



FAQ QUESTION #7

How does the spectrum of my light source affect the growth of my plants?

The spectrum of your light source is the light quality, which is the proportion of different wavelengths or colors. To quantify light for plant growth, rather than use energy fluxes or lux, we use photon flux density (PFD). Photosynthetic PFD (PPFD, 400-700nm) is most often used to quantify total light intensity (McCree 1972, Poorter et al 2012, Sager & McFarlane 1997, Figure 1). Spectrometers or spectroradiometers measure the spectrum or light quality (PFD at each wavelength), with their range often extending into the ultraviolet (< 400 nm) and far-red (> 700 nm) regions beyond PAR (Photosynthetically Active Radiation), in addition to also measuring total PPFD. For a fixed spectrum light source, the PFD proportions and ratios of different wavelengths (eg. %Blue, Red to Far-Red ratio (R:FR)) will not change with intensity. The light quality of your lighting system can affect the growth and development of your plants, termed light quality effects. Light quality and intensity can interact to affect plant growth. The proportions of different wavelengths relate to their respective intensity (PFD). For example, take two fixtures with equivalent PPFD output. One has 15% Blue and the other has 30% Blue. The PFD of Blue will be twice as

much in the 30% Blue fixture compared to the 15% Blue fixture. Photon flux density is sometimes called irradiance or quantum flux in the literature.

A) Ultraviolet Radiation (UV) (100-399nm)

Most of the incident ultraviolet radiation (UV) reaching plants growing outside is UV-A (315-399nm), a small amount of UV-B (280-315nm), with almost no detectable UV-C (100-280nm)(NASA 2001). UV photons below 400nm have a limited capacity to drive photosynthesis (McCree 1972), but they can affect plant growth and development from their high energy and photoreceptor effects. Similar to humans, plants are damaged/stressed by UV, especially at shorter wavelengths and higher intensity (PFD) (Roerber et al 2021). UV causes plants to upregulate antioxidants and vitamins to manage oxidative stress from high energy photons. UV-A photons activate cryptochrome and phototropin photoreceptors (Ahmad et al 2002, Briggs & Christie 2002, Christie 2007, Fraser et al 2017, Li & Kubota 2009). UV-B has its own photoreceptor (UVR8) which has an action peak of 300nm, causing hormonal changes to growth and development (Ballaré 2014, Díaz-Ramos et al 2018, Robson et al 2015, Roerber et al 2021). One effect of UV-B is to trigger plant's innate defense systems against pathogens and insect pests (Ballaré 2014, Ballaré et al 2012). UV can also affect morphology, generally causing plants to be more compact with smaller leaves, antagonizing the stem lengthening (shade-avoidance) effects of far-red (Fraser et al 2017, Robson et al 2015). If your plant growth goals are to relate pathogen tolerance experiments in growth chambers to the field, or require a more "outside like" morphology, consider including UV in your growth chamber.

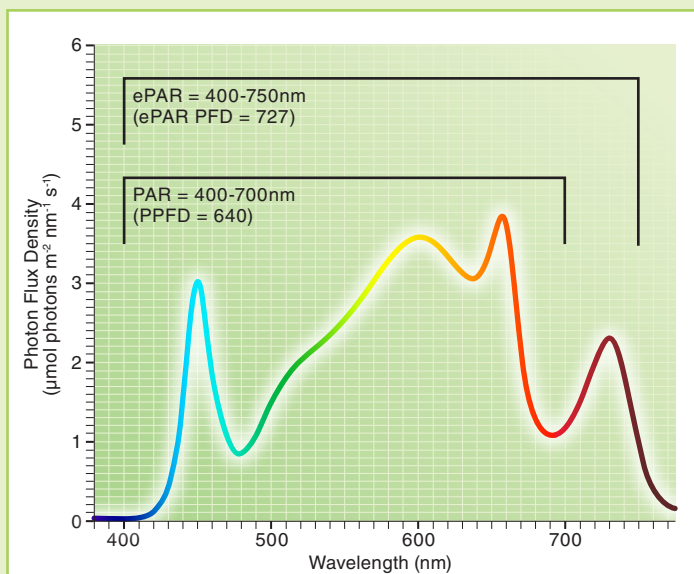


FIGURE 1: Spectrum of BioChamber's standard LED option. Spectrum is an average of 14 measurements taken in two FXC-10s and two FXC-19s in multi-tier modes, at shelf height (45 to 84cm from lights), at 20°C. Photosynthetic Photon Flux Density (PPFD) is the sum of PFD from 400-700nm (PAR). Extended PAR (ePAR) is the sum of PFD from 400-750nm.

