Review

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Light emitting diodes (LEDs) applied to microalgal production

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Light-emitting diodes (LEDs) will become one of the world's most important light sources and their integration in microalgal production systems (photobioreactors) needs to be considered. LEDs can improve the quality and quantity of microalgal biomass when applied during specific growth phases. However, microalgae need a balanced mix of wavelengths for normal growth, and respond to light differently according to the pigments acquired or lost during their evolutionary history. This review highlights recently published results on the effect of LEDs on microalgal physiology and biochemistry and how this knowledge can be applied in selecting different LEDs with specific technical properties for regulating biomass production by microalgae belonging to diverse taxonomic groups.

Light in microalgal production

Microalgal biomass is used as feed in aquaculture, bulk food, and as feedstock for food or feed supplements, nutraceuticals, and cosmetics, and has been considered as a promising feedstock for biofuel production [1,2]. Photoautotrophic growth of microalgae requires CO_2, a growth medium containing nutrients, such as nitrogen and phosphorus, and a light source. Under heterotrophic and mixotrophic conditions, many microalgal species are able to use organic matter as a source of carbon and other nutrients. Photosynthesis in photoautotrophic and mixotrophic microalgae can be driven by sunlight or artificial light. Although sunlight is the most cost-effective energy source for microalgal production, artificial light is still economically feasible when biomass is used as a feedstock for high-value products, such as food or feed supplements (e.g., carotenoids and n-3 polyunsaturated fatty acids) or nutraceuticals [1]. Artificial light also provides better regulation of the photosynthetic photon flux density (PPFD; see Glossary), photoperiod, and light spectra in microalgal production, which can result in gains in biomass productivity and quality, two key factors for the success of any agricultural or industrial product [2]. However, the use of artificial light sources comes at a cost, so their

improvement in terms of photosynthetic and electronic efficiency can provide a wider and cheaper array of products obtained from microalgal biomass [2]. This strategy has already been recognized as useful for horticulture [3].

Artificial lighting in microalgal research and production usually involves fluorescence lamps (FLs), which have wide emission spectra, including wavelengths with low photosynthetic activity for certain microalgae [2]. Alternatively, light-emitting diodes (LEDs) can be used [1,3,4]. LEDs are long-lasting (∼50 000 h), mercury-free, and fast-responding (nanosecond scale) artificial light sources emitting nearly monochromatic light at various wavelengths by virtue of solid-state electronics [3,4]. Hence, LEDs can also be applied to adjust the biochemical composition of the biomass produced by microalgae via single wavelengths at

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Glossary

Color rendering index (CRI): indicates how true the color of an irradiated object is revealed by a particular light source to human eyes.

Color temperature (K): denotes the trend of a light spectrum towards bluish or reddish wavelengths and is related to the irradiation spectrum of a heated Planck's black body at a given temperature (K). The human eye perceives a black body heated to 2000 K as having a reddish tint, whereas at 10 000 K a black body has a more bluish appearance.

Luminous efficacy (lm/W): efficiency of electrical power transformation to optical energy as perceived by the human eye. This measure is commonly used to compare light sources. The absorption spectrum of light-harvesting complexes of photosynthetic organisms [11] may differ from that of the human eye [4], and thus luminous efficacy is not a suitable indicator of the quality of a light source for photoautotrophic cultivation. Light sources with the same wattage and the same PCE can have very different luminous efficacy, depending on their spectrum. For conversion of luminous efficacy to μmol photons s^{-1} W^{-1}, see [1].

Photosynthetically active photon flux density (PPFD): amount of photosynthetic active photons in μmol striking a surface of $1 m^2$ in 1 s. The photosynthetically active wavelength range is 400–700 nm. However, algae and plants can be photosynthetically active between 380 and 750 nm. Measurement of the PPFD of light sources with narrow spectra using quantum sensors often causes significant over- or underestimation at certain wavelengths, and correction factors are essential [70,71].

Power conversion efficiency (PCE): ratio between the electrical optical output and input energy ($W_{output(optical)}$/W_{input}) of a illuminant as a percentage. When the absolute spectral irradiance (W m^{-2} nm^{-1}; obtained by radiometric measurements, for example) of an illuminant is known, PCE can be used to estimate the photon flux and photosynthetic efficiency.

White light: light composed of photons of different wavelengths among a broadband spectrum. It is usually evaluated in the human vision context via parameters such as the color temperature, color rendering index, or luminous efficacy.

λ$_a$ and λ$_e$: maximum absorption and emission wavelengths, respectively. λ$_{a\_red}$ and λ$_{a\_blue}$ are absorption peaks within the red and blue light ranges, respectively. λ$_{max}$ denotes the preferred wavelength for optimal growth (see Table S1 in the supplementary material online) or preferred wavelength for a metabolic effect (see Table 1 in the main text), whereas λ$_{min}$ denotes an alternative preferred wavelength that may be suboptimal.

