The best light spectrum for plant cultivation: a source of colourful arguments

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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 use of reductionism. Equating instantaneous rate of photosynthesis to crop yield is a prevailing but non-sensical 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 I describe in detail several of the mechanisms that have been ignored in early attempts to 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, with their multiple feedback loops and hierarchical organization.

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 considered in isolation: electricity to PAR efficiency (i.e., moles of photons per joule of electrical power), whole growth-cycle PAR to produce yield 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, CO_2 fertilization. Even the time course of the spot price of 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.

Currently if one considers advertising from LED manufacturers one can see three camps: companies still favouring blue plus red illumination as the most efficient (ams-Osram, Philips), those advertising white LEDs as very significantly improving yields (Nichia, Samsung, Bridgelight) and those not promoting either but providing LEDs based on both approaches (Luminus,...). The most recent advertising from Nichia recognizes much of the complexity of the problem. If we look at companies producing grow lamps, there is also great variation and in some cases advertising is not consistent between the LED as components and grow fixture divisions of the
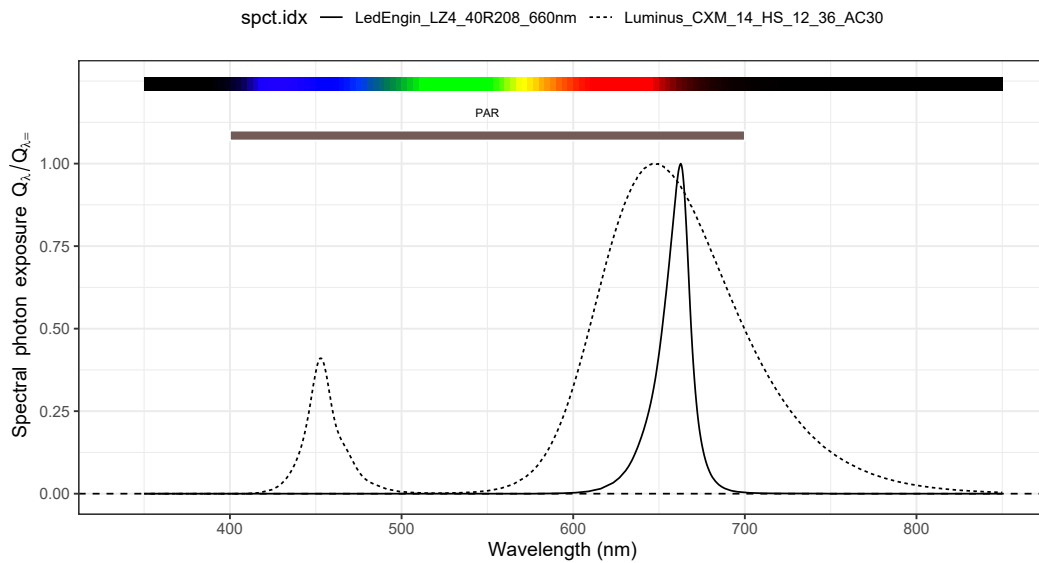
Figure 1: Emission spectrum of a "deep" red SMD LED (LedEngin-Osram, USA), and a "purple" blue plus red COB LED (Luminus, USA). Both LEDs sold for plant cultivation.

same companies (e.g., Osram). Valoya (Finland) has produced LED fixtures with broad spectra since its inception in 2009, but does not publish detailed spectra as part of fixture specifications. Other major suppliers have been less consistent in their offerings.

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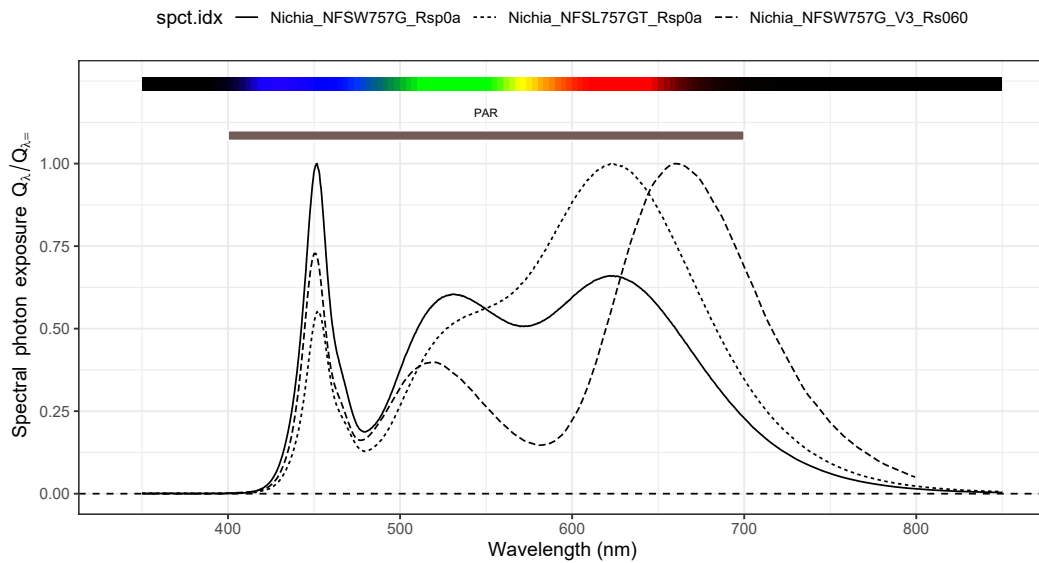
Figure 2: Emission spectra of three broad-spectrum SMD LED types for horticulture rated at 3000 K, 5000 K and 5300 K (Types NFSW757G-Rsp0a, NFSL757GT-Rsp0a, and NFSW757G-V3-Rs060, from Nichia, Japan).

