

The Light Spectrum for Plant Cultivation: A Source of Colourful Arguments

Running title: Light spectrum for plant cultivation

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Abstract

The concept of “wasted illumination” and its application to the design of light sources for plant cultivation is a good example of misuse of reductionism. Equating instantaneous rate of photosynthesis to crop yield is a prevailing but
5 nonsensical idea, and in the case of the design of red plus blue light sources an extreme case of ignoring the multiple regulatory mechanisms and interactions present in individual plants and crop canopies. The misconception about red plus blue LED growth lights has been challenged already, but in this article we describe in detail several of the mechanisms that have been ignored in early attempts to
10 optimize the spectrum of light sources for plant cultivation. They exemplify very well the dangers of a purely reductionist approach to scientific research that ignores the complexity inherent in biological systems, their multiple feedback loops and hierarchical organization. Translation of basic research results into applications that benefit growers is a complex up-scaling problem not amenable to
15 easy short-cuts.

The problem

What are the targets for the design of grow lights? Ultimately, growers’ net income and sustainable use of resources. Efficient energy use is relevant to both targets. The targets can be split into more specific targets, each of which cannot be
20 considered in isolation: conversion efficiency of electrical energy to photons (expressed as $\mu\text{mol J}^{-1}$), whole growth-cycle PAR to produce yield conversion efficiency, length of production cycle (i.e., greenhouse or indoor space occupation time), produce quality (i.e., income per unit produce), ancillary costs like cooling or heating, pest control, CO₂ fertilization. Even the time course of the spot price of
25 electricity through the day needs to be considered, and in the case of greenhouses, also the availability of natural light and its spectrum. Most of these secondary targets can be further split into sub targets as we will discuss below.

Considering advertising from LED (as electronic components) manufacturers one can see three camps: companies still favouring blue plus red illumination as the

30 most efficient, e.g., ams-Osram, those advertising white LEDs as very significantly
improving yields, e.g., Nichia, Samsung, Seoul Semiconductor, and Bridgelux, and
those not promoting either but selling LEDs aimed at both approaches, e.g.,
Luminus Devices, and Lumileds. Seoul Semiconductor currently advertises its
“Sunlike” white LEDs with a visible light emission spectrum similar to that of
35 sunlight as better for plant cultivation than ordinary white LEDs. Advertising from
Nichia for its recently released “Hortisolis” LEDs recognizes much of the
complexity of the problem.

Considering companies selling LED-based luminaires for horticulture, there is also
great variation and in some cases advertising is not consistent between the LED as
40 components and luminaire-producing divisions of the same companies, e.g.,
Osram. Valoya has produced LED fixtures with broad spectra since its inception in
2009, but only publishes spectra with very low wavelength resolution as part of
growth luminaire specifications. Nowadays, Valoya as some other major suppliers
of luminaires, e.g., Fluence and Signify/Philips horticulture, sells luminaires with
45 both types of spectra.

The arguments to defend one or the other approach vary to some extent, but blue
plus red illumination is most frequently justified by comparison to the in-vitro
absorption spectrum of chlorophyll, and white light tailored for plant cultivation
is justified based on yield comparisons, quality of produce and on improved work
50 conditions. These inconsistent arguments are reflected in the large variation
among the spectra of the LED fixtures offered to growers and the confusion about
their suitability for different production systems.

If we consider the current situation, both red plus blue and broad spectrum LEDs
and LED growth lamps are widely advertised as excellent for use in commercial
55 horticulture. There are variations around these two types of spectra but the two
approaches are different in concept and implementation. Red plus blue LED
fixtures most frequently use two types of LED chips, each type directly emitting
light in a narrow range of wavelengths in the red or blue region (Figure 1). Broad
spectrum LEDs rely on a second stage to broaden the range of emitted wavelengths
60 (Figure 2). They are in almost all cases blue or violet emitting LEDs coated with
fluorescent pigments. These pigments absorb the blue or violet radiation and
re-emit it at longer wavelengths, a process that decreases the conversion efficiency
of electrical energy into photons. Some LED fixtures use a combination of these

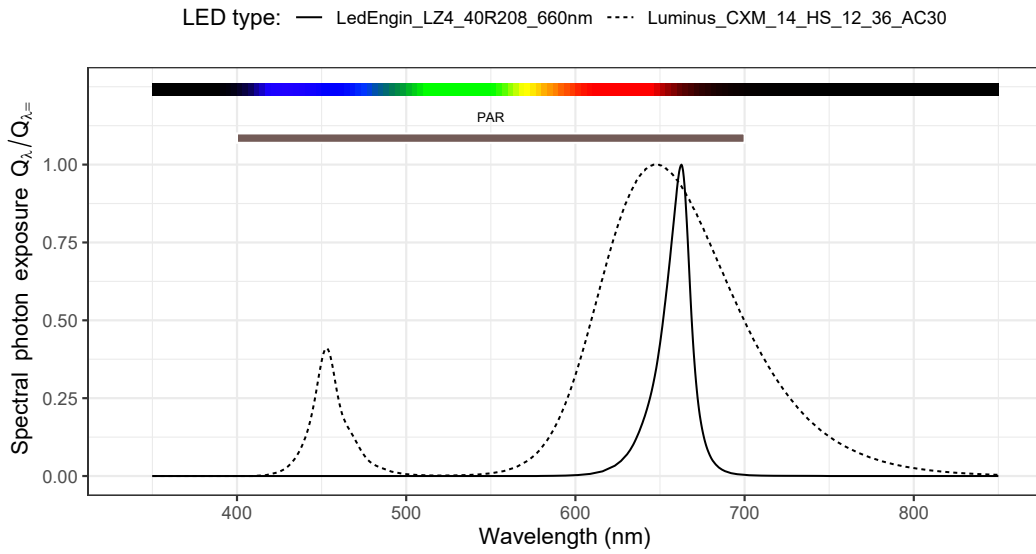


Figure 1: Emission spectrum of a “deep” red SMD LED (LedEngin-Osram, USA), and a “purple” blue plus red COB LED (Luminus Devices, USA). Both LEDs sold for plant cultivation.

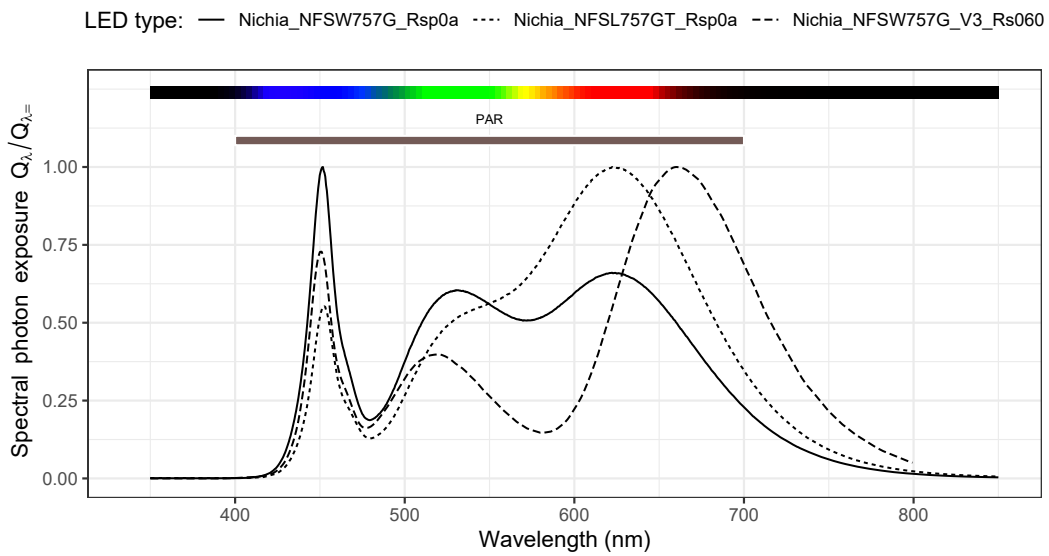


Figure 2: Emission spectra of three broad-spectrum SMD LED types for horticulture rated at 3000 K, 5000 K and 5300 K (Types NFSW757G-Rsp0a, NFSL757GT-Rsp0a, and NFSW757G-V3-Rs060, from Nichia, Japan).

approaches to increase the conversion efficiency by combining the use red LED
65 chips with broadband LED chips for blue plus green light (Figure 3).

As red photons carry less energy than photons of shorter wavelengths such as
blue or green, more photons can be generated, in principle, per joule of energy the
longer the wavelength. Any photon that is absorbed by a pigment, as long as it
carries enough energy to trigger excitation, contributes equally to a photochemical
70 reaction. In principle, absorbed red photons can be expected to be equally
effective in driving photosynthesis than absorbed blue or green ones. Thus, if we
ignore the optical properties of leaves and plant canopies, the regulatory effects of
light on plant growth and development, and the complexities of the
photochemistry and biochemistry of photosynthesis, we could conclude that pure
75 red light of a wavelength close to 650-680 nm would be best. It is clear that this is
far from correct, because we have ignored some fundamental aspects of plant's
photomorphogenesis and physiology. A recent study suggests as most efficient a
spectrum composed by 14% blue, 20% green and 66% red (Figure 6 in Kusuma
et al., 2020), while the authors also highlight the need to consider other factors in
80 addition to efficiency (Figure 3).

An argument that persists tenaciously, especially in advertising, is that red and
blue light are more efficiently absorbed by chlorophyll making them drastically
better at driving photosynthesis than other wavelengths, and consequently also
best for plant cultivation in horticulture. This idea has been taken to its extreme
85 in the controversial concept of "wasted illumination" used to describe
photosynthetically active radiation of other wavelengths than blue or red. The
design of light sources for plant cultivation using as criterion this idea is a clear
example of answering the wrong question.