Because UV PFD (and its hazards) increases dramatically moving closer to a given light fixture, a safety kill switch for UV fixtures is often required when the chamber door opens for user safety. Similarly, because the PFD of UV changes dramatically with distance from its fixture (similarly to PPFD and far-red PFD), careful monitoring of UV PFD at leaf level may be required as plants grow taller to ensure consistent UV PFD and/or proportion of UV. The desired effect/treatment may not be evident when UV PFD is too

low, whereas too high UV PFD may cause undesirable/artificial stress effects. Finally, UV can help manage pathogens and pests through direct stress and disinfecting effects. In this way UV-B exposure on plant surfaces manages pathogens and pests two-fold through direct stress effects and by upregulating plant's innate immune response (Huché-Théliér et al 2016, Neugart & Schreiner 2018, Wargent 2016). UV radiation can also effectively treat recycled irrigation and fertigation water (Sutton et al 2000). As for plant stress effects, the UV PFD reaching the growth area or plant surface, duration of exposure, innate pathogen UV tolerance, and UV peak wavelengths all factor into how effectively a treatment disinfects (Latorre et al 2012).

B) Violet/Blue/Cyan (400-500nm)

Some violet/blue/cyan light (hereafter blue) is essential for "normal" plant growth of most plant species, and NASA, who were among the first to grow plants under LEDs, realized this back in the 1990s, seeing a growth stimulus and more normal morphology when blue was added to red (Goins et al 1997, Yorio et al 1998). Blue light drives photosynthesis and contains the lowest wavelengths of the traditional definition of PAR (400-700nm), the wavelength range used to measure light intensity for plant growth (PPFD). Blue light drives plant growth in two ways; first chlorophylls strongly absorb blue light to energize photosynthesis, and second, a small amount of blue light induced stomatal opening stimulates net CO₂ assimilation (Matthews et al 2020, Zhen and Bugbee 2020b). Blue light activates photoreceptors (cryptochromes and phototropins) which help open stomata, direct growth towards light, guide stem and leaf growth, entrain the circadian system, and promote flowering in some short day plants (Devlin & Kay 1999, Jähne et al 2020, Runkle 2017). Blue and UV light also helps prevent intumescence in growth chamber grown plants, which are abnormal swollen growths on leaves and stems (Kubota et al 2017, Runkle 2017).

Although some blue light is considered essential by most users, at some point an increasing proportion and/or PFD of blue can cause noticeable morphological effects, largely the result of cryptochrome action. Cryptochrome mediated morphological effects can make plants more compact, reducing leaf area, stem elongation, and ultimately radiation capture. However, enhanced photosynthetic investment (increased leaf N and Rubisco), leaf anatomical efficiency, and performance (CO₂ assimilation and growth) from including some blue or a higher blue fraction often (though not always) negates any effect on overall growth and biomass (Britz & Sager 1990, Cammarisano et al 2021, Cope & Bugbee 2013, Cope et al 2014, Graham et al 2019, Hogewoning et al 2010, Mickens et al 2019, Ohashi-Kaneko et al 2006, Snowden et al 2016, Wang et al 2016, Westmoreland et al 2021, Ying et al 2020, Zheng & Van Labeke 2017). Red light works synergistically with blue light to inhibit hypocotyl, stem, and internode elongation. The pattern of increasing compactness with %Blue holds until 100% Blue where hypocotyls and internodes lengthen again, due to an absence of

red (Casal & Mazzella 1998, Hernández & Kubota 2016, Kong et al 2018, Kong et al 2019, Kong & Zheng 2020, Kong et al 2020, Sellaro et al 2009).

