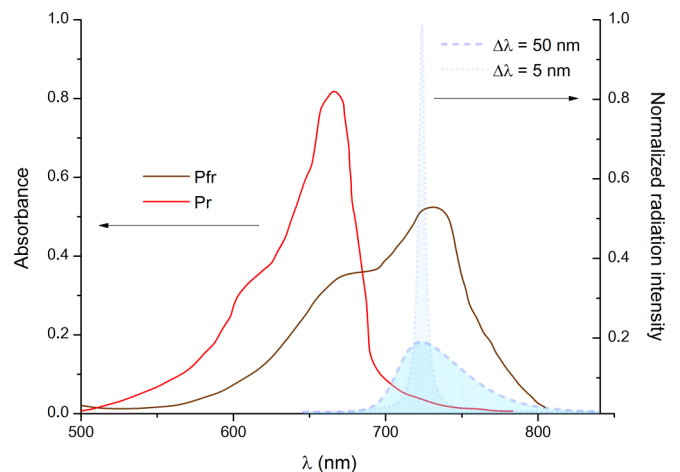


FIG. 2. Absorption spectra of the Pr and the Pfr form of plant phytochrome (according to [36]), and normalized spectra of the incandescent lamp with filters.

TABLE I. Coherence parameters of thermal light source with a frequency and spatial filters.

Variant	λ_{\max} , nm	$\Delta\lambda$, nm	L_{coh} , μm	r_{cor} , μm
I	730	5	107	18
II	730	5	107	6
III	730	50	11	18
IV	730	50	11	6

10 mm in diameter at a distance of 200 mm from the irradiated sample.

The use of thermal light source with the frequency and spatial filters made it possible to obtain quasimonochromatic waves with relatively high or low space-time coherence in the Pfr excitation regime (see Table I).

The results of irradiation were judged by the number and length of shoots formed on each explant. Measurements were carried out every 10 days for a month. Means and standard errors (error of the mean) are shown on graphs and histograms. The reliability of the differences between the experimental variants was calculated by means of the analysis of variance and quantitatively assessed by the level of significance of the “null hypothesis” p (the probability of equality of comparable values).

III. RESULTS

A. Influence of red and far-red light

The objective of this stage of research was to determine the sensitivity of the selected biological model to red and far-red light and the ability of its photoregulatory system to reversible photoconversion. The used semiconductor radiation sources (LEDs) provided the field coherence necessary for a pronounced photoinduced response: $L_{\text{coh}}; r_{\text{cor}} \geq D$.

In one group, biological samples were irradiated with red light only. Its influence led to a high stimulating effect. With all the irradiation regimes used, the length of the shoots increased by 1.5–3 times (Fig. 3, curve 660). The multiplication factor—the number of shoots formed per explant—changed

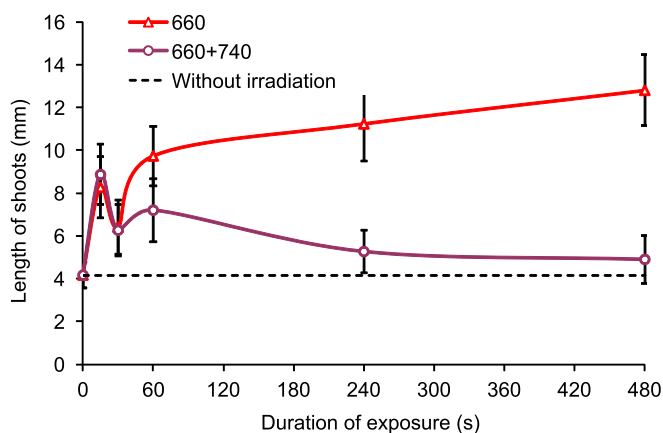


FIG. 3. Influence of red or combined (red and 1 min later far-red) light-emitting diode radiation on the length of shoots of blackberry explants. Cultivation period is 30 days.