Any plant scientist or agronomist, should know that there is much more behind
90 plants' growth than the absorption of light by a chlorophyll extract in a test tube.
There is certainly no lack of knowledge, in fact, nearly 60 years ago, they already
knew better. The output from Sylvania Gro-lux fluorescent tubes of the 1960's was
enhanced in blue and red light compared to both warm white or daylight
fluorescent tubes and only in some cases lead to increased growth. Marquis (1965)
95 stated in the discussion of his study on the growth of birch seedlings under these
three types of lamps: "The special fluorescent tubes (Gro-lux) did not produce
better growth of birch seedlings than the other tubes in spite of their high energy

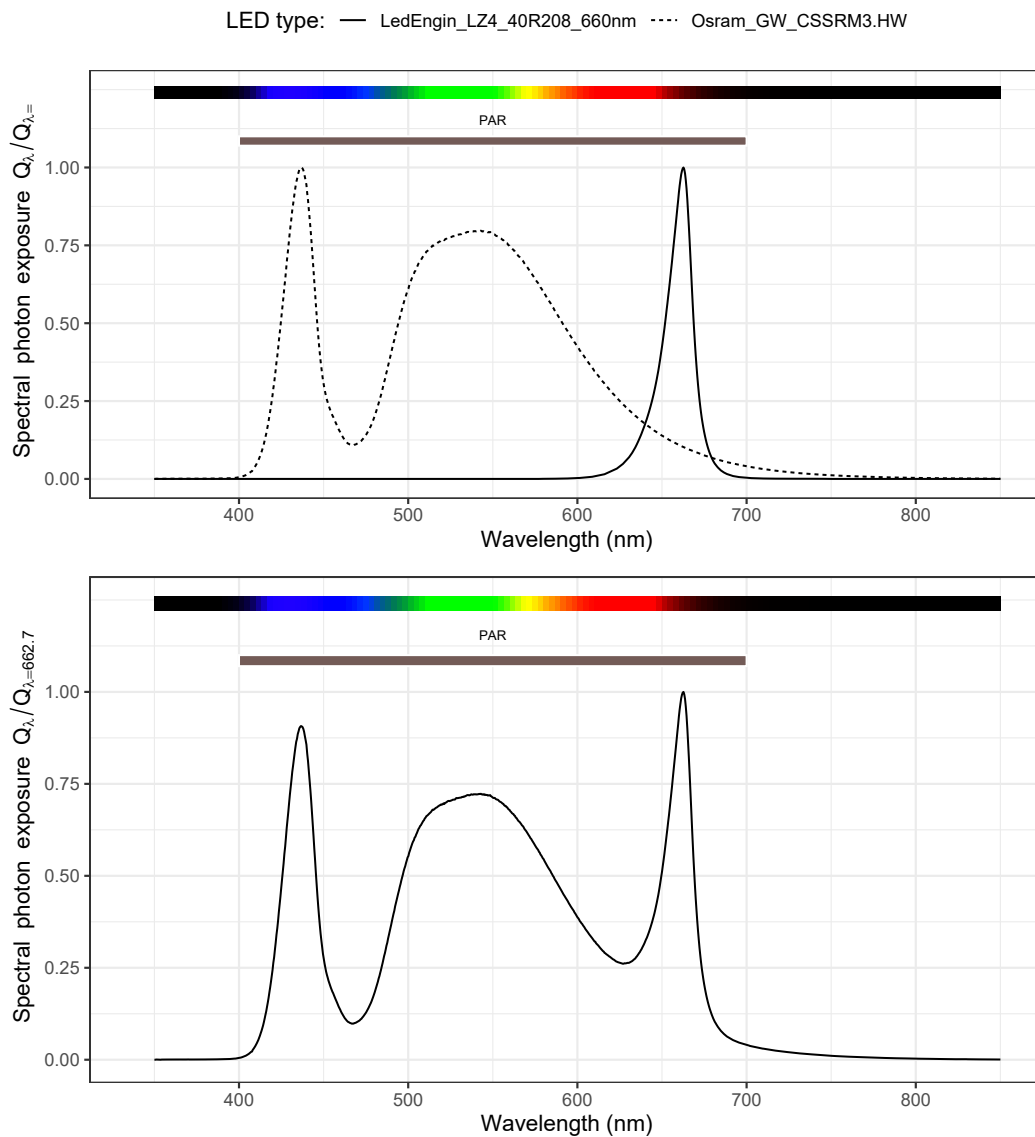


Figure 3: Spectra of narrow- and broadband LEDs and their combination. The spectra of Led Engin LZ4-40R208 leds emitting at 660 nm (nominal) and broad-spectrum Osram GW-CSSRM3-HW grow leds (top) were combined *in silico* in 4:1 proportion based on photon irradiance (bottom) to approximate the spectrum proposed by Kusuma et al., Fig. 6.

output in the regions of maximum chlorophyll absorption. Presumably yellow-green light is utilized in photosynthesis by birch seedlings to a much greater extent than is suggested by the spectral absorption characteristics of chlorophyll.” In the early 1970’s McCree’s research leading to his proposal for the use of PPFD (photosynthetic photon flux density, or PAR photon irradiance) as a useful measure of light for plants was conclusive in that the quantum efficiency of blue and green light was only slightly less than that of red light (McCree, 1972a,c). Obviously, in addition *slightly* more green light than red or blue light is reflected and transmitted by leaves (McCree, 1972a,c).

Fifty years have passed since PAR was proposed as a measure of light useful for plant growth. Nowadays, the use of PAR is almost universal, and PAR gives equal weight to blue, green and red photons, contradicting the idea that green light is wasted. PAR was designed as an approximate measure, useful in sunlight and artificial white light (McCree, 1976). Some recent work with LED light sources has questioned the relevance of the PAR definition for light sources that markedly differ from natural light (Zhen and Bugbee, 2020; Zhen et al., 2022). This serves as a reminder that PAR was never intended to faithfully represent the action spectrum of photosynthesis but rather to be an approximation, similar to illuminance for human vision, that would be within $\pm 10\%$ of the true value in a fair number of important species and conditions (McCree, 1976). The criticisms raised on PAR, however, relate to the limits at 400 nm and 700 nm, i.e., whether UV-A (wavelengths shorter than 400 nm) and FR (wavelengths longer than 700 nm) should be given some weight other than zero when estimating light useful for photosynthesis.

Evidence for the importance of plant morphology, and the key role of *leaf area ratio* (the ratio between the leaf area of a plant and its total dry biomass) as a determinant of whole-plant growth rate is far from new (Hunt, 1982; Kuroiwa et al., 1964; Sestak et al., 1971). Furthermore, the concept of harvest index (the ratio between harvestable biomass to total plant biomass) proposed by C. M. Donald has been used in agricultural research for 50 years (Hay, 1995, Figure 1). We also have been aware that the light spectral quality affects the morphology of plants (Smith, 1976) and the life-span of leaves (Rousseaux et al., 1996), and consequently has a bearing on both the growth, i.e., accumulation of biomass (Aphalo, 2010; Aphalo and Ballaré, 1995; Aphalo and Sadras, 2021; Casal, 2013a) and determination of the harvest index (Casal, 2013a). The importance of plant

morphology on light distribution within canopies (Monsi and Saeki, 1953) and of anatomy on light distribution within leaves has been also recognized for a
135 long-time (Vogelmann and Björn, 1984). Interestingly, experimental data, models and analyses addressing the problem and its complexity are also available in more recent scientific literature (e.g. Yoshida et al., 2016).

Clearly the problem is not lack of knowledge, but our failure to grasp the role played by complexity and the need to consider the context in which
140 photosynthesis takes place, i.e., ignoring interactions, levels of organization and temporal and spacial scales. So, to us an additional interesting question is how could so many people ignore what should have been obvious? Or at least obvious enough to require experimental evidence given that existing knowledge made the argument based on light absorption by chlorophyll implausible. We think the
145 answer is that designing a universally good spectrum is impossible. If we consider all factors involved, we end facing multiple problems instead of a single one. Consequently, the problem was drastically simplified to include only those aspects that can be thought as invariant over crop species, geographic locations and cultivation approaches. Thus, focus remained only in the in-vitro absorption
150 spectrum of chlorophyll, which is close to invariant, and the efficiency of LEDs measured as photons of per joule which is independent of the use cases. This oversimplification reduced a complex biological problem into a physicochemical one with a simple and exact answer. The difficulty is that this answer does not apply to the original question that was in need of an answer: what light spectrum
155 best fulfils growers' needs.

Why this misconception has persisted so tenaciously can be, likely, explained by human cognitive psychology. What makes a (pseudo-)scientific argument feel credible to non experts? a. Accompanying the text with a plot (any plot!), b. Internal coherence of the argument's logic and c. familiarity (See Cognitive easy, in
160 Kahneman, 2012, pp. 59-70). The argument relating good LED spectra to the chlorophyll absorbance spectrum in vitro is almost always presented together with a plot. The argument is internally coherent even though the spectrum of chlorophyll in vitro is not the main determinant of the photosynthetic rate and the photosynthetic rate is frequently not the main limitation on plant growth. The
165 argument has been repeated so many times that is now familiar to growers and sellers.

Biological systems are dominated by non-linear responses and interactions (Capra and Luisi, 2014). Feedback loops and intertwined signalling pathways are the norm. These systems have a hierarchical structure, with “behaviour” at higher levels of organization that is rarely predictable through simple extrapolation or summing of the result of activities at lower levels (Aphalo, 2010; Aphalo and Sadras, 2021). This complex regulation network and regulatory interactions have been tuned by natural and artificial selection to provide fitness and/or yield, respectively, under a certain range of environmental conditions (Sadras et al., 2021). Among these conditions, the light spectrum is used by plants as a source of information controlling the regulation of plant form and function. These regulatory responses depend on temporal and spatial integration of informational cues and signals carried by light as variation in its spectrum (color), flux rate, direction and timing. The information is in most cases dependent on environmental correlations that originate the “meaning” of cues and signals (Aphalo and Sadras, 2021). Consequently, we can not think just in terms of energy and quantum efficiency when choosing spectra, we need to be also aware that the properties of the spectrum will affect morphology, growth and development as a result of plant responses that have been selected under natural light as favorable to fitness.

It is too easy to forget, or not recognize, the wider implications of the data-analysis maxim “*Far better an approximate answer to the right question, which is often vague, than an exact answer to the wrong question, which can always be made precise.*” (Tukey, 1962, p. 13). Why would then anybody look for answers to approximate problems? We suggest this is because exact answers to oversimplified problems are much easier to communicate and grasp than approximate answers to complex problems, making exact answers more credible even when they do not address the right problem (Kahneman, 2012; Kahneman et al., 2021). Dealing with complexity and verbally communicating ideas about complex systems is inherently difficult for most humans and this can be traced back to how humans think (Grandin, 2022).

