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REVIEWS

Role of Green Light in Physiological Activity of Plants

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Abstract—Green light, along with other portions of the visible region of electromagnetic radiation, brings plants environmental information. Green light is a factor regulating the morphology of cells, tissues, and organs; photosynthesis; respiration and growth; and duration of stages of plant ontogenesis. This review summarizes the impact of the green light on the life of plants, and green light receptors and the mechanisms of its action are discussed.

Keywords: green light, phytochromes, cryptochromes, phototropins, Zeitlupe, heliochrome, rhodopsin, phytohormones, photomorphogenesis, photosynthesis, respiration, flowering

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INTRODUCTION

Plants have a fixed lifestyle and are constantly under the influence of a large number of external factors, among which the decisive role is played by light, because it is a source of energy for photosynthesis and a signal involved in the regulation of plant life. Light acts as a multifaceted factor, characterized by qualitative (wide range of wavelengths) and quantitative parameters (intensity, integrated daily radiation [1], photoperiod), as well as by direction. Light is important for the implementation of relevant programs for the development of plants (deetiolation, photomorphogenesis, photoperiodism, phototropism, etc.). Light is necessary for successful plant reproduction, since it controls the timing of seed germination, transition from the vegetative stage to flowering, and transition from fruiting to aging.

Light controls the functioning of endogenous regulation systems (genetic, enzymatic, trophic, hormonal, etc.), whose cumulative effect provides an adequate response of plants to the light conditions.

Evaluation of the absorption of radiant PAR energy by the whole leaf shows that its maximums are in blue (BL, 300–480 nm) and red (RL, 640–680 nm) regions, caused by the absorption of photosynthetic pigments. In this connection, the spectral composition of light changes under the canopy [2] and in the depth of planting, which gets radiation penetrating through the leaves of the upper stories, poor in blue and red rays and rich in green ones (GL, 510–565 nm) and far-red rays (FR, ~730 nm). Light in the shade is characterized by reduced ratios of RL/FR and BL/GL [3]. The biological significance of the phenomenon of GL is associated with the existence of dense aboveground phytocenoses [2–4]. Restriction in the absorption of green rays by chlorophyll (Chl) can play a positive role for the life of the lower leaves of plant crown and lower stories of phytocenosis.

As the optical system, the leaf is different from the pigment solution in two aspects: (1) local concentration of pigments in the chloroplasts and (2) diffuse nature of the distribution of plant tissues. The first feature in the structure of the leaf causes a local light absorption. The second feature is associated with the complexity of organization of cells and plant tissues, leading to light scattering with multiple internal reflection, and refraction leads to a substantial increase in the effective optical path of light to the plant tissues, leading to both increased absorption capacity and increased reflection of light [5]. Thus, the same amounts of pigments in apple fruit tissues absorb almost an order more light than these in the extract [6].

However, these features may be important only if GL will be used in the photosynthesis. According to some authors [4, 7], GL of high intensity does not limit photosynthesis processes but actively regulates growth processes. It can fully provide the life activity of several plants under irradiation from 300 to 400 μM/(m^2 s). Plants of *Triticum aestivum* and *Raphanus sativus*, e.g., accumulate greater biomass on GL compared with BL of the same intensity.

By now, a considerable amount of information was obtained on the role of RL and BL in plant life and on signal reception and transduction by RL and BL. The mechanisms of the action of GL on plant growth and

Abbreviations: BR—brassinosteroids; BL—blue light; Chl—chlorohhyll; FL—far-red light; GL—green light; P—phytochrome; RL—red light; WL—white light; YL—yellow light; ZR—zeatin riboside.

development, as well as the nature of GL receptor, remain unstudied.

LIFE PROCESSES IN PLANTS, CONTROLLED BY GREEN LIGHT

Green light regulates many vital processes of plants from seed germination to flowering (table). In addition, it is one of the factors that control plant reactions at "shade avoidance syndrome" (the growth of the stem and petiole elongation, flowering), allowing it to compete with neighbors in the dense phytocenosis [8]. However, GL may cause photodamage of photosynthetic pigments, since the maximum energy in the solar spectrum falls on the green light [6].

The green light is active in regulating seed germination. The seeds of *Lolium rigidum* remain at rest on imbibition in the light, but BL and GL activate their germination after dark stratification [9, 10]. There is evidence on the stimulating effect of short exposures to GL on seed germination. The species-specific response on GL was noted: species of the family *Cistaceae* were less sensitive to GL compared with the species of families *Compositae* and *Labiatae* [11].

A low-threshold nonphotosynthetic photomorphogenetic answer was found in single-celled algae *Scrippsiella trochoidea*: resting cysts required light for germination, and GL has the greatest effect [12].

The intensity of growth processes is largely dependent on cell division and expansion. It is shown that GL (with a maximum of 550 nm) makes interphase gap, breaking the mitotic phase of the cell cycle, and 50% reduction of cell elongation in *Lepidium sativum* [13]. Based on these results, one can explain the reason for the formation of a thin lamina with small mesophyll cells during long-term cultivation of certain plants in GL [4, 14]. However, the formation of the leaf surface at adaptation to GL is determined by genotype and duration of ontogenesis. Slow-growing species (*Bergenia crassifolia*) form smoller leaf surface on GL compared with white light (WL), RL, and BL, while the leaf surface area of more actively growing species (*Rhaponticum carthamoides*) on GL is comparable with that on RL. Leaf of monocots (*Avena sativa* and *A. fatua*) grows faster and longer on GL compared with that on BL [14]. GL increases the growth of plants of the genus *Fragaria* and their fruits [15].

The action of narrowband optical radiation (16 h photoperiod) at a wavelength of 522 nm (70 $\mu M/(m^2 s)$) reduced fresh and dry masses of leaves and roots of *Lactuca sativa*, which was associated with reduced intensity of photosynthesis, transpiration rate, and stomatal conductivity compared with RL (639 nm, 88 and 328 $\mu M/(m^2 s)$) and BL (470 nm, 80 and 328 $\mu M/(m^2 s)$). However, the effect of GL (180 $\mu M/(m^2 s)$) on net photosynthesis and the content of Rubisco was comparable with the action of RL (88 $\mu M/(m^2)$) [16].

It has been found in studying the effects of light (12 h photoperiod) at wavelengths ranging from 490 to 540 nm that the length of hypocotyl increased on GL in the seedlings of *Brassica oleracea*, but fresh and dry masses decreased compared with those for plants on BL and RL [17].