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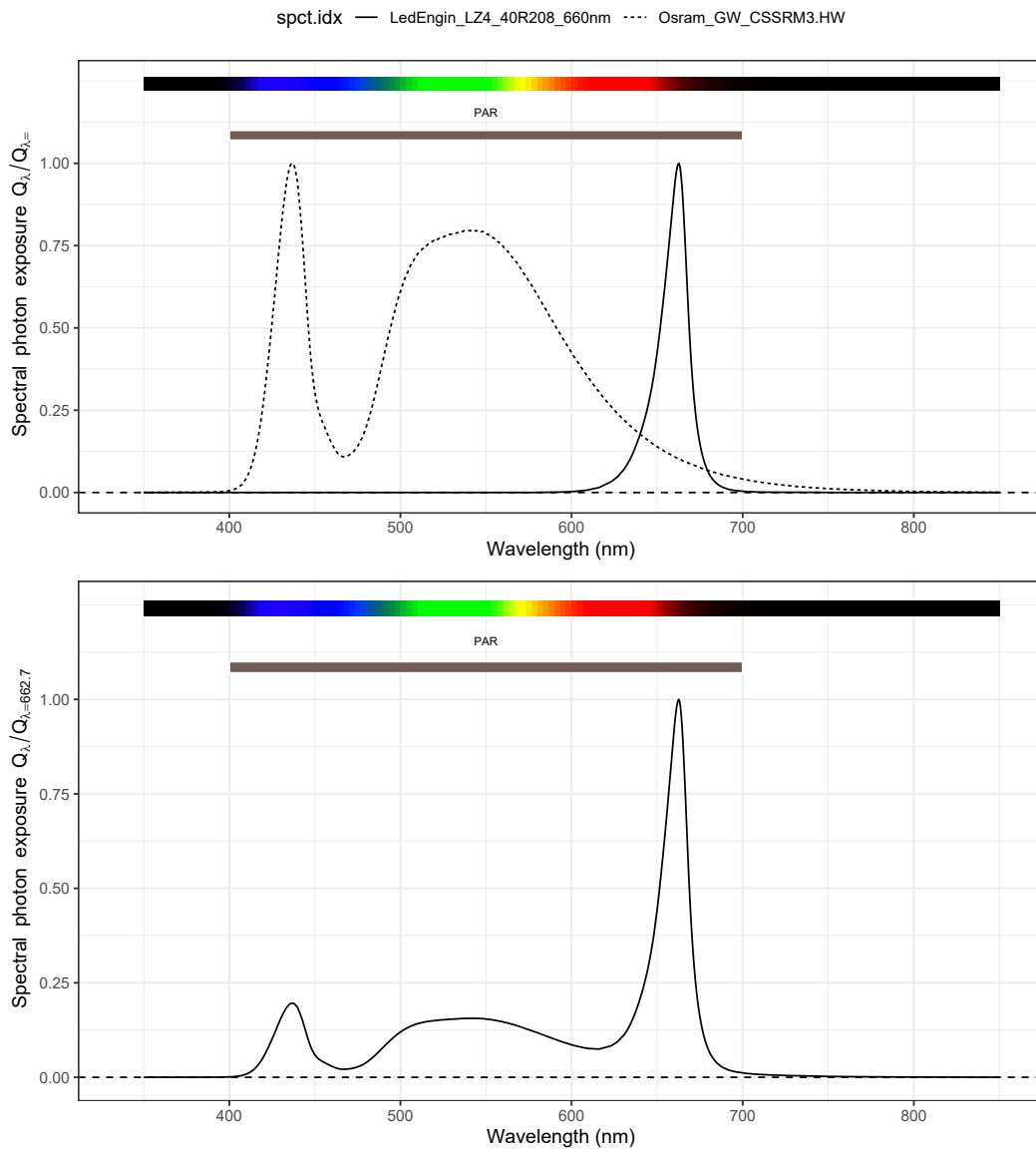
Figure 3: Spectra of narrow- and broadband LEDs and their combination. The spectra of Led Engin LZ4-40R208 leds emitting at 660 nm (nominal) and broadspectrum Osram GW-CSSRM3-HW grow leds (top) were combined *in silico* in 4:1 proportion based on photon irradiance (bottom) to approximate the spectrum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

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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 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 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, and anyone with high-school education, should know that there is much more behind 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) 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 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 (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,b). Obviously, in addition *slightly* more green light than red or blue light is reflected and transmitted by leaves (McCree, 1972a,b).

Nearly 50 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. 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). This serves as a reminder that PAR was never intended to faithfully represent the action spectrum of photosynthesis but rather to

be an approximation that would be within $\pm 10\%$ of the true value in a fair number of important species. The criticisms raised on PAR, however, relate to the limits at 400 nm and 700 nm, i.e., whether UV-A1 (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, 1978; 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 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 (Yoshida et al., 2016, e.g.).

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 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 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 with 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 spectrum of chlorophyll, which is close to invariant, and the efficiency of LEDs measured as photons of per joule which are 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 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 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 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 easy to forget the wise words usually attributed to John Tukey "An approximate answer to the right problem is worth a good deal more than an exact answer to an approximate problem" (). Why would then anybody look for answers to approximate problems? We think 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 (Box 1). 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. These multiple mechanisms interact in ways that make the problem of deciding on the best spectrum for artificial illumination for crop production very complex and for which given the current state of knowledge it is possible to provide only approximate answers difficult to translate into simple recipes applicable across different production systems. On the other hand the current state of affairs where recipes are based on a very approximate and flawed analysis of the problem can be seriously misleading and damaging.

The aim of this review is to characterize the "right problem(s)" considering the context under which crop plants are to grown vs. the one where they have evolved or have been artificially selected. We will next analyse the factors involved and assess the steps needed to reach a usable approximate answer. We will also justify our view that there 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.

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. 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."

Energy vs. photons

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 800 nm carries half as much energy as a violet photon at 400 nm. Of course, for real LEDs there are additional factors involved, as energy loss as heat is important. Nowadays specifications of LEDs intended for plant growth include a rating for photons per joule. This efficiency decreases with increasing temperature of the LEDs, and how strong this effect is depends on the type of LED. We will use as examples the new OSLON® 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 350 mA

and 74% at 700 mA, at 20 C, but this efficiency decreases, these are typical values corresponding to 3.8 μmol/J and 4.31 μmol/J depending on the "bins". If temperature of the LED die 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 expressed as photons lower, between 2.47 μmol/J and 2.91 μmol/J depending on the "bin". If temperature of the LED die 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 dies in a well designed fixture will be about 80–90 C 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 die. Their conversion efficiencies at 20 C are 61% at 350 mA and 55% at 700 mA and 2.17 μmol/J to 2.91 μmol/J, decreasing by approximately 13% at 120 C.

