Horticultural lighting – present and future challenges

P Pinho DSc[a], K Jokinen DSc[b] and L Halonen DSc[a]
[a] Lighting Unit, School of Electrical Engineering, Aalto University, Aalto, Finland [b] Plant Production Research, Horticulture, MTT Agrifood Research Finland, Piikkio¨, Finland

Received 14 July 2011; Revised 5 September 2011; Accepted 8 September 2011

There is an urgent need to find environmentally sustainable technologies that help to address the challenges related to increasing global demand for energy and food. Horticultural lighting allows for year-round cultivation of vegetable crops independent of weather conditions or season of the year. However, high energy prices, environmental impact and market competition are threatening this industry. Although understanding the principles and processes behind human responses to light and lighting is important, the investigation of similar aspects for plants deserves more attention from the lighting research community. This paper provides an overview of the present and future challenges facing horticultural lighting and food production in the context of a food- and fuel-hungry world.

1. The most important biochemical process on Earth

Certain living organisms, such as plants and algae, cannot directly process the energy gathered from solar radiation. Instead, it has to be first converted into chemical energy. This process is called photosynthesis and it is one of the oldest, most abundant and perhaps most important biochemical processes on Earth. During photosynthesis, the incident solar energy is converted into chemical energy used for the growth and development of plants. All life on earth depends either directly or indirectly on photosynthesis. Directly, photosynthesis provides oxygen (O_2) and biomass in the form of carbohydrates such as glucose ($C_6H_{12}O_6$), by decomposing water (H_2O) and reducing carbon dioxide (CO_2) in the atmosphere. Indirectly, photosynthesis is also the source of food, building materials and primary energy. The process uses the energy of light harnessed by specialised photoreceptors such as chlorophylls. The generic formula of photosynthesis is:

$$6H_2O + 6CO_2 + \text{light energy} \rightarrow C_6H_{12}O_6 + 6O_2 \qquad (1)$$

The energy in food, petroleum, natural gas, coal and firewood all came from the Sun via photosynthesis. Photosynthesis also has a vital role in regulating the life cycle on Earth. Therefore, there has been an increasing interest in re-engineering and mimicking natural photosynthesis towards artificial photosynthesis but with higher efficiency.[1–5] Unfortunately, in spite of its 3.7 billion years of existence, the conversion efficiency of oxygenic photosynthesis is still surprisingly low. The maximum conversion efficiency of natural photosynthesis (i.e. solar energy to biomass) in green plants has been estimated to be 4.6–6%.[6] If secondary processing such as growth is also considered, the efficiency will typically not exceed 1–2% under sunlight. Furthermore, increasing the conversion efficiency of natural photosynthesis occurring in plants and algae will not be easy to achieve in the short term, because of the various inherent inefficiencies involved.[7] However, increased food production may also be achieved by improving photosynthesis efficiency (i.e. the ratio of radiant energy stored in the form of carbohydrate to total intercepted radiant energy).[8] One possibility for optimizing the photosynthesis efficiency, and consequently plant productivity, may consist of using spectrally tailored artificial light sources which match the absorption spectra of the chlorophylls. Year-round plant production in closed environments may clearly benefit from this possibility.

2. The importance of light spectrum

The spectral influence of light on plant development was first reported around a century ago,[9] although earlier experiments had indicated the effects of specific wavelengths. In spite of this early discovery, the mechanisms controlling these responses are today still not completely understood. Additionally, the interaction and the nature of interdependence between certain groups of photoreceptors are not well understood.[10] One of the reasons for this is the complexity of the mechanisms mediating plant responses to light and the differences between plant species. Specialized photoreceptors in plants use the captured energy of light to mediate important biological processes. This mediation can take place in a variety of ways. Gathering environmental and sensory information as in vision processes or, in a more subtle way, setting the metabolic and circadian cycles of living organisms, are just a few examples (Figure 1).