The combined effect of BL, RL, and 24% of GL caused the strongest growth of the *L. sativa* plant. The growth of leaf area and dry mass decreased with increase in the proportion of GL from 24 to 86% in the total luminous flux [18].

The study on the light regulation of survival and subsequent development of in vitro culture of *Cymbidium insigne* plants demonstrated that the effect of different light spectral composition (WL, RL, BL, and GL) and two polysaccharides—chitosan H and hyaluronic acid (HA9)—accelerated the formation and increase in protocorm-like bodies (PLB). The highest PLB formation occurred among culture explants on a medium supplemented with chitosan H, and the rate of formation of shoot and root increased also. The increase in biomass PLB was noted when plants were treated with HA9 on GL [19].

It should be noted that there is a common pattern in the regulatory action of GL on morphogenesis *B. crassifolia, Rh. carthamoides, Lychnis chalcedonica*, and *Serratula coronata* plants. Green light, regulating cell growth and density of their packing in the mesophyll, reduced the total number of chloroplasts per unit of leaf surface area. The latter circumstance determines the weak assimilation of CO_2 in the leaf on GL [4, 14]. Meanwhile, the level of photosynthetic pigments in a single chloroplast increases. This regulation of the level of chloroplast pigments is probably directed at reducing their shading within the leaf.

The seedlings of higher plants orient their growth according to the direction of the light (phototropism), seeking to optimize the light exposure for photosynthetic organs. As a rule, phototropism is set by BL, but it is also effective on GL in *Arabidopsis thaliana*. Transmission mechanisms of phototropism signals vary in shoot and root, because some mutants (*nph1*) have a broken phototropism of shoot and root, while others (*rpt1* and *rpt2*) have a broken phototropism of root only [20]. Only phototropism of *A. thaliana* shoot is sensitive to GL [21]. The differences between the action of GL on phototropism of *A. thaliana* seedlings, grown under different conditions (in the light and in the dark), were shown. GL did not affect the regulation of root phototropism, caused by RL or BL. However, GL impulse significantly reduced positive BL phototropism in the hypocotyls of seedlings grown in the dark, increasing the rate of growth. In contrast, the impulse of GL increased significantly positive curvature in the hypocotyls of seedlings grown in the light without affecting the rate of growth [22].

Green light regulated the movement of chloroplasts (phototaxis) in the cell of diatom *Pleurosira lae-*

Life processes of plants controlled by green light

Process	Object	Source
Seed germination	*Lolium rigidum,* Cistaceae < Compositae, Labiatae, *Hordeum vulgare*	[9, 10, 11, 54]
Germination of cysts	*Scrippsiella trochoidea*	[12]
Cell cycle (interphase)	*Lepidium sativum*	[13]
Growth of cells and chloroplasts	*Avena sativa, A. fatua, Bergenia crassifolia, Rhaponticum carthamoides, Funaria hydrometrica*	[4, 14, 75]
Growth of leaf and cotyledons	*A. sativa, A. fatua, B. crassifolia, Rh. carthamoides, Lactuca sativa, A. thaliana*	[14, 16, 36, 37, 89, 91]
Growth of hypocotyl	*Brassica oleracea*	[17, 29, 31, 37, 89, 91]
Plant growth	genus *Fragaria, B. oleracea, Lactuca sativa*	[15, 17, 18, 90, 91]
Fruit growth	genus *Fragaria*	[15]
Formation and growth of protocorm-like bodies	*Cymbidium insigne* in vitro	[19]
"Shade avoidance syndrome"	*Arabidopsis thaliana*	[3, 61, 79–81]
Movement of leaves	*Albizzia pinnules*	[51]
Movement of stomata	*A. thaliana, phot1 phot2* mutant	[55, 56]
Phototropism of shoot and root	*A. thaliana*	[20, 21, 22]
Phototaxis of chloroplasts	*Pleurosira laevis*	[23]
Migration of phytoplankton during the day		[24]
Formation of chloroplast and mitochondria, chloroplast's photochemical activity		[27, 28]
Photoperiodism: plant flowering, FT mRNA levels	*Rudbeckia bicolor, Perilla ocymoides, Chenopodium rubrum, Nicotiana tabacum*	[25, 26, 82]
Transpiration and stomatal conductance	*L. sativa*	[16]
Photosynthesis	*A. sativa, A. fatua, B. crassifolia, Rh. carthamoides, Helianthus annuus, L. sativa*	[4, 14, 35, 36]
Net photosynthesis and Rubisco content	*L. sativa*	[16]
Accumulation of photosynthetic pigments	*A. sativa, A. fatua, B. crassifolia, Rh. carthamoides, A. thaliana*	[14, 29, 30, 31]
Respiration		[27]
Metabolism of carbohydrates and lipids	*Chlorella vulgaris in vitro, A. sativa*	[27, 34]
Accumulation of vitamin C, tocopherols, anthocyanins, and phenols; removal of free DPPH radicals	*L. sativa, Fagopyrum esculentum, A. thaliana*	[32, 33, 38]
Level of GA, IAA, and ABA phytohormones	*Lychnis chalcedonica, Rh. carthamoides, A. thaliana, Phaseolus vulgaris*	[3, 14, 29, 37, 54, 81, 86, 89–91]
Core microtubules	*A. thaliana*	[81]
Transcription of *XTH15, -16, -17, -19–22, CssPLA*$_2\alpha$ *and CsPLA*$_2\beta$, *PIF4*, and *PIF5* genes and plastid gene	*A. thaliana, Citrus sinensis, H. vulgare, A. thaliana, N. tabacum*	[3, 30, 39, 78, 80, 81]
Level and gradient of Ca^{2+}, cell polarity	*Funaria hydrometrica*	[75]
Transport of ions (protons, potassium)	*A. thaliana*	[55, 56, 81]
Resistance to strawberry anthracnose	genus *Fragaria*	[15]

vis [23]. It influenced photoperiodic responses of photosynthetic organisms, including phytoplankton vertical migration during the day [24], and flowering of annual plants (photoperiodism) [25]. In the context of a long day, faster formation and growth of the stem took place on GL, as well as budding of *Rudbeckia bicolor* compared with those on RL, BL, and WL; at the same time, on a short, 8-h day, *Perilla ocymoides* passed to budding more quickly on RL than on GL, BL, and WL [25]. A short exposure (5 min) to GL (554 nm) of *Chenopodium rubrum* short-day plants caused suppression of induction of flowering. Irradiation of short-day plants *Nicotiana tabacum* with GL during the induction of flowering inhibited their growth and flowering [26].