The determinants of plants’ growth and crop yield are many, and they interact. As we argue in detail below, the mechanism through which the light spectrum affects the growth of plants are many and most of them have been identified long ago. These multiple mechanisms interact in ways that make the problem of deciding on the best spectrum for artificial illumination for crop production very complex. Given the complexity of the problem and current state of knowledge it is only

possible to provide approximate answers. Furthermore, it is currently, and will remain in the future, difficult to translate experimental results into simple recipes applicable across different production systems. On the other hand the current
205 state of affairs where recipes are based on a very approximate and flawed analyses of the problem can be seriously misleading and damaging to growers.

The aim of this review is to characterize the “right question(s)” considering the context under which crop plants are to grown vs. the one where they have evolved or have been artificially selected (see Denison, 2012). We will next analyse the
210 factors involved and assess the steps needed to reach useful approximate answers. We will also justify our view that it will never be possible to reach the goal of a single all-encompassing answer to the right problem, because each crop species and type of production system generates a distinct “right problem” requiring a distinct approximate answer. Although we will not discuss this further in this
215 review, clear differences in responses exist among cultivars of a given crop (Kusuma et al., 2022) and among plant species.

We hope readers can keep in mind while reading this paper the words of John D. Cook (2008) “...you’ll probably face less criticism if you produce exact solutions to unrealistic problems than if you produce approximate solutions to realistic problems.
220 At least that’s what I’ve seen. I suppose this is because it takes less understanding to find fault with your solution than to evaluate your choice of problem to solve.”

Describing light

Colour vs. wavelength

Light is defined as electromagnetic radiation that can be perceived by the human
225 eye. ISO and CIE standards provide a mapping of wavelength ranges to colour names as seen by humans. Colours as defined in these standards are not used in plant sciences or agriculture. However, some of the same colour names are used to refer to wavelength ranges relevant to plants.

Another descriptor of light colour is colour temperature, expressed in degrees
230 kelvin. Colour temperature values are assigned by matching a lamp emission spectrum to the emission spectrum of a black body, *as perceived by human vision*. It is technically called, coordinated colour temperature or CCT, and higher

temperatures correspond to bluer colours and lower temperatures to redder colours.

235 Finally the colour reproduction index or CRI is based on comparing colours as seen by humans under standardized ‘ideal’ spectra of a similar CCT and actual illumination spectra, or alternatively, by actually observing “colour patches” under different light sources. Consequently, CRI is a measure of how much colours as seen by humans under a real light source deviate from how they are seen under an
240 ideal spectrum, with a value of 100 corresponding to undistorted perception of colours. Nowadays, CCT and CRI values are provided by most suppliers for lamps emitting white light. The procedure for the computation of CCT and CRI assumes that light is not far from being seen as white, thus, for some types of luminaires used for plant cultivation CCT and CRI are undefined.

245 Standard ISO21348 (Technical Committee ISO/TC 20, 2007) provides a convenient summary of mappings of wavelength ranges to names, including the split of ultraviolet (UV) radiation into UVC, UVB and UVA (Fig. 4). These wavelengths are for the most part not perceived by human vision. These definitions of UV are mostly based on the damage they can cause to organisms. Although not
250 standardized, in medicine it is common to split UVA into UVA1 (longer wavelengths) and UVA2 (shorter wavelengths). In spite of the existence since the 1930’s (Björn, 2015) of a international definition setting the boundary between UVA and UVB at 315 nm, the use of a non-standard limit at 320 nm coexists in the scientific literature, creating unnecessary confusion. This is so because in sunlight,
255 this shift by 5 nm makes a huge difference to UVB irradiance estimates, while it barely makes a difference for UVA irradiance estimates. Even though it is generally accepted that the longest wavelength limit of UVA is 400 nm, in relation to advertising for LED fixtures for plant cultivation and of LEDs as electronic components, LEDs with peak of emission at 405 nm or 410 nm are frequently
260 described as ‘UV LEDs’, creating a further source of misinformation.

Colour names as used in plant sciences are not standardized, and for a given name, drastically different to the corresponding ISO definitions described above (Fig. 4). There is no consensus within the plant research community about the use of light colour names, and definitions used tend to vary among publications.

265 Perception of light by plants’ through their numerous photoreceptors is complex, making it difficult to precisely match wavelength ranges to individual

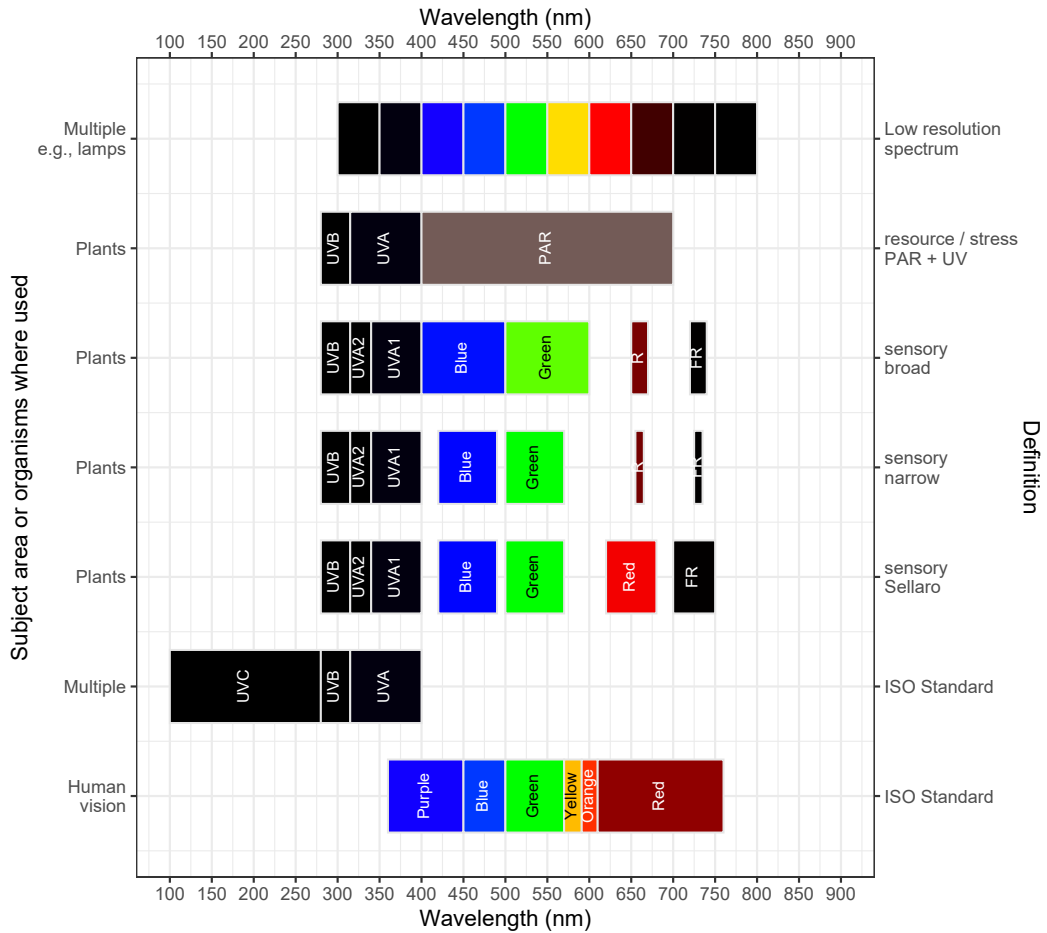


Figure 4: Wavelength and names of colours. Examples of “colour” definitions plotted against wavelength. The colour of the bars approximates the colour seen by humans averaged over wavelengths. Definitions in use for plants can emphasize light as a source of energy, labelled “resource / stress”, or light as a source of information, labelled “sensory”.

photoreceptors and plant responses. An exception, is the case of "red" and "far-red" with definitions that are predominantly used in studies involving the phytochrome photoreceptors (Smith, 1976). We must not rely just on names but
270 pay attention to the spectra of the light sources used. For example, we cannot assume that experiments using different UVA sources are comparable, as UVA1 and UVA2 radiation are perceived through different photoreceptors and UVA sources may emit either in the UVA1, UVA2 or in both regions (Rai et al., 2021).

In the case of plants, light is also a source of energy for photosynthesis, or if very
275 intense, light can cause damage to plants. McCree's definition of photosynthetically active radiation (PAR) is almost universally used in plant sciences (McCree, 1972b,c). On the other hand, how well PAR sensors of different brands and types match the theoretical PAR response varies widely (C Barnes et al., 1993; Ross and Sulev, 2000).

280 Figure 4 exemplifies some of the variation in the definitions used to describe the "colour of light". Given that definitions vary, and that the definitions used are too frequently not described in enough detail in publications, in this paper we rely on plots of the emission spectra of different light sources.

Energy vs. photons

285 For a more detailed discussion on LED technology used in horticulture see the recent review by Kusuma et al. (2020). The energy that a photon carries is proportional to the inverse of wavelength, so a far-red photon at 700 nm carries nearly half as much energy as a violet photon at 400 nm. This is reflected in the maximum possible quantum efficiencies, which for 400 nm and 700 nm photons
290 are $5.85 \mu\text{mol J}^{-1}$ and $3.34 \mu\text{mol J}^{-1}$, respectively. Of course, for real LEDs energy loss as heat is important at the LED chips and for luminaires also in the driver electronics. Nowadays specifications of LEDs intended for plant growth include a rating for their efficiency. This rating combines energy conversion efficiency and the changing energy per photon dependent on wavelength. The energy conversion
295 efficiency decreases with increasing temperature of LEDs, and how strong this effect is depends on the type of LED. We will use as examples the new OSOLON® Square LEDs for horticulture series (OSRAM Opto Semiconductors GmbH, Regensburg, Germany). The "hyper-red" (660 nm) type GH CSBRM4.24 has an

efficiency for conversion of electrical energy into radiant energy of between 80% at
300 350 mA and 74% at 700 mA, at 20 C, but this efficiency decreases, these are typical
values corresponding to 3.8 $\mu\text{mol}/\text{J}$ and 4.31 $\mu\text{mol}/\text{J}$ depending on the “bins”. If
temperature of the LED chip increases to 120 C, efficiency decreases by 18%. For a
“deep blue” LED in the same series, type GD CSBRM2.14, the efficiency for
conversion is almost the same 80% at 350 mA and 73% at 700 mA, but when
305 expressed as photons lower, between 2.47 $\mu\text{mol}/\text{J}$ and 2.91 $\mu\text{mol}/\text{J}$ depending on
the “bin”. If temperature of the LED chip increases to 120 C, efficiency decreases
by 12%. Given that the quantum yield of photosynthesis is rather similar at both
wavelengths, ignoring other things, longer wavelengths should be preferred. The
operating temperature of LED chips in a well designed fixture will be about 80-90 C
310 as higher temperature would compromise the life-span and lower temperatures
would require costly cooling. For a broader spectrum one could use LEDs like type
GW CSBRM3.HW together with the red ones instead of the blue ones (see Figure 3).
These blue plus green LEDs rely on secondary emission by “phosphors” to broaden
the spectrum of a blue LED chip. Their conversion efficiencies at 20 C are 61% at
315 350 mA and 55% at 700 mA and 2.17 $\mu\text{mol}/\text{J}$ to 2.91 $\mu\text{mol}/\text{J}$, decreasing by
approximately 13% at 120 C. As expected, efficiencies for luminaires are slightly
lower, as even the most efficient drivers incur in a loss of energy close to 10%.

