Seeing the lights for leafy greens in indoor vertical farming

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A B S T R A C T

Background: Agricultural production in controlled indoor farming offers a reliable alternative to food and nutrition supply for densely populated cities and contributes to addressing the impending food insecurity. Leafy vegetables, rich in vitamins, minerals, fibres and antioxidants, account for over half of the indoor farming operations worldwide. Light is the foremost environmental factor for plant growth and development, and the success of indoor farming largely depends on lighting qualities. The energy efficient light-emitting diode (LED) has been increasingly used in indoor farming systems.

Scope and approach: Here we provide an updated overview of the current indoor vertical farming systems, the mechanisms of light perception by photoreceptors, and the effects of LED spectra or intensity on growth and phytonutrient accumulation of leafy greens. We also outline the challenges in interpreting and applying the research findings in the field and highlight issues to be addressed.

Key findings and conclusions: Lighting quality and quantity can be manipulated to improve yield and phytonutrient contents of leafy greens. As responses of leafy greens to light are dependent on genotype and developmental stage, light recipe targeting different developmental stages should be formulated for different species for maximizing yield. While it has been known that blue wavelength has a more prominent positive impact on phytonutrient accumulation than red, little is known for other wavelengths. Moreover, recent findings that green wavelength inhibits plant growth in a blue-wavelength-dependent manner highlight the need for future research to investigate interactive effects of different wavelengths on modulating plant growth and metabolism.

1. Introduction

Light is central for the evolution and sustainability of life on our planet. For plants, light can be a source of energy and an environmental signal. Plants harness light energy from the sun to convert carbon dioxide and water into carbohydrates and release oxygen into the atmosphere. This process is called photosynthesis and occurs with the help of chlorophyll pigments in the leaves of land plants. Plants have also evolved many types of photoreceptors to perceive different light qualities, such as wavelength, intensity and duration, to regulate a broad range of developmental and physiological processes. The ability to sense and integrate information enables plants to elicit appropriate responses for optimal growth and reproduction in their dynamic environment.

The last century of mankind has seen huge leaps in science and technological innovation in the field of agriculture. The discovery of Mendelian genetics (1866), the Green Revolution (1940–1970) and the advent of biotechnology (1981) have changed the way how humans grow and produce food. With the world's population projected to grow from 7 billion in 2012 to 9.6 billion by 2050, the world will need to produce more food for the ever-growing population (Alexandratos & Bruinsma, 2012). With an uptrend in climate extremes and global warming, farmers are increasingly adopting farming in a controlled environment where environmental conditions including light and temperature can be regulated. Indoor farming, where sunlight is being replaced with artificial lighting, is proposed as the future of modern agriculture. We are beginning to see the benefits that indoor farming practices can bring to the local population and how they can contribute to the overall economy and global supply chain (Table 1). The advantages of indoor farming are apparent as recent technological advances have made it possible to grow crops without clearing land and control precisely the growing parameters. This will allow crops to be produced all year round as they are no longer reliant on weather patterns. In

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Table 1
Benefits of indoor vertical farming.

Factor	Advantages	Environmental	Social	Economics
Location	Proximity to supply and consumer market	Reduced use of natural resources	Fresh food readily available	Less energy cost
	Local workers employed	Less resources on transport	Increased employment rate	Wages for local people
Operation	Whole year round production	Independent of growing season	Stable food supply	Stable revenue
	Reduced water consumption	Less strain on natural resources	More water for drinking or other purposes	Less operating cost
	Reduced use of fertilizers and pesticides	Less pollution	Improved food quality	Less operating cost
Technology	High productivity	High space usage efficiency	Increased food supply	Higher revenue
	Scalability in food production	Saving the use of arable land	Stable food supply	Able to capture market forces

addition, this model of agriculture provides for reproducibility in yield and scalability in having more farms built in a similar fashion. The diversity in indoor vertical farming is generated from the domestic needs, innovations in farming technology and the availability of skilled labor.

In the indoor farming industry, there are mainly five types of crops being grown: leafy vegetables, tomatoes, herbs, flowers and microgreens. Currently, leafy vegetables account for more than half of the indoor farming operations worldwide. They have more nutrition per calorie than any other food and they are packed with vitamins, minerals, fibres and antioxidants. Recent studies have shown that different leafy vegetables grow differentially and accumulate different metabolites under specific light spectra and intensity. As the growing period of leafy vegetables is significantly longer than that of microgreens, the energy input for light per mass for growing leafy vegetables is considerably higher. However, due to the multitude of studies performed with varying parameters, it is by far hard to identify the optimal light parameters for efficient growing of different types of leafy vegetables.

In this review, we provide the most updated picture of the indoor farming industry and review various lighting conditions being used for growing leafy vegetables. We analyse the key lighting parameters for growing leafy vegetables efficiently and summarise the effects of light wavelength on photoreceptors and phytochemical profiles. In addition, we discuss the prospects for future research in light of new qualities of leafy vegetables.

2. Indoor vertical farming is the driving force for urban farming

Urban farming can be defined as the growing of crops primarily for domestic use within the boundary of a city or built-up areas. Similar to growing crops across large fields, it also involves processes such as production, processing and distribution of food. Over the last few decades, the focus on urban farming has increased significantly due to the effects of climate change and the need to bolster food security. The urban farming market can be segmented into different forms with increasing technological inputs: fields around urbanised areas, hoop houses, greenhouses and indoor farming with artificial lighting. For most of human history, farming has been an outdoor operation. Plants capture sunlight for energy and absorb water and nutrients from soil. With better technology, farmers have gradually been realizing the benefits to farming indoors with greenhouses such as growing plants all year round and better pest management.

To increase the yield further, the idea of using artificial light for

farming was proposed in the early 1900s. Traditional growers have used light from incandescent and high-intensity discharge (HID) lamps that resembled sunlight in terms of the wavelength spectrum. Even though the warm light produced from incandescent and HID lamps is good for vegetative growth, they are energy inefficient and produce a lot of heat. Thus, they are often used as supplemental lighting in greenhouses as they would not perform well where there is insufficient heat dissipation. It will be challenging to implement those technology in indoor vertical farming. The invention of LED solid-state lighting in the early 1960s, and the recent improvements in technology and pricing have made LED lights commercially feasible in indoor farming (Pattison et al., 2020; Pattison, Tsao, Brainard, & Bugbee, 2018; Pimputkar, Speck, DenBaars, & Nakamura, 2009). The benefits of LED lights include a decrease in electricity consumption, lower cost of ownership and the ease in implementing customised lighting recipe for different crops. The intensity and spectra control of LEDs allow for optimization of light quality to match the crop photosynthetic pigments and photoreceptors for efficiency. Even though vertical farms have higher start-up and operating cost, they produce more crops per unit area of land used.

The controlled environment of indoor farming ensures an optimised growing condition and provided a scalable way to reach economy-of-scale production. There are four main considerations in starting and maintaining an indoor vertical farm: location, cultivation type, types of crops, technology (Fig. 1).

2.1. Location

The location of an indoor farm can influence many aspects of the infrastructure and operation. In countries where land cost is high, the setting of an indoor farm can be placed in under-utilised spaces such as vacant buildings, underground, under road flyovers, etc. The closeness to urban population can greatly reduce the use of fossil fuels by minimizing food transportation and human labor movement. The time needed to deliver fresh food from the farm to the plate can also be shorter. In bringing nature closer to city, it will have access to skilled labor and generate employment.

2.2. Cultivation type

In indoor vertical farming as well as other modes of farming, there are mainly four different types of cultivation: soil-based, hydroponics, aquaponics and aeroponics. The market segmentation of indoor farming technology worldwide in 2019 is hydroponics (51%), aeroponics (20%), soil-based (13%), aquaponics (9%) and others (6%) (information from Statista). The selection of cultivation type often depends on the experience and technology readiness of the growers.

2.2.1. Soil-based
Plants are grown in soil trays where they can be moved. Soil provides plants with primary nutrients of nitrogen, phosphorus and potassium along with micronutrients such as copper, boron, zinc, manganese and molybdenum. The advantages of soil-based farming are that soil retains moisture well and can also provide aeration. With proper fertilization, soil can be used repeatedly for many cycles of crops. However, in doing so, soil cultivation requires a high degree of knowledge in field management, fertilization and pest management. All types of crops can be grown on soil depending on the soil type.

2.2.2. Hydroponics
Hydroponics is the growing of plants without soil as a medium while providing water and nutrients. The plants are held in net pots or on chemically inert media such as clay pellets, perlite, rock wool, etc. There are many variants of hydroponics where the roots can be suspended in solution full-time or fed with a flow of solution (Son, Kim, & Ahn, 2020). The use of hydroponics can greatly reduce the evaporative loss of water and thus conserve water usage. Though watering can be automated, the
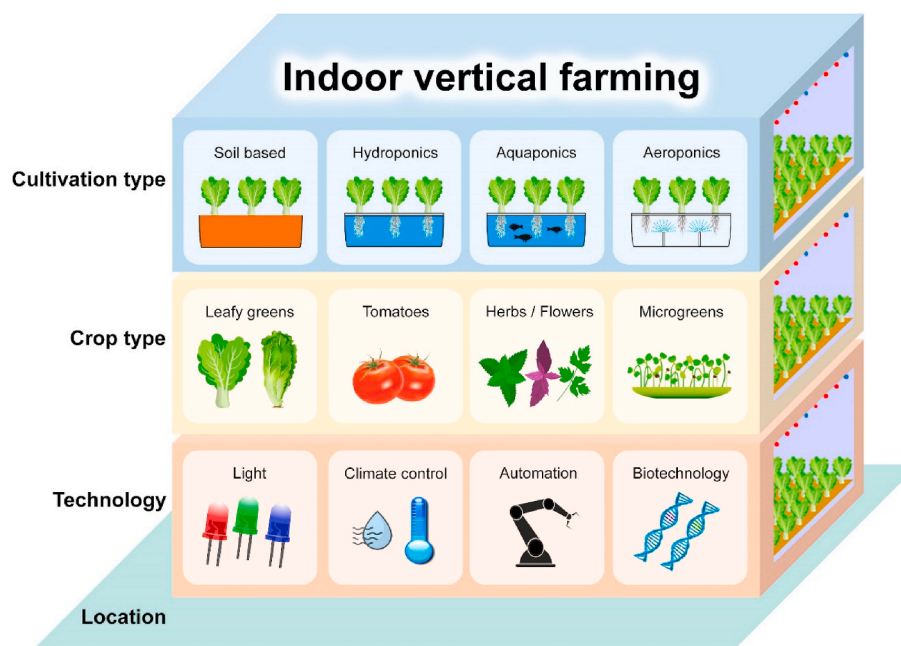
Fig. 1. Four main considerations in starting and maintaining an indoor vertical farm. Indoor vertical farming is the practice of producing food in a controlled environment with artificial lighting. This technique aims to maximise crops output in limited spaces independently of weather conditions. The four main considerations in starting and maintaining an indoor vertical farm are cultivation type, crop type, technology and location.

disruption of the system can significantly influence the outcome of the cycle. The cost of nutrients and electricity are higher compared to soil-based cultivation. The formula of the nutrient solutions will vary with the requirements of the specific vegetables being grown.