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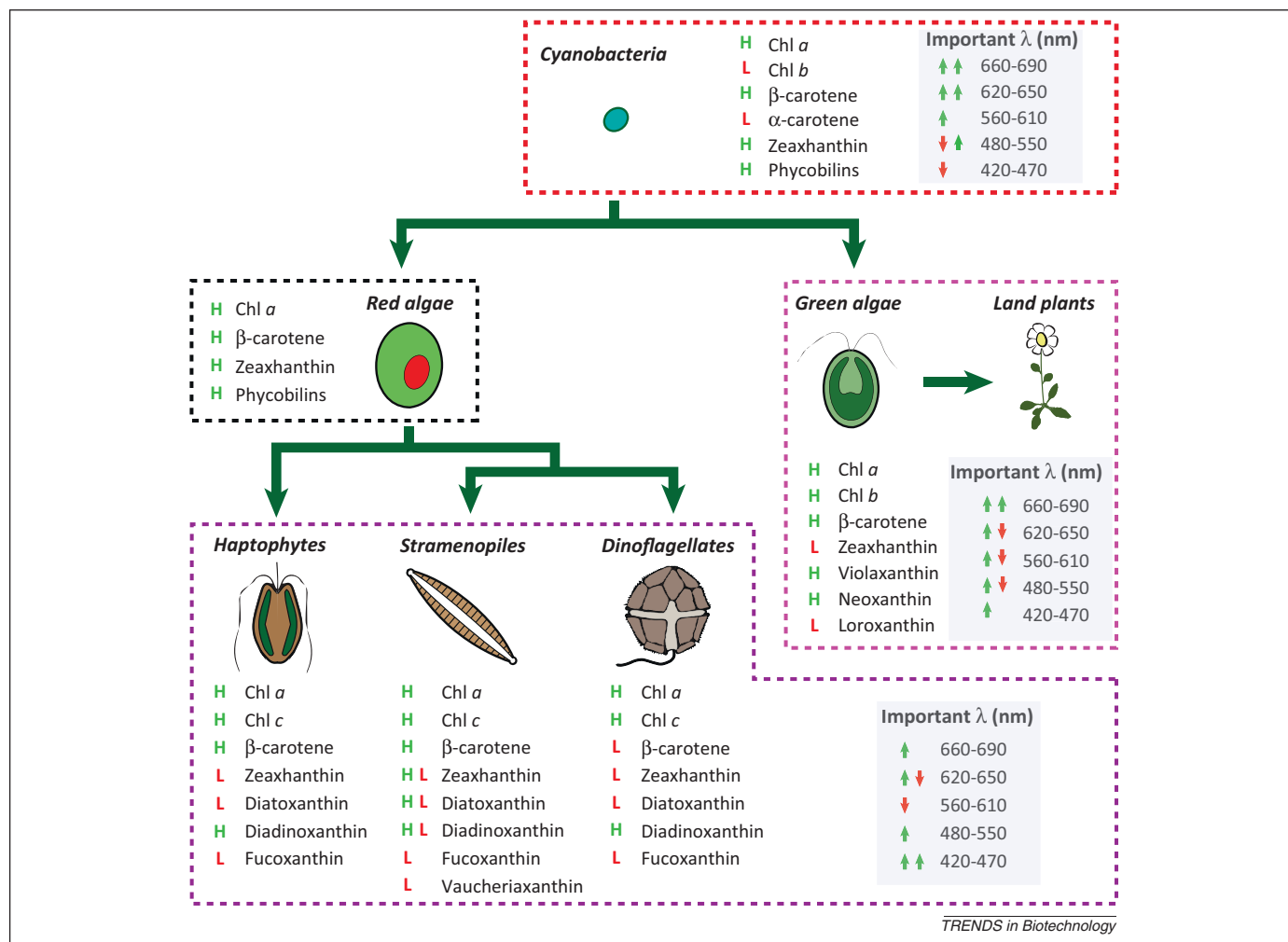
Figure 1. Approximate light requirements of microalgae according to results in Table S1 in the supplementary material, main pigments, and the evolutionary relationships among major microalgal megagroups [12–14]. Abbreviations: Chl, chlorophyll; H, high pigment content; L, low pigment content; H L, variation between high and low pigment contents among species.

different light intensities or pulse light frequencies [5–9]. Exposure of microalgae growing in photobioreactors to different light sources and the economic feasibility of this approach have been discussed previously [1,2,10,11]. However, the use of LEDs to supply specific light ranges for microalgal growth and to obtain high-value biochemical traits has not been reviewed extensively. LEDs will certainly become one of the world's most important light sources [4], so this review provides an overview of the application of various LED types to microalgal production.