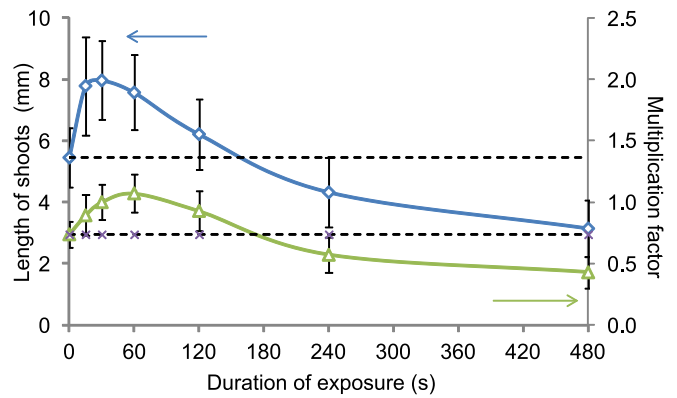


FIG. 4. Dependence of the length of shoots and the multiplication factor of blackberry explants on the time of irradiation with far-red (740 nm) light. Cultivation period is 20 days.

approximately in the same way. In another group of biological samples, combined irradiation was applied: first with the red light and then, after 1 min, with the far-red light. The suppression of the stimulation effect by longer wavelength radiation was also well pronounced (Fig. 3, curve 660 + 740). This form of response is characteristic of *phyB*-mediated photoregulatory processes.

The direct and reverse photoconversion rates were different. The stimulatory effect was noticeable already in the case of 15-s irradiation exposure. This indicates a sufficient accumulation of the Pfr form even at the lowest of the used exposures. Far-red light inhibition required a longer exposure time: differences in growth rates are noticeable for exposures longer than 1 min. In this case, growth indicators still remained above the reference level. The reason is probably associated with a high concentration of the Pfr form in cells and a lower rate of its reverse photoconversion: $\text{Pfr} \rightarrow \text{Pr}$.

Thus, the experiment carried out confirmed the suitability of the used biological model for further research.

B. Determination of the exposure duration

At the second stage of the study, the influence of exposure duration on the effectiveness of far-red light affecting explants in a neutral (nonactivated by red light) state was considered. The length and number of shoots irradiated with far-red light only depends on the exposure time. Reliable suppression of the growth of explants with respect to the intact (control) variant was observed at an irradiation duration of 480 s (Fig. 4). Therefore, this exposure was used in the further experiment as the main one.

C. Effect of far-red light coherence

The objective of the third experiment was to determine the effect of the coherent properties of radiation. To do this, explants were irradiated with beams of far-red light with different spatial and temporal coherence. The average cell size D was taken as the biological threshold for discrimination of the characteristic parameters of coherence [26]. The optical beams were formed in such a way that L_{coh} and r_{cor} were either smaller than or commensurate to D . That is, there are

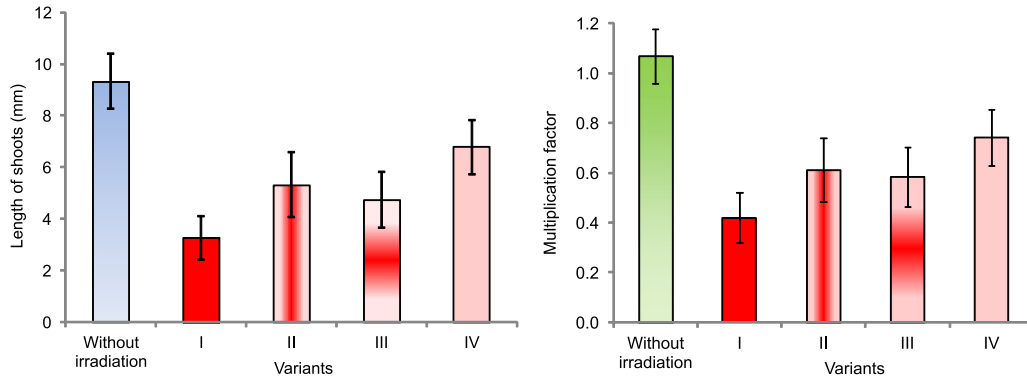


FIG. 5. Influence of the coherence of far-red (730 nm) light on the growth indices of blackberry explants. (I) $L_{\text{coh}} = 107 \mu\text{m}$, $r_{\text{cor}} = 18 \mu\text{m}$; (II) $L_{\text{coh}} = 10 \mu\text{m}$, $r_{\text{cor}} = 6 \mu\text{m}$; (III) $L_{\text{coh}} = 11 \mu\text{m}$, $r_{\text{cor}} = 18 \mu\text{m}$; and (IV) $L_{\text{coh}} = 11 \mu\text{m}$, $r_{\text{cor}} = 6 \mu\text{m}$. Exposure duration is 480 s, cultivation period is 20 days.

four variants of the experiment, the parameters of which are described in the methodological section.

