

**A REVIEW ON THE EFFECT OF SUPPLEMENTAL LIGHTING ON CROP
PRODUCTIVITY AND NUTRITIONAL QUALITY**

By

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Abstract

Recent developments in LED (light-emitting diode) technology have increased the viability of growing crops under artificial lighting with high efficiency. As LED lighting becomes more widely used, it is imperative to understand how LEDs affect plant development. This thesis presents a comprehensive literature review to evaluate the use of supplemental LED lighting of different light quality (different colors, i.e., different wavelengths of light) for controlled-environment agriculture (CEA). In-depth background is provided on the plant physiology underlying the effect of different wavelengths of light on plant growth and phytochemical (plant chemical) content, with an emphasis on various plant compounds with antioxidant effects and other health benefits for the human consumer. The input of plant photoreceptors (that absorb different wavelengths of light) into plant signaling networks is examined and how this effect of growth light quality is integrated with other aspects of the growth environment, such as light intensity, duration [photoperiod] of daily light exposure, nutrient level, CO₂ level, to orchestrate plant growth, development, and reproduction. The ratio of red to far-red light is used as an example to illustrate how the plant uses external input as information – in this case whether the growth environment supplies ample light (high red to far-red ratio) or limiting light (low red to far-red ratio due, e.g., to absorption of red light by upper layers of leaves in a canopy). These responses are, furthermore, linked to plant nutritional quality via resulting production of either high or low levels of compounds (antioxidants) needed in a high light environment. Corresponding analyses are done for green light (considering different wavelengths of green light with differential effects) and blue light. These results are placed into the context of central signaling networks that sense plant source/sink balance (balance between sugar source [mature leaves] and all sugar-consuming sink tissues of the plant), carbon/nitrogen

balance, and redox balance (balance between oxidants and antioxidants). In doing so, this literature synthesis places information on LED lighting for CEA into a mechanistic context of how plant productivity and nutritional quality varies in response to all aspects of the growth environment.

Introduction

In recent years, controlled environment agriculture (CEA) has become an increasingly popular farming technology, particularly in production of leafy greens, microgreens, and fruits (Lensing 2018). By growing plants indoors in controlled conditions, farmers aim to protect these crops from inclement weather and provide optimal growth conditions during cultivation (Lensing 2018). With large investments being made in CEA, such as USA-based AeroFarms that received a \$500 million evaluation in 2019 (Terazono and Fortado 2019), CEA appears to be the future of farming technology in certain contexts. Greenhouse-grown produce has long been a way for farmers to extend growing seasons, reduce transportation costs, and mitigate pesticide use (Tukker and Jansen 2006). However, until recently, supplemental light in greenhouses has been cost-prohibitive (Lensing 2018). This review integrates an evaluation of the engineering of novel lighting systems with mechanistic background on how plant productivity and nutritional quality is tied to the growth environment, with an emphasis on the light environment.

A New Generation of LEDs

As stated above, supplemental light in greenhouses was cost-prohibitive until recently (Lensing 2018). This was due to the inefficiency of available lighting systems, such as the

commonly used high-pressure sodium (HPS) lamp (Katzin et al. 2021). HPS lamps function through the arcing electricity through a sodium and mercury medium (Fig. 1) These systems have an average efficiency of $1.7\text{-}1.85 \mu\text{mol J}^{-1}$ (i.e 1.7 to 1.85 μmol of photons of photosynthetically active radiation, PAR, between 400-700 nm emitted per Joule of energy input; Katzin et al. 2021). This is a relatively low efficiency, which results from the substantial loss of energy as heat in HPS lamps (Nelson and Bugbee 2014).