Green light (480–570 nm) induced the resistance of plants from *Fragaria* genus to strawberry anthracnose (*Glomerella cinglata*). This was expressed in a reduced number of damages on the leaves [15].

Despite the fact that GL has an inhibitory effect on prolonged cultivation of plants, this portion of the electromagnetic radiation stimulates the processes accompanying seedlings' deetiolation in the early stages of ontogenesis.

In the early stages of morphogenesis, combination of GL+YL accelerated the formation of plastid membrane system up to the lamellar type, inclusive, and, subsequently, it began to slow down the transition to granal chloroplast [27]. Photochemical activity of chloroplasts is associated with a degree of membrane system formation. Hill reaction and its coupled noncyclic phosphorylation in the early stages of deetiolation (4 h) of cereal seedlings were more active on GL compared with those on RL and BL [28]. GL+YL had a significant influence on the formation of mitochondrial cristae, but their degradation was observed in the later stages [27].

Green light is involved in the regulation of the processes of photosynthesis, not only by modifying the structure of the photosynthetic apparatus but also through a change in the intensity of Chl synthesis. When the seedlings of *A. thaliana* were deetiolated on GL, the accumulation of photosynthetic pigments in cotyledons was noted [29, 30], their content per seedling increased with an increase in the intensity of light [31]. The level of pigment per unit of leaf area decreased in a large number of plant species during long-term adaptation on GL, but it increased in a single chloroplast [14].

The character of anthocyanin accumulation in hypocotyls of *Fagopyrum esculentum* [32] varied also depending on the intensity of selective light. Less anthocyanins accumulated under the influence of GL and BL of low-intensity than those on RL and FRL. The role of BL and GL in this process increased with an increase in the intensity of light. However, increasing intensity of additional GL light from 10 to 40 $\mu M/(m^2 s)$ in combination with BL+RL intensified its inhibiting effect on the accumulation of anthocyanin in *A. thaliana* [33].

The regulatory role of GL was revealed in energy processes [27]. Regulating carbohydrate metabolism of *Chlorella vulgaris* cell culture, GL increased the proportion of disaccharides, but it reduced the proportion of mono- and polysaccharides (starch). Increased duration of its action increased the level of starch and reduced that of disaccharides. Twofold increase in lipid synthesis under irradiation of *Ch. vulgaris* with GL+YL was accompanied by a two-fold decrease in the synthesis of carbohydrates [27]. There are data on the stimulating effect of 15-minute illumination with GL (535 nm) on the metabolism of ^{14}C-glucose in etiolated seedlings of *A. sativa* [34].

Green light changes the differential quantum yield of photosynthesis. When the leaf of *Helianthus annuus* was illuminated with RL, higher differential quantum yield of photosynthesis was marked on its adaxial side than that on the GL. The observed phenomenon is explained by differences in the absorption capacity of Chl for these two wavelengths. The differential quantum yield of photosynthesis decreased at additional lighting with GL or RL along with increasing intensity of white light. However, the decrease of photosynthesis takes place more actively on RL than that on GL, since GL can provide photosynthesis in chloroplasts, located deep in the leaf, where additional RL or BL are not able to penetrate, and is dissipated as a heat instead [3, 35]. The efficiency of GL in the photosynthesis depends on its intensity and quality. The rate of photosynthesis increases with increasing intensity of GL from 100 to 200 $\mu M/(m^2 s)$. Shorter-wavelength rays (510 nm) are more effective for photosynthesis than the long wavelength ones (532 nm) [36], whereas only long-wavelength rays are effective in the regulation of elongation in *L. sativa* leaf and *A. thaliana* cotyledons [36, 37].

Additional illumination of *L. sativa* plants with GL (505, 535 nm) and BL (455, 470 nm) with an intensity of 30 $\mu M/(m^2 s)$ in combination with WL increased the content of antioxidants (vitamin C and tocopherol) in a row 535 > 505 > 455 > 470 nm, the total content of anthocyanins in a row 505 > 455 > 470 > 535 nm, the total content of phenols in a row 505 > 535, 470 > 455 nm, and the ability for scavenging of free radicals DPPH in a row 535, 470 > 505 > 455 nm [38]. Following that, GL of certain wavelengths in the mixed light stream is sufficiently active in the biosynthetic processes of *L. sativa*.

Green light on par with other parts of the light spectrum of PAR, but with less activity, is involved in gene expression of low molecular secretory phospholipase $A_2\alpha$ ($CssPLA_2\alpha$) and β ($CsPLA_2\beta$) in *Citrus sinensis* [39], involved in various cellular processes.

Age-specific action of GL on leaf hormonal status was established in its ontogenesis [14]. Young growing leaves of *L. chalcedonica* and *Rh. carthamoides* are characterized by increased competence to hormones,

GL decreased the level of growth promoters—gibberellins (GAs) and indole-3-acetic acid (IAA) and increased the level of growth inhibitor abscisic acid (ABA), which probably determined the inhibition of leaf growth compared with RL and BL. Increased hormone level in all groups of adult leaves that finished their growth on GL had no effect on the growth processes, which may indicate a slowing of their synthesis and transport in the early stages of leaf development.

MECHANISMS OF GREEN LIGHT ACTION ON PLANTS

Green Light Reception

Photomorphogenetic effect of light on a plant is implemented through regulatory photoreceptors, which are composed of a light-absorbing pigment (chromophore), associated with an effector protein molecule (apoprotein). The absorption of light in the chromophore causes a change in the redox potential or the conformational state of apoprotein receptor that triggers the transduction of light signal through a chain of secondary mediators. Among them there are three photoreceptors of BL/UV-A (cryptochromes CRY1, CRY2, and CRY3 (or CRY-DASH)) [40], photoreceptors of BL (phototropins PHOT1 and PHOT2), photoreceptors of family ZTL/FKF1/LKP2 (or ZEITLUPE/FLAVIN-BINDING, KELCH, F-BOX1/LOV KELCH PROTEIN2) [41–43], and the photoreceptors of RL/FRL (phytochromes PHYA-E) [44]. Photoreceptor of UV-B—UVR8—was identified [45]. Photoreceptors of RL and BL are well studied now, but nature of GL receptor remains uncovered.

