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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, energy use efficiency). This part of the 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 significant 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 yields.

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 $E = h\nu$; in which $E$ is energy (Joules), $h$ is the Planck constant (6.62607015 × 10⁻³⁴ J·s), $c$ is the speed of light, and $\lambda$ 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 (PPFD) is the most commonly used measurement of light intensity, which refers to the number of photons (μmol) received on a specified area (m²) per second (μmol·m⁻²·s⁻¹), with 1 mol of photons consisting of 6.022 × 10²³ 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 m² (W·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 (μmol·m⁻²·s⁻¹) measures photons, whereas irradiance (W·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·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 (CO₂) 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; Kovichin et al. 2015; Thoma et al. 2020; Zheng et al. 2020). Many of these antioxidants and pigments are also highly...
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 Harbison 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 to plant health. 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. (Fig. 1A) 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. (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 in 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...
light 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; Starmatakis 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-Théléri et al. 2015; Thorna 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 light 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 pigments, 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, flavonoids 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 have as it if 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 among 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 cost of stomata (Frechilla et al. 2000; Mathews 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 (Lapworth et al. 2011; Lima 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 with 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
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 ultra-violet-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 ultra-violet (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. However, these effects need to be considered when designing the illumination recipe (Fig. 4), and this is also discussed in the Experimental Design analysis at the end of this article. FR up to 750 nm should be considered in the determination 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 Experimental Design analysis at the end of this article. FR up to 750 nm should be considered in the determination 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 Experimental Design analysis at the end of this article.
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), 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 (Courbetier 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; Simoes 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 with increased shoot and harvest yields of basil, cucumber, tomato, and lettuce (Yan et al. 2019). For flowering plants, while FR increased flowering, it also decreased chlorophyll content while decreasing internode length (Mcdonald et al. 2019). 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 (McDonald et al. 2019). Although there may not be a simple relationship between FR and chlorophyll content, both studies indicate that FR can have a significant impact on plant growth and development, affecting factors such as biomass, flowering, and chlorophyll content. This highlights the importance of optimizing the balance of red to FR for optimal growth and development.

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

<table>
<thead>
<tr>
<th>Author</th>
<th>Plants</th>
<th>R:B Range</th>
<th>Pigments</th>
<th>Secondary Metabolites</th>
<th>Other</th>
<th>Photosynthesis</th>
<th>Height</th>
<th>Leaf Area</th>
<th>Fresh Weight</th>
<th>Dry Weight</th>
<th>Partitioning</th>
<th>Flower/Fruit</th>
</tr>
</thead>
<tbody>
<tr>
<td>Yung et al. 2010</td>
<td>Tomato (Lycopersicon esculentum)</td>
<td>Total 10% (of sunlight + supplementary); 6%, 10%, 12% (24%)</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>↑</td>
<td>-</td>
<td>-</td>
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<tr>
<td>Polko et al. 2015</td>
<td>Basil (Ocimum basilicum)</td>
<td>R:B 0.7, 1.1, 1.5, 5.5, 0.5 (Fluorescent Lamp); R:B 0.7, 1.1, 1.5, 5.5, 0.5 (Fluorescent Lamp)</td>
<td>-</td>
<td>↑</td>
<td>-</td>
<td>↑ high nitrate at 0.5; ↑ high nitrate at 1.1</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>↑ (by R:B 1.5 only)</td>
<td>-</td>
</tr>
<tr>
<td>Yan et al. 2019</td>
<td>Lettuce (Lactuca sativa)</td>
<td>R:B 0.9, 1.8, 2.7, 3.6</td>
<td>-</td>
<td>↑ anthocyanins</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>↑ R:B 2.7, followed by 3.6, especially at higher DLI</td>
<td>↑ R:B 2.7, followed by 3.6, especially at higher DLI</td>
<td>-</td>
<td></td>
</tr>
<tr>
<td>Snowden et al. 2016</td>
<td>Radish (Raphanus sativus)</td>
<td>LED mixture</td>
<td>↑ at 500 PPFD</td>
<td>-</td>
<td>↓</td>
<td>↑ at 500 PPFD</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td></td>
<td>Tomato (Solanum lycopersicum)</td>
<td>LED mixture</td>
<td>↑</td>
<td>-</td>
<td>↓</td>
<td>↑ at 200 + 500 PPFD</td>
<td>-</td>
<td>-</td>
<td>-</td>
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<td>-</td>
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<tr>
<td></td>
<td>Cucumber (Cucumis sativus)</td>
<td>LED mixture</td>
<td>↑ at 500 PPFD</td>
<td>-</td>
<td>↑</td>
<td>↑ at 200 + 500 PPFD</td>
<td>-</td>
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<tr>
<td></td>
<td>Pepper (Capsicum annuum)</td>
<td>LED mixture</td>
<td>↑ at 500 PPFD</td>
<td>-</td>
<td>↑</td>
<td>↑ at 500 PPFD</td>
<td>-</td>
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<tr>
<td></td>
<td>Lettuce (Lactuca sativa)</td>
<td>LED mixture</td>
<td>↑ at 500 PPFD</td>
<td>-</td>
<td>↑</td>
<td>↑ at 200 + 500 PPFD</td>
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<tr>
<td></td>
<td>Soybean (Glycine max)</td>
<td>LED mixture</td>
<td>↑ at 500 PPFD</td>
<td>-</td>
<td>↑</td>
<td>↑ at 200 + 500 PPFD</td>
<td>-</td>
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<tr>
<td></td>
<td>Wheat (Triticum aestivum)</td>
<td>LED mixture</td>
<td>↑ at 500 PPFD</td>
<td>-</td>
<td>↑</td>
<td>↑ at 200 + 500 PPFD</td>
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</table>

