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Review – Thematic Issue

Considerations of utilizing far-red light in the production of leafy-green vegetables indoors

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Summary

Utilizing far-red (FR; 700–750 nm) light can increase the energy-use efficacy and economic viability of indoor vertical farms because it increases photosynthesis and promotes extension growth, which leads to greater photon capture and biomass accumulation. In addition, discrete FR light-emitting diodes (LEDs) offer high photon flux efficacy. However, trade-offs often exist with FR light including undesirable decreases in phytochemical concentrations, foliage coloration, and shelf life. Therefore, a comprehensive understanding of the potential advantages and disadvantages of FR light is important when utilizing FR light in indoor leafy-green vegetable production. A meta-analysis of scientific publications indicates that FR light increases leaf length to a greater degree than leaf area per plant. The analysis also showed that FR light promotes biomass accumulation but to a lesser extent than morphological alterations. This review discusses FR light descriptions and estimators and summarizes research-based information on its effects on leafy-green species grown under sole-source lighting including plant morphology, growth and biomass accumulation, phytochemical concentration, foliage pigmentation, and shelf and storage life. In addition, differences between FR light substitution and supplementation are discussed from both research and practical perspectives.

Keywords
controlled-environment agriculture, phytochemicals, phytochromes, pigmentation, plant factory, shade-avoidance response, shelf life, vertical farming

Significance of this study

What is already known on this subject?

- Far-red (FR) light generally promotes elongation growth and biomass accumulation of indoor leafy greens by inducing shade-avoidance responses.

What are the new findings?

- Based on a meta-analysis of published data, FR light increases leaf length to a greater degree than leaf area per plant, promotes biomass accumulation, but also decreases foliage coloration.

What is the expected impact on horticulture?

- This review discusses the potential and practical advantages and constraints of including FR in an indoor lighting spectrum when producing leafy green vegetables indoors, under sole-source lighting. Horticulture practitioners can better understand trade-offs that exist when delivering FR light to their crops.

Introduction

Plants perceive the photon spectrum through various photoreceptors and interpret the information to respond to the light environment. Phytochrome photoreceptors, which become active when absorbing red (R; 600–699 nm) light and become inactive when absorbing far-red (FR; 700–750 nm) light, play crucial roles in sensing shade created by nearby plants. Phytochrome exists as a photoequilibrium between the R-absorbing (P_R) and FR-absorbing (P_{FR}) forms, and its status can be estimated based on the photon spectrum and phytochrome absorption. Compared to sunlight, light that penetrates a plant canopy has a relatively higher proportion of FR than R light, which increases the relative amount of inactive phytochromes and creates a relatively low phytochrome photoequilibrium (Legris et al., 2016; Klose et al., 2020). In this shade (low R:FR light) environment, genes related to stem extension and leaf elongation growth are triggered to increase the capture of light.

Despite the important roles of FR light in regulating plant morphology, FR light has not been commonly utilized when growing plants indoors (without sunlight) in vertical farms. Until recently, the only way to deliver FR light was by incandescent (tungsten-filament) bulbs that are highly energy inefficient. However, the development of commercialized FR light-emitting diodes (LEDs) with narrow wavebands and a high photon flux efficacy enables the application of FR light indoors. FR LEDs are much less commonly used than white (W), blue (B; 400–499 nm), and R LEDs partly due to a lack of comprehensive information on the effects of FR light on indoor-grown crops such as leafy-green vegetables. Therefore, the effects of FR LEDs and FR light on the various aspects of indoor leafy greens production merits review.

FR light can increase the growth and biomass accumulation of various plant species including several indoor leafy-green vegetables such as lettuce (*Lactuca sativa*) and kale (*Brassica oleracea* and *Brassica napus*). For example, adding FR light to W light increased the shoot fresh mass of red-leaf lettuce 'Red Butter' and green-leaf lettuce 'Little Gem' by up to 97% and 79%, respectively (Li et al., 2021; Liu and Van Iersel, 2022). In addition, substituting 20 µmol m^{-2} s^{-1} of green (G; 500–599 nm) light with FR light increased the fresh mass of kale 'Siberian' by 13% (Meng et al., 2019). However, several studies have reported a slight decrease in indoor leafy green biomass when supplemented with FR light or when

other wavebands were substituted by FR light (Meng et al., 2019). Therefore, to clarify the effects of FR light on indoor leafy-green vegetable growth and biomass accumulation, the effects of FR light need to be comprehensively examined.

Along with the changes in morphology and growth, FR light also can induce phytochemical changes in indoor leafy-green species. For example, supplemental FR light decreased the concentrations of chlorophylls, anthocyanins, and carotenoids (xanthophylls and β-carotene) in lettuce 'Red Cross' (Li and Kubota, 2009). Similarly, supplemental FR light decreased chlorophylls, carotenoids, phenolics, flavonoids, and ascorbic acid in lettuce 'Tiberius' (Zou et al., 2023). Some of these phytochemicals are major phytopigments that determine the visual color of the leafy-green products. In addition, some have antioxidant activity, which can be health-promoting for humans and useful for plants to reduce oxidative damage and thus can increase shelf life (Zou et al., 2023). Since visual color, phytonutrient concentration, and shelf life of indoor leafy green vegetables can impact consumer preference and product marketability, the effects of FR light on these attributes also need to be reviewed.

