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 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 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

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,...). If we look that companies producing grow lamps, there is also great variation and in some cases advertising is not consistent between the LED as components and grow lamps divisions of the same companies (e.g., Osram). The arguments to defend one of the other approach vary to some extent, but blue plus red illumination is justified by comparison to the invitro absorption spectrum of chlorophyll, white light tailored for plant cultivation is justified based on yield comparisons for crops. The persistence of blue plus red illumination as a frequently used approach seems

We start by asking what are the real targets for the design of grow lights? Ultimately, growers' net income and sustainable use of resources. These 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. Anyway, we can already state that given the complexity of interactions, multiple factors and compromises involved, different spectra will be suitable for different situations. We also dare to say, that optimal spectra from the growers' perspective are those that fulfil the growers' target close enough under the broadest range of situations. Even for production 100% dependent on artificial light, it seems unwise to optimize lamp spectra to a single crop as the lamps have a long lifetime (20 or more years) during which market conditions may change in ways that make it desirable to cultivate a different species in the same facility.

If we consider the current situation, both red plus blue and broad spectrum LED growth lamps are widely advertised as excellent for use in commercial horticulture (Figs. 1, **??**). There are variations around these two types of spectra but these two approaches tend to be distinct in concept and implementation. Red plus blue lamps most frequently use two types of LEDs, each type directly emitting a narrow peak in the red or blue region. Broad´spectrum LEDs rely on a second stage to broaden the range of emitted wavelengths. 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. In addition, red photons carry less energy than photons of shorter wavelengths such as blue or green, so more photons can be generated, in principle, per joule of energy. Given that 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, red photons can be expected to be equally effective in driving photosynthesis than blue or green ones, as long as they are absorbed. 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 continuously day and night 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 addition to efficiency.

An argument still in use, especially in advertising, is that red and blue light are

more efficiently used in photosynthesis than other wavelengths (**exciteled2022**; **?**), and consequently also best for plant cultivation in horticulture and to the controversial concept of "wasted illumination" used to describe light outside these regions of the spectrum. The design of light sources for plant cultivation using as criterion this idea is a good example of gross misuse of reductionism. Next we will attempt to analyse how design could go so much astray when any plant scientist or agronomist should know that many important aspects were ignored. 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 useful way of measuring 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 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-A2 and FR should be given more weight.

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 deter-

minant 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) () and its importance in agriculture has been in use since …. We also have been aware that the light spectral quality affects the morphology of plants (Smith, 1976) and the life-span of leaves (??), and consequently has a bearing on both the growth, i.e., accumulation of biomass (Aphalo, 2010; Aphalo and Ballaré, 1995; Aphalo and Sadras, 2021) and determination of the harvest index (). 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).

Clearly the problem was not lack of information, but our failure to integrate it and consider the context in which photosynthesis takes place, i.e., ignoring interactions, levels of organization and temporal and spacial scales. So, to me the most interesting question is how could so many people have ignored what should have been obvious, or at least obvious enough that such justification was in need of a clear demonstration given all accumulated past evidence making it highly implausible. I think the answer is that attempting to design a universally good spectrum is not possible, because if we consider all factors involved, the problem becomes intractable (**Lumigrow2022**). So, everything that the problem was changed to deal only with those aspects that can be thought as invariant over crop species, geographic locations and cultivation approaches. So focus remained only in the in-vitro absorption spectrum of chlorophyll, which is close to invariant, and the efficiency of LEDs measured as mol per joule which is independent of the use cases. This oversimplification made it possible to think in terms that can make intuitively sense to both electrical engineers and users (see box XXX about credibility and graphical data displays). The problem is that the solutions proposed no longer apply to the actual problem in need of being solved.

Box 1. What makes that a (pseudo-)scientific argument is credible to non experts? a. Accompanying the text with a plot (any plot!) and b. Internal coherence of the argument's logic.

Biological systems are dominated by non-linear responses and interactions. 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), and what is most relevant here, the light spectrum is used by plants as a source of information. The responses, which depend on temporal and spatial integration of informational cues and signals, and that the information is in most cases dependent on environmental correlations. We can not think just in terms of energy and quantum efficiency when choosing spectra, we need to be aware that the properties of the spectrum will determine morphology, growth and development as a result of plant responses that have been selected as favorable to fitness in natural light.

Too frequently in biological research, participants 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" (). Ignoring the context under which plants are studied vs. the one where they have evolved, been artificially selected or crop production takes place generates good answers to approximate questions. The problem is that in most cases, these good answers are not applicable to the original or practical question that the research or analysis aimed to address.