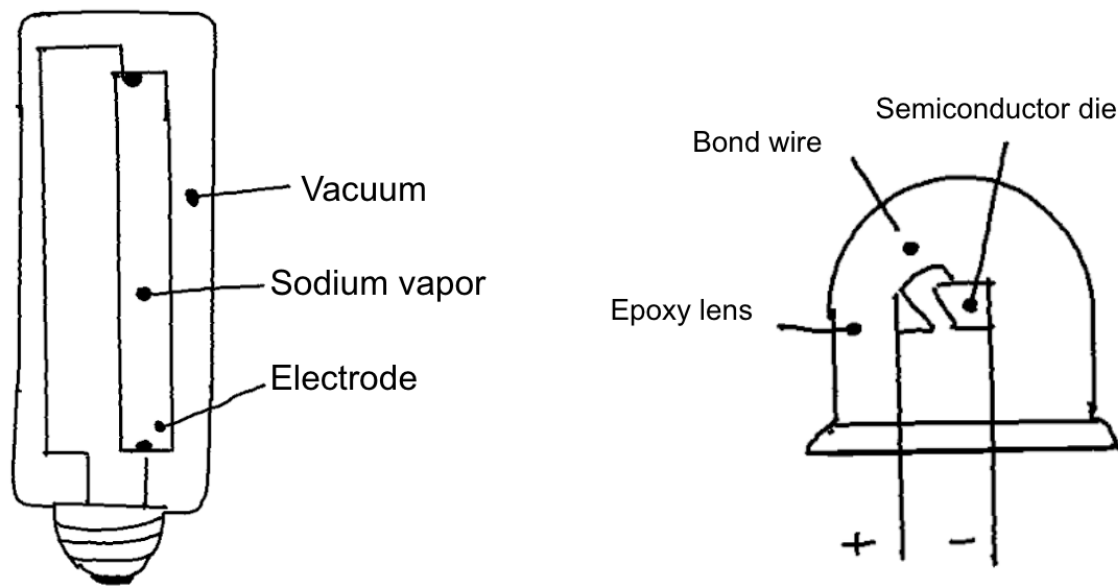


Figure 1: A comparison of the construction of High-Pressure Sodium (HPS) lightbulbs and Light Emitting Diodes (LEDs). HPS lamps have an average efficiency of $1.7\text{-}1.85 \mu\text{mol J}^{-1}$ of PAR while LEDs have an average efficiency of $3 \mu\text{mol J}^{-1}$ (Katzin et al. 2021, Kusuma et al. 2020).

Recent advances in LED technology have provided unique semiconductor diodes that are the first artificial lights capable of producing the full PAR spectrum (Olle and Viršile 2013). LEDs function by the activation of the semiconductor diode when current is applied which produces light (Fig. 1). LEDs are also more energy efficient, producing $3 \mu\text{mol J}^{-1}$, which represents a 40% saving in energy cost compared to HPS lighting (Kusuma et al. 2020). However, in practice LEDs save no more than 13% to 27% when compared to HPS after factoring in the increased

heating necessary to maintain optimal greenhouse temperature for plant cultivation with cool LEDs, which can be a substantial cost at high latitude with cold temperatures (Katzin et al. 2021). The advantages of LEDs, i.e, full spectrum control and reduced energy costs, nevertheless make CEA more feasible in northern latitudes that also require longer periods of supplementary light in winter months. Furthermore, LEDs can be tailored to produce a specific spectrum to optimize crop yield and nutritional quality, thus allowing CEA farmers to further reduce energy costs and maximize crop value (Viršilė et al. 2020). Optimized light treatments using LEDs may thus allow energy-efficient production of plants with higher contents of desired human micronutrients (Weaver et al. 2019; for more detail, see sections below). However, the level of customization provided by LED technology is not without its problems. In comparison to green or yellow LEDs, red, blue, and white LEDs have higher photon efficacy (defined as $\mu\text{mol PAR photons emitted per Joule, or } \mu\text{mol J}^{-1}$) because these latter wavelengths are absorbed by plants' photochemical systems at higher efficiency than the former wavelengths (Weaver et al. 2019). However, since various wavelengths of light provide not only energy input but also information input that alters plant form, function, and composition, completely contained CEA systems with 100% artificial lighting will likely need to provide additional wavelengths beyond red and blue (Viršilė et al. 2020). Additional wavelengths, such as green with its lower photosynthetic photon efficacy than that of red or blue, play other roles in plant metabolism. This review addresses the question of how wavelength affects plant growth and composition and builds on prior reviews (Kim et al. 2005; Wang and Folta 2013; Golovatskaya and Karnachuk 2015; Zhang et al. 2020) by addressing several gaps. The present review specifically addresses the interaction of several environmental factors that modulate plant growth and composition, such photoperiod,

wavelength, and lighting intensity in combination with yet other factors (e.g., pot size/root volume and resulting sink strength).

This review addresses the roles of less well-studied wavelengths in plant metabolism, such as green and far-red light, with a focus on selected plant constituents of interest to the CEA grower. Furthermore, only studies conducted using LED lighting were included. Plant constituents were selected that are (i) influenced by light quality and have roles (i) in photosynthesis, plant productivity and/or environmental resilience as well as (iii) serve as essential human micronutrients. These included vitamins, carotenoids, and phenolics.

Productivity, Desired Plant Outcomes and Nutritional Quality

When growing plants in CEA using artificial light, it is essential to first determine the desired outcome for the plant product. Plants utilize light as a signal to inform them about their environment and regulate their responses accordingly (Borthwick et al. 1952; Youvan and Marrs 1987; Wang et al. 2008; Lin et al. 2013). Thus, using artificial light to increase plant productivity must be based on an understanding of what spectral mixture optimizes development of the intended end product. The process and result of producing the desired plant outcome while accounting for the quality of the product and the cost of inputs is referred to as co-optimization (Fig. 2). Examples of potential desired outcomes depend on whether leafy greens or seed/fruit crops are produced, and may include leaf area production, biomass production, macro- and micronutrient content, and seed or fruit production (Youvan and Marrs 1987; Kim et al. 2004; Olle and Viršile 2013; Ji et al. 2016). Notably, these distinct measures of quantity and quality of yield respond differently to the light environment. For example, plants grown in the shade exhibit thinner, larger leaves with lower protein and phytochemical content, which allows the