Effects of light quality on algal growth

The number of photons at blue or red wavelengths that can be captured by a molecule of chlorophyll in an alga depends on the cellular architecture, pigment composition, and chloroplast arrangement. Interestingly, the evolutionary history of microalgae as purported by Keeling [12] seems to account for the preference of microalgae to grow under either blue ($\lambda \approx$ 420–470 nm) or red ($\lambda \approx$ 660 nm) light (Table S1 in the supplementary material online). This preference correlates well with the evolutionary megagroup of each microalga, which in turn seems to reflect the pigment composition of the light-harvesting complexes in their chloroplasts (Table S1 in the supplementary material online) [13]. As discussed by Keeling [12], a primary

endosymbiotic event between a eukaryote and a chlorophyll-*b*-containing ancestor of cyanobacteria gave rise directly or indirectly to most photoautotrophic eukaryotes (Figure 1). Cyanobacteria, especially those lacking chlorophyll *b*, use chlorophyll *a* ($\lambda_a \approx$ 430 and 680 nm) and accessory phycobiliproteins such as phycoerythrin ($\lambda_a \approx$ 550 nm) and phycocyanin ($\lambda_a \approx$ 620 nm), in light-harvesting protein–pigment (LHP) complexes [14]. As a result, cyanobacteria are able to utilize mostly red, yellow, and green light and, to a significantly lesser extent, blue light [12,15,16].

The first endosymbiotic event with the ancestor of cyanobacteria as the endosymbiont led to the appearance of chlorophytes (green algae) and rhodophytes (red algae) [17]. Red light is crucial for the growth of chlorophytes (and land plants) [13]. However, these organisms are able to utilize blue light more efficiently than cyanobacteria are, probably because of the loss of chlorophyll *b* by many cyanobacterial species [14] and a higher diversity of carotenoids in photosynthetic eukaryotes (Figure 1). As a trade-off, chlorophytes lack the ability to utilize yellow and green light extensively because they lost phycobilins during evolution [14]. Therefore, for chlorophyll-*a*-containing microalgae, major wavelengths are within the range 420–470 nm and/or 660–680 nm, and accessory

wavelengths are located below, between, or above these ranges. Exposure of microalgae to accessory wavelengths ($\lambda_e \approx 500$–630 nm) alone consistently leads to lower biomass production compared to growth under either blue ($\lambda_e \approx 430$–470 nm) or red ($\lambda_e \approx 660$ nm) LEDs [6,12,15,18–24]. Green ($\lambda_e \approx 525$–550 nm) LEDs were often found to be highly unsuitable for microalgae if used without additional light sources (Table S1 in the supplementary material online) [1,22,23,25,26].

Secondary endosymbiotic events involving heterotrophic eukaryotes and green algae gave rise to mixotrophic euglenids and chlorarachniophytes with a pigment composition and most probably light requirements similar to those of the ancestors of their plastids. Conversely, microalgae such as rhodophytes and glaucophytes are probably better adapted to shorter wavelengths (blue, green, yellow) than chlorophytes are because they retained phycobilins during evolution [12].

Cryptomonads and haptophytes (e.g., *Isochrysis*), belonging to the Hacrobia megagroup, and heterokontophytes (e.g., diatoms) and dinoflagellates, belonging to the Stramenopiles–Alveolata–Rhizaria (SAR) megagroup, are assumed to have evolved from secondary endosymbiosis of a heterotrophic eukaryote engulfing a rhodophyte, whereupon most species lost phycobilins. Instead, they developed a higher diversity of carotenoids and acquired chlorophyll *c*, a type of chlorophyll that absorbs strongly in the blue light range [27]. As a result, Hacrobia and SAR algae are usually better equipped for using bluish light compared to cyanobacteria and chlorophytes (Table S1 in the supplementary material online). Serial and tertiary endosymbiosis resulted in other eukaryotic photoheterotrophs (mostly dinoflagellates) with preferred wavelengths probably similar to those of the ancestors of their endosymbionts, although no studies on the light requirements of these microalgae have been found. Therefore, a shared evolutionary history of microalgae as suggested by Keeling's tree of endosymbiotic events [12] may provide information about the light requirements of algae within groups (Figure 1). For further information about pigments and their role in light harvesting for photosynthesis, see work by Cheng and Fleming [28] and Scholes *et al.* [29].

Effects of light quality on microalgal traits

In general, photons with a wavelength of 660–680 nm yield the highest quantum efficiencies in most plants and algae containing chlorophyll *a* ($\lambda_{a\_red} = 680$ nm) and/or *b* ($\lambda_{a\_red} = 660$ nm) [1,11]. The efficiency sharply decreases at longer wavelengths [30,31]. Interestingly, red to far-red light ($\lambda \approx 630$-750 nm) induces high growth rates and smaller cells by accelerating the cell cycle in many microalgae of diverse evolutionary lines [1,16,19,32–35]. However, far-red light can suppress volumetric biomass production when supplementing a broadband light source [34] because it regulates light-harvesting mechanisms in microalgae [35]. In terrestrial plants, far-red light promotes flowering, fruit development, and biomass production, but it can also cause growth arrest due to a complete breakdown of photosynthesis if not applied properly [36].