2.2.3. Aeroponics

Aeroponics is a variant of hydroponics and it involves growing of plants in an air or mist that is sprayed onto their roots several times an hour. The plants are usually supported by boards, foam sheets or other methods to suspend the plants in space. Aeroponics provides better aeration to the roots for the plants to grow faster. This type of cultivation would require precision sensing technology and strict dosing regime to maximise outcomes.

2.2.4. Aquaponics

Aquaponics is the growing of plants and fishes together in a system. The nutrient input for this system is by feeding fishes and converting the waste into nutrients for the plants. This rely on microbes and proper functioning microbes are the key in efficient conversion to nutrients for the plants. Thus, the start-up phase for an aquaponics system is much longer for the microbial population to grow up and stabilize. This will require a wide knowledge base in hydroponics, aquaculture and maintenance of microbes and nutrient levels.

2.3. Types of crop

The process of choosing crops should be part of a comprehensive feasibility study before setting out to build the farm. In 2017, the main crop types planted in the US and Canada are leafy greens (57%), tomatoes (16%), herbs (11%), flowers (10%) and microgreens (6%) (information from Agrilyst, 2017). As the operating cost for indoor vertical farming is higher compared to greenhouses and fields, it is important to note the crop cycle and select crops that are in high demand or niche crops that can fetch a higher value.

2.4. Technology

The implementation of technologies is often the key to a successful indoor vertical farm. Advancements in technologies such as LED lights, sensors and automation have enabled indoor farming to be more efficient and customised for growing specific crops. Unlike greenhouses, plants grown indoors rely exclusively on artificial lighting system for their growth. The energy cost in running lights can take up to 30% of the total energy cost, with the remaining is spent on climate control and system operations. The energy efficient LED has been increasingly used in indoor farming systems and the global LED grow light market is projected to grow from USD 1.13 billion in 2018 to USD 6.78 billion by 2026, with a compound annual growth rate (CAGR) of 24.9% (Verified Market Research, 2019). LEDs are basically specialised diodes similar to a PN junction diode that can pass current in its forward direction but block the flow of current in the reverse direction. Working in a forward biased method, an LED emits certain wavelength of light based on the semiconductor material used such as aluminium gallium arsenide phosphide for red, orange and yellow colors (Nair & Dhoble, 2015). With the addition of down-converting phosphors, these phosphors-converted LEDs can increase the photosynthetic efficiency of plants by matching the absorption spectra of chlorophylls (Fang et al., 2020; Huang & Guo, 2018; Liang et al., 2018; Liu, Zhang, Wu, Wang, & Li, 2017). This provides a viable alternative to using monochromatic LEDs. LED-based solid-state lighting is still being improved in its luminous efficiency and substantial increases are expected with a novel colour-mixed solid-state lighting technology (Pattison et al., 2018). With these advances in lighting technology, researchers and growers are experimenting with different spectral composition and crop varieties to optimize space and energy efficiency, as plants absorb wavelengths of light differentially and are able to perceive different light qualities such as wavelength, duration and intensity.

3. Light as a source of energy and an environmental signal

Light is one of the most important environmental factors that influence plant growth and development. Terrestrial sunlight consists of

ultraviolet (UV), visible light and infrared radiation, in which visible light accounts for almost half of the absorption spectrum (Abe, 2010). The wavelength of the UV radiation lies in the range of 100–400 nm, visible light in the range of 400–700 nm and infrared in the range of 700–1000 nm. Even though the terrestrial sunlight spectrum is wide, plants can only utilise the visible light spectrum as the sole source of energy for photosynthesis, and this narrow spectrum of electromagnetic radiation is defined as photosynthetically active radiation (PAR) (McCree, 1971, 1972). Interestingly, plants can sense and detect variations in the light intensity and spectral composition of their native environment to adjust their growth and developmental processes (Fiorucci & Fankhauser, 2017). This has given rise to various plant responses such as photomorphogenesis, photoperiodism and phototropism (Kendrick & Kronenberg, 2012; Vince-Prue, 1975; Whippo & Hangarter, 2006). Photomorphogenesis refers to the growth and development of plants. Photoperiodism is the ability of plants to track time. Phototropism enables plants to grow towards or away from a light source.

3.1. Light is harnessed by photosynthetic pigments

Plants use photosynthetic pigments in their leaves to capture energy from PAR to drive synthesis of sugar molecules. These photosynthetic pigments are present around the thylakoid membranes of chloroplasts to serve as primary electron donors in the electron transport chain (Anderson, 1986). Specifically, the photosynthetic pigments will absorb light and transfer the energy via resonance energy transfer to a specific chlorophyll pair in the reaction center of either P680 photosystem II or P700 photosystem I. In this light dependent reaction, water molecules are split to generate ATP and NADPH and release oxygen molecules as a by-product (Yachandra, Sauer, & Klein, 1996). In the following light-independent reaction in the stroma of chloroplasts, the energy from ATP and electrons from NADPH are used to convert carbon dioxide into glucose and other products through the Calvin cycle (Raines, 2003; Shoaf & Lium, 1976).

In plants, the most abundant photosynthetic pigments are chlorophyll a and chlorophyll b (Shoaf & Lium, 1976). The chlorophyll content is determined by mainly two methods, which are the absorption of light of isolated chlorophyll in aqueous acetone and the measurement of leaf reflectance and transmission level using a Soil Plant Analysis Development (SPAD) chlorophyll meter (Netto, Campostrini, de Oliveira, & Bressan-Smith, 2005). The approximate absorption maxima of chlorophyll a are at 430 nm and 662 nm and those of chlorophyll b are at 453 and 642 nm (Fig. 2) (Inskeep & Bloom, 1985). Due to the chemical structures of chlorophyll a and b, the absorption spectra are not uniform across PAR and they have minimal absorption in the 500–600 nm range, thus, reflecting the colors of light green and turquoise, respectively. In some plants, accessory pigments, such as carotenoids (carotenes and xanthophylls), are produced to help absorb light in the blue-green spectrum to enhance photosynthesis (Fig. 2) (Havaux, 1998). They can also serve as antioxidants to help absorb and dissipate excess light energy.

3.2. Different classes of plant photoreceptors

Response to light signals such as quality, quantity and photoperiod, are mediated by various types of plant photoreceptors, which transform these signals into metabolic and morphogenetic responses to ensure plant survival and reproduction. All photoreceptors other than UVR8 (UV RESISTANCE LOCUS 8) contain an organic molecule known as a chromophore that serves to absorb photons and may or may not be covalently bound. The chromophore determines the wavelength of light absorbed. Photoreceptors in plants can be classified by their chemical nature and photochemistry of their chromophore into at least five classes: UVR8 for perceiving UV-B light (280–320 nm); cryptochromes, photothropins and zeitlupes for blue/UV-A light (320–500 nm); phytochromes for perceiving red/far-red lights (600–750 nm) (Fig. 2).
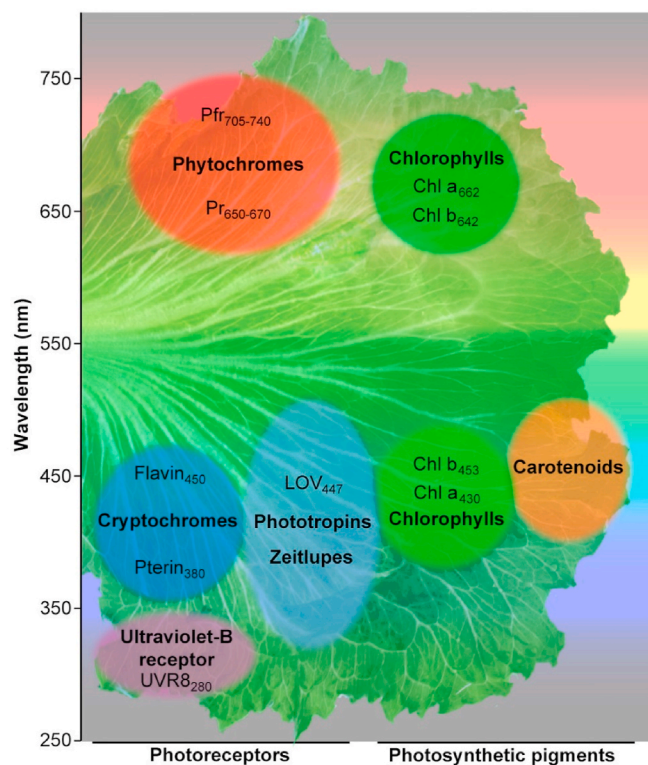

Fig. 2. Representative absorption spectra of primary classes of photosensitive molecules in plants. The absorption spectra of photoreceptors (phytochromes, cryptochromes, phototropins, zeitlupes, ultraviolet-B receptors) and photosynthetic pigments (chlorophylls and carotenoids) are shown. Absorbance peaks in each class of photosensitive molecules are given in subscript. Abbreviations: Chl, chlorophyll; LOV, light-oxygen-voltage domain; Pfr, far-red light-absorbing form of phytochrome; Pr, red light-absorbing form of phytochrome.