[] 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).
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 triggered 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 Pr form). Night-breaks of less than a few μmol·m⁻²·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 (Fias and Rajapakse 2005; Kaliarizoglou 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...
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

<table>
<thead>
<tr>
<th>Recipe</th>
<th>Spectra</th>
<th>Effects</th>
</tr>
</thead>
<tbody>
<tr>
<td>Increased UV</td>
<td>![Arrow](&lt;380 nm), blue for 400–500 nm, green for 500–600 nm, red for 600–700 nm, dark red for 700–750 nm</td>
<td>† Secondary metabolites</td>
</tr>
<tr>
<td>Increased Blue</td>
<td>![Arrow](&lt;400 nm), blue for 400–500 nm, green for 500–600 nm, red for 600–700 nm, dark red for 700–750 nm</td>
<td>† Secondary metabolites † Segment content † Colouration † Compadness † Biomass</td>
</tr>
<tr>
<td>Low R:B ratio</td>
<td>![Arrow](&lt;600 nm), blue for 400–500 nm, green for 500–600 nm, red for 600–700 nm, dark red for 700–750 nm</td>
<td>† Biomass ↓ Compadness</td>
</tr>
<tr>
<td>Increased Red</td>
<td>![Arrow](&lt;600 nm), blue for 400–500 nm, green for 500–600 nm, red for 600–700 nm, dark red for 700–750 nm</td>
<td>† Photosynthesis ↓ Flowering time</td>
</tr>
<tr>
<td>High R:B ratio</td>
<td>![Arrow](&lt;700 nm), blue for 400–500 nm, green for 500–600 nm, red for 600–700 nm, dark red for 700–750 nm</td>
<td>† Flowering time</td>
</tr>
<tr>
<td>Addition/increase of FR</td>
<td>![Arrow](&lt;800 nm), blue for 400–500 nm, green for 500–600 nm, red for 600–700 nm, dark red for 700–750 nm</td>
<td>† Photosynthesis ↓ Flowering time</td>
</tr>
<tr>
<td>High R:FR ratio</td>
<td>![Arrow](&lt;900 nm), blue for 400–500 nm, green for 500–600 nm, red for 600–700 nm, dark red for 700–750 nm</td>
<td>↓ Internode/ster length ↓ Petiole length ↓ Leaf length ↓ Hyponasty ↓ Biomass</td>
</tr>
<tr>
<td>Low R:FR ratio</td>
<td>![Arrow](&lt;1000 nm), blue for 400–500 nm, green for 500–600 nm, red for 600–700 nm, dark red for 700–750 nm</td>
<td>↓ Branching ↓ Leaf number ↓ Chlorophyll content ↓ Time to flowering</td>
</tr>
<tr>
<td>Addition/increase of Green</td>
<td>![Arrow](&lt;1200 nm), blue for 400–500 nm, green for 500–600 nm, red for 600–700 nm, dark red for 700–750 nm</td>
<td>↑ Photosynthesis</td>
</tr>
<tr>
<td>Low B:G Ratio</td>
<td>![Arrow](&lt;1400 nm), blue for 400–500 nm, green for 500–600 nm, red for 600–700 nm, dark red for 700–750 nm</td>
<td>↑ Stem length ↑ Petiole length ↑ Leaf length ↑ Hyponasty ↑ Biomass</td>
</tr>
<tr>
<td>Increased Light intensity</td>
<td>![Arrow](&lt;1600 nm), blue for 400–500 nm, green for 500–600 nm, red for 600–700 nm, dark red for 700–750 nm</td>
<td>↑ Growth ↑ Colouration ↑ Secondary metabolites</td>
</tr>
<tr>
<td>End of Day Red (EOD-R)</td>
<td>![Bar](&lt;1800 nm), blue for 400–500 nm, green for 500–600 nm, red for 600–700 nm, dark red for 700–750 nm</td>
<td>↓ Plant height</td>
</tr>
<tr>
<td>End of Day FR (EOD-FR)</td>
<td>![Bar](&lt;2000 nm), blue for 400–500 nm, green for 500–600 nm, red for 600–700 nm, dark red for 700–750 nm</td>
<td>↑ Flowering time</td>
</tr>
<tr>
<td>Night break</td>
<td>![Bar](&lt;2200 nm), blue for 400–500 nm, green for 500–600 nm, red for 600–700 nm, dark red for 700–750 nm</td>
<td>↑ Flowering time</td>
</tr>
</tbody>
</table>

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.
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; Tewolde et al. 2018).

Intracanopy LED lighting also has 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; Tewolde et al. 2018).

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 (Sirkkä 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 μmol·m⁻²·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. 2018).
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. 2020; Frantz et al. 2004; Goto 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; Ngobo 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).

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; Pennisi et al. 2020; Zou et al. 2020). 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; Chou 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). 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

![Figure 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 50% (blue), 75% (green), 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.](image-url)
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; Wanali 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 μmol·m⁻²·s⁻¹ total, or a supplementary light of 350 μmol·m⁻²·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 μmol·m⁻²·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.

**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 costs 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 μmol·m⁻²·s⁻¹ for a 18-h photoperiod with an LED efficacy of 2.5 μmol·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·m⁻² compared with HPS electricity costs of 210 USD·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 trends increasing 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 born 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 (Bayır 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.

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