The activities of photosynthetic pigments, such as chlorophylls and carotenoids are mostly related to light-harvesting and energy transduction during photosynthesis. Chlorophylls have maximum sensitivities in the blue and red regions, around 300–400nm and 600–700nm, respectively. Carotenoids such as

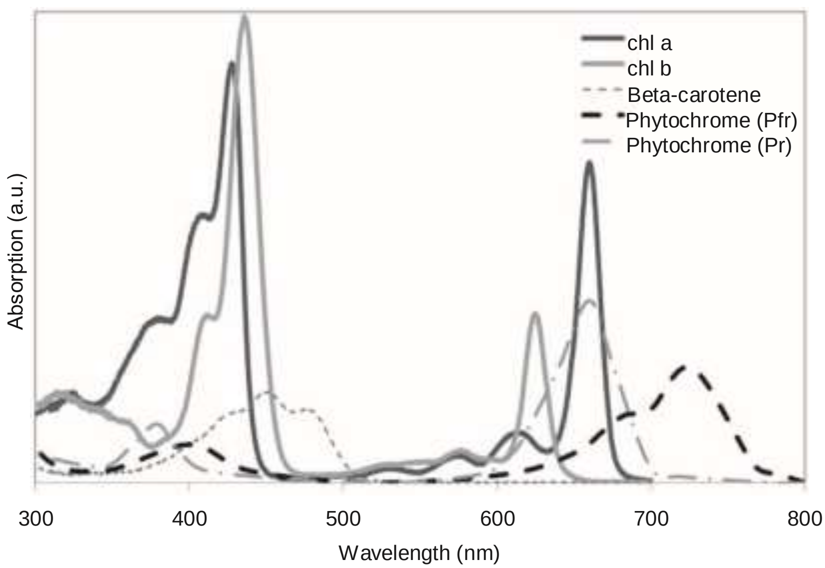

Figure 1 Absorption spectra of the most common photosynthetic and photomorphogenetic receptors in green plants: chlorophyll a (chl a), chlorophyll b (ch b), beta-carotene, phytochromes (Pfr and Pr)[11,12]

xanthophylls and carotenes absorb mainly blue-light and are also known as auxiliary photoreceptors of chlorophyll.[13]

The phytochrome photosystem includes the two interconvertable forms of phytochromes, Pr and Pfr, which have their sensitivity peaks in the red region at 660nmand in the far-red (700–800nm) region at 730nm, respectively. The importance of phytochromes can be evaluated by the different physiological responses in which they are involved, such as leaf expansion, neighbour perception, shade avoidance, stem elongation, seed germination and flowering induction. Photomorphogenetic responses mediated by phytochromes are usually related to the sensing of the light spectrum through the red (R) to far-red (FR) ratio (R/FR).[14] Plant photomorphogenesis refers to the change in form in response to the quality and quantity of radiation. Although shade-avoidance response is usually controlled by phytochromes through the sensing of the R/FR ratio, blue-light is also involved in the related adaptive morphological responses.[15]

Blue- and ultraviolet-A-sensitive photoreceptors are found in the cryptochrome signal transduction system. Blue light-absorbing pigments include both cryptochrome (e.g. cry1, cry2) and phototropins (e.g. phot1, phot2). Cryptochromes control plant morphology, gene expression, and the transition to flowering, contribute to leaf expansion and strongly inhibit stem elongation.[16] Cryptochromes have also been shown to be part of the circadian oscillator in animals.[17] They mediate a variety of light responses, including the entrainment of the circadian rhythms in flowering plants such as the Arabidopsis, in mammals and in small insects such as the Drosophila.[9] The magnetoperception, which is used by birds for orientation during their migratory journeys, is also a cryptochrome function.[18] Phototropins regulate the pigment content and the positioning of photosynthetic organs and organelles in order to optimize the light harvest and photoinhibition.[10] Although radiation at wavelengths below 300nmcan be highly harmful to the chemical bonds of molecules and to DNA structure, plants also absorb radiation in this region. The spectrum of photosynthetically active radiation (PAR) may be important to reduce the destructive effects of UV radiation.[19]