Red to far-red light can be detected by photoreceptors such as phytochromes in land plants and charophytes, as well as multiple light-sensing photoreceptors in cyanobacteria [37,38]. In free-swimming chlorophytes, no obvious genes encoding phytochromes have been found. Instead, an "animal-like" cryptochrome seems to be the long-sought-after red receptor in chlorophytes, although it is unable to detect far-red light [39]. This multitude of red/far-red photoreceptors in different evolutionary lines strongly indicates that caution must be used when extrapolating how the red or far-red light range is detected and how it regulates growth. Clearly, further research is needed to understand how different photosynthetic organisms detect and respond to this range of the electromagnetic spectrum.

For shorter wavelengths, blue light influences gene expression and several metabolic pathways in algae and plants via photoreceptors such as cryptochromes, phototropins, aureochromes, and neochromes [38–42]. Blue light is, for example, responsible for endogenous breakdown of carbohydrate reserves [43], which may explain why the haptophyte *Isochrysis* sp. T-ISO exposed to blue light and grown in a chemostat displayed lower carbohydrate content than when grown under other wavelengths [44]. However, the opposite or no significant effect has been obtained in green algae grown in batch culture [23,24]. Kim *et al.* found that changing the ratio between red and blue light affected nutrient utilization more than biomass production [22] because of increased enzyme activity such as carbonic anhydrase activation for hydrogen carbonate (HCO_3^-) uptake [45] or nutrient uptake due to activation of reductases for nitrite, nitrate, and phosphorus utilization [21,43,45,46]. Blue light, most probably via photoreceptors such as phototropins, seems to induce pigment accumulation in several species (Table 1) [7,26,39,46]. Moreover, because the energy of blue photons is higher than that required for photosynthesis [10], blue light might result in nonphotosynthetic quenching (NPQ), generating reactive oxygen species (ROS) [7]. Therefore, to protect the photosynthetic apparatus against ROS, algae and plants accumulate photoprotective pigments (e.g., xanthophylls) [3,7,11,47,48].

Lastly, increased green light content within a broadband light source can increase leaf photosynthesis and biomass production in land plants [3,49,50] because these photons can penetrate through the canopy and promote photosynthesis in leaves located below [12,16,51]. Mohsenpour and Willoughby demonstrated that green light could induce pigmentation in algae [51]. However, further research is needed before drawing a definitive conclusion about the effect of green light on algae.

LEDs for microalgal production

Light quality influences the growth and biochemistry of microalgae, so artificial lighting can be used to manipulate the final biomass for specific uses, particularly for high-end markets. To design an artificial lighting system for microalgal growth, the electronic and photosynthetic efficiency of FLs and LEDs must be considered. On conversion of an electric current to light in LEDs (Box 1) and FLs (Box 2), energy losses occur because of thermal dissipation and inward light reflection and reabsorption, among other factors. Reduction of such inefficiency has resulted in higher power conversion efficiency (PCE) for LEDs

Table 1. Light quality effects on microalgal biochemical composition at specific wavelengths

Light	λ_{max} (nm)	Alga	Effects	Refs
Blue	460–475	*Arthrospira platensis* (syn. *Spirulina platensis*)	Lowest chl and phycocyanin content in biomass compared to yellow, green, red, and white LEDs	[16]
	440–470	*Chlorella* sp.	Higher lipid content in biomass compared to red (650–680 nm) LEDs	[19]
	500	*Chlorella sp.*	Blue light induces slightly higher lipid production compared to red light	[46]
	470	*Dunaliella salina*	β-Carotene and lutein accumulation when blue light was supplemented with red (660 nm)	[7]
	470	*Haematococcus pluvialis*	Accumulation of red pigments	[20]
	380–470	*Haematococcus pluvialis*	Astaxanthin accumulation	[26]
	NA	*Isochrysis* T-ISO	Higher protein content and lower carbohydrate and chl content per cell compared to white FLs	[44]
	NA	*Isochrysis galbana*	Higher DHA and phospholipid content compared to red LEDs under intermittent light (f = 10 kHz)	[72]
	475	*Nannochloropsis oceanica* CY2f	Blue and red ($\lambda_e \sim$630 nm) LEDs showed highest EPA content in biomass compared to FLs and white and yellow LEDs	[73]
	470	*Nannochloropsis* sp.	Highest palmitoleic acid and lowest EPA content compared to red, green, and white LEDs under phototrophic conditions; highest total FAMEs per dry weight under blue, green, and white light, lowest under red when grown mixotrophically; similar FAME contents under phototrophic conditions	[6]
	450	*Nitzschia* sp.	Highest chl content compared to red (650 nm) and yellow (590 nm) LEDs	[74]
	NA	*Phaeodactylum tricornutum*	Lager pool of xanthophyll cycle pigments and higher chl *a* content compared to red and white LEDs (low light conditions)	[42]
	470	*Tetraselmis suecica* F&M-M33	Higher chl accumulation compared to cool white FLs and red, green, and blue LEDs; higher carbohydrate content for cells grown under blue compared to red LEDs	[23]
Green	NA	*Chlorella vulgaris*	Higher chl accumulation compared to blue, yellow, orange, and red broadband light spectra	[51]
	550	*Nannochloropsis* sp.	Higher AA content under phototrophic conditions compared to FLs and red and white LEDs	[6]
Red	660	*Botryococcus braunii* Bot-144	Evidence of higher carotenoid/chlorophyll ratio compared to blue and green LEDs	[25]
	660	*Chlorella* sp.	Highest biogas production compared to yellow, blue, and white LEDs	[5]
	660	*Mychonastes homosphaera* (syn. *Chlorella minutissima*)	Increased C18:2 and decreased C18:3 content in FAME; no fatty acid changes between FLs and white LEDs; total FAMEs unaffected among all light sources	[57]
	680	*Nannochloropsis* sp.	Higher oleic acid content compared to blue, green, and white LEDs under phototrophic conditions	[6]
	NA	*Tetraselmis suecica* F&M-M33	EPA content increased under red light compared to blue, green, and white LEDs	[23]
Far-red	NA	*Dunaliella salina* (syn. *D. bardawil*)	Higher carotenoid levels compared to cells grown under FLs	[34]

