



Estimating the quantum requirements for plant growth and related electricity demand for LED lighting systems

Marc Schmierer¹ · Holger Brueck² · Folkard Asch¹ · Joachim Sauerborn¹

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Abstract

Indoor plant production systems with artificial lighting are considered an emerging technology contributing to biomass-based value webs. The viability of this concept greatly relies on the energy requirements (ER, Watt) for lighting. We estimated the ER for plant growth by calculating the conversion efficiency of electricity to light of solid-state light-emitting diodes (LED) and the quantum requirements for plant growth of a fictional plant stand producing 2500 g of dry weight per m² of ground during 100 days, representing a high productivity benchmark of field crops. The quantum output ($\mu\text{mol s}^{-1} \text{W}^{-1}$) of eight LEDs of different colours varied between 0.78 for green and 2.54 for deep red. Uncertainty in the H⁺ demand for ATP synthesis during photosynthesis, the relative portion of photorespiration and the fraction of light intercepted by plant canopies (f_{abs}) were considered in a pessimistic (PA) and optimistic (OA) approach of calculation of ER. Cumulative ER were 606 and 265 kWh m⁻² for the PA and OA scenarios. The energy conversion efficiencies in the PA and OA scenarios were 2.07 and 4.72%. Estimates of energy savings by suppressing photorespiration and increasing f_{abs} vary between 24 and 38%. The peak daily ER were 9.44 and 4.14 kWh in the PA and OA scenarios. Results are discussed in the context of the design of lighting in indoor plant production systems and commercial greenhouses where natural fluctuation in solar radiation could be balanced by dimmable LED panels.

Keywords LED efficiency · Radiation use efficiency · Indoor plant production

1 Introduction

The 8.5 bn people living on earth in 2030 as projected with the medium fertility variant by the United Nations (2019) will aggravate the threat of food shortage. Climate change (Lobell et al. 2008), regional shortfall of freshwater availability (Falkenmark et al. 1997), and the foreseeable decline in fossil oil (OECD/IEA 2011) and high-grade rock phosphate resources (Cordell et al. 2009; Gilbert 2009) will both amplify food insecurity and challenge presently existing concepts of food production. Rice, wheat, maize, and barley form the backbone of the global food processing value chain, and the Food and Agriculture Organization of the

United Nations (FAO) estimates that annual world cereal production must increase by about 60% (Alexandratos and Bruinsma 2003) to meet the projected demand in 2050. This requires extension of arable land area (including land conversion), intensification of production by an increased and more efficient use of resources, such as nutrients and water (Tilman et al. 2011), and substantial improvements in harvest, transport, and storage technologies (Kitinoja et al. 2011). However, such an increase in production has to be considered in the context of the socio-economic framework conditions (Cohen 1997) and the external costs (e.g., greenhouse gas emissions, loss of biodiversity) related to these measures (Walsh 1991; Balmford et al. 2002).

Particularly external costs of food production (principally transport, energy demand of storage and food losses of vegetables) stimulated concepts of plant cultivation in contained indoor systems, where vegetable or crop plants are grown in artificial indoor systems comprising components for artificial lighting, nutrient supply and environmental control (temperature, CO₂ concentration and air humidity). Research on indoor growth systems were initiated in the frame of

✉ Marc Schmierer
marc.schmierer@uni-hohenheim.de

¹ Hans-Ruthenberg-Institute, Institute of Agricultural Sciences in the Tropics, University of Hohenheim, 70599 Stuttgart, Germany

² Research Centre Hanninghof, Yara International, Dülmen, Germany

space flight missions (Zabel et al. 2016) and are, with less sophisticated control over environmental factors, going to be established in commercial factories focusing on high-value crops such as vegetables (Shamshiri et al. 2018). A similar approach of plant cultivation is followed in proposed vertical farming concepts (Despommier 2011; Beacham et al. 2019) and some authors have specifically mentioned rice as a target crop for indoor staple food production (Germer et al. 2011; Song et al. 2018). These concepts seek to illustrate the feasibility of partially substituting food production on arable land. A central feature of such visionary indoor plant production systems is the evaluation of related energy demand. Studies on energy demand have to consider energy expenditure for temperature and humidity control and lighting systems with the latter being the preponderant item of energy balance sheets for indoor plant factories.