The response of biological samples depended on the ratios of the parameters L_{coh} and r_{cor} to the cell size D . The greatest inhibitory effect was obtained when the cells fit completely in the coherence volume of the quasimonochromatic wave field: $L_{\text{coh}}, r_{\text{cor}} \geq D$ (Fig. 5, variant I). After 20 days of cultivation on an artificial nutrient medium, the multiplication factor of shoots and their length lagged behind the control indicators (without irradiation) by a factor of 2.6–2.9 with high mathematical reliability ($p < 0.001$). In variant II, the coherence length was the same as in variant I: $L_{\text{coh}} = 107 \mu\text{m}$, but the field correlation radius was reduced by a factor of 3. In this case, the inhibitory effect in terms of the number and length of shoots decreased 1.5–1.6 times. A similar picture was observed at a shorter coherence length $L_{\text{coh}} = 11 \mu\text{m}$ (Fig. 5, variants III and IV). Thus, for the same spectral characteristics of the beams ($L_{\text{coh}} = \text{const}$), the response to far-red light depended on the spatial coherence of the light field.

Variant IV was characterized by the lowest field correlation; the cells were only partially fit in the volume of the field coherence ($L_{\text{coh}}, r_{\text{cor}} < D$) and the inhibitory effect was the weakest among the experimental variants. Pronounced differences in growth parameters (1.8–2 times at $p < 0.03$) were obtained in the variants with the highest and lowest light field coherence (Fig. 5, variants I and IV).

In accordance with the dependence of the influence of far-red light on the duration of irradiation (Fig. 4), the effect of coherence was more pronounced at a higher exposure. The length of shoots in the variants of the experiment with relatively high (variant I) and low (variant IV) spatiotemporal coherence differed 1.5 times at 240 s, and 2.1 times at 480 s (Fig. 6). A similar relationship, but with less pronounced differences, was observed when comparing variants I and II, where only the spatial coherence changed.

Differences in the morphological parameters of explants under irradiation with high- and low-coherent light were traced during the entire observation period (Fig. 7). They smoothed out over time, but remained quite noticeable. Thus, after 10 days of cultivation the ratio of the average lengths of shoots in the variants with the lowest (IV) and highest (I) coherence was 6, while on the 30th day it dropped to

1.5. At the same time, at the end of the observation period, the growth characteristics in variant I differed more from the control (without irradiation) than those in variant IV: by 1.9 and 1.3 times, respectively. Similar results were obtained for the shoot reproduction rate. Apparently, the coherence of far-red light affected not only the severity of the photoinhibiting effect, but also the duration of its retention.

IV. DISCUSSION

The results obtained indicate that the coherence of far-red radiation significantly affects the functional state of plants. In this case, the effect of quasimonochromatic light was more pronounced as the larger part of the cell was placed in the volume of the field coherence, i.e., in the region of space where the correlation of light waves is observed. The contributions of temporal and spatial coherence can be considered approximately equivalent. With equal values of L_{coh} , the limiting factor was r_{cor} and vice versa (in variants II and III, the growth indicators practically did not differ, Fig. 5).

Since the change in the temporal coherence of radiation is closely related to the width of its spectrum, in order to analyze the plant response, it is necessary to take into account the possible change in the balance of Pr and Pfr form under illumination by a source with a narrow or wide spectrum.

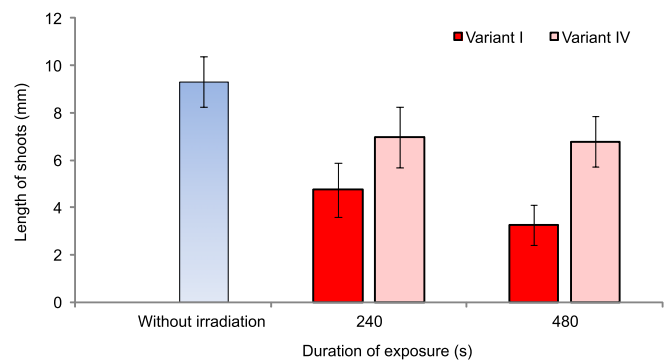


FIG. 6. Influence of the duration of irradiation with far-red light with relatively high (variant I) and low (variant IV) coherence on shoots growth inhibition in culture *in vitro*. Cultivation period is 20 days.