3.2.1. Ultraviolet light receptor UVR8

UVR8 is the only known plant photoreceptor that can mediate light responses to UV-B (280–320 nm) radiation (Kliebenstein, Lim, Landry, & Last, 2002). Intriguingly, UVR8 homologous proteins are present in all land plants, mosses and algae (Bowman et al., 2017). Upon perceiving UV-B signal by its two tryptophan residues Trp-285 and Trp-233, the inactive UVR8 dimer in the cytosol dissociates into two active monomers which can migrate into the nucleus to activate its downstream genes (Rizzini et al., 2011). The activation of UVR8 initiates plant stress responses such as biosynthesis of flavonoids, hypocotyl growth inhibition and suppression of leaf cell expansion (Jenkins, 2014). In tomato plants, the UVR8 homologous gene SlUVR8 plays essential roles in the biosynthesis of carotenoids and other UV-protective pigments in response to UV-B light (Li et al., 2018).

3.2.2. Cryptochromes

Cryptochromes are blue/UV-A photoreceptors and can be found in land plants and algae. Though cryptochromes share sequence similarity to DNA photolyases that use blue light to repair UV-induced DNA damage, they have no photolyase activity (Lin & Shalitin, 2003; Sancar, 2003). Cryptochromes bind to both pterin and flavin chromophores that can absorb light at 380 nm and 450 nm, respectively (Cashmore, Jarillo, Wu, & Liu, 1999). Cryptochromes are involved in many processes such as photoperiodic control of flowering, entrainment of circadian clock, plant stress responses to pathogens and shade avoidance (Chen, Chory, & Fankhauser, 2004). The overexpression of cryptochrome genes in tomatoes shows delayed flowering and increased flavonoids and lycopene content in fruits (Giliberto et al., 2005).

3.2.3. Phototropins and zeitlupes

Phototropins are serine/threonine kinases that can undergo auto-phosphorylation upon blue light irradiation (Christie, 2007). Phototropins can bind to two flavin mononucleotides with their two N-terminus LOV (Light, Oxygen and Voltage) domains and can exist in three different states LOV_{447}, LOV_{660} and LOV_{390} in a photocycle (Swartz et al., 2001). Phototropins regulate many developmental processes such as the bending of shoot toward blue light (positive phototropism), negative phototropism of roots, chloroplast movement, leaf expansion and stomatal opening (Christie, 2007). Similarly to phototropins, zeitlupes contain a LOV domain at the N-termini followed by an F-box and six kelch repeats at their C-termini (Somers, Schultz, Milnamow, & Kay, 2000). They regulate the period of circadian oscillation, photoperiodic flowering and hypocotyl elongation (Kim et al., 2007).

3.2.4. Phytochrome Pr and Pfr

Phytochromes function as red/far-red photoreceptors in plants. They are dimeric kinase proteins with covalently bonded bilin as their chromophore (Matsushita, Mochizuki, & Nagatani, 2003; Smith, 2000). Phytochromes can interconvert between an active form Pfr and an inactive form Pr depending on the light wavelength. Pr switches to Pfr upon excitation at 650–670 nm and Pfr can return to its inactive Pr state upon excitation at 705–740 nm (Nagatani, 2010; Shinomura, Uchida, & Furuya, 2000). The active Pfr form translocates from the cytosol to the nucleus to regulate light responsive gene expression (Li, Li, Wang, & Deng, 2011). Phytochromes regulate phototropism and many aspects of photomorphogenesis, such as seed germination, stem elongation, leaf expansion, biosynthesis of certain pigments, chloroplast development and flowering (Chory et al., 1996). In tomatoes deficient of phytochromes or bilin, the mutants display photomorphogenetic defects such as yellowing of leaves, elongated hypocotyl and reduced anthocyanin levels when grown under white light (Kendrick, Kerckhoffs, Van Tuinen, & Koornneef, 1997; Muramoto et al., 2005; Weller, Schreuder, Smith, Koornneef, & Kendrick, 2000). The ectopic expression of a phytochrome B gene from Chinese cabbage in Arabidopsis results in dwarfed plants and delayed flowering (Song et al., 2015).

4. Enhancing the quality of leafy greens through LED lighting

The development in LED lighting technology, allowing the flexible modifications of light spectra, has enabled the research and application of light quality in enhancing leafy green qualities in controlled environment for better growth, colour, flavour and phytonutrient content. The effects of LED spectra on the growth, development and metabolite accumulation of leafy vegetables have been intensively studied, especially in lettuce (Fig. 3 and Table 2). However, it is challenging to extract an optimal lighting recipe from all of this research due to inconsistent experimental parameters ranging from the precise spectral composition to the length of treatment. The findings that there are species-specific and even cultivar-specific differences also make it difficult to extrapolate research data from one species to another. There is nevertheless a general trend in the literature that suggests LED lights can be used to produce predictable outcomes as discussed below.

4.1. Red, blue light and plant growth

Studies conducted to understand the different spectral composition on improving biomass and quality of leafy vegetables have focused primarily on red and blue wavelengths, the absorptance maxima of chlorophyll (Fig. 2). Red light (RL) has the highest quantum yield, whereas blue light (BL) is considerably less efficient in driving photosynthesis (Inada, 1976; McCree, 1972). There is a significant loss of BL energy resulting from the absorption by non-photosynthetic pigments, including anthocyanin and accessory photosynthetic pigments that have inefficient energy transfer to chlorophyll (Terashima, Fujita, Inoue, Chow, & Oguchi, 2009). RL induces many physiological responses including leaf development, stomatal opening, chlorophyll and carbohydrate accumulations (Azad et al., 2020; Hogewoning et al., 2010; Lee, Son, & Oh, 2016; Yang, Seaton, Krahmer, & Halliday, 2016). BL influences photosynthetic activity by inducing stomatal opening (Zeiger, Talbott, Frechilla, Srivastava, & Zhu, 2002) and affecting chloroplast movement within the cell (Kasahara et al., 2002) in the short term while increasing stomata number and leaf thickness in the long term
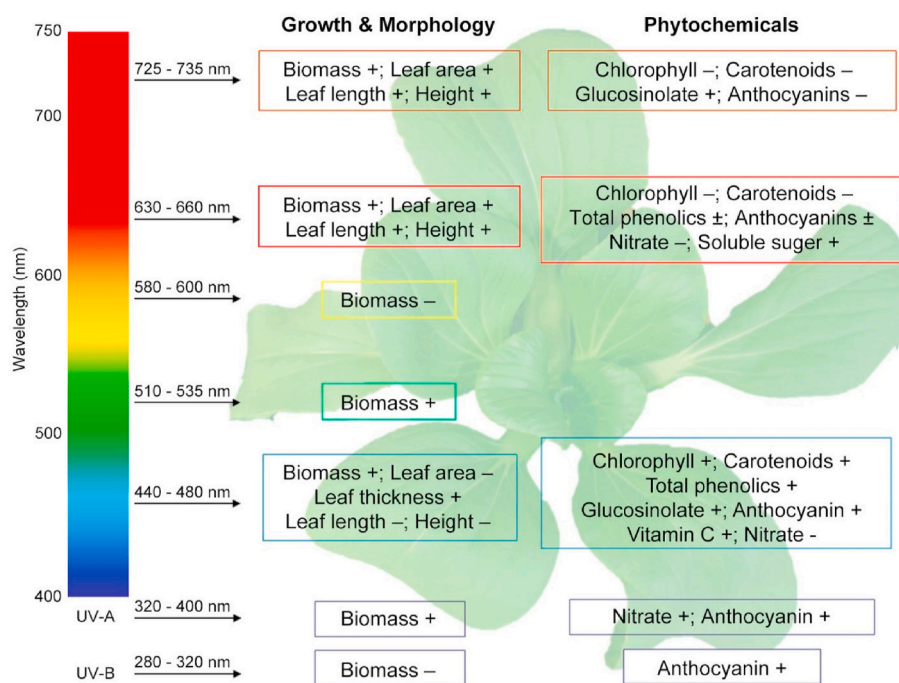
Fig. 3. Responses of leafy greens to different light quality. The effects of an increase in the specific wavelength ranges on growth and phytochemical contents in leafy greens are summarized. These are based on the general trend observed among studies discussed (Table 2). A positive effect is depicted by "+" sign while a negative impact is represented by "-" sign. A "±" sign denotes varying results.

Table 2
Effects of light spectrum on the growth and phytonutrient content of leafy greens.
All light sources are LEDs unless otherwise stated. The composition of white light is given if it was provided by the study cited. The number following each waveband indicates its percentage of the total photosynthetic photon flux density (PPFD) in $\mu mol \cdot m^{-2} \cdot s^{-1}$. The visible wavelengths used in studies cited have peaks typically in the range of 725–735 nm (Fr), 630–660 nm (R), 510–535 nm (G), 440–480 nm (B) unless otherwise stated.