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 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

There is a striking difference between the shape of the absorptance spectra for chlorophyll *in-vitro* (Fig. 4) and of leaves (Fig. 5), 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, 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 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,
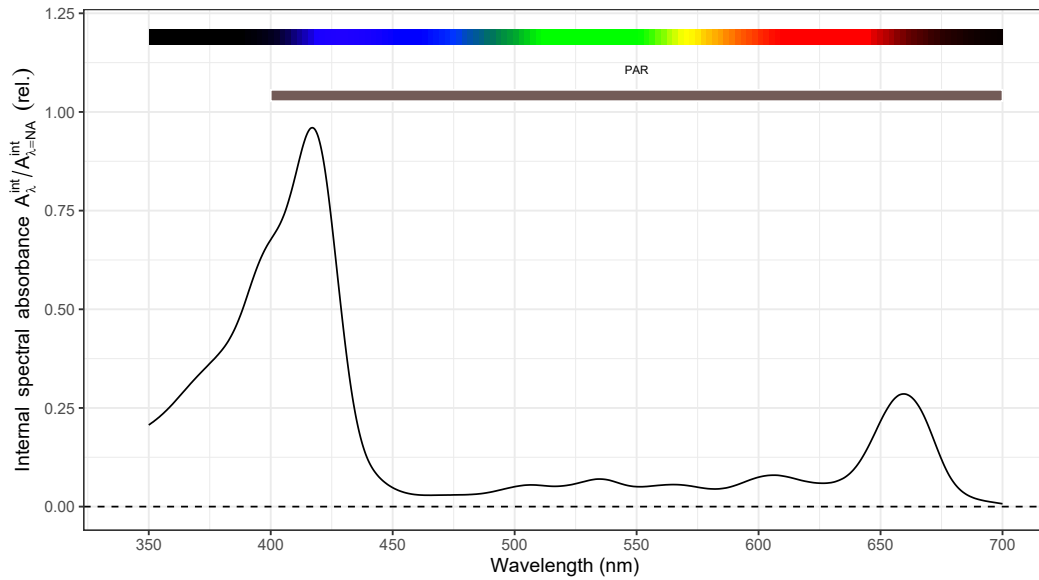
Figure 4: In vitro absorptance spectrum of chlorophyll *a* in methanol (Data described in Dixon et al., 2005).

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,
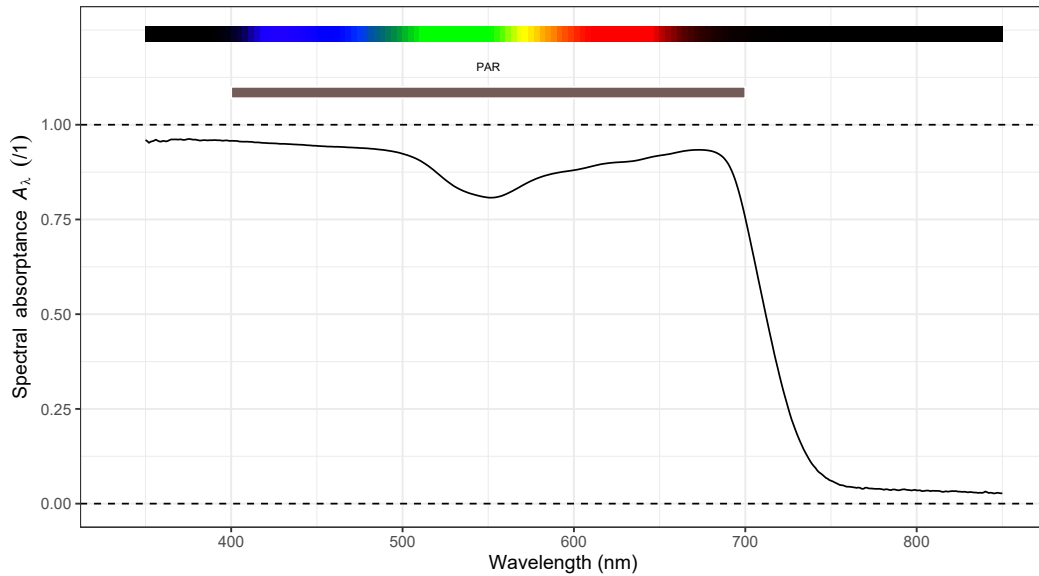
Figure 5: In-vivo absorptance of the adaxial surface of a *Betula ermanii* leaf from the first flush (Data from Noda, 2013).

Action spectrum of photosynthesis

Dimming based on pulse width modulation 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 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.

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. The 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 photosythesis per plant dry mass. As we will discuss in later sections, 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. 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 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 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. Given the high energy involved, it is also a process that is highly regulated to prevent damage by surplus energy.

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 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 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 reported (Zhen et al., 2018; Zhen and Iersel, 2017). 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
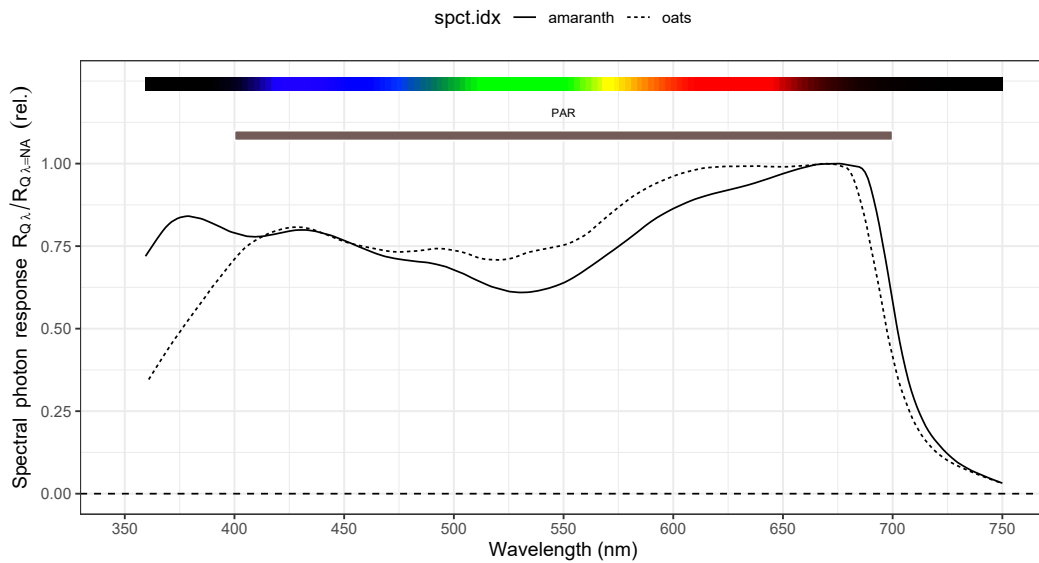
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Figure 6: Action spectra for photosynthetic oxygen evolution in leaf tissues of *Amaranthus edulis* and *Avena sativa* (Data from McCree, 1972a) expressed on a *photon base*.

regulation of the balance between light reactions and carbon reactions (Neha Rai et al. unpublished). This balance is crucial to the efficient functioning of photosythesis and preventing damage by excess excitation.