Here, we describe the physical properties of FR LEDs and discuss FR light descriptions and estimators. In addition, we describe overall trends of how FR light regulates plant morphology, growth, and biomass accumulation of indoor leafy-green vegetables. We also describe the effects of FR light on quality attributes of such crops such as phytochemical content, foliage color and texture, and shelf and storage life. Finally, we mention additional considerations about incorporating FR LEDs in indoor leafy-green production.

Physical properties of FR LEDs

LEDs have a heterostructure consisting of positive (p) and negative (n) types of semiconductors, which allow electron flow between the two. When the electrons coming from an n-type semiconductor are combined with holes in a p-type semiconductor, the electrons dissipate part of their energy. Some proportion of the dissipated energy is converted into light and enables LEDs to emit light. The materials of semiconductors determine the color of emitted light. LEDs made with semiconductors composed of aluminum gallium indium phosphide (AlGaInP) and aluminum gallium arsenide (AlGaAs) can efficiently generate FR light and are used for making discrete FR LEDs (Samsung Electronics, 2022a; ams-OSRAM, 2023a).

Discrete FR LEDs emit a relatively narrow waveband of light with a peak around 727 to 735 nm (Figure 1A). W LEDs can also emit FR light, but this is at the entails of the emitted spectrum and most of the FR light has a wavelength <720 nm. For example, when considering the 400–800 nm waveband, cool-W and warm-W LEDs emit about 3% and 11% as FR light, respectively. Therefore, the only practical way to deliver a spectrum enriched with FR light indoors is with FR LEDs. In addition, since the emission and centroid wavelength of currently marked FR LEDs aligns with the action spectrum of the P_{FR} (active) form of phytochrome (Figure 1A), they effectively regulate growth and morphology in indoor leafy-greens production.

FR photons have less energy than those in the photosynthetically active radiation (PAR; 400–700 nm) waveband because of their longer wavelengths, according to the Planck equation ($E=hc/\lambda$, where E is photon energy, h is the Planck constant, c is the speed of light in a vacuum, and λ is the wavelength). Partly because of the low energy of FR photons, modern FR LEDs have a photon flux efficacy as high as the efficacy of R LEDs and higher than the efficacy of B and W LEDs (Figure 1B). This means that FR LEDs can produce a greater number of photons per unit of energy input (μmol J^{-1}) than most other types of LEDs. Therefore, if photons generated by FR LEDs can be equally or more efficiently used by plants compared to those generated by other types of LEDs, their utilization can increase electricity-use efficacy in indoor leafy-greens production.

FR light descriptions and estimators

FR light is commonly defined as the photon flux density (PFD) within a 100-nm waveband and is reported as the number of FR photons per square meter and second (μmol m^{-2} s^{-1}). However, practically all morphological and photosynthetic responses to FR are with photons within a 50-nm waveband, from 700 to 750 nm, and thus, some recent studies have reported this waveband. Some older publications

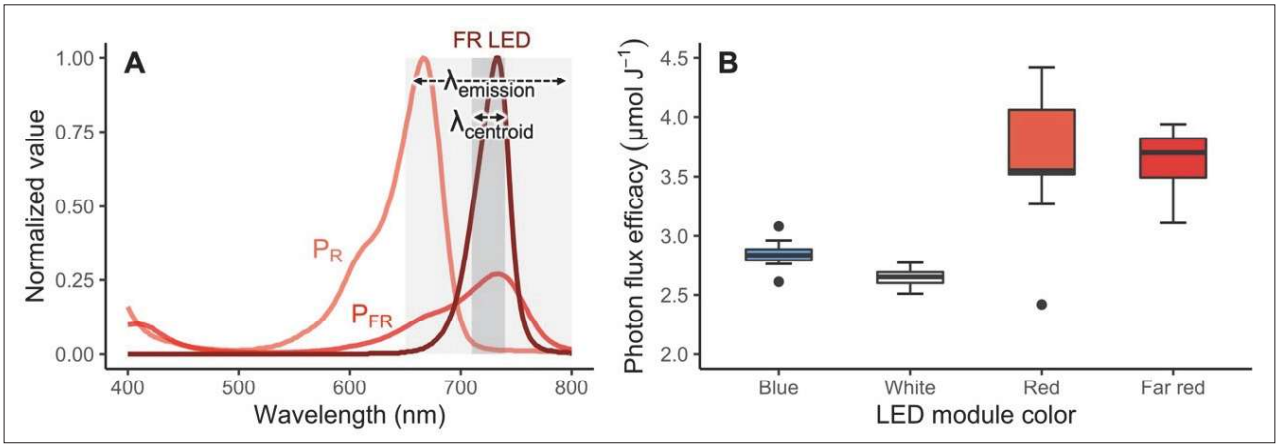


Figure 1. The emission ($\lambda_{emission}$) and centroid ($\lambda_{centroid}$) spectrum of common far-red (FR) LEDs compared to the action spectrum and normalized response of two different phytochrome monomers, the red (R) and FR absorbing forms (P_R and P_{FR}, respectively) (A) and photon flux efficacy of common commercial LEDs for horticultural use at a forward current of 350 mA and a junction temperature of 25°C (B). Boxes, lines in boxes, round symbols, and whiskers represent the interquartile range, median, outliers, and minimum and maximum values excluding outliers, respectively. Photon efficacy and emission and centroid wavelength data were derived from manufacturer websites (LUMILEDS, 2021; Samsung Electronics, 2022b; ams-OSRAM, 2023b; CREE LED, 2023). The action spectrum and the normalized response of phytochrome monomers are from Sager et al., 1998.

have reported an even shorter waveband for FR light, e.g., 725–735 nm, however, this excludes potential direct photosynthetic responses with short-wavelength FR photons and thus is not recommended. We suggest publications measure and report the FR-PFD as a 50-nm waveband and then optionally as a 100-nm waveband.