	Lighting conditions	Plant and sampling stage	Effects on growth and morphology	Effects on primary and secondary metabolism	Reference
Far-red	Fr (160 $\mu mol\ m^{-2}\ s^{-1}$) as supplement to W fluorescent (WF) lamp with R/FR = 0.5; 300 $\mu mol\ m^{-2}\ s^{1}$; 12 h light	Lettuce (*Lactuca sativa* cv. Red Cross) 12 DAT (22 DAP)	Compared to WF, dry weight, stem length, leaf length and leaf width were significantly increased by 15%, 14%, 44% and 15%, respectively.	Compared to WF, Fr decreased anthocyanins, carotenoids and chlorophyll levels by 40%, 11% and 14%, respectively.	(Li & Kubota, 2009)
	B, R, Fr or WF lamp at different PPFD of 1, 10, & 100 $\mu mol\ m^{-2}\ s^{-1}$; continuous light	Russian kale (*Brassica napus* L. var. pabularia) 4 DAP	Hypersensitive to Fr light with the shortest hypocotyls compared to B, R and WF, even at a very low PPFD of 1 $\mu mol\ m^{-2}\ s^{1}$.	Fr treatment results compared to other wavelengths: - the highest level of anthocyanin at all PPFD (~2 - 10-fold increase) - the lowest chlorophyll level for PPFD = 10 and 100 $\mu mol\ m^{-2}\ s^{-1}$ - the highest level of total glucosinolates (18 - 42% higher)	(Carvalho & Folta, 2014)
	Fr as supplement to R and B with different R/Fr ratios of 0.7, 1.2, 4.1 and 8.6. $B_{20}R_{80}$; PPFD = 135 $\mu mol\ m^{-2}\ s^{-1}$; 12 h light	Lettuce (*Lactuca sativa* cv. Sunmang) 12 and 24 DAT (26 and 38 DAP)	Compared to $B_{20}R_{80}Fr_0$, R/Fr of all ratios increased leaf area, leaf length and shoot dry weight with the second lowest R/FR ratio of 1.2 producing the highest dry weight (38% increase in shoot and 40% increase in root).	Compared to $B_{20}R_{80}Fr_0$, Fr caused a decrease in chlorophyll content in all treatments (>20% decrease).	(Lee et al., 2016)
	Fr (35 $\mu mol\ m^{-2}\ s^{-1}$) supplemental to W ($B_{20}G_{38}R_{42}$); 180 $\mu mol\ m^{-2}\ s^{-1}$; 18 h light	Lettuce (*Lactuca sativa* cv. Outedgeous) 28 DAT	Compared to W, leaf area, shoot diameter and shoot dry weight were increased by 28%, 17% and 15%, respectively with supplemental Fr.	Compared to W, chlorophyll content was decreased by 24% while there was no difference in carotenoid or flavonoid content under Fr supplementation.	(Mickens et al., 2018)
	W ($B_{20}G_{48}R_{32}$) and W + Fr (34 $\mu mol\ m^{-2} \cdot s^{-1}$); 180 $\mu mol\ m^{-2} \cdot s^{-1}$; 18h light	Red pak choi (*Brassica rapa* var. Chinensis Rubi F1) 28 DAT	No significant changes in shoot dry weight with Fr treatment.	Fr reduced chlorophyll and anthocyanin contents.	(Mickens et al., 2019)
Red	R (130 $\mu mol\ m^{-2}\ s^{1}$) as supplement to WF; 300 $\mu mol\ m^{-2}\ s^{1}$; 12 h light	Lettuce (*Lactuca sativa* cv. Red Cross) 12 DAT (22 DAP)	No significant changes in leaf morphology and shoot dry weight.	Phenolics concentration was increased by 6% with supplemental R.	(Li & Kubota, 2009)
	R_{100} and WF; 100 $\mu mol\ m^{-2}\ s^{-1}$; 14 h light	Lettuce (*Lactuca sativa* L. cv. Banchu Red Fire 7 DAT (17 DAP)	R_{100} treatment results compared to WF: - 33% increase in the leaf area - 30% increase in the shoot dry weight	R_{100} treatment results compared to WF: - 14% decrease in carotenoid content - 69% decrease in chlorogenic acid level - 25% decrease in anthocyanin level - 49% decrease in total antioxidant	(Johkan et al., 2010)
	R (625 nm), B and G at R_{100}, $B_{10}R_{90}$, $B_{20}R_{80}$, $B_{30}R_{70}$, $G_{10}R_{90}$, $B_{10}G_{10}R_{80}$, $B_{20}G_{10}R_{70}$, $B_{30}G_{10}R_{60}$; 150 $\mu mol\ m^{-2}\ s^{-1}$; 16 h light	Lettuce (*Lactuca sativa* cv. Green-skirt) 25 DAT (39 DAP)	R_{100} produced plants with the longest and widest leaves.	ND	(Kang et al., 2016)
	R (636 nm) and B at R_{100}, $B_{20}R_{80}$, $B_{25}R_{75}$, $B_{50}R_{50}$, $B_{25}R_{75}$ & B_{100}; 550 $\mu mol\ m^{-2}\ s^{-1}$; 12 h light	Rapeseed (*Brassica napus* L. cv. Zhongshuang 11 21 DAT (28 DAP)	Compared to $B_{75}R_{25}$, R_{100} and $B_{25}R_{75}$ caused abnormal leaf development with wrinkled blade and down-rolled margin, and decrease in leaf thickness by 38% (palisade layer reduced to one)	Higher starch content in R dominated spectrum and 50% decreases in chlorophyll and carotenoid contents for R_{100} and B_{100} compared to $B_{75}R_{25}$.	(Chang et al., 2016)

Red	W, R, B or B + R (B$_{30}$R$_{70}$); 300 µmol m^{-2} s^{-1}; 14 h light	Lettuce (*Lactuca sativa* cv. Grizzly) 60 DAT	Compared to W, - 80% decrease in dry mass under R$_{100}$ - deformed leaves with excessive hypocotyl elongation and failure of heading formation.	Compared to W, - 80% decrease in total phenolics under R$_{100}$ - 70% increase in vitamin C under R$_{100}$	(Amoozgar et al., 2017)
	R and R + B (B$_{10}$R$_{90}$); 300 µmol m^{-2} s^{-1}; 16 h light	Tatsoi (*Brassica rapa* var. rosularis)	80% increase in dry weight under B$_{10}$R$_{90.}$	3-fold decrease in flavonols and 2-fold increase in soluble sugar under B$_{10}$R$_{90.}$	(Virsile et al., 2019)
	R and B at B$_{17}$R$_{83}$, B$_9$R$_{91}$, B$_5$R$_{95}$ and R$_{100}$; 200 µmol m^{-2}s^{-1}; 16 h light	Lettuce (*Lactuca sativa* L. cv. Buttercrunch), spinach (*Spinacia oleracea*), basil (*Ocimum basilicum*), kale (*Brassica oleracea* var. acephala) 35 DAT	Increasing RL fraction resulted in tall plants with wide, pale green leaves and long petioles. Tallest plant with lowest dry mass under R$_{100}$ except for spinach.	Lowest total chlorophyll content, carotenoid content and antioxidant capacity under R$_{100}$.	(Naznin et al., 2019)
	R and B at B$_{83}$R$_{17}$, B$_{75}$R$_{25}$, B$_{50}$R$_{50}$, B$_{25}$R$_{75}$ and B$_{17}$R$_{83}$; 90 µmol m^{-2} s^{-1}; 16 h light	Lettuce (*Lactuca sativa* var. Lollo rosso) 10 or 20 DAT (25 or 35 DAP)	Increasing RL fraction resulted in an increase of height and leaf area but a decrease in dry weight with the highest and lowest values under B$_{17}$R$_{83.}$	Increasing RL fraction resulted in an increase in carbohydrate content but a decrease in the contents of chlorophyll, carotenoid, anthocyanin, chlorogenic acid and flavonoid, and the effects were most obvious under B$_{17}$R$_{83.}$	(Azad et al., 2020)
Green	Green fluorescent lamp (G*) as supplement to BR: B$_{14}$R$_{86}$ and B$_{14}$G*$_{23}$R$_{63}$; 150 µmol m^{-2} s^{-1}; 18 h light.	Lettuce (*Lactuca sativa* cv. Waldmann's Green) 28 DAP	Compared to B$_{14}$R$_{86}$, supplemental G* increased leaf area and dry weight by 31% and 46%, respectively.	ND	(Kim et al., 2004)
	W (B$_{11}$G$_{41}$R$_{48}$), B$_{12}$G$_2$R$_{86}$ and B$_{14}$G$_{23}$R$_{63}$; 200 µmol m^{-2} s^{-1}; 16 h light.	Lettuce (*Lactuca sativa* cv. Waldmann's Green) 21 DAP	Increasing GL from 2 to 41% resulted in 28% increase in stem length but without any effect on dry weight.	ND	(Snowden et al., 2016)
	W (B$_{20}$G$_{48}$R$_{32}$) supplemented with B, G, R (635 nm) or Fr; 180 µmol m^{-2} s^{-1};18 h light	Lettuce (*Lactuca sativa* cv. Outredgeous) 14, 21 and 28 DAT	WG (B$_{17}$G$_{57}$R$_{25}$) treatment increased biomass early in the growth cycle (14 and 21 DAT), while WR (B$_{16}$G$_{38}$R$_{46}$) increased biomass later in the cycle.	No significant effect of green on the content of macronutrients and micronutrients.	(Mickens et al., 2018)
	W (B$_7$G$_{29}$R$_{54}$Fr$_{10}$), B, G, R (639 + 664 nm) at G$_{33}$R$_{67}$, B$_{11}$R$_{89}$, B$_{19}$G$_{33}$R$_{48}$, B$_{33}$R$_{67}$, B$_{33}$G$_{33}$R$_{33}$, B$_{56}$R$_{44}$, B$_{56}$G$_{33}$R$_{11}$; 180 µmol m^{-2} s^{-1}; 20 h light	Lettuce (*Lactuca sativa* cv. Rouxai) 30 DAT	G decreased shoot dry mass by 20% or more when BL was over 33%.	G did not significantly affect the levels of macronutrient and micronutrient.	(Meng et al., 2020)
	W (R$_{44}$B$_{12}$G$_{44}$), WF (R$_{35}$B$_{24}$G$_{41}$), R$_{88}$B$_{12}$, R$_{76}$B$_{24}$ and R$_{51}$B$_{49}$; 224 µmol m^{-2} s^{-1}; 16 h light	'Siberian' and 'Scarlet' kale (*Brassica napus* var. *pabularia*) 18 and 25 DAT (32 and 39 DAP)	G decreased shoot fresh weight (21-28%) and plant height under 24% B in both cultivars.	G increased and decreased anthocyanin levels in green kale under 12% B and 24% B, respectively. G decreased levels of anthocyanin, phenolics and carotenoids in red kale.	(Dou et al., 2020)
Blue	B (476 nm, 130 µmol m^{-2} s^{-1}) as supplement to white fluorescent lamps; 300 µmol m^{-2} s^{-1}; 12 h light	Lettuce (*Lactuca sativa* cv. Red Cross) 12 DAT (22 DAP)	Compared to WF, stem length and leaf length were decreased with no significant effect on dry weight.	Compared to WF, anthocyanin and carotenoid concentrations were increased by 6 - 8%.	(Li & Kubota, 2009)