The action spectra of photosynthesis shown in Figures 6 and 7, as most 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 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, 1972b), with an example reproduced in Fig. 6. This variation is positively correlated with specific leaf area (McCree, 1972b) and most likely related to the accumulation in the epidermis of flavonoids 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; Barnes et al., 2016). It remains to be studied if a link exists between this rhythm
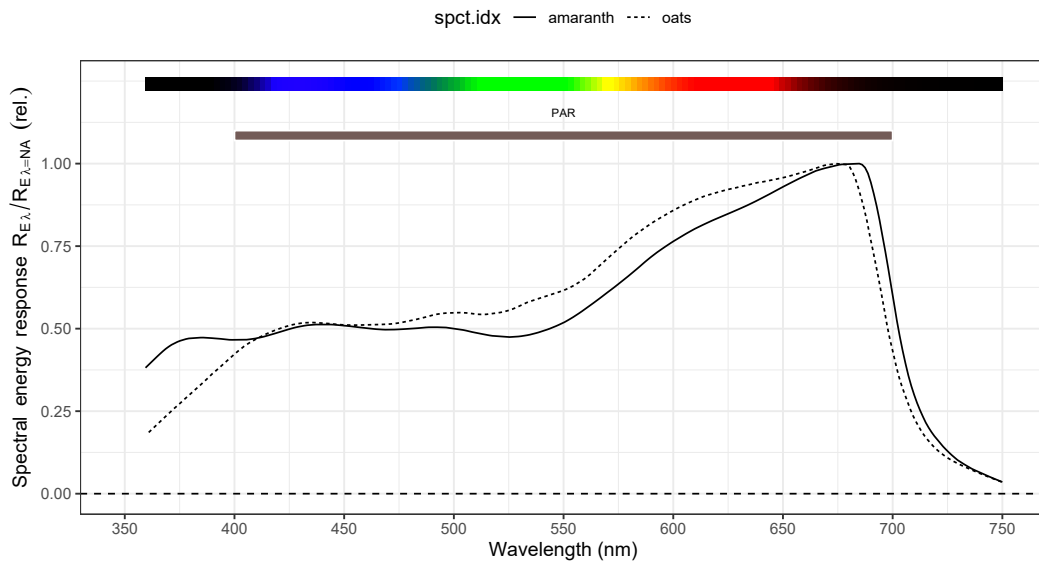
Figure 7: Action spectra for photosynthetic oxygen evolution in leaf tissues of *Amaranthus edulis* and *Avena sativa* (Data from McCree, 1972a) expressed on an *energy base.*

and photosynthesis in sunlight early and late in the day.

Growers' cost for artificial light is proportional to energy use rather than photons, so it makes sense to re-express the action spectrum of photosynthesis on an energy base (Figure 7). 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 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 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, 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). Grow lights poor in blue can enhance water use efficiency in

greenhouses (Kotiranta et al., 2015). In cold climates a lower transpiration rate decreases the need for ventilation to control air humidity, and consequently can decrease the energy needed for heating. On the other hand partly closed stomata can reduce the photosynthetic rate at a given CO_2 concentration in the greenhouse air by increasing the mesophyll to air concentration difference.

Light and plant morphology

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 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 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 system of plants to the environment in which they evolved—i.e. natural, usually mixed-species, vegetation canopies under sunlight.

More investment in leaf area results in faster growth

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, 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 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 production of new leaf area leads 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 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 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 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 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 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 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 bal-

ance 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 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

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 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 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 perceived through photoreceptors.

Physiology of leaves

Photosynthesis is a tightly regulated process that undergoes acclimation. Acclimation is effected by relative and absolute changes in pigment concentrations (e.g. chlorophyll a : chlorophyll b 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 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 limiting factor for plant growth or crop yield. It is well documented that in many situations the rate of photosynthesis remains below its potential maximum as a result of negative feedback from sinks. Compensatory increases in photosynthesis rate of remaining leaves after partial defoliation has 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 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 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).

Taming complexity

One way to deal with complexity in mechanism is to search for an approximate empirical answer: to simply compare crop performance under light of different spectra (Folta and Childers, 2008; Kim et al., 2004; Kotiranta et al., 2015; Yoshida et al., 2016). We need to exclude the least promising candidate spectra from empirical comparisons can be based on an analysis of the mechanisms involved in combination with empirical observations both from controlled empirical 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.

A spectrum with 14% blue, 20% green and 66% red has been proposed for high efficacy (Kusuma et al., 2020) of which we show a possible implementation in Figure 3.

Conclusion

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 the lifespan of a crop. Furthermore, 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 not a useful criterion for deciding on the best spectrum of illumination for efficient plant production under LEDs or other artificial light sources.

The wavelength of light affects every single step in the cascade of processes linking electric power use to growers' net income.

$$Q_{\text{PAR}} = P_{\text{electrical}} \times \epsilon; \epsilon = f(\lambda, ...) \tag{1}$$

$$Q_{\text{PAR}}^{\text{intercepted}} = Q_{\text{PAR}} \times k; k = f(\lambda, ...) \tag{2}$$

$$Q_{\text{PAR}}^{\text{leaf incident}} = Q_{\text{PAR}}^{\text{intercepted}}/L; L = f(Q_{\text{PAR}}, \lambda, ...) \tag{3}$$

$$Q_{\text{PAR}}^{\text{leaf absorbed}} = Q_{\text{PAR}}^{\text{leaf incident}} \times (1 - \mathcal{R} - \mathcal{T}); \mathcal{R} = f(Q_{\text{PAR}}, \lambda, ...); \mathcal{T} = f(Q_{\text{PAR}}, \lambda, ...) \tag{4}$$

$$A^{\text{leaf}} = f(Q_{\text{PAR}}^{\text{leaf}}, \lambda, t, \chi_{\text{a}}^{\text{c}}, ...) \tag{5}$$

$$A^{\text{plant}} = A^{\text{leaf}} \times L; L = f(Q_{\text{PAR}}, \lambda, ...) \tag{6}$$

$$\text{Biomass} = A^{\text{plant}} - R; R = f(Q_{\text{PAR}}, \lambda, ...) \tag{7}$$

$$\text{Yield} = \text{Biomass} \times h; h = f(Q_{\text{PAR}}, \lambda, ...) \tag{8}$$

$$\text{Income} = \text{Yield} \times q; q = f(Q_{\text{PAR}}, \lambda, ...) \tag{9}$$

$$\text{Costs} = P_{\text{electrical}} + W + S \tag{10}$$

$$\text{Income}_{\text{net,daily}} = (\text{Income} - \text{Costs})/l; l = f(Q_{\text{PAR}}, \lambda, t, \chi_{\text{a}}^{\text{c}}, ...) \tag{11}$$

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). Domesticated plants have continued to be grown mostly under daylight or a combination of daylight and artificial light. Their 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.