Current LED fixtures

Currently lamps 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 lamps used for general illumination in houses or public spaces. We here give examples, starting with spectra most different to sunlight to those most similar.

Both types of growth lamps are still widely available commercially. The argument used to justify the design of blue and red lamps is based on the in-vitro absorption spectrum of chlorophyll, disregarding what is known about the action spectrum of photosynthesis itself and the indirect effects of light on growth through the modulation of morphology and physiology. All wavelengths of light from the UV-C to the NIR are relevant for plant growth, development or health.

Figure 8 shows an approximation to the spectrum for "suggested fixture for high efficacy", proposed by Kusuma et al. 2020, Fig. 6 obtained by combining *in silico* the emission spectra of two types of LEDs, designed to be used together. It also
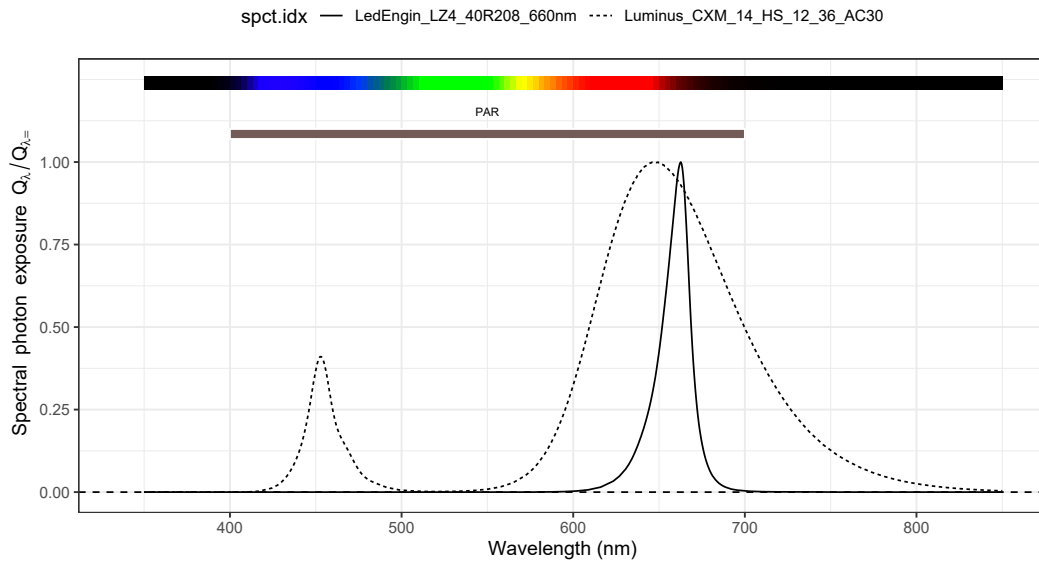
Figure 1: Emission spectrum of a "deep" red SMD LED (LedEngin-Osram, USA), and a "purple" blue plus red COB LED (Luminus, USA). Both LEDs sold for plant cultivation.
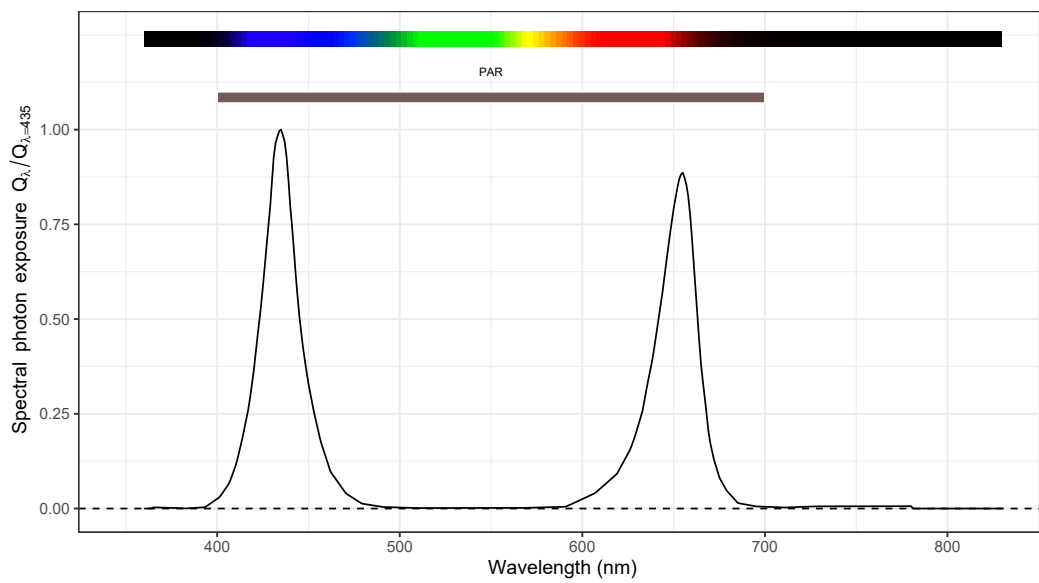