Rhodopsins are believed to be regulatory pigments of GL in some algae. Two rhodopsin function as phototaxis receptors of low and high intensity light in eukaryotic alga *Chlamydomonas reinhardtii*: sensory rhodopsins A and B (CSRA and CSRB) [46]. CSRA has an absorption maximum near 510 nm and regulates the reactions under the action of a high intensity light. On the contrary, CSRB has an absorption maximum at 470 nm and controls the reactions saturated at low intensity light. Somatic cells of multicellular alga *Volvox carteri* contain rhodopsin, managing the phototaxis mode of the organism and encoded by *VOP* gene (*VOLVOOPSIN*) [47]. VOP protein is homologous to opsin of unicellular alga *Ch. reinhardtii* (chlamyopsin) and to a full family of animal opsin. The existence of two photoreceptors was shown for the diatom *P. laevis* that regulate the migration of the chloroplast in the cell, with peaks in the spectrum of action at 450 and 540 nm [23]. The presence of the photoreceptor RcaE was established on the basis of the action spectra of phycobilins' biosynthesis in cyans during complementary chromatic adaptation (CCA); it is similar to plant phytochromes and controls the process of CCA and absorbs RL (640 nm) and GL (550 nm) [48].

The aftereffect of FR inhibits the effect of GL on the metabolism of ^{14}C-glucose in etiolated seedlings of *A. sativa*, as well as the level of phytohormones IAA and GA during the deetiolation of bean seedlings, suggesting phytochrome as one of GL receptors, which is in a photostationary state [34, 37]. The threshold intensity of GL for the excitation of phytochrome is 2.5 times higher than that for RL and is 1.33 $\mu M/(m^2\ s)$ for the studied reactions. The action of GL at doses that saturate the phytochrome effect, is close to the regulatory action of RL [49].

The participation of other portions of the spectrum was shown for the phytochrome photoconversions on par with RL/FR. BL slows further elongation of *Sinapis alba* and *L. sativa* hypocotyls in the mixed light flux that was set by the phytochrome [50]. On the other hand, BL causes an increase in the content of the phytochrome and partially reduces the percentage of the active form of the phytochrome in the hypocotyl loop of *Vigna radiata*. In addition, it was found that the inhibition of hypocotyl elongation in *Trifolium repens*, caused by short-term action of FR, was completely canceled under the action of GL in addition to FR [50]. The combined effect of GL+FR reduces the amount of reversible phytochrome (P) in the seeds of *T. repens*, leading to an increase in the intensity of hypocotyl elongation.

Specific GL photoreceptor, differing from the phytochrome, was suggested as a regulatory pigment, controlling the germination of *L. rigidum* seeds, since BL and GL interrupt the rest regardless of FR. Interruption of the seed rest can be established with GL and without the participation of cryptochrome [9, 10].

It was shown in the study on nyctinastic movements of *Albizzia pinnules* lamina that BL slowed the process of dark slows nyctinasty with increased potrion of photon flux. RL or GL were not effective individually. However, in the case of low-intensity blue light (BL), RL and GL interacted with BL, increasing its efficiency. At high intensity of blue light, GL reduced its efficiency [51]. The author suggested the existence of heliochrome—a pigment absorbing GL.

The sensitivity of plants to GL can be provided by a group of photoreceptors (cryptochromes CRY1 and CRY2 [40, 52], phototropins PHOT1 and PHOT2, and ZTL/FKF1/LKP2 [40–43]) binding semireduced flavins [2, 53].

GL-dependent intramolecular electron transfer from adenine to lumiflavin, leading to the photoreduction of the latter, was proposed as a primary reaction of the mechanism of CRY1 light activation. According to some authors [2], the cycle of CRY1 conversion in *A. thaliana* at light consists of light dependent transition between three interchangeable redox forms of FAD (FAD, FADH•, and FADH-); among them, a stable neutral form of flavo semiquinone (FADH•) is considered to be an intermediate link in transmission of receptor signals. Meanwhile, other authors [53] believe that the cofactor may

exist in four different redox-forms: oxidized (FAD), anion semiquinone (FAD-), neutral semiquinone (FADH•), and anionic hydroquinone (FADH-). According to the time of life (2 ns), only the anionic flavin of hydroquinone can be the functional state of the receptor, because the lifetime of the neutral semiquinone is only 135 ps.

The formation of a more reduced form of flavin allows photoreceptors to absorb GL/YL (500–630 nm) in addition to the blue light. Activation of cryptochrome by BL may be slowed down by GL, which is determined by the change in the redox state of cofactor.

Phototransformations were marked for phototropins and receptors of family ZTL/FKF1/LKP2 [42, 43]. When a photon is absorbed, FMN photoexcitation of LOV domain occurs at the D_{450}, which leads to the formation of short-living triplet state of L_{660} that gives the metastable tioadduct of isoalloxazine FMN ring with a conservative cysteine (^{39}Cys PHOT1)—the state S_{390}. In the darkness, FMN returns gradually to its original state [43].

Partial reversal of the inhibitory action of BL on seed germination of barley by green light indicates the participation of cryptochrome [54]. GL reverses the opening of stomata, caused by BL, in a double mutant *phot1 phot2* of *A. thaliana* [55, 56] that is insensitive to FR, which is an additional proof of GL involvement in the regulation of CRY1 functioning.

The level of plant photoreactions is determined by cell concentration of photoreceptors; thus, an overexpression of *CRY1* leads to increased sensitivity of seedlings to GL [57], and a mutation in *HY4* gene reduces their sensitivity to this spectral region [29, 58]. Full sensitivity of transgenic plants to GL is lower than that for BL. The intensity of radiation required for 50% inhibition of hypocotyl elongation in CRY1-overexpressed seedlings of *N. tabacum* is 0.75 μM/(m^2 s) of BL compared with 4.00 μM/(m^2 s) of GL [57].

Nph1 mutants, defective at the early stage of phototropism signaling transmission, mediated by BL and GL, have no most likely photoreceptor of BL and GL–PHOT1 [21].

A reversion of the reaction controlled by phytochrome was shown by a light of a another quality, different from FRL [59]. Increased (10–15%) germination of wild-type *A. thaliana* seeds, as well as *phyA* and *phyB* mutants under the action of RL+GL, is attributed by the authors to a synergistic effect of either PHYA and PHYB, or PHYA, PHYB, and other phytochromes.

Two groups of plant reactions were identified, based on the analysis of the facts on the reception and action of GL in the plant: reactions on GL, dependent and independent of CRY [60, 61].

According to the latest data, thioflavines were found, which absorb light with a peak at 500 nm, i.e., at longer wavelength compared to known lumiflavines in natural photoreceptors of BL [62]. It is believed that the time of their existence is sufficient for photochemical reactions.