Since the commercial release of the first red LEDs in 1968, the development of solid-state LEDs has progressed rapidly. Projections indicate that, due to energy savings, LEDs may displace all traditional lamps for general illumination within the next few decades (Haitz and Tsao 2011). As compared with the successful implementation of solid-state LEDs in technical applications (e.g., indicator lights, room and street lighting, screens and flashlights), LED technology starts to be widely used in greenhouses (Shamshiri et al. 2018). While low radiant efficiency and the effects of light quality on growth and photo-morphogenesis of plants due to the few available wavelengths restricted the use of first generation LEDs in greenhouses (Bula et al. 1991), current LED lighting systems for plant growth match high-pressure sodium (HPS) lamps in terms of electrical efficiency and light quality. HPS lamps are gas-discharge lamps that use excited sodium to emit light of a relative broad spectrum. In growth environments which exclusively rely on artificial lighting, LEDs could be a prime technology, especially since light intensity can be adjusted to the plants' specific demand while the thermal load for the plants is lower than with HPS lamps (Folta et al. 2005; Massa et al. 2008; Morrow 2008).

Information about the plants' energy demand for growth is essential for future design of LED-based lighting systems. We present calculations of the quantum requirements (moles of plant usable light quanta needed to produce a certain amount of biomass) for plant growth and combine this with related electric energy demand for indoor environments equipped with LED lighting. By using a standard data set of plant growth parameters, our approach allows for an approximate estimation of temporal dynamics of energy demand of LED lighting fields in indoor-growth environments.

2 Materials and methods

2.1 Estimating cumulative electric energy requirements

In the following, we present equations which enable the reader to calculate the energy demand for their crop and growth environment of interest.

Equations 1–4 summarize classical approaches of crop growth physiology and can be applied to any crop of interest, from greenhouse vegetables to broad acre crops. Equation 3 can be used to quantify daily crop growth rates by fitting curve parameters to the crop's expected yield and growth duration. Equations 2 and 4 are useful to adjust energy content of crop organs during the growth period. For further details, readers are encouraged to consult the cited crop growth publications.

Equations 5–7 specify how crop energy demand is converted to LED performance. With advances in LED development, technical specifications will necessarily change, but the basic approach will stay as outlined.

The cumulative electric power requirement [ER, Watt hour (m² ground)⁻¹] is here defined as the ratio of the quantum requirements [QR, mol quanta (m² ground)⁻¹] for the built-up of dry mass over time and the conversion efficiency of electricity to light (CO_{Eff}, mol quanta Watt⁻¹) and can be calculated by Eq. 1.

$$ER = QR/CO_{Eff} \quad (1)$$

2.2 Estimating quantum requirements

QR was calculated according to Eq. 2:

$$QR = (dY \times GLU_{reqG.} + Y \times GLU_{reqM.}) \times 0.0\bar{3} \times (a + b\Phi) \times (1 + 1 - f_{abs}), \quad (2)$$

where construction costs for daily dry weight formation [dY, g DW (m² ground)⁻¹ day⁻¹] are expressed in glucose requirements [GLU_{reqG.}, g glucose (g DW)⁻¹]. Carbon costs for maintenance respiration [GLU_{reqM.}, g glucose (g DW)⁻¹] are related to standing biomass [Y, g DW (m² ground)⁻¹] and 0.0 $\bar{3}$ is a conversion factor from g glucose to mol C considering the molar stoichiometry of carbon and glucose (72/180=0.4) and the conversion from g C to mol C (0.4/12=0.0 $\bar{3}$). The conversion from glucose to mol C is necessary for calculating daily QR for carboxylation which is defined by the term (a + bΦ) and depends on the relative rate of oxygenation to carboxylation (Φ). The term f_{abs} is the portion of incident light which is absorbed and used in photosynthesis by the plant canopy. E.g., with a value of f_{abs}

of 0.8, the term $1 + 1 - f_{abs}$ is 1.2, indicating that QR is 20% higher than if it were in a situation of complete absorption of quanta by the plant surface.

