

# Toward an optimal spectrum for photosynthesis and plant morphology in LED-based crop cultivation

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## 17.1 Introduction

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Photobiologically active radiation refers to photons between 280 and 800 nm (Dörr et al., 2020), as these photons can drive photosynthesis (a process that turns water and CO<sub>2</sub> into oxygen and carbohydrates) and/or excite a suite of photoreceptors that modulate plant development. This biologically active region can be broadly split into six regions: UV-B (280–320 nm), UV-A (320–400 nm), blue (400–500 nm), green (500–600 nm), red (600–700 nm), and far-red (700–800 nm).

Sunlight and conventional electric light sources (e.g., high-pressure sodium and metal halide lamps) provide minimal opportunity to manipulate the light spectrum. Recent developments in high efficiency narrow spectrum light-emitting diodes (LEDs) enable precise control of plant growth and development by creating ‘light recipes.’ In this chapter we discuss general principles of plant spectral responses, focusing on photosynthetic efficiency, plant shape, and secondary metabolite production.

## 17.2 Photosynthesis overview

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Plants evolved under broad spectrum sunlight—the ultimate energy source for all life on the Earth. About half of the photons in solar radiation that reaches the Earth’s surface falls into the biologically active region, with peak output in the range that is visible to the human

eye (approximately 400–700 nm). For photosynthesis, photons must be of sufficient energy for photochemical reactions but must not contain too much energy to cause damage to the photosynthetic apparatus. Coincidentally (but perhaps not surprisingly), photons in the visible region of about 400–700 nm fit this requirement and are known as photosynthetically active radiation (PAR).

Photosynthesis is dependent on the amount of photons plants receive, which is commonly quantified in two ways: (1) the instantaneous photosynthetic photon flux density (PPFD;  $\mu\text{mol m}^{-2} \text{s}^{-1}$ ), and (2) the cumulative number of photons received over a day—called the daily light integral (DLI;  $\text{mol m}^{-2} \text{d}^{-1}$ ). Crop yield shows a strong linear correlation with the total amount of light intercepted by the plant canopy both in the field under sunlight (Gifford et al., 1984; Monteith, 1977) and in indoor agriculture under LEDs (Zhen and Bugbee, 2020a). However, photons of different wavelengths do not drive photosynthesis with equal efficiency (expressed as moles of  $\text{CO}_2$  fixed per mole of photons absorbed). This was known from pioneering studies on photosynthesis under monochromatic light (Emerson and Lewis, 1943; Hoover, 1937). Classic studies by McCree (1971) and Inada (1976) found that red photons are most efficient for photosynthesis, followed by green and blue photons, while photosynthetic efficiency decreases significantly on the edges of the PAR region (Fig. 17.1C). The results from these classic studies should be interpreted with caution because the studies were conducted on single leaves under low light due to technical limitations at the time. More recent studies examine the photosynthetic responses at canopy level under higher light, which we discuss in detail below.

### 17.3 Morphology overview

Plants are sessile organisms that must acclimate to their local growing environment. Among the environmental factors, light plays a central role in their development. Some characteristics of the light environment are more constant such as modifications caused by an overhead canopy, while others fluctuate substantially on a timescale of seconds (e.g., cloud cover or leaf movement in the wind). Additionally, there are seasonal changes in the PPFD and photoperiod (or daylength). Plants possess a suite of photoreceptors (proteins coupled with a photon absorbing chromophore) that are sensitive to specific photons. Plants sense the light signals (i.e., changes in PPFD, spectrum, and photoperiod) via their photoreceptors and modify their development accordingly. These modifications can include a number of key changes over a plant's life cycle, including seed germination, plant shape, phytochemical composition, biomass allocation, flowering, and seed-setting (Kendrick and Kronenberg, 1994).

Under natural environments, changes in light spectral quality primarily occur between full sun versus vegetative shade. Table 17.1 provides some typical values of the spectral composition of sunlight and shade light. Compared to full sunlight, shade light is notably enriched in far-red, which is caused by filtration of most of the photons in the PAR region by the top layers of a plant canopy for photosynthesis. These shifts in spectral ratios are thus accompanied by a significant overall decrease in total photon flux density that can reach 95% or greater (Casal, 2012). Shade conditions can simply be the presence of neighboring plants that reflect a small amount of additional far-red (Ballare et al., 1987). Species tend to respond differently to shade or changes in spectral quality, such as rapid elongation of stems in order