Cytochromes, carotenoids, some forms of chlorophylls, anthocyanins, and betalains can act as nonregulatory pigments absorbing GL. The data on the inhibitory effect of GL+YL on oxidative processes suggest the components of the respiratory chain—cytochromes (whose reduced forms have α- and ß-bands of absorption in the green region of the spectrum, 545–600 nm and 520–535 nm, respectively)—to be nonregulatory photoreceptors [63]. Carotenoids can also absorb the green region of the spectrum as a result of the shift in their spectrum—electrochromic effect—associated with the disturbance of the energy levels of the molecule due to the appearance of light-induced transmembrane fields [64]. Base bands of electrochromic differential spectrum were observed in the thylakoids at 478 and 518 nm. Some xanthophylls, e.g., fucoxanthin of brown, golden, and diatomic algae can absorb light in the range of 500–590 nm in vivo [63].

The forms of secondary carotenoids resistant to photodegradation were found in algae and terrestrial plants—these are retro- and keto-carotenoids (such as rhodoxantin) with **extra-plastid and extra-thylakoid** localization that are not involved in the absorption and transmission of light energy by chlorophyll molecules. They are able to absorb a significant part of **PAR** in the green region of the spectrum [6]. Rhodoxantin forms effective irradiation traps in the leaves of *Aloe arborescens* in a broad band of 450–600 nm, in which the solar radiation penetrates most deeply into the leaf tissue.

Green light may affect the redox reactions, since the formation of products occurs during the reduction of pigments (chlorophyll *a*, pheophytin α, phthalocyanine) by ascorbic acid with an absorption maximum at 530 nm [65]. Anthocyanins can be called among the nonregulatory GL pigments. The leaves containing anthocyanins absorb GL well enough. The reflective capacity of the leaves in green spectral range of irradiation reduces with increasing content of anthocyanin [66]. It was found in the study on the optical properties of leaves of five species—*Acer platanoides, Cotoneaster alaunica, Corylus avellana, Cornus alba*, and *Parthenocissus quinquefolia*—that anthocyanin has in vivo absorption maxima between 537 and 542 nm, showing the red shift of 5–20 nm compared with the corresponding maxima in acidic medium of water-methanol extracts [67]. Maximum absorption of cyanidin, dominant aglycone of anthocyanins from the leaves and fruits, giving them a red color, is approximately 525 nm. The rate of linear electron transport in ETC of chloroplasts in the leaves of *Corylus avellana* is characterized by a high positive correlation with endogenous content of anthocyanins [6].

Betalains (betacyanins) constitute a separate group of water-soluble nitrogen-containing compounds (alkaloids) that are present in plants of the nine families of the order Caryophyllales. The absorption spectra of betacyanins are characterized by a broad band with a

maximum around 539–543 nm, bathochromic shift of the absorption maximum to 550 nm is possible as a result of intramolecular copigmentation [68]. Exogenously added amaranthine (betacyanin) increases the electron transport by noncyclic pathway (Hill reaction) in isolated chloroplasts of *Amaranthus cruentus* [69].

Signal Transduction of Green Light

Phytochrome can be converted by GL into a biologically active form absorbing FRL [70]; therefore, GL is able to start a chain reaction with a lower efficiency than that under RL. Reactions on GL are usually low-energy photoreactions [70], whereby PHYB can act as one of the receptors that regulate these reactions.

The movement of the light-activated form of photoreceptor (Pfr) from the cytoplasm to the nucleus is an essential step in the transduction of light signal by phytochrome (P or PHY). It was shown on the isolated nuclei of a single-celled green alga *Acetabularia acetabulum* that the moving of PHYA occurs by a specific transport protein FHY1 (FAR-RED-ELONGATED HYPOCOTYL 1), being also actively exported from the nucleus [71], and by FHL (FHY1-LIKE) [72]. Phytochromes localized in the nucleus are associated with specific protein complexes, called photobodies. The size and distribution of these structures are regulated by the intensity and duration of illumination, and they are included in the adjustment of phytochrome signal transduction [72].

Active conformer PHY Pfr exported into the nucleus, physically interacts in the light with PIF transcription regulators, causing a decrease in the accumulation of transcription factors in the cell, accompanied by changes in the transcription of certain genes and the onset of light development (deetiolation). The interaction between Pfr and PIF causes not only rapid decomposition of PIF but also relatively slower decrease in the levels of PHYB photoreceptor under prolonged illumination. It was found that seven of 15 members of the PIF subfamily (PIF3, PIF1, PIF4, PIF5, PIF6, PIF7, and PIF8) interact with PHYB in a RL/FR photo-reversible way [8]. It was proven experimentally that, in the shadow light signals, including these from GL, the content of PHYTOCHROME INTERACTING FACTOR 4 (PIF4) and PIF5 proteins increases [3].

It is believed that PIF4 mediates the regulation of SHB1 (SHORT HYPOCOTYL UNDER BLUE1) of *A. thaliana* hypocotyl elongation and the expression of *CHLOROPHYLL a/b BINDING PROTEIN3* or *CHALCONE SYNTHASE* genes under the influence of RL, since overexpression of ***SHB1*** enhances the expression of *PIF4* [73]. Obtained data [3, 73] indicate the involvement of PHY in the signal transduction of GL.

Form of flavin of CRY1 photoreceptor restored on BL can absorb GL. The absorption of GL by cryptochrome slows its activation with blue light.

CRY1 signal transduction is associated with moving the light activated form from the nucleus to the cytoplasm, and the transmission of CRY1 signals may include both nuclear and cytoplasmic reactions, since early transmission of CRY1 signals is still able to function in the nucleus. In contrast, CRY2 localizes in the nucleus, both in the dark and in the light. It was shown that CRY1 and CRY2 are exposed to BL-dependent phosphorylation and that the phosphorylation status may be closely related to their regulatory functions [73]. It is important that the members of PIFq group of proteins (PIF1, PIF3, PIF4, and PIF5) also slow the photomorphogenetic development of the seedlings on BL and PIF4 and PIF5 suppress the lower level of BL phototropin sensor that controls phototropism [8].

Photoreceptors (PHYA and PHYB) can transmit and enhance the light signal through the activation of secondary cytoplasmic mediators (G-proteins, cGMP, Ca^{2+}, calmodulin, phospholipases D, protein phosphatases, protein kinases), causing another type of cellular activity, including the regulation of gene expression [74]. The main function of the cytoplasmic protein SHORT UNDER BLUE1 that binds calcium is the transmission of cryptochrome signals, but it also modulates PHYA-set Pfr reaction [73].