Figure 2: Emission spectrum of a red plus blue LED lamps for plant cultivation (RAY bar, AnthoSpec, Fluence-Osram, Austin, TX, USA).
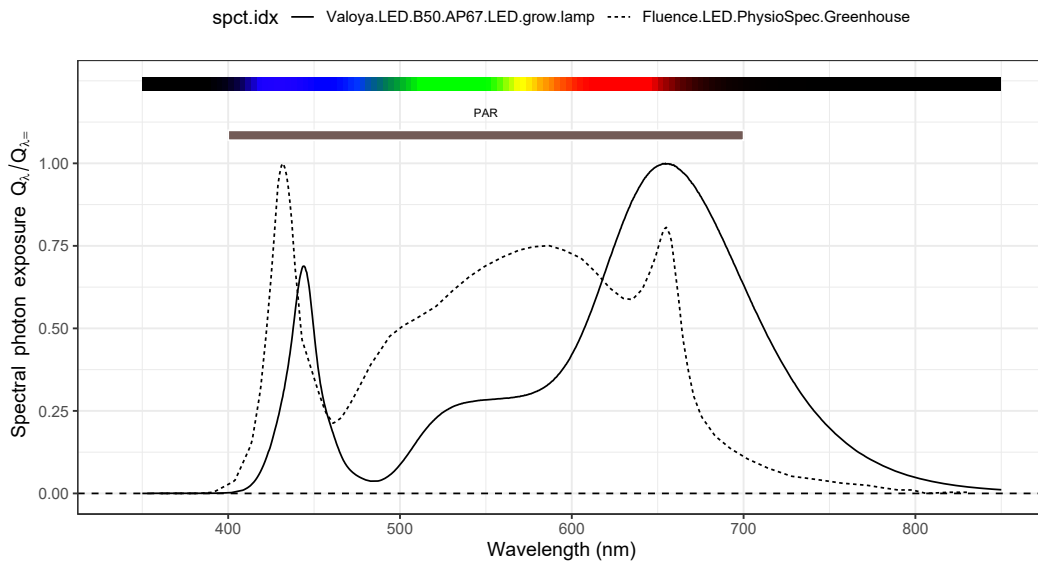
Figure 3: Emission spectra of two broad spectrum LED luminaires for plant cultivation (B50 AP67, Valoya, Finland; RAY bar, PhysioSpecGreenhouse, Fluence-Osram, Austin, TX, USA.).
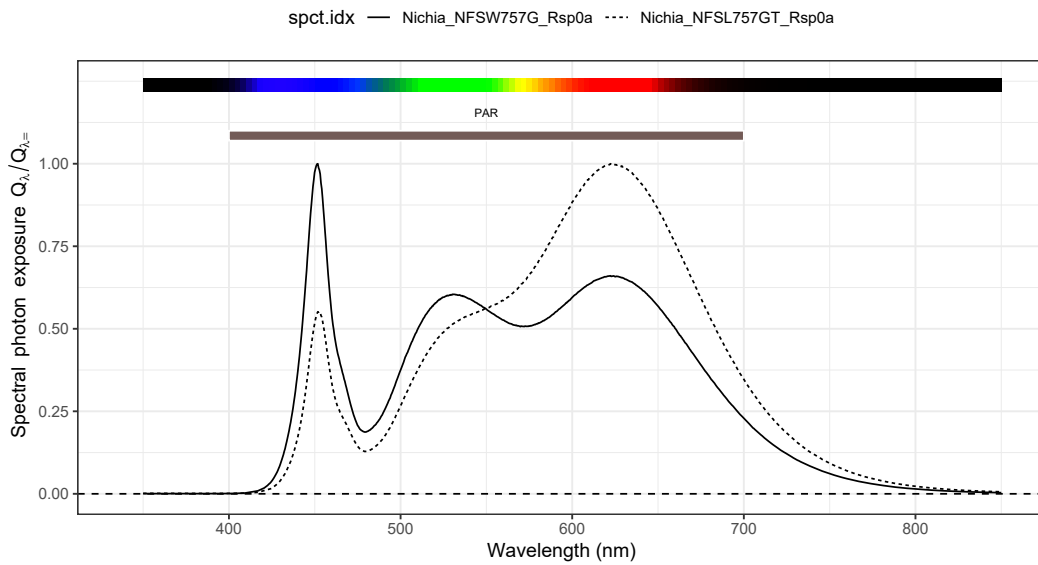
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Figure 4: Emission spectra of two broad spectrum SMD LEDs for horticulture rated