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UV-A/BLUE-LIGHT RESPONSES IN ALGAE

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INTRODUCTION

All life on earth depends on light. A variety of photoreceptors capture the light for a wide range of reactions. Photosynthetic organisms absorb the light necessary for energy transformation and charge separation facilitating photosynthesis. In addition to the bulk pigments there are a great diversity of photoreceptors present in minute concentrations that control development, metabolism and orientation of plants und microorganisms. (Shropshire and Mohr 1983, Senger 1987a, Kendrick and Kronenberg 1994). Based on its spectral absorbance, the well-studied phytochrome system acts in the RL region as well as in the UV-A/BL region where the above mentioned reactions are mediated by a variety of photoreceptors whose natures are largely unknown.

Phyllogenetically the UV-A/BL photoreceptors seem to be more ancient pigments that eventually were replaced by the phytochrome system. However, there are many reports that suggest a coaction between the UV-A/BL receptors and the phytochrome system. In several cases the UV-A/BL activation is the prerequisite for the phytochrome reaction (for a review see Mohr 1994). Historically it was the German botanist Julius Sachs who first discovered in 1864 that phototropism in plants was due to BL reactions. It took over 70 years until Bünning (1937) and Galston and Baker (1949) rediscovered the BL response. Since then, an ever-increasing attention has been paid to this effect.

Two international conferences in 1979 and 1983 have been entirely dedicated to the BL phenomenon (Senger 1980 and 1984). In this contribution, the general aspect of UV-A/BL responses and especially the responsiveness of algae will be covered. There are numerous review articles covering the various aspects of UV-A/BL action and the photoreceptors involved (Senger and Briggs 1981, Kowallik 1982, Richter 1984, Senger 1987a, Senger and Lipson 1987, Galland and Senger 1988a and 1988b, Galland and Senger 1991, Galland 1992, Gualtieri 1993, Kaufman 1993, Senger and Schmidt 1994).

GENERAL ASPECTS OF UV-A/BLUE-LIGHT EFFECTS

The best, and easiest, approach to study UV-A/BL effects is action spectroscopy. Action spectra calculated from fluence-rate response curves for an array of wavelengths provide both absorption

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Abbreviations: ALA = 5-aminolevulinic acid; BL = blue light; Chl = chlorophyll; LHC = light-harvesting complex; LIAC = light-induced absorbance change; RL = red light;

characteristics of photoreceptors involved and thresholds of the given responses (Schäfer and Fukshansky 1984, Galland 1987). Out of numerous effects, we present a selection of action spectra that document that UV-A/BL responses can be observed in higher plants, ferns, mosses, algae, fungi and cyanobacteria (Fig. 1). The variety in the shape of the action spectra indicates that UV-A and BL must excite a number of different photoreceptors. Nevertheless, it is obvious that peaks around 370, 450 and 480 nm are typical. Documentation in the UV region, especially below 350 nm, is still insufficient, because in many laboratories light sources and filters to produce the desired wavelength are not available.

Photomorphogenic responses are observed throughout the entire spectral region; ranging form UV-B to far-red light (Fig. 2). Therefore, the coaction between photoreceptors has to be expected in plants growing under a natural light regime. Indeed, coactions between UV-B and UV-A on the one hand (Fernbach and Mohr 1992, Caldwell et al. 1994) and UV-A/BL and phytochrome on the other hand (Mohr 1980 and 1994) have been reported. The obvious variety in UV-A/BL effects is accompanied by an even wider range of intensities evoking these effects (Fig. 3). This range covers at least 12 orders of magnitude and thus, in the natural environment, weak moon light, as well as strong sun-light, can trigger UV-A/BL responses.

Although action spectroscopy is a straight forward approach to identify photoreceptors regulating photobiological responses, several points have to be considered if conclusions are to be drawn with respect to the behavior of a plant in its natural environment. Under daylight conditions, both the fluence rates and the spectral composition of solar light change due to a number of factors such as solar angle (time of day, season), atmospheric turbidity, scattering, cloudiness, the ozone concentration, the plant canopy and, in the case of aquatic plants, the absorption characteristics of their aquatic environment (Caldwell 1981, Jeffrey 1981, Smith 1981). Furthermore, distinct wavelengths of the solar spectrum are absorbed by different photoreceptors simultaneously. Thus, the final response of a plant to the light environment is the sum of reactions influenced by the factors listed above and can hardly be mimicked in the laboratory.

The Nature of UV-A/Blue-light Receptors

Non-photosynthetic responses of plants to light are regulated via a variety of photoreceptors encompassing UV/BL receptors (Dörnemann and Senger 1984, Galland and Senger 1991, Senger and Schmidt 1994), phytochrome (Pratt et al. 1990, Quail 1991, Furuya 1993), rhodopsin (Foster et al. 1984, Hegemann et al. 1991, Gualtieri 1993) and phycochromes (Bogorad 1975, Björn and Björn 1976). Phytochrome has been well characterized on the protein and gene level. The present knowledge about UV-A/BL receptors, by contrast, still derives from physiological investigations on UV-A/BL responses, analyses of photoreceptor mutants, chemical analyses of pigments, characterization of the optical properties of putative chromophores, in particular light-induced absorbance changes (LIACs), and the elucidation of the signal transduction chain (Galland and Senger 1988a and 1988b, Galland 1992, Liscum and Hangarter 1991, Kaldenhoff et al. 1993, Kaufman 1993, Palmer et al. 1993a and 1993b).