In the case of supplementary illumination, when daylight contributes a major portion of the energy, the importance of the spectrum used for artificial 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 source of information ac-

quired through photoreceptors. In this second situation there are two possible approaches: breeding plants to grow well under energy-efficient artificial light sources or optimize the spectrum and how it varies through the day and grow cycle so as to convey information conducive to the desired morphology while minimizing the use of energy-inefficient wavelengths. Informed application of these two approaches will require a good understanding of plant photomorphogenesis and its genotypic variation within and across species. A difficulty that also creates an avenue for solutions is that there are carry-over effects through the life-time of a plant and from the parental generation to sibblings. This complexity, makes a reasoned approach very challenging but simultaneously makes it possible to envisage management protocols based on conveying information with less efficient wavelengths only during critical periods of development, or critical times of the day. Consequently, in our opinion it will be possible with new management practices to decouple energy use efficiency from photomorphogenesis, but only if enough research and development effort is put into it.

If we learn in detail how and when plants' regulatory mechanisms are most responsive to light of different wavelengths, we will be able to design light sources optimized for crop production on a much more solid ground than we currently can. No spectrum can be expected to be best for all crops, plant development stages or even times of the day. The possibility of adjusting the spectrum in "grow lights" would solve the problem only after suitable open-access recipes are devised and systems easy to centrally program become available to growers. It remains to be seen if the cost of LED chips compared to driver electronics and heat sinks becomes so low that the cost penalty of having unpowered LEDs in luminaires becomes economically viable.

The question discussed here is not the only fallacy affecting current applied plant research and the applications proposed for basic plant research. Too 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 for agriculture (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 photosynthetic rate and light use efficiency—e.g. through genetic engineering or selection for high photosynthetic rate in isolated plants or under unrealistic growing conditions.

Acknowledgements

References

Anderson, JM, Chow, WS, Park, YI (1995). The grand design of photosynthesis: Acclimation of the photosynthetic apparatus to environmental cues. *Photosynthesis Research* 46, 129–139. DOI: 10.1007/bf00020423.

Anten, NPR (2004). Optimal Photosynthetic Characteristics of Individual Plants in Vegetation Stands and Implications for Species Coexistence. *Annals of Botany* 95, 495–506. DOI: 10.1093/aob/mci048.

Anten, NPR, Schieving, F, Medina, E, Werger, MJA, Schuffelen, P (1995). Optimal leaf area indices in C_3 and C_4 mono- and dicotyledonous species at low and high nitrogen availability. *Physiologia Plantarum* 95, 541–550. DOI: 10.1111/j.1399-3054.1995.tb05520.x.

Aphalo, PJ (2010). On how to disentangle the contribution of different organs and processes to the growth of whole plants. *Journal of Experimental Botany* 61, 626–628. DOI: 10.1093/jxb/erp398.

Aphalo, PJ, Ballaré, CL (1995). On the importance of information-acquiring systems in plant-plant interactions. *Functional Ecology* 9, 5–14. DOI: 10.2307/2390084.

Aphalo, PJ, Gibson, D, Di Benedetto, AH (1991). Responses of growth, photosynthesis, and leaf conductance to white light irradiance and end-of-day red and far-red pulses in *Fuchsia magellanica* Lam. *New Phytologist* 117, 461–471. DOI: 10.1111/j.1469-8137.1991.tb00010.x.

Aphalo, PJ, Lehto, T (1997). Effects of light quality on growth and N accumulation in birch seedlings. *Tree Physiology* 17, 125–132. DOI: 10.1093/treephys/17.2.125.

Aphalo, PJ, Sadras, VO (2021). Explaining preemptive acclimation by linking information to plant phenotype. *Journal of Experimental Botany*. DOI: 10.1093/jxb/erab537.

Barnes, PW (2017). Understanding the ecological role of solar ultraviolet radiation in the life (and death) of terrestrial plants. *UV4Plants Bulletin*, 8–15. DOI: 10.19232/uv4pb.2016.2.12.

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Barnes, PW, Flint, SD, Tobler, MA, Ryel, RJ (2016). Diurnal adjustment in ultraviolet sunscreen protection is widespread among higher plants. *Oecologia* 181, 55-63. DOI: 10.1007/s00442-016-3558-9.

Blackman, GE, Wilson, GL (1951). Physiological and Ecological Studies in the Analysis of Plant Environment. VII. An analysis of the differential effects of light intensity on the net assimilation rate, leaf-area ratio, and relative growth rate of different species. *Annals of Botany* 15, 373-408. DOI: 10.1093/oxfordjournals.aob.a083288.

Bone, RA, Lee, DW, Norman, JM (1985). Epidermal cells functioning as lenses in leaves of tropical rain-forest shade plants. *Applied Optics* 24, 1408-1412.

Brelsford, CC, Morales, LO, Nezval, J, Kotilainen, TK, Hartikainen, SM, Aphalo, PJ, Robson, TM (2018). Do UV-A radiation and blue light during growth prime leaves to cope with acute high-light in photoreceptor mutants of *Arabidopsis thaliana*? *Physiologia Plantarum* 165, 537-554. DOI: 10.1111/ppl.12749.

Capra, F, Luisi, PL (2014). *The Systems View of Life*. Cambridge University Press. 514 pp.

Casal, JJ (2013a). Canopy Light Signals and Crop Yield in Sickness and in Health. *ISRN Agronomy* 2013, 1-16. DOI: 10.1155/2013/650439.

Casal, JJ (2013b). Photoreceptor Signaling Networks in Plant Responses to Shade. *Annual Review of Plant Biology* 64, 403-427. DOI: 10.1146/annurev-arplant-050312-120221.

Cook, JD (2008). *Approximate problems and approximate solutions*. URL: https://www.johndcook.com/blog/2008/07/10/approximate-problems-and-approximate-solutions/.

Dale, MP, Causton, DR (1992). The ecophysiology of *Veronica chamaedrys*, *V. montana* and *V. officinalis*. 1. Light quality and light quantity. *Journal of Ecology* 80, 483-492. DOI: 10.2307/2260692.

Dixon, JM, Taniguchi, M, Lindsey, JS (2005). PhotochemCAD 2: a refined program with accompanying spectral databases for photochemical calculations. *Photochemistry and photobiology* 81, 212-213. DOI: 10.1562/2004-11-06-TSN-361.

Ehleringer, J, Forseth, I (1980). Solar Tracking by Plants. *Science* 210, 1094-1098. DOI: 10.1126/science.210.4474.1094.

Ehleringer, JR, Cook, CS (1984). Photosynthesis in Encelia farinosa Gray in Response to Decreasing Leaf Water Potential. *Plant Physiology* 75, 688–693. DOI: 10.1104/pp.75.3.688.

Folta, KM, Childers, KS (2008). Light as a Growth Regulator: Controlling Plant Biology with Narrow-bandwidth Solid-state Lighting Systems. *HortScience* 43, 1957–1964.

Hay, RKM (1995). Harvest index: a review of its use in plant breeding and crop physiology. *Annals of Applied Biology* 126, 197–216. DOI: 10.1111/j.1744-7348.1995.tb05015.x.