The photoreceptors mentioned above are the most investigated and therefore their role in control of photosynthesis and growth is known reasonably well, even at the molecular level. However, there is evidence of the existence of other photoreceptors, the activity of which may have a significant role in mediating important physiological responses in the plant. Recently, a new chlorophyll photoreceptor has been discovered, isolated and designated as chlorophyll f (chl f).[20] This chlorophyll present is in addition to the other four previously known ones (chl a, chl b, chl c and chl d). The optical absorption spectrum of chl f has a red-shifted absorption peak at 706nm. This finding suggests that photosynthesis extends further into the infrared region than previously thought. The first photoreceptor protein specifically absorbing ultraviolet-B (UV-B) has also been recently identified in Arabidopsis plants.[21] This discovery may contribute to the study of the potential impacts on terrestrial plants of an increase in solar UV-B radiation reaching the Earth's surface. UV-B is known to affect the growth and development of plants (e.g. hypocotyl elongation, dry weight, leaf area, photosynthetic activity and flowering).[22]

The effects of yellow–green (500–600nm) light on plant development are still controversial. Some studies have reported that yellow (580–600nm) light appears to inhibit lettuce growth by suppressing chlorophyll or chloroplast formation.[23] Other studies conclude that green light can improve lettuce development and revert the blue-light stimulated stomatal opening.[24] In general, the existing knowledge supports the conclusion that green light sensory systems adjust development and growth in orchestration with red and blue sensors.[25,26] These findings suggest also that red and blue combinations of light alone may not provide the ultimate solution for the optimal growth of some specific plants such as lettuces.[27]

3. Conventional light sources in horticulture

Artificial light sources were used to grow plants before the invention of incandescent lamp, with some of the earliest reports in the year 1861.[28] The use and usefulness of incandescent lamps in horticultural lighting has been limited. The reasons are the low electrical efficiency, low light emission, unbalanced spectrum (reduced emission in the blue region) and short lifetime. The growth control of ornamental plants is one of the applications where incandescent lamps are still used. Floral initiation can be achieved with long day responsive species using overnight exposure to low light levels from incandescent lamps.[29] The high amount of far-red radiation emitted is used to control the photomorphogenetic responses through the mediation of the phytochromes.

Fluorescent lamps are frequently used in growth rooms for plant propagation in vitro. The blue radiation emitted is indispensable to achieve a balanced morphology for most crop plants through the mediation of the cryptochrome family of photoreceptors.[30]

Metal halide lamps can be used in plant growth to totally replace daylight or for partially supplementing it during periods of low availability. The inclusion of metal halides during manufacture allows the spectrum of the radiation emitted to be optimized to some extent.

The high-pressure sodium (HPS) lamp has provided the ‘horsepower’ for year-round crop production in greenhouses. The reasons are related to the high radiant emission, low price, long life time, high light emission and high electrical efficiency. HPS lamps are mainly used as supplemental light sources supporting vegetative growth. However, their spectrum is not optimal for promoting the most efficient photosynthesis and normal plant morphology in commercial plant production, resulting in excessive leaf and stem elongation.[31,32] The low R/FR ratio and low blue-light emission in comparison with other sources induce excessive stem elongation to most of the crops grown under HPS lighting. In the past, sulphur lamps have been considered the prime candidate for the development of hybrid lighting systems for bioregenerative life support in space.[33] The typical system electrical efficiency of both technologies is close to 30%. However, in spite of the high efficiency shown and long lifetimes, the use of sulphur lighting systems has been hindered by high costs and the lifetime of magnetrons, which poses reliability problems.[34]

Some examples of typical photon flux efficacy, electrical efficiency and luminous efficacy of conventional lamps and light-emitting diode (LED) components are shown in Figure 2. The photon flux efficacy is the ratio between the total emitted number of moles of photons per second and the total input power. Theelectricalefficiencyistheratiobetweenthe total radiant power within the PAR region (400–700nm) and the total input power.