Blue	B_{100}, $B_{50}R_{50}$ and WF; 100 µmol m^{-2} s^{-1}; 14 h light	Lettuce (*Lactuca sativa* L. cv. Banchu Red Fire 7 DAT (17 DAP)	Compared to WF: - 44% decrease in the leaf area under B_{100} - 67% decrease in the shoot dry weight under $B_{50}R_{50}$	Compared to WF, - 16% increase in carotenoid content under $B_{50}R_{50}$ - 1.5-fold increase in chlorogenic acid under B_{100} and $B_{50}R_{50}$ - 3-fold increase in anthocyanin levels under $B_{50}R_{50}$ - 2-fold increase in total antioxidant capacity under $B_{50}R_{50}$	(Johkan et al., 2010)
	B_0R_{100}, B_8R_{92}, $B_{16}R_{84}$ and $B_{24}R_{76}$ at PPFD = 210 µmol m^{-2} s^{-1}; 12 h light.	Chinese kale (*Brassica oleracea* var. alboglabra Bailey) 18 DAT (22 DAP)	The highest leaf number, leaf area, leaf mass per unit area, and shoot and root fresh weight and dry weight were observed under $B_{16}R_{84}$.	$B_{16}R_{84}$ resulted in the highest light-saturated photosynthetic CO_2 assimilation rate and stomatal conductance. No significant differences in total chlorophyll and carotenoid content among different BR treatments.	(He et al., 2015)
	W and $B_{30}R_{70}$; 300 µmol m^{-2} s^{-1}; 14 h light	Lettuce (*Lactuca sativa* L. cv. Grizzly) 60 DAT	Compared to W, 75% increase in shoot dry mass under $B_{30}R_{70}$.	Compared to W: - 2-fold increase in total chlorophyll and carotenoid content under $B_{30}R_{70}$. - 70% increase in vitamin C under $B_{30}R_{70}$	(Amoozgar et al., 2017)
	White, B_5R_{95}, and $B_{20}R_{80}$. For $B_{20}R_{80}$ with a varying duration of treatment: 30, 25, 20 and 15 days before harvest. PPFD at 250 µmol m^{-2} s^{-1}; photoperiod not specified	Kale (*Brassica oleracea* var. acephala). 37 DAT	Increasing B fraction produced shorter and more compact kale but with limited impact on yield.	Similar levels of total chlorophyll, carotenoid, and glucosinolate across all treatments.	(Metallo et al., 2018)
	B at different PPFD (0, 50, 100 & 150 µmol m^{-2} s^{-1}) to supplement glasshouse growth (PPFD at noon 1000 µmol m^{-2} s^{-1}); 12 h with B (6:00 - 18:00)	Pak choy (*Brassica rapa* subsp. Chinensis var. communis L. cv. Green- and Red-leaf) 10 DAT (40 DAP)	Compared to B_0, there was 35% increase in dry weight in red pak choi under B_{50}.	Compared to B_0, - vitamin C: at least 5-fold higher in both cultivars under B_{100} - glucosinolates: 75% increase under B_{150} in red pak choi only - total chlorophyll and carotenoids: 20% increase under B_{50} in red pak choi only - nitrate: 50% decrease under B_{150} in red pak choi only	(Zheng et al., 2018)
	B (460 nm, 0, 50, 100, and 150 µmol m^{-2} s^{-1}) as supplement to greenhouse growth conditions	Chinese kale (*Brassica oleracea* var. alboglabra Bailey) 10 DAT (50 DAP)	Compared to B_0, B_{50} and B_{100} resulted in a similar increase in stem diameter (8%), plant height (39%) and shoot DW (34%), while B_{150} produced less than 10% increase in stem diameter and plant height and no significant effect on shoot DW.	Compared to B_0: - chlorophyll and vitamin C content increased by 12% and 54%, respectively, under B_{50} - total phenolics and anthocyanin increased by 27% and 131%, respectively, under B_{150}.	(Li et al., 2019)
	White ($B_{20}G_{48}R_{32}$), R (630 & 660 nm) and B (460 nm); PPFD at 180 µmol m^{-2}·s^{-1}; 18h light	Red pak choi (*Brassica rapa* var. Chinensis, Rubi F1) 28 DAT	Highest biomass and leaf area under $B_{25}R_{75}$.	Highest relative anthocyanin accumulation under $B_{25}R_{75}$	(Mickens et al., 2019)
	W ($B_7G_{29}R_{54}Fr_{10}$), B, G, R (639 + 664 nm) at $G_{33}R_{67}$, $B_{11}R_{89}$, $B_{19}G_{33}R_{48}$, $B_{33}R_{67}$, $B_{33}G_{33}R_{33}$, $B_{56}R_{44}$, $B_{56}G_{33}R_{11}$; 180 µmol m^{-2} s^{-1}; 20 h light	Lettuce (*Lactuca sativa* L.cv. Rouxai) 30 DAT	Compared to $G_{33}R_{67}$, there was 46% and 54% decrease in dry mass at $B_{56}R_{44}$ and $B_{56}G_{33}R_{11}$, respectively. Plant diameter decreased linearly by about 20% with an increasing B. Leaves were narrowest under $B_{56}G_{33}R_{11}$.	An increase in B increased red foliage coloration and the accumulation of macronutrients (e.g., nitrogen & magnesium) and micronutrients (e.g., zinc & copper).	(Meng et al., 2020)
	B and R at $B_{83}R_{17}$, $B_{75}R_{25}$, $B_{50}R_{50}$, $B_{25}R_{75}$ and $B_{17}R_{83}$; 90 µmol m^{-2} s^{-1}; 16h light	Lettuce (*Lactuca sativa* var Lollo rosso) 10 or 20 DAT (25 or 35 DAP)	Plant height, leaf area and biomass were negatively correlated with the proportion of B with the lowest values at $B_{83}R_{17}$.	Levels of chlorophyll, carotenoids, chlorogenic acid, flavonoids and anthocyanin were positively correlated with the proportion of B with the highest values at $B_{83}R_{17}$.	(Azad et al., 2020)

Blue	$B_{25}R_{75}$ and W; 160 µmol m^{-2} s^{-1}; 12h light	Choy sum (*Brassica rapa* subsp. chinensis var. parachinensis) One-leafed, two-leafed and adult (30 DAP) stage	29% increase in relative growth rate at one-leafed seedling stage under $B_{25}R_{75}$ but no significant differences in the subsequent stages.	No significant differences in glucosinolate content.	(Tan et al., 2020)
	W ($R_{44}B_{12}G_{44}$), WF ($R_{35}B_{24}G_{41}$), $R_{88}B_{12}$, $R_{76}B_{24}$ and $R_{51}B_{49}$; 224 µmol m^{-2} s^{-1}; 16 h light	'Siberian' and 'Scarlet' kale (*Brassica napus* var. *pabularia*) 18 and 25 DAT (32 and 39 DAP)	Leaf area, plant height and shoot FW were decreased when B was increased from 12% to 49%.	The concentrations of anthocyanin and phenolics were highest under $R_{76}B_{24}$ and $R_{51}B_{49}$ in green kale but were unaffected by changing B fraction in red kale.	(Dou et al., 2020)
UV	UV-A (18 µmol m^{-2}·s^{-1}) as supplement to WF; 300 µmol m^{-2} s^{-1};12 h light.	Lettuce (*Lactuca sativa* L. cv. R Cross) 12 DAT (22 DAP)	No significant effect on growth parameters.	Anthocyanins concentration increased by 11% under UV-A.	(Li & Kubota, 2009)
	UV-A (3.7 W) and UV-B (4.2 W) as supplement to W; 185 µmol m^{-2} s^{-1}; 12 h light	Lettuce (*Lactuca sativa* L. cv. Hongyeom) 7 DAT (37 DAP) Continuous UV-A treatment for 7 days and only 4 h of UV-B treatment per day for 7 days.	Compared to W, shoot DW increased under UV-A until day 6 while shoot growth was inhibited under UV-B. UV-B also induced significant morphology disorder (wilting and necrosis) even after 1 day of 4 h treatment	Both UV-A and UV-B (2 DAT) induced the accumulation of phenolic compounds and antioxidants.	(Lee et al., 2014)
	$B_{10}R_{88}Fr_2$ and $B_{10}R_{86}Fr_2$ with 6 µmol m^{-2} s^{-1} supplemental UV-A; 300 µmol m^{-2} s^{1}; 16 h light	Green and red leaf lettuce (*Lactuca sativa* L. cv. 'Lobjoits Green Cos' and 'Red Cos') 27 DAP	No significant increase in dry weight with treatment.	UV-A increased nitrite level by 5-fold in Green Cos.	(Virsile et al., 2020)

Blue (B), DAP (day after planting), DAT (day after treatment), DW (dry weight), ND (not determined), Far-red (Fr), Green (G), Red (R), White (W), White Fluorescent (WF).

(Hogewoning et al., 2010; Wang, Lu, Tong, & Yang, 2016). BL is also known to increase the chlorophyll content (Hogewoning et al., 2010; Johkan, Shoji, Goto, Hashida, & Yoshihara, 2010; Matsuda, Ohashi-Kaneko, Fujiwara, & Kurata, 2007). A greater fraction of BL is associated with the development of "sun-type" leaf characterized by a high leaf thickness and photosynthetic capacity (Hogewoning et al., 2010; Matsuda et al., 2007). BL also regulates several plant morphogenic responses including leaf expansion and shoot elongation (Li & Kubota, 2009; Metallo, Kopsell, Sams, & Bumgarner, 2018). Both RL and BL wavelengths can therefore directly affect plant yield by their positive impact on photosynthesis that increases carbon availability for plants and indirectly by giving rise to plant architecture favorable for light interception, which in turn promotes photosynthesis.

A combination of red and blue LEDs routinely used in indoor farming has a relatively higher production efficiency compared to other light sources such as fluorescent lamps with the same light irradiance (Amoozgar, Mohammadi, & Sabzalian, 2017; Johkan et al., 2010; Lee et al., 2016). The optimal ratio between BL and RL is crucial in determining plant productivity and a low B/R ratio generally favours biomass accumulation. In a background of RL, 25% of BL ($B_{25}R_{75}$) has produced red pak choi with greater biomass, leaf area and anthocyanin accumulation compared to white LED (Mickens et al., 2019), while lettuce ('Grizzly') grown under $B_{30}R_{70}$ has 75% increase in biomass when compared to those under white LED (Amoozgar et al., 2017). Kale grown under $B_{20}R_{80}$ increases by 12.5% in dry mass compared to those under white light and shows significant morphological alteration with shorter and more compact plants, which is consistent with BL's roles in inhibiting extension growth (Metallo et al., 2018). The above-ground dry weight is almost doubled in tatsoi when RL is supplemented with 10%

BL (Virsile et al., 2019). In Chinese kale, a 2–3 fold increase in leaf area and shoot dry weight has been reported when RL was supplemented with 18% BL (He, Qin, Liu, & Choong, 2015).

