HortScience 58(2):180–196. 2023. https://doi.org/10.21273/HORTSCI16823-22

LED Lighting: A Grower's Guide to Light Spectra

John D. Stamford, Jim Stevens, Philip M. Mullineaux, and Tracy Lawson
School of Life Sciences, University of Essex, Colchester, Essex, CO4 3SQ, United Kingdom

Keywords. LED lighting, lighting regime, grower, light, morphology, physiology, intracanopy, supplementary, red:blue ratio, red:far-red ratio, shade avoidance, energy costs, productivity

Abstract. **For many growers, established and newcomers, the determination of the optimal light spectrum for growing crops can be challenging and highly dependent on crop species and variety. With the increased popularity of LED lighting, the capability to fine-tune a light spectrum has never been greater. Here, we break down the fundamental roles of the major spectral regions (ultraviolet, blue, green, red, and far-red) and explain the effect on plant growth, yield, and crop quality (i.e., greenness, coloration, flavor) when applied in isolation or combination. The first part of this review examines plant responses to light stimuli and the potential benefits for growers. We also discuss how LED lighting can be used to manipulate plant growth and development to improve crop productivity and/or value. We suggest some basic LED light "recipes" that could be used by growers to deliver specific growth effects and provide an easy-to-use visual reference guide. The second part of this review explores the impact of light treatments on crop productivity. Increased productivity is weighed against the ongoing costs associated with various light treatments, modeled in the context of UK electricity pricing.**

Light is an essential resource for all plants, providing the energy necessary for photosynthesis, the process that enables plants to grow. However, light also plays a major role in influencing plant morphology and physiology, which is dependent not just on light intensity but also the spectral quality (color) of light. The effects of intensity and quality on plant performance and morphology are discussed in this review, with emphasis on how light can be used to improve the quality and quantity of crop yield.

Light is typically discussed in terms of light particles, or photons. Photons have specific wavelengths, ranging from the short wavelengths of the electromagnetic spectrum such as gamma and X-rays (<10 nm), to the long wavelengths of radio and microwaves (>1 mm). Visible light ranges between wavelengths of 400 and 700 nm (Fig. 1A). The wavelength of a photon is inversely correlated to the energy of that photon, with shorter wavelengths having higher energy, as described by Planck's equation of $E = hc/\lambda$; in which E is energy (Joules), h is the Planck constant ($6.62607015 \times 10^{-34}$ J·s), c is the speed of light, and λ is wavelength. The approximate relationship between wavelength and visible light as seen by the human eye is illustrated by the corresponding colors in Fig. 1A. When referring to the quantity of incident light on a plant, the photon flux density (PFD) is the most commonly used measurement of light intensity, which refers to the number of photons (µmol) received on a specified area (m^2) per second ($\mu mol \cdot m^{-2} \cdot s^{-1}$), with 1 mol of photons consisting of 6.022×10^{23} photons.

In the leaf, light between 400–700 nm (Fig. 1A), a region of the electromagnetic spectrum which is referred to as photosynthetically active radiation (PAR), is absorbed by various plant pigments. The total PFD for light within the PAR (400–700 nm) region is referred to as photosynthetic photon flux density (PPFD) and is the measurement used when assessing the impacts of light intensity on plant growth. However, recently there has been considerable debate regarding the definition of PAR, with suggestions that it should be extended to include far-red (FR) wavelengths up to 750 nm (Zhen et al. 2022; Zhen and Bugbee 2020a, 2020b; Zhen and van Iersel 2017). Other measurements commonly used include irradiance, in units of Watt per m^2 ($W \cdot m^{-2}$), which measures the overall power (referred to as radiant flux) received per unit area. The difference between PPFD and irradiance is that PPFD ($\mu mol \cdot m^{-2} \cdot s^{-1}$) measures photons, whereas irradiance ($W \cdot m^{-2}$) measures energy. The two are interconvertible bearing in mind that the energy of a photon depends on its wavelength as per Planck's equation. Lux is another measurement often provided by lighting manufacturers, which indicates the amount of lumens per square meter. The measure of lumens is weighted to the sensitivity of the human eye to each wavelength. Thus, given the same output of light in terms of irradiance ($W \cdot m^{-2}$), a green light will have a higher lux reading than a blue or red light. Red and blue wavelengths are particularly important to plants, and therefore PPFD or irradiance based units should be employed when referring to light intensity relative to crop performance, and lux should not be used unless a fixed spectrum is used and the relationship between PPFD and lux under that spectrum known.

Absorption of light for photosynthesis is predominantly due to chlorophyll pigments, which have absorbance peaks in red and blue wavelengths, with accessory pigments extending absorption to the other wavelengths in the visible spectrum (Lichtenthaler and Buschmann 2001). Photosynthesis is the process by which light energy (from the sun or electric lamps) is used to convert carbon dioxide (CO_2) and water into sugars, which are required for all plant growth and maintenance. Thus, light is clearly crucial in maintaining high rates of photosynthesis and plant growth.

Although light is essential for photosynthetic processes, too much light can be damaging, particularly in conjunction with other environmental stressors. Plants are sessile organisms and are unable to move rapidly in response to changing environmental cues or threats, including excess light energy (i.e., where more light energy is absorbed than can be usefully harnessed for electron transport). They have therefore developed an array of mechanisms to monitor and respond to environmental conditions to ensure survival and reproductive success (Casal 2013; Jenkins 2017). Both light intensity and spectral quality are triggers to which plants respond and adjust on both short- and long-term scales. For instance, plants have developed mechanisms to dissipate light energy in excess of that required for photosynthesis. One primary means of dissipating excess excitation energy is through pigments such as carotenoids, which dissipate absorbed light energy as heat (a process known as nonphotochemical quenching). This aids in preventing excess light energy from producing reactive oxygen species (ROS) and free radicals, which can significantly damage proteins, lipids and pigments, and subsequently reduce photosynthetic performance (Latowski et al. 2011; Murchie and Lawson 2013; Mullineaux et al. 2018; Murchie and Harbinson 2014). ROS accumulation is prevented by a battery of antioxidants such as ascorbic acid (vitamin C) and α-tocopherol (vitamin E; Mullineaux et al. 2018). Other pigments such as anthocyanins, which give leaves a distinctive purple color, also assist in reducing light absorption by photosynthetic pigments and can act as antioxidants helping to remove ROS (Chalker-Scott 1999; Kovinich et al. 2015; Thoma et al. 2020; Zheng et al. 2020). Many of these antioxidants and pigments are also highly

---

Received for publication 8 Aug 2022. Accepted for publication 11 Oct 2022.

This work was supported by Hy4Dense, a project that has received funding from the Interreg 2 Seas programme 2014-2020, co-funded by the European Regional Development Fund under subsidy contract no. 2S05-030. Phillip A. Davey is thanked for spectral measurements of light sources.

Current address of J.S.: Vertical Future, 3 Creekside, London, SE8 4SA, United Kingdom.

T.L. is the corresponding author. E-mail: tlawson@essex.ac.uk.

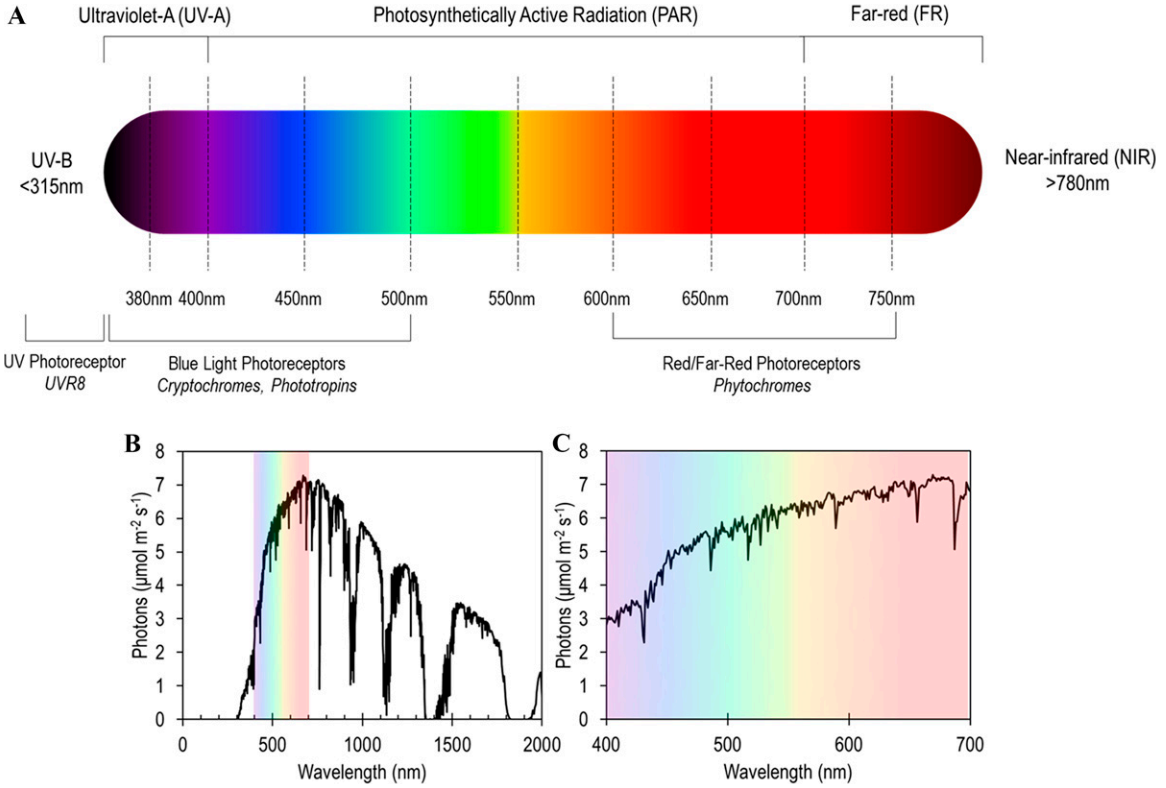


Fig. 1. (**A**) Wavelengths of the electromagnetic spectrum absorbed by plants and used to drive photosynthesis. Three main regions are identified: ultraviolet, associated with potentially damaging high energy photons of light; photosynthetically active radiation (PAR), the spectra that is absorbed by plant pigments to provide light energy for photosynthesis; and far-red (FR) light, associated with lower-energy photons of light. Key photoreceptors and their associated absorption spectra are also identified, showing the regions of ultraviolet, blue, red, and FR light detection by associated photoreceptors. Cryptochromes and phototropins have a role in blue light sensing—for instance, as used in phototropism or the increase in plant pigments to protect from high light intensity. Phytochromes are responsible for FR and red light sensing—for instance, to regulate plant growth in response to an increase in FR light associated with shade. UVR8 senses ultraviolet light and, much like blue light receptors, is involved in regulating high light to ultraviolet-protective pigments. (**B**) The photon flux density of irradiating sunlight per nanometer wavelength, based on the average for the 48 contiguous U.S. states over a period of 1 year, with (**C**) a close-up look at the visible spectra showing higher light intensities in green, orange, and red wavelengths than those of blue wavelengths, exhibiting a total photosynthetic photon flux density of 1739 $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$. The photon flux density was calculated based on the ASTM G-173 reference spectra, accessible at nrel.gov/grid/solar-resource/spectra-am1.5.html.

desired by some crop growers and retailers, due to the nutritional and visual attractiveness of these products to consumers.

These photoprotective mechanisms assist in maintaining optimal rates of photosynthesis under periods of high light (Murchie and Harbinson 2014; Murchie and Lawson 2013; Murchie and Ruban 2020). Thus, light intensity and subsequent photo-protective mechanisms have a major impact on plant growth. Low light intensity can limit plant growth, whereas too much light can be detrimental and damage plants, but additionally the speed of recovery from fluctuations in light intensity through management of nonphotochemical quenching capacity is linked to sustained rates of photosynthesis and yield (Casal 2012; Chavan et al. 2020; Kromdijk et al. 2016).

Other examples of environmental cues that influence plant development include changes in daylength, as experienced in spring and autumn months, which are major signals that plants use to determine seasons and flowering time (Johansson and Staiger 2015). The spectral quality of light is another key aspect that influences plant growth. Plants are able to detect the presence and intensity (or quantity) of light in specific spectral regions, typically grouped into ultraviolet, blue, red, and FR (Fig. 1A), through photoreceptors such as phototropins, cryptochromes, and phytochromes (Fig. 1A). Changes in light spectral quality, which, for example, can arise due to shading from other plants, result in the activation and deactivation of signaling pathways, leading to changes to plant growth, morphology, or performance.

Light sources: natural and electrical. Light from the sun is refracted and absorbed by atmospheric particles, such as water as it passes through Earth's atmosphere. This absorption affects the spectrum of sunlight that reaches the surface of Earth. A typical surface solar spectrum (Fig. 1B) exhibits a large peak corresponding to wavelengths of visible light. The visible spectrum (Fig. 1C) has increasingly higher intensities of green, orange, and red (wavelengths from 500 to 700 nm) relative to blue. However, sunlight is not always available or of sufficient intensity for growing certain crops or at particular times of the season. Supplementary lighting, which refers to electric lamps used to supplement sun-lit plants, is often employed by growers in greenhouses and polytunnels when natural light is limited due to low transmission through glass or plastic coverings, cloud cover, shading from nearby structures, and when natural light levels are low (e.g., winter months) (Chavan et al. 2020; Palmer and van Iersel 2020). Supplementary lighting is also used to extend the daylength to induce flowering in long day (short night) plants or to maximize flowering by optimizing the daylength for day-neutral plants (Hidaka et al. 2014). In some cases, all a crop's lighting requirements may be met with electric lamps, a common approach in the increasing use of controlled environment agriculture, which are sometimes referred to as "plant factories"—large warehouses composed of tall stacks of hydroponic systems also referred to as vertical farms (Kozai et al. 2019; Touliatos et al. 2016).

Several lighting options are available to growers (Fig. 2), each with different spectral qualities. In addition to ambient sunlight, there is the option of high-pressure sodium (HPS), metal halide (MH), fluorescent or light emitting diode (LED) lights, each with advantages and disadvantages for specific situations, most commonly relating to spectral output. HPS lighting is rich in orange–red wavelengths (Fig. 2D) with small amounts of blue and green, whereas MH lights typically have peaks in blue, green, and orange wavelengths (Fig. 2E). Most electric lamps emit

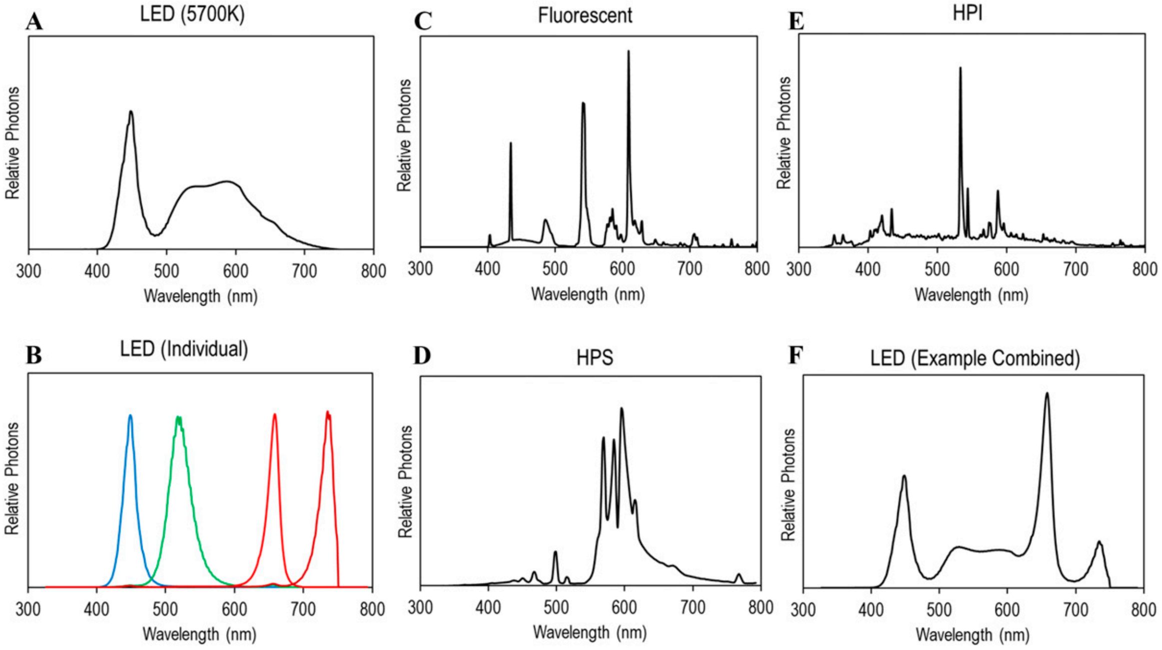


Fig. 2. Example spectra of common light sources for the purpose of plant growth. (**A**) A typical white light-emitting diode (LED) with a color temperature of 5700 K. (**B**) A selection of LEDs for the wavelengths of 450 nm (blue), 520 nm (green), 660 nm (red), and 735 nm (far-red). These are common wavelengths used by many manufacturers; however, many more wavelengths are available. Actual relative intensities will vary between manufacturers, and a uniform maximum intensity is shown here for illustration purposes. (**C**) A fluorescent bulb. (**D**) A high-pressure sodium (HPS) lamp used for supplementary lighting. (**E**) HPI, a type of metal halide light. (**F**) An example LED spectrum, composed of the spectra of panels A and B, demonstrating the flexibility afforded by LED lighting. Spectra for each light source type was measured in-house at the University of Essex, showing the relative photon flux density for each light source, and therefore the light intensity between light sources in this figure are not directly comparable. Calculated red:blue ratios can be found in Supplementary Table 1.

heat energy along with useful irradiance, which either has to be managed within greenhouse climate control systems or used as part of the heating system (Bakker et al. 2006; Firfiris et al. 2012). LED lighting is opening up new avenues for growers, allowing almost complete flexibility in the control of the light spectrum, intensity, and scheduling. Not only do LEDs offer unparalleled control over the lighting spectrum, but the reduced loss of energy to heat output contributes to the lower energy consumption of LED lights, with reported reductions of up to 20% to 35% compared with conventional HPS, greatly reducing energy consumption relative to traditional illumination systems (Kaukoranta et al. 2017; Pattison et al. 2018; Särkkä et al. 2017). As a result, LEDs have quickly overtaken other light sources as the first choice for many growers, especially given their spectral flexibility and ability to vary intensity. Unlike MH or HPS, LEDs can also turn on and off at will, whereas other types of lighting often requires a substantial (10–15 min) period of warming up and cooling down, and therefore cannot be switched rapidly. Having said this, LEDs do not have as long a history of use for growing plants as other lights, and therefore the relationship between LED spectra and crop performance is relatively unknown and untested. Furthermore, the impact of LEDs on crop growth will differ in crop varieties and growth environments, such as temperature, nutrients, irrigation, and humidity, and therefore it can be difficult to draw a concrete conclusion as to the effects of light on crop yield. However, general trends can be identified and used as a baseline for further fine-tuning. In addition to this, the associated initial costs with transitioning to a LED-based setup means that uptake so far has been limited.