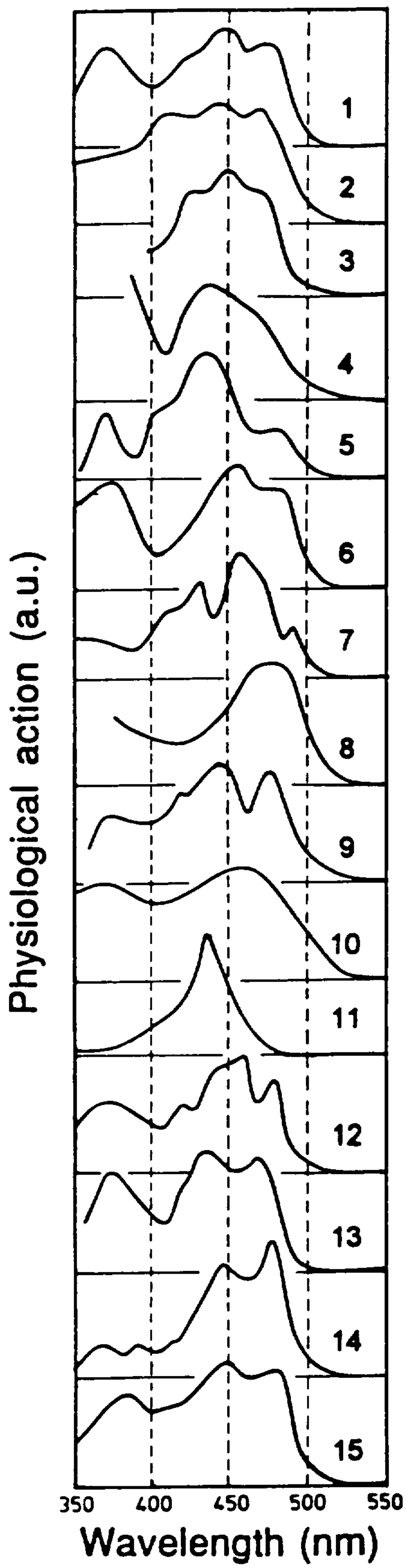

Fig. 1. Action spectra displaying the widespread distribution of UV-A/BL-regulated physiological processes among plants and fungi. (1) Phototropism of *Avena sativa* coleoptile, 10° and (2) 0° (Shropshire Jr. and Withrow 1958); (3) light-induced absorbance change (LIAC) in *Brassica oleracea var. botrytis* (Widell et al. 1983); (4) photoinactivation of indole acetic acid in *Pisum sativum* (Galston and Baker 1949); (5) germination of spores of the fern *Pteris vittata* (Sugai et al. 1984); (6) chloroplast rearrangement in the moss *Funaria hygrometrica* (Zurzycki 1967); (7) hair whorl formation of *Acetabularia mediterranea* (Schmid 1984); (8) cortical fibre reticulation in *Vaucheria sessilis* (Blatt and Briggs 1980); (9) formation of 5-aminolevulinic acid in *Chlorella protothecoides* (Oh-hama and Senger 1978); (10) carbohydrate decrease in *Chlorella vulgaris* (Kowallik and Schänzle 1980); (11) DNA-photoreactivation in *Anacystis nidulans* (Saito and Werbin 1970); (12) perithecial formation in the fungus *Gelasinospora reticulispora* (Inoue and Watanabe 1984); (13) photoreactivation of nitrate reductase in *Neurospora crassa* (Roldan and Butler 1980); (14) carotenogenesis in *Neurospora crassa* (DeFabo et al. 1976); (15) phototropism in *Phycomyces blakesleeanus* (Lipson et al. 1984).The physiological action is given in arbitrary units (a.u.).