The equation is conceptually very similar to the radiation use efficiency (RUE) approach of Amthor (2010), where detailed explanations of energy demand calculations can be found.

QR was calculated for a fictional highly-productive plant stand producing 2500 g DW (m² ground)⁻¹ over 100 days.

We assumed for our calculations that 500 g of DW are invested in the root system (relative root allocation factor of 0.2) and 50% of the aboveground biomass is invested in final grain yield. Detailed dry mass allocation coefficients for crops and vegetables are reported in Haenel et al. (2020). This hypothetical crop would realize a grain yield of 1000 g (m² ground)⁻¹. This yield level (equivalent to 10 tons of grain per hectare) represents a high productivity benchmark of field crops such as rice and wheat. For indoor plant production, and particularly vegetables, similarly high growth rates are realistic and the estimated QR presented in this paper are, therefore, representative for a highly productive plant species in general. QR varies over time as growth rate and chemical composition of plants change. In order to consider this, a fictional growth dynamic of a plant stand was calculated with the symmetric expolinear function suggested by Goudriaan, cited in Yin et al. (2003):

$$dY = \frac{c_m}{r_m} \ln \frac{1 + e^{r_m(t-t_0)}}{1 + e^{r_m(t-t_0 - w_{max}/c_m)}} \tag{3}$$

Values used were 40 for the maximum growth rate c_m , 0.2 for the maximum relative growth rate in the expolinear phase r_m , 20 for the time when linear growth begins, t_0 , and 2500 for final weight w_{max} . Of the aforementioned values the maximum growth rate of 40 g m⁻² per day is a high but reasonable value (Lambers and Poorter 1992) and 0.2 and 20 were selected to create a reasonable shape of the growth curve. Values of target yield and maximum growth rate for different environments can be easily adjusted for other plant species. Carbon costs for growth (GLU_{ReqG}) were calculated from information about ash-free heat of combustion (ΔH_C , J kJ⁻¹) of grain (18.5), stem (17.5) and root (16.5) (Amthor 2010) according to Griffin (1994):

$$GLU_{ReqG} = [(0.06968DH_C - 0.065)(1 - AC) + 7.5(k_N \times Nc/14.0067)](1/E_g), \tag{4}$$

with ash content (AC, g g⁻¹) of grain (0.015) and straw (0.044) taken from Jørgensen et al. (2007). The straw data were assumed to represent those of leaf, stem and root tissue. N content (g g⁻¹), in a simplified approach, was assumed to be constant over time with values of 0.04 (leaf) and 0.02 (root, stem, grain). A k_N value (considering costs of N

Table 1 Coefficients for calculating the quantum requirements (a, b), the ratio of oxygenation to carboxylation (Φ) and the fraction of light absorbed by leaves (f_{abs}) in the pessimistic (PA) and optimistic (OA) approach

Scenario	a	b	Φ	f_{abs}
	Dimensionless			
PA	12	13.5	0.28	0.70
OA	9	10.5	0.05	0.95

assimilation) of 5 (sole nitrate–N supply) and $E_g = 0.87$ were used (see Griffin 1994). The assumed GLU_{ReqG} were 1.287, 1.219, and 1.149 g glucose (g DW)⁻¹ for grain, stem and root tissue, respectively. Experimental estimates of maintenance respiration rates vary from 15 to 50 mg Glu g⁻¹ DW day⁻¹ (Loomis and Amthor 1999). We took a value of 30 mg Glu g⁻¹ DW.

Uncertainty in the calculations of daily QR arises from factors which can be technically manipulated such as the environmental CO₂ concentration (variable rate of oxygenation to carboxylation, Φ) as well as the fraction of light absorbed by the plant canopy (f_{abs}). Additionally, uncertainty in QR exists as ‘true’ quantum costs for production of energy and reducing equivalents is not clear. This is considered by a pessimistic (PA) and optimistic (OA) approach (see Table 1 and text below).