Monochromatic RL environment, however, triggers abnormal plant morphology in lettuce, spinach, kale and basil that includes the development of elongated hypocotyl, long petioles and thin wide leaves with reduced chlorophyll content (Amoozgar et al., 2017; Johkan et al., 2010; Kang, Park, Park, & Son, 2016; Naznin, Lefsrud, Gravel, & Azad, 2019). The impaired development seen in these studies resembles those associated with shade avoidance response that is triggered by low light, a high red to far-red (R/Fr) ratio, low BL or high green light levels in the environment (Wang, Gao, Liu, Fan, & Ma, 2020). Since none of these known triggers are present in the above studies, the absence of BL is likely the cause of the impaired development observed (Kang et al., 2016). Such negative impact on plant growth could result from the lack of coaction among different photoreceptors in regulating normal development, which is perhaps compounded by a dysfunctional photosynthetic machinery in the absence of BL (He et al., 2015; Hogewoning et al., 2010).

Too much BL in the irradiance can also have an adverse effect on plant growth and development. When the proportion of blue LED exceeds 11% in a broad-spectrum background, dry mass and leaf area are decreased for lettuce ('Waldmann's Green'), radish and pepper (Cope, Snowden, & Bugbee, 2014). Similar parameters in two other cultivars of lettuce ('Rouxai' and 'Green Skirt') as well as kale are also negatively correlated with the amount of BL in a red background (Dou, Niu, Gu, & Masabni, 2020; Kang et al., 2016; Meng, Boldt, & Runkle, 2020). An increase from 16 to 24% of BL leads to the reduction in the leaf area and dry weight of Chinese kale grown in a red background (He et al., 2015).

A lower level of irradiance does not seem to negate the effect of high fraction of BL on lettuce ('Lollo Rosso') growth as the leaf area and shoot dry weight decrease significantly as BL fraction is increased from 25% to 50% at 90 μmol m^{-2} s^{-1} (equivalent to 5% of full sunlight) (Azad et al., 2020). Spinach seems to be more vulnerable to BL-induced negative effects compared to lettuce and komatsuna (*Brassica rapa* var. perviridis) as severe reduction in dry weight has been observed under blue fluorescent lamp (Ohashi-Kaneko, Takase, Kon, Fujiwara, & Kurata, 2007). There is thus a species-specific sensitivity to BL and the minimum amount of BL in a red background that is required for proper vegetative development varies for each species or cultivars and needs to be determined to ensure optimal productivity.

4.2. Other visible wavelengths and plant growth

4.2.1. Green wavelength

Green light (GL), unlike RL and BL, can penetrate deeper into a leaf (Sun, Nishio, & Vogelmann, 1998) and canopy (Massa et al., 2015). A higher fraction of GL may thus stimulate photosynthesis deep within a leave and canopy layer, increasing whole-plant photosynthesis. Such increase in photosynthesis is not possible with excess RL or BL due to their strong absorption by chlorophyll in the upper part of the leaf (Terashima et al., 2009). This unique contribution of GL to photosynthesis suggests that it may be beneficial to plant growth and development when used to supplement red and blue irradiation, especially for vegetables that form thick canopy. GL can also act as a shade signal (Sellaro et al., 2010; Zhang, Maruhnich, & Folta, 2011) and it can antagonize a number of BL-induced responses including inhibition of extension growth (Folta, 2004) and stimulation of stomata opening (Talbott, Nikolova, Ortiz, Shmayevich, & Zeiger, 2002).

There is a considerable lack of studies on the effect of supplemental GL on leafy vegetables species other than lettuce, and even these are inconclusive regarding the physiological benefits of GL. A blue and red background (B$_{16}$R$_{84}$) with 24% GL from green fluorescent lamp (B$_{15}$G$_{24}$R$_{61}$) has been shown to increase lettuce ('Waldmann's Green') yield (Kim, Gregory, Raymond, & John, 2004), whereas in another study, an increase of up to 30% green LED light does not influence the dry mass in the same cultivar (Snowden, Cope, & Bugbee, 2016). This discrepancy may be attributed to the different sources of GL used since fluorescent light could confound the effect of GL with associated increases in diffused light and leaf temperature (Snowden et al., 2016). The effect of GL on growth has also been examined at different growth stages. For example, the biomass and shoot diameter of lettuce ('Outredgeous') are significantly increased at 14- and 21-day-after-sowing (DAS) but such effects are no longer significant at maturity (28 DAS) compared to those grown under white LED, suggesting that GL stimulates an early rapid growth of lettuce (Mickens et al., 2018). Similarly, there is significant increase of leaf area in lettuce ('Red Cos') seedlings (3-w-old) with the inclusion of GL in the blue and red irradiance compared to those grown under blue and red only, but this fails to translate to an increase in biomass for mature plants (5-w-old) (Samuoliene, Virsile, Haimi, & Miliauskiene, 2020). These imply that supplemental GL favours growth at seedling stage but as the plant grows and matures, it becomes less sensitive to the growth-promoting effect of GL. In addition, a negative effect of GL (33.3%) on growth of lettuce ('Rouxai') has been found to be dependent on the high BL fraction (33.3%) since lower BL fraction (11.1% or 0%) diminishes such effect (Meng et al., 2020). This inhibitory effect of GL on growth that is dependent on high BL fraction has also been reported in kale (Dou et al., 2020). Thus, the interaction between GL and BL further adds to the complexity in delineating the GL effect quantitatively. Nonetheless, the inclusion of GL is helpful in the dichromatic background of red and blue in a closed production system as it can improve the visual quality by creating a more pleasant white light output that is less harsh on human eyes, making crop inspection more straightforward (Massa, Kim, Wheeler, & Mitchell, 2008).

4.2.2. Yellow wavelength

Yellow light (YL, 580–600 nm) is poorly absorbed by any of the photosynthetic pigments and we know relatively little about the effect of YL on photosynthesis as compared to other wavelengths. Research using green fluorescent lamp includes 500–600 nm wavelengths and therefore contains YL (Dougher & Bugbee, 2001; Kim et al., 2004). These coupled with the low efficiency of yellow LEDs (Jiang et al., 2019) could explain the scarcity of studies exploring the use of YL in the cultivation of leafy greens. Yellow wavelength (ranging from 20 to 30% of photosynthetic photon flux density (PPFD) = 200 and 500 μmol m^{-2} s^{1}) from high-pressure sodium lamp and metal halide lamp has been reported to inhibit growth in lettuce ('Grand Rapids') by suppressing chlorophyll formation (Dougher & Bugbee, 2001), while a more recent study shows minimal effect of YL (6.7% of PPFD = 300 μmol m^{-2} s^{1}) on lettuce ('Red & Green Cos') growth and biomass production (Virsile et al., 2020). In another cultivar ('Green Oakleaf'), supplemental YL (30% of PPFD = 135 μmol m^{-2} s^{1}) inhibits growth compared to those under white LED (Chen, Xue, Guo, Wang, & Qiao, 2016). Thus, YL negatively impacts on lettuce growth at high fraction. The effect of YL on the growth of other leafy greens as well as on the accumulation of phytonutrients await further investigation. Such studies will be facilitated with the recent development of a more efficient light source (Jiang et al., 2019).

4.2.3. Far-red wavelength

Far-red (Fr) light is minimally absorbed by leaves and it has a low quantum efficiency in photosynthesis on its own (McCree, 1972). Recent studies have revealed that Fr light can drive photosynthetic activity in photosystem II (Pettai, Oja, Freiberg, & Laisk, 2005; Thapper, Mamedov, Mokvist, Hammarström, & Styring, 2009) and enhance photosynthesis under shorter wavelength by promoting a balanced excitation of the two photosystems (Zhen & van Iersel, 2017). Fr can also act as a photomorphogenic signal by modulating phytochrome activity as Fr converts phytochromes to their inactive forms (Pr; Fig. 2). Fr can thus modulate RL responses; in particular, R/Fr ratio can be altered to control flowering (Craig & Runkle, 2013) and a low R/Fr ratio can elicit shade-avoidance responses (Franklin, 2008).

Studies conducted on the effect of Fr have largely supplied additional Fr irradiance (35–160 μmol m^{-2} s^{-1}) in addition to the total PPFD in the comparison treatment while keeping the PPFD of the PAR region constant (Lee et al., 2016; Li & Kubota, 2009; Mickens et al., 2018). Increase in biomass has been reported for three different cultivars of lettuce grown under supplemental Fr and this is correlated with an increase in leaf area and leaf length, likely enhancing light interception (Lee et al., 2016; Li & Kubota, 2009; Mickens et al., 2018). There is, however, the possibility that the increase in growth observed could have resulted from the increased photosynthetic activity due to the additional irradiance of Fr light supplied compared to the controls. Intriguingly, all three studies have also reported reduction in chlorophyll content that are attributed to a dilution effect resulting from rapid leaf expansion. This reduction in leaf chlorophyll content by Fr has also been reported in red pak choi even though Fr does not increase yield and leaf areas compared to other treatments (Mickens et al., 2019). Fr treatment also results in the lowest level of chlorophyll accumulation in kale seedlings compared to white, blue or red light (Carvalho & Folta, 2014). Fr could thus be inhibitive on the synthesis of chlorophyll.

4.3. Light quality and phytochemicals

Leafy greens are rich in essential nutrients such as vitamins and minerals, and a diverse group of health-promoting secondary metabolites. The latter has garnered much interest largely due to their antioxidant activity in detoxifying reactive oxygen species that would otherwise cause oxidative damage to bio-molecules, contributing to the development of cancer, neurodegenerative, ageing-related and cardiovascular diseases (Barnham, Masters, & Bush, 2004; Liguori et al., 2018; Sosa et al., 2013). Extensive studies have illustrated the utility of LED

lighting technology in enhancing accumulation of various phytonu-trients (Fig. 3 and Table 2) and we shall elaborate on this with an emphasis on secondary metabolites.