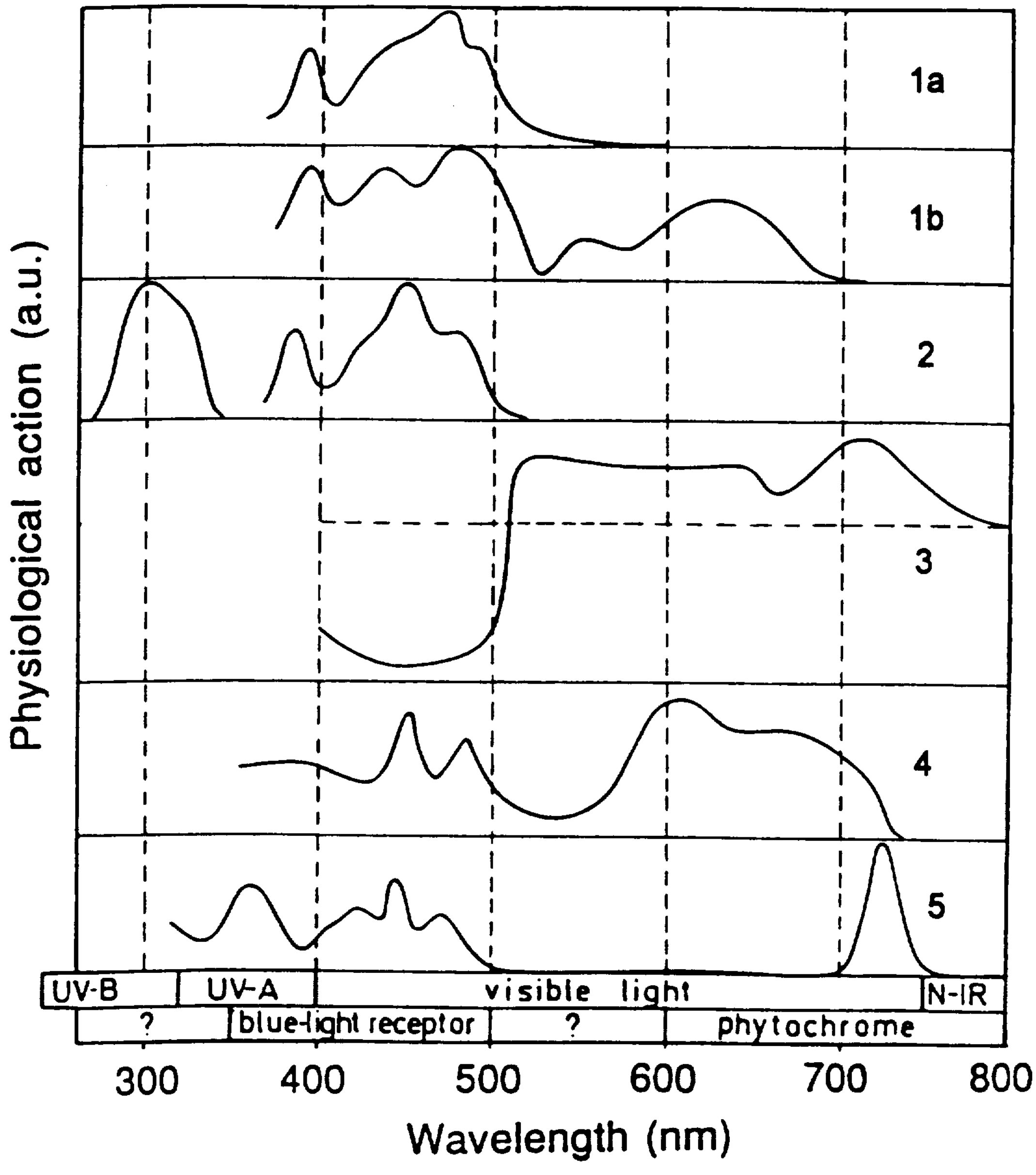

Fig. 2. Action spectra of physiological responses (in arbitrary units, a.u.) depending on the excitation of different photoreceptors. (1a) Chlorophyll accumulation in dark-grown *Scenedesmus* (Brinkmann and Senger 1978a) and (1b) after 2 h preillumination with BL (Brinkmann and Senger 1978b); (2) induction of conidiation in *Alternaria* by UV-B light and its reversion by BL (Kumagai 1983); (3) morphogenetic index L/W (ratio length to width of fern protonema) in *Dryopteris filix-mas* (Mohr 1956); (4) light-induced sensitization to geotropic stimulus in maize roots (Klemmer and Schneider 1979); (5) high-irradiance response (HIR) of light-inhibition of hypocotyl elongation in *Lactuca sativa* (Hartmann 1967).