Higher energy wavelengths from UV-B to blue (280-500nm) preferentially cause oxidative stress compared to the rest of PAR (500-700nm), potentially photoinhibiting or photodamaging the light harvesting complex of photosynthesis, which can reduce the rate of photosynthesis and growth (Oguchi et al 2021, Takahashi et al 2010). Prior exposure to UV/blue is critical to acclimate both to these wavelengths and to higher PFD in general (Brelford et al 2019, Pattison et al 2018, Roeber et al 2021). The darker green leaves, increased production of anthocyanins (red/purple/blue coloration), vitamins, and other anti-oxidants commonly associated with growth under UV/blue light allow plants to cope with these high energy photons and are part of the acclimation response (Chen et al 2006, Giliberto et al 2005, Li & Kubota 2009, Meng & Runkle 2019a, Son & Oh 2013). Not surprisingly, both the cryptochromes and UVR8 photoreceptors are intimately involved with many of these acclimatory processes (Brelford et al 2019, Roeber et al 2021). Prior exposure to UV/blue light is something to consider when moving plants from one growth area to another. Horticulturists and greenhouse growers gradually transition plants started in growth chambers or greenhouses outside into direct sunlight. A plant's innate ability to respond and acclimate to increasing UV/blue PFD and overall PFD will depend on its evolutionary and breeding history and other environmental growth conditions, namely temperature. High and low stressful temperatures exacerbate oxidative damage and can impair a plant's ability to acclimate to UV/blue photons, especially stressful chilling temperatures (Lambers & Oliveira 2019b, Lambers & Oliveira 2019c).

Blue light morphological effects are highly species specific and can be sensitive to either the PFD or proportion of blue (%Blue). For some species blue PFD is a better predictor of blue light morphological effects whereas for others the proportion (%Blue) is a better predictor. Blue light morphological effects can become evident at >20% Blue and the compactness effects are generally more pronounced at lower overall PFD (Cope & Bugbee 2013, Cope et al 2014, Hernández & Kubota 2016, Snowden et al 2016). Whether more or less blue light morphological effects are desirable depends on your plant growth goals.

C) Green/Yellow/Amber (501-600nm)

Green light (501-565nm) is used for photosynthesis and growth but is absorbed about 15-20% less than other wavelengths within PAR for single leaves (Liu & van Iersel 2021). Because of its increased transmission and reflectance, green light penetrates deeper into plant canopies and can help drive photosynthesis in lower leaves, especially at higher green PFD and overall PFD (Liu & van Iersel 2021, Massa et al 2015). At lower overall PFD green light can also partially inactivate and decrease the activity of cryptochromes (UV/

blue light). In this way green light induces shade avoidance effects of lengthening stems, internodes, and petioles, similar to far-red (Folta 2004, Kusuma et al 2021, Meng et al 2019, Sellaro et al 2010, Wang & Folta 2013, Zhang et al 2011). Green light also has distinct circadian effects (Battle & Jones 2020), and can delay flowering in some short day plants when applied as day extension lighting (Meng & Runkle 2019b). As wavelengths move closer to 600nm, leaf absorption of yellow/amber light (565-600nm) becomes greater than green and closer to other regions within PAR (Liu & van Iersel 2021), and begins to trigger phytochrome photoreceptors similarly to red. Finally yellow/amber light has some potentially unique effects at 595nm that are a current area of research (Yavari & Lefsrud 2019).

D) Orange/Red (601-700nm)

Orange/red (hereafter red) light drives photosynthesis most efficiently and chlorophylls strongly absorb red light (McCree 1972). Because of this photosynthetic efficiency and initial LED availability, the first plant growth experiments with LEDs used only red (Morrow 2008). We now know that a broader spectrum that includes violet to red (and often far-red) is desirable for most plant growth goals across a wide range of plant species. Red light triggers phytochrome photoreceptors, and a high proportion of red (%Red) and/or high red to far-red ratio (R:FR) generally promotes investment into leaves and roots over stem growth (Holmes & Smith 1975, Keiller & Smith 1989, Maliakal et al 1999). Together with UV/blue, red acts to shorten stems, internodes, and petioles, whereas in the absence of sufficient UV/blue, a red enriched spectrum can result in longer stems compared to a spectrum balanced with appreciable UV/blue (Casal & Mazzella 1998). In contrast to 100%Blue, 100%Red light results in compact plants. A high proportion of red and little far-red can keep long-day plants in a vegetative state for longer and delay flowering compared to light sources with more far-red and/or a lower proportion of red (Runkle & Heins 2001).