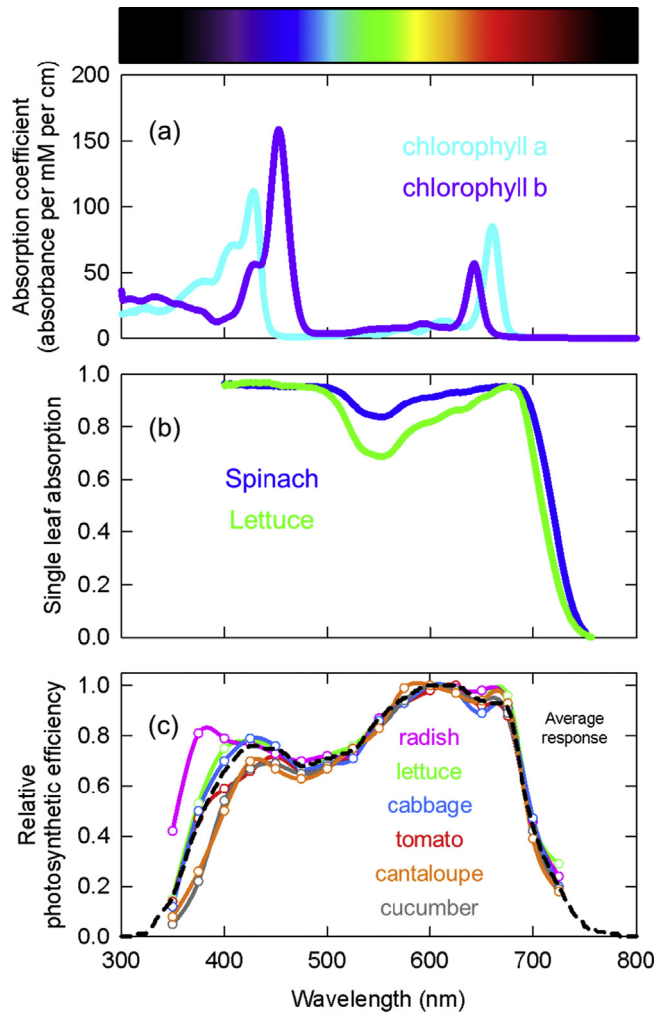


FIGURE 17.1 (A) Absorption coefficients of chlorophylls extracted with diethyl ether, (B) light absorption in leaves, and (C) spectral effect of photosynthesis. Relative photosynthetic efficiency curves of diverse species are redrawn from data by McCree, K.J., 1971. *The action spectrum, absorbance and quantum yield of photosynthesis in crop plants. Agric. Meteorol.* 9, 191–216.

to outgrow neighbors or expansion of leaves (often making the leaves thinner at the same time) to increase light capture (Gommers et al., 2013). The response of a specific species is dependent on the type of environment under which it evolved, for example, forest under-stories or open fields.

For morphological development, these broad categories can be grouped into photons that make plants more compact (UV-B, UV-A, blue, and red) or less compact (green and far-red). These six categories are admittedly crude, as development is actually dependent on photoreceptor absorption (Fig. 17.2). For example, a UV-A photon at 330 nm is unlikely

**TABLE 17.1** Typical spectral composition of the photobiologically active radiation under full sun and canopy shade environments. In addition to the shifts in spectral ratios, both the photosynthetic photon flux density (PPFD) and biological photon flux density (BPFD) decrease substantially under shade. Different photon categories are expressed as a percentage of the total biologically active radiation.

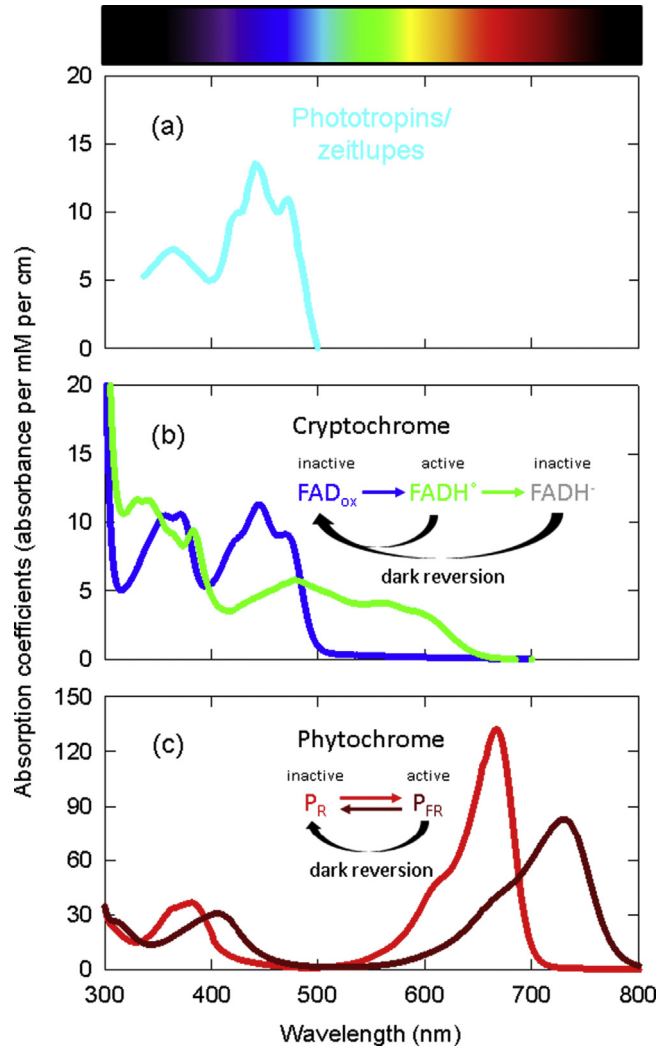
	Full sun	Vegetation shade
UV-B (280–320 nm)	0.2%	0.1%
UV-A (320–400 nm)	5%	3%
Blue (400–500 nm)	19%	6%
Green (500–600 nm)	25%	10%
Red (600–700 nm)	27%	7%
Far-red (700–800 nm)	24%	74%
PPFD (400–700 nm)	2100 ( $\mu\text{mol m}^{-2} \text{s}^{-1}$ )	25 ( $\mu\text{mol m}^{-2} \text{s}^{-1}$ )
BPFD (280–800 nm)	3000 ( $\mu\text{mol m}^{-2} \text{s}^{-1}$ ; 100%)	100 ( $\mu\text{mol m}^{-2} \text{s}^{-1}$ ; 100%)

to have the same effect on plant growth and development as a UV-A photon at 395 nm. Likewise, a far-red photon at 730 nm is expected to have a significantly different effect on development than a far-red photon at 780 nm. Despite this, these coarse categories are still useful as the peak absorbance of different photoreceptors roughly fall into the specified photon categories.