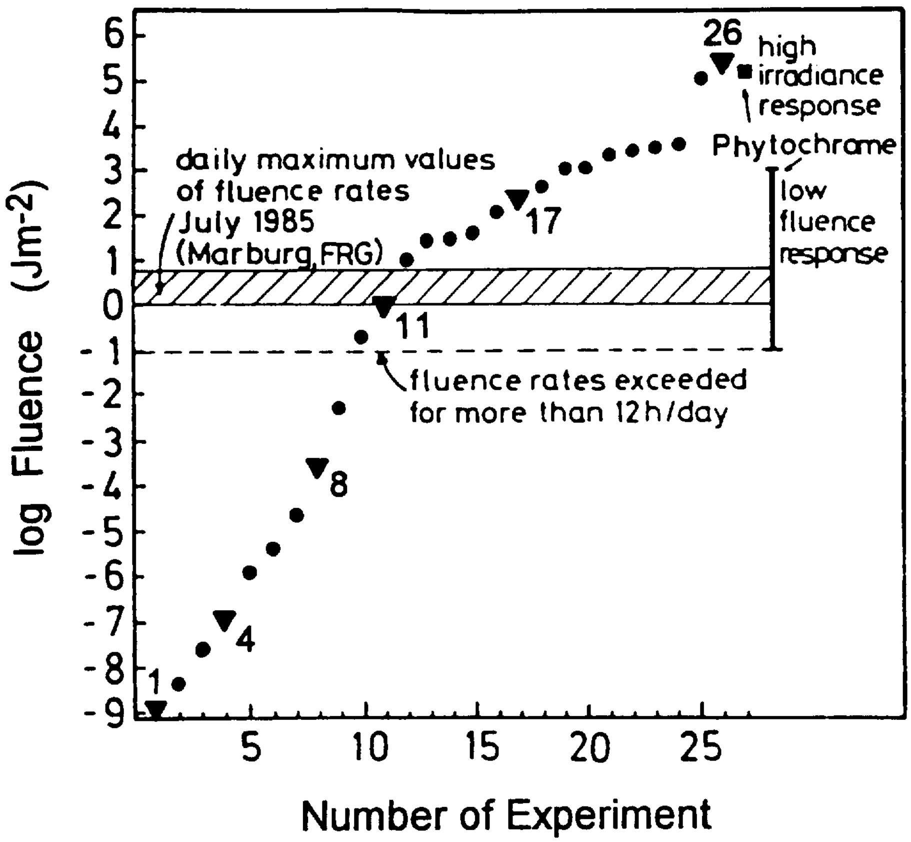

Fig. 3. Range of fluences inducing UV-B-, UV-A- and BL-controlled reactions. Closed triangles indicate the following experiments: (1) phototropism of *Phycomyces*; (4) oxgen uptake of *Chlorella*; (8) anthocyan synthesis in *Sorghum*; (11) inhibition of spore germination in *Pteris vittata*; (17) light-induced absorbance change (LIAC) in membrane fractions of corn and *Neurospora*; (26) adaptation of the photosynthetic apparatus in *Scenedesmus*. A description of the entire set of experiments is provided by Senger and Schmidt (1994)

According to the action spectra of UV-A/BL responses and physico-chemical properties of the putative pigments, pterins (Galland and Senger 1988a) and flavins (Galland and Senger 1991) as well as carotenoids (Zeiger et al. 1993, Zeiger 1994), are favoured to be the chromophores of the UV-A/BL receptors. Analysis of photoreceptor mutants of the fungus *Phycomyces* (Hohl et al. 1992a and 1992b) and investigations on the alga *Euglena* (Brodhuhn and Häder 1990, Schmidt et al. 1990, Sineshchekov et al. 1994) provide evidence for the involvement of pterins and flavins in controlling phototropism and phototaxis, respectively. Reduced Flavin ($FADH^-$) and methenyltetrahydrofolate have already been shown to constitute the chromophores of some DNA photolyases (reviewed by Kim and Sancar 1993). Recently, an interesting contribution was provided by Ahmad and Cashmore (1993), who showed that a protein homologous to the DNA photolyase exists in *Arabidopsis*. However, the association of the native protein with chromophore(s) and photoreceptor function remain to be proven.

In general, three experimental approaches are advisable to elucidate the nature of the UV-A/BL receptors: generation and complementation of photoreceptor mutants (Adamse et al. 1988, Liscum et al. 1992, Chory 1991, 1992 and 1993), development of a LIAC-based purification procedure (Widell 1987, Galland 1992), and the indirect access via the immediate effectors, e.g. G poteins (Schäfer and Briggs 1986, Galland 1991, Terryn et al. 1993, Kaufman 1994).

GREEN ALGAL RESPONSES TO UV-A AND BLUE LIGHT

Since Kowallik (1965) introduced studies on the wavelength-dependent metabolism of *Chlorella* into the field of UV-A/BL research, green algae are among the best studied objects in this field (Senger 1987a). Research in our group has focussed on the unicellular green alga *Scenedesmus obliquus*, particularly on UV-A/BL control of chlorophyll biosynthesis (Oh-hama and Senger 1975, Senger 1987b, Dörnemann 1992), expression of the genes encoding the apoproteins of the light-harvesting complex of photosystem II (Hermsmeier et al. 1991 and 1992) and the development and light-adaptation of the photosynthetic apparatus (Senger and Bauer 1987, Humbeck et al. 1988).

Action spectra of chlorophyll accumulation, synthesis of 5-aminolevulinic acid, respiration, carbohydrate degradation, and accumulation of total cellular proteins (Fig. 4) display the important role of UV-A and BL in regulating fundamental cellular processes in *Scenedesmus*. The absorption characteristics of the UV-A/BL-receptor chromophore(s) are defined by peaks around 390, 450 and 480 nm.

An interesting finding was that, besides the UV-A/BL receptor, a second photoreceptor is present which absorbs at 410 and 650 nm (Fig. 4.2). This violet/RL receptor has a marked lower threshold as compared with the UV-A/BL receptor and operates in an antagonistical manner (compare Fig. 4.1 and 4.2). Activation of the UV-A/BL receptor results in an increase in chlorophyll, the apoproteins of the light-harvesting complexes and their messenger RNAs. The violet/RL receptor reverses these effects (Hermsmeier et al. 1991, Thielmann and Galland 1991, Thielmann et al. 1991). Furthermore, the receptor antagonism dramatically influences the light-adaptation of the photosynthetic apparatus.