at 3000 K and 5000 K (Types NFSW757G-Rsp0a and NFSL757GT-Rsp0a, Nichia, Japan).
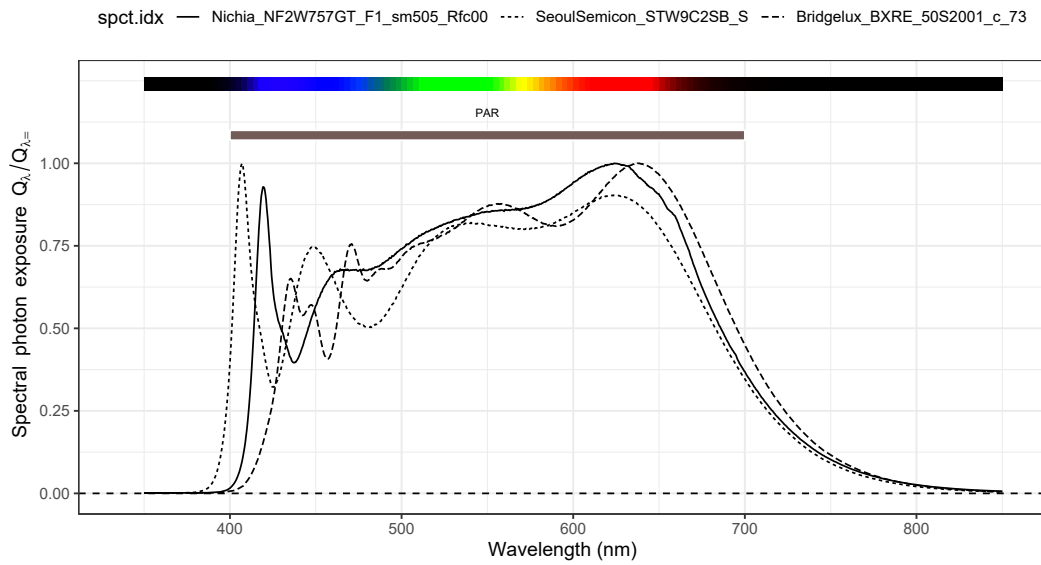
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Figure 5: Emission spectrum of 5000 K SMD LEDs marketed as "similar to sunlight" and sold for museum displays and general illumination (Nichia, Japan; Seoul Semiconductors, Korea; Bridgelux, USA). These three types of LED differ mainly in the violet region.
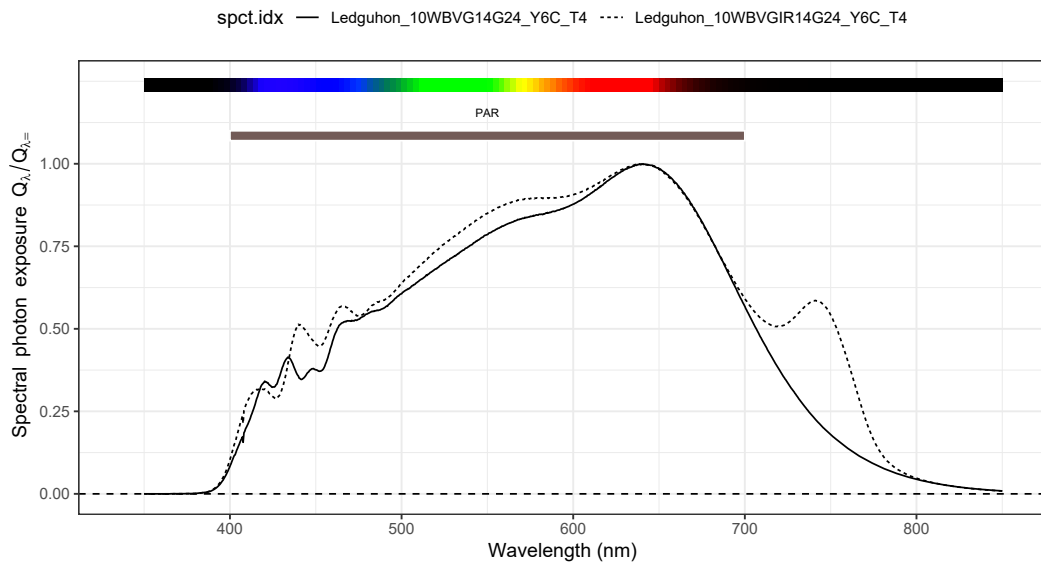