LED Light Growth Spectra: The PAR Region

The importance of red and blue light. Red (600–700 nm) and blue (400–500 nm) wavelengths are the primary wavelengths employed in most LED based lighting systems as they are most strongly absorbed by plant pigments (including chlorophylls) for photosynthesis (Lichtenthaler and Buschmann 2001; McCree 1971). Red light is more efficiently used in photosynthesis than blue light (McCree 1971) due to several factors. First, absorbed high-energy blue light is transferred to lower energy chromophores in the photosynthetic reaction center, with the remainder of that energy lost as heat, and thus absorbed blue light delivers the same amount of energy for photochemistry as absorbed red light (Heldt 2005; Mirkovic et al. 2017). Second, blue light is absorbed not just by chlorophyll but also other pigments such as carotenoids, which have an absorption spectrum that overlaps with chlorophyll, mainly in the blue spectral region; however, there is low efficiency in the transfer of energy from carotenoids to chlorophyll (Lichtenthaler and Buschmann 2001; Mirkovic et al. 2017; Peterman et al. 1997; Stamatakis et al. 2014). Thus, blue light is associated with the production of compounds to aid in the dissipation of excess absorbed light energy, referred to as secondary metabolites (Huché-Thélier et al. 2015; Thoma et al. 2020), which are often associated with increased nutritional value or are contributing factors to the taste and flavor of vegetables and fruits. Additionally, a higher pigment content due to blue light has been shown to improve the recovery of plants exposed to ultraviolet stress (Hoffmann et al. 2015).

However, narrow-band red or blue light is often associated with poor plant performance and growth (Larsen et al. 2020; Ouzounis et al. 2016; Trouwborst et al. 2016; Zhang et al. 2019). Growth under narrow-band red light can give rise to “red light syndrome” in part due to a lack of blue light receptor mediated photomorphogenesis (Larsen et al. 2020), which reduces rates of photosynthesis and photosynthetic capacity (Hogewoning et al. 2010). The addition of blue light to narrow-band red light can return plants to “normal” photosynthetic rates within a matter of days, although morphological changes due to red light syndrome are not always fully recovered (Trouwborst et al. 2016; Wang et al. 2016b). Narrow-band light can alter plant morphology and improve certain desirable traits—for example, increased fresh and dry weight of shoots (Johkan et al. 2010; Wollaeger and Runkle 2015) and increased plant height (Hirai et al. 2006; Johkan et al. 2010; Rabara et al. 2017; Wollaeger and Runkle 2015) have been reported in plants grown under narrow-band red light. Similarly, narrow-band blue light can increase root dry weight and pigment content, which conferred an advantage for transplanted lettuce plants (*Lactuca sativa*; Johkan et al. 2010), and, depending on species, increased stem elongation, dry mass, and leaf area (Hernández and Kubota 2016; Hirai et al. 2006). For example, elongation under narrow-band blue has been reported for many microgreens, which improves microgreen crop desirability to consumers (Brazaitytė et al. 2021; Ying et al. 2020b). The general effect of narrow-band light is best illustrated in marigold, an ornamental plant, which produced taller stems and greater or increased internode lengths under narrow-band blue; however, dry weight was higher under narrow-band red light (Heo et al. 2002). However, in the majority of cases, the combination of both red and blue light within a growth spectrum results in improved overall crop growth and better performance than narrow-band red or blue. Therefore, the determination of the optimal ratio between red and blue light (R:B ratio) is one of the most important characteristics of a growth light spectrum. However, the specific ratio of red to blue depends on the crop; the desired outcome for the grower; and balance between growth rates, biomass, compaction, and pigmentation.

Although a standardized light spectrum may not exist, many LED manufacturers typically produce "grow lights" with a spectrum of ∼80% red and 20% blue (R:B of 4) (Särkkä et al. 2017). On the other hand, the light spectrum for standard (cool) white 5700 K LEDs, which is a common white LED used for growing plants, have a R:B ratio of 0.66 (40% red, 60% blue). Therefore, the first question a grower transitioning to LED lighting is likely to ask is, "What ratio of red and blue light should I be using?"

A summary of responses by common crops to different R:B ratios is shown in Tables 1 and 2, with the effects separated depending on whether the light source is sole-source (i.e., provided entirely artificially by electric lamps, without sunlight; Table 1) or supplementary (Table 2). For sole source red + blue LED lighting, a clear trend emerges for increased pigment content with increased blue—namely, anthocyanins and chlorophyll content (Table 1), although there are some cases in which too much blue was associated with decreased chlorophyll content (Naznin et al. 2019; Pennisi et al. 2019; Son and Oh 2015). Likewise, although blue was associated with increased secondary metabolites (Naznin et al. 2019; Son and Oh 2015; Ying et al. 2020a), a higher red:blue ratio has also been shown to increase certain secondary metabolites, for example, flavanols in basil (*Ocimum basilicum*; Pennisi et al. 2019). Morphologically, increasing the fraction of blue light leads to more compact plants, as shown by decreases in plant height and leaf area, and thus a resulting decrease in fresh/dry weight and thicker leaves (Table 1).

Under supplementary lighting, the story remains the same (Table 2) in that higher fractions of blue light result in higher photosynthetic capacity and rates. As with sole source lighting, the increasingly compact size of plants grown under high supplementary blue fractions are also prone to lower biomass. Compaction in plants with increasing fractions of blue are mostly likely the results of poorer light interception (due to smaller canopies), which ultimately lowers biomass (Izzo et al. 2021; Kaiser et al. 2019a). Therefore, it has been suggested that the addition of supplementary blue light is only optimal up to a certain amount (Kaiser et al. 2019a).

While these general trends hold true and reliably allow for R:B ratios to be determined to best suit desired crop performance and characteristics, there are some additional factors to consider. For instance, in fruit-bearing crops such as strawberry (*Fragaria* ×*ananassa*) and sweet pepper (*Capsicum annuum*), higher rates of photosynthesis were observed under lower R:B (higher blue), however higher fruit yield was found under higher R:B (higher red) (Naznin et al. 2019; Piovene et al. 2015). The decrease in fruit yield despite high photosynthesis in plants grown in a high compared with low R:B ratio may be due to greater partitioning of assimilates to leaves instead of the fruits, which can also occur in crops grown under high light intensity (Trouwborst et al. 2011). It has also been proposed that a higher fraction of blue light causes the plant to behave as if it is under a higher light intensity (Lichtenthaler et al. 1980), supporting higher chlorophyll content and photosynthetic capacity (Table 1), indicating that plants perceive light intensity as blue light (Matsuda et al. 2007; Zhang et al. 2019).

In summary, it is clear there are discrepancies between studies, with differing optimal R:B ratios observed for the same species. The variation seen between studies is likely due to the variations in experimental conditions such as PPFD, addition or omission of wavelengths such as green and FR, nutrient availability, temperature, and other environmental factors, as well as species and choice of cultivar. Although LED lighting offers complete spectral freedom, this comes at the expense of spectral consistency between growers and setups, which can make it difficult to unravel the effects of differing spectral conditions on crop performance. Despite this, there is an overall trend for greater biomass with increasing fractions of red light, whereas higher fractions of blue tend to increase photosynthetic capacity, which is beneficial under higher light intensities (e.g., under sunlight) (Hogewoning et al. 2010; Kaiser et al. 2019a; Kang et al. 2021), pigment content, and secondary metabolite synthesis (Tables 1 and 2). Although these general trends are worth adhering to (and a basic protocol for determining the optimal R:B ratio is provided in Fig. 3), it is also worth keeping in mind that the response to increasing red:blue ratios can vary based on species, cultivar, and environmental conditions.

Green light. Altough often overlooked, green light is also important for plant performance (Fig. 4). Typically defined as the region of light wavelengths from 500 up to 600 nm (Fig. 1A), green light is able to penetrate deeper into the leaf, driving photosynthesis in lower layers that may be limited by the absorption of red and blue light by pigments in the upper leaf layers (Smith et al. 2017; Terashima et al. 2009). Enhanced green light has been associated with increased plant growth in lettuce and increased yield in tomato (*Solanum lycopersicum*; Kaiser et al. 2019b; Kim et al. 2004). A greater proportion of green may be beneficial at higher PPFD values (i.e., 1000 $\mu mol \cdot m^{-2} \cdot s^{-1}$) because a proportion of the absorbed blue and red light in the upper leaf layers at high light intensities will be dissipated as heat, thus reducing photosynthetic efficiency, whereas the lower absorbance of green in the upper layers allows greater penetration to the lower layers where it can be absorbed more efficiently, driving photosynthetic processes (Liu and van Iersel 2021). Green light also has other roles in regulating plant performance, for instance by reducing the accumulation of nitrates by increasing nitrate assimilation (Bian et al. 2018).

Green light has also been reported to counteract many processes initiated by red or blue irradiance (Folta and Maruhnich 2007). For example, green light reversed blue light–induced stomatal opening, resulting in closure of stomata (Frechilla et al. 2000; Matthews et al. 2020), and this mechanism has demonstrated potential in improving plant water use and drought tolerance in tomato (Bian et al. 2019). Finally, too much green light in comparison with blue light can have consequences on plant morphology (Wang and Folta 2013), triggering shade avoidance responses in basil, resulting in rapid growth at the expense of pigment content and compactness (Schenkels et al. 2020).

Spectra Beyond PAR

Ultraviolet. As mentioned in the opening section, photons of light with shorter wavelengths have higher energy. Therefore, blue and ultraviolet light have the highest energy out of all the wavelengths considered in this review (Fig. 1). Blue light is used in photosynthesis, but too much blue light triggers plant defense mechanisms to protect the plant significant damage to proteins and pigments (Latowski et al. 2011; Mullineaux et al. 2018; Murchie and Harbinson 2014).

Although ultraviolet light can be even more damaging owing to higher energy than blue and is not used directly in photosynthesis, it can also be beneficial to growers. Many plants respond to ultraviolet (and similarly to increasing intensities of blue light) by producing secondary metabolites—compounds not directly involved in normal growth and development, but which aid in plant defenses to external threats such as high light stress, disease, and herbivory (Huché-thélier et al. 2015). For instance, chemical growth regulators are often applied to cucumber (*Cucumis sativus*) to modify plant growth and fruit yield (Tantasawat et al. 2015), with one common use of growth regulators being to reduce plant size without affecting overall fruit yield. Applying ultraviolet-B (280–315 nm) light to cucumber as an alternative to these growth regulators demonstrated that while at low doses of ultraviolet-B no major impact on fruit yields were observed, more compact

Table 1. The responses of crops grown under controlled environments with different combinations of red and blue light. When an exception is mentioned, the specific treatment goes against the overall trend, and in some cases may have the highest or lowest values.

Author	Plants	R:B Range	Pigments	Secondary Metabolites & Volatiiles	Other	Photosyn-thesis	Other Physiology	Specific Leaf Weight	Height	Leaf Area	Fresh Weight	Dry Weight	Partitioning	Flower/Fruit
Hogewoning 2010	Cucumber (*Cucumis sativus*)	Blue (%): 0%, 7%, 15%, 22%, 30%, 50%, 100%	↑ chl. content per area (however, decrease on a dry weight basis)	-	-	↑, except for B100%	-	-	-	-	↑ leaf mass per unit leaf area	-	-	-
Matsuda et al. 2007	Spinach (*Spinacia oleracea*)	%B: 0, 1%, 33%, 50%	-	-	↑ N content	↑	-	-	-	-	-	↑	-	-
Pennisi et al. 2019	Basil (*Ocimum basilicum*)	R:B: 0.5, 1, 2, 3, 4	↑ chl. content	↑ flavonoid except for R:B pf 4	↑ mineral uptake	-	↓ stomatal conductance	-	-	-	↑	-	-	-
Naznin et al. 2019	Lettuce (*Lactuca sativa*)	Blue (%): 17%, 5%, 5%, 0%	↑ carotenoids, chl. at specific %B	-	↑ antiox.	-	-	-	-	-	-	-	-	-
	Spinach	Blue (%): 17%, 5%, 5%, 0%	↑ carotenoids, chl. at specific %B	-	↑ antiox.	-	-	-	-	-	-	-	-	-
	Kale (*Brassica oleracea*)	Blue (%): 17%, 5%, 5%, 0%	↑ carotenoids, chl. at specific %B	-	↑ antiox.	-	-	-	-	-	↑	-	-	-
	Basil	Blue (%): 17%, 5%, 5%, 0%	↑ carotenoids, chl. at specific %B	-	↑ antiox.	-	-	-	-	-	-	-	-	-
	Sweet pepper (*Capsicum annuum*)	Blue (%): 17%, 5%, 5%, 0%	↑ carotenoids	-	↑ antiox.	-	-	-	-	-	↑ except for 100% red	↑	-	↑ flower + fruit, except for 100% red
Brazaitytė et al. 2021	Mustard (microgreen; *Brassica juncea*)	B(%):R(%); 0:100, 10:90, 25:75, 50:50, 75:25, 100:0	Bell curve skewed towards blue. Blue decreases anthocyanin	-	↑ macro & micro nutrients. Lower nitrates with more blue, but bell shaped response overall	-	-	-	↓ except for 100% blue	Peak at 25% blue 75% red (excluding 100% Blue which was highest)	-	↑ R75% or higher, except for 100% Blue	-	-
	Kale (microgreen; *Brassica napus*)	Blue (%): 0%, 25%, 50%, 75%, 100%	Bell curve skewed towards blue. No change to anthocyanin	-	No effects on nitrates or nitrites	-	-	-	B100%, R100% longer hypocotyl than R+B	-	50/50, red skew	-	Higher shoot:root for 100% Blue or 100% Red	-
Liang et al. 2021	Cucumber	Blue (%): 0%, 25%, 50%, 75%, 100%	-	-	-	↑	-	-	↓ (100%B highest)	↑	↑ except for 100% blue	↑ except for 0% and 100% blue	NC	-
	Tomato (*Solanum lycopersicum*)	Blue (%): 0%, 25%, 50%, 75%, 100%	-	-	-	↑	-	-	↓ (0%B Highest)	-	↑ except for 100% blue	↑ except for 0% and 100% blue	↑ to leaves, slight decrease at 100% blue	-
Hernández & Kubota 2016	Cucumber Seedlings	Blue %: 0%, 10%, 20%, 30%, 50%, 75%, 100%	↑ except for 100B	-	-	↑ 30% blue	↑ stomatal conductance	-	↓ except for 100B	↓ except for B100% and R100%	↓ except for B100% and R100%	↓ except for B100% and R100%	-	-
Izzo et al. 2021	Lettuce	Blue %: 0%, 7%, 26%, 66%, 10%	↑ except for 100B	-	-	↑ except for 100B	↑ stomatal conductace except for 100B	-	-	↓ except for 100B	↓ except for 100B	↓ except for 100B	↓ root dry mass, lowest at 100% blue	-
Ying et al. 2020	Cabbage	Blue (%): 5%, 10%, 15%, 20%, 25%, 30%	↑ purple coloration	-	-	-	-	-	-		slight increase at 15B	slight increase at 15B	-	-
	Kale	Blue (%): 5%, 10%, 15%, 20%, 25%, 30%	↑ purple coloration	-	-	-	-	-	↓ hypocotyl length	↓ cotyedon area	-		-	-
	Rocket (*Eruca Sativa*)	Blue (%): 5%, 10%, 15%, 20%, 25%, 30%	↑ purple coloration	-	-	-	-	-	↓ hypocotyl length	↓ cotyedon area	-		-	-
	Mustard	Blue (%): 5%, 10%, 15%, 20%, 25%, 30%	↑ purple coloration	-	-	-	-	-	-		-		-	-
Wang et al. 2016b	Lettuce	R:B: B, 1, 4, 8, 12, R	↑ chlorophyll	-	↑ starch and sucrose content	↑	-	-	-	↑	-	↑	↑ leaf number	-
Son & Oh 2015	Red Leaf Lettuce	Blue (%): 13%, 24%, 34%	↑ chl. Content	↑ phenol, antioxidant capacity	-	↑ (an increase after 13% blue)	-	↑ (sharp increase after 13% blue)	-	↓ (sharp drop after 13% blue)	↓	↓	-	-
	Green Leaf Lettuce	Blue (%): 13%, 24%, 34%	↓ (chl. Content sharp drop after 13% blue)	-	-	-	-	↑ (sharp increase after 13% blue)	-	↓ (sharp drop after 13% blue)	↓ (24 and 34% the same)		-	-
Signore et al. 2020	Rocket (*E. Sativa*) and Wild Rocket (*Diplotaxis tenuifolia*)	Blue (%): 0%, 25%, 100%	-	-	↓ Nitrates	-	-	-	-	-	-	-	-	-

↑/↓ indicates an increase under increasing blue or a decrease under increasing red. ↓/↑ indicates a decrease under increasing blue or an increase under increasing red. B = Blue; Chl = chlorophyll; R = red.

plants with higher levels of antioxidants, and phenolic and flavonoid content were found (Qian et al. 2020), although too high a dose of ultraviolet-B can also negatively impact yield (Qian et al. 2020; Topcu et al. 2018). These photoprotective benefits from ultraviolet exposure, due to increased secondary metabolites, have been reported to improve performance under dynamic environments such as those experienced outside in the field. For example, in a study in which lettuce seedlings were grown with the addition of ultraviolet-B, performance and yield was greatly improved after transplanting to a field environment (Wargent et al. 2011).