The LEDs described in the previous paragraph are some of the most efficient
currently available. A simple analysis based on photons per joule indicates that to
320 maximize energy use efficiency we should prefer longer wavelengths for plant
cultivation. However, can we really assume that photons of different wavelengths
contribute equally to plant growth and crop yield as long as they are absorbed by
chlorophyll?

Chlorophyll in vitro vs. in planta

325 There is a striking difference between the shape of the absorptance spectra for
chlorophyll *in-vitro* (Fig. 5) and of leaves (Fig. 6), even though the main light
absorbing pigment in leaves is chlorophyll. There are multiple reasons behind this
difference: 1) light absorbed by other pigments than chlorophyll contributes to the
optical properties of a leaf, as well as reflection and structural optical phenomena,
330 and 2) absorption in a homogeneous solution differs from absorption in an
heterogeneous medium: the structure of leaves is such that the path of photons

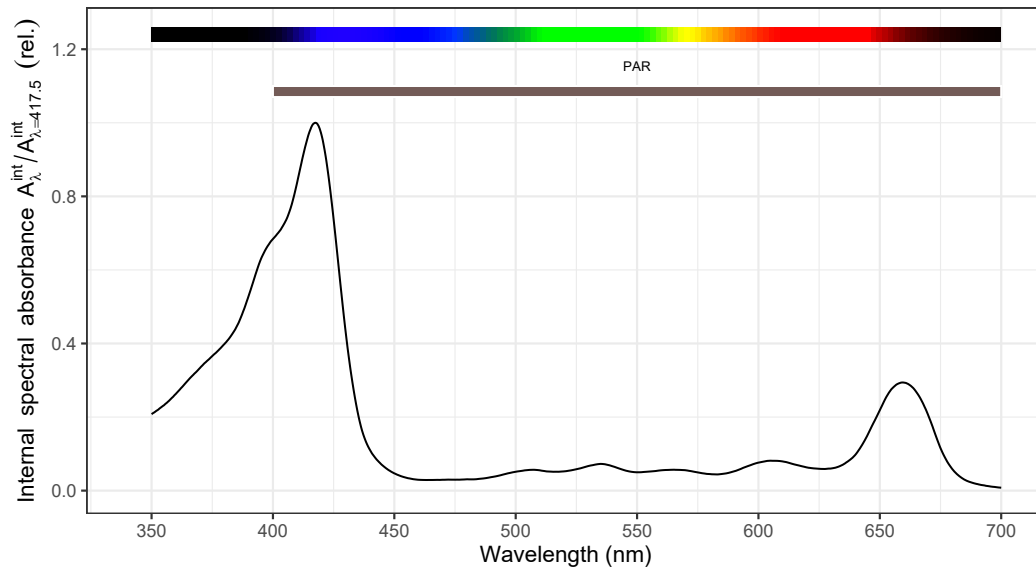


Figure 5: In vitro absorbance spectrum of chlorophyll *a* in methanol (Data described in Dixon et al., 2005).

inside a leaf unless rapidly absorbed is longer than a straight pass across the leaf. Internal scattering enhances the probability of photons impinging on pigment molecules, while the fact the chlorophyll is concentrated in discrete organelles, the chloroplasts allows photons' traversal through tissue regions with low pigment concentration, invalidating the expectations of Beer-Lambert law of light extinction. The tissue structure of leaves, especially in the case of shade-plants can even "trap" photons or in some cases direct them to specific cells through lens-like effects (Bone et al., 1985). Leaves look green to us because reflection and transmission of green photons is higher than for other wavelengths, but the difference in absorption is rather small. Plants have acquired during evolution optical and photochemical traits that greatly enhance the "harvest" and use of photons at wavelengths weakly absorbed by chlorophyll molecules. As we will see next, the absorption spectrum of a leaf is much closer in shape than that of chlorophyll in vitro to the action spectrum of photosynthesis. Light absorption by leaves, and to an extent of shape of the absorption spectrum, depend on the concentration of multiple pigments, pubescence, epidermal waxes, number of mesophyll cell layers and concomitant leaf thickness, size of cells and air spaces within the leaves. These leaf features are all dependent on the light spectrum through the action of photoreceptors responsive to UV, blue, green, red and far-red wavelengths.

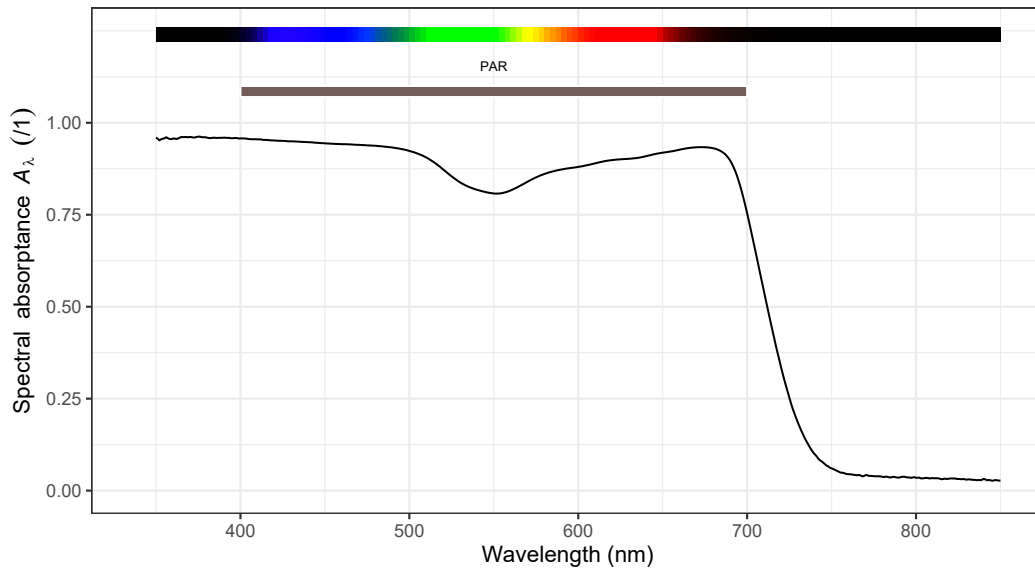


Figure 6: In-vivo absorbance of the adaxial surface of a *Betula ermanii* leaf from the first flush (Data from Noda, 2013).

The responses just described contribute to efficient canopy photosynthesis by modifying both the penetration of light into the canopy and adjusting the allocation of resources to leaf photosynthetic capacity based on the prevailing PAR irradiance at different depths in the canopy (e.g. Terashima and Hikosaka, 1995).

355 Action spectrum of photosynthesis

It is known that the light response curve of photosynthesis differs between plant canopies and individual leaves, with light saturation for canopy photosynthesis almost never reached even in full sunlight, but this has been frequently ignored during the design of LEDs for plant cultivation (Jou et al., 2015, e.g.). The
 360 allocation of resources, including photosynthates and nitrogen, within a canopy affects their use efficiency (Niinemets, 2007). The amount of leaf area per unit ground area, the thickness of leaves, their content of chlorophyll and photosynthetic enzymes and how they are displayed within the canopy, all affect the rate photosynthesis per plant dry mass. As we will discuss in later sections,
 365 both irradiance and spectral composition of light regulate the expression of all these traits, thus having a very strong impact on the relative growth rate (Aphalo

and Lehto, 1997). In nature the light spectrum and irradiance change with depth in the canopy and these responses to light have evolved such that use of multiple resources is efficient, making the scaling up from leaves to canopies difficult.

370 However, there is little if any information available about the action spectrum for canopy photosynthesis. Thus, unwillingly, we need to base this section on the action spectrum for photosynthesis of individual leaves or parts of leaves.

Not all the radiation absorbed by a leaf is converted into chemical energy through photosynthesis. Quantum efficiency of photosynthesis has a theoretical maximum
375 of *ca.* 10% and is in practice at its best only *ca.* 5%. To drive photosynthesis, photons need to be first absorbed by a pigment. In photochemical reactions, a photon needs to carry enough energy to drive the excitation of the absorbing molecule, but once this threshold is surpassed, one absorbed photon will drive one excitation event. This leads to the expectation that on an energy basis red
380 light should be more efficient at driving photosynthesis than blue or green light. However, the photochemistry of photosynthesis is a complex process, requiring multiple photons per C atom fixed, and multiple pigments participating (Shevela et al., 2017). Given the high energy involved, it is also a process that is highly regulated to prevent damage by surplus energy (Sharkey, 2020).