4. Horticultural LED lighting

Conventional light sources cannot be spectrally controlled without the inefficient and limited utilization of additional filters. Furthermore, the control of the light output is also limited, reducing the possibility of versatile lighting regimes such as pulsed operation or full dimming. The LED does not suffer from these

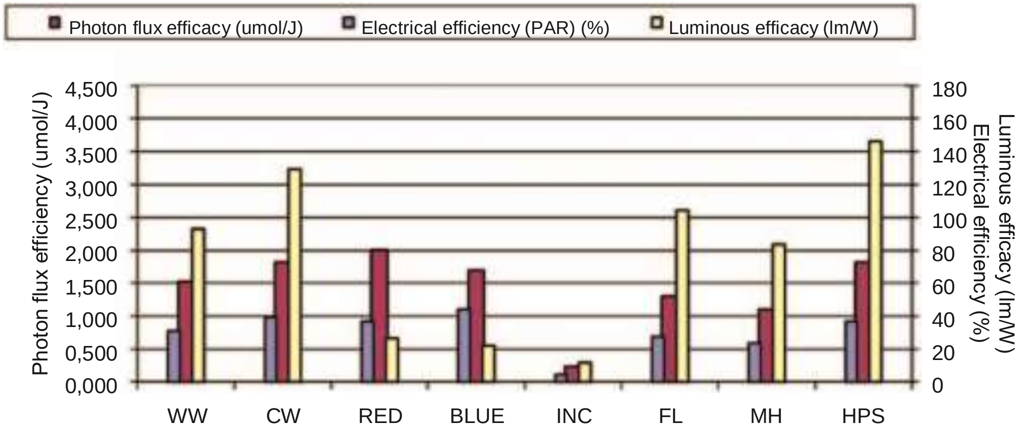

Figure 2 Typical photon flux efficacy, electrical efficiency and luminous efficacy in 2010 of phosphor-converted warm-white (WW) and cool-white (CW) LEDs with correlated colour temperatures (CCTs) of 2600K and 6000K, respectively; red and blue LEDs with peak wavelengths at 660nmand 450nm, respectively; and conventional incandescent lamp (INC); 35-Wlinear T5 fluorescent lamp (FL); 400-Wmetal halide lamp (MH); and 400-WHPS lamp

Note: The luminous efficacy and electrical efficiency values are partially based on the product catalogues of different manufacturers and on targets and milestones set by the Solid State Lighting Multi Year Program Plan of the US Department of Energy[35]

limitations. LEDs have emerged as a potentially energy-efficient, viable and promising technology for use in horticultural lighting. The use of LEDs in plant production applications offers completely novel opportunities for optimization of plant growth and development that can be achieved through more versatile and appropriate control of the quantity, periodicity and spectrum of the light provided. This optimization can be tailored to the specific needs of each crop species and their production conditions.

The investigation of the influence of the spectrum of LED lighting on plant development has initially been mainly focused on the red and blue regions of the electromagnetic spectrum[36,37] due to the earlier realization of viable red and blue LED-light sources with high energy efficiency. Another reason for this focus was that the important photosynthetic photoreceptors such as chlorophyll-a and cryptochromes have their absorption peaks in the red and blue spectral regions, respectively. These absorption peaks can be easily matched with LEDs with appropriate peak wavelengths. These two aspects are crucial in the promotion of the efficient photosynthesis and the balanced morphology of the plants.

The current challenges faced by the greenhouse industry are related to market needs, environmental impact and energy. The energy efficiency of greenhouses is one of the aspects that LED lighting can help to improve.

Energy efficiency improvements can be attained by maintaining or minimizing the inputs (e.g. energy, fertilizers, water and CO_2), while maximizing or maintaining the outputs (e.g. edible biomass per unit area). Consequently, the lighting regime should allow for the maximum crop productivity while reducing or maintaining the electricity consumption. Therefore, after the appropriate light spectrum in terms of crop growth and development has been defined, the second most important design aspect of LED luminaires is the maximization of electrical efficiency. Although apparently contradictory, the utilization of the most energy-efficient luminaire may not necessarily lead to the highest energy-saving performance of the lighting installation. The light distribution of the luminaires and the mounting height of the installation may also be optimized to maximize the efficient use of energy. LEDs allow the optimization of both aspects. In this way, the application efficiency can be enhanced using light where it is needed (i.e. on the plants) while reducing light pollution. The sort of light distribution required to achieve this goal is dependent on the morphological structure (i.e. height, size and shape) of the crop species to be lit.