Hikosaka, K, Hirose, T (1997). Leaf angle as a strategy for light competition: Optimal and evolutionarily stable light-extinction coefficient within a leaf canopy. *Ecoscience* 4, 501–507. DOI: 10.1080/11956860.1997.11682429.

Hunt, R (1978). *Plant Growth Analysis*. London: Edward Arnold, 67.

Kahneman, D (2012). *Thinking, Fast and Slow*. Penguin Books Ltd (UK). 512 pp.

Kim, HH, Goins, GD, Wheeler, RM, Sager, JC (2004). Green-light supplementation for enhanced lettuce growth under red- and blue-light-emitting diodes. *HortScience : a publication of the American Society for Horticultural Science* 39, 1617–1622.

Kotiranta, S, Siipola, S, Robson, T, Aphalo, P, Kotilainen, T (2015). LED lights can be used to improve the water deficit tolerance of tomato seedlings grown in greenhouses. *Acta Hortic.*, 107–112. DOI: 10.17660/actahortic.2015.1107.14.

Kuroiwa, S, Hiroi, T, Takada, K, Monsi, M (1964). Distribution ratio of net photosynthate to photosynthetic and non-photosynthetic systems in shaded plants. *Botanical Magazine, Tokyo* 77, 37–42. DOI: 10.15281/jplantres1887.77.37.

Kusuma, P, Pattison, PM, Bugbee, B (2020). From physics to fixtures to food: current and potential LED efficacy. *Horticulture Research* 7. DOI: 10.1038/s41438-020-0283-7.

Laisk, A, Oja, V, Eichelmann, H, Dall'Osto, L (2014). Action spectra of photosystems II and I and quantum yield of photosynthesis in leaves in State 1. *Biochimica et Biophysica Acta (BBA) - Bioenergetics* 1837, 315–325. DOI: 10.1016/j.bbabio.2013.12.001.

Lichtenthaler, HK, Buschmann, C, Fietz, H, Bach, T, Kozel, U, Meier, D, Rahmsdorf, U (1981). Photosynthetic activity, chloroplast ultrastructure, and leaf characteristics of high-light and low-light plants and of sun and shade leaves. *Photosynthesis Research* 2, 115–141.

Lysenko, VS, Varduny, TV, Simonovich, EI, et al. (2014). Far-Red Spectrum of Second Emerson Effect: A Study Using Dual-Wavelength Pulse Amplitude Modulation Fluorometry. *American Journal of Biochemistry and Biotechnology* 10, 234–240. DOI: 10.3844/ajbbsp.2014.234.240.

Mansfield, TA, Meidner, H (1966). Stomatal Opening in Light of Different Wavelengths: Effects of Blue Light Independent of Carbon Dioxide Concentration. *Journal of Experimental Botany* 17, 510–521. DOI: 10.1093/jxb/17.3.510.

Marquis, DA (1965). *Artificial light sources differ in effect on birch seedling growth*. Research rep. Upper Darby, PA: U.S., 1–6. 6 pp.

McCree, KJ (1972a). Significance of Enhancement for Calculations Based on the Action Spectrum for Photosynthesis. *Plant Physiology* 49, 704–706. DOI: 10.1104/pp.49.5.704.

McCree, KJ (1972b). The action spectrum, absorptance and quantum yield of photosynthesis in crop plants. *Agricultural Meteorology* 9, 191–216. DOI: 10.1016/0002-1571(71)90022-7.

Monsi, M, Saeki, T (1953). Über den Lichfaktor in den Pflanzengesellschaften und seine Bedeutung für die Stoffproduktion. *Japanese Journal of Botany* 14, 22–52.

Muraoka, H, Koizumi, H, Pearcy, RW (2003). Leaf display and photosynthesis of tree seedlings in a cool-temperate deciduous broadleaf forest understorey. *Oecologia* 135, 500–509. DOI: 10.1007/s00442-003-1227-2.

Niinemets, Ü (2007). Photosynthesis and resource distribution through plant canopies. *Plant, Cell and Environment* 30, 1052–1071. DOI: 10.1111/j.1365-3040.2007.01683.x.

Noda, H (2013). *Reflectance and transmittance spectra of leaves and shoots of 22 vascular plant species and reflectance spectra of trunks and branches of 12 tree species in Japan*. Version ERDP-2013-02.1.1. From R package 'photobiologyPlants' version 0.4.2, available through CRAN. JaLTER, Japan Long Term Ecological Re-

search Network, http://www.jalter.org. URL: http://db.cger.nies.go.jp/JaLTER/metacat/metacat/ERDP-2013-02.1.1/jalter-en.

Novoplansky, A, Cohen, D, Sachs, T (1990). How portulaca seedlings avoid their neighbors. *Oecologia* 82, 490–493. DOI: 10.1007/BF00319791.

Ovaska, J, Ruuska, S, Rintamaki, E, Vapaavuori, E (1993). Combined Effects of Partial Defoliation and Nutrient Availability on Cloned Betula pendula Saplings .2. Changes in Net Photosynthesis and Related Biochemical Properties. *Journal of Experimental Botany* 44, 1395–1402.

Poorter, H, Remkes, C (1990). Leaf area ratio and net assimilation rate of 24 wild species differing in relative growth rate. *Oecologia* 83, 553–559. DOI: 10.1007/BF00317209.

Rai, N, O'Hara, A, Farkas, D, et al. (2020). The photoreceptor UVR8 mediates the perception of both UV-B and UV-A wavelengths up to 350 nm of sunlight with responsivity moderated by cryptochromes. *Plant, Cell & Environment* 43, 1513–1527. DOI: 10.1111/pce.13752.

Rousseaux, MC, Hall, AJ, Sánchez, RA (1996). Far-red enrichment and photosynthetically active radiation level influence leaf senescence in field-grown sunflower. *Physiologia Plantarum* 96, 217–224.

Sadras, V, Alston, J, Aphalo, P, et al. (2021). Making science more effective for agriculture. In: *Advances in Agronomy*. Vol. 163. Elsevier. Chap. 4, 153–177. DOI: 10.1016/bs.agron.2020.05.003.

Sestak, Z, Catsky, J, Jarvis, PG (1971). *Plant photosynthetic production: manual of methods*. English. The Hague: Junk, 819.

Shackel, KA, Hall, AE (1979). Reversible Leaflet Movements in Relation to Drought Adaptation of Cowpeas, *Vigna unguiculata* (L.) Walp. *Australian Journal of Plant Physiology* 6, 265–276. DOI: 10.1071/pp9790265.

Smith, H (1976). *Light and Plant Development*. London: Butterworths.