Carbon demand for growth and maintenance is equivalent to the required rate of carboxylation, V_C per unit ground area, which can be expressed as $(a + b\Phi)$. This term quantifies the required production rates of energy (ATP) and reducing equivalents [NAD(P)H] sustaining the rates of carboxylation and oxygenation according to von Caemmerer and Farquhar (1981). The required rate of ATP consumption is $(3 + 3.5\Phi)V_C$. We assumed that either three or four H⁺ are required for the synthesis of 1 ATP (Sacksteder et al. 2000). Consequently, rates of proton production were $(9 + 10.5\Phi)V_C$ or $(12 + 13.5\Phi)V_C$ in the optimistic and pessimistic approaches, respectively (Table 1). Relative rates of photorespiration (Φ) were assumed to be 0.28 or 0.05 under ambient or high atmospheric CO₂ concentrations (Lambers and Poorter 1992), respectively with the ambient CO₂ concentration used in the PA scenario. The fraction of quanta which are absorbed by leaves (f_{abs}) depends on reflective properties of the leaf surface and the absorption efficiency which depends on pigment density (Evans and Poorter 2001). An additional source of inefficient quanta absorption is the portion of ground coverage and reflective properties of the ground surface. In the OA scenario we assume a fraction of absorbed quanta of 0.95, which would represent an optimized indoor design with permanent complete ground cover and use of highly reflective material of the growth chamber inner surfaces. A value of 0.70 was assumed in the PA scenario. This

value is representative for field crops which do not reach full canopy cover (Lambers and Poorter 1992). In indoor systems such low values could be realized if floor or wall materials are not highly reflective.

Conversion efficiency of electricity to biomass (ϵ ; J/kJ) was calculated by dividing the cumulated energy of plant biomass by the electricity demand for LED lighting. An energy content of 18.1 kJ (g DW)⁻¹ (Jørgensen et al. 2007) was assumed for plant biomass.

2.3 Calculation of conversion efficiency of electricity to light of LEDs

LED suppliers usually specify the efficacy of illuminants in terms of the photometric luminous flux. For the calculation of photosynthetically active quanta ($\mu\text{mol PPFd m}^{-2} \text{s}^{-1}$), we first converted the photometric luminous flux to the physical luminous flux. The relationship between photometric and physical luminous flux is given by:

$$\Phi_v = K_m \int_{380\text{nm}}^{780\text{nm}} \frac{de^{(\lambda)}}{d\lambda} \times V(\lambda) d\lambda, \quad (5)$$

where Φ_v is the photometric luminous flux in Watt, Φ_e is the physical luminous flux in Lumen for a specific wavelength λ and $V(\lambda)$ is the luminous efficiency function of the human eye (photopic) in Lumen per Watt with its highest value K_m of 683.002 l/W at a wavelength of 555 nm.

For the conversion, we determined the relative spectral power distribution $S(\lambda)$ of LED spectra reported in specific datasheets of Osram (Osram Opto Semiconductors GmbH & Co., Regensburg, Germany). The graph of the spectral distribution from the datasheet was converted to a monochromatic image and the numerical values of the distribution were estimated by self-written software with a resolution of 1 nm. The total physical luminous flux of the LED was then calculated according to Eq. 6:

$$\Phi_e = \frac{\Phi_v}{\sum_{380\text{nm}}^{780\text{nm}} K_m \times V(\lambda) \times S(\lambda)}, \quad (6)$$

with Φ_v given in the specific datasheet. Subsequently, $\Phi_e(\lambda)$ was calculated by multiplying the relative spectral power distribution $S(\lambda)$ for each wavelength with the formerly calculated total physical luminous flux of the illuminant.

For the calculation of photosynthetically active quanta, the photonic energy per wavelength was calculated as:

$$E = \phi \times \frac{hc}{\lambda}, \quad (7)$$

where h is the Planck constant and c is the speed of light. The number of quanta per wavelength was calculated by

dividing the numerical values of the power distribution for each wavelength by the dedicated photonic energy. Finally, the number of photosynthetically active quanta was calculated by integrating all photons between 400 and 700 nm.

It should be noted that the brightness values given in the datasheets are typical values measured under the specified test conditions. For detailed information about test conditions and measuring inaccuracy, information provided in the datasheets should be considered. Due to production related fluctuations in certain LED parameters such as peak wavelength and optical flux, LEDs from a particular model are usually classified into different wavelength and brightness groups. The values presented in this paper usually refer to LEDs that are specified as ‘typical’ in the data sheets.