In addition to the FR-PFD, the R to FR PFD ratio (R:FR), FR fraction [FR-PFD/(R+FR-PFD)], and estimated phytochrome photoequilibrium (PPE) are used to measure and estimate the effects of FR light on modulating plant growth and morphology. FR-PFD can be used as an estimator of the effects of FR light on plant morphology when the PFDs of additional light wavebands remain constant (Meng and Runkle, 2019; Liu and Van Iersel, 2022). However, FR-PFD has limitations in estimating the effects of FR light on plant morphology and photosynthesis when B, G, and/or R PFDs change because photoreceptor (e.g., chlorophyll and phytochrome) responses also depend on other wavebands (Figure 1A).

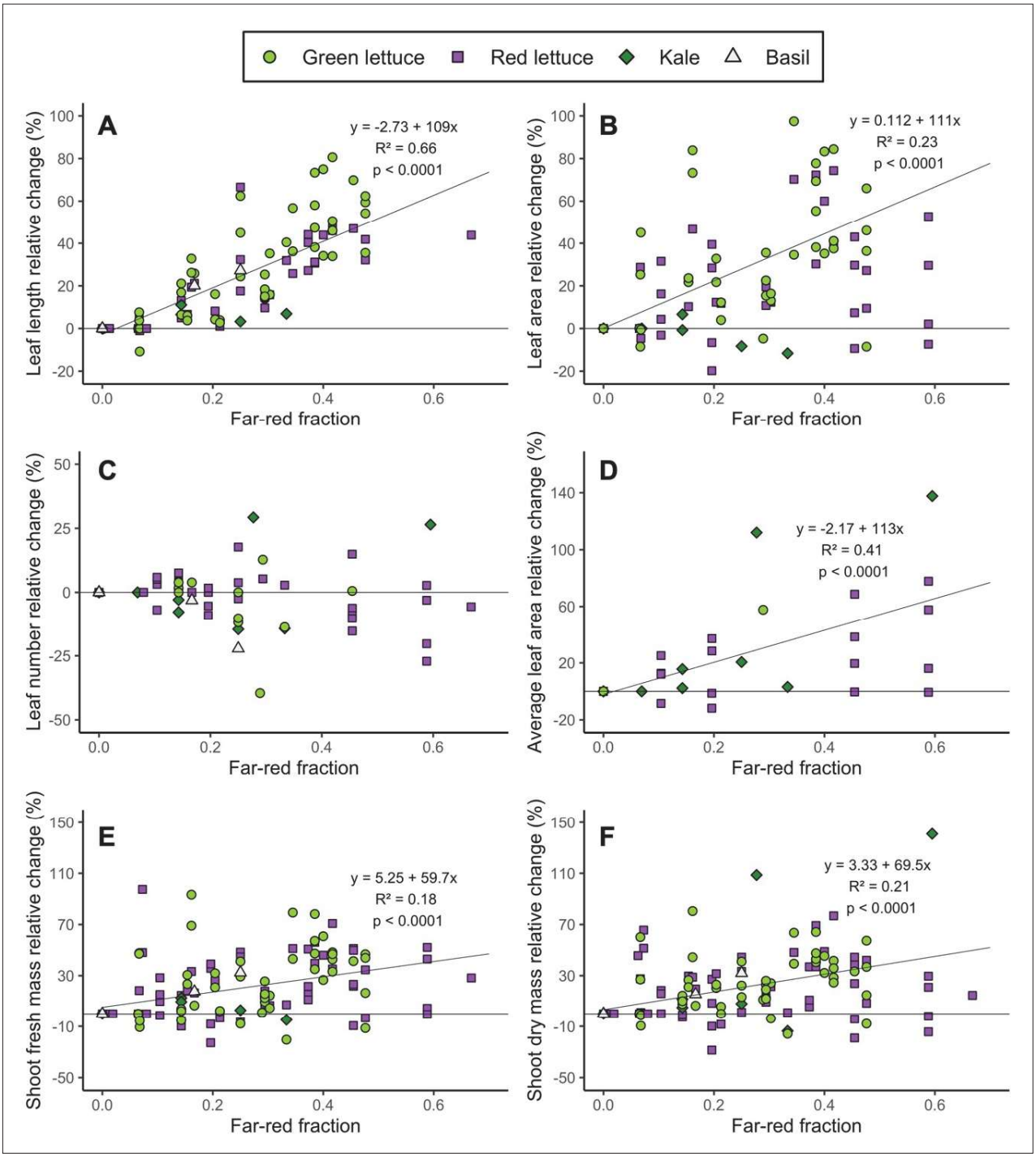


Figure 2. Meta-analysis of the relative change in leaf length (A), leaf area per plant (B), leaf number per plant (C), average leaf area (D), shoot fresh mass (E), and shoot dry mass (F) affected by far-red (FR) light fractions in indoor sole-source LED lighting experiments. The FR fraction is based on its photon flux density relative to the combined photon flux density of red and FR light. The correlation coefficient (R^2), regression equation, and p value are presented for each biometric data. The data used for the meta-analysis is from Li and Kubota, 2009; Stutte et al., 2009; Lee et al., 2015, 2016; Meng et al., 2019; Meng and Runkle, 2019, 2020; Kong and Nemali, 2021; Li et al., 2021; Liu and Van Iersel, 2022; Kang et al., 2023.