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Figure 6: Emission spectrum of 4000 K COB LEDs marketed as "similar to sunlight" and useful for plant cultivation (Ledguhon, China). These two types of LED differ mainly in the far-red.
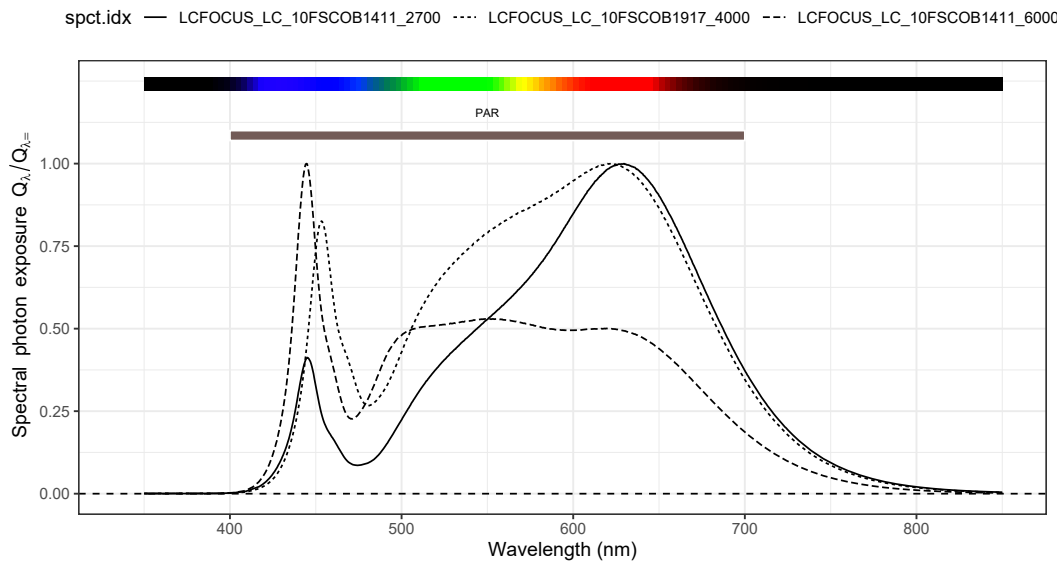
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Figure 7: Emission spectrum of 10W COB LEDs marketed as "for hydroponics" with nominal color temperatures of $2700\,K$, $4000\,K$ and $6000\,K$ (LCFOCUS, China). These two types of LED differ mainly in the balance between blue and red light.