385 Not only chlorophyll *a* and chlorophyll *b* participate in the capture of photons. The energy of photons absorbed by carotenoids is transferred to chlorophylls and through these to the reaction centers. Blue radiation absorbed by carotenoids is only partly transferred to reaction centers, but on the other hand this “loss”, that is also under regulation, can provide protection as blue light is especially effective
390 in inducing photoinhibition (Laisk et al., 2014). As photosystems I and II (PSI and PSII) function in series, a better balance between the rates of reactions at these two steps can enhance overall quantum efficiency (Laisk et al., 2014). As the ratio between chlorophyll *a* and chlorophyll *b* is different in PSI and PSII, this balance depends on the wavelength of light. Although action spectra are usually measured
395 with monochromatic light, the balance between excitation of PSI and PSII can be enhanced by illumination with far-red light in addition to shorter wavelengths—a phenomenon called “Second Emerson Effect” (Lysenko et al., 2014). In the case of different sources of white light the enhancement has been shown to be up to 7% (McCree, 1972a). A similar enhancement for red plus blue LEDs was recently
400 reported (Zhen et al., 2018; Zhen and van Iersel, 2017) leading to the proposal of an extended definition of photosynthetically active radiation (ePAR) (Zhen et al.,

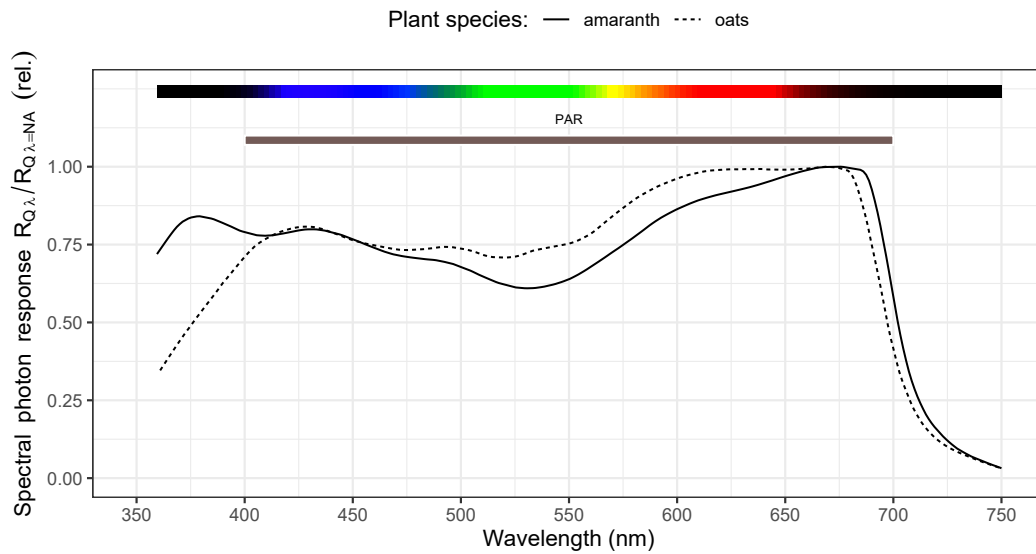


Figure 7: Action spectra for photosynthetic oxygen evolution in leaf tissues of *Amaranthus edulis* and *Avena sativa* (Data from McCree, 1972a) expressed on a *photon base*.

2021, and references therein). In addition, the acclimation of the photosynthesis machinery to make best use of a given irradiance depends on the perception of blue light through cryptochromes, which contributes to the regulation of the balance between light reactions and carbon reactions (Brelsford et al., 2018; Rai, 2020; Yan, 2021). This balance is crucial to the efficient functioning of photosynthesis and preventing damage by excess excitation.

Because the light response of photosynthesis by individual chloroplasts saturates at lower irradiances and more abruptly than that of leaves and that of leaves saturates at lower irradiances and more abruptly than that of canopies, optical properties and optical phenomena play an important role in determining the photosynthetic rate of leaves and canopies. This can lead to at first sight to a surprising observation: the shape of the action spectrum of photosynthesis depends on the irradiance, and thus under high irradiance green photons can drive leaf photosynthesis more efficiently than blue photons (e.g. Liu and van Iersel, 2021). Light penetration within a canopy depends on how diffuse the light is, thus light that is more diffuse can enhance whole-canopy photosynthesis (Durand et al., 2021; Li and Yang, 2015, and references therein).

The action spectra of leaf photosynthesis shown in Figures 7 and 8, as most
420 available action spectra, have been measured using monochromatic light. This is
informative about mechanisms but not a fully valid estimate for the action of
specific wavelengths when they are components of a broad spectrum or of a
spectrum with multiple peaks like that of most artificial light sources. Subtractive
and additive action spectra remain to be measured, as the quantification of the
425 effect of relatively small changes in PAR irradiance is technically difficult.

The role of UV-A radiation in driving photosynthesis depends on the species
considered and growing conditions (McCree, 1972c), with an example reproduced
in Fig. 7. This variation is positively correlated with specific leaf area (McCree,
1972c) and most likely related to the accumulation in the epidermis of flavonoids
430 and phenolic acids which might afford protection from stress damage at the cost
of impeded photosynthesis in the UV-A. In some plant species a diurnal rhythm
with large relative amplitude has been observed in epidermal UV-A transmittance
(Barnes, 2017; PW Barnes et al., 2016). It remains to be studied if a link exists
between this rhythm and photosynthesis in sunlight early and late in the day.

435 Dimming based on pulse width modulation (Aphalo, 2018) could reduce the
efficiency of photosynthesis in some situations (Tennessen et al., 1995), such as
with the usual frequencies of less than 1 kHz, low duty cycle and high irradiance
during pulses. Acclimation of photosynthesis and morphological responses to
pulsed light remain little studied while PWM dimming is frequently used due to its
440 low impact on the efficiency of the conversion of electrical power into light. The
choice of frequencies between 100 Hz and 1000 Hz is based on what pulsing is
invisible to humans. We currently cannot include the effect of pulsing in a
quantitative assessment due to a gap in current knowledge.

Growers' cost for artificial light is proportional to energy use rather than photons,
445 so it makes sense to re-express the action spectrum of photosynthesis on an
energy base (Figure 8). We saw above that the energy conversion efficiency of
modern deep-blue and hyper-red LEDs is similar, with larger variation within types
than between them. As we concluded based on the properties of LEDs, we also
here can conclude from the perspective of photosynthesis, that longer
450 wavelengths are expected to be used more efficiently. In both cases, the
justification is based on quantum physics while the *in-vitro* absorption spectrum
of chlorophyll is of little relevance, as it is very different in shape to the action

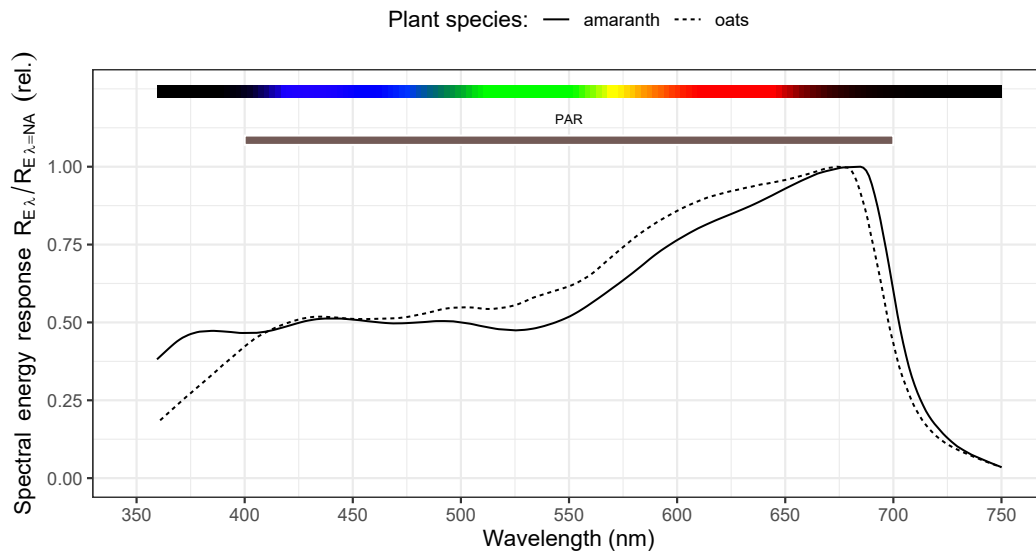


Figure 8: Action spectra for photosynthetic oxygen evolution in leaf tissues of *Amaranthus edulis* and *Avena sativa* (Data from McCree, 1972a) expressed on an *energy base*.

spectrum of photosynthesis. Thus from the perspective of energy use there is no doubt that longer wavelengths are to be preferred, however, as we will see next,
 455 light is also a source of information for plants.

Stomata and water use efficiency

At equal photon irradiance stomata tend to open more in blue light than in red light, especially if PAR irradiance is relatively low (Mansfield and Meidner, 1966; Zeiger et al., 1981). LED luminaires emitting light poor in blue can enhance water
 460 use efficiency in greenhouses (Kotiranta et al., 2015). The effects of stomatal conductance on photosynthesis and water use are non-linear and rather different in shape because of the different resistances affecting the flow of carbon dioxide and water vapour. In cold climates a lower transpiration rate decreases the need for ventilation to control air humidity, and consequently can decrease the energy
 465 needed for heating. On the other hand partly closed stomata can reduce the photosynthetic rate at a given CO₂ concentration in the greenhouse air by increasing the mesophyll to air concentration difference. However, the negative

effect on photosynthesis tends to be small when PAR irradiance and thus the rate of photosynthesis are not very high.

470 **Plant morphology and development**

Even disregarding the importance of morphology for produce quality, it cannot be ignored that changes in plant morphology have a very large impact on both relative and absolute growth rates (e.g. Aphalo et al., 1991). As light quality (colour) has a very profound effect on plant morphology, wavelengths less
475 efficiently used in photosynthesis can have non-the-less a positive bearing on light use efficiency for plant growth. Light plays a key role in the sensory ecology of plants. Photomorphogenesis of plants is controlled through the join action of a large and variable number of photoreceptors. The exact number of photoreceptors varies among plant species (e.g. 14 described in *Arabidopsis thaliana*) but taken
480 together are in most species capable of perceiving radiation all the way from UVB to near IR regions. These photoreceptors are the multiple entrances to a downstream signalling network that in concert conforms a sensory system that regulates gene expression, metabolism, catabolism, morphogenesis and development of plants (Casal, 2013b). Natural selection has tuned the sensory
485 system of plants to the environment in which they evolved—i.e. natural, usually mixed-species, vegetation canopies under sunlight. LED illumination with mixes of pure blue and red light falls outside the conditions under which natural selection has worked during evolution, thus plant responses under these conditions can be thought of as “accidental”. This probably explains the huge differences between
490 tomato and cucumber in their responses to different mixing ratios of red and blue light (Liang et al., 2021).

An important notion is that of critical stages/phases of development in annual field crops. In many cases availability of resources or exposure to informational cues can have major impact on yield or produce quality during relatively short
495 critical periods/stages of development and weak impact at other times during the growth cycle (e.g., Fischer, 1985, in wheat). Compensatory changes in yield components can play an important role in overcoming periods of low irradiance induced by shading (e.g., Labra et al., 2017, in canola). Growth light management needs to take this into account.