The extensive use of HPS lamps excessively increases the ambient temperature of the greenhouse in the intensive cultivation of high-wire crops like tomato and cucumber. To diminish the negative effects of high temperatures on crop growth, regular ventilation is required, resulting in a decrease in the fed CO_2 as well as a loss of energy. The reduced CO_2 concentration decreases the rate of photosynthesis and consequently plant productivity, ultimately impairing the overall energy efficiency of the greenhouse production. The high energy efficiency potential of LEDs can offer an important contribution to address this problem. Based on the latest updates on technological roadmap targets for LED's efficiencies, the photosynthetic efficacy of red LEDs is estimated to be double that of the HPS lamp by the year 2020, as shown in Figure 3.

5. Challenges and opportunities in horticultural lighting

There are three global problems that mankind is currently facing, for which solutions have to be urgently found: The continuously increasing demand for food and energy, the need to control CO_2 emissions in order to reduce the greenhouse effect and climate change together with the related increase in natural disasters. The increasing demand for energy and the strong global dependence on fast-depleting fossil fuels have led to high prices for oil and electricity. Furthermore, this situation has not been helpful in promoting a fast recovery from the most recent global economic recession that started in December 2007 in the USA.

Similar to energy, food production has also been under pressure with an unprecedented rise in prices during the years 2007 and 2008. According to the Food and Agriculture Organization, the increase in international prices of food in 2010 was closer to the peak reached in 2008. It is estimated that at the current pace of

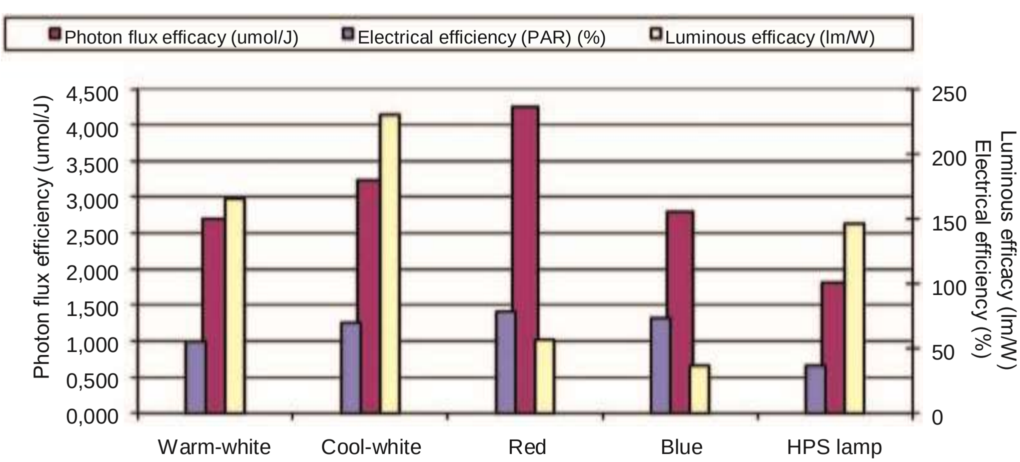

Figure 3 Estimates of photon flux efficacies, electrical efficiencies and luminous efficacies by the year of 2020 for a phosphor-converted warm-white (2500K CCT) and cool-white (5500K CCT) LEDs; red (660nm) and blue (450nm) LEDs; and a conventional 400-WHPS lamp

food demand, the production rates per hectare will need to be improved by 50% if disaster is to be avoided.[38] Therefore, it is of utmost importance to find ways to produce food efficiently, sustainably and safely to feed future generations. Cultivation of food in close proximity to the consumers and in controlled environments such as greenhouses, phytotrons and plant factories is one possibility that needs to be seriously considered. Food cultivation in closed and controlled environments allows for the optimization of the main plant growth parameters such as the abiotic conditions (i.e. temperature, water, humidity, CO_2 and light). Additionally, this solution allows for year-round safe production of food independent of the weather conditions or season of the year. Year-round production will significantly increase the annual crop productivity (kg/m^2) and consequently make land use more efficient. In Scandinavia, the yearround productivity of cucumber has been increased from $50kg/m^2$ to $250kg/m^2$ annually by utilizing modern cultivation methods and lighting technologies. However, energy is required in order to realize and maintain this artificial and complex growth environment. Although the environmental impact and market competitiveness are currently important aspects in year-round greenhouse food cultivation, the fundamental issue is still energy and energy efficiency.