There are three well-studied classes of photoreceptors that modulate development. These are (1) the phytochromes, which have peak absorbance in the red and far-red regions, although they can absorb from 300 to 800 nm; (2) the cryptochromes, which primarily absorb in the UV-A, blue, and green regions; and (3) the phototropins, which primarily absorb in the UV-A and blue regions (Fig. 17.2). Plants also contain other photoreceptors including UV RESISTANCE LOCUS8 (UVR8), which responds to UV-B photons; and zeitlupes, which respond to blue/UV-A photons, but these are less well studied (Folta and Carvalho, 2015; Galvão and Fankhauser, 2015).

## 17.4 General effects of spectrum

For the remainder of this chapter, we discuss the general effects of the six categories of photons (UV-B, UV-A, blue, green, red, and far-red) on the photosynthesis and development of crops. Note that photons below 280 nm (UV-C; 100–280 nm) can be generated with electric lamps, conventionally with high-pressure mercury lamps and now UV-C LEDs have become available. These high-energy ionizing photons have germicidal effects and may be applied in short flashes to stimulate plant resistance to pathogens (Aarouf and Urban, 2020) and to control branching and height of ornamental plants (Bridgen, 2016), but they tend to be highly damaging and can reduce yields (Lee et al., 2014). Their applications in crop cultivation need to be further studied.



**FIGURE 17.2** Absorption coefficients of three major families of photoreceptors that modulate plant development. (A) Phototropins and zeatolupes. (B) Absorption coefficients for the cytochrome chromophore (FAD) in the oxidized ( $\text{FAD}_{\text{ox}}$ ) and neutral radical ( $\text{FADH}^\bullet$ ) states. (C) Absorption coefficients for the  $\text{P}_\text{R}$  and  $\text{P}_{\text{FR}}$  forms of phytochrome. Straight colored arrows indicate photoreceptor activation or deactivation upon photon absorption and curved black arrows indicate dark (meaning light-independent) reversion. Dark reversion rate is dependent on the concentration of oxygen in cryptochrome (Müller and Ahmad, 2011) and on temperature in phytochrome (Klose et al., 2020). (A) Data from Ahmad, M., Grancher, N., Heil, M., Black, R.C., Giovani, B., Galland, P., Lardemer, D., 2002. Action spectrum for cryptochrome-dependent hypocotyl growth inhibition in *Arabidopsis*. *Plant Physiol.* 129 (2), 774–785; Salomon, M., Christie, J.M., Knieb, E., Lempert, U., Briggs, W.R., 2000. Photochemical and mutational analysis of the FMN-binding domains of the plant blue light receptor, phototropin. *Biochemistry* 39 (31), 9401–9410; (B) data were kindly provided by Müller, P., Bouly, J.P., Hitomi, K., Balland, V., Getzoff, E. D., Ritz, T., Brettel, K. (2014). ATP binding turns plant cryptochrome into an efficient natural photoswitch. *Sci. Rep.* 4 (1), 1–11 for more detail; (C) curves redrawn from data by Kelly, J.M., Lagarias, J.C., 1985. Photochemistry of 124-kilodalton *Avena* phytochrome under constant illumination in vitro. *Biochemistry* 24 (21), 6003–6010; Lagarias, J.C., Kelly, J.M., Cyr, K.L., Smith Jr, W.O., 1987. Comparative photochemical analysis of highly purified 124 kilodalton oat and rye phytochromes in vitro. *Photochem. Photobiol.* 46 (1), 5–13.

### 17.4.1 UV-B (280–320 nm)

The classification of UV-B photons begins at 280 nm, as this is the shortest wavelength of photons from the Sun that can penetrate through the Earth's atmosphere. The long wavelength cutoffs for UV-B are either based on studies on sunburn (315 nm) or skin cancer (320 nm) in humans (Kusuma et al., 2020). We use 320 nm since this covers a broader range of photons that are potentially damaging to plants, but perhaps better metrics are needed for plant-based responses. It is important to use UV-B with caution as it creates hazardous conditions to both plants and workers.

#### 17.4.1.1 Photosynthesis

UV-B is generally detrimental to photosynthesis and plant growth as it causes damage to photosynthetic apparatus, primarily photosystem II (Jansen et al., 1998; Tyystjärvi, 2008). Damages to DNA, proteins (including the key photosynthetic enzyme Rubisco) and cell membranes often occur under moderate to high intensity UV-B radiation. Exposure to UV-B can also induce thickening of leaves and cuticle layers, a decrease in chlorophyll content and an increase in UV-B screening pigments, all of which may further affect photosynthesis by altering the leaf optical properties and distribution of PAR within the leaves (Bornman and Vogelmann, 1991).