The initiation of protonema polarity was marked during the germination of spores of moss *Funaria hydrometrica* in the light of different spectral composition, which was accompanied by a change in the distribution of Ca^{2+} second messenger in the apical cells and by their growth [75]. Active cell growth under BL was associated with the maximum content of Ca^{2+} and its pronounced apical-basal gradient. The gradient of Ca^{2+} of the same intensity is mitigated on RL and GL due to its immobilization, resulting in a partial loss of cell polarity and reduce in the rate of their growth. The minimal level of Ca^{2+} was noted on GL.

Light signal transduction and production of ROS turns on in the process of plant transition from heterotrophic to autotrophic growth. ROS may be involved in the transmission of molecular signals that regulate numerous developmental processes, including cell death. It was shown that the transcriptional modules PIF1/PIF3-HY5/HYH participate in the exchange between the signaling pathways of different light spectrum and ROS, which is one of the mechanisms of plant adaptation to the light conditions of the environment [76].

PAR1 (PHYTOCHROME RAPIDLY REGULATED1) and PAR2 [77] were named among the positive factors functioning in multiple signaling pathways of photoreceptors during deetiolation of seedlings enhancing this process. The accumulation of transcripts of these proteins is suppressed by PHYA, PHYB, and CRY1 under the influence of FR, RL, and BL, respectively. PAR1 and PAR2 act at a lower level than COP1 does; however, COP1 determines their proteolysis in 26S proteasome. Localization of COP1 varies in the light with the participation of various

transduction pathways of light photoreceptors, and it is exported from the nucleus to the cytoplasm. This determines the accumulation of HY5 transcription factor in the light and causes the activation of the transcription of genes that are required in order to maintain the photomorphogenesis. Since PHYB and CRY1 absorb GL, these reactions may be involved in GL signal transduction.

The cascade mechanism turns on in response to the action of light that triggers the gene expression of "positive" regulators of photomorphogenesis. The influence of GL on the transcription of plastid genes in the etioplasts of the first leaves of *Hordeum vulgare* seedlings during deetiolation is shown. Treatment with GL (545 nm, 120 μM/(m^2 s)) for 16 h increases the transcription of ten genes by 2.0–3.5 times. The activation of transcription was observed for three genes of PS II, gene of Rubisco large subunit, ATP synthase complex, F subunit of NADP · H-plastoquinone oxidoreductase, as well as for "household" genes—genes of 16S and 23S ribosomal RNA, genes encoding β-subunit of plastid RNA polymerase of bacterial type (*rpoB*) and transport RNA (*trnE-Y*) [30].

At the same time, the treatment with short single impulse of GL with the intensity from 0.1 to 100 μM/(m^2 s) led to a decrease in the dark transcription of chloroplast genes *psa*A, *psb*D, and *rbs*L (respectively, the transcripts of the proteins of PS I, PS II, and stroma) in *A. thaliana* and *N. tabacum* [78]. The expression of nuclear genes *Elip* and *Lhcb*, whose transcripts were not detected in the dark or after the impulse of GL increased in *phyAphyB* mutant in response to GL impulse.

Downregulation of plastid protein synthesis with a short impulse of GL [78], as well as the support of stem growth with GL [61], are considered to be a manifestation of a way of development that is different from the normal way of photomorphogenetic development resembling a program of partial etiolation.

"Shade avoidance syndrome" was noted in light-loving plants that grow in the shade of larger plants, enriched with GL and FRL. This plant reaction is associated with intensive elongation of shoot and leaf petioles, more vertical position of leaves on the stem, lower branching, and accelerated flowering in the case of a constant shading [3, 79, 80]. Perhaps, this same phenomenon is observed in hypocotyl elongation under the effect of GL in the initial stages of deetiolation of *A. thaliana* seedlings [61]. This syndrome affects the expression of certain genes. The transcripts of *HAT4* and *PIL1* genes are accumulated under illumination conditions with low ratio of RL/FRL rays, which could serve as excellent indicators for reactions sensitive to GL. However, wild-type plants do not increase the level of HAT4 and PIL1 transcripts in response to GL, indicating the absence of fully synchronous responses on the action of FRL and GL [79]. GL signals cause partial etiolation of a plant, independent from CRY1-2, PHYA, and PHYB. At the same time, GL signals initiate gene expression, whose profiles resemble the profiles of gene expression, mediated by FR. The exception is that CRY receptors block the changes in gene expression in the presence of GL and in the absence of FR.

It was shown that PAR1 and PAR2 are the negative factors in the shade avoidance syndrome of *A. thaliana* [77].

Rapid elongation of shoot and leaf petioles in the shadow is determined by a change in the mechanisms of cell wall elongation. Changes in cell wall plasticity are associated with two major protein families—expansins and xyloglucan endo-transglycosylases/hydrolases (XET). The role of these proteins in the reactions on two signals, fixed in the shade, low ratio of RL/FRL and GL rays (so-called "green shadow") was studied in *A. thaliana* [80]. A quick exit of protons into the apoplast, compared with the control on WL, was shown in petioles treated with "green shadow." Cell wall elongation induced by acidification depended on the activity of XET, which increased in petioles placed in the shade. Five *XET* genes (XET9, -15, -16, -17, and -19) are positively regulated by light with a low ratio of RL/FRL, while a significant increase in expression in response to a "green shade" was shown also for the latter four and *XET22*. *XET* were also weakened or shade avoidance reactions to these light signals were lost in the mutants of *A. thaliana* with the defects in two of these genes, indicating the important role of *XET* genes in the regulation of growth by GL.

Further decoding of the regulation mechanism of leaf petiole elongation in *A. thaliana* in the process of shade avoidance showed that a great role in the regulation of expression of *XET* genes is played by microtubules that are located in the core cells [81].

The regulation of potassium channels is called one of the mechanisms of stomata movement regulation with GL, because the sensitivity of stomata to GL is observed only in the morning, when the movement of the guard cells is determined by the attraction of potassium in them as an osmotic [56].

Green light on par with other portions of PAR spectrum is involved in the gene expression of low molecular secretory phospholipase A2a (*CssPLA2a*) and b (*CsPLA2b*) in *C. sinensis* [39], which is involved in various cellular processes, including the transmission of light signals, lipid metabolism, injury reactions, pathogen-plant interaction, transmission of defense signals, fruit dropping, auxin-regulated reactions, and stomatal movement.

We know about the delay of plant flowering under the effect of GL [25, 26], since the flowering is controlled by CRY2, and the levels of *FT (FLOWERING LOCUS T)* mRNA are reduced in *cry2* mutant [82]. It should be noted that the inhibition of GL occurs only in the presence of the CRY2 and BL, since GL inhibits the expression of *FT* gene by inactivating BL receptor.