Energy accounts for a substantial proportion of the total production costs in yearround crop production in greenhouses. The electricity contribution to overhead costs may, in some crops, reach approximately 30%.[39] Typically, electrical appliances consume around 20% of total energy, which is used mainly by artificial lighting while the rest of the energy is mostly used for heating. Although renewable wood-based products are increasingly used for greenhouse heating, fossil fuels are still significant energy sources. Fossil fuels are the main contributor to the CO_2 foot-print of greenhouse products. Thus, the necessity of using fossil fuels is the main negative factor in terms of environmental impact. However, in terms of market competiveness, the situation is the opposite. Costs related to electricity consumption are significantly higher than costs resulting from the use of fossil fuels for heating. By reducing the energy inputs (e.g. light, temperature and fertilizers), important reductions on costs may be achieved with a corresponding impact at consumer prices. These reductions can be achieved through a wide range of developments and improvements. One of them is through the development of crops that require lower energy inputs. Another approach is through the improvement of the energy efficiency of appliances such as light sources. Until now, there has been little or no increase in the intrinsic conversion efficiency of the absorbed radiation into plant dry matter (i.e. biomass) by individual leaves.[8,38] Improvement of the conversion efficiency may be sought using appropriate control of light spectrum, quantity and periodicity. Unlike cultivation in open fields, in the near future, the lighting conditions in closed environments are expected to be fully controlled. Semiconductors, such as LEDs, are the ideal candidates for the implementation of these lighting environments in the near future. Improving productivity in controlled environment may, in the future, be achievable also by implementing multilayer cultivation systems. These systems are intended to make efficient use of the required land area for the cultivation of several crop species. In that way, higher spatial plant density and consequently improved plant productivity per unit area can be achieved in comparison to the conventional approach with just one growth layer. LED lighting will be a key aspect for market competiveness of multilayer growing systems. The daylight contribution in these growing environments can be significantly less than that in conventional single-layer cultivation used nowadays. Therefore, more artificial lighting will be required to compensate for the loss of daylight, increasing the energy demand per unit area. LEDs are the ideal light sources to be integrated into multilayer cultivation due to their small size, controllability, electrical efficiency and absence of heat radiation which allows for mounting distances closer to the plants.

6. A short note on metrics

The spectral power distribution of solar radiation, as measured at the surface of the Earth, has a broad wavelength band between around 280nmand 2500nm. However, only 50% of the radiation reaching the surface is PAR.[40] PAR, according to the Commission Internationale de L'Eclairage recommendations comprises the radiation in the wavelength region between 400nmand 700nmof the electromagnetic spectrum.[41] The laws of photochemistry can generally express the way that plants harvest radiation. The dual character of radiation makes it behave as an electromagnetic wave when propagating in space and as particles (i.e. a photon or quantum of radiant energy) when interacting with matter. The photoreceptors are the active elements mainly located in the leaves of plants. Some known photoreceptors such as chlorophylls are responsible for the photon capture and for conversion of its energy into chemical energy. Due to the photochemical nature of photosynthesis, the photosynthetic rate, which represents the amount of O_2 evolution or the amount of CO_2 fixation per time unit, correlates well with the number of photons falling per unit area per second on a leaf surface. Therefore, the recommended quantities for PAR are based on the quantum system and expressed using the number of moles (mol) or micromoles (mmol) of photons. The recommended term to report and quantify instantaneous measurements of PAR is the photosynthetic photon flux (PPF) or photosynthetic photon flux density. These give the number of moles of photons falling at a surface per unit area per unit time. In spite of all this, a fundamental question should be raised in relation to measurement of PAR: 'Why do we need to measure PAR in plant growth applications?' If the only reason is to compare the relative photosynthetic rates of plants growing under the same light spectrum, then the present system should be sufficient. However, if the photosynthetic performance of different light sources is to be compared, then the presently used metrics based on the quantum system are erroneous, not coherent and therefore fail. The reason for the failure is that the spectrum of the light influences the plant photomorphogenesis as well as photosynthesis. Therefore, light sources with different spectra can photosynthetically perform differently even though identical PPF is provided to the same plant species. Perhaps a novel and more coherent approach should take into account the spectral response curve for the photosynthesis of the specific crop to be lit. The establishment of a coherent measurement system to quantify radiation in plant growth is desirable in order to allow for more appropriate design, characterization, comparison and optimization of luminaires and installations for plant growth in the future. Additionally, with respect to the economics of this, it is expected that a coherent metrology will better forecast and correlate investments in lighting with the expected benefits. Finally, it is desirable that a new metrology improves the interoperability, interchangeability and reproducibility of results in plant research.