Interestingly, when ultraviolet-A light was used as a direct replacement for blue light, tomato growth was increased due to several morphological adaptions, including greater leaf area and steeper leaf angles, which in turn improved light interception and led to improvements in biomass (Zhang et al. 2020). However, such ultraviolet-A replacement also decreased secondary metabolites production and resulted in lower photosynthetic capacity (Zhang et al. 2020), in contrast to what usually occurs when ultraviolet is added. This contradiction is most likely due to the absence of blue light eliciting a low-light (Hogewoning et al. 2010) or shade avoidance response, which signals the plant to focus on physical growth to escape the shade of neighboring vegetation, rather than an effect of ultraviolet (Keller et al. 2011; Pedmale et al. 2016; Zhang et al. 2020). This suggests that there is still plenty to explore with more unorthodox combinations of wavelengths, such as a red and ultraviolet light based spectra.

Far-red light. FR wavelengths (700 to ~900 nm) are known to be important for photosynthesis through the preferential absorption of these wavelengths by PSI, which drives higher electron flow through PSI, and, as a result, improves electron transfer through the entire electron transport chain, which would otherwise be a bottleneck (Pettai et al. 2005; Zhen and Bugbee 2020a, 2020b; Zhen and van Iersel 2017; Zhen et al. 2022); therefore, FR up to 750 nm should be considered in the definition of PAR. However, there are both photosynthetic and photomorphogenic effects of FR that need to be weighed when considering the addition of this spectrum to a lighting recipe (Fig. 4), and this is also discussed in the economic analysis toward the end of this article.

Shade perception and the shade avoidance response. FR light is not readily absorbed by plant pigments and the majority is reflected or transmitted. Light below the top of the canopy (i.e., in shade) is therefore enriched in FR light and lower in PAR, affecting the ratio of red to FR (R:FR). Environments enriched in FR can trigger a shade avoidance response via the phytochrome photoreceptors, which sense the relative quantities of red and FR light (Legris et al. 2019; Leivar and Quail 2011). FR rich environments thus lead to morphological and developmental changes to plant growth that aid the plant in seeking unshaded light (Fig. 5), commonly by increasing internode, stem,

Table 2. The responses of crops grown with different combinations of supplementary red and blue light.

Author	Plants	R:B Range	Pigments	Secondary Metabolites	Other	Photosynthesis	Height	Leaf Area	Fresh Weight	Dry Weight	Partitioning	Flower/Fruit
Kaiser et al. 2019a	Tomato (*Solanum lycopersicum*)	Total B% (of sunlight + supplementary): 0%, 6%, 12%, 24%	-	-	-	↑	-	-	-	Fruit & Shoot: Increase up to 6%, decrease above 12%. ↓ Stem dry weight	-	-
Piovene et al. 2015	Basil (*Ocimum basilicum*)	R:B: 0.7, 1.1, 1.5, 5.5, 0.5 (Fluorescent Lamp)	-		↑ high nitrate at 5.5	↑	-	-	↑	-	-	-
	Strawberry (*Fragaria × Ananassa*)	R:B: 0.7, 1.1, 1.5, 5.5, 0.5 (Fluorescent Lamp)	-	↑ improved antioxidant capacity at 0.7	↑ high nitrate at 1.1	↑	-	-	↑ (for R:B 1.5 only)	-	-	↑ highest fruit yield at R:B 1.1, 0.7, than 1.5
Yan et al. 2019	Lettuce (*Lactuca sativa*)	R:B: 0.9, 1.8, 2.7, 3.6	↓ anthocyanins	-	↓ nitrates except for 3.6	↑	-	-	↑ R:B 2.7, followed by 3.6, especially at higher DLI	↑ R:B 2.7, followed by 3.6, especially at higher DLI	-	-
Snowden et al. 2016	Radish (*Raphanus sativus*)	LED mixture	↑ at 500 PPFD	-	-	↑ at 500 PPFD	↓ Trend	↓ at 500 PPFD	-	-	-	-
	Tomato (*Solanum lycopersicum*)	LED mixture	↑	-	-	-	↓	↓ at 200 + 500 PPFD	-	↓ at 200 + 500 PPFD	-	-
	Cucumber (*Cucumis sativa*)	LED mixture	↑	-	-	↑ at 200 + 500 PPFD	↓	↓ at 500 PPFD	-	↓ at 500 PPFD	-	-
	Pepper (*Capsicum annum*)	LED mixture	↑ at 500 PPFD	-	-	↑ at 500 PPFD	↓	↓ at 500 PPFD	-	↓ at 500 PPFD	-	-
	Lettuce (*Lactuca sativa*)	LED mixture	-	-	-	↑ at 500 PPFD			-	N.S. Trend ↑ at 500 PPFD	-	-
	Soybean (*Glycine max*)	LED mixture	-	-	-	-	↓		-	↓ at 500 PPFD	-	-
	Wheat (*Triticum aestivium*)	LED mixture	-	-	-	-			-	N.S. Trend ↓ at 500 PPFD	-	-

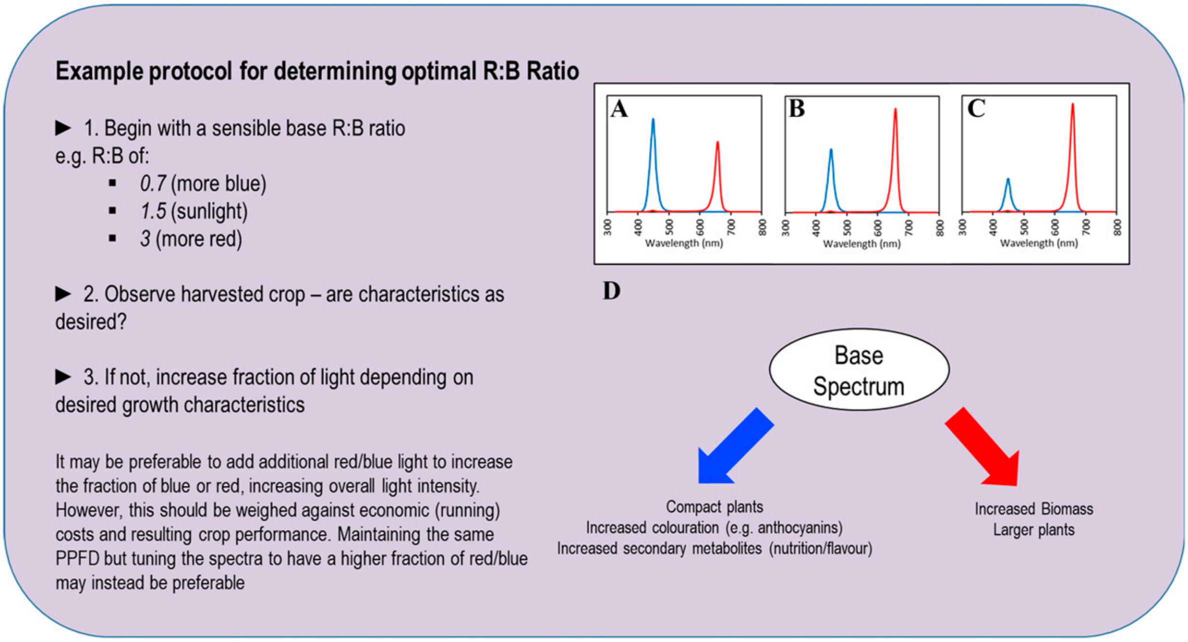
↑/↓ indicates an increase under increasing blue or a decrease under increasing red. ↓/↑ indicates a decrease under increasing blue or an increase under increasing red. B = blue; R = red; Chl. = chlorophyll; DLI = daily light integral; PPFD = photosynthetic photon flux density (400 nm–700 nm).

petiole, and leaf length; earlier flowering (Casal 2012; Casal et al. 2014); increased hyponasty, in which leaves grow vertically rather than horizontally to locate red-rich light; (Polko et al. 2011); and reductions in leaf number and branching (Wang et al. 2013). The effects of FR are also dependent on other wavelengths, with more-pronounced shade avoidance responses under either low light intensity or a high B:R ratio (Meng and Runkle 2019). Shade avoidance responses may also depend on the blue-to-green ratio, mostly via the increase in green light (Meng et al. 2019; Sellaro et al. 2010; Wang and Folta 2013; Zhang et al. 2011). Also, shade avoidance can be initiated by the upward reflection of FR rich light from vegetation and soil below the canopy (Green-Tracewicz et al. 2011), which may have implications for intercanopy supplementary lighting and the effects of greenhouse floor reflection if FR is added to an overhead lighting spectrum.

FR illumination can also affect disease responses. Whereas red light improved disease resistance in tomato, cucumber, broad bean (*Vicia faba*), watermelon (*Citrullus lanatus*), and roses (*Rosa ×hybrida*) through the regulation of plant defense hormones such as salicylic acid (Nagendran and Lee 2015; Rahman et al. 2003; Suthaparan et al. 2010; Wang et al. 2010; Yang et al. 2015, 2018), FR light reduced resistance to *Botrytis cineria* in tomato and powdery mildew in cucumber, indicating that the balance of red to FR is also important for optimizing resistance to plant disease (Courbier et al. 2021; Ji et al. 2019; Shibuya et al. 2011; Wang et al. 2010).

Due to the energy required for rapid growth, the shade avoidance response also lowers leaf chlorophyll content (Meng and Runkle 2019; Smith and Whitelam 1997). Although less chlorophyll may not affect photosynthetic output (Heraut-Bron et al. 1999; Kalaitzoglou et al. 2019), consumers prefer deep greenness in leafy crops such as rocket/arugula (common names for both *Eruca sativa* and *Diplotaxis tenuifolia*; Siomos and Koukounaras 2007). On the other hand, a high R:FR ratio will elicit an inverse shade avoidance response, increasing chlorophyll content while decreasing height and internode length (McMahon et al. 2019).

FR treatments for manipulating crop development and yield. As a result of both its photosynthetic activity and shade avoidance response, the addition of FR can increase biomass (Yang et al. 2020). FR has been associated with increased shoot weight and leaf expansion in seedlings and harvest yields of basil and lettuce (Jin et al. 2021; Meng and Runkle 2019). For fruiting plants, while FR increased the partitioning of dry weight into the stem and thus led to taller plants in both tomato and pepper (*C. annuum*), a higher fruit mass was also reported in tomato (Brown et al. 1995; Kalaitzoglou et al. 2019; Kim et al. 2019a; Lanoue et al. 2022). Although FR showed little effect on pepper fruit yield, it did induce longer internode length, which may prevent deformation of fruit shape (Lanoue et al. 2022). FR also interacts with the daily light integral (DLI), influencing the



Example protocol for determining optimal R:B Ratio

► 1. Begin with a sensible base R:B ratio
e.g. R:B of:
- *0.7* (more blue)
- *1.5* (sunlight)
- *3* (more red)

► 2. Observe harvested crop – are characteristics as desired?

► 3. If not, increase fraction of light depending on desired growth characteristics

It may be preferable to add additional red/blue light to increase the fraction of blue or red, increasing overall light intensity. However, this should be weighed against economic (running) costs and resulting crop performance. Maintaining the same PPFD but tuning the spectra to have a higher fraction of red/blue may instead be preferable

Fig. 3. An example protocol outlining the steps for determining the optimal red-to-blue (R:B) ratio for crops. This example protocol can be used for plants that a grower has not grown under light-emitting diode lighting before and serves as a starting point for determining the optimal R:B ratio. In the first step, three base ratios are suggested, with higher proportions of blue (**A**) or red (**C**), or a R:B ratio similar to sunlight (**B**). The base ratio to choose depends on whether, for instance, biomass or secondary metabolites are the primarily factor desired (**D**). The second step is to assess the crop that has been grown under one of the base regimes. Are plants grown with sufficient biomass, compaction, coloration, and desired secondary metabolites? The third step is to adjust the R:B ratio (e.g., for a base R:B of 3, adjust from 3 to 5 for more red, or 3 to 1.5 for more blue). Repeat steps 2 and 3 until the optimal (or close to optimal) R:B ratio is determined.

induction of flowering. Plants grown at a low DLI with FR exhibit more rapid flowering than treatments without FR, whereas at a higher DLI, flowering time is more rapid with or without FR light (Garrett Owen et al. 2018). However, in one study, blue light attenuated FR associated growth, alleviating morphological changes such as increased plant height, but did not affect flowering time (Park and Runkle 2019).

The application of red or FR as night-breaks can trigger a phytochrome response in plants, in which narrow-band red or FR light leads to the conversion of phytochrome to either the Pfr or Pr form of phytochrome and subsequent downstream signaling (Fig. 5) and thus has been shown to delay or trigger flowering (Borthwick et al. 1952; Hendricks and Borthwick 1967). In short day (long night) plants, the application of a FR flash during the night increases the length of the night (due to the phytochrome being pushed toward the Pr form), whereas the opposite is required for long day (short night) plants, in which a flash of red during the night will stimulate flowering (phytochrome is trigger toward the Pfr form). These manipulations can be reversed by the application of the opposite flash (Borthwick et al. 1952; Hendricks and Borthwick 1967). For example, if the nighttime break of a FR flash is followed by a red flash in the short day plant, flowering will not occur (as the plant will still experience a short night as the phytochrome will be mostly in the Pfr form). Night-breaks of less than a few $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ of light have been used to initiate earlier flowering and increasing fruit yield in tomato (Cao et al. 2016). The effectiveness of night-breaks for manipulating growth may depend on varieties, as it has been shown that early bolting varieties of spinach are more sensitive to night-breaks than late-bolting varieties (Hamamoto et al. 2004).

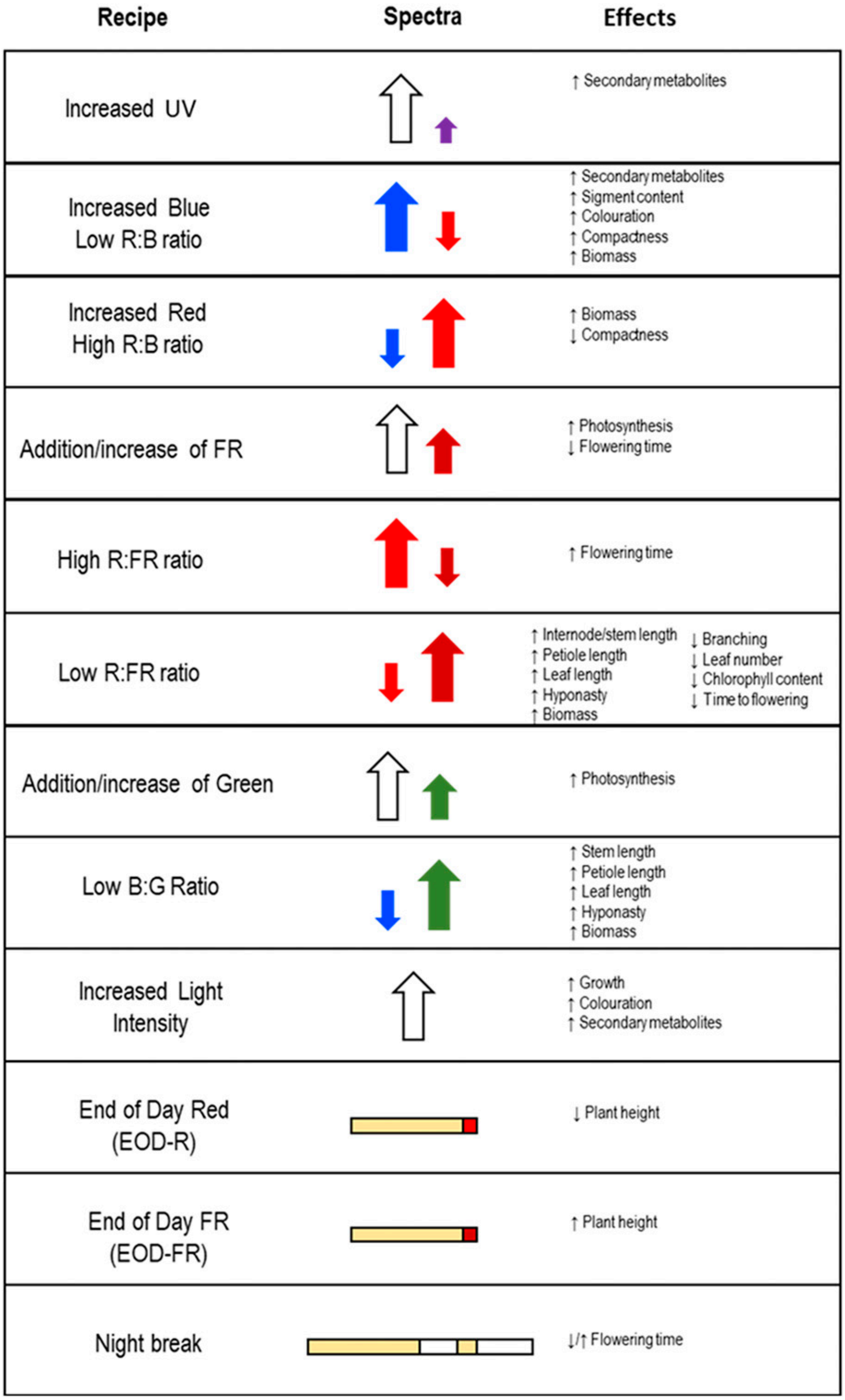
There are indications that daytime grow light spectra may also affect the sensitivity of plants to night-break light treatments (Higuchi et al. 2012). Interestingly, the intensity of FR can complicate the phytochrome driven responses because Pr forms of phytochrome can absorb a small amount of FR light, which is magnified at higher intensities (Kusuma et al. 2021).

Similar to night-breaks, "end of day" (EOD) red or FR treatments applied at the end of the photoperiod when growth lights are usually turned off trigger a phytochrome response in plants, which could provide a promising alternative to day-long application of FR spectra. EOD treatments aim to elicit a response similar to a full-day FR treatment but without the associated energy cost or full shade avoidance response, although the boost to photosynthesis as seen when FR is mixed in with the growth spectrum is not observed (Ilias and Rajapakse 2005; Kalaitzoglou et al. 2019; Zhen and Bugbee 2020a). For instance, an EOD red or FR treatment can either elicit (FR) or halt (red) the shade avoidance response and subsequently influence plant height of tomato and poinsettia (*Euphorbia pulcherrima*; Cao et al. 2016; Islam et al. 2014). This EOD technique has applications in grafting, with EOD FR used to promote stem expansion in tomato without loss of leaf area (Chia and Kubota 2010) or EOD red to prevent excessive stem elongation in ornamentals (Islam et al. 2014). Another use of EOD FR light is to decrease the length of time required before the onset of flowering in strawberry, although this can depend on FR dose and daylength (Zahedi and Sarikhani 2016).