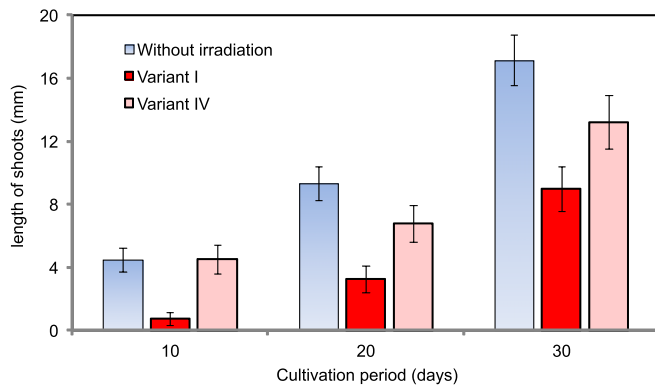


FIG. 7. Changes in the length of shoots of blackberry explants after their irradiation with far-red light with relatively high (variant I) and low (variant IV) coherence. Duration of irradiation is 480 s.

A priori, it could be assumed that illumination with a wider spectrum should cover the absorption region of the Pr form (Fig. 2) and lead to the transformation of the red form into the far-red form, which reduces the inhibition efficiency. We calculated the absorption efficiency of Pr and Pfr forms for each of the sources in the range from 300 to 850 nm. The ratio of the integral absorption efficiency (absorption with regard to the intensity of the source at a given wavelength) Pfr:Pr for the narrowband source was 12.2:1, while for the broadband it was 14.1:1. Thus, from the point of view of the balance between Pfr and Pr forms, a more coherent (narrow-band) beam is under conditions less favorable for inhibition, but its action (comparison of variants I and III, and variants II and IV, Fig. 5) is more efficient.

Let us note, however, that the phytochrome form balance Pfr:Pr upon absorption of light in a living organism may differ from the estimates based on the spectra of the isolated phytochrome. Therefore, to clarify the influence of coherent properties, the variants in which the spatial coherence changed with a fixed temporal (fixed frequency spectrum) one are most indicative. Variants of experiment I and II, as well as III and IV (Fig. 5), corresponded to this condition. In each of these pairs, the radiation spectrum remained constant, and the correlation radius of the light beam differed by a factor of 3. Varying the spatial coherence (and, accordingly, the correlation properties of radiation) significantly influenced the growth response of irradiated explants: it changed by 50–60%. A similar picture was earlier observed for the same culture under the action of red light [26]. The data obtained on the action of far-red light (Fig. 5) confirm that the correlation properties of radiation play an important role in photoregulatory processes. The effect of light coherence is probably associated with an increase in the *phyB* photoconversion efficiency and a larger accumulation of Pfr or Pr form.

The direct and reverse photoconversion of phytochrome pass through a number of intermediate states differing in absorption spectra and lifetime [38,39]. Unlike the direct photoconversion, the reverse one can also proceed in the dark, but at a lower rate [38]. The results shown in Figs. 3 and 4 allow us to conclude that in order to obtain a reliable biological response, the action of light with a wavelength of 740 nm should be sufficiently long (exceed several minutes). This

explains why in our experiments the effect of the far-red light coherence under irradiation for 240 s is less pronounced than that for 480 s (Fig. 6). Earlier, a slightly different picture was observed in the red region of the spectrum: the differences in the biological effect of high and low coherent light became mathematically reliable already at 16–64 s [26,28]. One can assume that this behavior is a consequence of the higher rate of accumulation of the Pr form in explants, which is consistent with the *in vivo* phytochrome studies [40].

Phytochromes are involved in the regulation of a wide range of biological processes, in particular, the control of the synthesis and transport of phytohormones, both at the level of gene expression and processes in biomembranes [41–43]. The feature of the chosen biological model was that in the taken culture medium the explants did not form roots where cytokinins are predominantly synthesized. These hormones stimulate cell division and are involved in the regulation of plant growth and development. In the absence of roots, the source of cytokinins was an artificial nutrient medium containing 6-benzylaminopurine. The dependence of the length and number of shoots on the statistical ordering (coherence) of the far-red light (Fig. 5) indicates that the correlation properties of radiation are capable of affecting the transport of hormones in plant cells through chemical signaling cascades.