A last important aspect is related to the definition of the PAR spectral range. The discovery of the new red-shifted chlorophyll photoreceptor (chl f) with an absorption peak extending up to 750nmand with a maximum at 706nmindicates that the definition of the PAR spectral region between 400nmand 700nmis not entirely correct. The discovery of chl f suggests that photosynthesis extends further into the infrared region than previously thought and therefore the lighting metrics should be updated accordingly. For instance, the efficiency of blue

LEDs increases approximately 6% if an extended PAR region (i.e. 300–800nm) is considered. A similar increase happens with HPS lamps where the electrical efficiency can increase by more than 10% if the infrared limit of PAR is extended from 700nmto 830nm.

7. Concluding remarks and future aspects

In this paper, we have given a broad overview of current and future challenges facing horticultural lighting. The utilization of artificial lighting in controlled or closed growth environments offer great opportunities for the cultivation of food year-round, locally, safely and independently of the increasing unfavourable extreme weather conditions resulting from global warming and climate change. New lighting technologies such as LEDs will have a vital role in the implementation of optimized lighting regimes and novel growing systems for improved plant growth and productivity. However, to make full use of the potential offered by LEDs in horticultural lighting, it is necessary to fully understand the mechanisms and processes mediating plant responses to light. Photosynthesis is one of these processes. Photosynthesis is of utmost importance to mankind and to the preservation of the natural environment. In future, the optimization of photosynthesis and more specifically the efficient conversion of radiation into biomass will offer new possibilities to increase food production. Exploring crop productivity limits and improving the energy efficiency and costs of light in horticultural production are additional goals. Improved metrics and measuring methods to properly quantify PAR are indispensable to define light costs in horticulture and allow for interoperability, interchangeability and reproducibility of results.

References

1 Kalyanasundaram K, Graetzel M. Artificial photosynthesis: biomimetic approaches to solar energy conversion and storage. Current Opinion in Biotechnology 2010; 21: 298–310.

2 Anemaet I, Bekker M, Hellingwerf K. Algal photosynthesis as the primary driver for a sustainable development in energy, feed, and food production. Marine Biotechnology 2010; 12: 619–629.

3 Gust D, Moore TA, Moore AL. Solar fuels via artificial photosynthesis. Accounts of Chemical Research 2009; 42: 1890–1898.

4 Blankenship RE, Tiede DM, Barber J, Brudvig GW, et al. Comparing photosynthetic and photovoltaic efficiencies and recognizing the potential for improvement. Science 2011; 332: 805–809.

5 Wang X, Koyama Y, Kitao O, Wada Y, Sasaki S, Tamiaki H, Zhou H. Significant enhancement in the power-conversion efficiency of chlorophyll co-sensitized solar cells by mimicking the principles of natural photosynthetic light-harvesting complexes. Biosensors and Bioelectronics 2010; 25: 1970–1976.

6 Zhu X, Long SP, Ort DR. What is the maximum efficiency with which photosynthesis can convert solar energy into biomass?. Current Opinion in Biotechnology 2008; 19: 153–159.

7 Larkum A. Limitations and prospects of natural photosynthesis for bioenergy production. Current Opinion in Biotechnology 2010; 21: 271–276.

8 Long SP, Zhu X, Naidu SL, Ort DR. Can improvement in photosynthesis increase crop yields?. Plant, Cell and Environment 2006; 29: 315–330.

9 Cashmore AR, Jarillo JA, Wu YJ, Liu D. Cryptochromes: blue light receptors for plants and animals. Science 1999; 284: 760–765.