Suárez, N (2010). Leaf lifetime photosynthetic rate and leaf demography in whole plants of *Ipomoea pes-caprae* growing with a low supply of calcium, a 'non-mobile' nutrient. *Journal of Experimental Botany* 61, 843–855. DOI: 10.1093/jxb/erp351.

Tennessen, DJ, Bula, RJ, Sharkey, TD (1995). Efficiency of photosynthesis in continuous and pulsed light emitting diode irradiation. *Photosynthesis Research* 44, 261–269. DOI: 10.1007/bf00048599.

Vogelmann, TC, Björn, LO (1983). Response to directional light by leaves of a sun-tracking lupine (*Lupinus succulentus*). *Physiologia Plantarum* 59, 533–538. DOI: 10.1111/j.1399–3054.1983.tb06276.x.

Vogelmann, TC, Björn, LO (1984). Measurement of light gradients and spectral regime in plant tissue with a fiber optic probe. *Physiologia Plantarum* 60, 361–368.

Yoshida, H, Mizuta, D, Fukuda, N, Hikosaka, S, Goto, E (2016). Effects of varying light quality from single-peak blue and red light-emitting diodes during nursery period on flowering, photosynthesis, growth, and fruit yield of everbearing strawberry. *Plant Biotechnology* 33, 267–276. DOI: 10.5511/plantbiotechnology.16.0216a.

Zeiger, E, Field, C, Mooney, HA (1981). Stomatal openning at dawn: possible roles of the blue light response in nature. In: H Smith, ed. *Plants and the Daylight Spectrum*. London: Academic Press, 391–407.

Zhen, S, Bugbee, B (2020). Substituting Far-Red for Traditionally Defined Photosynthetic Photons Results in Equal Canopy Quantum Yield for CO2 Fixation and Increased Photon Capture During Long-Term Studies: Implications for Re-Defining PAR. *Frontiers in Plant Science* 11. DOI: 10.3389/fpls.2020.581156.

Zhen, S, Haidekker, M, Iersel, MW van (2018). Far-red light enhances photochemical efficiency in a wavelength-dependent manner. *Physiologia Plantarum*. DOI: 10.1111/ppl.12834.

Zhen, S, Iersel, MW van (2017). Far-red light is needed for efficient photochemistry and photosynthesis. *Journal of Plant Physiology* 209, 115–122. DOI: 10.1016/j.jplph.2016.12.004.

Additional examples of LED and LED fixture spectra

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, starting with spectra most different to sunlight to those most similar. See also the spectra in Figures 1, 2 and
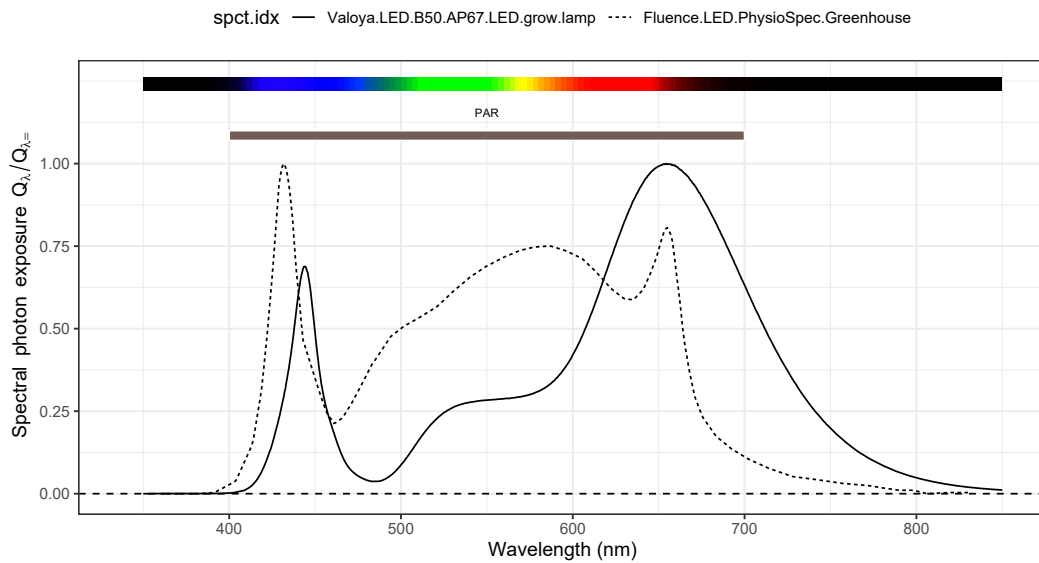
Figure 8: Emission spectra of two broad spectrum LED luminaires for plant cultivation (B50 AP67, Valoya, Finland; RAY bar, PhysioSpecGreenhouse, Fluence-Osram, Austin, TX, USA.).

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3.