The software for the estimation of the relative spectral power distribution from the LED datasheets was written in C++. For image analysis, we used the Qimage class provided by the Qt framework version 4.7.4 (<http://qt-project.org/>). Binaries and source code are available from the authors on request. Information about four LED types and a combination from deep red and deep blue LEDs and for HPS (SON-T 400 W, PHILIPS, The Netherlands) are summarized in Table 1. The quantum output for LEDs was calculated for different colours and varied between 0.83 for true green and 2.64 for deep red. Calculations are presented for HPS lamps, cool white LEDs, and a combination of deep red and blue LEDs with a red:blue photon ratio of 5:1. Distribution of electrical energy between deep red and blue LEDs was 4.29:1. For the calculation of energy requirement, LED efficiency was recalculated to operating temperatures at 60 °C as stated in the datasheets.

3 Results and discussion

The ER of indoor plant production systems with exclusive LED lighting have not been reported so far. The cumulative ER per unit ground area with exclusive LED lighting is, according to our estimates, between 265 and 606 kWh for a growth cycle of 100 days and 2500 g DW production (Table 3). The calculated ER can be used for dimensioning energy supply systems required to power LED lighting fields of indoor plant production units like those intensively investigated in the context of controlled environment life support systems (Bugbee 1992) and vertical farming concepts (see “Introduction”). In this paper, we want to elucidate the connection between light supply by technical means and the production of biomass. Plenty of articles on vertical farming exist in the market of scientific literature. In our opinion, most of them lack specific information on the processes we discuss in our paper and are by trend more visionary. Here, we want to make a contribution that this changes in the future. Comparable calculations and estimations of light

and energy supply for biomass production was presented by Pattison et al. (2018). However, this paper addresses the topic on a more economical approach and the model applied is by nature parametric, while our approach focuses on the mechanistic of the photosynthetic stoichiometry. Further, our method also catches the dynamics of the quantum demand over time. For the estimation of the economic feasibility of plant production under artificial lighting, the parametric model is absolutely sound and, with solid estimations available for the given parameters, maybe even more reliable than our model. However, our approach is rendered unique by consequently connecting electric efficiency with a mechanistic model of the stoichiometry of photosynthesis and the back-calculation of quantum demand for plant growth over time.

The pronounced differences in ER between the two scenario calculations indicate that, by a combination of management practices such as CO₂ enrichment and use of reflective materials, substantial energy savings can be achieved. The peak daily ER were 9.44 and 4.14 kWh m⁻² in the PA and OA scenarios, respectively, and were substantially lower at the beginning and end of the growth cycle (Fig. 1). This highly dynamic ER during the growth cycle suggests that LED lighting fields should be designed to meet this variable and plant growth stage-specific energy supply. This could be a significant contribution to energy saving in greenhouses and indoor plant growth systems and could be achieved by either dimming the LED light field or by moving plants into a demand-defined light environment supplied by LED panels in separate sectors of the indoor growth facility. This could further include the option of supplying spectrally different

light composition and, by that, exploiting ontogenetic-specific photo-morphogenetic effects.