#### 17.4.1.2 Development

Although UV-B induces damage at high intensities, lower intensity UV-B can act as a beneficial stress (Neugart and Schreiner, 2018), increasing the production of beneficial secondary metabolites including anthocyanins, phenolics, and flavonoids. These compounds act as 'sunscreen,' absorbing the UV radiation primarily in the epidermal layers before it can damage the photosystems. Additionally, these compounds have antioxidant properties, scavenging reactive oxygen species (Jansen et al., 1998). Many of these molecules change the overall pigmentation of the plant and can promote human health, potentially increasing the value of the crop (Schreiner et al., 2012).

Even though UV-B may improve crop quality, its application tends to decrease stem and leaf expansion (Wargent et al., 2009a,b; Yao et al., 2006). Together with the decreases in photosynthesis, these decreases in leaf area (reduced photon capture) can lead to yield reductions. The effects of UV-B on both morphology and secondary metabolite synthesis depend on the background growth light intensities (DLIs), with larger impacts at lower DLIs (Dou et al., 2019; Warner and Caldwell, 1983).

Many of these responses to UV-B are mediated through the UVR8 photoreceptor, which regulates the expression of hundreds of genes (Favory et al., 2009), but some UV-B responses are also mediated by independent mechanisms (Coffey et al., 2017; Wargent et al., 2009a). Measurement of a transcript downstream of UVR8 activation showed that the action spectrum of this photoreceptor drops by about 310 nm (Brown et al., 2009).

Intumescence is a physiological disorder that occurs in certain cultivars of crops (e.g., Maxifort tomato) cultivated in greenhouses and plant factories. It manifests as small blisters on the surface of leaves, and at the microscopic level, these protrusions are caused by cell hypertrophy (Williams et al., 2014). Although the cause for this disorder is not well understood, UV-B has been shown to decrease its severity (Kubota et al., 2017).

Increased cuticle thickness and changes in phytochemical composition in plants grown with UV-B may also increase their resistance to fungal pathogens and diseases (Raviv and Antignus, 2004).

### 17.4.2 UV-A (320–400 nm)

A commonly used violet LED with a peak at about 405 nm and with 10%–50% of its output below 400 nm (depending on operating conditions) has sometimes been marketed as a UV LED (Samuolienė et al., 2020). LEDs with peaks between 365 and 400 nm can be manufactured with higher efficiency than UV-B LEDs, but the efficiency decreases with decreasing peak wavelength. Distinctions between longer and shorter wavelength UV-A photons are important as the effects of UV-A vary considerably with wavelength.

#### 17.4.2.1 Photosynthesis

UV-A photons are of lower energy than UV-B photons and are thus less damaging (Verdaguer et al., 2017). Additionally, the longer wavelength UV-A photons can be absorbed by photosynthetic pigments (chlorophyll and carotenoids) and drive photosynthesis. McCree (1971) found that photosynthetic efficiency of UV-A photons decreased rapidly with decreasing wavelength from 400 to 350 nm (Fig. 17.1C). Although, some species (e.g., radish and sugar beet) were shown to use UV-A photons with relatively high efficiency, and plants grown in growth chambers without prior UV-A exposure generally used UV-A more efficiently than field grown plants (McCree, 1971). Interestingly, Mantha et al. (2001) showed that shorter wavelength UV-A photons (peak around 340 nm) can enhance leaf photosynthesis through fluorescence emission of violet, blue, and green photons, which are absorbed by photosynthetic pigments. This effect is more pronounced under low light situations when photosynthesis is not light saturated.

Plants accumulate UV-absorbing compounds (notably in the upper epidermis) upon UV exposure as a photoprotective mechanism. Therefore, both the photosynthetic efficiency and the potential photoinhibitory effects of UV-A decrease as crops acclimate to UV-A. It is important to note that there is large variation in species sensitivity to UV radiation (Fig. 17.1C). From the standpoint of optimizing photosynthetic efficiency, more studies are needed to better understand whether it is beneficial to include UV-A photons in greenhouses and indoor agriculture.

#### 17.4.2.2 Development

Plant responses to UV-A photons have been less well studied compared to UV-B, and the studies thus far have shown both beneficial and detrimental effects. With the continued development of LED technology, studies in controlled environments are beginning to fill in the gaps in knowledge regarding the responses to UV-A and the underlying mechanisms (Verdaguer et al., 2017).

Under sole-source LED light, leaf area was increased by supplementation with UV-A photons between 365 and 400 nm in both lettuce (Chen et al., 2019) and tomato (Kang et al., 2018; Khoshimkhujiev et al., 2014). By contrast, other studies have shown no effect of UV-A on leaf area in cucumber, soybean, and lettuce (Samuolienė et al., 2020; Yao et al., 2006).



Supplemental UV-A has also been shown to increase stem length in tomato (Kang et al., 2018), decrease stem length in soybean (Yao et al., 2006), and have no effect in cucumber (Jeong et al., 2020; Yao et al., 2006). The effects were similarly inconsistent on fresh and dry mass, either showing increases (Kang et al., 2018; Lee et al., 2014) or no changes (Jeong et al., 2020; Li and Kubota, 2009; Samuolienė et al., 2020). These inconsistencies are not simply explained by species differences because studies on the same species (e.g., lettuce) have provided conflicting results (Chen et al., 2019; Li and Kubota, 2009; Samuolienė et al., 2020). The specific intensity of both PAR and UV-A likely contributed to the differences.

In addition to altering morphology, UV-A has been shown to contribute to secondary metabolite production. Mariz-Ponte et al. (2019) found that UV-A, not UV-B, increased flavonoids and phenolic concentrations in tomato fruits. UV-A also induces secondary metabolite production in lettuce (Lee et al., 2014; Li and Kubota, 2009), with higher doses being more effective (Chen et al., 2019).