4.3.1. Phenolic acids and flavonoids

Secondary metabolites are vital to the maintenance of plant fitness as they function in the protection of plants against biotic (for example, microbial pathogen and herbivory) and abiotic stresses (for example, high light and drought). They also contribute to the organoleptic quality (colour, taste, and aroma) of plant-derived products. There are three main categories of secondary metabolites in plants, which are 1) phe-nolics, 2) carbon-based terpenoids and 3) nitrogen or sulfur containing compounds such as the alkaloids or glucosinolates, respectively. These are produced from pathways of different primary metabolites including glycolysis, pentose phosphate pathway and shikimate pathway (Pott, Osorio, & Vallarino, 2019, Fig. 4). Light affects the accumulation of secondary metabolites directly via influencing the expression levels of structural as well as regulatory genes involved in the biosynthesis of these compounds (Cominelli et al., 2008; Fuglevand, Jackson, & Jen-kins, 1996; Morales et al., 2013). As carbohydrates are basic compounds required to produce secondary metabolites, light also influences the accumulation of secondary metabolites indirectly by affecting the availability of carbohydrate through photosynthesis even though excess carbohydrate has been reported to be "a necessary but insufficient trigger for increased secondary metabolism" (Fajer, Bowers, & Bazzaz, 1992).

The most studied phenolic compounds with regards to the lighting quality effect on leafy greens are phenolic acids and flavonoids, a very diverse class of secondary metabolites that can be largely divided into colourless and colored compounds (for example, anthocyanins and fla-vanols). Some phenolic acids and colourless flavonoids absorb radiation primarily in the UV-B range, whereas anthocyanins are pigments that absorb light in the blue-green wavelengths and thereby provides attractive colorations to many fruits and vegetables, including various red/purple varieties of lettuce, kale and pak choi. These compounds can serve as sunscreen protecting plants against harmful UV light and in the case of anthocyanins, they are also known to protect photosynthetic plant tissues against photoinhibition by attenuating the amount of light from reaching the chlorophyll (Steyn, Wand, Holcroft, & Jacobs, 2002).

The positive impact of blue wavelengths on secondary metabolism is well-documented. BL has been consistently shown to enhance the accumulation of phenolic compounds in several species of leafy greens ranging from lettuce, pak choi, Chinese kale to tatsoi at seedling or adult growth stages (Li et al., 2019; Li & Kubota, 2009; Qian et al., 2016; Vaštakaitė et al., 2017; Zheng et al., 2018). Notably, the BL-induced anthocyanin accumulation may be inhibited by the addition of green wavebands although this inhibition is genotype-dependent (Carvalho & Folta, 2016). As these phenolics can function as UV screen, it is little surprising that UV light is also effective in stimulating the accumulation of such compounds (Lee, Son, & Oh, 2014; Li & Kubota, 2009). Both supplemental UV-A and UV-B enhance the accumulation of anthocya-nins in lettuce but UV-B induces wilting and necrosis with just one day of 4 h UV-B treatment (Lee et al., 2014; Li & Kubota, 2009). Meanwhile, RL has a modest effect on the accumulation of total phenolics in lettuce (Li & Kubota, 2009), while a 3-day pre-harvest RL treatment has a more pronounced effect on the level of total phenolics in lettuce grown in greenhouse conditions in winter (Samuoliene, Sirtautas, Brazaitytė, Viršilė, & Duchovskis, 2012). However, similar treatment does not alter the level of total phenolics in spinach and rocket (Bliznikas et al., 2012). RL thus has a less pronounced positive impact on total phenolics as compared to BL or UV and in fact, an increase in the proportion of RL is largely correlated with a decrease in the accumulation of anthocyanins,
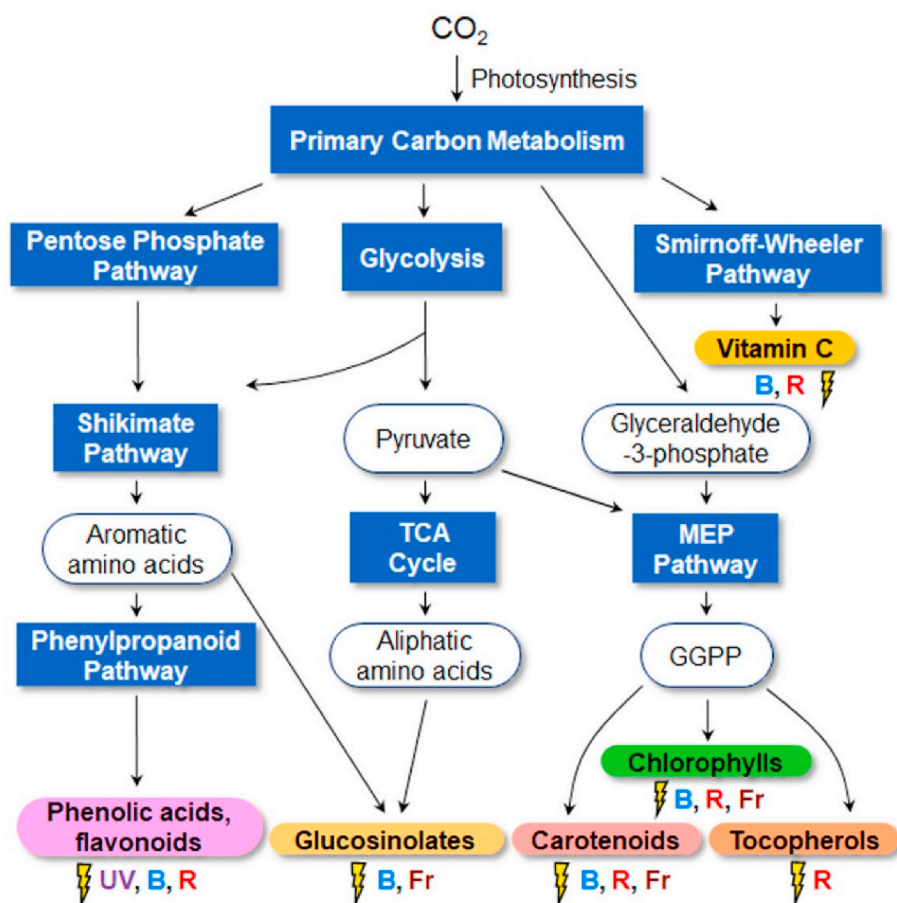

Fig. 4. A brief overview of the biosynthesis of phy-tonutrients. The simplified diagram illustrates the interconnectedness between the primary and sec-ondary metabolic pathway. Blue boxes and white rounded rectangles represent chemical pathways and intermediates, respectively. Colored rounded rectan-gles represent phytonutrients or bioactive com-pounds. The light spectra that have been reported to influence the accumulation of phytonutrients are indicated below (see also in Table 2). Abbreviations: B, Blue light; Fr, Far-red light; GGPP: Geranylgeranyl pyrophosphate; MEP: Methylerythritol phosphate; R: Red light; TCA: Tricarboxylic acid; UV, Ultraviolet light.

chlorogenic acid and flavonoid compounds in lettuce (Azad et al., 2020).

The BL- and UV-mediated changes in phenolic compound levels may be attributed to their ability to induce the gene expression of phenyl-alanine ammonia lyase (PAL), a key enzyme involved in the first step of the phenylpropanoid pathway that serves as the starting point for the biosynthesis of a wide range of phenolic compounds, and to enhance PAL activity post-transcriptionally (Cominelli et al., 2008; Guo & Wang, 2010; Lee et al., 2014; Morales et al., 2013). Both spectra have also been found to induce the transcript accumulation of chalcone synthase, the first enzyme committed to the flavonoid pathway and a number of genes involved in anthocyanin biosynthesis (Cominelli et al., 2008; Fuglevand et al., 1996; Morales et al., 2013). These transcriptional regulations are believed to be mediated by cryptochromes (Fuglevand et al., 1996) and may also involve the UV-B specific photoreceptor, UVR8 (Morales et al., 2013).

4.3.2. Glucosinolates

Glucosinolates are unique to brassicas and their breakdown products are potential protective agents against carcinogenesis and heart disease (Fujioka, Fritz, Upadhyaya, Kassie, & Hecht, 2016). Total glucosinolate levels are similar for kale and choy sum grown under blue and red LEDs with those cultivated under white LEDs (Metallo et al., 2018; Tan et al., 2020) but similar dichromatic environment has been reported to elevate the total glucosinolate level by two folds in sprouting broccoli compared to those grown under the full-spectrum fluorescent/incandescent light (Kopsell, Sams, Barickman, & Morrow, 2014). UV-B irradiation can also be used to increase levels of glucosinolates in broccoli sprouts (Mewis et al., 2012). The positive impact of monochromatic Fr, R or B on the accumulation of total glucosinolates has also been reported in Russian kale seedlings (Carvalho & Folta, 2014). Moreover, short period BL treatment has been shown to increase total glucosinolate levels. A 10-day preharvest treatment with blue LEDs at different photon flux (50, 100 and 150 μmol m^{-2} s^{-2}) of greenhouse-grown pak choi has been shown to result in a modest increase in total glucosinolates (10–17%) in the green variety and a marked increase (35–75%) in red pak choi (Zheng et al., 2018). There are thus genotype-dependent differences of the stimulatory effect of BL on the accumulation of glucosinolates. Moreover, it is likely that sustained maintenance of high levels of glu-cosinolates induced by blue light throughout the growth cycle is meta-bolically costly and hence short-term pre-harvest treatment with monochromatic blue light may represent a better option in enhancing the accumulation of glucosinolates in some species of leafy greens such as choy sum or kale.

4.3.3. Carotenoids

Carotenoids are a family of antenna pigments that are crucial in light harvesting by absorbing in the blue-green (480–580 nm) spectral region. These pigments are essential for the photoprotection of chlorophylls against excess light by quenching their energetic triplet state. Xantho-phylls (including lutein) and β-carotene (the precursor for vitamin A) are two major carotenoids and besides antioxidant effects, they are also vital in reducing the risk of age-related eye diseases (Abdel-Aal, Akhtar, Zaheer, & Ali, 2013).