500 **More investment in leaf area results in faster growth**

Obviously, only light that is intercepted by foliage contributes to photosynthesis, so that even under field conditions crop production is closely and consistently related to the amount of light intercepted by the crop canopy but not to irradiance (Monteith, 1981). Interception increases with the growth and expansion of leaves
505 and decreases with their senescence. It also depends of the angle at which leaves are displayed.

Photosynthesis can be quantified using different bases for expression (e.g. Aphalo et al., 1991, and references therein). In practice, it is more convenient to express gas-exchange per unit leaf area than per unit leaf- or plant dry-mass. However,
510 from the perspective of the plant's efficiency of use of resources for growth, only expression on a mass basis is directly relevant. Two ratios link photosynthesis per unit leaf area to photosynthesis per unit plant mass (Dale and Causton, 1992). Specific leaf area (SLA), or area of leaf per unit leaf dry mass: high SLA results in higher photosynthesis per unit leaf dry mass for the same rate of photosynthesis
515 per unit leaf area. Leaf mass ratio (LMR): the fraction of total plant dry mass that is in leaves. The larger the LMR the faster the relative growth rate will be as long as there are no other limits to growth, such as PAR irradiance and supply of water and mineral nutrients.

Relatively small increases in the fraction of photosynthates allocated to the
520 production of new leaf area lead to a much larger difference in whole-plant accumulated growth, as it works like "compound interest" by accelerating the relative growth rate (Blackman and Wilson, 1951; Poorter and Remkes, 1990). Depending on the prevailing irradiance and degree of scattering of light, and the total leaf area per unit ground area (called leaf-area index, LAI), the SLA of leaves
525 leading to optimal use of radiation will be different (Anten, 2004; Anten et al., 1995).

In addition to allocation of photosynthates to new leaves, the total leaf area of a plant depends on the demography of leaves (Suárez, 2010, and references therein). That is to say, that the number of leaves present at a given time on a plant
530 depends both on the rate of formation of new leaves and the rate at which old leaves die. The spectrum of light and irradiance contribute to the regulation of the morphology of the plant as a whole, the morphology and size of individual leaves,

and the demography of leaves in a plant. Plants growing as neighbours affect each others' light environment, not only with respect to the amount of light but also
535 with respect to the light spectrum, and consequently affect each other's morphology, growth and development (Anten, 2004; Aphalo and Ballaré, 1995).

Display of leaves

The positioning of leaves in 3D space, their location on the horizontal and vertical planes, and the angle of the blade surface with respect to the horizontal and with
540 respect to the cardinal points, determine the irradiance it receives. Two effects are involved, shading among leaves and the decrease in irradiance according to the "cosine law" on surfaces not perpendicular to the direction of the light beam (Monsi and Saeki, 1953). Depending on the prevailing irradiance and degree of scattering of light and total leaf area per ground area, the display of leaves leading
545 to maximal growth and/or successful competition for light with neighbours will be different (Hikosaka and Hirose, 1997). Furthermore, the optimal angle will depend on the depth within the canopy as irradiance and scattering change with depth by the presence of the plants' own leaves and stems and those of its neighbours. The display of leaves can directly affect photosynthesis through its effect on the
550 irradiance incident on the leaf surface (i.e. absorbed photons per leaf area) and also indirectly through effects on leaf display and optical properties on the energy balance and consequently temperature of leaves. Leaf display is regulated by light through photoreceptor-dependent changes in leaf-blade angle, height and inclination of stems and petioles, plant water-status and temperature (Muraoka
555 et al., 2003; Novoplansky et al., 1990). In some plant species leaf display changes dynamically through the day (e.g. tracking of the sun position from sunrise to sunset) (Ehleringer and Forseth, 1980; Shackel and Hall, 1979; Vogelmann and Björn, 1983).

Optical properties of leaves

560 The concentration of chlorophyll and auxiliary pigments per unit leaf area is an important, but not the only, determinant of the absorption spectrum of whole leaves. How these pigments are distributed within a leaf affects how effective they are at absorbing photons. Furthermore, accumulation of white waxes on the

cuticle at the surface of leaves, sometimes forming optically tuned structures, and
565 the presence of light-coloured pubescence can increase reflectance decreasing the
number of photons available for photosynthesis. These features that reduce the
number of photons available for absorption by photosynthetic pigments can,
paradoxically, lead to increased rates of net photosynthesis by their moderating
effect on leaf temperature (Ehleringer and Cook, 1984). The thickness of the
570 palisade mesophyll that most efficiently captures photons depends on
illumination conditions, with thicker leaves with multiple layers of palisade
parenchyma being an acclimation and/or adaptation to growth under high
irradiance (Lichtenthaler et al., 1981). The regulation of these changes in leaf
optical properties and morphology are in part mediated by cues in solar radiation
575 perceived through photoreceptors.

Physiology of leaves

Photosynthesis is a tightly regulated process that undergoes acclimation (Shevela
et al., 2017, and references therein). Acclimation is effected by relative and
absolute changes in pigment concentrations (e.g. chlorophyll *a* : chlorophyll *b*
580 ratio and total chlorophyll concentration per unit leaf area), changes in the
stoichiometry of different components of the photosynthetic “machinery” (e.g.
electron transport capacity, antenna molecules per reaction centre). Although
regulation through feedback plays a key role, once again, pigment composition,
photosynthetic antenna size, and abundance of photosynthetic enzymes are also
585 regulated through the interaction of multiple photoreceptors (Anderson et al.,
1995; Brelsford et al., 2018; Rai et al., 2020).

Sink to source feedback

Another key point to consider is that photosynthetic rate is not necessarily the
main limiting factor for plant growth or crop yield (Passioura, 2020). It is well
590 documented that in many situations the rate of photosynthesis remains below its
potential maximum as a result of negative feedback from sinks. In tomato, the
balance between source vs. sink limitation depends on cultivar, irradiance, light
quality and stage of development (Ji et al., 2020; Li et al., 2015). Compensatory
increases in photosynthesis rate of remaining leaves after partial defoliation has

595 been observed in tree saplings (Ovaska et al., 1993). In crop breeding although
high yielding cultivars tend to have higher photosynthetic rate, attempts to
increase yield by selecting for high photosynthesis rate have in most cases failed
(Sadras et al., 2021). In other words the number of growing points in a plant and
their growth rate are frequently the main limitation to growth and or yield outside
600 the laboratory. This dynamic balance between sources of photosynthates and
sinks available for their use is once again under regulation mediated at least in
part by photoreceptors (Casal, 2013a).

Timing

Maternal effects in plants were first described more than 100 years ago (see Roach
605 and Wulff, 1987). That there are carry-over effects of light through the life-time of
a plant and from the parental generation to offspring (Yan et al., 2020) creates
difficulties for the design of relevant experiments but also opens an avenue for
management-based solutions. Time-of-day has been observed to play a major role
in responses to light sensed by plants (Casal et al., 1990; Sellaro et al., 2011; Wang
610 et al., 2020), and interactions among sensed wavelengths (Moriconi et al., 2018)
and light sensing and temperature (Casal and Qüesta, 2018). This additional
complexity, makes a reasoned approach very challenging but simultaneously
makes it possible to envisage management protocols based on conveying
information with wavelengths less efficient for photosynthesis only during critical
615 periods of development, or critical times of the day.

The spot price of electricity varies in time, in some situations even greatly through
the course of a single day and coordinated management of irradiance, ambient
CO₂ and air temperature can optimize energy use (Ottosen et al., 2003). In the case
of vertical farming with no contribution of natural light, management of crop
620 illumination to minimize energy costs needs to take into account both its role as
source of energy for photosynthesis and its role as an informational cue that
regulates morphology and development of plants. Research on when plants'
regulatory mechanisms are most responsive to light of different wavelengths is
needed before the design of light regimes optimized for crop production can be
625 based on mechanistic understanding. In an experiment with lettuce cultivated
under different temporal regimes of red plus blue LED illumination, Chen et al.
(2019) observed effects of timing on growth rate and produce quality that were

unrelated to the daily light integral or the length of the photoperiod. The effect of timing of light quality needs to be further assessed.

630 The possibility of adjusting in real-time the spectrum in luminaires used for crop cultivation would solve the problem only after suitable recipes are devised, and hopefully encoded in a shareable non-proprietary format, and deposited in on-line open-access repositories so that all growers, large and small, have free access to them.

635 **Taming complexity**

Plants have evolved under sunlight and/or shade light, and have become adapted to using changes in the spectrum and irradiance of daylight as informational cues for the achievement of fitness (Aphalo and Ballaré, 1995; Aphalo and Sadras, 2021). Informational cues and signals are noisy, and through evolution, plants
640 have acquired complex signalling pathways that combine multiple sensory inputs as a mechanism to more reliably acquire information (Casal, 2009). Plants extensive and complex use of light as a source of information, makes any attempt at optimizing light source spectra based only on the photochemistry of photosynthesis or photosynthesis per unit leaf area of individual leaves futile.

645 The harvestable product is only rarely the whole biomass. We are interested in the yield of harvested produce—determined by the harvest index together with accumulated biomass—and its quality—nutritional value, colour, flavour, texture, post-harvest shelf life—. As discussed above the link between producers' aims and the in-vitro absorption spectrum of chlorophyll is very tenuous, and consequently
650 not a useful criterion for deciding on the best spectrum of illumination for efficient plant production under LEDs or other artificial light sources.

To tame this complexity we have to consider the individual steps linking photosynthesis of leaves to growers' net income, and assess which of these steps are influenced by the wavelength of light crop plants are exposed to. Although
655 this approach does not describe the intricate physiological mechanisms and feedback loops involved, it informs us about what is “dangerous” to ignore and what is “interesting” to study in empirical and mechanistic approaches to research aiming to be useful or relevant to crop production.