Adaptation to BL induces a weak-light (shade) phenotype, i.e., among other things, decreased respiration and photosynthetic capacity, lower compensation point of photosynthesis and increased pigment contents combined with higher light-harvesting capacity relative to electron transport capacity. Cells adapted to RL, by contrast, exhibit a strong-light (sun) phenotype whose characteristics are opposite to those of the weak-light cells (Senger and Bauer 1987, Humbeck et al. 1988).

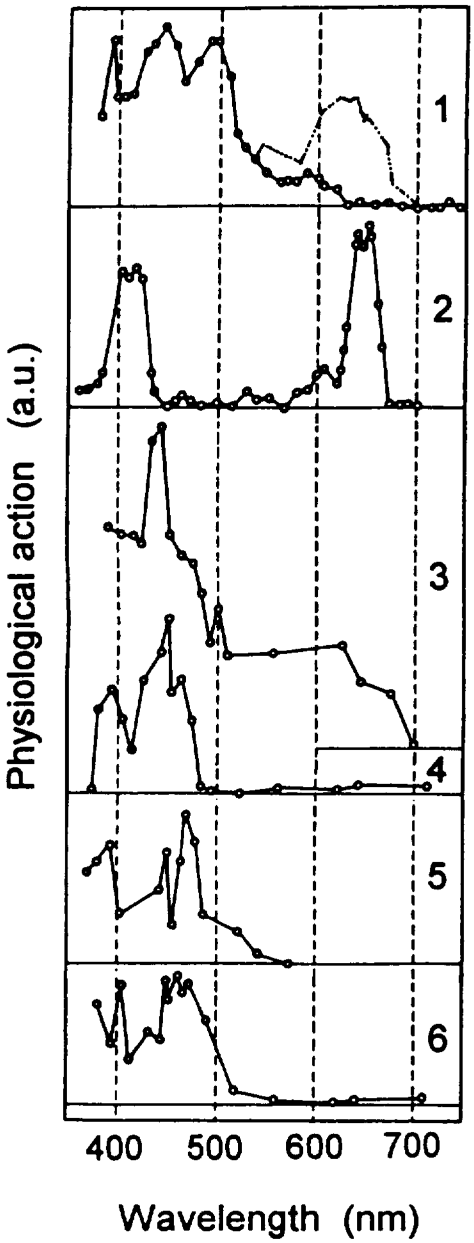

Fig. 4. Action spectra verifying UV-A /BL regulation of fundamental anabolic and catabolic processes in the unicellular green alga *Scenedesmus obliquus*. (1) Induction of chlorophyll (Chl) biosynthesis under high fluence rates (2 mol m^{2} s^{1}; dotted line: after 2 h preirradiation) relative to a dark control (Thielmann et al. 1991, Brinkmann and Senger 1980), (2) inhibition of Chl biosynthesis under low fluence-rate conditions (4·10^{3} mol m^{2} s^{1}) relative to a dark control (Thielmann and Galland 1991), (3) formation of 5-aminolevulinic acid (ALA), the committed step in Chl biosynthesis (Oh-hama and Senger 1975), (4) enhancement of mitochondrial respiration by UV-A and BL, (5) light-induced decrease in total carbohydrates, (6) light-dependent accumulation of proteins (Brinkmann and Senger 1978a).

Considering all these data it can be stated that UV-A and BL regulate numerous essential processes within the *Scenedesmus* cell (Fig. 5). The different biochemical reactions promoted by UV-A and BL finally result in an enhanced photosynthetic efficiency and the formation of components that constitute the photosynthetic apparatus.

Light Requirements of Algae

As in higher plants, the photosynthetic apparatus of algae and cyanobacteria use light between 400 and 700 nm to drive photochemical reactions. To achieve optimum growth of algae and cyanobacteria under laboratory conditions, proper light sources have to be applied for the illumination of autotrophic cultures.

As indicated by the in vivo absorption spectra of selected members of cyanobacterial and algal taxa (Fig. 6), artificial lighting systems should generally emit high portions of BL and RL to saturate photosynthesis. The majority of algal classes contain peripheral light-harvesting antennae that absorb BL and RL due to their contents of carotenoids, Chl *a* and Chl *b* or Chl *c*. In red algae and cyanobacteria, by contrast, phycobiliproteins serve as light antennae. Phycoerythrin and phycocyanobilin, which constitute the chromophores of the phycobiliproteins, extend the absorption range covered by Chl *a* to the green and orange region of the spectrum (Fig. 6.1-6.3). This should be taken into consideration if a lighting system is established for the cultivation of cyanobacteria and red algae. By choosing one or the other type of artificial light sources, specific systematic groups of algae can be enhanced in growth in favour of others.