Currently the majority of LED lighting in glasshouses does not include FR. The omission of FR can lead to the inverse shade avoidance response described earlier; more compact plants have lower biomass, attributed to a reduced leaf area and subsequent low light interception and to an absent photosynthetic effect (Kalaitzoglou et al. 2019; Zhen and Bugbee 2020a). A certain amount of FR (the amount is dependent on species and overall lighting spectra) appears to be required to generate desirable traits (e.g., photosynthesis boost, biomass, and larger leaf area), but not too much to reduce chlorophyll content, promote excessive elongation, or alter flowering time. The intensity and balance of red and FR should therefore be fine-tuned to manage the potential gain or loss in productivity, flowering time and fruit yield, stem elongation, and other effects on plant morphology. Thus, FR and red treatments are powerful tools to manipulate crop performance.

Supplementary and Intracanopy Lighting

Supplementary lighting. The aim of supplementary lighting is to increase light intensity on lower intensity or cloudy days and/or to extend the photoperiod during autumn, spring, and winter months, or even year-round whenever the photoperiod needs to be extended. Supplementary lighting can also be used to modify the light environment by



Recipe	Spectra	Effects
Increased UV		↑ Secondary metabolites
Increased Blue Low R:B ratio		↑ Secondary metabolites ↑ Sigment content ↑ Colouration ↑ Compactness ↑ Biomass
Increased Red High R:B ratio		↑ Biomass ↓ Compactness
Addition/increase of FR		↑ Photosynthesis ↓ Flowering time
High R:FR ratio		↑ Flowering time
Low R:FR ratio		↑ Internode/stem length ↑ Petiole length ↑ Leaf length ↑ Hyponasty ↑ Biomass ↓ Branching ↓ Leaf number ↓ Chlorophyll content ↓ Time to flowering
Addition/increase of Green		↑ Photosynthesis
Low B:G Ratio		↑ Stem length ↑ Petiole length ↑ Leaf length ↑ Hyponasty ↑ Biomass
Increased Light Intensity		↑ Growth ↑ Colouration ↑ Secondary metabolites
End of Day Red (EOD-R)		↓ Plant height
End of Day FR (EOD-FR)		↑ Plant height
Night break		↓/↑ Flowering time

Fig. 4. Some of the major modifications to the light-emitting diode (LED) growth spectra and their resulting effect. The effects listed here are generalized, not exhaustive, and are dependent on species and other environmental factors. In the 'Spectra' column, arrow colors refer to spectral region, typically; purple for ultraviolet light (<380 nm), blue for 400–500 nm, green for 500–600 nm, red for 600–700 nm, dark red for 700–750 nm. White arrows refer to the general spectrum a grower has previously chosen for their plants. Arrow sizes represent the approximate quantity of light. For end-of-day (EOD) and night-break treatments, the boxes colored yellow represent light, white boxes represent night, and colored boxes represent a light treatment without any other light source.

altering its spectral composition, such as alteration of the R:B ratio, against a background of sunlight. Supplementary lighting for greenhouses traditionally uses HPS lamps, which are enriched in red and orange wavelengths. However, LED lighting is quickly gaining favor with growers due to lower running costs and increased flexibility, as well as the ability to customize spectral output. Additionally, supplementary LED lighting has also been shown to promote higher biomass production and more partitioning to reproductive organs than HPS lamps. Plants grown under HPS have higher leaf temperatures due to the greater heat output of HPS lamps and thus, in addition to higher transpiration rates, may exhibit morphological changes to improve heat dissipation, such as smaller leaves to improve heat loss via convection and conduction (Chaves et al. 2002; Kim et al. 2019a; Wang et al. 2019). Supplementary lighting of all types (i.e., LED, HPS) has been shown to improve fruit yield in tomato (Gómez et al. 2013) and phytochemical content in strawberry (Choi et al. 2015). Likewise, in leafy

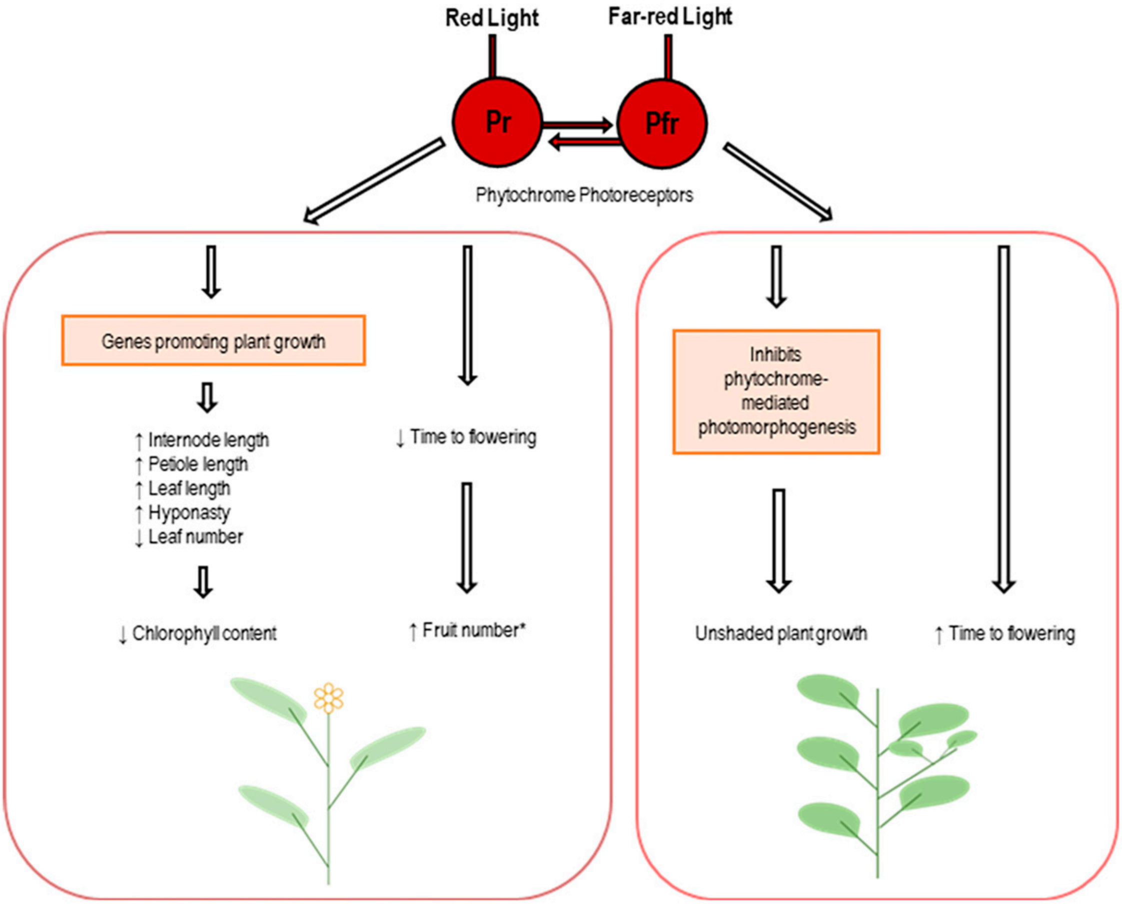


Fig. 5. Some of the major phytochrome-mediated effects due to red or far-red light. Red light converts the Pr form of phytochrome to the Pfr form, which regulates normal unshaded growth. Far-red light converts the Pfr form of phytochrome to the Pr form, which promotes signaling pathways that promote plant growth and flowering. Upward arrow denotes an increase, whereas a downward arrow denotes a decrease. * An effect that has not been demonstrated in all relevant crops.

crops supplementary lighting showed an increased length and yield of pea shoots (*Pisum sativum*; Kong et al. 2019) and improved flavor, nutrient content, and yield of pak choi (*Brassica campestris* ssp. *chinensis* var. *communis*; Zheng et al. 2018).

Intracanopy LED lighting. Although traditionally set up this way, supplementary light does not have to be exclusively above the canopy and face downward. Within-canopy supplementary lighting has received growing interest and refers to the inclusion of LED strips within the canopy (intracanopy) to increase photosynthesis throughout the plant. This technique is being increasingly used by growers to increase productivity and yield of tall crops such as pepper (Jokinen et al. 2012) and tomato, as well enhancing flavor (Gómez et al. 2013; Kim et al. 2019b; Tewolde et al. 2018). Intracanopy lighting has also been used to increase biomass and yield in crops such as cowpea (*Vigna unguiculata* ssp. *unguiculata*; Frantz et al. 2000) and cucumber (Pettersen et al. 2010). This technique benefits from the advancements of LEDs thanks to the cooler temperature of LEDs over other light sources (Gómez and Mitchell 2016a)

Fluctuating light and shade-flecks due to shading from the upper canopy have been associated with reduced growth (Kaiser et al. 2018; Vialet-Chabrand et al. 2017); however, the addition of intracanopy lighting can improve light distribution throughout the canopy (Frantz et al. 2000; Pettersen et al. 2010), increasing photosynthesis in lower leaves that would otherwise present a significant metabolic burden for the plant (Frantz et al. 2000). It should be noted that any increases in photosynthesis by intracanopy lighting remain sensitive to the choice of light spectrum (Murakami et al. 2013), and fine-tuning of light spectra may affect rates of photosynthesis more than morphology and fruit yield (Gómez and Mitchell 2016b). Although intracanopy lighting is another tool for light spectrum-based manipulation of plant morphology and performance, we note that evidence of impact remains ambiguous. Intracanopy lighting in cucumber was less effective than overhead supplementary lights in improving yields; leaf curling and a greater partitioning of dry matter to leaves rather than fruit adversely affected productivity (Trouwborst et al. 2011). Therefore, a combination of overhead and intracanopy light may be optimal (Särkkä et al. 2017).

Other Considerations for LED Lighting

Light intensity. Light intensity plays a pivotal role in determining plant growth, with too high a light intensity having consequences for crop quality through the initiation of plant defense mechanisms and morphological changes to reduce high light induced stress (Demmig-Adams and Adams 1992; Larsen et al. 2020; Mullineaux et al. 2018). Some of the effects of excessive light include decreased chlorophyll content, photodamage, damaged leaves and fruits, suboptimal growth, and reduced yield (Ferrante and Mariani 2018; Nguyen et al. 2019). During winter months, both photoperiod and light intensity are especially crucial, as the low winter sun results in a reduction in overall light intensity throughout the course of the shorter day, which can affect overall growth rates and flowering (Johansson and Staiger 2015).

The definition of “high” light intensity is dependent on the species and environment, with some plants having highest yield at light intensities as low as 90 $\mu mol \cdot m^{-2} \cdot s^{-1}$ (e.g., the medicinal herb *Anoectochilus formosanus*; Ma et al. 2010). However, pushing light intensity toward the upper limit of a crop’s known range is important for secondary metabolite production, which is often produced in response to high light to aid in the dissipation of excess absorbed light energy and improves taste and nutritional content in many crops (Ma et al. 2010; Thoma et al.

2020; Zou et al. 2020). Lettuce grown under higher levels of electric lamp lighting is susceptible to tipburn due to calcium limitation in fast-growing leaves (Sago 2016). The mechanism of tipburn onset has been associated with rapid plant growth driven by higher light intensities and long daylengths, with that rapid growth and cell expansion resulting in lower calcium concentration in the inner leaf and subsequent development of tipburn (Sago 2016). Therefore, if tipburn is prevalent, it may be suitable to provide localized supply of air to improve transpiration rates and thus nutrient uptake and flow (Ahmed et al. 2020; Frantz et al. 2004; Goto and Takakura 1992). Other solutions, such as selection of tipburn resistant varieties (Birlanga et al. 2021) or a reduction in temperature to slow growth (Choi et al. 2000), may also prevent onset.

The selection of a light intensity and DLI is a key choice that a grower has to make. Several models, such as for hydroponic salads (Walters and Lopez 2021) and leafy microgreens (Jones-Baumgardt et al. 2020), have thus been produced that attempt to predict the impact of light intensity on growth parameters such as fresh and dry mass, plant height, and photosynthetic performance.

Photoperiod. Photoperiod refers to the period of light that a plant experiences. Many growers have to determine the optimal daylength under which to grow their crops, with longer photoperiods generally corresponding to increased growth rates (Adams and Langton 2005) due to a higher integrated dose of light or DLI. The response to photoperiod varies across species, with both increases and decreases in leaf area possible (Adams and Langton 2005). However, as a general rule, many crops are typically grown under a long daylength, usually 16 h (Pennisi et al. 2020) because this generally corresponds to the longer daylengths during summer months; however, daylengths used can range from anywhere between 12 to 22 h.

It has been suggested that a longer photoperiod at a lower light intensity ("Long/Low") may be more photosynthetically efficient than a short photoperiod at a high light intensity ("Short/High"), at the same daily light integral (Elkins and van Iersel, 2020). Plants grown under a Long/Low treatment showed increased biomass and higher chlorophyll content despite lower photosynthetic rates, although it should be noted that a number of crops, such as lettuce and chicory (*Cichorium intybus*), may be suboptimal at daylengths of 20 h or more, whereas others such as spinach (*Spinacia oleracea*) are prone to bolting above daylengths of 14 to 16 h (Adams and Langton 2005; Chun et al. 2001; Elkins and van Iersel 2020; Palmer and van Iersel 2020; Pennisi et al. 2020; Weaver and van Iersel 2020). The mechanism behind the "Long/Low" is due to the lower light intensity improving the efficiency of photosynthesis (Weaver and van Iersel 2020), with less absorbed light energy dissipated as heat. The importance of photoperiod is especially apparent in flowering crops, in which flowering is initiated when the photoperiod reaches a critical daylength. Short day plants flower when the photoperiod is short (and night is long), whereas long day plants flower when the photoperiod is long (night is short).

Elsewhere, continuous light has been proposed as a technique to increase plant biomass and yield either due to higher cumulative rates of photosynthesis or by distributing the light dose across the photoperiod and increasing photosynthetic efficiency (Lefsrud et al. 2006; Proietti et al. 2021; Shibaeva et al. 2022). However, the effect of continuous lighting can, depending on species, be detrimental to growth and yield through reduced performance—for instance, due to reduced pigment content (Lefsrud et al. 2006) or to stress or injury (Gaudreau et al. 1994; Murage and Masuda 1997; Van Gestel et al. 2005). Fruiting vegetables such as pepper can be vulnerable to injury from continuous lighting (Demers and Gosselin 1999), although cucumber has been shown to support growth under continuous lighting (Lanoue et al. 2021). This is especially the case for tomato, which is susceptible to damage when grown under continuous lighting (Demers et al. 1998). However, there are genes that confer tolerance to continuous lighting, allowing for cultivars to be bred specifically for this purpose (Velez-Ramirez et al. 2014, 2015). Although the longer days may translate into marginally higher yields, they may not necessarily offset the increased running costs associated with that daylength, as indicated by the significantly lower energy use efficiency observed with increasing photoperiod (Pennisi et al. 2020). Alternating between 12 h of narrow-band red and 12 h of narrow-band blue light over a 24-h period has been used to improve yields and harvest quality in lettuce (Ohtake et al. 2018), and in tomato, such growth conditions had no adverse effects (Lanoue et al. 2019). Similarly, the addition of green light to the spectrum in a continuous lighting regime has been identified as a mechanism to reduce nitrate accumulation in hydroponically grown lettuce (Bian et al. 2018).

Pre- and postharvest light treatments. Another use of light treatments is to improve the quality of harvested crop by applying specific light treatments during the days before or after harvest. Preharvest regimes can be used to manipulate plants during growth; for example, increasing the proportion of blue light in the days before harvest in lettuce and other leafy greens (with the growth spectra before this tuned toward promoting biomass) resulted in increased production of secondary metabolites and improved appearance and flavor. A similar approach, using blue or red light to increase light intensity, promoted fruit ripening and improved quality of tomatoes and certain leafy greens (Bliznikas et al. 2012; Ngcobo et al. 2020; Nicole et al. 2016). Likewise, preharvest illumination by FR has been used to improve postharvest cold tolerance of tomato fruit, due to higher synthesis of the plant hormones abscisic acid and jasmonic acid as a result of a low R:FR ratio, thus improving fruit quality during storage (Affandi et al. 2020; Wang et al. 2016a). Similarly, an application of a 4-day ultraviolet-B treatment before harvest maintained the nutritional quality of basil during storage by increasing the polyphenol and antioxidant content (Nascimento et al. 2020).

When the supply of nitrogen is in excess of what the plant requires, which often occurs when fertilizer (including hydroponic nutrient solutions) is used, an accumulation of nitrates in plants can occur (Anjana and Iqbal 2003;

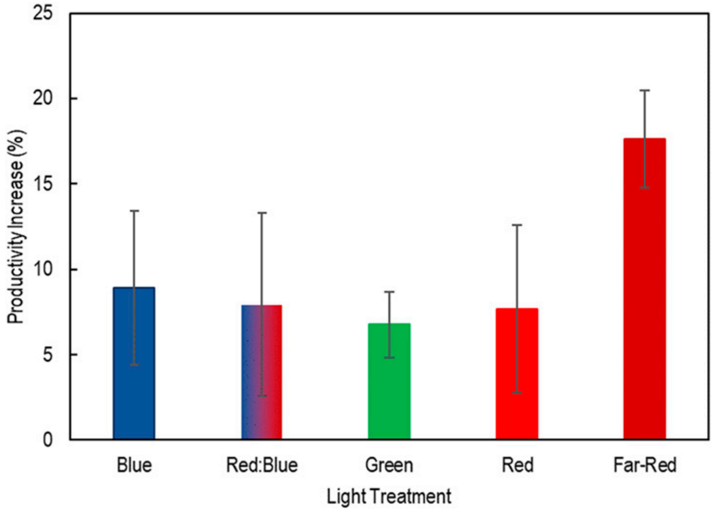


Fig. 6. Productivity increase (mean of leaf area, leaf number, biomass, height) from changes in light spectral quality for horticultural crops (e.g., spinach, lettuce, rocket) from a control "white" light source to a specific treatment. Control light sources are, for example, high-pressure sodium (HPS), white, or red+blue light-emitting diodes (LEDs). Productivity changes are calculated where some portion of the control light is replaced by the spectrum named. Note that for RB interventions, we assume that 100% of the control (i.e., HPS) lighting is replaced with a new red + blue spectrum LED. For monochromatic treatments, we estimate that 20% (blue), 20% (green), 50% (red), and 12.5% (far-red) of the control spectrum is replaced (see text). Error is standard error of average values as reported in the literature. All data sources can be found in the Supplementary Materials.