The wavelength of light affects most steps in the cascade of processes linking

660 electric power, $P_{\text{electrical}}$, use to growers' net income, $\text{Income}_{\text{net,daily}}$,

$$\begin{aligned}
 Q_{\text{PAR}} &= P_{\text{electrical}} \times \epsilon; \epsilon = f(\lambda, \dots) \\
 Q_{\text{PAR}}^{\text{intercepted}} &= Q_{\text{PAR}} \times k; k = f(\lambda, \dots) \\
 Q_{\text{PAR}}^{\text{leaf incident}} &= Q_{\text{PAR}}^{\text{intercepted}} / L; L = f(Q_{\text{PAR}}, \lambda, \dots) \\
 Q_{\text{PAR}}^{\text{leaf absorbed}} &= Q_{\text{PAR}}^{\text{leaf incident}} \times (1 - \mathcal{R} - \mathcal{T}); \mathcal{R} = f(Q_{\text{PAR}}, \lambda, \dots); \mathcal{T} = f(Q_{\text{PAR}}, \lambda, \dots) \\
 A^{\text{leaf}} &= f(Q_{\text{PAR}}^{\text{leaf absorbed}}, \lambda, t, \chi_a^c, \dots) \\
 A^{\text{plant}} &= A^{\text{leaf}} \times L; L = f(Q_{\text{PAR}}, \lambda, \dots) \\
 M^{\text{plant}} &= A^{\text{plant}} - R; R = f(Q_{\text{PAR}}, \lambda, \dots) \\
 Y^{\text{plant}} &= M^{\text{plant}} \times h; h = f(Q_{\text{PAR}}, \lambda, \dots) \\
 Y^{\text{area}} &= Y^{\text{plant}} \times d \\
 I^{\text{area}} &= Y^{\text{area}} \times q; q = f(Q_{\text{PAR}}, \lambda, \dots) \\
 C^{\text{area}} &= P_{\text{electrical}} + W + S \\
 \text{Income}_{\text{net,daily}} &= (\text{Income} - \text{Costs}) / l; l = f(Q_{\text{PAR}}, \lambda, t, \chi_a^c, \dots)
 \end{aligned}$$

where ϵ is a conversion efficiency dependent on multiple factors including wavelength, λ ; the number of PAR photons intercepted, $Q_{\text{PAR}}^{\text{intercepted}}$, depends on the fraction of ground area occluded by foliage, k ; the average PAR irradiance on the surface of leaves, $Q_{\text{PAR}}^{\text{leaf incident}}$, is given by the average number of *intercepted* PAR
665 photons divided by the leaf area, L ; not all these photons are absorbed, the absorbed photons, $Q_{\text{PAR}}^{\text{leaf absorbed}}$, are decreased according to the reflectance, \mathcal{R} , and transmittance, \mathcal{T} , of the leaves. Photosynthesis of leaves, A^{leaf} , can be integrated into photosynthesis per plant, A^{plant} , and converted into biomass accumulated per plant, M^{plant} , by subtracting respiration, R , and other mass losses. Yield, Y^{plant} , is
670 determined by the harvest index, h , giving the fraction of harvestable biomass. Yield per cultivation area, Y^{area} , is obtained by multiplying by the planting density, d (e.g., plants per square meter). Income, is dependent on produce quality, q , through its effect on price. The costs incurred include that of electrical power used for illumination, $P_{\text{electrical}}$, use of water, w , and space, s , and possibly energy for
675 heating. What is economically relevant to growers, is the net income per unit time and area, which depends on the length of the crop growth cycle, or the length of time, l , a greenhouse or vertical farming facility is occupied.

One way of dealing with great complexity in mechanism is to search for an

approximate empirical answer, treating much of the system as a *black box*: we can
680 simply compare crop performance under light with different spectra (Folta and
Childers, 2008; Kim et al., 2004; Kotiranta et al., 2015; Yoshida et al., 2016; Zou
et al., 2020). When using this approach, we need to exclude the least promising
candidate spectral and irradiance conditions to make such studies possible and
results tractable. Exclusion can be based on an analysis of the mechanisms
685 involved in combination with previous knowledge about mechanisms and
empirical observations both from controlled experiments and informal knowledge
based on growers' experience. We should also, at least initially, include spectra
that are different enough for us to expect measurable differences in plants'
performance. In addition, the design of the experiments, including replication,
690 should ensure that most differences relevant to production have a high probability
of being detected. We should correspondingly avoid interpreting lack of statistical
significance itself as a demonstration of *lack of difference or no effect* of
treatments.

Alternatively, if focusing on mechanisms, it must be realized that up scaling
695 responses observed at molecular or physiological level of organization to crop
performance in a commercial setting is far from direct and in most cases
impossible without further research at higher levels of organization. Relevance to
applications also depends on what we study and in what context we study it. Key
basic knowledge crucial for guiding mechanistic and empirical research at crop
700 level is, perhaps surprisingly, mostly lacking. Examples of major gaps in
knowledge that hinder up scaling are that 1) polychromatic action spectra of
photosynthesis are unavailable, 2) the dependency of the shape of the action
spectrum of leaf photosynthesis on irradiance remains to be described, 3)
response- or action spectra for crop growth or yield, or even canopy
705 photosynthesis, are lacking, 4) how the action spectrum of photosynthesis
acclimates in plants grown under artificial light of unnatural spectra, such as red
plus blue, remains to be studied and 5) knowledge about the role of timing during
the photoperiod and crop cycle of exposure to light of different wavelengths is
very scant.

710 Up scaling of mechanistic understanding is challenging not only because of the
dimension and intricacy of the problem, but also because up scaling across
disciplines requires effective communication among researchers from fields of
science that rely on different paradigms and methods. As described by Passioura

breaking the barriers to effective translational is challenging and needs to be
715 encouraged through changes in the rewards systems of scientific research
including how research outcomes are reviewed and evaluated. Bridging the gap
between disciplines requires practitioners familiar with the paradigms, methods
and language used in multiple disciplines, and an ability to see the details within
the frame of the bigger picture, or fitting the pieces of the puzzle together.
720 Education targets and evaluation methods are selecting against persons with these
abilities entering or succeeding in academia (Grandin, 2022).

No spectrum can be expected to be best for all crops, plant development stages or
even times of the day. A spectrum with 14% blue, 20% green and 66% red has been
proposed for high efficacy (Kusuma et al., 2020). However, relative efficiency of
725 light of different colours depends on irradiance (Liu and van Iersel, 2021) and on
the characteristics of individual cultivars (Kusuma et al., 2022). Thus, it is unlikely
that a consistently superior recipe catering for many crops and production
systems will ever be found. However, based on evolutionary history of crop plants,
performance across species and cultivars can be expected to be more consistent
730 under white-light spectra similar to daylight than under unnatural spectra
(Denison, 2012). In any case, there is much that can be improved by combining the
formulation of hypotheses about promising spectra with their empirical testing in
different crop systems.

Conclusion

735 Even in the unlikely case of the production aim being maximum biomass
accumulation, the simplistic idea that light of wavelengths not maximally
absorbed by chlorophylls is “wasted illumination” is a fallacy. In practice we are
not interested in maximising the instantaneous rate of photosynthesis of
individual leaves, but instead we aim at maximising energy-use-efficiency through
740 the lifespan of a crop, or more realistically, growers’ net income.

Efficiency of luminaires, measured as PAR photons output per energy input
(usually expressed in $\mu\text{mol J}^{-1}$) even if relatively easy to measure and understand,
is only one step in a long chain of events, and thus should not be the main or only
concern when deciding on the spectrum used for plant cultivation. Similarly, the
745 daily light integral (DLI) is a simple summary that ignores light quality and timing

of the light during the day, thus it should not be used as the main or only descriptor of light availability.

In the case of supplementary illumination, when daylight contributes a major portion of the energy, the importance of the spectrum used for artificial
750 illumination is not crucial but can be still important. In greenhouses in winter at high latitudes and for vertical farming, artificial light becomes the only or main source of information acquired through photoreceptors controlling development, growth and morphology of plants. In this second situation there are two possible approaches: breeding plants to grow well under energy-efficient artificial light
755 sources or optimizing the spectrum and how it varies through the day and through the crop growth cycle so as to convey information conducive to the desired morphology while minimizing the use of energy-inefficient wavelengths.

Whatever the approach aimed at, in research or production, identifying the “right question” to study is a precondition to success. We should not ignore that in many
760 cases in agriculture and other complex production systems approximate empirical answers to the right questions are the most relevant both to individual growers and for global food production. Any management or breeding proposals based on up scaling or translation of mechanistic understanding will always need to be considered as hypotheses, and subjected to thorough tests under real cropping
765 conditions before adoption. This necessary translation step is not amenable to easy short-cuts. Pretending that easy shortcuts exist, when not available, harms growers’ interests and the credibility of scientific research.

The question discussed here is not the only fallacy affecting current applied plant research or proposals for applications of outcomes from basic plant research. Too
770 many other cases exist where as in the present example, losing sight of the crop and focusing on a single process within plants muddles the understanding of what matters in practice to agriculture (Passioura, 2020; Sadras et al., 2021). It should be noted, that much of the same argumentation presented in the current paper applies to other attempts at increasing crop productivity by enhancing the
775 photosynthetic rate and light use efficiency—e.g. through genetic engineering or selection for high photosynthetic rate in isolated plants or under growing conditions drastically different to those used by growers.

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785 repository and open source code available at GitHub (see Aphalo, 2014–2023, for
details).

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Additional examples of LED and LED fixture spectra

1105 Currently LEDs and LED fixtures with hugely different emission spectra are being sold as specially suitable for plant cultivation. A few of them, do not even differ significantly in their spectrum from spectra recommended for general illumination in houses or public spaces. We here give examples, of both spectra different and similar to sunlight. See also the spectra in Figures 1, 2 and 3.

The spectra shown above are just a small sample out of the many different spectra

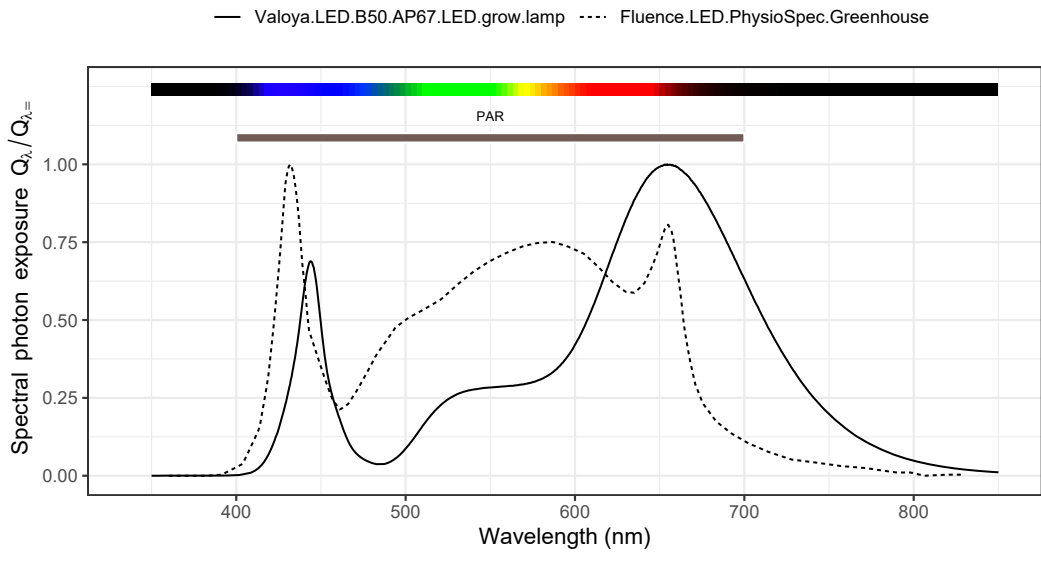


Figure 9: Emission spectra of two broad spectrum LED luminaires for plant cultivation (B50 AP67, Valoya, Finland; RAY bar, PhysioSpecGreenhouse, Fluence, Austin, TX, USA.).