The R:FR and FR fraction are estimators that consider both R and FR light and are widely used in studies with FR light. The R:FR can usually estimate the effects of FR light on plant morphology even when both the R and FR PFD change (Lee et al., 2016). However, the estimating power of the R:FR decreases when greater than 10 (i.e., when the relative proportion of R-PFD to FR-PFD is significantly high; Kusuma and Bugbee, 2021a) and when the B-PFD (or B light fraction) differs substantially among treatments (Runkle and Heins, 2001). On the other hand, the FR fraction can estimate FR light effects even when the relative proportion of R-PFD to FR-PFD is high, making it a more versatile estimator than the R:FR.

Although the R:FR and FR fraction are powerful and practical estimators for morphological responses, they only consider R and FR light and disregard the responses to B and G light (Figure 1A). PPE considers B and G light along with R and FR light (Sager et al., 1998). Therefore, PPE can be used to estimate morphological responses of plants to FR light based both on the light environment and photophysiological responses of plants. However, precise calculations of PPE require light spectrum data measured at least in a 2 nm resolution. In addition, the PPE can be a less powerful descriptor when there are meaningful changes to the B light environment.

Recent studies have highlighted the need for improving PPE calculations. For example, accounting for spectral distortion that occurs within leaves due to pigments and cell walls and using internal spectral composition within leaves can enhance the estimating power of PPE (Kusuma and Bugbee, 2021b). Additionally, a three-state PPE model, which considers the dimerization of phytochrome monomers, can improve its estimating power, especially when combined with the calibration of spectral distortion within leaves. Furthermore, PPE can be affected by temperature (Jung et al., 2016; Legris et al., 2016), which indicates that temperature may need to be considered when calculating PPE in different temperature environments.

Effects of FR light on plant morphology

FR light is absorbed by a group of plant pigments, chlorophylls, and a group of plant photoreceptors, phytochromes (Figure 1A). FR light induces changes in plant morphology such as stem elongation, leaf expansion, hyponasty, and apical dominance, which are collectively called the shade-avoidance response or shade-avoidance syndrome (Franklin, 2008). The shade-avoidance response is stimulated by FR light primarily via phytochrome, particularly via phytochrome B (phyB) in light-grown plants. phyB photoreceptors are dimetric chromoproteins that exist in two homo (P_R-P_R or P_{FR}-P_{FR}) forms or one hetero form (P_{FR}-P_R) (Klose et al., 2020).

When P_{FR}-P_{FR} dimers absorb FR light, they are sequentially converted to P_{FR}-P_R and P_R-P_R dimers. P_R-P_R dimers are biologically inactive and reduce the activity inhibition and degradation of a basic helix-loop-helix transcription factor phytochrome-interacting factor 4 (PIF4) caused by active phytochromes. The high activity and stability of PIF4 increase the expression of auxin biosynthesis genes and auxin levels in plant tissues, which can lead to leaf elongation and expansion (Franklin et al., 2011). In addition, FR light can increase the concentration of bioactive gibberellin, which increase the expression of PIF-downstream genes by degrading a PIF inhibitor, DELLA proteins (Bou-Torrent et al., 2014). Ethylene and brassinosteroids can co-regulate shade-avoidance responses with auxin under low FR light (Pierik et al., 2009; Kozuka et al., 2010).

Extension growth responses of plants to FR light have been reported for indoor leafy-green species grown under sole-source LED lighting. An increase in FR-PFD and thus an increase in FR fraction generally increased the leaf length and leaf area per plant of green- and red-leaf lettuce, kale, and sweet basil (*Ocimum basilicum*) (Figure 2A, B). The degree of increase in leaf length and leaf area per plant was greater at higher FR fractions. Therefore, when a greater amount of FR light is used in indoor leafy-greens production, a canopy becomes closed earlier than when less or no FR light is delivered. Thus, harvest timing and/or planting density may need to be changed when FR light is incorporated in production.

There is greater response variation to a high FR fraction in the promotion of leaf area per plant than in leaf length (Figure 2A, B). The greater response variability in leaf area per plant can be attributed to variability in leaf number to FR light (Figure 2C, D). For example, a high FR fraction decreased the leaf number of red-leaf lettuce 'Sunmang' by up to 20% and 27% (Lee et al., 2015, 2016). Similarly, a high FR fraction decreased the leaf number of green-leaf lettuce 'Amadeus', kale 'Siberian', and basil 'Genovese' (leaves on the main stem) by up to 40%, 10%, and 13%, respectively (Meng and Runkle, 2019; Meng et al., 2019; Kong and Nemali, 2021). In contrast, a high FR fraction increased the leaf number of kale 'Manchoo Collard' and sweet and holy basil (*Ocimum tenuifolium*) (total leaves in a plant) by 28%, 106%, and 296%, respectively (Watjanatepin and Sritanauthaikorn, 2020; Kang et al., 2023). The responses of leaf number to FR light did not show clear trends in red-leaf lettuce 'Rouxai' and 'Cherokee' and green-leaf lettuce 'Rex' (Meng and Runkle, 2019; Meng et al., 2019).

Table 1. The effects of far-red light on the relative change in the phytochemical concentrations on a mass basis (for example, mg g^{-1}) of indoor leafy-green vegetables grown under sole-source LED lighting.