Abbreviations: AA, arachidonic acid; chl, chlorophyll; EPA, eicosapentaenoic acid; FAME, fatty acid methyl ester; FL, fluorescent lamp; NA, spectrum not available or broadband spectrum.

(up to 50%) [4] compared to gas-discharge lighting technologies such as FLs (~30%) (Table S2 in the supplementary material online) [52,53].

At present, cool white phosphor-converted-LEDs (pc-LEDs) yield the highest PPFD per input wattage (PPFD/W) among white LEDs and can be highly photosynthetically active because of their blue emission peak ($\lambda_e \approx$ 440-460 nm) [54], which almost perfectly fits the blue absorption spectrum of LHP in many plants and algae [11,55,56]. Both FLs and pc-LEDs emit light within the range of photosynthetically important long wavelengths ($\lambda_e >$ 650 nm), whereas most color-mixed-LEDs (cm-LEDs) display a sharp decrease in light emission at shorter wavelengths [4]. Furthermore, white pc-LEDs and FLs emit a broad spectrum of light with high photon release in the blue and green spectral ranges that decreases at $\lambda_e >$ 650 nm. pc-LEDs and FLs have similar emission spectra, so pc-LEDs might be well suited for FL replacement within the same color temperature range without causing significant changes in algal growth rates and biochemical properties.

This replacement would lead to more competitive energy usage for biomass production (Table S2 in the supplementary material online) [1,55,57]. Nevertheless, unlike FLs or pc-LEDs, single-color LEDs usually have higher PCE because they can emit at specific wavelengths without the use of phosphor layers and thus avoid losses (>30%) for conversion of higher- to lower-energy photons [4]. However, single-color LEDs emitting within the green–amber light range often have very low PCE, a problem known as the green gap or green–yellow gap [58].

In addition, more photons are usually released by LEDs emitting at longer wavelengths (e.g., red), resulting in higher PPFD/W ratios than for LEDs emitting at shorter wavelengths (e.g., blue) [1], because blue photons are more energetic than red photons. Specifically, red (λ_e = 660 nm) LEDs can emit double the number of photons that blue LEDs emit, whereas green LEDs emit approximately three times fewer photons than red LEDs do [5,18,58–60]. At face value, these results suggest that 660-nm red LEDs are able to sustain biomass growth with the highest energy

Box 1. How LEDs work

LEDs are semiconductor devices consisting of a positive (P doped) layer and a negative (N doped) layer (Figure IA). The P layer has an excess of electron holes in the valence band because of the presence of acceptor dopant atoms; the N layer has excess electrons in the conduction band owing to the presence of donor dopant atoms. When N and P semiconductors are brought together, excess carriers diffuse to the opposite side, resulting in a depletion region without free carriers. Application of an opposite voltage allows electrons from the N side and holes from the P side to enter the depletion region and recombine. This recombination corresponds to de-excitation of an electron from the conduction band to the valence band, and a photon with the corresponding difference in energy (energy gap between the bands) can be released. A blue–green