Photons from the violet LED (peak at about 405 nm) are at the cusp of photosynthetic activity (Fig. 17.1) and photoinhibition (Takahashi et al., 2010). In one study these photons were shown to have no effect on leaf area and yield when applied supplementally (Samuolienė et al., 2020).

The UVR8 photoreceptor does not appear to induce responses beyond UV-B, instead the cryptochromes are most likely involved in responses to UV-A photons (Wade et al., 2001). The absorbance spectrum for cryptochrome activation (FAD<sub>ox</sub> in Fig. 17.2B, described in further detail below) shows one peak around 350 nm and another peak at about 450 nm, with a valley between 375 and 425 nm, indicating that longer wavelength UV-A photons (~375–400 nm) are likely not as effective in regulating plant development compared to shorter wavelength UV-A and longer wavelength blue photons. The studies discussed in this section generally use supplementation of UV-A photons between 365 and 400 nm. It is possible that adding blue photons (around 450 nm) would have had the same or even greater effect.

### 17.4.3 Blue (400–500 nm)

#### 17.4.3.1 Photosynthesis

Blue photons are most efficiently absorbed by leaves (Fig. 17.1B) and are often thought to be needed for efficient photosynthesis due to their role in inducing stomatal opening. Interestingly, studies on the spectral response of photosynthesis found that blue photons tend to have the lowest photosynthetic efficiency among photons in the PAR region. For example, McCree (1971) reported that the average photosynthetic efficiency of blue photons was 17%–28% lower than red and green photons in diverse species. Similarly, Hogewoning et al. (2012) found that the photosynthetic efficiency of blue photons in cucumber was about 30% lower than red photons. In addition to chlorophylls, blue photons are absorbed by non-photosynthetic pigments (e.g., anthocyanins and flavonoids) as well as photosynthetic carotenoids, which transfer excitation energy to chlorophylls with reduced efficiency (Frank and Cogdell, 1996; Siefermann-Harms, 1985). This largely accounts for the lower photosynthetic efficiency of blue photons.



Compared to red and green photons, absorption of blue photons primarily occurs in the upper cell layers of the leaves at the top of a plant canopy (Vogelmann and Evans, 2002). This nonuniform light distribution within a plant canopy leads to reduced photosynthetic efficiency (Melis, 2009). In addition, high-intensity blue light can induce chloroplast movement to the side walls parallel to the light direction (inducing a 'stacked' orientation), causing a decrease in light absorption, and thus a decrease in photosynthetic rate (Haupt and Scheuerlein, 1990; Kagawa et al., 2001).

It is well known that blue light, often applied as a short pulse, induces fast stomatal opening (Assmann et al., 1985). A recent study found that when varying the fractions of red and blue photons, blue light-induced stomatal opening minimally enhanced steady-state photosynthesis and consistently decreased water use efficiency under medium and high light intensities (Zhen and Bugbee, 2020b). Additional studies are needed to elucidate the role of blue light in photosynthesis, stomatal regulation, and water use of crops grown under electric lights, especially if dynamic lighting strategies (e.g., fluctuating light levels and spectra) are implemented.

#### 17.4.3.2 Development

Blue photons act on three families of photoreceptors to modulate plant development: cryptochromes, phototropins, and zeitlupes. Cryptochromes and zeitlupes control plant development through modulation of gene expression, while phototropins act through association with cell membranes (Galvão and Fankhauser, 2015; Lin, 2000). Responses mediated by phototropins include phototropism, stomatal opening, chloroplast reorientation, and leaf movement (Christie, 2007). Zeitlupes play a role in flowering (Galvão and Fankhauser, 2015). The effects of blue photons on photomorphogenesis and secondary metabolite production (the focus of this section) are primarily controlled by cryptochromes.

Many studies conducted in controlled environments have shown that increasing the fraction of blue photons, especially between 10% and 50%, often causes leaf area and stem length to decrease, thus leading to decreases in yield (Hernández and Kubota, 2016; Kang et al., 2016; Meng et al., 2019, 2020; Snowden et al., 2016; Son and Oh, 2013, 2015; Wang et al., 2016). Less commonly, studies have found no effect on yield from increasing the fraction of blue photons (Li and Kubota, 2009; Snowden et al., 2016).

Because leaf area and yield generally decrease with increasing blue photon fraction, lower fractions of blue photons may be preferred. However, studies show that growing plants in the absence of blue photons often lead to low chlorophyll concentrations and excessive stem elongation (Son and Oh, 2013; Snowden et al., 2016; Yorio et al., 2001). Leaf area and crop yield in the absence of blue photons have been reported to increase in some species (Meng et al., 2020; Son and Oh, 2013; Wang et al., 2016) but decrease in others (Hernández and Kubota, 2016; Snowden et al., 2016; Yorio et al., 2001). Therefore, the decision of whether or not to completely remove blue photons may be species dependent.

One of the key regulators in flavonoid and anthocyanin synthesis is the enzyme chalcone synthase. The expression of this enzyme is partially controlled by cryptochromes (Wade et al., 2001). Thus, blue photons have been shown to increase the production of secondary metabolites including phenolics and flavonoids (Li and Kubota, 2009; Son and Oh, 2013, 2015).