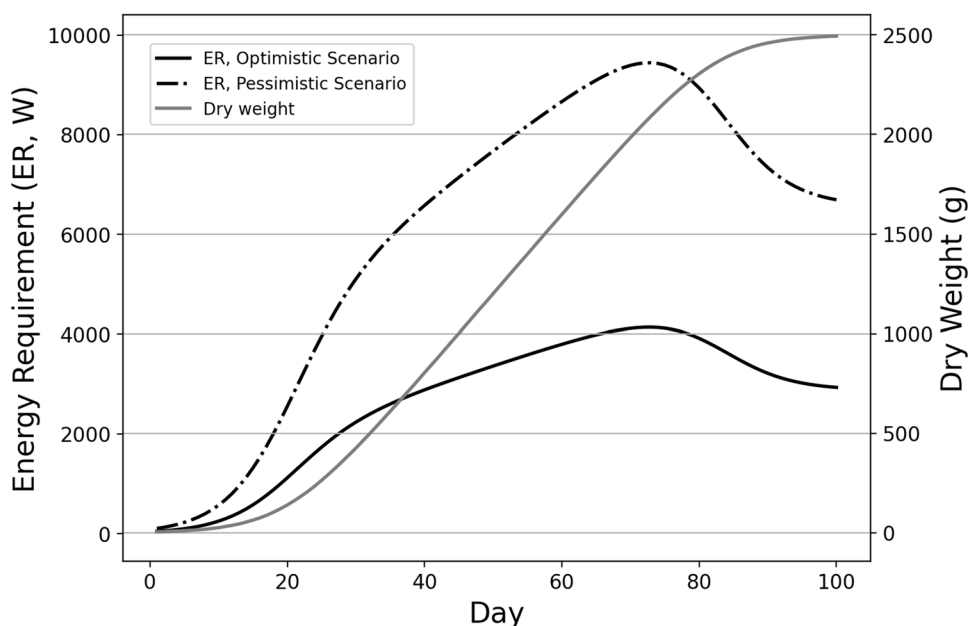
A theoretical maximum energy conversion efficiency of photosynthetically active light (400–740 nm) at the plant surface of C3 plants of 9.5% (Zhu et al. 2008; Amthor 2010) has been derived from consideration of biophysical and biochemical principles of CO₂ assimilation. Relating the time-integrated energy accumulation of the scenario crop to the electric energy demand, the energy conversion efficiencies in the PA and OA scenarios were 2.07 and 4.72%. These values are unavoidably lower than the theoretical maximum energy conversion efficiency due to the energy losses along the physical transformation of electricity to quanta. LEDs vary in efficiency of plant-available Watt per Watt of electricity

Table 2 Peak wavelength (λ_{peak}), efficiency (W plant available per W of electricity) and photon conversion efficiency of electricity to quanta (CO_{Eff}, 400–700 nm) of five different commercially available LEDs

Visible color	λ_{peak} nm	Efficiency W W ⁻¹	CO _{Eff} $\mu\text{mol J}^{-1}$
Hyper red	660	0.46	2.55
Blue	470	0.57	2.18
Deep blue	451	0.50	1.89
True green	521	0.18	0.78
Cool white	445/555	0.28	1.35
Hyper red:blue (5:1)	470/660	0.48	2.47
HPS (SON-T, 400 W)	n.a.	0.29	1.53

LEDs at typical test conditions (forward current: 350 mA, temperature: 25 °C), a combination of deep red and deep blue and a High Pressure Sodium lamp (SON-T, 400 W)

Fig. 1 Temporal dynamics of dry mass formation (DW, g m⁻²; solid grey line), and energy requirements [ER, kWh (m² ground)⁻¹ day⁻¹] of the fictional plant stand. ER were calculated with the optimistic (OA, solid black line) and pessimistic (PA, broken line) approach as outlined in Table 1



and in CO_{Eff} , with lower values of true green LEDs and the highest in deep red and blue LEDs (Table 2).

As indicated by differences in ER of the PA and OA scenarios by varying f_{abs} and the ratio of carboxylation to oxygenation (Φ), technical options are relevant for energy savings. High CO_2 environments are commercially used in order to suppress photorespiration. By reducing Φ from 0.28 to 0.05, the ER was reduced from 606 to 437 kWh m^{-2} and ϵ increased by 38% (Fig. 2). Although high CO_2 environments appear as a feasible option for reducing energy costs and water requirements, the role of photorespiration in stress tolerance (Bauwe et al. 2010) and putative effects of CO_2 enrichment on nutrient uptake and assimilation, and grain composition and quality (Fangmeier et al. 1999; Erda et al. 2005) must be considered in an integrated management approach.