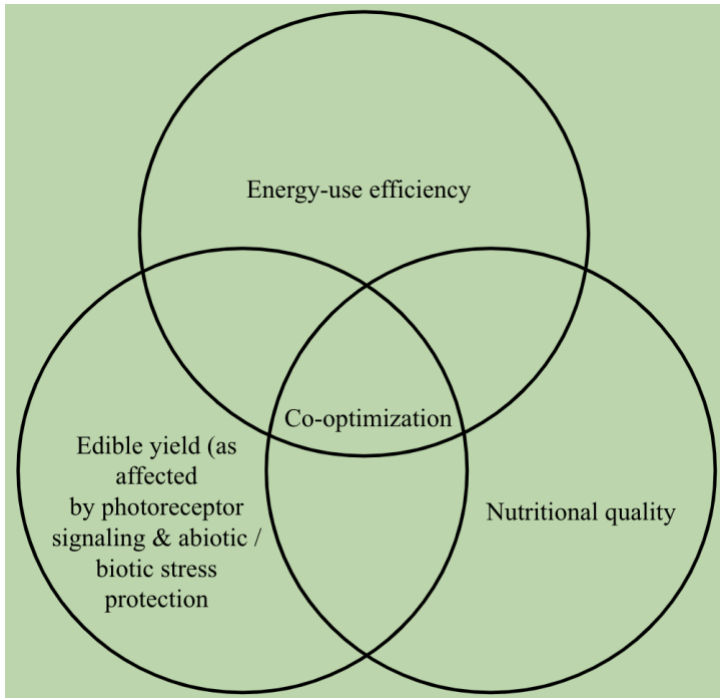


Figure 2: Venn diagram of co-optimization. While plants can be tailored to grow in a desired way, this process is a balance between the inputs, edible yield (e.g., fruit size, leaf area) and the nutrient density of the product.

plant to maximize photon capture at the expense of constituents (proteins and protective antioxidants) that would be necessary to produce more biomass in higher light (Allen and Richardson 1968; Kang, Zhang, et al. 2016). Plants also utilize light quality and photoperiod (the length of time for which the plant is exposed to light on a daily basis) to determine when to

germinate, reproduce, and, in the case of annuals, complete their life cycle (Borthwick et al. 1952). These plant responses to light are highly dependent on species, thus making it necessary to optimize spectral mix for given species. For example, winter annuals like spinach germinate under environmental conditions typical for fall and complete their life cycle before conditions indicate the onset of summer; summer annuals like sunflower germinate in environments typical for spring conditions and complete their life cycle under typical fall conditions (Yorio et al. 2001; Wang et al. 2008). The following section presents an overview of how spectral quality of growth light affects plants, via pigments and photoreceptors involved, and their functions and composition.

Photosynthetic Pigments, Signaling Photoreceptors, and Their Functions

Photosynthetic pigments

The primary light-absorbing pigments of plant photosynthesis are chlorophylls that selectively absorb red (650-700 nm) and blue (400-475 nm) wavelengths (Avital et al. 2006; Heddad et al. 2006; Eichhorn Bilodeau et al. 2019 ; see Fig. 3). In a dilute solution in a test tube (Fig. 3), chlorophylls absorb mainly red and blue light, but in a leaf packed with chlorophyll, chlorophyll-binding, light-collecting proteins alter chlorophyll's molecular structure, which alters the range of wavelengths absorbed (Kang, Park, et al. 2016). This largely closes the gap in the green region of PAR (Golovatskaya and Karnachuk 2015). Moreover, chlorophyll *b* (Chl *b*) absorbs more light than chlorophyll *a* (Chl *a*) in the green range of the light spectrum, and thus further closes the green gap (Kaiser et al. 2019). Plants adapted to, and/or growing in, different light environments exhibit different ratios of Chl *a* to Chl *b* (Allen and Richardson 1968; Nishio 2000; Folta and Maruhnich 2007). Sun-loving species have high Chl *a/b* ratios; shade-tolerant species have low Chl *a/b* ratios (Allen and Richardson 1968; Nishio 2000). This difference offers benefits in these respective light environments, with shade environments enriched in green light that filters through overlapping canopies as stated above (Allen and Richardson 1968; Kang, Zhang, et al. 2016).