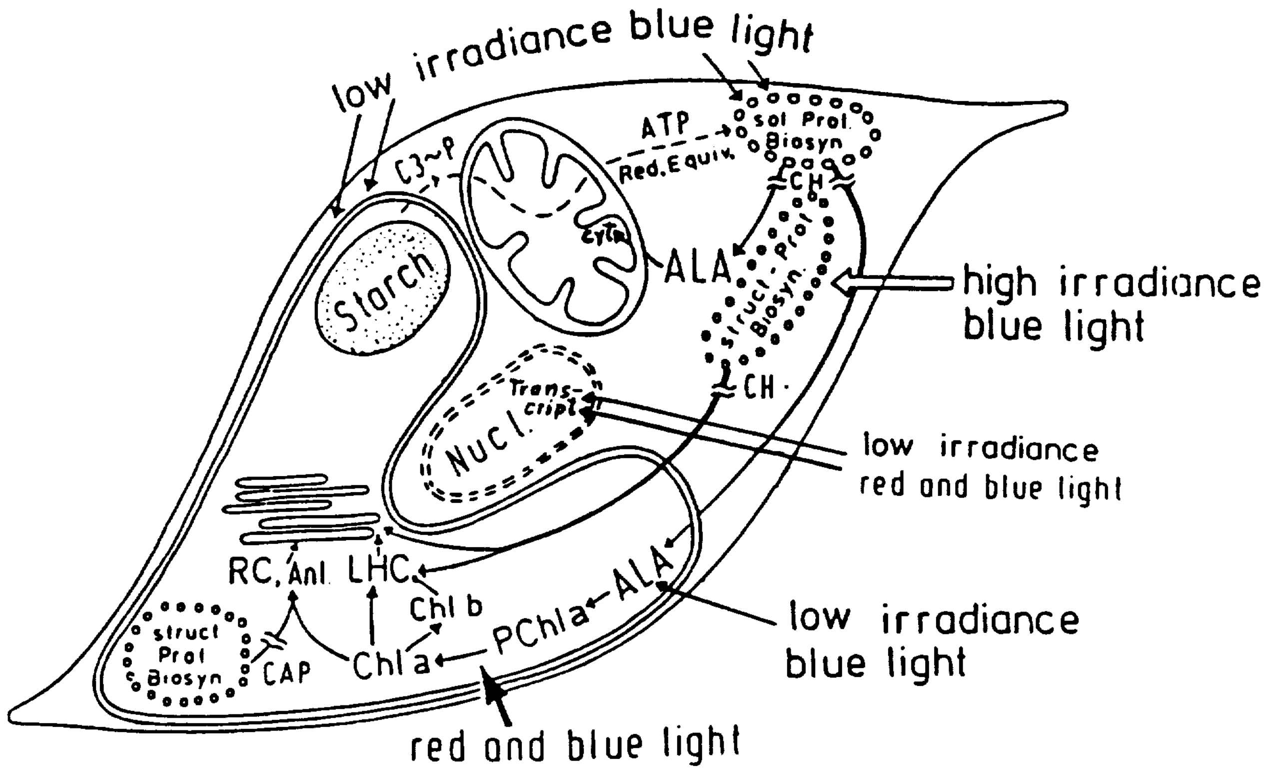

Fig. 5. Target sites of photocontrol of intracellular processes in *Scenedesmus obliquus*. Low- and high-irradiance blue and red light regulate transcription of nuclear genes, e.g. genes encoding the light-harvesting chlorophyll *a/b*-binding proteins, starch degradation, synthesis of soluble and structural proteins, formation of 5-aminolevulinic acid (ALA) and transformation of protochlorophyllide *a* (PChl *a*) into chlorophyllide *a*.

Apart from the importance of light as the primary source of energy, light plays the key role in photomorphogenesis and light-adaptation as described above. Beside the irradiance the ratio of BL to RL determines whether the photosynthetic apparatus is directed towards weak- or strong-light acclimation. During acclimation pronounced changes occur in the molecular organization of thylakoid membranes.