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

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 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. In the remainder of this article we discuss the transformations involved in the conversion of electrical energy into commercial yield and growers' profit highlighting the gaps in knowledge and the difficulties involved in basing argumentation on only partial aspects of a mechanistically very
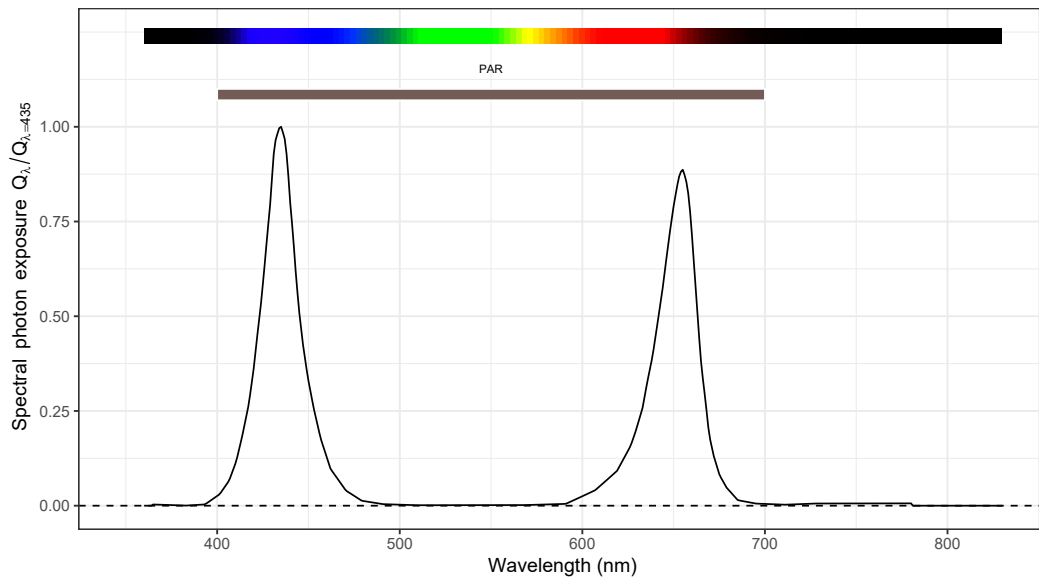
Figure 9: Emission spectrum of a red plus blue LED lamps for plant cultivation (RAY bar, AnthoSpec, Fluence-Osram, Austin, TX, USA).
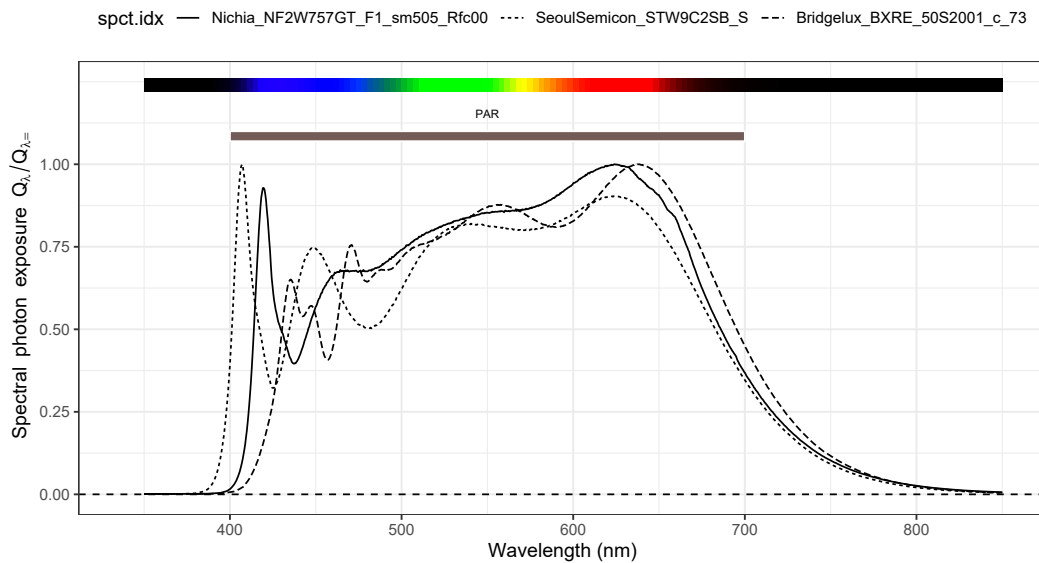

Figure 10: Emission spectrum of 5000 K SMD LEDs marketed as "similar to sunlight" and sold for museum displays and general illumination (Nichia, Japan; Seoul Semiconductors, Korea; Bridgelux, USA). These three types of LED differ mainly in the violet region.
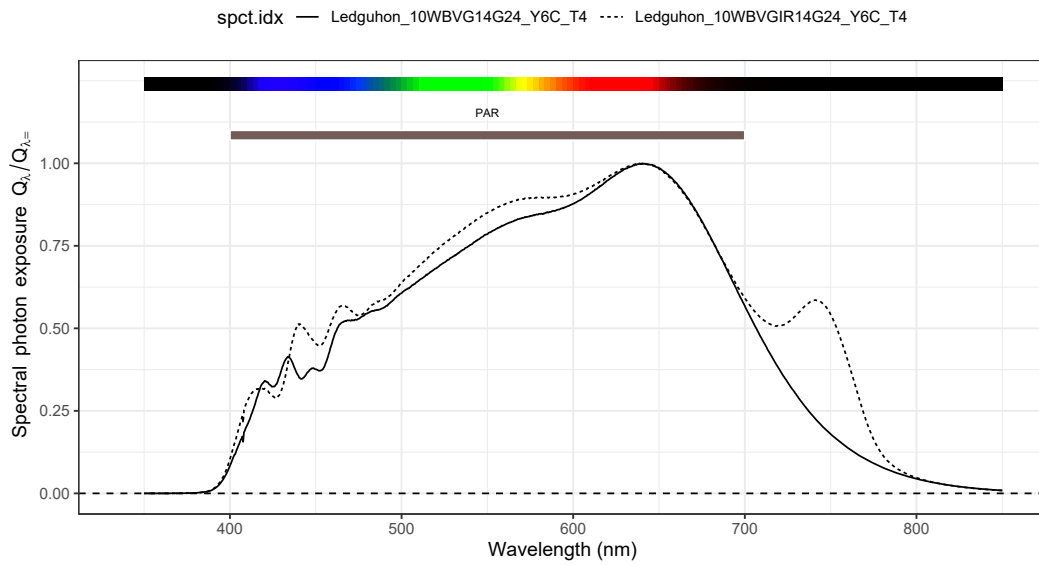
.

Figure 11: 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.
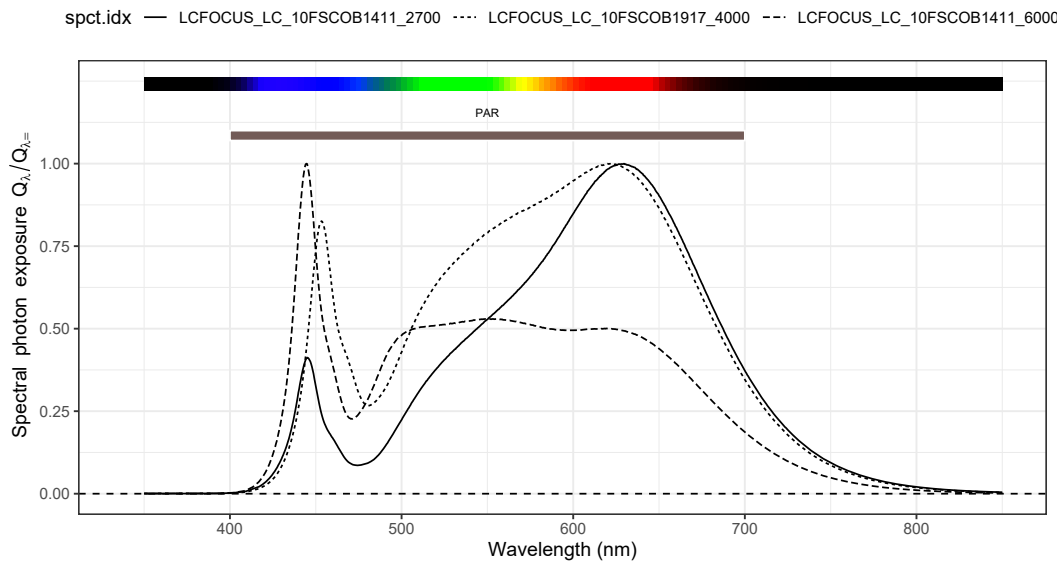
.

Figure 12: 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 two types of LED differ mainly in the balance between blue and red light.

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complex problem.