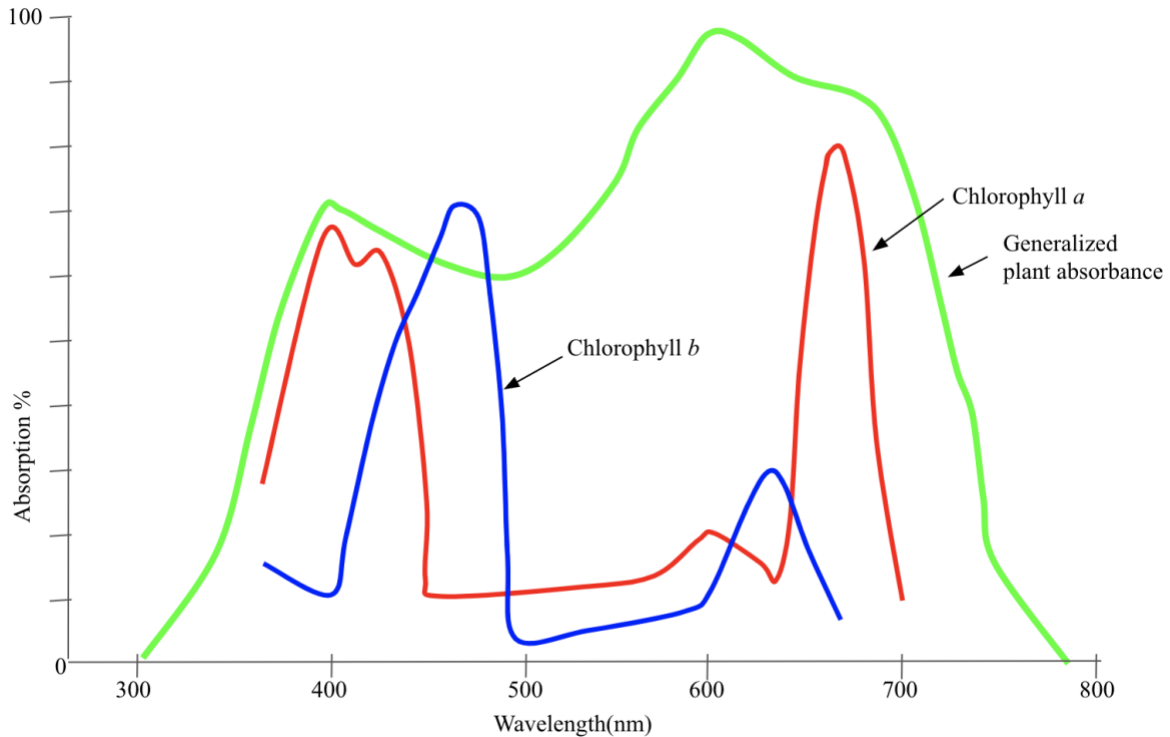


Figure 3: Absorption percent as a function of wavelength of light in nanometers. Chlorophyll absorption was recorded in dilute solution in a test tube. The difference between the chlorophyll absorption and the generalized plant absorption is a result of the effects of chlorophyll binding proteins which alter the structure of chlorophyll and broaden the absorption spectrum. Data derived from (Avital et al. 2006; Heddad et al. 2006; Eichhorn Bilodeau et al. 2019)

Signaling Photoreceptors

While the carbon fixation driven by the range of wavelengths absorbed by chlorophyll in a leaf is essential to growth, signaling photoreceptors collect light that informs plant morphogenesis, i.e., the way plant development and cell differentiation occurs through its life cycle (Johkan et al. 2012; Kang, Park, et al. 2016). Photoreceptors such as phytochromes, ultraviolet-B receptor (UVR8), phototropins, and cryptochromes (Avital et al. 2006; Heddad et al. 2006; Eichhorn Bilodeau et al. 2019) (Fig. 3) respond to light quality (specific wavelengths) and provide additional input into the same signaling networks that are also receiving input from plant source-sink balance (Demmig-Adams et al. 2017 Current Opinion, 2022 Photosynthetica).

Source-sink balance reflects the balance between photosynthetic activity of the plant (as the sugar source) in response to, e.g., light intensity and CO₂ level, and the utilization of sugar in the plant's sinks (e.g., growing tissues and storage organs), which is strongly affected by, e.g., the availability of water and nutrients like nitrogen and others (Venkateswarlu and Visperas 1987; Demmig-Adams et al. 2017, 2022). The complexity of this regulatory system allows the plant to integrate all aspects of the environment into the control of growth, development, and defense (Wang et al. 2011). In other words, the signaling networks that receive input from signaling photoreceptors also receive input from other environmental signals as well as endogenous signals (Fig. 4). This organization allows the plant to integrate input from multiple aspects of its environment with its own developmental state (Wang et al. 2011; Lin et al. 2013). Conversely, this means that light quality must be considered in the context of light intensity, photoperiod, CO₂ supply, nutrient supply, and other environmental variables. This complexity limits generalizations about lighting quality, particularly in comparisons across species.