E) Far-Red (701-750nm)

Far-red (701-750nm) photons drive photosynthesis when added to PAR (400-700nm), but do little on their own (McCree 1972, Zhen & Bugbee 2020a, Zhen & van Iersel 2017). Adding far-red while maintaining a R:FR \geq 1.2, even while maintaining total PFD (400-750nm) the same, can also stimulate leaf expansion in some species (Park & Runkle 2017, Zhen & Bugbee 2020c). Through the effects of phytochrome photoreceptors, including appreciable far-red in your lighting will almost invariably elongate the stems of most species (Demotes-Mainard et al 2016, Morgan et al 1980, Park & Runkle 2017). In long-day plants, including appreciable far-red will invariably shorten the time to flower compared to growth under the same light source without far-red (Demotes-Mainard et al 2016, Runkle & Heins 2001). This far-red stimulation of flowering has also been reported for some short-day and day-neutral plants as well (Craig & Runkle 2013, Izawa et al 2000, Reid et al 1967,

Schwend et al 2015). While adding some far-red may stimulate growth and promote timely flowering, at some point additional far-red may cause tall spindly plants with reduced leaf investment that flower pre-maturely, reducing overall growth and biomass (Holmes & Smith 1975, Keiller & Smith 1989, Maliakal et al 1999). This effect is called the shade avoidance syndrome and is most pronounced in obligate sun plants (shade avoiders) at lower overall PPFD (Franklin 2008, Hersch et al 2014, Hitz et al 2019).

Including far-red in your electric light source will create a light environment somewhere on the continuum from subtle phytochrome effects to a pronounced shade-avoidance response. Historically, the Red to Far-Red ratio (R:FR), the phytochrome PhotoStationary State (PSS), and/or the %Far-Red (%FR) have all been used to predict the extent of phytochrome effects and shade avoidance (Sager et al 1988, Smith 1982). A R:FR \geq 1.2 (direct sunlight) may be considered a safe ratio for not inducing the shade avoidance response in most species. However some species, like the model plant *Arabidopsis*, can show a pronounced shade avoidance response at a R:FR of 1 when grown at 150 PPFD (Franklin & Whitelam 2005, Friesen 2020, Lambers & Oliveira 2019a, Park & Runkle 2017, Smith 2000). The far-red fraction is a newer parameter that may be a more universal indicator of the intensity of phytochrome effects across plant species and electric light sources (Kusuma & Bugbee 2021). When added to PAR (400-700nm), far-red (701-750nm) photons act equivalently to PAR photons to drive photosynthesis when included up to around 30% (of 400-750nm) in several crop species. Currently extended PAR (ePAR, sum of photons from 400-750nm) has been proposed as another light intensity measurement to report alongside PAR (DLC, 2021, Zhen & Bugbee 2020c, Zhen et al 2021, Figure 1). Because of far-red's ubiquitous effects on growth, morphology, and flowering time, we offer far-red on the majority of our equipment. For our standard LED lighting option, far-red is independently dimmable, allowing you to optimize the amount and proportion of far-red for your plant growth goals.

Questions to ask yourself when deciding whether to include or adjust the far-red PFD (% intensity) with our standard LED lighting option:

- Do I want to stimulate photosynthesis and overall growth, leaf expansion, and elongation of stems, internodes, and petioles?
- Do I want to achieve a spectrum closer to sunlight?
- If I'm working with flowering time in a long-day or other phytochrome sensitive photoperiodic plant, do I want to shorten the time to flowering, or have some control over when plants flower?

For a more detailed discussion of how far-red affects plant growth, and how to adjust the amount and proportion of far-red inside your growth chamber, please read: How far-red photons affect plant growth and development: a guide to optimize the amount and proportion of far-red under sole-source electric lights. (Friesen 2020, https://www.biochambers.com/pdfs/far_red.pdf)

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