Phytochemicals[a]	Relative change[b]	*n*[c]	Species	References
Chlorophylls	−24.6 ± 4.0%	7	Red- and green-leaf lettuce and kale	Li and Kubota, 2009; Kong and Nemali, 2021; Li et al., 2021; Kang et al., 2023
Anthocyanins	−29.1 ± 8.5%	5	Red- and green-leaf lettuce	Li and Kubota, 2009; Stutte et al., 2009; Kong and Nemali, 2021; Li et al., 2021
Carotenoids	−9.2 ± 5.4%	7	Red- and green-leaf lettuce and kale	Li and Kubota, 2009; Kong and Nemali, 2021; Li et al., 2021; Kang et al., 2023

[a] The average far-red fraction of light treatments used in the studies was 0.39, 0.23, and 0.39, for chlorophyll, anthocyanin, and carotenoid concentrations, respectively.
[b] Mean ± standard error.
[c] The number of samples used for the meta-analysis.

The effect of FR fraction on the morphology of some indoor leafy-green species is dependent upon other wavebands, especially B light. Cryptochromes (cry) are a group of flavoproteins that absorb B light and can mediate B light-related responses in plants (Cashmore et al., 1999). Similar to the active form of phytochrome, a high B light signal generated from cry can degrade and inhibit the function of PIF4, which restricts leaf elongation and expansion (Ahmad et al., 1995). Conversely, a low B-light signal reduces the degradation and function inhibition of PIF4. Therefore, shade avoidance-related signals generated by high FR light and a low B-PFD can merge at PIF4, and thus FR and B light signals can interact (Pedmale et al., 2016). For example, the effects of FR light on increasing leaf length were greater at a high B:R and high photosynthetic PFD (PPFD; 400–700 nm) than at a lower B:R or PPFD (Meng and Runkle, 2019). Similarly, the effects of additive FR light on increasing leaf area were significant when 26 µmol m^{-2} s^{-1} of B light was included in the background spectrum (Lee et al., 2016), but not when B light was excluded (Lee et al., 2015).

Several studies conducted with Arabidopsis (*Arabidopsis thaliana*) suggest that the effect of FR light on morphological changes can be more pronounced at higher air temperatures (Jung et al., 2016; Legris et al., 2016). Similar to FR light, a high temperature can revert the P_{FR}-P_{FR} dimers formed by R light into P_{FR}-P_R and P_R-P_R dimers. The rate of high temperature-induced reversion from P_{FR}-P_{FR} to P_{FR}-P_R dimers is significantly lower than the reversion rate from P_{FR}-P_R to P_R-P_R dimers. This is because high-temperature effects on phytochrome reversion can be greater when P_R monomers are more predominant (under high FR light) than P_{FR} monomers.

Effects of FR light on growth and biomass accumulation

As mentioned above, FR light can impact the morphology of indoor leafy-green species grown under sole-source LED lighting. Increased leaf elongation and expansion can improve the light capture of a plant and thus, increase whole-plant photosynthesis. In addition, challenging the conventional definition of PAR and PPFD, FR photons with a relatively short wavelength (e.g., <731 nm) can be as effective (within limits) as those in the PAR waveband by exciting photosystem (PS) I and thus balancing the electron flow between PSII and PSI (Zhen et al., 2019; Zhen and Bugbee, 2020). The effectiveness of FR photons in driving photosynthesis and inducing leaf elongation and expansion can both increase crop growth and biomass accumulation.

Similar to leaf length and leaf area per plant, an increase in FR-PFD and thus an increase in FR fraction generally increased shoot fresh and dry mass of green- and red-leaf lettuce, kale, and basil (Figure 2E, F). The degree of mass increase was generally greater at higher FR fractions. However, the magnitude of FR-induced increases in shoot fresh and dry mass were less than those for leaf length and leaf area per plant (Figure 2). This discrepancy can be at least partly attributed to a decrease in the concentration of chlorophylls in an FR-enriched spectrum (Table 1). Antenna chlorophylls in photosystems surround reaction centers (where photosynthesis-related photochemical reactions occur) and transfer the light energy they absorb to them. Therefore, decreases in chlorophyll concentration can negatively influence growth and biomass accumulation. A high FR PFD and fraction generally decreased the chlorophyll concentration on both a mass and area basis (Table 1, Figure 3). Accessory pigments such as carotenoids and anthocyanins can also absorb and deliver light energy to the reaction center of a photosystem. The concentration of carotenoids and anthocyanins also generally decreased under high FR light and fraction (Table 1).

The relatively greater effect of FR light on leaf size than on biomass accumulation can change specific leaf mass (SLM; usually g dry mass cm^{-2} leaf area) and affect leaf texture. A low SLM normally means leaves are thin, and vice versa. Adding FR light by 12, 25, 87, and 149 µmol m^{-2} s^{-1} to background light composed of a B-PFD at 26 µmol m^{-2} s^{-1} and R-PFD at 104 µmol m^{-2} s^{-1} (increasing FR fraction from 0.0 to 0.6) decreased the SLM of red-leaf lettuce 'Sunmang' by 14%, 14%, 26%, and 22%, respectively, 12 days after treatment (Lee et al., 2016). However, adding FR light at 15, 32, 110, or 189 µmol m^{-2} s^{-1} to background light composed only of R light at 132 µmol m^{-2} s^{-1} (increasing FR fraction from 0.0 to 0.6) had a less notable influence on the SLM of the same lettuce cultivar (Lee et al., 2015). Considering that the only difference between these two experiments was the inclusion of B light, the B-PFD apparently influences FR light-induced changes in SLM.