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includes a simulated almost matching spectrum obtained by combining two types of SMD LEDs sold for use in luminaires for plant cultivation.

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
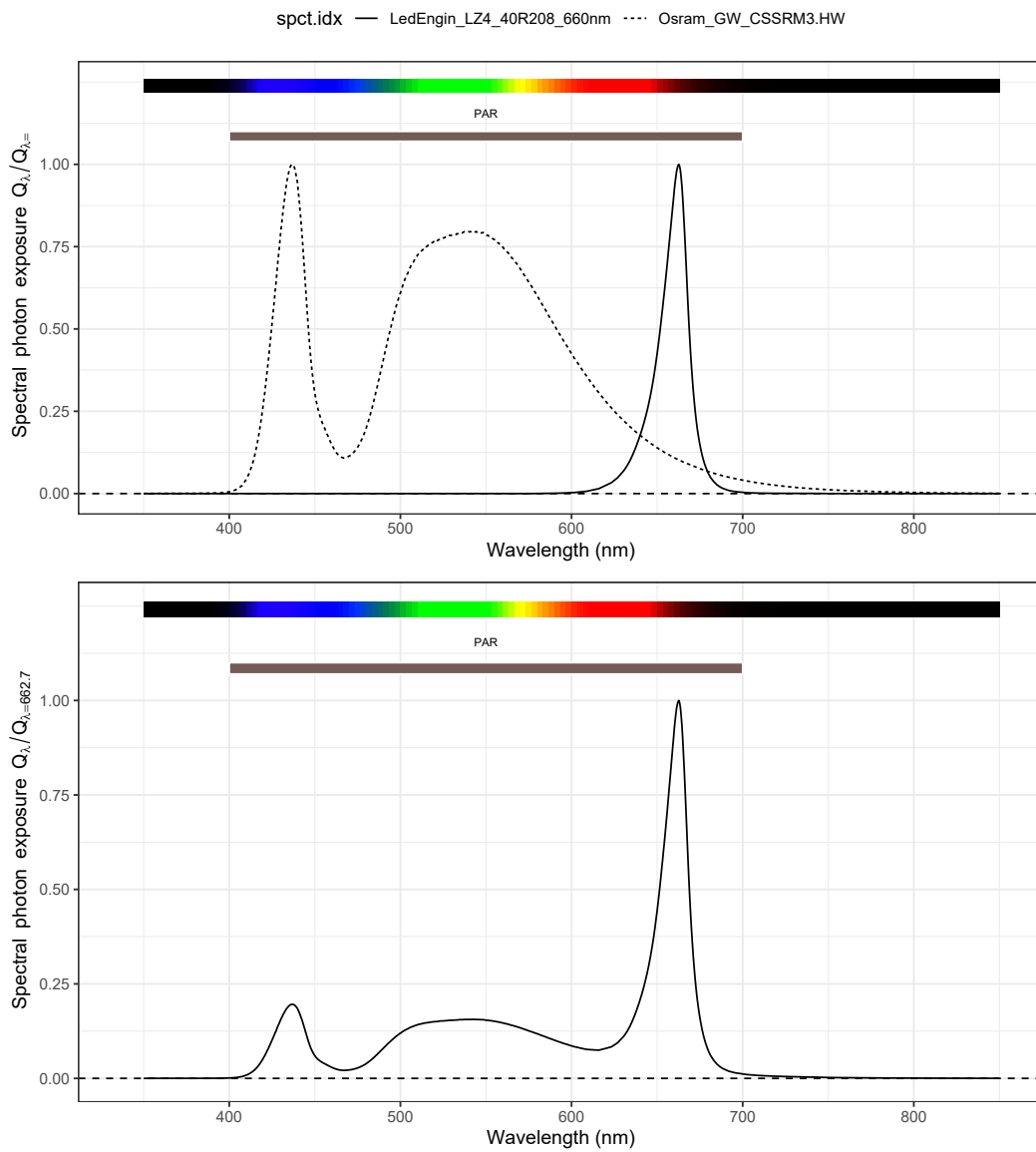
Figure 8: Emission spectrum approximating the one proposed by Kusuma et al., Fig. 6. The spectra of Led Engin LZ4-40R208 leds emitting at 660 nm (nominal) and broad-spectrum Osram GW-CSSRM3-HW grow leds (top) were combined *in silico* in 4:1 proportion based on photon irradiance (bottom).