The absorption of light by the plant canopy (f_{abs}) is relevant for the system's ER as an increase of f_{abs} from 0.70 to 0.95 increased ϵ by 24% (Fig. 2). As summarized in

Amthor (2010), dense canopies might absorb 90–95% of photosynthetic active radiation (PAR), but so called inactive PAR absorption by pigments not involved in photosynthetic carbon assimilation may reduce the effective absorption to a certain, yet not well quantified, extent. A value of 0.95 in the OA scenario would imply that all quanta emitted by LEDs were absorbed by leaves and that only 5% of quanta were lost by conversion to heat and fluorescence. In order to minimize unproductive losses of light in greenhouses or indoor factories, plant density should be adjustable over the growth period to maximize canopy cover during the growth period. Secondly, the use of highly reflective surfaces surrounding plants can minimize losses by reflectance of plant canopies and increase the fraction of diffuse light. As shown by Tubiello et al. (1997), high levels of diffuse light can RUE by equalizing the high and low radiation levels at the upper and lower layers of the canopy, respectively. However, given that newer findings by Brodersen et al. (2008) suggest an increase of leaf level

Fig. 2 The energy conversion efficiencies (ϵ) of a fictional plant stand producing 2500 g total DW m^{-2} during a growth cycle of 100 days. Calculations are based on the pessimistic approach (PA), and stepwise changes in parameters listed in Table 1 under the optimistic approach (OA), or with all parameters changed according to the OA scenario (a, b: quantum requirements, Φ : the ratio of oxygenation to carboxylation, f_{abs} : the fraction of light absorbed by leaves)

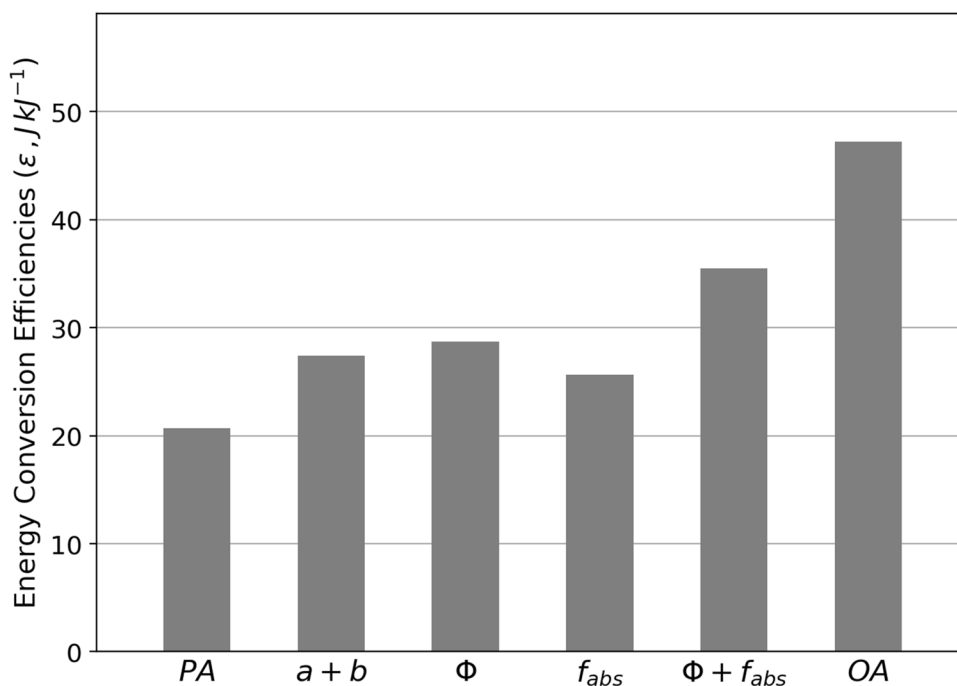


Table 3 Cumulative energy requirement (ER) for a dry weight formation of 2500 g m^{-2} during a crop growth cycle of 100 days for plants growing in an indoor system under the PA/OA scenarios as described in Table 1

ER	PA	a + b	Φ	f_{abs}	$\Phi + f_{\text{abs}}$	OA
kWh m^{-2}	606	458	437	489	353	265

Calculations were based on CO_{Eff} of the a combination of deep red and blue LEDs with a red:blue photon ratio of 5:1 (Osram Opto Semiconductors GmbH & Co., Regensburg, Germany) (see Table 2)

a, b quantum requirements, Φ the ratio of oxygenation to carboxylation, f_{abs} the fraction of light absorbed by leaves

photosynthesis under high direct light levels compared to equal irradiances of diffuse light for high light grown leaves, it seems plausible to focus on the development of an integrated lighting environment with respect to both the position of the light sources as well as to the light-directional quality. Technically, all the management options are feasible (Table 3).