## 17.4.4 Green (500–600 nm)

### 17.4.4.1 Photosynthesis

Green photons are often perceived as less efficient for photosynthesis than red and blue photons, largely due to the minimal absorption of green photons by chlorophylls. This lower absorption/higher reflectance is what gives leaves their green color. However, chlorophyll absorption spectra are quantified with extracted pigments in a solvent. Light absorption of a leaf differs from that of extracted chlorophyll solution because leaf chlorophylls are concentrated in chloroplasts (see Fig. 17.1A compared to Fig. 17.1B). This uneven distribution of chlorophylls within leaf cells flattens the absorption of strongly absorbed red and blue photons while only marginally reducing absorption of weakly absorbed green photons (also known as ‘sieve effect’; see Terashima et al. (2009) for more details). On the other hand, the diffusive nature of plant tissues (light is reflected/scattered at the interfaces of cell walls and intercellular air spaces) increases the light path length inside the leaf and thus increasing the overall absorptance of photons, especially green (Vogelmann, 1993). Zhen and Bugbee (2020c) reported that leaf absorptance of green photons ranged from 77% to 88% for a number of crop species, including lettuce, spinach, and tomato. In comparison, leaf absorptance of those species was around 95% in the blue region and 88%–93% in the red region. Thus, it is a misconception that ‘green leaves do not (efficiently) absorb green photons.’

On the basis of absorbed photons, McCree (1971) found that photosynthetic efficiency of green photons was 20% higher than blue photons and equivalent to red photons. Note that the values were determined from the average response of 22 diverse species grown in growth chambers and the measurements were made at 25 nm intervals under low light conditions. Under high light, strongly absorbed red and blue photons tend to oversaturate upper cell layers of the leaf while ‘starving’ the bottom leaf cells, resulting in reduced leaf photosynthetic efficiency. Because green photons are not as strongly absorbed by chlorophylls, they can penetrate deeper into the leaf (and canopy) (Brodersen and Vogelmann, 2010), driving photosynthesis deep within the leaf (Sun et al., 1998). As a result, green photons may be more efficient for leaf photosynthesis than red and blue photons when added to high light (Liu and van Iersel, 2021; Terashima et al., 2009).

At canopy level, the difference in light absorption between green and red (and blue) photons is expected to be smaller than the differences within a leaf (Paradiso et al., 2011). Furthermore, the more uniform light distribution within the canopy under green photons likely lead to higher canopy photosynthetic efficiency. Measurements of photosynthetic efficiency at canopy level will help to further elucidate the value of green photons for photosynthesis and crop productivity.

### 17.4.4.2 Development

The past two decades of photobiological studies have revealed a potential role of green photons in morphogenesis. The flavin adenine dinucleotide (FAD) chromophore embedded in cryptochrome has three states:  $\text{FAD}_{\text{ox}}$ , the oxidized state;  $\text{FADH}$ , the semireduced neutral radical state; and  $\text{FADH}^-$ , the fully reduced state. Of these three states,  $\text{FADH}$  is the active form, while  $\text{FAD}_{\text{ox}}$  and  $\text{FADH}^-$  are both inactive (Ahmad, 2016).  $\text{FAD}_{\text{ox}}$  absorbs most prominently in the blue region, converting it into active  $\text{FADH}$  (Fig. 17.2B). As the active form,  $\text{FADH}$  inhibits stem expansion. The absorption spectrum of  $\text{FADH}$  shows a high absorbance

of green photons, which lead to the inactivation of cryptochrome (to  $\text{FADH}^-$ ). Thus, green photons have been suggested to induce shade avoidance responses by reversing blue photon-induced decreases in plant size. A decrease in B:G ratio tends to occur in canopy shade (Smith et al., 2017). Shade avoidance in response to green has been supported mainly by studies in *Arabidopsis thaliana* (Bouly et al., 2007; Zhang et al., 2011).

Because green photons may reverse the effects of blue photons, it may be expected that increasing the fractions of green photons (while the blue fraction remains constant) will increase leaf area. This effect was observed in an early study that investigated responses of lettuce to green photons (Kim et al., 2004), but subsequent studies in horticultural species have shown minimal responses to green photons (Hernández and Kubota, 2016; Kang et al., 2016; Snowden et al., 2016; Son and Oh, 2015), and in some cases, plant diameter/leaf area actually decrease (Meng et al., 2020; Snowden et al., 2016). Overall, increasing the fraction of green photons has been observed to minimally affect leaf area and stem/petiole elongation in horticultural species.

Green photons have been observed to reverse blue photon-induced anthocyanin accumulation (Meng et al., 2019; Zhang and Folta, 2012), but this effect is not consistent (Meng et al., 2020).

## 17.4.5 Red (600–700 nm)

### 17.4.5.1 Photosynthesis

Red photons are efficiently absorbed by chlorophylls and are among the most efficient for photosynthesis, especially under low to medium light intensities. Additionally, red LEDs typically have higher photon efficacy (moles of photon output per joule of input energy, see Chapter 7) compared to blue and green LEDs, which contributes to their prevalence in plant factories. However, red photons become less efficient for leaf (and likely canopy) photosynthesis than green photons under high light intensities (Terashima et al., 2009; also see discussion in Section 17.4.4.1 on green photons). Unlike green photons, red photons are primarily absorbed by the top layer of leaves in a canopy, thus exposing them to often excessive light levels. Photosynthetic efficiency decreases with increasing PPFD as plants dissipate an increasing fraction of the absorbed light as heat—a photoprotective mechanism against potential oxidative damages under high light (Ruban, 2015).