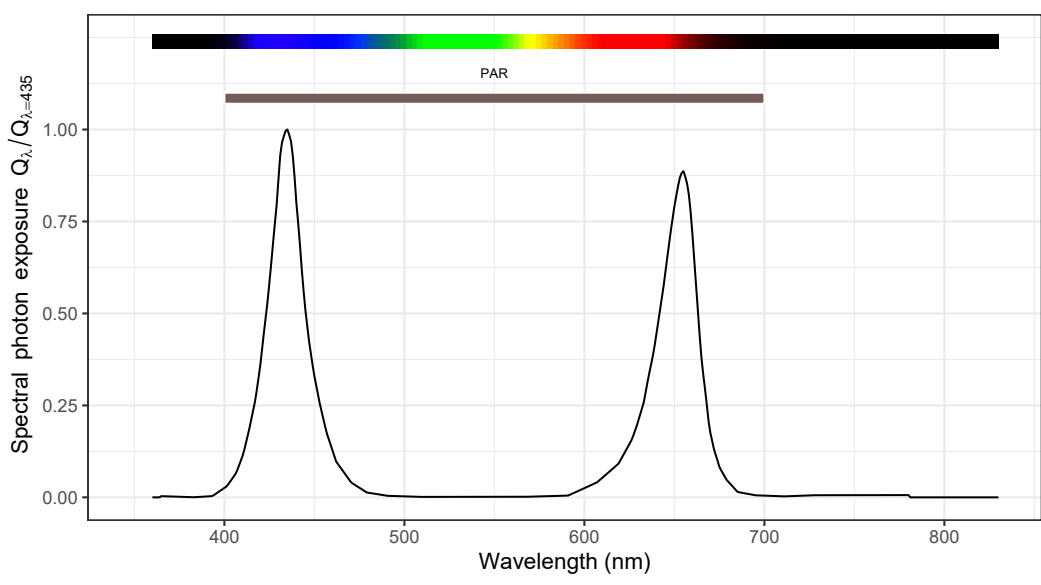


Figure 10: Emission spectrum of a red plus blue LED luminaire for plant cultivation (RAY bar, AnthoSpec, Fluence, Austin, TX, USA).

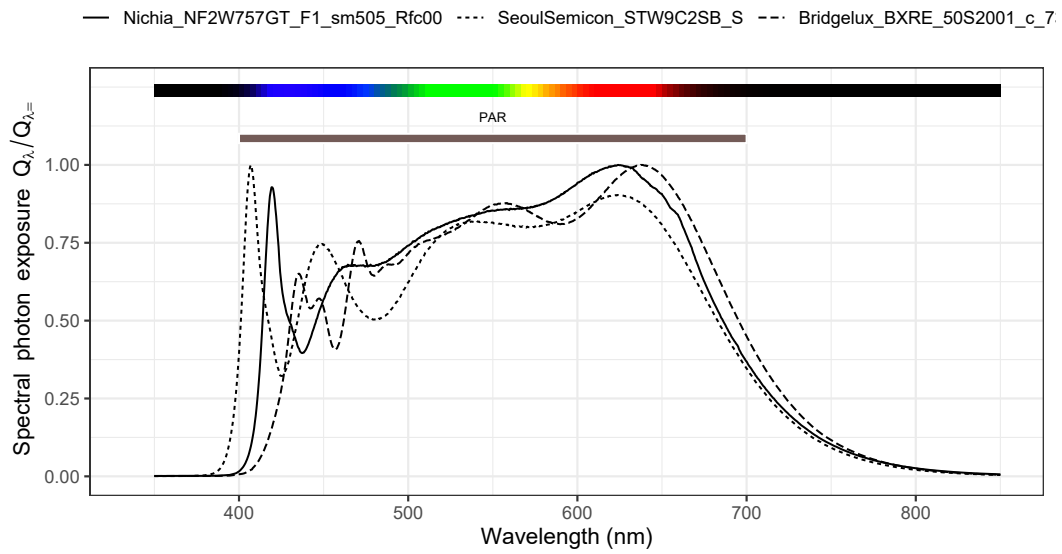


Figure 11: Emission spectrum of 5000 K SMD LEDs marketed as “similar to sunlight” and sold for museum displays and general illumination (Nichia, Japan; Seoul Semiconductors, Korea; Bridgelux, USA). These three types of LED differ mainly in the violet region.

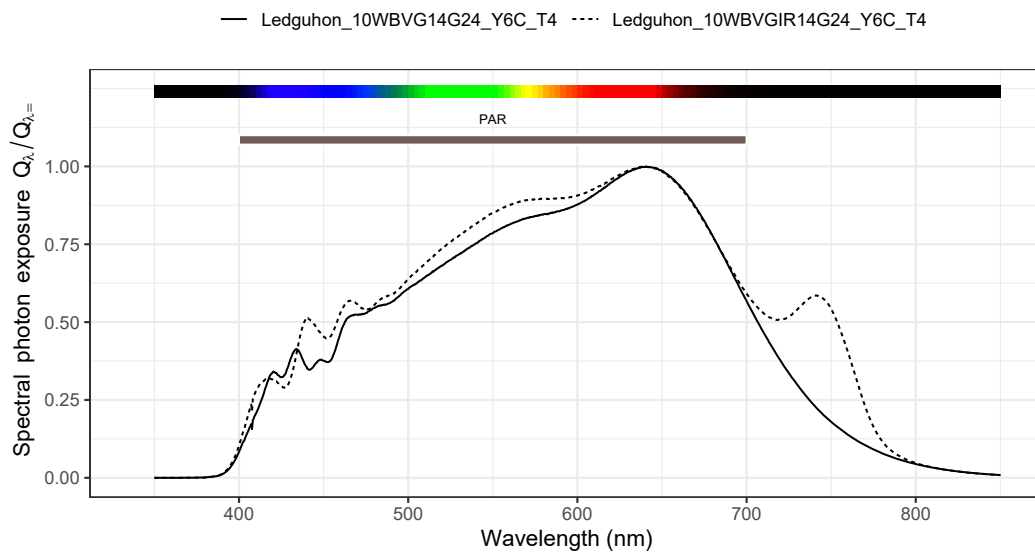


Figure 12: Emission spectrum of 4000 K COB LEDs marketed as “similar to sunlight” and useful for plant cultivation (Ledguhon, China). These two types of LED differ mainly in the far-red.

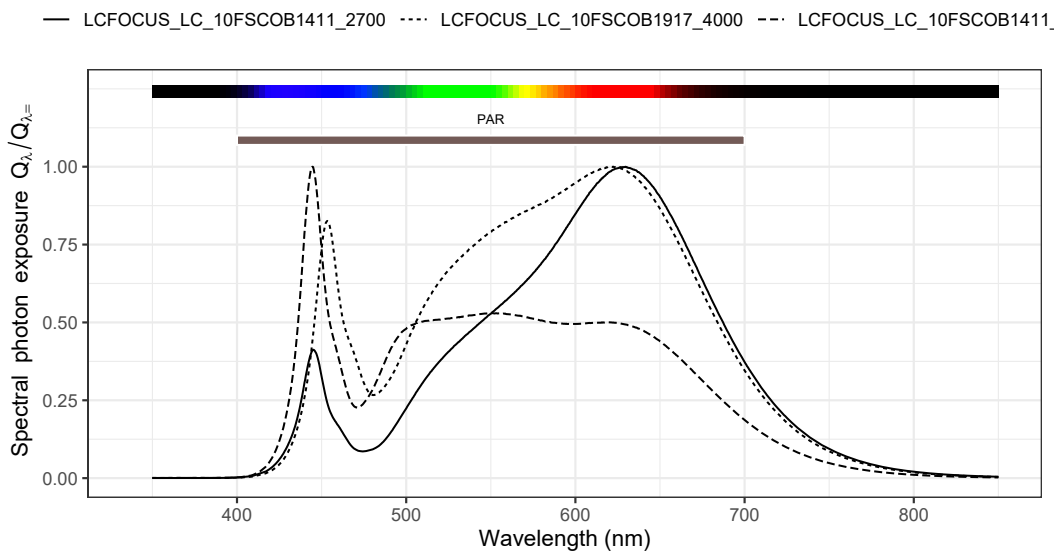


Figure 13: Emission spectrum of 10W COB LEDs marketed as “for hydroponics” with nominal color temperatures of 2700 K, 4000 K and 6000 K (LCFOCUS, China). These types of LED differ mainly in the balance between blue and red light.

of LEDs. We do not have any accepted way of describing such spectra in numbers, or of predicting plants’ responses to them with any detail. The ISO standard for
 1110 light colour names as a function of wavelength is based on human vision. LED suppliers use fantasy names like “hyper red”, “lime”, “deep blue”, “royal blue”, and “cool blue”. While blue plus red LED arrays are described as “purple”. There is large variation in what spectra are considered to be narrow, broad or similar to sunlight.

1115 The most common difference between LEDs for plant cultivation and general illumination is the use of shorter wavelength blue or “deep blue” (435 nm instead of 460 nm) and longer wavelength for red or “hyper red” (660 nm instead of 630 nm). Frequently, but not always, LEDs for plant cultivation emit more far-red (near 735 nm) than LEDs for general illumination. This is simply because in
 1120 the case of illumination the target is human vision and the measure of efficiency is in lumens per watt which is better for wavelengths closer to green.