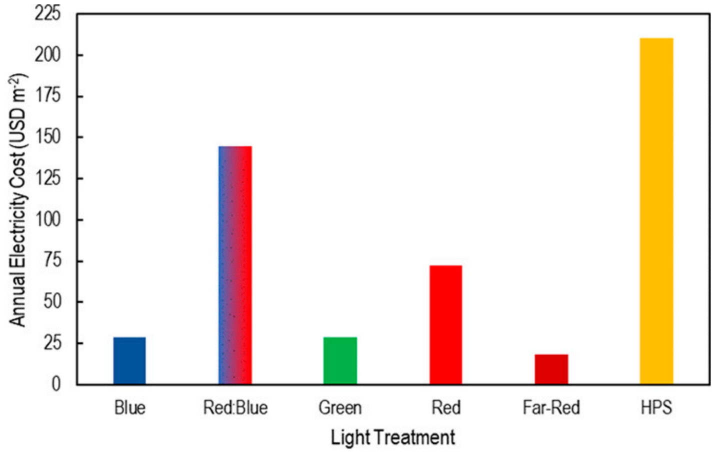


Fig. 7. Annual electricity cost of light-emitting diodes (LED) use (m^{-2}) based on usage implied in research papers (see Supplementary Materials). Red, blue, green, and far-red may be given to replace (part of) baseline R:B or white light (see Fig. 6). Costs are based on 18 $h \cdot d^{-1}$ of 250 $\mu mol \cdot m^{-2} \cdot s^{-1}$ total PFD, with light treatments as described in Fig. 6. Electricity price is based on a medium-sized electricity user in the United Kingdom in the first quarter of 2022 including Climate Change Levy, a tax on energy used by nondomestic users; growers in receipt of feed-in tariffs or similar incentives might find ways to reduce input costs. Results assume 2.5 $\mu mol \cdot J^{-1}$ efficacy of LED units and 1.75 $\mu mol \cdot J^{-1}$ efficacy of high-pressure sodium units (Kusuma et al. 2020), and 6570 h use per annum (i.e., 18-h days), no credit is given for the white light/R:B light replaced.

Maynard et al. 1976). Excess nitrates can pose serious hazards to human health, and nitrate content is therefore regulated (e.g., by the EU; European Food Safety Authority 2008). This is especially concerning for leafy vegetables, in which the whole plant is consumed (Anjana and Iqbal 2003). New LED approaches to prevent nitrate accumulation from reaching high levels have been developed in recent years; for instance, the application of red light spectra, 5 d of continuous lighting before harvest, or 48 h of continuous red-rich lighting have all been shown to decrease nitrate levels in various leafy vegetables, with some varieties of rocket also showing an increase in the secondary metabolite glucosinolate, which is a key flavor compound (Nicole et al. 2016; Signore et al. 2020; Wanlai et al. 2013).

Interestingly, treatments can also be applied after a crop has been harvested, known as postharvest treatments. The aim of applying postharvest treatments is to maintain photosynthetic activity in harvested crop and delay deterioration, thereby increasing shelf life and quality. Approaches include applying low levels of white light, which maintained chlorophyll, antioxidant, and flavonoid content and delayed senescence (Hasperué et al. 2016). Pulses of low light have also delayed senescence in harvested broccoli, maintaining quality (Favre et al. 2018). This area of research promises to reduce food waste in the supply chain and increase the value of crops sold and is likely to become a ubiquitous intervention in modern food production systems.

Temperature interactions with growth light conditions. When determining the optimal growth light intensity, one key consideration is the temperature of the growth environment. Higher temperatures increase reaction rates for photosynthetic enzymes (Berry and Bjorkman 1980), although this is only true up to a point; too high a temperature can instead damage plants and reduce photosynthetic rates (Berry and Bjorkman 1980; Lu et al. 2017; Matthews and Lawson 2019; Stevens et al. 2021). Temperature remains important for tracking crop growth and developmental stages: "growing degree days" is calculated based entirely on daily temperature and is a key metric used to track and predict crop growth (McMaster and Wilhelm 1997; Yang et al. 1995). The optimal temperature range, as well the maximum and minimum temperatures for some common crops, were listed by Ferrante and Mariani (2018) and can be used to determine the ideal temperature of a growth environment for a specific crop.

A study by Zhou et al. (2019) examined the relationship between light intensity and temperature and suggested that lettuce grown at lower temperatures (i.e., 15 °C day/11 °C night) were better suited for lower light intensities (i.e., 350 to 500 $\mu mol \cdot m^{-2} \cdot s^{-1}$ total, or a supplementary light of 350 $\mu mol \cdot m^{-2} \cdot s^{-1}$ during winter months). Likewise, increasing temperatures (35 °C day/25 °C night) were suggested to be paired with higher light intensities (up to 500–600 $\mu mol \cdot m^{-2} \cdot s^{-1}$), as experienced by field crops from late spring to early autumn. This approach would be especially useful for balancing heating and cooling requirements with light intensity—for instance, in greenhouses or plant factory installations—to ensure that energy use is not excessive due to an incorrect balance between temperature and lighting.

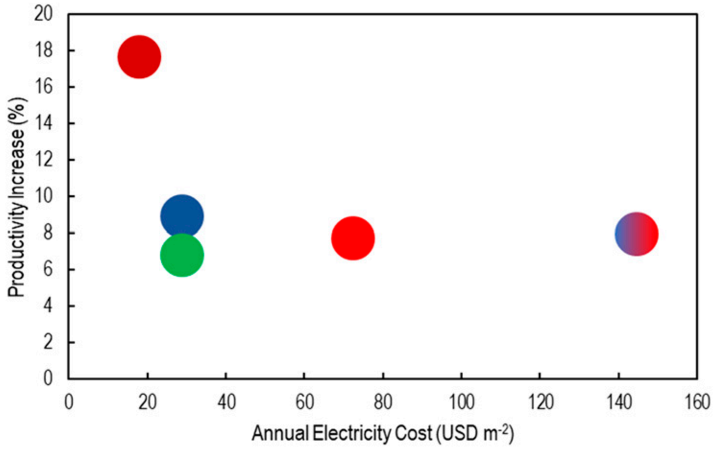


Fig. 8. Comparison of yield increase (Fig. 6) against electricity costs (Fig. 7). Dot color corresponds to light treatments, darker red dot corresponds to far-red light; bright red dot, red light; blue dot, blue light; green dot, green light; blue-red gradient dot, a mixture of both red and blue light. The benefits of using far-red light dominate all other options for marginal cost in this model. However, the link between spectral intervention and cost implication remains complex. The initial cost of moving to LED lighting (Red+Blue) is a considerable barrier to investment notwithstanding ongoing declines in installation cost; nevertheless, LEDs typically offer a decrease in cost in excess of 50% compared with high-pressure sodium (Nelson and Bugbee 2014) and may be attractive in their own right. Given the presence of an existing white or R:B lighting system, augmentation of particular spectra appears attractive. Far-red, blue, and, to a lesser extent, green augmentation offer the potential for attractive increases in yield yet only modest increases in running costs.

LED Lighting: Is There a Price to Pay?

The previous sections of this article have outlined the effects of different light spectra on plant responses and plant morphology in the context of horticulture, yield, and quality (Fig. 4). The translation of the basic research into implementable outputs for growers is more difficult to compare, with relatively few investigations into the costs of implementing lighting solutions compared with their benefits in terms of increased productivity or quality (Nelson and Bugbee 2014; Pattison et al. 2018).

As we have emphasized in this review, it can be difficult to compare findings and outcomes in the literature owing to variability in daylength, light intensity, species, and controls between experiments. However, what has received less attention is the variety of choices available and the subsequent economic performance. LEDs have higher initial costs compared with more traditional lighting systems such as HPS; however, the costs of LEDs have recently decreased and are expected to continue to decrease and at a faster rate than other light sources (Kusuma et al. 2020; Nelson and Bugbee 2014). Compared with supplementary HPS, one study reported that replacing HPSs with LED lights resulted in a 75% reduction in lighting costs per fruit grown (Gómez et al. 2013). Furthermore, additional cost savings can be made by dynamically regulating supplementary light intensity, based on forecasted solar light levels and electricity price for the day ahead, and this has been shown to have no negative effects on plant growth or visual quality while reducing overall greenhouse costs (Sørensen et al. 2020).

The economies of lighting are crop dependent. Leafy salads, which are not always considered high value, are cost-effective to produce because input light energy is converted into vegetative biomass, most of which is harvested and sold (Pattison et al. 2018). However, only a fraction of input light energy is converted into harvestable fruit in a range of crops such as tomato and other vegetables (Pattison et al. 2018).

Here, we review the literature, to compare electricity costs associated with different light treatments to their final effect on crop yield, given that electricity is one of the largest variable cost a grower is likely to face (Graamans et al. 2018) and is predicted to increase greatly over the coming years. Other qualities that may be desirable to growers that increase value without increasing yield, such as coloration, freshness, taste, and flavor, will not be included in this comparison for simplicity; however, the importance of these elements should not be forgotten. Therefore, optimizing for both yield and quality may involve trade-offs.

The literature reports a wide range of growth and yield metrics for the effectiveness of light treatments, including height, leaf area, leaf number, shoot length, the fresh and dry weight of shoots and total dry weight. Most of these metrics have been collected from studies on crops such as spinach, rocket and lettuce (see Supplementary Materials). We have only included studies that used light interventions in which light treatments replaced some or all of the control lighting (i.e., white or R:B LED, HPS control) with the relevant narrow-band spectrum (i.e., red, blue, green, FR; Fig. 6).

To compare the associated running costs of each of these treatments, we used the 2022 first quarter UK electricity price (Department for Business, Energy & Industrial Strategy, 2022). A number of assumptions were made, based on what is typically reported in the literature: for R+B interventions, we assumed 100% of the preexisting "white lights" (which includes fluorescent, HPS) was replaced with red and blue LEDs. For narrow-band LED treatments, we assumed 50% of the preexisting "white lights" (which includes LED, fluorescent, HPS) was replaced with red LEDs, 20% of the preexisting "white lights" replaced with green; 20% replaced with blue; and 12.5% replaced with FR LEDs. We considered only the ongoing cost of the replacement light and based our assumptions on a constant total output of 250 $\mu mol \cdot m^{-2} \cdot s^{-1}$ for a 18-h photoperiod with an LED efficacy of 2.5 $\mu mol \cdot J^{-1}$ (Fig. 7).

The result of this literature review highlights two treatments that stand out for their potential to increase crop yield (Fig. 6), compared with running costs (Figs. 7 and 8). First, FR light, which has traditionally fallen outside the definition of PAR (Zhen et al. 2021), shows the greatest increase in plant productivity relative to electricity costs (Fig. 8). However, for leafy crops such as spinach, the caveat is that flowering time may be shortened depending on treatment (FR added to growth spectra, EOD FR, etc.). Second, the replacement of HPS lights with a combination of blue, red+blue, or red LEDs alone (Fig. 6) shows considerable promise, with annual red+blue LED electricity costs of 144 $USD \cdot m^{-2}$ compared with HPS electricity costs of 210 $USD \cdot m^{-2}$ (Fig. 7).

Considerations and possible recommendations. The major barrier to initial investment into LED lighting remains the high investment cost of replacing existing HPS or fluorescent lighting with narrow-band LEDs. LED lighting is associated with reductions in electricity use due to reduced heat loss and thus offers considerable efficiency gains compared with HPS systems (Nelson and Bugbee, 2014), which, combined with trending increases in electricity prices (Department for Business, Energy & Industrial Strategy 2022; Eurostat 2022), may offset the initial investment cost of transitioning to LEDs. However, the reduction of heat loss from LED lights is often associated with greater energy use by greenhouse heating systems to compensate for the lack of heat emitted from lighting, especially during winter months. Despite these considerations, using LEDs still reduces overall energy use within a greenhouse compared with HPS (Katzin et al. 2021; Kaukoranta et al. 2017).

Adding a FR spectrum to the existing white or red:blue spectrum offers the most attractive yield uplift; however, this does not account for any changes to the quality of crop, such as chlorophyll and other pigment content and other aspects of morphology (Fig. 4). Adding blue light (or optimizing the red:blue ratio, a species-dependent problem) also offers large benefits to the grower. However, all the treatment recommendations noted here come with nonphotosynthetic risks. Growers must consider developmental and photomorphogenic consequences of varying spectral quality that have been covered elsewhere in this article (Fig. 4).

There are wider impacts of these choices to be borne in mind. For example, in the United Kingdom, recent events such as Brexit, the COVID-19 pandemic, and global logistical issues with shipping have demonstrated the fragility of supply chains across borders (Coleman et al. 2022; Zurayk et al. 2022). LED lighting, as mentioned throughout this review, can extend the growing period of crops in greenhouses and allow for year-round production in controlled environments, increasing the production of locally grown produce, which is generally less susceptible to these issues, although not totally problem free (Bayir et al. 2022).

LED lighting therefore is not only beneficial to improving crop yield and quality, but additionally supports locally grown produce and thus improves food security, while reducing carbon emissions from transportation, a metric many producers, retailers, and consumers take into account in their buying habits.

Conclusion

Many manufacturers focus on delivering a lighting spectrum based on a basic white or simple red and blue spectrum, while other spectral regions that are important for primary and secondary metabolism, such as green and FR, are often neglected. Here, we have laid out the foundations on the range of available lighting spectra, from the addition of FR to the balance between red and blue light, with the effects these lights have on plant growth and performance. Finally, we have also briefly investigated some of the economic benefits due to productivity increases based on the information available in the literature. Here, we have shown that the addition of FR light has the highest impact on productivity and the lowest ongoing electricity cost. The replacement of lighting such as HPS with LEDs may appear expensive compared with the predicted yield increase but there are also significant cost savings associated with the removal of HPS lights. Hardware costs for lighting continue to fall, and we believe tremendous scope remains to improve productivity, increase quality, and reduce waste in glasshouses and vertical farms through the use of tuned lighting "recipes." As yet, no systematic survey exists in the public domain that takes advantage of the inherent dynamism offered by LED lighting to enhance yield. Thus growers and technologists are in uncharted waters where important intellectual property remains on the table that could significantly improve profitability and sustainability.

References Cited

Adams, S.R. and F.A. Langton. 2005. Photoperiod and plant growth: A review. J. Hortic. Sci. Biotechnol. 80(1):2–10, https://doi.org/10.1080/14620316.2005.11511882.

Affandi, F.Y., J.C. Verdonk, T. Ouzounis, Y. Ji, E.J. Woltering, and R.E. Schouten. 2020. Far-red light during cultivation induces postharvest cold tolerance in tomato fruit. Postharvest Biol. Technol. 159:111019, https://doi.org/10.1016/j.postharvbio.2019.111019.

Ahmed, H.A., T. Yu-xin, and Y. Qi-chang. 2020. Lettuce plant growth and tipburn occurrence as affected by airflow using a multi-fan system in a plant factory with artificial light. J. Therm. Biol. 88:102496, https://doi.org/10.1016/j.jtherbio.2019.102496.

Anjana, S.U. and M. Iqbal. 2003. Nitrate accumulation in plants, factors affecting the process, and human health implications. A review. Agron. Sustain. Dev. 27:45–47, https://doi.org/10.1051/agro:2006021.

Bakker, J.C., H.F. De Zwart, and J.B. Campen. 2006. Greenhouse cooling and heat recovery using fine wire heat exchangers in a closed pot plant greenhouse: Design of an energy producing greenhouse. Acta Hortic. 719:263–270, https://doi.org/10.17660/ActaHortic.2006.719.29.

Bayir, B., A. Charles, A. Sekhari, and Y. Ouzrout. 2022. Issues and challenges in short food supply chains: A systematic literature review. Sustainability 14(5):3029, https://doi.org/10.3390/su14053029.

Berry, J. and O. Bjorkman. 1980. photosynthetic response and adaptation to temperature in higher plants. Annu. Rev. Plant Physiol. 31(1):491–543, https://doi.org/10.1146/annurev.pp.31.060180.002423.

Bian, Z., R. Cheng, Y. Wang, Q. Yang, and C. Lu. 2018. Effect of green light on nitrate reduction and edible quality of hydroponically grown lettuce (*Lactuca sativa* L.) under short-term continuous light from red and blue light-emitting diodes. Environ. Exp. Bot. 153:63–71, https://doi.org/10.1016/j.envexpbot.2018.05.010.

Bian, Z., X. Zhang, Y. Wang, and C. Lu. 2019. Improving drought tolerance by altering the photosynthetic rate and stomatal aperture via green light in tomato (*Solanum lycopersicum* L.) seedlings under drought conditions. Environ. Exp. Bot. 167:103844, https://doi.org/10.1016/j.envexpbot.2019.103844.

Birlanga, V., J.R. Acosta-Motos, and J.M. Pérez-Pérez. 2021. Genotype-dependent tipburn severity during lettuce hydroponic culture is associated with altered nutrient leaf content. Agronomy 11(4):616, https://doi.org/10.3390/agronomy11040616.

Bliznikas, Z., A. Žukauskas, G. Samuoliene, A. Viršile, A. Brazaityte, J. Jankauskiene, P. Duchovskis, and A. Novičkovas. 2012. Effect of supplementary pre-harvest LED lighting on the antioxidant and nutritional properties of green vegetables. Acta Hortic. 939:85–91, https://doi.org/10.17660/ActaHortic.2012.939.10.

Borthwick, H.A., S.B. Hendricks, M.W. Parker, E.H. Toole, and V.K. Toole. 1952. A reversible photoreaction controlling seed germination. Proc. Natl. Acad. Sci. USA 38(8):662–666, https://doi.org/10.1073/pnas.38.8.662.

Brazaitytė, A., J. Miliauskienė, V. Vaštakaitė-Kairienė, R. Sutulienė, K. Laužikė, P. Duchovskis, and S. Małek. 2021. Effect of different ratios of blue and red led light on brassicaceae microgreens under a controlled environment. Plants 10(4):801, https://doi.org/10.3390/plants10040801.