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yield and growers' profit highlighting the gaps in knowledge and the difficulties involved in basing argumentation on only partial aspects of a mechanistically very complex problem.

Energy vs. photons

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. So, nowadays specifications of LEDs intended for plant growth include a rating for photons per watt. This efficiency decreases with increasing temperature of the LEDs, and how strong this effect is depends on the type of LED. We will use for 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 8). 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, so this analysis indicates that if we assume that the wavelength of light is irrelevant to plant morphogenesis and that the quantum efficiency of photosynthesis is independent of wavelength, to maximize energy use efficiency we

should prefer longer wavelengths for plant cultivation. But are these assumptions valid?

Chlorophyll in vitro vs. in planta

There is a striking difference between the shape of the *in-vitro* absorptance spectra for chlorophyll (Fig. 9) and of leaves (Fig. 10), 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, 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 (**??**). 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,

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
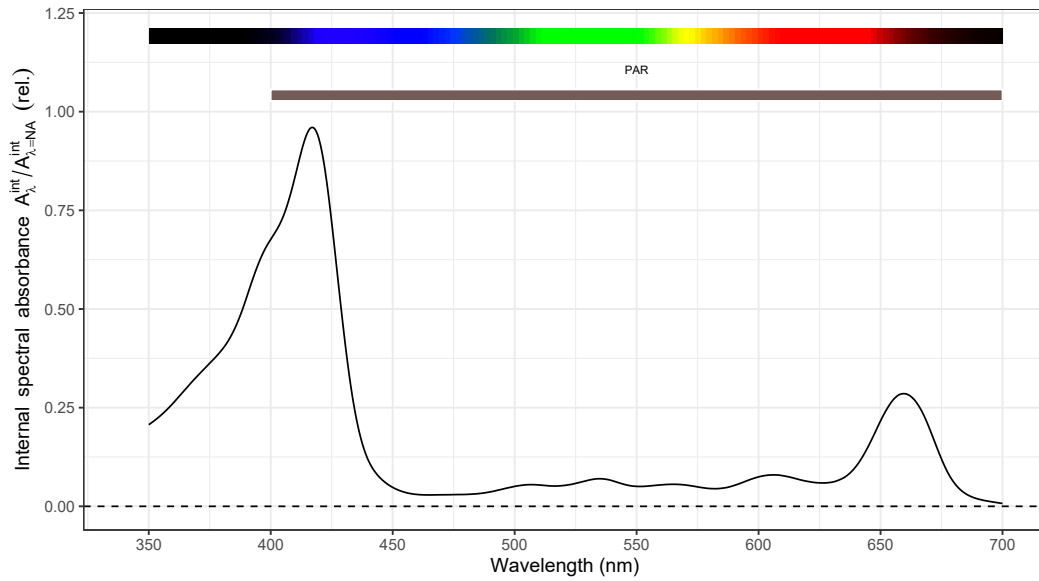
Figure 9: In vitro absorptance spectrum of chlorophyll *a* in methanol (Data described in Dixon et al., 2005).
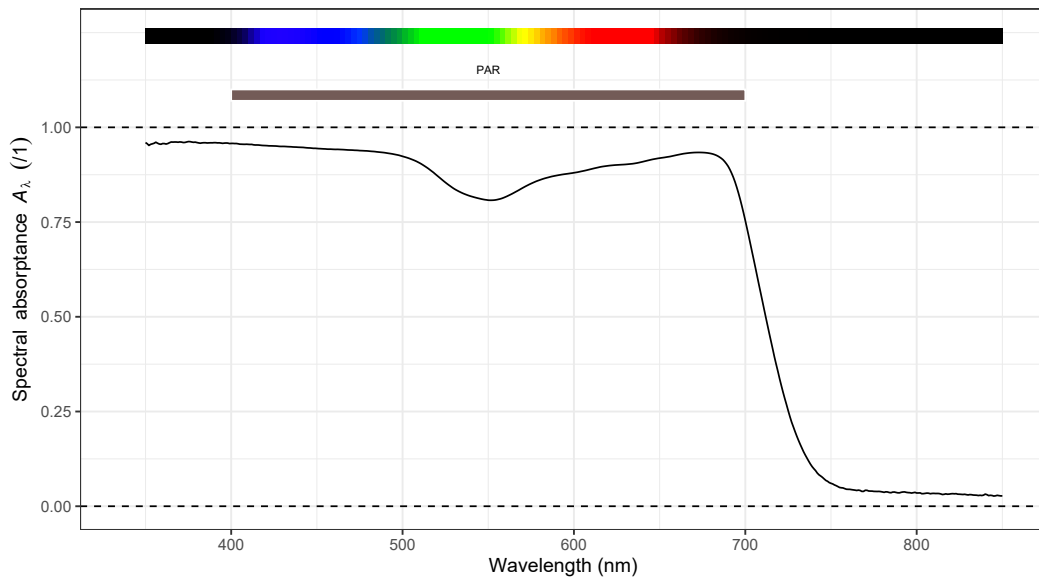

Figure 10: In-vivo absorptance of the adaxial surface of a *Betula ermanii* leaf from the first flush (Data from Noda, 2013).