(365–550 nm) InGaN semiconductor has a wider energy gap than an orange–red (560–650 nm) emitting AlGaInP diode or a red–infrared (630–940 nm) GaAlAs chip (Figure IB). Thus, recombination of semiconductor materials controls the wavelengths (color and energy of emitted light). To increase the efficiency, most (high-power) LED chips are built up in heterostructures with a more complex internal structure comprising more than one semiconductor material, which can also include multiple quantum wells. Further information on the theoretical background and application of these techniques is available in the literature [52,54,75,76]. White LEDs can be obtained by combining different LED chips in color-mixed LEDs (cm-LEDs) or by coating single blue chips with a photon-converting layer in phosphor-converted LEDs (pc-LEDs) [4].
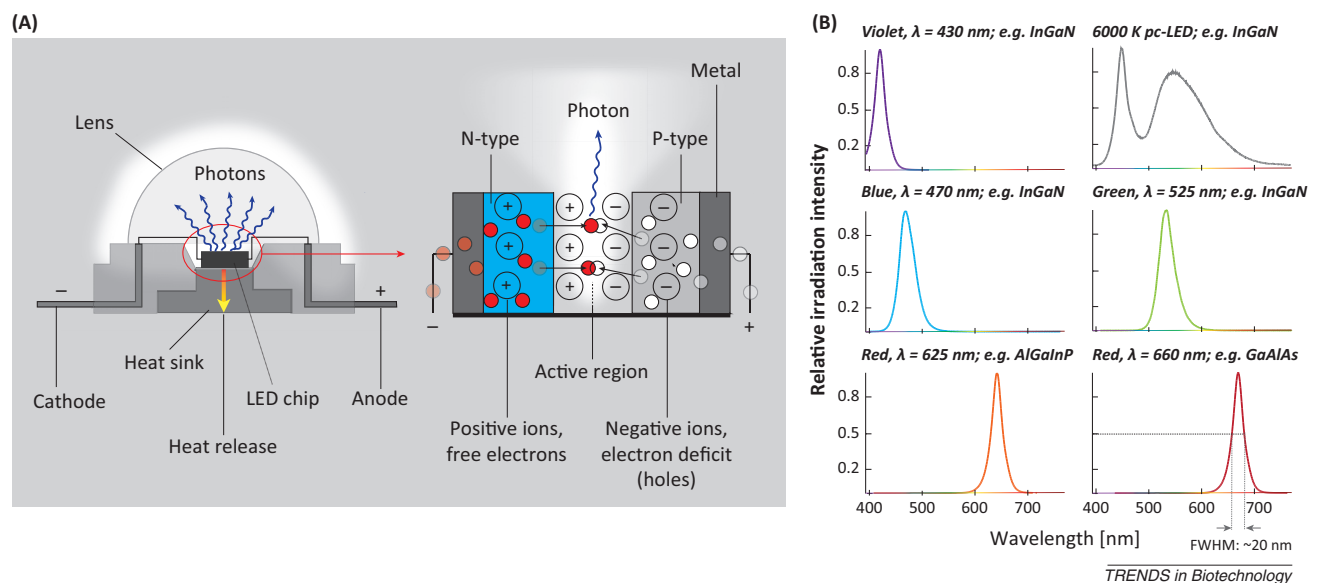
Figure I. (A) Simplified diagram showing how low-power (homostructured) LEDs work. (B) Emission spectra for different LEDs. The full width at half-maximum (FWHM) corresponds to the wavelength difference (usually 20 nm) for which the LED attains 50% of its maximum intensity.

efficiency [1]. However, LEDs with $\lambda_e > 680$ nm also release photons with photosynthetically inefficient wavelengths ($\lambda_e > 695$ nm) [31,61], leading to lower photon utilization by the algae and thus less biomass production per input wattage. Nevertheless, caution is needed because PPFD/W ratios and PCE may vary with the LED manufacturer. Finally, the fast response time of LEDs compared to that of FLs can also be beneficial, because LEDs can be used to grow algae under customized flashing light via pulse width modulation (PWM; Box 3), which increases biomass production [8,62,63] and might allow algae to exceed the proposed maximum photosynthetic efficiency of 17% [1].

Tailored light sources

Spectral matching

To maximize photosynthetic efficiency, all photons released from a light source should be captured by the photosynthetic apparatus of microalgae. A strategy to achieve a high level of light utilization is complete spectral matching of a light source to the photosynthetically active spectrum (PAS). However, this strategy can only yield an approximation because PAS measurement for microalgae is still difficult [30]. Determination of a general PAS for

single taxonomic groups or megagroups, as done for green algae [64], may help to estimate the light quality required for a species belonging to a specific taxon. Absorption spectra of intact cells, however, are easier to obtain and may give a rough idea of the light quality needed for optimal growth. Comparison of the wavelengths of absorption peaks [65,66] and the preferred wavelengths (λ_{max} and λ_{min}) for growth (Table S1 in the supplementary material online) of algae within a given megagroup reveals a relatively good spectral match. However, the wavelength of the highest absorption peak seldom matches the preferred wavelength for optimal growth (either 420–470 or 660–670 nm) of cyanobacteria and green algae. These species usually show better growth and biomass production under 660-nm LEDs (Table S1 in the supplementary material online), whereas maximum absorption often occurs in the blue range of the electromagnetic spectrum [65,66]. This is because the absorption spectra of cells include the contributions of all cellular components able to absorb or scatter light, which may not necessarily contribute to the light-harvesting processes needed for photosynthesis and thus may mask the true light requirements for growth of a specific microalga.

Box 2. How fluorescent lights work

Electrodes located at each side of an FL are heated to induce emission of electrons into the space in front of the electrodes in a process called thermionic emission (Figure IA) [53]. An electric field is thereby built up and accelerates the electrons until their energy is high enough to excite gaseous mercury atoms, distributed in the space between the electrodes, from the ground stage to a higher energetic level. An excited mercury atom falls back to its ground stage and releases the energy difference by emitting a photon with energy of ∼5.5 eV (8.83×10^{-19} J). This high-energy UV photon can then be absorbed by the phosphor coating on the inside of the tube and is transformed into less energetic visible and photosynthetically active light (380–750 nm or 1.7–3.2 eV).