Brown, C.S., A.C. Schuerger, and J.C. Sager. 1995. Growth and photomorphogenesis of pepper plants under red light-emitting diodes with supplemental blue or far-red lighting. J. Amer. Soc. Hort. Sci. 120(5):808–813, https://doi.org/10.21273/JASHS.120.5.808.

Cao, K., L. Cui, L. Ye, X. Zhou, E. Bao, H. Zhao, and Z. Zou. 2016. Effects of red light night break treatment on growth and flowering of tomato plants. Front. Plant Sci. 7:1–8, https://doi.org/10.3389/fpls.2016.00527.

Casal, J.J. 2012. Shade avoidance. Arabidopsis Book 2012(10): https://doi.org/10.1199/tab.0157.

Casal, J.J. 2013. Photoreceptor signaling networks in plant responses to shade. Annu. Rev. Plant Biol. 64:403–427, https://doi.org/10.1146/annurev-arplant-050312-120221.

Casal, J.J., A.N. Candia, and R. Sellaro. 2014. Light perception and signalling by phytochrome A. J. Expt. Bot. 65(11):2835–2845, https://doi.org/10.1093/jxb/ert379.

Chalker-Scott, L. 1999. Environmental significance of anthocyanins in plant stress responses. Photochem. Photobiol. 70(1):1–9, https://doi.org/10.1111/j.1751-1097.1999.tb01944.x.

Chavan, S.G., C. Maier, Y. Alagoz, J.C. Filipe, C.R. Warren, H. Lin, B. Jia, M.E. Loik, C.I. Cazzonelli, Z.H. Chen, O. Ghannoum, and D.T. Tissue. 2020. Light-limited photosynthesis under energy-saving film decreases eggplant yield. Food Energy Secur. 9(4):1–18, https://doi.org/10.1002/fes3.245.

Chaves, M.M., J.S. Pereira, J. Maroco, M.L. Rodrigues, C.P.P. Ricardo, M.L. Osório, I. Carvalho, T. Faria, and C. Pinheiro. 2002. How plants cope with water stress in the field. Photosynthesis and growth. Ann. Bot. (Lond.) 89(7):907–916, https://doi.org/10.1093/aob/mcf105.

Chia, P. and C. Kubota. 2010. End-of-day far-red light quality and dose requirements for tomato rootstock hypocotyl elongation. HortScience 45(10):1501–1506, https://doi.org/10.21273/HORTSCI.45.10.1501.

Choi, H.G., B.Y. Moon, and N.J. Kang. 2015. Effects of LED light on the production of strawberry during cultivation in a plastic greenhouse and in a growth chamber. Scientia Hort. 189:22–31, https://doi.org/10.1016/j.scienta.2015.03.022.

Choi, K.Y., K.Y. Paek, and Y.B. Lee. 2000. Effect of air temperature on tipburn incidence of butterhead and leaf lettuce in a plant factory, p. 166–171. In: C. Kubota and C. Chun (eds.). Transplant production in the 21st century. Springer, Dordrecht, the Netherlands. https://doi.org/10.1007/978-94-015-9371-7_27.

Chun, C., M. Toinaga, and T. Kozai. 2001. Floral development and bolting of spinach as affected by photoperiod and integrated photosynthetic photon flux during transplant production. HortScience 36(5):889–892, https://doi.org/10.21273/hortsci.36.5.889.

Coleman, P.C., F. Dhaif, and O. Oyebode. 2022. Food shortages, stockpiling and panic buying ahead of Brexit as reported by the British media: A mixed methods content analysis. BMC Public Health 22:206, https://doi.org/10.1186/s12889-022-12548-8.

Courbier, S., B.L. Snoek, K. Kajala, L. Li, S.C.M. Van Wees, and R. Pierik. 2021. Mechanisms of far-red light-mediated dampening of defense against Botrytis cinerea in tomato leaves. Plant Physiol. 187(3):1250–1266, https://doi.org/10.1093/plphys/kiab354.

Demers, D.A., M. Dorais, C.H. Wien, and A. Gosselin. 1998. Effects of supplemental light duration on greenhouse tomato (*Lycopersicon esculentum* Mill.) plants and fruit yields. Scientia Hort. 74(4):295–306, https://doi.org/10.1016/S0304-4238(98)00097-1.

Demers, D.A. and A. Gosselin. 1999. Supplemental lighting of greenhouse vegetables: Limitations and problems related to long photoperiods. Acta Hortic. 481:469–473, https://doi.org/10.17660/actahortic.1999.481.54.

Demmig-Adams, B. and W.W. Adams. 1992. Photoprotection and other responses of plants to high light stress. Annu. Rev. Plant Physiol. Plant Mol. Biol. 43(1):599–626, https://doi.org/10.1146/annurev.pp.43.060192.003123.

Department for Business Energy & Industrial Strategy. 2022. Prices of fuels purchased by non-domestic consumers in the United Kingdom excluding/including CCL (QEP 3.4.1 and 3.4.2). https://www.gov.uk/government/statistical-data-sets/gas-and-electricity-prices-in-the-non-domestic-sector [accessed 8 Aug 2022].

Elkins, C., and M.W. van Iersel. 2020. Longer photoperiods with the same daily light integral improve growth of rudbeckia seedlings in a greenhouse. HortScience. 55(10):1676–1682. https://doi.org/10.21273/HORTSCI15200-20.

European Food Safety Authority. 2008. Nitrate in vegetables—Scientific opinion of the panel on contaminants in the food chain. EFSA J. 689:1–79, https://doi.org/10.2903/j.efsa.2008.689.

Eurostat. 2022. Gas prices for non-household consumers—bi-annual data (from 2007 onwards). https://ec.europa.eu/eurostat/web/products-datasets/-/nrg_pc_202 [accessed 8 Aug 2022].

Favre, N., A. Bárcena, J.V. Bahima, G. Martínez, and L. Costa. 2018. Pulses of low intensity light as promising technology to delay postharvest senescence of broccoli. Postharvest Biol. Technol. 142:107–114, https://doi.org/10.1016/j.postharvbio.2017.11.006.

Ferrante, A. and L. Mariani. 2018. Agronomic management for enhancing plant tolerance to abiotic stresses: High and low values of temperature, light intensity, and relative humidity. Horticulturae 4(3):21, https://doi.org/10.3390/horticulturae4030021.

Firfiris, V., P.G. Kougias, C. Nikita-Martzopoulou, and G.G. Martzopoulos. 2012. Performance of a covered closed loop shallow geothermal greenhouse heating system. Acta Hortic. 952:457–462, https://doi.org/10.17660/ActaHortic.2012.952.57.

Folta, K.M. and S.A. Maruhnich. 2007. Green light: A signal to slow down or stop. J. Expt. Bot. 58(12):3099–3111, https://doi.org/10.1093/jxb/erm130.

Frantz, J.M., R.J. Joly, and C.A. Mitchell. 2000. Intracanopy lighting influences radiation capture, productivity, and leaf senescence in cowpea canopies. J. Amer. Soc. Hort. Sci. 125(6):694–701, https://doi.org/10.21273/jashs.125.6.694.

Frantz, J.M., G. Ritchie, N.N. Cometti, J. Robinson, and B. Bugbee. 2004. Exploring the limits of crop productivity: Beyond the limits of tipburn in lettuce. J. Amer. Soc. Hort. Sci. 129(3):331–338, https://doi.org/10.21273/jashs.129.3.0331.

Frechilla, S., L.D. Talbott, R.A. Bogomolni, and E. Zeiger. 2000. Reversal of blue light-stimulated stomatal opening by green light. Plant Cell Physiol. 41(2):171–176, https://doi.org/10.1093/pcp/41.2.171.

Garrett Owen, W., Q. Meng, and R.G. Lopez. 2018. Promotion of flowering from far-red radiation depends on the photosynthetic daily light integral. HortScience 53(4):465–471, https://doi.org/10.21273/HORTSCI12544-17.

Gaudreau, L., J. Charbonneau, L.P. Vezina, and A. Gosselin. 1994. Photoperiod and photosynthetic photon flux influence growth and quality of greenhouse-grown lettuce. HortScience 29(11):1285–1289, https://doi.org/10.21273/hortsci.29.11.1285.

Gómez, C. and C.A. Mitchell. 2016a. Physiological and productivity responses of high-wire tomato as affected by supplemental light source and distribution within the canopy. J. Amer. Soc. Hort. Sci. 141(2):196–208, https://doi.org/10.21273/jashs.141.2.196.

Gómez, C. and C.A. Mitchell. 2016b. In search of an optimized supplemental lighting spectrum for greenhouse tomato production with intracanopy lighting. Acta Hortic. 1134:57–62, https://doi.org/10.17660/ActaHortic.2016.1134.8.

Gómez, C., R.C. Morrow, C.M. Bourget, G.D. Massa, and C.A. Mitchell. 2013. Comparison of intracanopy light-emitting diode towers and overhead high-pressure sodium lamps for supplemental lighting of greenhouse-grown tomatoes. HortTechnology 23(1):93–98, https://doi.org/10.21273/horttech.23.1.93.

Goto, E. and T. Takakura. 1992. Supplying air to inner leaves. Am Soc Agric. Engineers 35(2): 641–645.

Graamans, L., E. Baeza, A. van den Dobbelsteen, I. Tsafaras, and C. Stanghellini. 2018. Plant factories versus greenhouses: Comparison of resource use efficiency. Agric. Syst. 160:31–43, https://doi.org/10.1016/j.agsy.2017.11.003.

Green-Tracewicz, E., E.R. Page, and C.J. Swanton. 2011. Shade avoidance in soybean reduces branching and increases plant-to-plant variability in biomass and yield per plant. Weed Sci. 59(1):43–49, https://doi.org/10.1614/ws-d-0-00081.1.

Hamamoto, H., H. Shimaji, and T. Higashide. 2004. Earlier-bolting spinach cultivars respond to a wider spectrum of night-break light for bolting than later-bolting cultivars. Nogyo Kisho 60(3):191–195, https://doi.org/10.2480/agrmet.60.191.

Hasperué, J.H., L.M. Rodoni, L.M. Guardianelli, A.R. Chaves and G.A. Martínez. 2016. Use of LED light for Brussels sprouts postharvest conservation. Scientia Hortic. 213(14):281–286.

Heldt, H.-W. 2005. Plant biochemistry. 3rd ed. Elsevier Academic Press.

Hendricks, S.B. and H.A. Borthwick. 1967. The function of phytochrome in regulation of plant growth. Proc. Natl. Acad. Sci. USA 58(5):2125–2130, https://doi.org/10.1073/pnas.58.5.2125.

Heo, J., C. Lee, D. Chakrabarty, and K. Paek. 2002. Growth responses of marigold and salvia bedding plants as affected by monochromic or mixture radiation provided by a light-emitting diode (LED). Plant Growth Regulat. 38(3):225–230, https://doi.org/10.1023/A:1021523832488.

Heraut-Bron, V., C. Robin, C. Varlet-Grancher, D. Afif, and A. Gucker. 1999. Light quality (red:-far-red ratio): Does it affect photosynthetic activity, net CO_2 assimilation, and morphology of young white clover leaves? Can. J. Bot. 77(10):1425–1431, https://doi.org/10.1139/cjb-77-10-1425.

Hernández, R. and C. Kubota. 2016. Physiological responses of cucumber seedlings under different blue and red photon flux ratios using LEDs. Environ. Exp. Bot. 121:66–74, https://doi.org/10.1016/j.envexpbot.2015.04.001.

Hidaka, K., A. Okamoto, T. Araki, Y. Miyoshi, K. Dan, H. Imamura, M. Kitano, K. Sameshima, and M. Okimura. 2014. Effect of photoperiod of supplemental lighting with light-emitting diodes on growth and yield of strawberry. Environ. Control Biol. 52(2):63–71, https://doi.org/10.2525/ecb.52.63.

Higuchi, Y., K. Sumitomo, A. Oda, H. Shimizu, and T. Hisamatsu. 2012. Day light quality affects the night-break response in the short-day plant chrysanthemum, suggesting differential phytochrome-mediated regulation of flowering. J. Plant Physiol. 169(18):1789–1796, https://doi.org/10.1016/j.jplph.2012.07.003.

Hirai, T., W. Amaki, and H. Watanabe. 2006. Action of blue or red monochromatic light on stem internodal growth depends on plant species. Acta Hortic. 711:345–349, https://doi.org/10.17660/actahortic.2006.711.47.

Hoffmann, A.M., G. Noga, and M. Hunsche. 2015. High blue light improves acclimation and photosynthetic recovery of pepper plants exposed to UV stress. Environ. Exp. Bot. 109:254–263, https://doi.org/10.1016/j.envexpbot.2014.06.017.

Hogewoning, S.W., G. Trouwborst, H. Maljaars, H. Poorter, W. van Ieperen, and J. Harbinson. 2010. Blue light dose—Responses of leaf photosynthesis, morphology, and chemical composition of *Cucumis sativus* grown under different combinations of red and blue light. J. Expt. Bot. 61(11):3107–3117, https://doi.org/10.1093/jxb/erq132.

Huché-thélier, L., L. Crespel, J. Le, P. Morel, S. Sakr, and N. Leduc. 2015. Light signaling and plant responses to blue and UV radiations—Perspectives for applications in horticulture. Environ. Exp. Bot. 121:22–38, https://doi.org/10.1016/j.envexpbot.2015.06.009.

Ilias, I.F. and N. Rajapakse. 2005. The effects of end-of-the-day red and far-red light on growth and flowering of *Petunia ×hybrida* 'Countdown Burgundy' grown under photoselective films. HortScience 40(1):131–133, https://doi.org/10.21273/HORTSCI.40.1.131.

Islam, M.A., D. Tarkowská, J.L. Clarke, D.R. Blystad, H.R. Gislerød, S. Torre, and J.E. Olsen. 2014. Impact of end-of-day red and far-red light on plant morphology and hormone physiology of poinsettia. Scientia Hort. 174(1):77–86, https://doi.org/10.1016/j.scienta.2014.05.013.

Izzo, L.G., M.A. Mickens, G. Aronne, and C. Gómez. 2021. Spectral effects of blue and red light on growth, anatomy, and physiology of lettuce. Physiol. Plant. 172(4):2191–2202, https://doi.org/10.1111/ppl.13395.

Jenkins, G.I. 2017. Photomorphogenic responses to ultraviolet-B light. Plant Cell Environ. 40(11): 2544–2557, https://doi.org/10.1111/pce.12934.

Ji, Y., T. Ouzounis, S. Courbier, E. Kaiser, P.T. Nguyen, H.J. Schouten, R.G.F. Visser, R. Pierik, L.F.M. Marcelis, and E. Heuvelink. 2019. Far-red radiation increases dry mass partitioning to fruits but reduces Botrytis cinerea resistance in tomato. Environ. Exp. Bot. 168:103889, https://doi.org/10.1016/j.envexpbot.2019.103889.

Jin, W., J.L. Urbina, E. Heuvelink, and L.F.M. Marcelis. 2021. Adding far-red to red-blue light-emitting diode light promotes yield of lettuce at different planting densities. Front. Plant Sci. 11:60997, https://doi.org/10.3389/fpls.2020.609977.

Johansson, M. and D. Staiger. 2015. Time to flower: Interplay between photoperiod and the circadian clock. J. Expt. Bot. 66(3):719–730, https://doi.org/10.1093/jxb/eru441.

Johkan, M., K. Shoji, F. Goto, S.-N. Hashida, and T. Yoshihara. 2010. Blue light-emitting diode light irradiation of seedlings improves seedling quality and growth after transplanting in red leaf lettuce. HortScience 45(12):1809–1814, https://doi.org/10.21273/HORTSCI.45.12.1809.

Jokinen, K., L.E. Särkkä, and J. Näkkilä. 2012. Improving sweet pepper productivity by LED interlighting. Acta Hortic. 956: 59–66, https://doi.org/10.17660/ActaHortic.2012.956.4.

Jones-Baumgardt, C., D. Llewellyn, and Y. Zheng. 2020. Different microgreen genotypes have unique growth and yield responses to intensity of supplemental *PAR* from light-emitting diodes during winter greenhouse production in southern Ontario, Canada. HortScience 55(2):156–163, https://doi.org/10.21273/HORTSCI14478-19.

Kaiser, E., S. Matsubara, J. Harbinson, E. Heuvelink, and L.F.M. Marcelis. 2018. Acclimation of photosynthesis to lightflecks in tomato leaves: Interaction with progressive shading in a growing canopy. Physiol. Plant. 162:506–517, https://doi.org/10.1111/ppl.12668.

Kaiser, E., T. Ouzounis, H. Giday, R. Schipper, E. Heuvelink, and L.F.M. Marcelis. 2019a. Adding blue to red supplemental light increases biomass and yield of greenhouse-grown tomatoes, but only to an optimum. Front. Plant Sci. 9:2002, https://doi.org/10.3389/fpls.2018.02002.

Kaiser, E., K. Weerheim, R. Schipper, and J.A. Dieleman. 2019b. Partial replacement of red and blue by green light increases biomass and yield in tomato. Scientia Hort. 249:271–279, https://doi.org/10.1016/j.scienta.2019.02.005.

Kalaitzoglou, P., W. van Ieperen, J. Harbinson, M. van der Meer, S. Martinakos, K. Weerheim, C.C.S. Nicole, and L.F.M. Marcelis. 2019. Effects of continuous or end-of-day far-red light on tomato plant growth, morphology, light absorption, and fruit production. Front. Plant Sci. 10:1–11, https://doi.org/10.3389/fpls.2019.00322.

Kang, C., Y. Zhang, R. Cheng, E. Kaiser, Q. Yang, and T. Li. 2021. Acclimating cucumber plants to blue supplemental light promotes growth in full sunlight. Front. Plant Sci. 12:1–14, https://doi.org/10.3389/fpls.2021.78246.

Katzin, D., L.F.M. Marcelis, and S. van Mourik. 2021. Energy savings in greenhouses by transition from high-pressure sodium to LED lighting. Appl. Energy 281:116019, https://doi.org/10.1016/j.apenergy.2020.116019.

Kaukoranta, T., L.E. Särkkä, and K. Jokinen. 2017. Energy efficiency of greenhouse cucumber production under LED and HPS lighting. Acta Hortic. 1170:967–972, https://doi.org/10.17660/ActaHortic.2017.1170.124.