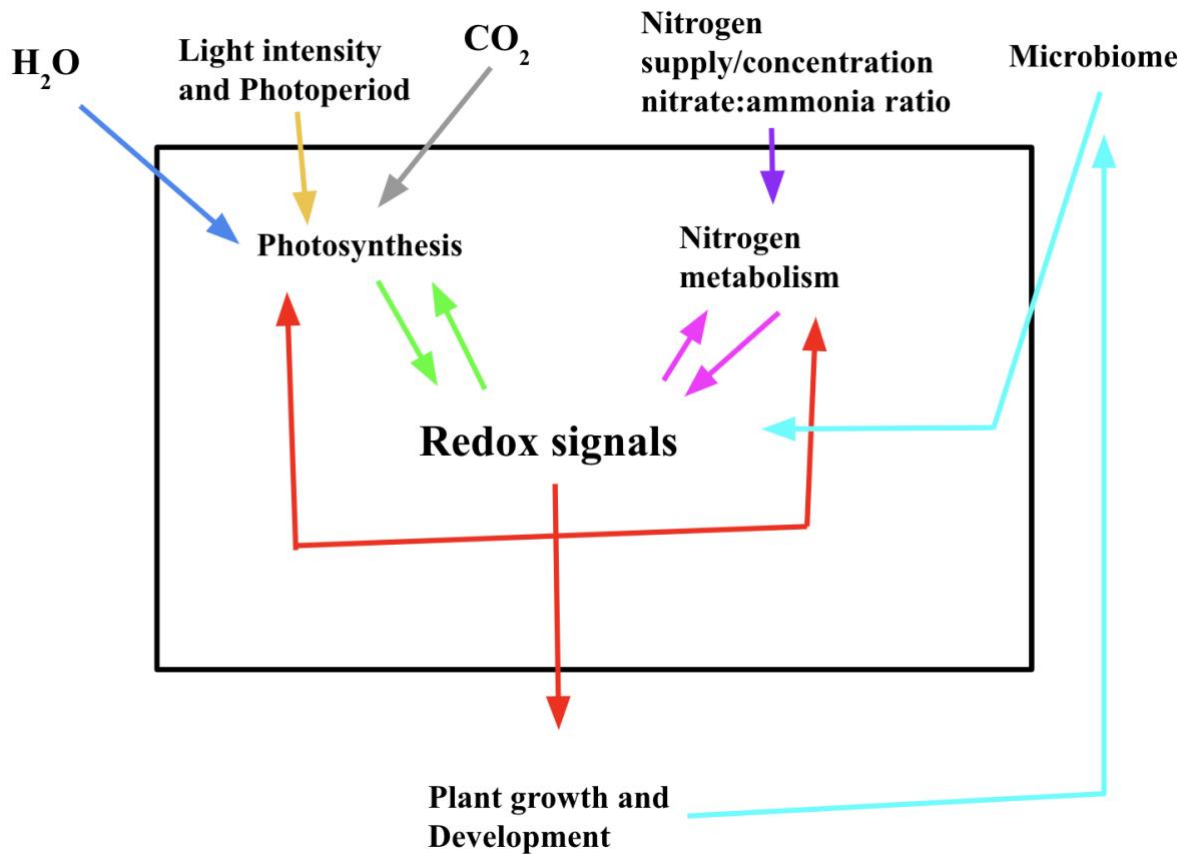


Figure 4: Diagram of plant signaling pathways. Photosynthesis is regulated through inputs such as, water availability, light intensity, photoperiod, and CO₂. Through redox signaling photosynthetic rate, plant growth, and morphology are regulated. Additionally, nitrogen and the microbiome influence plant growth and development through other redox signals. (Demmig-Adams et al, 2022)

Effect of red to far-red ratio

Daylength/photoperiod informs about seasons and the resulting need for timing of flowering, reproduction, and (for annuals) life cycle completion. Light quality informs the plant primarily on whether it is in a shaded environment with light supply limiting to photosynthetic activity or in a high-light environment with light supply that saturates photosynthesis or exceeds what can be used in photosynthesis. Notably, the phytochrome photoreceptor is involved both in measuring daylength and in signaling wavelength composition (Oguchi et al. 2011). Concerning photoperiod, daylength changes indicate changing seasons and help regulate processes like germination, reproduction, and senescence (Borthwick et al. 1952; Youvan and Marrs 1987). The

direction of these changes varies among plant species and groups, such as summer versus winter annuals as described above. In addition, light quality can be used to trigger these processes through phytochrome signals. As first shown by Borthwick et al. (1952), lettuce seeds (*Lactuca sativa L.*) irradiated during germination required the lowest light exposure to stimulate germination at wavelengths between 640-680 nm. The system of sensitivity to red and far red wavelengths is driven by the ratio of the phytochrome forms P_R (red form of phytochrome) and P_{FR} (far-red form of phytochrome) that are converted interchangeably by absorption of red and far red light, respectively (Fig. 5) (Brazaitytė et al. 2016).