Furthermore, although including a high fraction of red photons in grow lights can result in energy savings, the cost of red LEDs (i.e., initial capital investment) is relatively high. White LEDs are fairly efficient and less expensive as they are widely used for human lighting. Kusuma et al. (2020) suggested that a white LED enriched with red photons may be best suited for plant factories considering the photon efficacy and luminaire cost. Broad spectrum white light is gaining popularity over a combination of blue + red light for horticulture lighting as it is easier to diagnose pests, diseases, nutritional disorders under white light; it also creates a more pleasant light environment for workers. The green photons emitted by white LEDs may also improve photosynthetic efficiency at canopy level.

### 17.4.5.2 Development

Red photons act on the photoreceptor phytochrome to modulate plant development. The effect of red photons is often discussed in tandem with far-red, either through the R:FR ratio,



**FIGURE 17.3** Photobleaching of medical cannabis inflorescence under a high fraction of red photons (approximately 75% or greater). *Photo courtesy of Mitchell Westmoreland.*

or phytochrome photoequilibrium, which is an estimated ratio of active phytochrome ( $P_{FR}$ ) to total phytochrome ( $P_R + P_{FR}$ ). Issues with these common metrics were recently reviewed in [Kusuma and Bugbee \(2021\)](#).

Absorbance of red photons by  $P_R$  (the inactive form of phytochrome) converts it into the active  $P_{FR}$  form. This active form then goes on to modulate plant development via regulation of gene expression.  $P_{FR}$  inhibits the expression of genes related to cell wall expansion and the hormones auxin, gibberellin, and brassinosteroids ([de Lucas and Prat, 2014](#)). Therefore, red photons tend to decrease cell expansion in leaves and stems.

It has been observed that photobleaching may occur under a high fraction of red photons ([Fig. 17.3](#)). The exact cause of this phenomenon is unknown, as longer wavelength photons do not typically induce photobleaching ([Takahashi et al., 2010](#)). Due to the widespread use of 660 nm red LEDs in horticulture, research should focus on the mechanism causing this effect in order to identify potential remedies.

#### 17.4.6 Far-red (700–800 nm)

##### 17.4.6.1 Photosynthesis

The spectral response of photosynthesis is traditionally quantified under monochromatic light. Far-red photons have long been considered inactive for photosynthesis due to their low photosynthetic efficiency when applied alone ([Emerson and Lewis, 1943](#); [McCree, 1971](#)). However, spectral responses determined under monochromatic lights do not account for synergistic action among photons of different wavelengths. Synergism among wavelengths on photosynthesis was first discovered by [Emerson et al. \(1957\)](#), who found that the photosynthetic rate under simultaneous illumination of photons above 680 nm and

shorter wavelength light was greater than the sum of the rates from applying each light separately—a phenomenon now known as the Emerson Enhancement Effect. This finding contributed to the identification of two photosystems in photosynthesis, both of which are required to be stimulated in order for photosynthesis to operate (Duysens and Ames, 1962; Hill and Bendall, 1960; Myers, 1971). In fact, to achieve optimal photosynthetic efficiency, the two photosystems need to operate at matching rates. The significance of wavelength synergy in photosynthetic efficiency has received little attention until recently with the current definition of PAR (400–700 nm) excluding far-red photons.

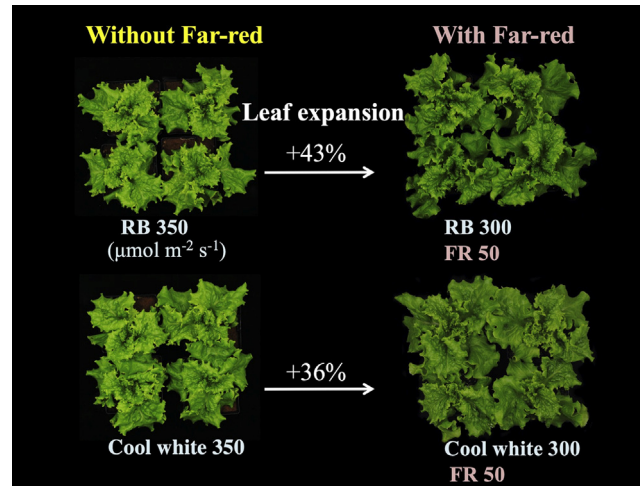
Several recent studies using narrow spectra LEDs have shown that far-red photons added to shorter wavelength photons (e.g., red and blue) synergistically increase leaf photochemical efficiency (Zhen and van Iersel, 2017) and photosynthetic rate (Hogewoning et al., 2012; Murakami et al., 2018). This is because shorter wavelength photons from 400 to 680 nm tend to overexcite one of the photosystems (PSII), while longer wavelength far-red photons preferentially excite the other photosystem (PSI) (Evans, 1987; Laisk et al., 2014; Zhen et al., 2019). Combining far-red with shorter wavelength photons helps restore the balance of excitation between the two photosystems, leading to synergistic enhancement of photosynthetic efficiency (Zhen and van Iersel, 2017). Furthermore, both short- and long-term studies of canopy photosynthesis indicated that far-red photons (700–750 nm) are equally efficient for photosynthesis at canopy level when up to ~40% of those photons were applied with 400–700 nm photons (Zhen and Bugbee, 2020a, 2020c). These recent findings warrant reconsideration of the photosynthetic value of far-red photons and argue for a new definition of PAR that extends to 750 nm (Zhen et al., 2021).