Keller, M.M., Y. Jaillais, U.V. Pedmale, J.E. Moreno, J. Chory, and C.L. Ballaré. 2011. Cryptochrome 1 and phytochrome B control shade-avoidance responses in Arabidopsis via partially independent hormonal cascades. Plant J. 67(2):195–207, https://doi.org/10.1111/j.1365-313X.2011.04598.x.

Kim, H.H., G.D. Goins, R.M. Wheeler, and J.C. Sager. 2004. Green-light supplementation for enhanced lettuce growth under red-and blue-light-emitting diodes. HortScience 39(7):1617–1622, https://doi.org/10.21273/hortsci.39.7.1617.

Kim, H.J., M.Y. Lin, and C.A. Mitchell. 2019a. Light spectral and thermal properties govern biomass allocation in tomato through morphological and physiological changes. Environ. Exp. Bot. 157:228–240, https://doi.org/10.1016/j.envexpbot.2018.10.019.

Kim, H.J., T. Yang, S. Choi, Y.J. Wang, M.Y. Lin, and A.M. Liceaga. 2019b. Supplemental intracanopy far-red radiation to red LED light improves fruit quality attributes of greenhouse tomatoes. Scientia Hort. 261:108985, https://doi.org/10.1016/j.scienta.2019.108985.

Kong, Y., D. Llewellyn, and Y. Zheng. 2019. Response of growth, yield, and quality of edible-podded snow peas to supplemental led lighting during winter greenhouse production. Can. J. Plant Sci. 99(5):676–687, https://doi.org/10.1139/cjps-2018-0288.

Kovinich, N., G. Kayanja, A. Chanoca, M.S. Otegui, and E. Grotewold. 2015. Abiotic stresses induce different localizations of anthocyanins in Arabidopsis. Plant Signal. Behav. 10(7):2–5, https://doi.org/10.1080/15592324.2015.1027850.

Kozai, T., G. Niu, and M. Takagaki (eds.). 2019. Plant factory: An indoor vertical farming system for efficient quality food production. Academic Press.

Kromdijk, J., K. Glowacka, L. Leonelli, S.T. Gabilly, M. Iwai, K.K. Niyogi, and S.P. Long. 2016. Improving photosynthesis and crop productivity by accelerating recovery. Science 354(6314):857–861, https://doi.org/10.1126/science.aai8878.

Kusuma, P., P.M. Pattison, and B. Bugbee. 2020. From physics to fixtures to food: Current and potential LED efficacy. Hort. Res. 7:56, https://doi.org/10.1038/s41438-020-0283-7.

Kusuma, P., F.M. Westmoreland, S. Zhen, and B. Bugbee. 2021. Photons from NIR LEDs can delay flowering in short-day soybean and *Cannabis*: Implications for phytochrome activity. PLoS One 16:1–17, https://doi.org/10.1371/journal.pone.0255232.

Lanoue, J., C. Little, and X. Hao. 2022. The power of far-red light at night: Photomorphogenic, physiological, and yield response in pepper during dynamic 24 hour lighting. Front. Plant Sci. 13:1–19, https://doi.org/10.3389/fpls.2022.857616.

Lanoue, J., J. Zheng, C. Little, B. Grodzinski, and X. Hao. 2021. Continuous light does not compromise growth and yield in mini-cucumber greenhouse production with supplemental led light. Plants 10(2):1–18, https://doi.org/10.3390/plants1002037.

Lanoue, J., J. Zheng, C. Little, A. Thibodea, B. Grodzinski, and X. Hao. 2019. Alternating red and blue light-emitting diodes allows for injury-free tomato production with continuous lighting. Front. Plant Sci. 10:1–14, https://doi.org/10.3389/fpls.2019.01114.

Larsen, D.H., E.J. Woltering, C.C.S. Nicole, and L.F.M. Marcelis. 2020. Response of basil growth and morphology to light intensity and spectrum in a vertical farm. Front. Plant Sci. 11:1–16, https://doi.org/10.3389/fpls.2020.597906.

Latowski, D., P. Kuczyńska, and K. Strzałka. 2011. Xanthophyll cycle—A mechanism protecting plants against oxidative stress. Redox Report: Communications in Free Radical Research. 16(2):78–90, https://doi.org/10.1179/174329211X13020951739938.

Lefsrud, M.G., D.A. Kopsell, R.M. Augé, and A.J. Both. 2006. Biomass production and pigment accumulation in kale grown under increasing photoperiods. HortScience 41(3):603–606, https://doi.org/10.21273/hortsci.41.3.603.

Legris, M., Y.Ç. Ince, and C. Fankhauser. 2019. Molecular mechanisms underlying phytochrome-controlled morphogenesis in plants. Nat. Commun. 10:5219, https://doi.org/10.1038/s41467-019-13045-0.

Leivar, P. and P.H. Quail. 2011. PIFs: Pivotal components in a cellular signaling hub. Trends Plant Sci. 16(1):19–28, https://doi.org/10.1016/j.tplants.2010.08.003.

Liang, Y., C. Kang, E. Kaiser, Y. Kuang, Q. Yang, and T. Li. 2021. Red/blue light ratios induce morphology and physiology alterations differently in cucumber and tomato. Scientia Hort. 281:109995, https://doi.org/10.1016/j.scienta.2021.109995.

Lichtenthaler, H.K. and C. Buschmann. 2001. Chlorophylls and carotenoids: Measurement and characterization by UV-VIS. Curr. Prot. Food Anal. Chem. 1:F4.3.1–F4.3.8, https://doi.org/10.1002/0471142913.

Lichtenthaler, H.K., C. Buschmann, and U. Rahmsdorf. 1980. The importance of blue light for the development of sun-type chloroplasts, p. 485–494. In: H. Senger (ed.). The blue light syndrome. Springer, Berlin and Heidelberg, Germany.

Liu, J. and M.W. van Iersel. 2021. Photosynthetic physiology of blue, green, and red light: Light intensity effects and underlying mechanisms. Front. Plant Sci. 12:619987, https://doi.org/10.3389/fpls.2021.619987.

Lu, T., Z. Meng, G. Zhang, M. Qi, Z. Sun, Y. Liu, and T. Li. 2017. Sub-high temperature and high light intensity induced irreversible inhibition on photosynthesis system of tomato plant (*Solanum lycopersicum* L.). Front. Plant Sci. 8:1–16, https://doi.org/10.3389/fpls.2017.00365.

Ma, Z., S. Li, M. Zhang, S. Jiang, and Y. Xiao. 2010. Light intensity affects growth, photosynthetic capability, and total flavonoid accumulation of Anoectochilus plants. HortScience 45(6): 863–867, https://doi.org/10.21273/hortsci.45.6.863.

Matsuda, R., K. Ohashi-Kaneko, K. Fujiwara, and K. Kurata. 2007. Analysis of the relationship between blue-light photon flux density and the photosynthetic properties of spinach (*Spinacia oleracea* L.) leaves with regard to the acclimation of photosynthesis to growth irradiance. Soil Sci. Plant Nutr. 53(4):459–465, https://doi.org/10.1111/j.1747-0765.2007.00150.x.

Matthews, J.S.A. and T. Lawson. 2019. Climate change and stomatal physiology. In: J.A. Roberts (ed.). Annual Plant Reviews online. https://doi.org/10.1002/9781119312994.apr0667.

Matthews, J.S.A., S. Vialet-Chabrand, and T. Lawson. 2020. Role of blue and red light in stomatal dynamic behaviour. J. Expt. Bot. 71(7):2253–2269, https://doi.org/10.1093/jxb/erz563.

Maynard, D.N., A.V. Barker, P.L. Minotti, and N.H. Peck. 1976. Nitrate accumulation in vegetables. Adv. Agron. 28:71–118.

McCree, K.J. 1971. The action spectrum, absorptance and quantum yield of photosynthesis in crop plants. Agric. Meteorol. 9:191–216, https://doi.org/10.1016/0002-1571(71)90022-7.

McMahon, M.J., J.W. Kelly, D.R. Decoteau, R.E. Young, and R.K. Pollock. 2019. Growth of *Dendranthema ×grandiflorum* (Ramat.) Kitamura under various spectral filters. J. Am. Soc. Hort. Sci. 116(6):950–954, https://doi.org/10.21273/JASHS.116.6.950.

McMaster, G.S. and W.W. Wilhelm. 1997. Growing degree-days: One equation, two interpretations. Agr. For. Meteorol. 87(1):291–300.

Meng, Q., N. Kelly, and E.S. Runkle. 2019. Substituting green or far-red radiation for blue radiation induces shade avoidance and promotes growth in lettuce and kale. Environ. Exp. Bot. 162:383–391, https://doi.org/10.1016/j.envexpbot.2019.03.016.

Meng, Q. and E.S. Runkle. 2019. Far-red radiation interacts with relative and absolute blue and red photon flux densities to regulate growth, morphology, and pigmentation of lettuce and basil seedlings. Scientia Hort. 255:269–280, https://doi.org/10.1016/j.scienta.2019.05.030.

Mirkovic, T., E.E. Ostroumov, J.M. Anna, R. Van Grondelle, and G.D. Govindjee Scholes. 2017. Light absorption and energy transfer in the antenna complexes of photosynthetic organisms. Chem. Rev. 117(2):249–293, https://doi.org/10.1021/acs.chemrev.6b00002.

Mullineaux, P.M., M. Exposito-Rodriguez, P.P. Laissue, and N. Smirnoff. 2018. ROS-dependent signalling pathways in plants and algae exposed to high light: Comparisons with other eukaryotes. Free Radic. Biol. Med. 122:52–64, https://doi.org/10.1016/j.freeradbiomed.2018.01.033.

Murage, E.N. and M. Masuda. 1997. Response of pepper and eggplant to continuous light in relation to leaf chlorosis and activities of antioxidative enzymes. Scientia Hort. 70(4):269–279, https://doi.org/10.1016/S0304-4238(97)00078-2.

Murakami, K., R. Matsuda, and K. Fujiwara. 2013. Effects of supplemental lighting to a lower leaf using light-emitting diodes with different spectra on the leaf photosynthetic rate in sweet pepper. Nogyo Kisho 69(2):55–63, https://doi.org/10.2480/agrmet.69.2.2.

Murchie, E.H. and T. Lawson. 2013. Chlorophyll fluorescence analysis: A guide to good practice and understanding some new applications. J. Expt. Bot. 64(13):3983–3998, https://doi.org/10.1093/jxb/ert208.

Murchie, E.H. and J. Harbinson. 2014. Non-photochemical fluorescence quenching across scales: From chloroplasts to plants to communities, p. 553–582. In: B. Demmig-Adams, G. Garab, W. Adams III, Govindjee (eds.). Non-photochemical quenching and energy dissipation in plants, algae and cyanobacteria. Springer, Dordrecht, the Netherlands. https://doi.org/10.1007/978-94-017-9032-1.

Murchie, E.H. and A.V. Ruban. 2020. Dynamic non-photochemical quenching in plants: From molecular mechanism to productivity. Plant J. 101(4): 885–896, https://doi.org/10.1111/tpj.14601.

Nagendran, R. and Y.H. Lee. 2015. Green and red light reduces the disease severity by *Pseudomonas cichorii* JBC1 in tomato plants via upregulation of defense-related gene expression. Phytopathology 105(4):412–418, https://doi.org/10.1094/PHYTO-04-14-0108-R.

Nascimento, L.B.D.S., C. Brunetti, G. Agati, C.L. Iacono, C. Detti, E. Giordani, F. Ferrini, and A. Gori. 2020. Short-term pre-harvest uv-b supplement enhances the polyphenol content and antioxidant capacity of *Ocimum basilicum* leaves during storage. Plants 9(6):1–19, https://doi.org/10.3390/plants9060797.

Naznin, M.T., M. Lefsrud, V. Gravel, and M.O.K. Azad. 2019. Blue light added with red LEDs enhance growth characteristics, pigments content, and antioxidant capacity in lettuce, spinach, kale, basil, and sweet pepper in a controlled environment. Plants 8(4):93. https://doi.org/10.3390/plants8040093.

Nelson, J.A. and B. Bugbee. 2014. Economic analysis of greenhouse lighting: Light emitting diodes vs. high intensity discharge fixtures. PLoS One 9(6):e99010, https://doi.org/10.1371/journal.pone.0099010.

Ngcobo, B.L., I. Bertling, and A.D. Clulow. 2020. Preharvest illumination of cherry tomato reduces ripening period, enhances fruit carotenoid concentration and overall fruit quality. J. Hortic. Sci. Biotechnol. 95(5):617–627, https://doi.org/10.1080/14620316.2020.1743771.

Nguyen, T.P.D., T.T.H. Tran, and Q.T. Nguyen. 2019. Effects of light intensity on the growth, photosynthesis and leaf microstructure of hydroponic cultivated spinach (*Spinacia oleracea* L.) under a combination of red and blue LEDs in house. Agric. Technol. Thail. 15(1):75–90.

Nicole, C.C.S., F. Charalambous, S. Martinakos, S. Van De Voort, Z. Li, M. Verhoog, and M. Krijn. 2016. Lettuce growth and quality optimization in a plant factory. Acta Hortic. 1134: 231–238, https://doi.org/10.17660/ActaHortic.2016.1134.31.

Ohtake, N., M. Ishikura, H. Suzuki, W. Yamori, and E. Goto. 2018. Continuous irradiation with alternating red and blue light enhances plant growth while keeping nutritional quality in lettuce. HortScience 53(12):1804–1809, https://doi.org/10.21273/HORTSCI13469-18.

Ouzounis, T., E. Heuvelink, Y. Ji, H.J. Schouten, R.G.F. Visser, and L.F.M. Marcelis. 2016. Blue and red LED lighting effects on plant biomass, stomatal conductance, and metabolite content in nine tomato genotypes. Acta Hortic. 1134:251–258, https://doi.org/10.17660/ActaHortic.2016.1134.34.

Palmer, S. and M.W. van Iersel. 2020. Increasing growth of lettuce and mizuna under sole-source LED lighting using longer photoperiods with the same daily light integral. Agronomy 10(11):1659, https://doi.org/10.3390/agronomy10111659.

Park, Y. and E.S. Runkle. 2019. Blue radiation attenuates the effects of the red to far-red ratio on extension growth but not on flowering. Environ. Exp. Bot. 168:103871, https://doi.org/10.1016/j.envexpbot.2019.103871.

Pattison, P.M., J.Y. Tsao, G.C. Brainard, and B. Bugbee. 2018. LEDs for photons, physiology and food. Nature 563(7732):493–500, https://doi.org/10.1038/s41586-018-0706-x.

Pedmale, U.V., S.S.C. Huang, M. Zander, B.J. Cole, J. Hetzel, K. Ljung, P.A.B. Reis, P. Sridevi, K. Nito, J.R. Nery, J.R. Ecker, and J. Chory. 2016. Cryptochromes interact directly with PIFs to control plant growth in limiting blue light. Cell 164(1–2):233–245, https://doi.org/10.1016/j.cell.2015.12.018.

Pennisi, G., F. Orsini, M. Landolfo, A. Pistillo, A. Crepaldi, S. Nicola, J.A. Fernández, L.F.M. Marcelis, and G. Gianquinto. 2020. Optimal photoperiod for indoor cultivation of leafy vegetables and herbs. Eur. J. Hortic. Sci. 85(5):329–338, https://doi.org/10.17660/eJHS.2020/85.5.4.

Pennisi, G., S. Blasioli, A. Cellini, L. Maia, A. Crepaldi, I. Braschi, F. Spinelli, S. Nicol, J.A. Fernandez, C. Stanghellini, L.F.M. Marcelis, F. Orsini, and G. Gianquinto. 2019. Unraveling the role of red:blue LED lights on resource use efficiency and nutritional properties of indoor grown sweet basil. Front. Plant Sci. 10:1–14, https://doi.org/10.3389/fpls.2019.00305.

Peterman, E.J.G., C.C. Gradinaru, F. Calkoen, J.C. Borst, R. Van Grondelle, and H. Van Amerongen. 1997. Xanthophylls in light-harvesting complex II of higher plants: Light harvesting and triplet quenching. Biochemistry 36(40): 12208–12215, https://doi.org/10.1021/bi9711689.

Pettai, H., V. Oja, A. Freiber, and A. Laisk. 2005. Photosynthetic activity of far-red light in green plants. Biochim. Biophys. Acta Bioenerg. 1708(3):311–321, https://doi.org/10.1016/j.bbabio.2005.05.005.

Pettersen, R.I., S. Torre, and H.R. Gislerød. 2010. Effects of intracanopy lighting on photosynthetic characteristics in cucumber. Scientia Hort. 125(2):77–81, https://doi.org/10.1016/j.scienta.2010.02.006.

Piovene, C., F. Orsini, S. Bosi, R. Sanoubar, V. Bregola, G. Dinelli, and G. Gianquinto. 2015. Optimal Red: Blue ratio in led lighting for nutraceutical indoor horticulture. Scientia Hort. 193:202–208, https://doi.org/10.1016/j.scienta.2015.07.015.

Proietti, S., S. Moscatello, F. Riccio, P. Downey, and A. Battistelli. 2021. continuous lighting promotes plant growth, light conversion efficiency, and nutritional quality of *Eruca vesicaria* (L.) Cav. in controlled environment with minor effects due to light quality. Front. Plant Sci. 12: https://doi.org/10.3389/fpls.2021.730119.

Qian, M., E. Rosenqvist, A.-M. Flygate, I. Kalbina, Y. Teng, M.A.K. Jansen, and Å. Strid. 2020. UV-A light induces a robust and dwarfed phenotype in cucumber plants (*Cucumis sativus* L.) without affecting fruit yield. Scientia Hort. 263:109110, https://doi.org/10.1016/j.scienta.2019.109110.

Rabara, R.C., G. Behrman, T. Timbol, and P.J. Rushton. 2017. Effect of spectral quality of monochromatic LED lights on the growth of artichoke seedlings. Front. Plant Sci. 8:1–9, https://doi.org/10.3389/fpls.2017.00190.

Rahman, M.Z., Y. Honda, and S. Arase. 2003. Red-light-induced resistance in broad bean (*Vicia faba* L.) to Leaf spot disease caused by *Alternaria tenuissima.* J. Phytopathol. 151(2): 86–91, https://doi.org/10.1046/j.1439-0434.2003.00685.x.