Long-term growth under monochromatic BL or RL have deleterious effects on the total content of both chlorophyll and carotenoids in leafy greens including rapeseed, lettuce, spinach and kale, with concomitant negative impacts on biomass accumulation (Amoozgar et al., 2017; Chang et al., 2016; Naznin et al., 2019). A dichromatic spectral composition of red and blue is optimal for the accumulation of these pigments. For example, total chlorophyll and carotenoid content of lettuce is more than double under $B_{30}R_{70}$ compared to that under white or R_{100} (Amoozgar et al., 2017). A higher B/R ratio has also been re-ported to enhance the accumulation of both pigments in three different lettuce cultivars when the effects of different ratios of B/R were exam-ined (Azad et al., 2020; Spalholz, Perkins-Veazie, & Hernández, 2020). When red pak choi grown in the greenhouse has been supplemented

with BL (50 μmol m^{-2} s^{-1}) for 10 days before harvest, there is an 20% increase in both pigments but further increase in the dose of BL has a negative impact on the pigment levels (Zheng et al., 2018). This stim-ulatory effect of moderate dose of BL is likely species-dependent as minimal effect has been observed in the green variety of pak choi in the same study (Zheng et al., 2018) or kale with similar treatment (Li et al., 2019). Similarly, the growth under white or dichromatic BR environ-ment has resulted in kale with similar accumulation of both pigments (Metallo et al., 2018).

4.3.4. Anti-nutritional compounds

While the manipulation of light spectrum could enhance the accu-mulation of phytonutrients in leafy greens, there is a risk of enriching non-target phytochemicals including nitrates and oxalates under such growth environment. Nitrate is a natural component of plant tissues that could be harmful to human health when daily intake exceeds certain threshold as nitrate is a source of carcinogenic nitrosamines via nitrites (Bruning-Fann & Kaneene, 1993). Spectral combinations of blue and red that are favorable for plant growth and photosynthesis result in low level of nitrates likely due to an increase in sugars that provide energy and carbon skeleton for nitrogen metabolism (Bian, Cheng, Wang, Yang, & Lu, 2018; Virsile et al., 2019; Zheng et al., 2018). RL has also been re-ported to stimulate nitrate reductase activity that could lead to a decrease in nitrate level (Signore, Bell, Santamaria, Wagstaff, & Van Labeke, 2020). On the contrary, UV-A and low light environment (100 μmol m^{-2} s^{-1}) have been reported to enhance nitrate level by 3–5 fold (Virsile et al., 2019, 2020). Oxalate salt is a natural substance derived from oxalic acid in many plants and it is a substance of concern for human health because soluble oxalate can lead to the formation of kidney stones (Franceschi & Nakata, 2005). Oxalate level is high in spinach (800–1257 μmol/gFW) (Siener, Hönow, Seidler, Voss, & Hesse, 2006) while low in lettuce (0.01–0.17 μmol/gFW) (Miyagi, Uchimiya, & Kawai-Yamada, 2017). The accumulation of oxalate is thus of relevance for indoor cultivation of spinach. In spinach, low light intensity has been shown to enhance oxalate level by 25% (Proietti, Moscatello, Leccese, Colla, & Battistelli, 2004). Therefore, levels of anti-nutritional com-pounds in plant products must be assessed especially when low light cultivation is used.

4.4. Light intensity and photoperiod

Most studies with LEDs have been conducted using PPFD between 150 and 300 μmol m^{-2} s^{-1} (7.5–15% of full sun). Higher irradiance within limits is generally correlated with a higher growth rate of leafy greens as it provides additional photons to drive photosynthesis result-ing in increased biomass accumulation. This is exemplified by an almost linear increase in tatsoi dry weight and leaf area when the PPFD (con-sisting of 10% BL) has been increased from 100 to 300 μmol m^{-2} s^{-1} and beyond which an increase in PPFD has little effect on these parameters (Virsile et al., 2019). Irradiance higher than 300 μmol m^{-2} s^{-1} may have reached a light saturation point with a decrease in photosynthetic effi-ciency and hence a decline in light use efficiency. Similar linear in-creases in kale and spinach biomass have also been reported as irradiance was raised from 125 to 620 μmol m^{-2} s^{-1} but the phytonu-trients accumulation including lutein, β-carotene and chlorophyll was saturated at 335 μmol m^{-2} s^{-1} for kale, and 200 μmol m^{-2} s^{-1} for spinach (Lefsrud, Kopsell, Kopsell, & Curran-Celentano, 2006).

Photoperiod is an environmental cue that regulates flowering (Bao et al., 2019; Chen et al., 2020; Li, Liu, Teo, Shen, & Yu, 2020; Liu, Li, Teo, Zhang, & Yu, 2019). It has been modulated to promote flowering in indoor ornamental crops (Lopez, Meng, & Runkle, 2020) and shorten generation time in crop breeding (Jähne, Hahn, Würschum, & Leiser, 2020). However, photoperiod is a relatively unexplored parameter in studies determining the lighting effect on the indoor cultivation of leafy greens. This is likely due to the less pronounced effect of photoperiod on the growth and phytonutrients accumulation when compared to light

quality and quantity (Kang, KrishnaKumar, Atulba, Jeong, & Hwang, 2013; Viršilè et al., 2019). This indicates that photoperiods routinely used (14–18 h light) are already at the optimal levels and thus any deviation has not yielded significant benefits during vegetative growth of leafy greens.

Even though all tested daily light integrals are only a fraction of that of the full sun, leafy greens grow well under such so-called low light conditions. As demonstrated by the above studies, a higher irradiance may result in higher biomass, but the accumulation of phytonutrients could be saturated at a lower irradiance. Furthermore, electric lighting can account for a significant production cost and thus there is little incentive to use high PPFD or prolonged photoperiod in a closed production system in order to make such system economically viable and environmentally sustainable.

4.5. Postharvest preservation

Postharvest treatment of leafy greens with different visible light wavelengths improves the preservation of vegetables by maintaining the nutritional and sensory quality. Continuous white LED treatment at low irradiance ($10\,\mu mol\,m^{-2}\,s^{-1}$) could delay senescence and increase levels of glucosinolates in postharvest pak choi as the expression of genes related to photosynthesis, chlorophyll and glucosinolate synthesis is upregulated when compared to those stored under dark (Yan et al., 2020). Even 1 h pulses of either white or red fluorescent light (20–25 $\mu mol\,m^{-2}s^{-1}$) daily resulted in purple kale with higher nutrients including chlorophyll, soluble sugar and protein compared to untreated control (Barcena, Martinez, & Costa, 2019). UV light has also been used successfully in sterilizing plant products (Deng et al., 2019). There are thus broad applications associated with light quality for the postharvest preservation of vegetables.

5. Summary and future perspectives

Closed production systems using a basal lighting of blue and red LEDs are conducive to high yield of leafy greens with enhanced accumulation of phytonutrients. BL has a more prominent positive influence on the accumulation on phytonutrients than RL while there is a significant knowledge gap of the influence of other wavelengths. The synergistic effects of different wavelengths on photosynthesis (Zhen & van Iersel, 2017) also means there is scope for improving the productivity of this system by incorporating green and Fr wavelengths, for instance, which could optimize photosynthesis despite our lack of understanding of the interaction among different wavelengths. Moreover, instead of using a one-size-fits-all approach, lighting recipes targeting different growth stages should be determined for different species. For example, a high fraction of BL seems to be essential for seedling establishment in lettuce (Johkan et al., 2010), while the inclusion of green and Fr wavelengths with a decrease in BL fraction following seedling establishment could promote rapid leaf expansion which increases the radiation capture. As GL can penetrate deeper into the canopy, GL irradiation would be beneficial following canopy closure and for high density planting, whereas BL treatment could increase the accumulation of phytonutrients before harvest.

The global indoor farming industry was valued at USD 26.8 billion in 2018 and is projected to grow at a CAGR of 9.19% from 2019 to 2025 (Grand View Research, 2019). It will continue to grow amidst uncertainties such as climate change and food supply chain disruption. In this emerging field, we are expecting to see research and development expenses taking up bulk of the early operating expenses of companies in this industry, and new players, other than growers, taking niche roles such as incubators or technology providers to support the indoor farming ecosystem.

Indoor farming technology is now rapidly evolving in numerous aspects. The first generation of indoor farming has focused on the controlling and monitoring of lighting, nutrients, temperature and humidity. We are beginning to see growers implementing new technologies to collect and analyse data to optimize yield. This can be classified under plant phenotyping which is an emerging field that links physiology to genomics and agronomy (Fiorani & Schurr, 2013). Plant phenotyping using hyperspectral imaging involves the acquisition of certain reflected light wavelengths to determine the profile of certain groups of molecules (Fahlgren, Gehan, & Baxter, 2015). This non-invasive metabolomics method can provide useful real-time information to growers regarding plant development and stress conditions. A recent study has reported a non-invasive, real-time remote sensor that could track crop growth based on chlorophyll fluorescence (at red and far-red wavelength) and the resulting data could be integrated into tunable LED lighting control systems (Urschel & Pocock, 2018). In other cases, reflectance near the near-infrared range is mostly influenced by the leaf structure and reflectance in the ultraviolet range can determine the content of phenolics and flavonoids (Brugger et al., 2019; Slaton, Raymond Hunt, & Smith, 2001). In addition, the current indoor agriculture mainly relies on legacy crop varieties selected or bred for field conditions, under which breeding for phenotypic stability and the resulting consistent production are priorities in a changing environment (Folta, 2019). Most crop varieties currently produced in indoor farms are not the ideal cultivars suited for controlled environments, under which breeding priorities focus on a different set of plant traits, including growth rate, crop yield and phytonutrient level. There is thus a need to breed varieties for controlled environment farming. The rapidly developing gene editing technology could be key to develop these new varieties. With a multi-level technological strategies of optimal light wavelength selection, genomics and automation, we are seeing the light for leafy greens and expect new players in the market.

Funding

Declaration of competing interest

The authors declare that there is no conflict of interest regarding the publication of this article.

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