The energy difference (40–70%) is dissipated as heat, which drastically limits the FL efficiency [53]. Figure IB shows emission spectra for different FL types. The spectra of grow-light FLs have high levels of red light (630–680 nm) matching the chlorophyll *a* and *b* absorption peaks within the red spectral range. Therefore, these FLs can be used in growing photosynthetic organisms, although they are more expensive and less energetically efficient than FLs with major emission at shorter wavelengths (e.g., cool daylight FLs) [10]. The spectra of warm white FLs may not be suitable for growing algae in an energy-efficient manner because a significant proportion of their emission lies outside the major photosynthetic ranges (420–450 and 630–690 nm).
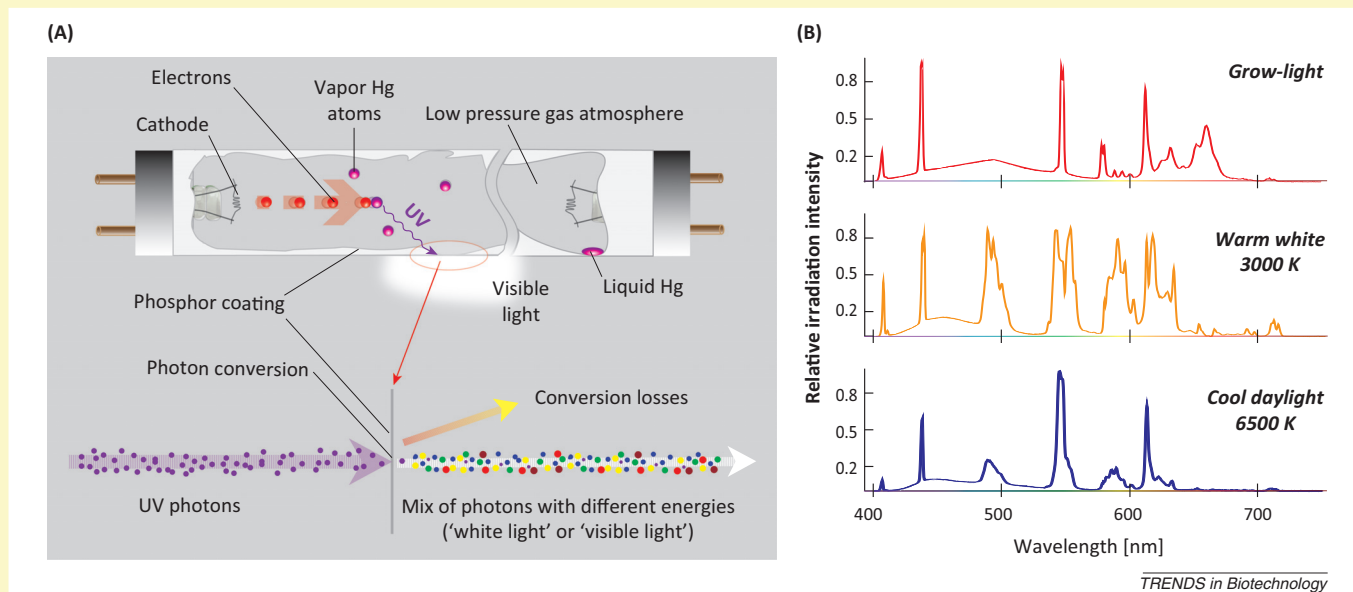
Figure I. **(A)** Simplified diagram showing how fluorescent lamps (FLs) work. **(B)** Emission spectra for different FL types, including grow-lights, warm white FL, and cold daylight FLs.

Light quality and design of LED usage

A tailored LED-based light source for high-volume production at the present state of the art might include pc-LEDs as a good starting point because their broadband phosphor emission at $\lambda_e \approx 560$ nm (Box 1) covers the green, yellow, and amber (500–610 nm) wavelength ranges. Violet–blue (preferably 420–450 nm) and red (660–670 nm) wavelengths can then be further adjusted to the species selected for cultivation. However, white pc-LEDs, especially those with cooler color temperatures, also emit photons with $\lambda_{e\_blue} \approx 440$–460 nm (Box 1), so the levels of blue light available are higher. Moreover, as previously discussed, the taxonomy of the selected microalga may be used to predict the most important LEDs for growth (Figure 1 and Table S1 in the supplementary material online) or production of specific biochemicals (Table 1). Concerning red-to-blue ratios, land plants showed optimal biomass production when red LED light was supplemented with 10–30% blue light [67]. This suggests that similar red and blue ratios may also be suitable for green algae, because their plastids are closely related to those of terrestrial plants in terms of structure, metabolism, and biochemical composition. This assumption seems to be correct, because mixing of red and blue photons in this proportion has often increased biomass production compared to red light alone [7,21,60,68]. Regarding other taxa such as cyanobacteria

and SAR microalgae, higher blue light content may be needed. However, a relative dearth of studies on red-to-blue ratios for these species means that no final conclusion is possible.