Effects of FR light on phytopigments and foliage coloration

As briefly mentioned above, FR light can modulate the concentration of phytopigments (such as chlorophylls) in indoor leafy-green species grown under sole-source electric lighting (Table 1). Chlorophylls, anthocyanins, and carot-

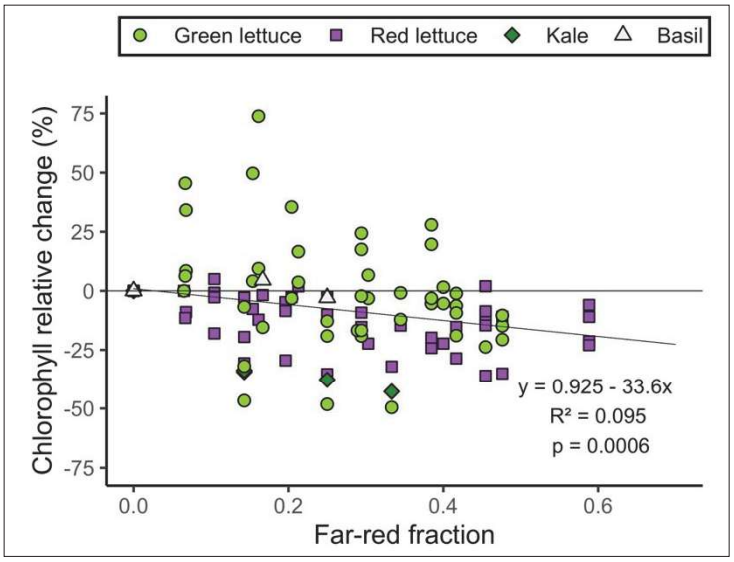


Figure 3. Meta-analysis of the relative change in chlorophyll concentration on an area basis affected by far-red light fractions in indoor sole-source LED lighting experiments. The correlation coefficient (R^2), regression equation, and p value are presented. The data used for the meta-analysis is from Lee et al., 2015, 2016; Meng et al., 2019; Meng and Runkle, 2019; Kong and Nemali, 2021; Liu and Van Iersel, 2022.

enoids are major phytopigments with green, red (and purple), and orange colors, respectively. Phytopigment contents in plant tissue can affect the nutritional value and flavor of indoor leafy-green products. In addition, phytopigments play a key role in determining their visual color. Therefore, understanding the effects of FR light on phytopigment concentration is important for consumer preference and product marketability.

FR light generally decreased the chlorophyll concentration of green- and red-leaf lettuce and kale. For example, adding 10 µmol m^{-2} s^{-1} of FR light decreased the chlorophyll concentration of red-leaf lettuce 'Red Butter' by 23% (Li et al., 2021). The addition of 154 µmol m^{-2} s^{-1} of FR light decreased the chlorophyll concentration of red-leaf lettuce 'Red Cross' by 12% (Li and Kubota, 2009). Similarly, adding FR light at 37, 185, and 332 µmol m^{-2} s^{-1} decreased the chlorophyll concentration of kale 'Manchoo Collard' by 29%, 33%, and 41%, respectively (Kang et al., 2023). Also, substituting B and R light with FR light decreased the chlorophyll concentration of green-leaf lettuce 'Amadeus' by 23% (Kong and Nemali, 2021).

PIFs mediate the light-induced changes in chlorophyll biosynthesis. Specifically, PIF1 and 3 negatively regulate chlorophyll biosynthesis (Stephenson et al., 2009; Tang et al., 2012). A high FR fraction can inhibit the breakdown of PIFs by decreasing the proportion of active-form phytochromes, and thus suppress chlorophyll biosynthesis. In addition, an experiment conducted with Arabidopsis showed that a relatively high proportion of FR to R light can induce senescence and decrease chlorophyll concentration (Tian et al., 2020).

Anthocyanin concentration, which is regulated by high-energy wavelengths (e.g., B light), can also be affected by FR light. In green- and red-leaf lettuce grown under sole-source LED lighting, a high FR fraction generally decreased anthocyanin concentration (Table 1). For example, adding 10, 20, and 154 µmol m^{-2} s^{-1} of FR light decreased the anthocyanin concentration in red-leaf lettuce 'Yanzhi', 'Outredgeous', and 'Red Cross', by 24%, 50%, and 40%, respectively (Li and Kubota, 2009; Stutte et al., 2009; Li et al., 2021). In addition, substituting B and R light with FR light decreased the anthocyanin concentration by 31% in green-leaf lettuce 'Amadeus' (Kong and Nemali, 2021). However, adding 10 µmol m^{-2} s^{-1} of FR light did not change the anthocyanin concentration in red-leaf lettuce 'Red Butter' (Li et al., 2021).

In contrast with indoor leafy greens, many studies conducted with Arabidopsis seedlings showed that anthocyanin biosynthesis can be promoted under FR light (Li et al., 2014). Similarly, anthocyanin concentration in kale 'Red Russian' seedlings increased under high FR light (Carvalho and Folta, 2014). These contrasting responses can be attributed to different dominant types of phytochrome. While phytochrome A (phyA) plays a dominant role in the de-etiolation of seedlings, phyB is predominant in light-grown plants. During de-etiolation, FR light promotes anthocyanin biosynthesis by activating phyA and accumulating promoters of anthocyanin biosynthetic genes such as dihydroflavanol reductase (Liu et al., 2015). In light-grown plants, low phyB activity under a high proportion of FR light can reduce the degradation of PIF 4 and 5, which are negative regulators of anthocyanin biosynthetic genes and repress anthocyanin biosynthesis (Liu et al., 2015).