Based on the above said and other known facts of light signal transduction through phytochromes and cryptochromes involving nuclear genome [83], as well as on a possible absorbtion of GL by these sensory pigments, one can also imagine GL signal transmission. Each photoreceptor is suggested to have multiple signaling pathways of the lower level in photomorphogenesis.

More complex interactions of various regulatory and nonregulatory systems are formed in the process of long-term plant adaptation to the light conditions. The presence of several GL photoreceptors with overlapping absorption spectra may cause the change in the force of responses to the action of GL of varying intensity. The rate of formation of Chl and carotenoids decreased in *hy4* mutant in the absence of highly energetic CRY1 photoreceptor during deetiolation [30] and at constant GL (48 $\mu M/(m^2)$) compared with the original line of *A. thaliana* Landsberg *erecta* (L*er*) ecotype [29]. A twofold increase in GL intensity increased the content of all groups of pigments, reducing the differences between the lines [30, 31]. The latter fact is explained with both regulatory reactions due to other GL photoreceptors that are different from CRY1 and energy saturation of biosynthetic reactions.

There are effective mechanisms of accurate regulation of Chl biosynthesis in plants. Two transcription factors derived from transposase were identified as positive controls of Chl biosynthesis in *A. thaliana*: FHY3 (FAR-RED ELONGATED HYPOCOTYL3) and FAR1 (FARRED IMPAIRED RESPONSE1) [84]. FHY3 binds directly to the promoter and activates the expression of *HEMB1*, encoding a dehydrogenase of 5-aminolevulinic acid (ALAD) of Chl biosynthetic pathway. It was shown that PIF1 interacts physically with FHY3 DNA binding domain and thereby partially inhibits the expression of *FHY3/FAR1* activated by HEMB1. Light activates the expression of *FHY3*, thereby increasing the level of HEMB1 transcript and the level of ALAD protein, determining the accumulation of protochlorophyll and subsequent synthesis of chlorophyll. It can be assumed that, since GL increases the Chl content in plants, this mechanism can be used to regulate its biosynthesis under GL.

The interaction between transmission pathways of "sugar signals" (sucrose) and light signals (BL, RL and FR) has been shown at the present time in the regulation of the three target genes involved in nitrogen assimilation—asparagine synthetase (*ASN1* and *ASN2*) and glutamine synthetase (*GLN2*)—in plants [85]. Light cancels the regulatory effect of sucrose on gene expression of *ASN1* and *GLN2* in etiolated seedlings. In contrast, sucrose cancels the regulatory effect of light on the expression of *ASN2* and *GLN2* in plants grown in the light. The effect of GL on the condition of CRY1 can also change the interaction of transmission pathways of these two signals.

Green light is involved in the regulation of endogenous level of phytohormones, supporting the synthesis and redistribution of auxin and decomposition of DELLA proteins and increasing the expression of genes activated by auxins, gibberellins, and brassinosteroids [3]. Furthermore, the distribution of auxins is controlled by microtubules of core cells [81] and, possibly, by ethylene level [8].

The growth and development rates are decreased under GL in the plants of light mutants (*hy1, hy3, hy4*) in the absence of phytochrome or CRY1 compared with the original line, indicating the role of these receptors in GL signal transduction. Organs of small sizes are formed in mutant plants, and their competence to the photoperiodic induction of flowering reduces. In addition, GL reduces the growth and development of *ga4-1* and *det2* mutant plants, characterized by impaired synthesis of GA and brassinosteroids, respectively [30, 31, 86]. Exogenous brassinolide restores the "etiolated phenotype" of hypocotyls of *det2* mutant with impaired synthesis of brassinosteroids under GL [31], which is probably due to the expression of specific genes [30, 87].

Another proof of the involvement of hormonal growth regulators in the mechanism of action of photoreceptors includes the following data. The expression of *ARR4 (AUTHENTIC RESPONSE REGULATOR4)* gene is regulated not only by phytochrome PHYB but also by phytohormone cytokinin, which may indicate the interaction between light and hormone-dependent cascades of signal transmission through ARR4 [88]. At the heart of GL regulatory action on the growth of leaf, seedling, and the whole plant are changes in their hormonal composition, determined by genotype or exogenous regulators [14, 29, 86, 89–91]. The activation of the first leaf elongation during deetiolation under GL (30 min) of seedlings of a bipartite plant (*Phaseolus vulgaris*) was accompanied by a temporary increase in the content of IAA and the sum of gibberellins (GA_1 + GA_3), followed by a change in the pool of gibberellins ($GA_4 + GA_7$), as well as by a temporary reduction in the level of ABA. The growth rate of the leaf in the dark retained under similar conditions in the seedlings of a monocot (*A. sativa*). The growth rate was maintained by IAA and zeatin riboside (ZR), synthesized in etiolated leaves, with a parallel increase in the level of ABA and inactive gibberellin GA_9 and reduce in the level of active GA_1 [86]. There was a species-specific response to GL. The action of GL of a shorter duration (1 minute) was required to enhance IAA and GA_9 in bean leaf more sensitive to GL than that for oat leaf (30 min).

The level of hormones is controlled by GL in germinating seeds, too. Thus, GL (57.5 $\mu M/(m^2 s)$) partially reversed the inhibitory effect of BL of same intensity on seed germination, reducing the ABA content in them [54], which suggests the involvement of CRY1 and, thus, the realization of the process due to reduced gene expression of 9-cis-epoxycarotenoid dioxygenase that synthesizes ABA, as well as gene

expression of 8'-hydroxylase involved in seed imbibition [92].

Different in magnitude and direction response growth reaction of plants to light may be due to either different competence (state of photoreceptors), or the interaction of the various components of signal transduction (hormonal complex). For example, the level $GA_1 + GA_3$ and IAA synthesized in etiolated seedling did not change in the absence of CRY1 photoreceptor in the *hy4* mutant of *A. thaliana* during deetiolation under GL, but the level of free ABA decreased due to active binding. The facts show a violation of GL signal transduction in the absence of CRY1 involving hormones from these groups [89].

At the same time, the deficit of reactive forms of $GA_1 + GA_4$ in *ga4-1* mutant plants of *A. thaliana* caused the decrease in the content of IAA and increase in the level of ZR and ABA compared with original line L*er* [90]. The increase in the deficit of IAA and the accumulation of inactive precursor of gibberellins (GA_9) during the adaptation of *ga4-1* to GL, as well as the data [93] on the interaction of GA and IAA at the level of their biosynthesis, suggest an inhibitory effect of GL on the synthesis of gibberellins on the level of β-hydroxylase.