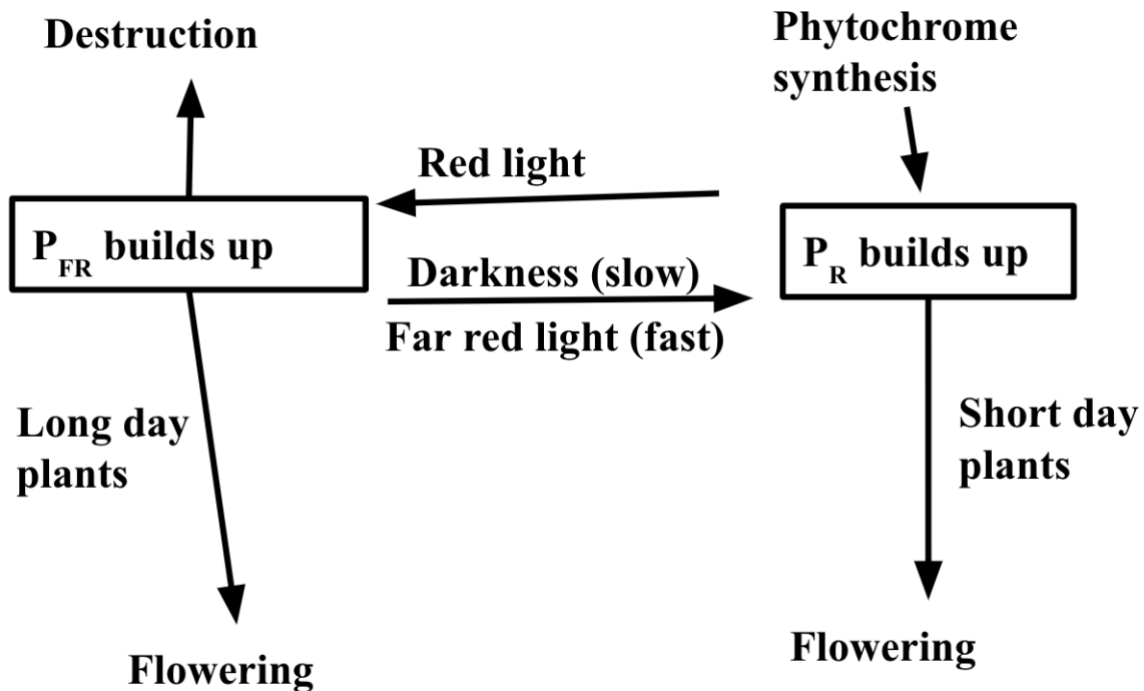


Figure 5: Diagram of phytochrome signaling. P_{FR} (phytochrome far-red form) builds up as red light is absorbed while P_R (phytochrome red form) builds up when far red light or darkness occurs. Both forms of the phytochrome are shown to induce flowering in plants. Short-day plants are those that require a photoperiod of less than 12 hours to begin flowering while long day plants require less than 12 hours of night to begin flowering. (Oguchi et al. 2011; Brazaitytė et al. 2016)

Green light as a signal

Similar to red and far-red light, green light is also associated with growth regulation (Terashima et al. 2009; Bian et al. 2018; Zhang et al. 2011; Folta and Maruhnich 2007; Kim et al. 2004). Green light is absorbed by mesophyll cells (inner leaf tissue, Fig. 6) (Powles 1984; Vogelmann et al. 1991; Terashima et al. 2001; Terashima et al. 2009). The preferential absorption of red and blue wavelengths by chloroplast in the upper mesophyll layers (Folta and Maruhnich 2007; Wang et al. 2008; Wang and Folta 2013) leads to an enrichment in green wavelengths of the light that penetrates the deeper, self-shaded layers of the mesophyll tissue, where most of the absorption of green light – mainly by Chl *b* – takes place (Terashima et al. 2001; Terashima et al. 2009; Oguchi et al. 2011). Both whole plants growing in the forest understory, and individual cells located in a leaf below a layer of other cells, produce more chlorophyll *b* and absorb significant levels of green light (Allen and Richardson 1968; Terashima et al. 2001; Wang et al. 2008; Terashima et al. 2009). Whether or not, and to what extent, green light will stimulate plant growth can thus be expected to vary with plant species and growth conditions. For example, plant species that form tiered, multi-layer canopies and have thick, multilayer leaves may be expected to exhibit growth stimulation by addition of green light, whereas plant species that form rosettes or vines and/or have thinner leaves may not (Zhang et al. 2011; Johkan et al. 2012; Golovatskaya and Karnachuk 2015).

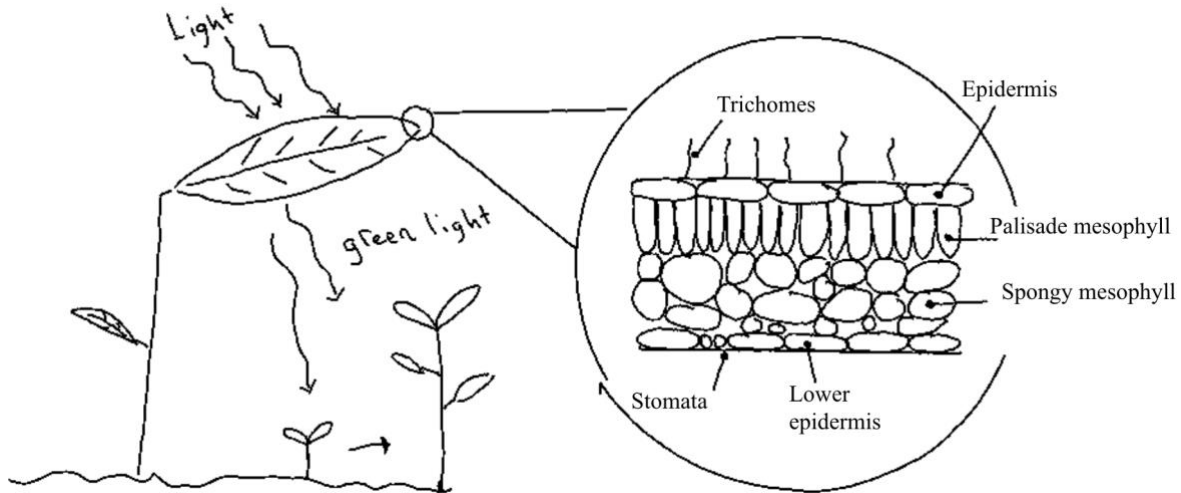


Figure 6: Left diagram represents green light transmittance through the canopy which can promote growth in the understory. Right inset of generalized leaf architecture with common leaf structures. Green light is shown to play a role in understory photosynthesis and signaling pathways, and functions similarly in the palisade and spongy mesophyll tissue. (Terashima et al. 2001; Wang et al. 2008; Terashima et al. 2009)