The result of the excitation of plant organisms by coherent (in particular case far-red) light was preserved for a period significantly (tens of thousands of times) longer than the exposure time (Fig. 7). Such a long-term preservation of the action of the stimulus is possible only in the presence of some bistable system with stable feedbacks. In genetics, this effect was first shown on the lactose operon of bacteria [44,45]. The essence of the phenomenon lies in the occurrence of a feedback between two operons through their gene products. Expression of genes of one operon causes the synthesis of repressor proteins that suppress transcription of genes of another operon and vice versa. This form of information transfer is called a two-operone trigger. Mathematical modeling in works [46,47] showed that bistable biological systems are very stable and can exist for a long time in a dissipative environment. These systems are very diverse in function and lifetime. For example, phenotypic variability under certain conditions persists not only for one generation, but is also inherited at the epigenetic level [48,49]. At the metabolic level, the trigger form of control is observed during membrane transport of the extracellular substrate [50].

The dependence of phytochrome-mediated reactions on the coherence of light may have a certain biological function associated with the response to coherent biophotons. An example is the interaction of chemically isolated organisms through biochemiluminescence shown in a large number of works [11–14,21,24,51,52]. Communication in this case is carried out through the cells' own radiation, which, as a rule, has an extremely low intensity. It is known that weak luminous fluxes can be distinguished (detected) against the background of a powerful stochastic hindrance (which is natural illumination) only if they have a higher coherence [53]. Thus, the phenomenon of optical intercellular interaction is an indirect confirmation of the coherence of biophotons. Another proof is the weakening of the optical interaction of cells if a stochastic phase screen, which reduces the spatial

coherence of the transmitted radiation, was installed between them [13,14].

Another important element of the optical communication system is the phase detector, capable of responding to the statistical ordering of radiation. Its presence in the cell is evidenced by the dependence of photoinduced reactions on the coherence of light. This property of cells was experimentally determined by us in the early 1990s [54], but to explain the mechanism of the phenomenon, it is necessary to accumulate experimental data. Stimulation with red light [26–28], similar to the inhibition by far-red light shown in this work, depends on coherence. The spectral ranges used and the reversible nature of the photoinduced reactions indicate the participation of phytochrome, while the influence of the statistical properties of radiation suggests that this chromoprotein can be a phase detector element.

A possible structure connecting the elements of the phase detector can be membranes: cytoplasmic, nuclear, endoplasmic reticulum membrane. Most of the phytochrome molecules, combining with the chemical signal of nuclear localization (NLS), come from the cytoplasm to the cell nucleus, where they are involved in the regulation of gene expression [42,55]. A certain amount of phytochrome directly or with the participation of phototropin interacts with the cytoplasmic membrane [43]. This connection is confirmed by the presence of fast photoinduced reactions, which are significantly ahead of epigenetic processes. The sensitivity to the direction of light is also membrane mediated, which is impossible at the nuclear level. Linear dichroism (dependence on the plane of polarization of light) in plant cells indicates nonchaotic, anisotropic attachment of photoreceptors to the membrane [31]. The electrostatic binding of phytochrome to membranes that affect its properties is also considered [56]. Biological membranes are distributed throughout the volume of the cell and its periphery (cytoplasmic membrane). They have cooperative properties and, in the presence of the corresponding chromoproteins, can potentially provide recognition of the coherence of light

waves. This structure corresponds to the delocalization of the phase detector elements on the cell size scale.

Another organelle dispersed throughout the cell is the cytoskeleton. It also has a connection with phytochrome and is involved in its translocation into the nucleus [57]. It cannot be ruled out that components of the cytoskeleton can participate in the operation of the phase detector.

V. CONCLUSIONS

In this work, it was shown that the photoregulatory effect of far-red light is associated with its statistical properties. The biological response induced by the Pfr \rightarrow Pr transition depends on the spatial or temporal coherence of light in the same way as in the direct Pr \rightarrow Pfr photoconversion. Therefore, one can speak in a broader aspect about the role of light coherence in photoregulatory processes.

Attention to coherent processes in biology is growing every year. However, it concentrates mainly around coherent states at the molecular and electronic levels. Much less attention is paid to the cell level. This issue seems to us extremely important, since the statistical properties of light significantly affect the functional state of living organisms. We have carried out a number of studies in this area. The response to the coherent properties of light was observed in bacteria, fungi, and plants. In all cases, it had common features. The larger the part of the cell placed in the volume of field coherence was, the more pronounced was the photoinduced response.

These studies cannot be considered complete. The ability of other chromoproteins to respond to the statistical properties of radiation remains to be determined. The questions of how the generation and recognition of coherent photons occurs in a cell are becoming topical.

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