CONCLUSIONS

In conclusion, it should be noted that GL, along with other portions of the visible region of the electromagnetic radiation, carries information about the environment to the plants. It is the factor that regulates the morphology of cells, tissues, and organs; the processes of photosynthesis, respiration, and growth; and the duration of the stages of plant ontogenesis.

The number of photoreceptors that are in an active state is an important component of light signaling, which is capable of signal transmission. Lifetime of the active state of photoreceptor involved in signaling is limited due to the return of the chromophore to standard state and/or due to degradation of the photoreceptor in the state activated by illumination. It was shown that the time of half-life of CRY1 and CRY2 signaling transmission state is, therefore, between 5 and 16 minutes [94].

From the standpoint of modern ideas about the functioning of photoreceptors, one can assume the simultaneous participation of several photoreceptors (CRY1-2, PHOT1-2, ZTL / FKF1 / LKP2, PHYA-B, etc.) in the regulatory role of GL that are differently activated by the illumination and interact with each other. In particular, the illumination-dependent interaction of CRY1 and PHYB photoreceptors was shown [95]. CRY1 interacts with inactive form of Pr PHYB, but it does not interact with Pfr activated by RL or with chromophore of unbound form of the enzyme. The interaction is also regulated by the light activation of CRY1, Pr PHYB interacts only with the free form of CRY1, but it does not interact with the photostimulated protein. There is a hypothesis that the interaction of PHYB/CRY1 in plants starts a tuning of reactions to the action of light of different spectral composition at RL/FRL and BL/UV-A. GL absorbed by cryptochromes and phytochromes, especially by PHYB, causes a change in the state of photoreceptors—it inactivates cryptochromes and activates phytochromes.

The induction of expression of *CHS* gene (CHS is the first enzyme on the biosynthetic pathway of flavonoids and anthocyanins) reduces in *phyA phyB* mutant, indicating the need of phytochromes for full induction of *CHS* gene by CRY1. The observed lack of GL action on the level of *CHS* expression is believed to be the result of interference between the reduced level of CRY1 activity and elevated levels of active Pfr [94]. Since CRY1 and PHYB absorb GL, these receptors can be used to adjust the plant response to changing ratio of BL/GL in the environment [70].

HRB1 (HYPERSENSITIVE TO RED AND BLUE1) protein was identified among the components of the lower level of photoreceptors in *A. thaliana* [96], which is localized in the nucleus and belongs to the family Di19 (Drought induced 19). The activity of HRB1 is required for the induction of *PIF4* expression by RL and BL. HRB1 and PIF4, participating together in the regulation of reactions by RL and BL, may be the links where the chains of signal transmission by RL and BL cross. The same mediator can modify the GL signal transduction by photoreceptors, since GL increased the content of PIF4 [3].

There is proof of the possible interactions between UVR8 and cryptochromes [97]. UVR8 is required for the accumulation of transcripts of genes included in UV-protection, oxidative stress, and hormone signal transduction. Under the natural irradiance with UV-A, UVR8 probably interacts with UV-A/BL signaling pathways in order to reduce the level of the transcript initiated by UV-B, and to accumulate PDX1 protein (PYRIDOXINE BIOSYNTHESIS1). Pre-irradiation with GL (530 and 570 nm), unlike RL, did not increase the resistance of the photosynthetic apparatus to UV radiation [98], which may be due to the inactivation of cryptochrome.

The inclusion of one or another photoreceptor in combined light stream will depend on the intensity of GL. GL may reduce the effectiveness of BL in the regulation of processes through receptors that bind flavins. The duration of reversion in the light and in the dark will vary depending on the number of flavin groups in a molecule of the receptor (1 for CRY1-2 and ZTL/FKF1/LKP2 or 2 for PHOT1-2) [43, 94] and, therefore, the state of the receptor at any given time will also vary.

This representation explains the reaction of plants of different levels and their focus in response to the action of GL. In addition, there is the opportunity to participate in the regulatory function of GL and little-known photoreceptors, containing thioflavine cofactors [62].

The impact of GL on energetic processes may be further realized through the other pigments absorbing medium-wavelength region of PAR [6, 63–69].

Generalization of the entire data enables us to represent the possible ways of GL signal reception and transduction in plants in a single branched chain. GL affects the processes occurring in plants through the regulatory pigments (PHYA-B, CRY1-2, PHOT1-2, ZTL/FKF1/LKP2, and/or unknown specific GL receptors) and other pigments that absorb medium-wavelength region of PAR (chlorophyll *a* + ascorbate, phycobilins, carotenoids, secondary carotenoids, anthocyanins, betalains, cytochromes). Photosynthetic pigments implement the energy action of GL on the metabolic processes. Excess GL is absorbed by secondary carotenoids, anthocyanins, and betalains.

Regulatory pigments trigger a cascade of secondary messengers on GL that activate the genome (nuclear, chloroplast, mitochondrial) and control the activity of the processes of plant life.

The reverse effect of the products of metabolism (photosynthesis and respiration) on the state of the photoreceptors is possible. For example, the photochemical activity of small metabolites, including NADPH, NADH, and ATP, serves to maintain the photoreduction of CRY [99] as a GL receptor, whereas the reverse reaction of flavin dark reoxidation in the protein of cryptochrome of *A. thaliana* (AtCRY1) may be carried out with molecular oxygen [100].

The regulatory function of GL is implemented ahead of its energy function, since the GL signal activates the network of secondary mediators through PHYA-B, CRY1, and other GL receptors that absorb light with a wavelength of 515–553 nm, as well as the hormonal system of regulation, including a program of plant photomorphogenesis coupled with the formation of the photosynthetic apparatus.

The growth and development of plant structural elements of different levels (subcellular, cellular, organ, organism) determine donor-acceptor relations between them and affect the intensity and direction of metabolism.

The ability to absorb GL allows plants to fully assess the lighting conditions and to respond adequately to the changes in their phytocenosis during the day or season. The mechanisms of stomata movement, germination, and circadian rhythms are not by chance controlled by the ratio of GL/BL [24, 25, 39, 54]. GL is especially important in the early stages of plant ontogenesis, since the correct evaluation of light conditions enables the turning on of an adequate development program for the regulation of the size and morphological structure of the seedling.

Further study on the mechanisms of GL action on plant life will enhance the understanding of photoregulatory and photobiological processes of the organisms.

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