Furthermore, green light apparently provides regulatory input that has an effect on plant morphology (the plant form) (Folta and Maruhnich 2007). Although a green specific photoreceptor remains to be identified, green wavelengths can apparently counteract the signaling from the phytochrome system (Shinomura et al. 1996) and inhibit the phytochrome responses expected from supplementary red light (Tanada 2006). Provisionally titled ‘heliochrome,’ this inhibitory pigment has not yet been fully characterized. It should also be noted that, just as had been found for far-red light, green light – as a signal that the plant is in a light-limiting environment – promotes leaf area expansion (more area to intercept PAR) and lowers biomass production (and nutritional quality for the consumer) per unit of area (Johkan et al. 2012; Kaiser et al. 2019).

Production of Antioxidants and Other Phytochemicals

Excess absorbed light and dissipation as thermal energy

Plants dissipate excess absorbed light (that cannot be used in photochemistry) non-photochemically as harmless heat (Powles 1984; Baker and Bowyer 1994; Demmig-Adams et al. 2020). This is a vital survival strategy because accumulation of excess excitation energy leads to the formation of reactive oxygen species (ROS) that, in larger amounts, can damage macromolecules and, in smaller amounts, modulate gene expression and can trigger photosynthetic downregulation and growth declines (Demmig-Adams et al. 1996; Demmig-Adams and Adams 2006; (Zhang et al. 2011; Johkan et al. 2012; Golovatskaya and Karnachuk 2015). Although increasing levels of ROS may first induce synthesis of greater amounts of antioxidants, the subsequent downregulation of chlorophyll levels can eventually trigger early senescence, downregulation of growth, and photosynthesis altogether (Demmig-Adams et al. 2022). In addition to regulating the allocation of absorbed light to photochemistry versus non-photochemical dissipation as heat (Fig. 7), plants adjust the amount of light they absorb by regulating their light-harvesting capacity (chlorophyll content via regulating gene expression of Chl *a/b*-binding proteins) (Demmig-Adams and Adams III 2006; Oguchi et al. 2011; Stewart et al. 2021). Furthermore, excess absorbed light (rising ROS levels) increases gene expression of proteins that are antioxidant enzymes or serve in the production of antioxidant metabolites (such as carotenoids, vitamin C and vitamin E) that either prevent ROS formation (via non-photochemical dissipation involving carotenoids) or detoxify ROS and other reactive species (Z. et al. 2012; Demmig-Adams et al. 2020b). Whereas surplus light can have unwanted effects (Oguchi et al. 2011, Kang, Zhang, et al. 2016), use of some excess light is necessary to increase

nutritional quality with increased vitamin/carotenoid production (Demmig-Adams et al. 1996; Demmig-Adams et al. 2020b).

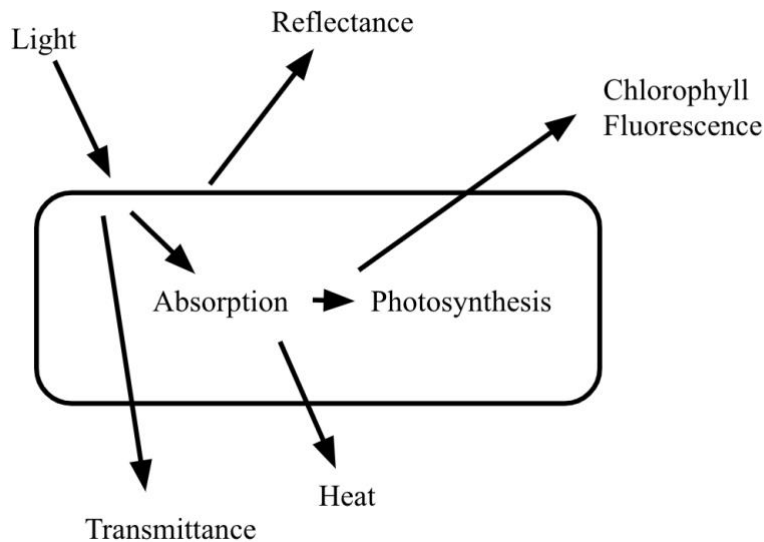


Figure 7: Plant mechanisms in response to light and excess light. Absorption, reflectance and transmittance represent the primary response but fluorescence and heat are also crucial mechanisms to mitigate damage to the photosystem. (Demmig-Adams et al. 1996; Demmig-Adams and Adams 2006; Zhang et al. 2011; Johkan et al. 2012; Golovatskaya and Karnachuk 2015)

Carotenoids

Enhanced carotenoid production, which is associated with photoprotective capacity (Demmig-Adams et al. 1996, 2020a), responds to light supply in two ways. The formation of zeaxanthin requires excess light absorbed by chlorophyll which triggers conversion of the zeaxanthin precursor violaxanthin to zeaxanthin (Demmig-Adams et al. 2020b). Excess light of any wavelength absorbed by chlorophyll, lowers intra-thylakoid pH and triggers the conversion of violaxanthin to the photoprotector zeaxanthin catalyzed by violaxanthin de-epoxidase (VDE) (Demmig-Adams et al. 2020b). Zeaxanthin is connected to photoreceptors in the human eye and

must be obtained from plants (Kvansakul et al. 2006). Furthermore, elevated carotenoid content substantially increases the nutritional value of the crop as carotenoids are connected to lowered risk of cardiovascular disease, reducing inflammation, and increased cognitive function (Arab and Steck 2000; Bian et al. 2019; Demmig-Adams et al. 2020b). In addition to excess light absorbed by chlorophyll, lower levels of blue light absorbed by photoreceptors in this region also stimulates carotenoid synthesis (Hoffmann et al. 2016; Kamal et al. 2020) although these results vary among species.