Compared with chlorophyll and anthocyanin concentrations, a high FR fraction has less of an effect on carotenoid concentration and differs by plant species (Table 1). For example, adding 154 µmol m^{-2} s^{-1} of FR light decreased the carotenoid (xanthophylls and β-carotene) concentration of red-leaf lettuce 'Red Cross' by 14% (Li and Kubota., 2009). Also, substituting B and R light with FR light decreased the carotenoid concentration of green-leaf lettuce 'Amadeus' by 31% (Kong and Nemali, 2021). However, the addition of FR light had no significant impact on the carotenoid concentration of red-leaf lettuce 'Yanzhi' and 'Red Butter' and kale 'Manchoo Collard' (Li et al., 2021; Kang et al., 2023). Carotenoid biosynthesis can be upregulated when PIFs are degraded (Toledo-Ortiz et al., 2010). Thus, the FR light-induced decrease in carotenoid concentration in some plant species could have been caused by less degradation of PIFs under a high FR fraction, which can downregulate carotenoid biosynthesis.

Decreases in chlorophyll and anthocyanin concentration can reduce foliage coloration. A high FR fraction can decrease leaf redness (CIE *a** value) partly due to the loss of anthocyanin contents (Tables 1 and 2). Similarly, a high FR fraction can increase leaf yellowness (CIE *b** value) because of less chlorophyll and anthocyanin content. However, changes in phytopigment concentration do not necessarily fully explain changes in foliage coloration. For example, even though the anthocyanin concentration of red-leaf lettuce 'Yanzhi' decreased by 24% when 10 µmol m^{-2} s^{-1} of FR light was added, the leaf redness increased by 20% (Li et al., 2021).

Effects of FR light on shelf and storage life

Phytochemicals such as chlorophylls, anthocyanins, carotenoids, and phenolics have antioxidant capacity and can reduce oxidative damage in plants (Kähkönen and Heinonen, 2003; Stahl and Sies, 2003; Lanfer-Marquez et al., 2005). Therefore, vegetables rich in such phytochemicals can tolerate oxidative stress and thus have a long shelf life. A decrease in phytochemicals such as chlorophylls and anthocyanins caused by FR light (Table 1) can decrease the shelf life of indoor leafy-green products. For example, at a storage temperature of 16°C, the addition of 50 µmol m^{-2} s^{-1} of FR light during cultivation increased the rate of postharvest deterio-

Table 2. The effects of far-red light on the relative change in the leaf coloration (redness and yellowness) of indoor leafy-green vegetables grown under sole-source LED lighting.

Leaf color[a]	Relative change[b]	*n*[c]	Species	References
Redness	−38.4 ± 28.7%	19	Red- and green-leaf lettuce and basil	Meng and Runkle, 2019, 2020; Meng et al., 2019; Li et al., 2021
Yellowness	17.6 ± 6.4%	16	Red- and green-leaf lettuce and basil	Meng and Runkle, 2019, 2020; Meng et al., 2019; Li et al., 2021

[a] The average far-red fraction of light treatments used in the studies was 0.25 for leaf redness (CIE *a** value; greenness-redness from −128 to 127) and 0.23 for leaf yellowness (CIE *b** value; blueness-yellowness from −128 to 127).

[b] Mean ± standard error.

[c] The number of samples used for the meta-analysis.