Because far-red photons are of lower energy, they can achieve a high photon efficacy (Kusuma et al., 2020, Chapter 7). As far as photosynthetic efficiency is concerned, it is cost-effective to include far-red photons in the grow light in plant factories.

#### 17.4.6.2 Development

Plants are highly sensitive to far-red photons. As discussed in Section 17.4.5.2 on red photons, far-red interacts with plant development through the photoreceptor phytochrome. While phytochrome activation ( $P_R$  to  $P_{FR}$ ) is most sensitive to red photons, phytochrome inactivation ( $P_{FR}$  to  $P_R$ ) is most sensitive to far-red (Fig. 17.2C). When phytochrome is inactivated, the inhibition of gene expression related to cell wall expansion and hormone synthesis is lifted (de Lucas and Prat, 2014; Legris et al., 2019). This leads to more leaf expansion and/or stem elongation depending on the species.

Supplementation with far-red in sole-source lighting has been shown to increase fresh and dry mass of lettuce in tandem with an increase in leaf area (Lee et al., 2016; Meng and Runkle, 2019), and these responses tend to be more pronounced at higher fractions of far-red. However, due to the increase in photosynthesis from far-red, it is difficult to separate the effect on leaf expansion (thus more photon capture) from that on photosynthesis. Other studies that substitute far-red rather than supplement far-red still show an increase in leaf expansion and dry mass (Fig. 17.4; Zhen and Bugbee, 2020a). In contrast, ornamental species geranium and snapdragon were shown to increase leaf area with far-red substitution but without an increase in dry mass (Park and Runkle, 2017). Although lettuce has been shown to increase leaf area in response to far-red, a decrease in leaf area is often reported in shade-avoiding species (Casal, 2012). In species that are adapted to



**FIGURE 17.4** Lettuce ‘Waldmann’s Dark Green’ grown under blue + red (top left) or cool white LEDs (bottom left). When replacing 15% of the red/blue or white photons with far-red photons (total photon flux remained constant), leaf expansion of lettuce significantly increased without any reductions in canopy photosynthetic efficiency. The increased radiation capture with far-red led to higher yield. *For more details see Zhen, S., Bugbee, B., 2020a. Substituting far-red for traditionally defined photosynthetic photons results in equal canopy quantum yield for CO<sub>2</sub> fixation and increased photon capture during long-term studies: implications for re-defining PAR. Front. Plant Sci. 11, 1433.*

high light like tomato and cucumber, far-red tends to increase stem and/or petiole elongation (Kalaitzoglou et al., 2019; Meng et al., 2019; Park and Runkle, 2017). This may not be desirable in plant factories.

Plant responses to far-red also interact with the background PPFD and temperature. The reversion of active P<sub>FR</sub> back to inactive form of P<sub>R</sub> can occur independent of light in a temperature-dependent manner, with faster reversion rate at higher temperature. This is known as thermal reversion of phytochromes, and the effect is more pronounced under lower PPFDs (Sellaro et al., 2019). This effect means that plant responses to far-red (elongation) are expected to be more pronounced at both higher temperatures and lower PPFD.

In addition to these effects on morphology, one recent study found that supplemental far-red increased fruit yield of tomatoes, possibly through increased fruit sink strength and dry mass partitioning to the fruits (Ji et al., 2020).

Far-red can be applied near the end-of-day to mimic the relative increase in far-red under natural conditions (Kasperbauer, 1971). These end-of-day far-red treatments are still used to this day as an energy-saving method to alter development in greenhouse and indoor crop production, but it tends to be less effective than far-red applied over the entire photoperiod (Kalaitzoglou et al., 2019; Morgan and Smith, 1978).

Far-red supplementation was reported to decrease anthocyanins and/or carotenoids (with no effect on phenolics) in lettuce (Li and Kubota, 2009; Zou et al., 2019) and also caused carotenoid concentration to decrease in tomato (Kalaitzoglou et al., 2019). By contrast, Lee et al. (2016) saw an increase in the concentration of phenolics with increasing far-red.



## 17.5 Concluding remarks

LED-based crop production enables precise control of the light environment (intensity, spectrum, and photoperiod) to optimize growth, modulate plant morphology and beneficial secondary metabolites synthesis. With an increasing number of high efficiency LEDs of distinct spectral peaks becoming available, there is a need for more research-based information on creating light ‘recipes’ for various crops that have different desirable traits and are harvested for roots, leaves, flowers, fruits, and/or secondary metabolites. In terms of optimal spectrum for photosynthesis, most of the data thus far are collected using monochromatic lights on single leaves under low light. More recent studies show that the responses differ at canopy level and under different light intensities and spectral combinations (synergistic responses). Importantly, photosynthetic responses also interact with morphological and physiological changes mediated by an array of photoreceptors during long-term crop cultivation. Spectral effects on plant development vary significantly among species, spectral peaks, intensity, duration, and timing of application. Additionally, the spectral responses interact with other environmental factors such as temperature, water, and nutrient availability. Lastly, the photon efficacy of the LED luminaire should be considered as it plays a large role in determining the cost of lighting. Continued research efforts in both academia and private sectors are necessary toward the development of optimal spectra for crop production in plant factories.

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