Sago, Y. 2016. Effects of light intensity and growth rate on tipburn development and leaf calcium concentration in butterhead lettuce. HortScience 51(9):1087–1091, https://doi.org/10.21273/HORTSCI10668-16.

Särkkä, L.E., K. Jokinen, C.O. Ottosen, and T. Kaukoranta. 2017. Effects of HPS and LED lighting on cucumber leaf photosynthesis, light quality penetration and temperature in the canopy, plant morphology and yield. Agric. Food Sci. 26(2):101–109, https://doi.org/10.23986/afsci.60293.

Schenkels, L., W. Saeys, A. Lauwers, and M.P. De Proft. 2020. Green light induces shade avoidance to alter plant morphology and increases biomass production in *Ocimum basilicum* L. Scientia Hort. 261:109002, https://doi.org/10.1016/j.scienta.2019.109002.

Sellaro, R., M. Crepy, S.A. Trupkin, E. Karayekov, A.S. Buchovsky, C. Rossi, and J.J. Casal. 2010. Cryptochrome as a sensor of the blue/green ratio of natural radiation in Arabidopsis. Plant Physiol. 154(1):401–409, https://doi.org/10.1104/pp.110.160820.

Shibaeva, T.G., E.G. Sherudilo, A.A. Rubaeva, and A.F. Titov. 2022. Continuous LED lighting enhances yield and nutritional value of four genotypes of Brassicaceae microgreens. Plants 11(2):1–14, https://doi.org/10.3390/plants11020176.

Shibuya, T., K. Itagaki, M. Tojo, R. Endo, and Y. Kitaya. 2011. Fluorescent illumination with high red-to-far-red ratio improves resistance of cucumber seedlings to powdery mildew. HortScience 46(3):429–431, https://doi.org/10.21273/hortsci.46.3.429.

Signore, A., L. Bell, P. Santamaria, C. Wagstaff, and M.-C. Van Labeke. 2020. Red light is effective in reducing nitrate concentration in rocket by increasing nitrate reductase activity, and contributes to increased total glucosinolates content. Front. Plant Sci. 11:604, https://doi.org/10.3389/fpls.2020.00604.

Siomos, A.S. and A. Koukounaras. 2007. Quality and Postharvest Physiology of Rocket Leaves. Fresh Prod. 1(1):59–65.

Smith, H. and G.C. Whitelam. 1997. The shade avoidance syndrome: Multiple responses mediated by multiple phytochromes. Plant Cell Environ. 20(6):840–844, https://doi.org/10.1046/j.1365-3040.1997.d01-104.x.

Smith, H.L., L. Mcausland, and E.H. Murchie. 2017. Don't ignore the green light: Exploring diverse roles in plant processes. J. Expt. Bot. 68(9):2099–2110, https://doi.org/10.1093/jxb/erx098.

Snowden, M.C., K.R. Cope, and B. Bugbee. 2016. Sensitivity of seven diverse species to blue and green light: Interactions with photon flux. PLoS One 11(10):1–32, https://doi.org/10.1371/journal.pone.0163121.

Son, K.H. and M.M. Oh. 2015. Growth, photosynthetic and antioxidant parameters of two lettuce cultivars as affected by red, green, and blue light-emitting diodes. Hort. Environ. Biotechnol. 56(5):639–653, https://doi.org/10.1007/s13580-015-1064-3.

Sørensen, H.K., D. Fanourakis, G. Tsaniklidis, D. Bouranis, A.R. Nejad, and C.O. Ottosen. 2020. Using artificial lighting based on electricity price without a negative impact on growth, visual quality or stomatal closing response in *Passiflora.* Scientia Hort. 267:109354, https://doi.org/10.1016/j.scienta.2020.109354.

Stamatakis, K., M. Tsimilli-Michael, and G.C. Papageorgiou. 2014. On the question of the light-harvesting role of β-carotene in photosystem II and photosystem I core complexes. Plant Physiol. Biochem. 81:121–127, https://doi.org/10.1016/j.plaphy.2014.01.014.

Stevens, J., M. Faralli, S. Wall, J.D. Stamford, and T. Lawson. 2021. Stomatal responses to climate change. In: K. Becklin, K. Ward, and D.A. Way (eds.). Photosynthesis, respiration and climate change. Springer. https://doi.org/10.1007/978-3-030-64926-5.

Suthaparan, A., S. Torre, A. Stensvand, M.L. Herrero, R.I. Pettersen, D.M. Gadoury, and H.R. Gislerød. 2010. Specific light-emitting diodes can suppress sporulation of *Podosphaera pannosa* on greenhouse roses. Plant Dis. 94(9):1105–1110, https://doi.org/10.1094/PDIS-94-9-1105.

Tantasawat, P.A., A. Sorntip, and P. Pornbungkerd. 2015. Effects of exogenous application of plant growth regulators on growth, yield, and in vitro gynogenesis in cucumber. HortScience 50(3):372–382, https://doi.org/10.21273/hortsci.50.3.374.

Terashima, I., T. Fujita, T. Inoue, W.S. Chow, and R. Oguchi. 2009. Green light drives leaf photosynthesis more efficiently than red light in strong white light: Revisiting the enigmatic question of why leaves are green. Plant Cell Physiol. 50(4):684–697, https://doi.org/10.1093/pcp/pcp034.

Tewolde, F.T., K. Shiina, T. Maruo, M. Takagaki, T. Kozai, and W. Yamori. 2018. Supplemental LED inter-lighting compensates for a shortage of light for plant growth and yield under the lack of sunshine. PLoS One 13(11):1–14, https://doi.org/10.1371/journal.pone.0206592.

Thoma, F., A. Somborn-Schulz, D. Schlehuber, and V. Keuter. 2020. Effects of light on secondary metabolites in selected leafy greens: A review. Plant Metabolism and Chemodiversity 11:1–15, https://doi.org/10.3389/fpls.2020.00497.

Topcu, Y., A. Dogan, H. Sahin-Nadeem, E. Polat, Z. Kasimoglu, and M. Erkan. 2018. Morphological and biochemical responses of broccoli florets to supplemental ultraviolet-B illumination. Agric. Ecosyst. Environ. 259:1–10, https://doi.org/10.1016/j.agee.2018.02.027.

Touliatos, D., I.C. Dodd, and M. Mcainsh. 2016. Vertical farming increases lettuce yield per unit area compared to conventional horizontal hydroponics. Food Energy Secur. 5(3):184–191, https://doi.org/10.1002/fes3.83.

Trouwborst, G., S.W. Hogewoning, O. van Kooten, J. Harbinson, and W. van Ieperen. 2016. Plasticity of photosynthesis after the "red light syndrome" in cucumber. Environ. Exp. Bot. 121:5–82, https://doi.org/10.1016/j.envexpbot.2015.05.002.

Trouwborst, G., A.H.C.M. Schapendonk, K. Rappoldt, S. Pot, S.W. Hogewoning, and W. van Ieperen. 2011. The effect of intracanopy lighting on cucumber fruit yield—Model analysis. Scientia Hort. 129(2):273–278, https://doi.org/10.1016/j.scienta.2011.03.042.

Van Gestel, N.C., A.D. Nesbit, E.P. Gordon, C. Green, P.W. Paré, L. Thompson, E.B. Peffley, and D.T. Tissue. 2005. Continuous light may induce photosynthetic downregulation in onion—Consequences for growth and biomass partitioning. Physiol. Plant. 125(2):235–246, https://doi.org/10.1111/j.1399-3054.2005.00560.x.

Velez-Ramirez, A.I., W. van Ieperen, D. Vreugdenhil, and F.F. Millenaar. 2014. Continuous-light tolerance in tomato is graft-transferable. Planta 241(1):285–290, https://doi.org/10.1007/s00425-014-2202-3.

Velez-Ramirez, A.I., W. van Ieperen, D. Vreugdenhil, and F.F. Millenaar. 2015. Continuous-light tolerance in tomato is graft-transferable. Planta 241(1):285–290, https://doi.org/10.1007/s00425-014-2202-3.

Vialet-Chabrand, S., J.S.A. Matthews, A.J. Simkin, C.A. Raines, and T. Lawson. 2017. Importance of fluctuations in light on plant photosynthetic acclimation. Plant Physiol. 173(4):2163–2179, https://doi.org/10.1104/pp.16.01767.

Vialet-Chabrand, S., J.S.A. Matthews, A.J. Simkin, C.A. Raines, and T. Lawson. 2017. Importance of fluctuations in light on plant photosynthetic acclimation. Plant Physiol. 173(4):2163–2179, https://doi.org/10.1104/pp.16.01767.

Walters, K.J. and R.G. Lopez. 2021. Modeling growth and development of hydroponically grown dill, parsley, and watercress in response to photosynthetic daily light integral and mean daily temperature. PLoS One 16:1–16, https://doi.org/10.1371/journal.pone.0248662.

Wan, Y. and K.M. Folta. 2013. Contributions of green light to plant growth and development. Amer. J. Bot. 100(1):70–78, https://doi.org/10.3732/ajb.1200354.

Wang, C., J. He, T.H. Zhao, Y. Cao, G. Wang, B. Sun, X. Yan, W. Guo, and M.H. Li. 2019. The smaller the leaf is, the faster the leaf water loses in a temperate forest. Front. Plant Sci. 10:1–12, https://doi.org/10.3389/fpls.2019.00058.

Wang, F., Z. Guo, H. Li, M. Wang, E. Onac, J. Zhou, X. Xia, K. Shi, J. Yu, and Y. Zhou. 2016a. Phytochrome a and b function antagonistically to regulate cold tolerance via abscisic acid-dependent jasmonate signaling. Plant Physiol. 170(1):459–471, https://doi.org/10.1104/pp.15.01171.

Wang, H., Y.P. Jiang, H.J. Yu, X.J. Xia, K. Shi, Y.H. Zhou, and J.Q. Yu. 2010. Light quality affects incidence of powdery mildew, expression of defence-related genes and associated metabolism in cucumber plants. Eur. J. Plant Pathol. 127(1):125–135, https://doi.org/10.1007/s10658-009-9577-1.

Wang, H., Z. Zhang, H. Li, X. Zhao, X. Liu, M. Ortiz, C. Lin, and B. Liu. 2013. CONSTANS-LIKE 7 regulates branching and shade avoidance response in Arabidopsis. J. Expt. Bot. 64(4):1017–1024, https://doi.org/10.1093/jxb/ers376.

Wang, J., W. Lu, Y. Tong, and Q. Yang. 2016b. Leaf morphology, photosynthetic performance, chlorophyll fluorescence, stomatal development of lettuce (*Lactuca sativa* L.) exposed to different ratios of red light to blue light. Front. Plant Sci. 7:1–10, https://doi.org/10.3389/fpls.2016.00250.

Wanlai, Z., L. Wenke, and Y. Qichang. 2013. Reducing nitrate content in lettuce by pre-harvest continuous light delivered by red and blue light-emitting diodes. J. Plant Nutr. 36(3):481–490, https://doi.org/10.1080/01904167.2012.748069.

Wargent, J.J., E.M. Elfadly, J.P. Moore, and N.D. Paul. 2011. Increased exposure to UV-B radiation during early development leads to enhanced photoprotection and improved long-term performance in Lactuca sativa. Plant Cell Environ. 34(8):1401–1413, https://doi.org/10.1111/j.1365-3040.2011.02342.x.

Weaver, G. and M.W. van Iersel. 2020. Longer photoperiods with adaptive lighting control can improve growth of greenhouse-grown ‘Little Gem’ lettuce (*Lactuca sativa*). HortScience 55(4):573–580, https://doi.org/10.21273/HORTSCI14721-19.

Wollaeger, H.M. and E.S. Runkle. 2015. Growth and acclimation of impatiens, salvia, petunia, and tomato seedlings to blue and red light. HortScience 50(4):522–529, https://doi.org/10.21273/hortsci.50.4.522.

Yan, Z., D. He, G. Niu, Q. Zhou, and Y. Qu. 2019. Growth, nutritional quality, and energy use efficiency of hydroponic lettuce as influenced by daily light integrals exposed to white versus white plus red light-emitting diodes. HortScience 54(10):1737–1744, https://doi.org/10.21273/HORTSCI14236-19.

Yang, F., Q. Liu, Y. Cheng, L. Feng, X. Wu, Y. Fan, M.A. Raza, X. Wang, T. Yong, W. Liu, J. Liu, J. Du, K. Shu, and W. Yang. 2020. Low red/far-red ratio as a signal promotes carbon assimilation of soybean seedlings by increasing the photosynthetic capacity. BMC Plant Biol. 20(1):1–12, https://doi.org/10.1186/s12870-020-02352-0.

Yang, S., J. Logan, and D.L. Coffey. 1995. Mathematical formulae for calculating the base temperature for growing degree days. Agr. For. Meteorol. 74(1–2):61–74, https://doi.org/10.1016/0168-1923(94)02185-M.

Yang, Y.X., M.M. Wang, Y.L. Yin, E. Onac, G.F. Zhou, S. Peng, X.J. Xia, K. Shi, J.Q. Yu, and Y.H. Zhou. 2015. RNA-seq analysis reveals the role of red light in resistance against Pseudomonas syringae pv. tomato DC3000 in tomato plants. BMC Genomics 16(1):1–16, https://doi.org/10.1186/s12864-015-1228-7.

Yang, Y.X., C. Wu, G.J. Ahammed, C. Wu, Z. Yang, C. Wan, and J. Chen. 2018. Red light-induced systemic resistance against root-knot nematode is mediated by a coordinated regulation of salicylic acid, jasmonic acid and redox signaling in watermelon. Front. Plant Sci. 9:1–13, https://doi.org/10.3389/fpls.2018.00899.

Ying, Q., Y. Kong, C. Jones-Baumgardt, and Y. Zheng. 2020a. Responses of yield and appearance quality of four Brassicaceae microgreens to varied blue light proportion in red and blue light-emitting diodes lighting. Scientia Hort. 259:108857, https://doi.org/10.1016/j.scienta.2019.108857.

Ying, Q., Y. Kong, and Y. Zheng. 2020b. Overnight supplemental blue, rather than far-red, light improves microgreen yield and appearance quality without compromising nutritional quality during winter greenhouse production. HortScience 55(9):1468–1474, https://doi.org/10.21273/HORTSCI15196-20.

Zahedi, S.M. and H. Sarikhani. 2016. Effect of far-red light, temperature, and plant age on morphological changes and induction of flowering of a ‘June-bearing’ strawberry. Hort. Environ. Biotechnol. 57(4):340–347, https://doi.org/10.1007/s13580-016-0018-8.

Zhang, T., S.A. Maruhnich, and K.M. Folta. 2011. Green light induces shade avoidance symptoms. Plant Physiol. 157(3):1528–1536, https://doi.org/10.1104/pp.111.180661.

Zhang, Y., E. Kaiser, Y. Zhang, J. Zou, Z. Bian, Q. Yang, and T. Li. 2020. UVA radiation promotes tomato growth through morphological adaptation leading to increased light interception. Environ. Exp. Bot. 176:104073, https://doi.org/10.1016/j.envexpbot.2020.104073.

Zhang, Y., E. Kaiser, Y. Zhang, Q. Yang, and T. Li. 2019. Red/blue light ratio strongly affects steady-state photosynthesis, but hardly affects photosynthetic induction in tomato (*Solanum lycopersicum*). Physiol. Plant. 167(2):144–158, https://doi.org/10.1111/ppl.12876.

Zhen, S. and B. Bugbee. 2020a. Far-red photons have equivalent efficiency to traditional photosynthetic photons: Implications for redefining photosynthetically active radiation. Plant Cell Environ. 43(5):1259–1272, https://doi.org/10.1111/pce.13730.

Zhen, S. and B. Bugbee. 2020b. Substituting far-red for traditionally defined photosynthetic photons results in equal canopy quantum yield for CO_2 fixation and increased photon capture during long-term studies: Implications for redefining PAR. Front. Plant Sci. 11:1–14, https://doi.org/10.3389/fpls.2020.581156.

Zhen, S., M.W. van Iersel, and B. Bugbee. 2022. Photosynthesis in sun and shade: The surprising importance of far-red photon. New Phytol. 236:538–546, https://doi.org/10.1111/nph.18375.

Zhen, S., M. van Iersel, and B. Bugbee. 2021. Why far-red photons should be included in the definition of photosynthetic photons and the measurement of horticultural fixture efficacy. Front. Plant Sci. 12:10–13, https://doi.org/10.3389/fpls.2021.693445.

Zhen, S. and M.W. van Iersel. 2017. Far-red light is needed for efficient photochemistry and photosynthesis. J. Plant Physiol. 209:115–122, https://doi.org/10.1016/j.jplph.2016.12.004.

Zheng, X.T., Z.C. Yu, J.W. Tang, M.L. Cai, Y.L. Chen, C.W. Yang, W.S. Chow, and C.L. Peng. 2020. The major photoprotective role of anthocyanins in leaves of Arabidopsis thaliana under long-term high light treatment: Antioxidant or light attenuator? Photosynth. Res. 148:25–40, https://doi.org/10.1007/s11120-020-00761-8.

Zheng, Y., Y. Zhang, H. Liu, Y. Li, Y. Liu, Y. Hao, and B. Lei. 2018. Supplemental blue light increases growth and quality of greenhouse pak choi depending on cultivar and supplemental light intensity. J. Integr. Agric. 17(10):2245–2256, https://doi.org/10.1016/S2095-3119(18)62064-7.

Zhou, J., P.P. Li, J.Z. Wang, and W. Fu. 2019. Growth, photosynthesis, and nutrient uptake at different light intensities and temperatures in lettuce. HortScience 54(11):1925–1933, https://doi.org/10.21273/HORTSCI14161-19.

Zou, T., C. Huang, P. Wu, L. Ge, and Y. Xu. 2020. Optimization of artificial light for spinach growth in plant factory based on orthogonal test. Plants 9(4):490, https://doi.org/10.3390/plants9040490.

Zurayk, R., A.A.K. Yehya, and R.A. Bahn. 2022. Fragility and resilience in food systems: What can we learn from the COVID-19 crisis? In: R. Shaw and A. Gurtoo (eds.). Global Pandemic and Human Security. Springer, Singapore. https://doi.org/10.1007/978-981-16-5074-1_10.