The success of increasing biomass productivity via tailored supplemental artificial light depends on environmental parameters for photosynthesis such as PPFD, light path length, CO_2 concentration, pH, macro- and micronutrient availability, and temperature, among other factors [2,35]. For example, nitrogen starvation can cause chromatic adaptation of cyanobacteria and red algae, resulting in degradation of phycobilisomes (phycobilin-containing light-harvesting complexes) and leading to diminished green light absorption [35]. Furthermore, the light path length of the bioreactor can influence the choice of wavelengths coming from a light source. A higher proportion of green–amber wavelengths might be beneficial for green and SAR algae grown in photobioreactors with a long light path or high-density cultures because photon absorption is lower, so they can travel deeper into the culture. In turn, the same light quality might be unsuitable for algae growing in flat panel photobioreactors with shorter light paths or low-density cultures. Lastly, Miao *et al.* concluded that the light saturation point for *Skeletonema costatum* is lower for a suitable than for an unsuitable light source [69]. If this result is confirmed in other species, growth of

Box 3. Dimming of LEDs

The PPFD of LEDs can be controlled by PWM or AM, also referred to as continuous current reduction (CCR) [77,78]. PWM entails the use of alternating states in which the current is completely turned either on or off. At a fixed frequency, the relative duration of the on-period (duty cycle) can be regulated. A low duty cycle of 10% means that the LED is on for 10% of the on-and-off cycle. Alternatively, AM is achieved by reducing the current intensity, which in turn leads to decreased light output [77,78]. The luminous efficacy of the two dimming methods varies, though AM can reach 200% of the nominal efficacy of an LED provided by the supplier when dimmed to 10% of its nominal current. Conversely, at the same dimming level, PWM provides only 70% of the nominal efficacy [77]. AM dimming can be used to prevent photoinhibition during early growth stages because photons are emitted continuously over time at low PPFD. By contrast, PWM-dimmed LEDs emit almost all photons within the LED capacity in a short duty cycle of flashing light, during which microalgae can be exposed to the fully available PPFD [8]. Because photosynthesis does not require continuous lighting [8,62] and microalgae can display satisfactory photosynthetic rates even if the duration of the dark cycle is increased [62], PWM may be used as an effective tool for controlling microalgal growth. In addition, an increase in the instantaneous maximum PPFD within the duty cycle of flashing LEDs by increasing the voltage (overloading) and/or the amount of LEDs will probably not result in photoinhibition and the released photons may penetrate deeper into highly concentrated algal cultures, increasing biomass productivity with lower electrical power consumption [8]. However, both dimming methods can shift λ_e by ~10 nm [77,78] and may change the photon capture when these peaks move towards or away from the optimal LHP absorption range, thus affecting microalgal growth. It is questionable which dimming method produces the highest biomass per input energy, because both have the aforementioned advantages and disadvantages. High-frequency PWM with AM-controlled LEDs may be implemented to reduce wavelength shifts and combine the advantages of both methods [78].

microalgae at lower PPFD with lower energy consumption could be possible if tailored light sources are selected for specific microalgal strains, growth phases, or photobioreactors.

Concluding remarks and future perspectives

Over the last few years, the prices of LED-based lamps have significantly decreased; nevertheless, LED lighting systems are still four times more expensive than FLs on average. However, this higher initial cost can be offset by the longer lifetimes and often better energy efficiency of LEDs compared to FLs. LED lighting technology is thus a feasible option for microalgal cultivation, in particular when supplemental light is needed for faster production of biomass and accumulation of specific biochemical components. As a result, research on microalgae grown under LEDs of different colors has strongly increased over the last 2–3 years. However, the combined application of different LEDs has seldom been studied, especially for LEDs emitting between 500 and 630 nm or above 700 nm (far-red region). Unfortunately, in many studies that used white LEDs, information about the emission spectra used is rarely mentioned, so meaningful comparisons are not possible. Moreover, optical density measurements for biomass determination in experiments with microalgae under different light qualities might be prone to error because the cell size and pigment composition can strongly change with light quality. Measurements of the PPFD of LEDs with narrow bandwidths using quantum sensors may also lead

to errors because the responses of these sensors vary across the photosynthetically active range (400–700 nm). Thus, research on the application of LEDs in microalgal production should use properly calibrated spectroradiometers whenever feasible. Despite these problems, future research on LED use is promising and may lead to higher energy efficiency for indoor microalgal cultivation and improved reliability of research on the light requirements of biological and molecular processes in photosynthetic organisms. Furthermore, cultivation of microalgae in a highly energy-efficient manner can be envisaged using dimmed LEDs controlled by a combination of high-frequency PWM and amplitude modulation (AM) (Box 3). This application would require a greater number of LEDs to maintain the PPFD needed for cultivation. Nevertheless, because LEDs are not fully exploited when dimmed, heat generation is reduced, prolonging the lifetime of LED modules and possibly rendering LED cooling unnecessary, which are two critical factors for successful application of LEDs in microalgal production.

Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.tibtech.2014.06.001.

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