10 Spalding EP, Folta KM. Illuminating topics in plant photobiology. Plant, Cell and Environment 2005; 28: 39–53.

11 Du H, Fuh RA, Li J, Corkan A, Lindsey JS. PhotochemCAD: A computer-aided design and research tool in photochemistry. Photochemistry and Photobiology 1998; 68: 141–142.
12 Sager JC, Smith WO, Edwards JL, Cyr KL. Photosynthetic efficiency and phytochrome photoequilibria determination using spectral data. Transactions of the American Society of Agricultural Engineers 1988; 31: 1882–1889. 13 Pinho P, Moisio O, Tetri E, Halonen L. Photobiological aspects of crop plants grown under light emitting diodes. Proceedings of the CIE Symposium 04, LED Light Sources: Physical Measurements and Visual and Photobiological Assessment – Tokyo, Japan, Jun 7–8: 2004: 71–74. CIE Publication x026:2004, Vienna: CIE, 2004.
14 Fankhauser C. The phytochromes, a family of red/far-red absorbing photoreceptors. The Journal of Biological Chemistry 2001; 276: 11453–11456.
15 Christophe A, Moulia B, Varlet-Grancher C. Quantitative contributions of blue light and PAR to the photocontrol of plant morphogenesis in Trifolium repens (L.). Journal of Experimental Botany 2006; 57: 2379–2390.
16 Folta KM, Childers KS. Light as a growth regulator: Controlling plant biology with narrow-bandwidth solid-state lighting systems. HortScience 2008; 43: 1957–1964.
17 Christie JM, Briggs WR. Blue light sensing in higher plants. The Journal of Biological Chemistry 2001; 276: 11457–11460.
18 Mouritsen H, Janssen-Bienhold U, Liedvogel M, Feenders G, Stalleicken J, Dirks P, Weiler R. Cryptochromes and neuronal-activity markers colocalize in the retina of migratory birds during magnetic orientation. Proceedings of the National Academy of Sciences of the United States of America 2004; 101: 14294–14299.
19 Krizek DT. Influence of PAR and UV-A in determining plant sensitivity and photomorphogenic responses to UV-B radiation. Photochemistry and Photobiology 2004; 79: 307–315.
20 Chen M, Schliep M, Willows RD, Cai Z, Neilan BA, Scheer H. A red-shifted chlorophyll. Science 2010; 329: 1318–1319.
21 Rizzini L, Favory J, Cloix C, Faggionato D, O'Hara A, Kaiserli E, Baumeister R, Scha¨ fer E, Nagy F, Jenkins GI, Ulm R. Perception of UV-B by the Arabidopsis UVR8 Protein. Science 2011; 332(6025): 103–106.
22 Tevini M, Teramura AH. UV-B effects on terrestrial plants. Photochemistry and Photobiology 1989; 50: 479–487.
23 Dougher TA, Bugbee B. Evidence for yellow light suppression of lettuce growth. Photochemistry and Photobiology 2001; 73: 208–212.
24 Kim HH, Goins GD, Wheeler RM, Sager JC. Stomatal conductance of lettuce grown under or exposed to different light qualities. Annals of Botany 2004; 94: 691–697.
25 Folta KM, Maruhnich J. Green light: A signal to slow down or stop. Journal of Experimental Botany 2007; 58: 3099–3111.
26 Wang Y, Noguchi K, Terashima I. Photosynthesis-dependent and -independent responses of stomata to blue, red and green monochromatic light: Differences between the normally oriented and inverted leaves of sunflower. Plant and Cell Physiology 2011; 52: 479–489.
27 Massa GD, Kim H, Wheeler RM, Mitchell CA. Plant productivity in response to LED lighting. HortScience 2008; 43: 1951–1956.
28 Wheeler RM. A historical background of plant lighting: An introduction to the workshop. HortScience 2008; 43: 1942–1943.
29 Yanagi T, Yachi T, Okuda N, Okamoto K. Light quality of continuous illuminating at night to induce floral initiation of fragaria chiloensis L. CHI-24-1. Scientia Horticulturae 2006; 109: 309–314.
30 Goins GD, Yorio NC, Sanwo MM, Brown CS. Photomorphogenesis, photosynthesis, and seed yield of wheat plants grown under red light-