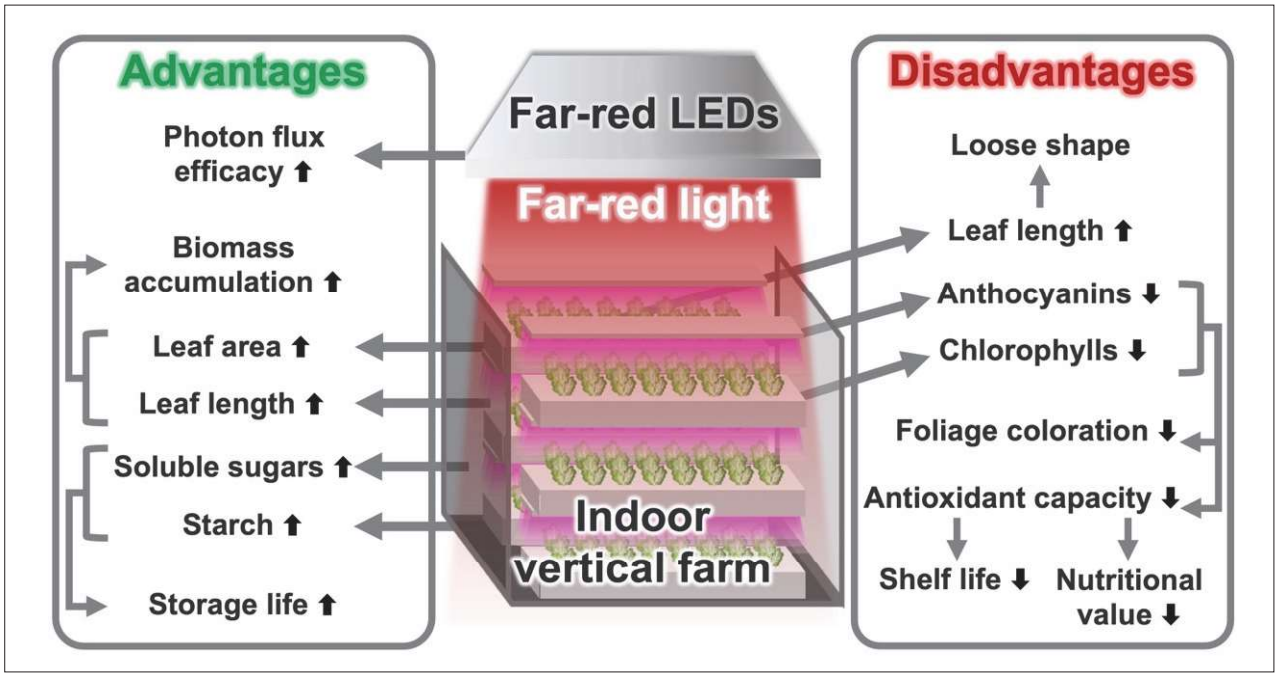


Figure 4. The potential advantages and disadvantages of utilizing far-red (FR) LEDs in indoor leafy-green vegetable production. FR light-induced changes in each parameter (↑ and ↓ refer to increase and decrease, respectively) are shown. The effects of FR light on soluble sugar and starch contents were observed when FR light was supplemented rather than substituted for another waveband.

ration and visual quality loss (yellowing and browning) of green-leaf lettuce 'Tiberius' (Zou et al., 2023). The authors attributed the decrease in shelf life caused by FR light to an increase in reactive oxygen species (hydrogen peroxide and superoxide anion) caused by decreases in non-enzymatic antioxidants such as chlorophylls, carotenoids, phenolics, and some enzymatic antioxidants. However, the effect of FR light on shelf life can vary by crop because different plant species can have different phytochemical responses to FR light. For example, adding 12, 25, 87, and 149 μmol m^{-2} s^{-1} FR light increased the concentration of a group of non-enzymatic antioxidants, phenolics, in red-leaf lettuce 'Sunmang' by 9%, 14%, 22%, and 52% respectively, which increased antioxidant capacity and can lengthen shelf life (Lee et al., 2016).

The storage temperature (<5°C) of leafy greens is generally lower than that at which vegetable products are displayed on market shelves (Gross et al., 2016). Therefore, metabolites in plants that function as osmoprotectants, such as soluble sugars, can lengthen storage life (Courbier et al., 2020; Larsen et al., 2023; Zou et al., 2023). The addition of FR light can increase the soluble sugar content. For example, the addition of FR light at the end of day increased the soluble sugar in lettuce 'Tiberius' (Zou et al., 2021). Similarly, adding 10 μmol m^{-2} s^{-1} of FR light during cultivation increased soluble sugar by 89% in lettuce 'Red Butter' (Li et al., 2021). Adding 50 μmol m^{-2} s^{-1} of FR light during cultivation did not accelerate the rate of postharvest deterioration at 4°C partly due to increased soluble sugar under FR light (Zou et al., 2023). Similarly, adding 180 μmol m^{-2} s^{-1} of FR light during cultivation increased soluble sugar and starch content in basil 'Emily' and inhibited the overall visual quality loss during storage at 4°C (Larsen et al., 2023). As such, FR light during cultivation can positively influence storage life.

FR light supplementation versus substitution

Most of the published studies with FR light in vegetable production utilized FR supplementation, which refers to the addition of FR light to the background light, thus increasing the total PFD (TPFD). Fewer studies have substituted a portion of the background light with FR light, maintaining a fixed TPFD. FR supplementation requires additional energy, whereas FR substitution can maintain or decrease energy load due to the high photon flux efficacy of FR LEDs (Figure 1B). As such, FR supplementation and substitution are similar in that FR light is utilized, but one maintains a PPFD and increases the TPFD while the other maintains a TPFD and decreases the PPFD.

FR substitution can be more adequate than FR supplementation for evaluating the effects of FR light from the perspectives of similar energy consumption and the same TPFD. However, since it is not practical to substitute sunlight with FR light in greenhouses, only FR supplementation has been used in greenhouse vegetable production research. In contrast, FR substitution is viable for indoor vertical farming research. Considering the few published studies with FR substitution (Meng et al., 2019; Meng and Runkle, 2020; Kong and Nemali, 2021), further research is needed to investigate the explicit effects of FR light more comprehensively.

Conclusions

Increasing demand for fresh vegetables due to the rapidly increasing global population increases the use of resources in vegetable production. Thus, it is important to improve resource-use efficacy in agriculture for better sustainability. While indoor vertical farms have higher water and nutrient solution use efficacy than field and greenhouse production (Barbosa et al., 2015; Avgoustaki and Xydis, 2020), they have significantly higher energy loads than conventional vegetable production systems primarily due to electric lighting and air conditioning (Graamans et al., 2018). Because of the high energy demand for electric lighting alone, indoor vertical farms have a two- to five-fold higher carbon footprint than field agriculture (Al-Chalabi, 2015). Therefore, improving the efficacy of electric lighting in indoor vertical farms has

become key for increasing the economic viability and improving the sustainability of indoor vertical farms.

The utilization of FR light generated by discrete FR LEDs is a promising method for improving electric lighting efficacy for two reasons: 1) FR LEDs have high photon flux efficacy and 2) FR light can increase the growth and biomass accumulation of indoor leafy-green species. However, even though FR LEDs and light have advantages, they can induce undesired changes in morphology (elongated leaves, petioles, and stems), phytonutrient concentrations (low chlorophyll and anthocyanin concentration), foliage coloration (pale colors), and shelf life (fast postharvest quality deterioration) (Figure 4). Therefore, the trade-offs between increases in biomass accumulation and decreases in quality attributes should be considered when utilizing FR light in indoor vertical farms. Also, since the effects of FR light are dependent upon crop species and other environmental factors, such as B-PFD and air temperature, more research is needed to determine appropriate FR light regimens in various production situations.

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