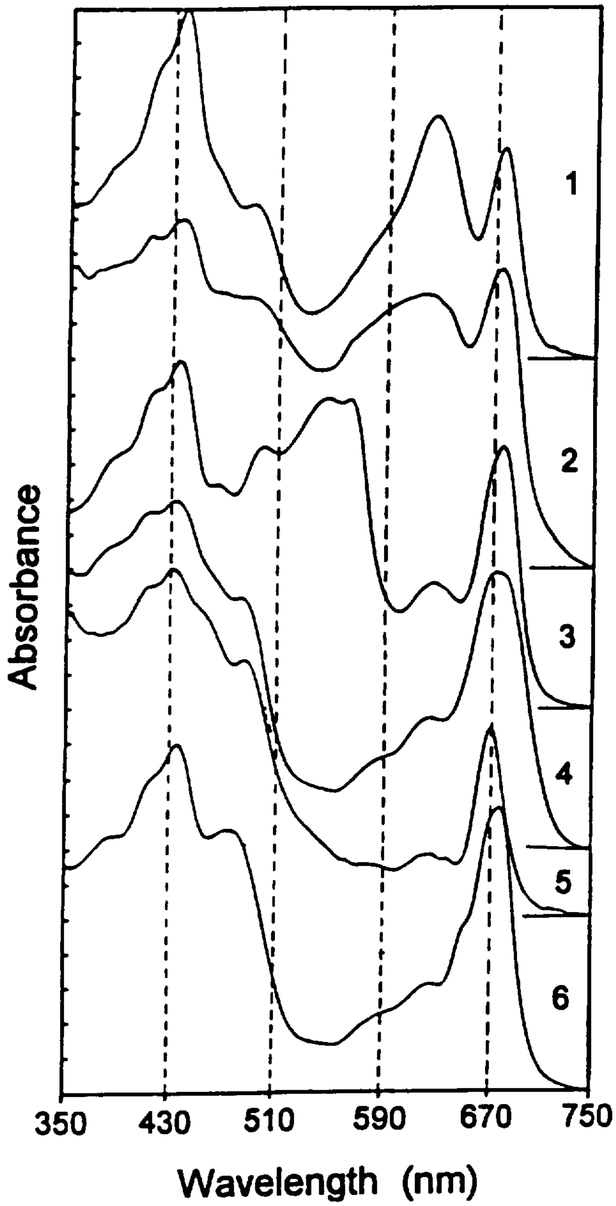

Fig.6. In vivo absorption spectra of the cyanobacteria *Anacystis nidulans* (1) and *Tolypothrix spec.* (2), the red alga *Porphyridium cruentum* (3), *Euglena gracilis* (4), the diatom *Cyclotella meneghiniana* (5) and the green alga *Scenedesmus obliquus* (6).

Therefore, in experiments dealing with the composition of the photosynthetic apparatus, the spectral distribution of the incident light should favour the absorption and excitation of relevant photoreceptors. Attention also has to be given to the intensity of the light source. On one hand, the applied fluence rates must provide sufficient net photosynthesis and, on the other hand, fluence rates inducing photoinhibition or even photodestruction of pigment-protein complexes must be avoided. Therefore, it is recommended to apply irradiance slightly exceeding the light-saturation point of photosynthesis. This ensures optimum growth and saves energy. The light-saturation point is usually determined by plotting photosynthetic oxygen evolution against irradiances. Since light-saturation points vary greatly among different algal species, it is necessary to carry out this procedure for each species of interest.

Practical Applications

The aquatic environment of the algae is characterized by an imbalance of the spectral distribution depending on the type of water, e.g. blue-, green- and orange/red-water seas (Jeffrey 1981 and 1984). A comparison of the spectrum of solar light with the spectrum of a blue-water sea in 5 m depth shows that the spectrum is shifted in favour of shorter wavelengths (Fig.7.1 and 7.2). In the case of laboratory cultures, absorption of water can be neglected since distilled water is used for the preparation of culture media and applied volumes are to small to absorb light significantly. For the set up of experiments which do not aim at daylight simulation, the choice of commercial available lamp types depends only on criteria discussed in the preceding chapters.

Emission spectra of selected lamp types are collected in Fig. 7. Due to their spectral imbalance, common incandescent lamps are fairly useless as a light source for photosynthetic organisms

(Fig. 7.3). Many laboratories use fluorescent lamps because of low running costs, long lifetime, high luminous efficiency and the availability of a great variety of lamp types with different emission properties. However, a substantial decrease in output necessitates replacement after approximately one year. The BIOLUX lamp (Osram, Berlin) simulates solar light to a certain degree (Fig. 7.4) and is recommendable for many biological applications. Because of its balanced spectral emission the BIOLUX lamp is a useful light source for the cultivation of cyanobacteria and red algae which show a high absorption throughout the entire spectrum (confer Fig. 6). The FLUORA lamp (Osram, Berlin) is well suited for cultivation of Chl *a/b*-type plants and algae since this lamp mimics the absorption spectrum of their photosynthetic apparatus (Fig. 7.5).

Fluorescent lamps have high luminous efficiencies but do not emit high irradiances of light. Under certain conditions where high irradiances are demanded, e.g. for the illumination of aquaria deeper than 50 cm, metal-halide or mercury lamps should be prefered to fluorescent lamps. For aquarists a number of mercury-lamp types, e.g. the HQL series (Osram, Berlin; Fig. 7.6) are available which provide both, high irradiances and an unaffected colour of aquatic plants and animals. Xenon lamps also provide high irradiances of light with a spectral emission similar to solar light. However, they emit high amounts of UV-C, UV-B and infra red (IR) and produce ozone which has to be exhausted. Their use requires UV- and heat-absorbing filters which again decrease luminous efficiency and increase costs.

Experimental ecological plant research necessitates sophisticated sunlight simulators which precisely mimic the solar radiation with respect to intensity, spectral balance and direction of light (Warrington et al. 1978, Holmes 1984, Björn 1994, Caldwell and Flint, this volume).