Antioxidant vitamins and phenolic antioxidants

In plants, antioxidants lower the levels of ROS and other radicals/reactive species, and this function is also essential in human health because neither antioxidant vitamins nor carotenoids or phenolics can be synthesized de novo by humans and must thus be consumed with the diet (Jacob and Sotoudeh 2002; Demmig-Adams et al. 2020a). High intensity light has been shown to increase antioxidant production such as vitamin C (ascorbic acid) and vitamin E (tocopherols) (Z. et al. 2012; Demmig-Adams et al. 2020a). Low levels of blue light also trigger synthesis of multiple phenolic antioxidants in the phenylalanine ammonia lyase (PAL) pathway (PAL is the key enzyme in the phenol synthesis pathway) (Jiang et al. 2021; Kolton et al. 2022). Supplemental blue light (430 nm) at an intensity of $50 \mu\text{mol m}^{-2} \text{s}^{-1}$ increased vitamin C yield in Chinese kale (*Brassica alboglabra*) compared to supplemental light of the same intensity with red and green wavelengths (Jiang et al. 2021). These findings indicate that antioxidant production per se could be attained without high light intensities.

Conclusions

Given the granular control that CEA systems allow over the final plant product, alterations to the lighting environment through intensity and wavelength should be exploited to improve nutritional quality and other desired plant outcomes. Although variation in plant response to wavelength is both species and environment (e.g. water, nutrient, and space availability) dependent, the use of supplemental lighting presents numerous advantages. Despite the importance of the aforementioned environmental conditions to the success of plant production, altering the lighting environment is an under-utilized avenue of improving product quality. Particularly, the application of finishing treatments of light to improve the nutritional quality (Stewart et al. 2021) appears to balance the tradeoffs created by light stress and growth response. Furthermore, the importance of pot size is often overlooked, limiting the ability of plants to develop to their full potential or altering the expected outcome. CEA's utilizing supplemental lighting should first develop successful methods in full spectrum because misinterpreting wavelength changes as success or failure is commonly driven by root limitation or drought stress. Although red and blue wavelengths predominantly drive photosynthetic response, addition of green wavelengths should be explored, particularly in shade tolerant varieties. However, the importance of green wavelengths remains one of the major gaps in photosynthetic research. Further work on plant response to wavelength is certainly crucial to realize the gains of specific wavelength application in agricultural systems. While many authors primarily focus on results of wavelength applications, more attention to methods and growth conditions could further the application and replication of results. The variation in plant response is incredibly specific to these conditions and limited reporting of growth conditions limits how broadly the results can be applied.

With global human population, land use and water consumption increasing steadily, CEA systems create an important technology to increase resource-use efficiency. By utilizing climate-controlled environments and supplemental light, CEAs are also capable of expanding growing seasons to year-round harvests and preventing losses from extreme temperatures and drought (Nataliia et al. 2015). CEAs require less space to produce a similar amount of certain crops like leafy produce, with Aero farms reporting production of 40% more lettuce in the same space compared to a conventional farm (Terazono and Fortado 2019). Although CEAs are not a replacement for all conventional farming techniques, particularly grain agriculture, within the niche of leafy greens and fruits CEAs can provide major benefits. With further improvements, such as reduced water usage in hydroponic media and supplemental lighting designed specifically for plants to co-optimize light-use efficiency and nutritional quality, CEAs provide a solution to feeding the growing world population. Implementation of CEA agriculture has the potential to reduce the impact of farming on natural resources (Kim et al. 2005; Nataliia et al. 2015). However, because around 67% of all CEAs still rely on electricity generated by fossil fuels (Nataliia et al. 2015), most plants grown with supplemental lighting actually have a greater carbon footprint than their field-grown cousins. Fortunately, as the power grid becomes more sustainable and renewables become more affordable, CEAs will likely become more environmentally friendly (Kim et al. 2005; Kusuma et al. 2020). However, with much of CEAs still using regular fossil fuel power, CEAs – particularly those with 100% artificial lighting – are currently not environmentally friendly.

While CEA systems require refinement to become fully sustainable, the advantages outweigh the downsides. By having granular control over the light received by the plant, farmers can use knowledge of wavelength effects to produce greater high-quality yields. Although more

research is needed, e.g., on the effects of green light depending on species, modulating lighting has a profound effect on crop yield and nutritional quality. Advances in LED technology developed the possibility for more modern lighting systems. By utilizing these tools, agriculture of the future may be not too far away.

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