Temperature control is one of the major items of energy balance sheets in greenhouse and indoor plant factory management and has not been assessed in our calculations. Calculated energy requirements cannot be considered as a fixed value under variable environmental temperatures since, due to temperature effects on solubility of gases, high temperature environments will increase the quantum requirements by higher rates of photorespiration [see Amthor (2010) for details]. Although technical aspects of temperature control and related energy costs are not considered here, the relevance is not at all questioned.

Additionally, to technical options for minimizing ER, some bio-physical processes of plant growth are highly relevant to improve estimates of real ER. Firstly, the quantum requirement is under debate as electron transport in the light reaction part of photosynthesis is apparently not simply a linear transport but has a constitutive or facultative operation of cyclic electron flow. Furthermore, the costs of ATP synthesis are not clear but transport of four H^+ through the chloroplastic ATP synthase may be required per ATP with up to 12 H^+ transported into the thylakoid lumen per 8 quanta absorbed (Sacksteder et al. 2000; Amthor 2010). In our PA and OA scenarios, 15.78 and 11.94 quanta per rate of carboxylation would be required, estimates which are higher (PA) or comparable (OA) to the estimates used by Amthor (2010). Clarification of the quanta/ATP stoichiometry is not only of scientific interest but affects the QR and thus ER for LED based lighting systems. ER would decrease from 606 (PA) to 458 $kWh\ m^{-2}$ if proton costs for ATP synthesis were lower than assumed in the PA scenario. In line with Sacksteder et al. (2000), we assume in our calculations, that energy demand during photosynthesis is defined by the ATP demand. By this we explicitly exclude the possibility of ATP import into the chloroplasts during the light phase and assume that the surplus of reducing equivalents is exported to the cytosol via the malate/oxalacetate shuttle (Scheibe 2004).

Maintenance respiration is a significant component of the plant's carbon economy and conceptually reflects all carbon costs related to ensure functionality of cells in terms of membrane potentials, pH regulation, de-toxification, and repair and turnover of structure and enzymes. Though clear in a biological sense, estimates of carbon

costs of maintenance are methodologically difficult but are roughly of similar cumulative glucose requirements than those invested in growth respiration over a complete growth cycle (Loomis and Amthor 1999). In consideration of the functions supported by maintenance respiration, costs are evidently not constant per unit plant DW but expected to increase in stressful environments, with increasing N content of tissue and towards maturity. Relevance of maintenance respiration in our calculations is indicated by the peak energy demand at 73 days after sowing, while peak growth rate occurred at 52 days after sowing. This is due to the increasing relevance of maintenance respiration with plant age, keeping the ER at 100 days after sowing at high values. We likely overestimate cumulative ER in both scenarios as senescence of plant tissue and re-translocation from vegetative organs to grain will reduce ER during the generative growth phase.

4 Conclusions

The calculation of ER as outlined can be applied to any crop once the growth dynamics and energy content of plant organs is known, which often is the case. Unlike other lighting systems, LEDs are easily dimmable and can therefore be adjusted to the plants' demand which could substantially reduce energy costs. For example, we can see dimmable LEDs in a greenhouse to supply supplementary light to the natural one, if by season or cloud conditions, the QR (calculated from a model as outlined here in principle) is not sufficient. The basic approach of our calculations is valid for any vertical farming concept and already existing greenhouses. Relevance of our findings is highest for concepts of completely self-contained growth environments, since in traditional greenhouses the energy demand for thermal control is more relevant than energy requirements for lighting. Logically, hybrid systems with transitory supply of light through transparent surfaces will reduce the energy estimates of our study. With a more consolidated understanding of energy demand and conversion efficiency by plants, the construction of appropriate LED-based light fields should be possible. However, and as indicated by our consideration of pessimistic and optimistic approaches, the design of environmental conditions in sealed systems is far from trivial and plants are transferred into a combination of bio-physical factors (e.g., permanent light and high CO_2) for which information is sparse in terms of presently used mechanistic plant growth models.

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