The best approximation of a standard daylight spectrum, so far known, renders a sunlight simulator developed by Seckmeyer and Payer (1993). Daylight simulation is achieved by the combination of 184 lamps of the metal-halide, quartz-halogen, BL-emitting and UV-B-emitting type, filters and reflectors in an appropriate spatial arrangement. Although the growth chamber of this apparatus is laid out for the cultivation of land plants it should be possible to adapt it to the cultivation of algae. However, simulation of fluctuations of the solar spectrum depending on meteorological and astronomical parameters remains an unsolved problem.

CONCLUSIONS

As for higher plants, growth and development of algae depend on light. Besides the light necessary to facilitate photosynthesis, UV-A/BL is of specific necessity for the normal development of algae. Spectral output of artificial light sources should match as close as possible the absorption cross section of the pigments responsible for photosynthesis and morphogenesis. The irradiances of the incident light should not exceed saturating values for photosynthesis to avoid photooxidation. By choosing the appropriate light source one or the other taxonomic group can be enhanced or suppressed in growth and development in comparison to others.

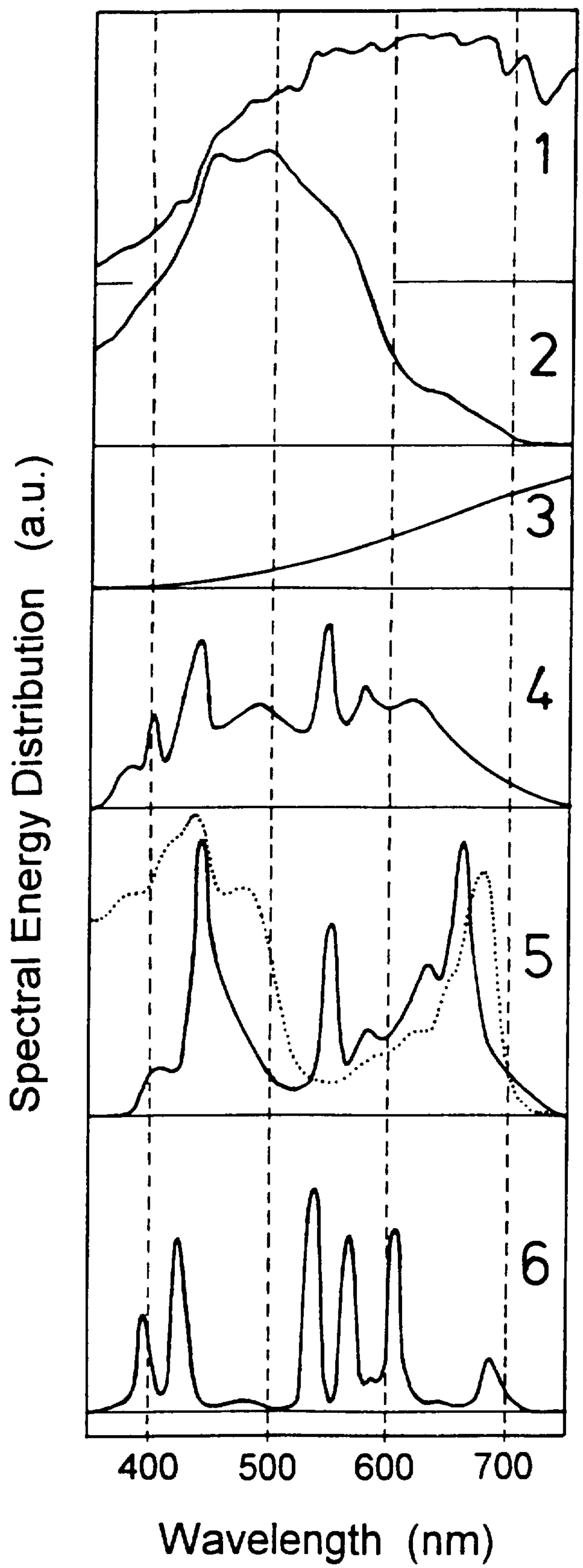

Fig.7. Comparison of the spectral energy distribution of solar light in the air (1) and in 5 m depth of a blue-water sea (2) with the corresponding spectra of technical light sources (3-6). (3) Spectrum of incandescent lamp; (4) fluorescent lamp BIOLUX 72 (Osram, Berlin); (5) fluorescent lamp FLUORA 77 (Osram, Berlin), the dotted line indicates the in-vivo absorption spectra of the unicellular green alga *Scenedesmus obliquus*; (6) mercury lamp HQL DE LUXE (Osram, Berlin).With respect to the spectral emission the BIOLUX light source is suitable to mimic natural daylight, while the FLUORA lamp is a recommendable light source for illuminating land plants and aquatic specimen. The HQL DE LUXE lamp exhibits a high output in the short wavelength range and between 520 and 620 nm and therefore provides maximum excitation of insect rhabdomer cells and retinal cells of mammals. As indicated by (3) incandescent light is not sufficient to cover the spectral range of photobiological processes.

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