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
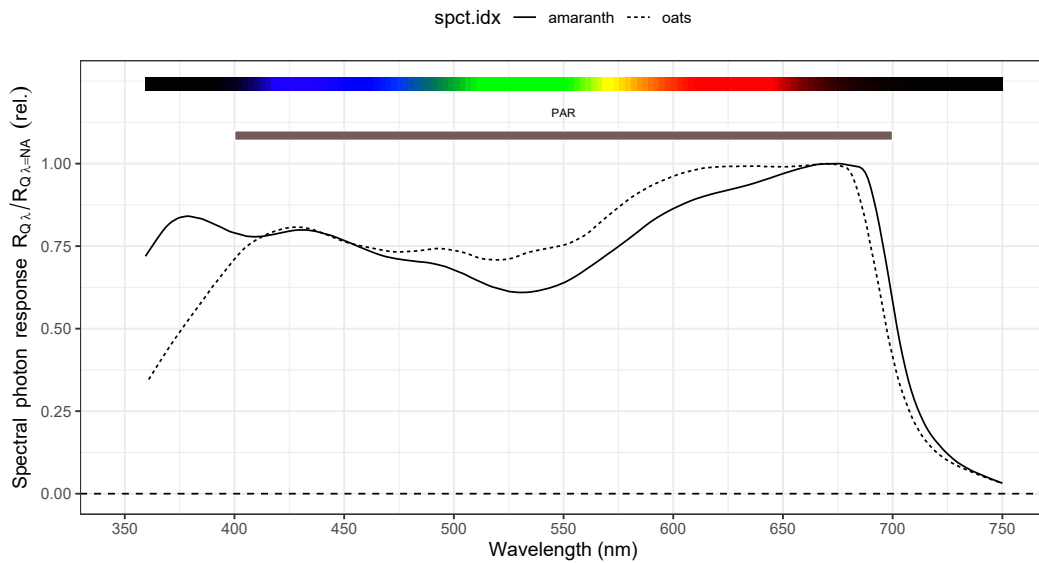
Figure 11: Action spectra for photosynthetic oxygen evolution in leaf tissues of *Amaranthus edulis* and *Avena sativa* (Data from McCree, 1972a) expressed on a *photon base*.

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 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 11 and 12, as most avail-

able 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. 11. 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 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 12). 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

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 pho-
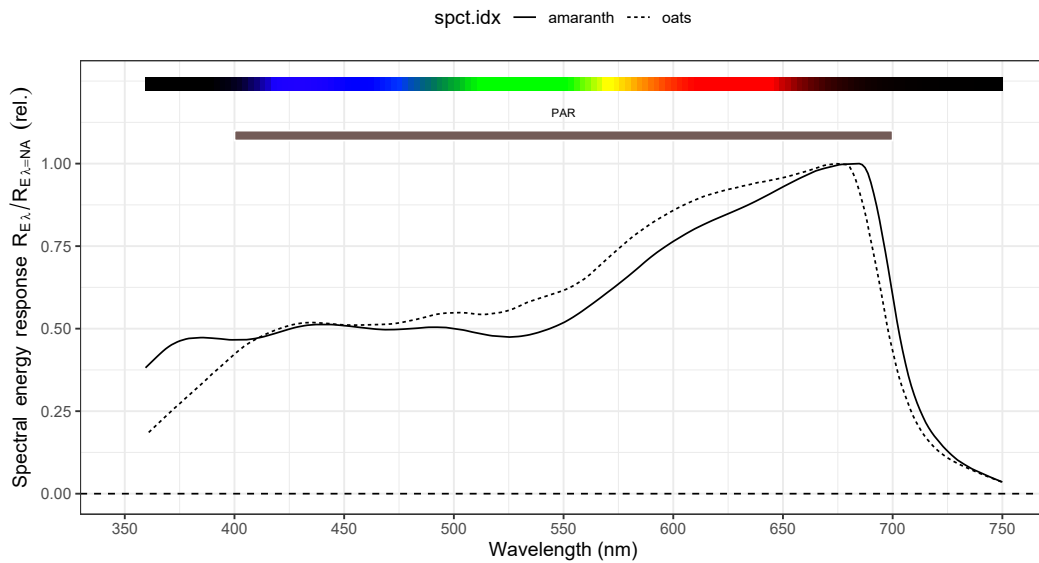
Figure 12: Action spectra for photosynthetic oxygen evolution in leaf tissues of *Amaranthus edulis* and *Avena sativa* (Data from McCree, 1972a) expressed on an *energy base*.

tosynthesis 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, 2013). 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", accelerating the relative growth rate (??). However, 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

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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 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 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 (??). 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 cen-

tre). Although some regulation is through feedback, once again, pigment composition, photosynthetic antenna size, and abundance of photosynthetic enzymes are regulated through the interaction of multiple photoreceptors (**??**).

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 (). 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 (). 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 ().

Taming complexity

The best thing about being a statistician is that you get to play in everyone's backyard. (John w. Tukey)

   The greatest value of a picture is when it forces us to notice what we never expected to see. (John W. Tukey)

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 autocite???. 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 acquired 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 so-

lutions 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.

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