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Far-red photons have equivalent efficiency to traditional photosynthetic photons: Implications for redefining photosynthetically active radiation

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Abstract

Far-red photons (701–750 nm) are abundant in sunlight but are considered inactive for photosynthesis and are thus excluded from the definition of photosynthetically active radiation (PAR; 400–700 nm). Several recent studies have shown that far-red photons synergistically interact with shorter wavelength photons to increase leaf photochemical efficiency. The value of far-red photons in canopy photosynthesis has not been studied. Here, we report the effects of far-red photons on single leaf and canopy photosynthesis in 14 diverse crop species. Adding far-red photons (up to 40%) to a background of shorter wavelength photons caused an increase in canopy photosynthesis equal to adding 400–700 nm photons. Far-red alone minimally increased photosynthesis. This indicates that far-red photons are equally efficient at driving canopy photosynthesis when acting synergistically with traditionally defined photosynthetic photons. Measurements made using LEDs with peak wavelength of 711, 723, or 746 nm showed that the magnitude of the effect was less at longer wavelengths. The consistent response among diverse species indicates that the mechanism is common in higher plants. These results suggest that far-red photons (701–750 nm) should be included in the definition of PAR.

KEYWORDS

Chl *d* and *f*, Emerson enhancement, far-red, photosynthetically active radiation, photosystems, whole-plant/canopy photosynthesis

1 | INTRODUCTION

Crop yield is largely determined by three factors: radiation capture, photosynthetic efficiency at which the absorbed photons are converted into biomass, and dry matter partitioning to the harvested portion of the crop, that is, harvest index (Bugbee & Monje, 1992; Gifford, Thorne, Hitz, & Giaquinta, 1984). As the efficiency of

radiation capture and harvest index for major crops are approaching their theoretical maxima, the improvement of photosynthetic efficiency is projected to play a central role in improving crop productivity to meet the rising global demand for food and bioenergy in the coming decades (Long, Zhu, Naidu, & Ort, 2006; Zhu et al., 2010; Ort et al., 2015). Multiple approaches to improve photosynthesis have been considered and/or implemented, including optimization of light utilization, minimizing photorespiratory losses (Hanson, Lin, Carmo-silva, & Parry, 2016; Schuler, Mantegazza, & Weber, 2016; South, Cavanagh, Liu, & Ort, 2019), accelerating relaxation of photoprotective thermal energy dissipation (Kromdijk et al., 2016),

Abbreviations: CEF, cyclic electron transport; g_s , stomatal conductance; LAI, leaf area index; LED, light emitting diode; PAR, photosynthetically active radiation; *PFD*, photon flux density; P_{gross} and P_{net} , gross and net photosynthetic rate; *PPFD*, photosynthetic photon flux density integrated over 400 to 700 nm; R_{dark} , dark respiration.

and increasing the efficiency of carboxylation enzyme RuBisCO (see reviews by Long et al., 2006; Kubis & Bar-Even, 2019).

Among the efforts to optimize photosynthetic light utilization, reducing the size of light harvesting antenna of photosystems was reported to result in improved photosynthetic efficiency, especially in high-density crop cultivation under high light (Melis, 2009; Kirst et al., 2018). This was achieved through increasing the uniformity of canopy light distribution, thus relieving the upper canopy from absorbing an excess amount of light that would otherwise be wastefully dissipated as heat.

Distinct from the reduction of antenna size, another approach to potentially increase photosynthetic efficiency is to expand the solar spectrum that can be used for photosynthesis (Blankenship & Chen, 2013). Oxygenic photosynthesis in plants, algae, and cyanobacteria are generally thought to only use photons from 400 to 700 nm, known as the photosynthetically active radiation (PAR). Chen and Blankenship (2011) noted that the amount of photosynthetic photons could increase by 19% if crop plants can utilize far-red photons between 700 and 750 nm, potentially leading to marked increase in crop yield.

In oxygenic photosynthetic organisms, chlorophyll *a* (Chl *a*) is nearly exclusively used as the primary electron donor (i.e., specialized chlorophylls that perform charge separation) in the photochemical reaction centres (Björn, Papageorgiou, Blankenship, & Govindjee, 2009). The reaction centre chlorophylls in photosystems I and II (PSI and PSII) absorb maximally around 700 and 680 nm, respectively, and are denoted as P700 and P680 (Barber & Archer, 2001; Kok, 1961). A small number of long wavelength ($\lambda > 700$ nm) absorbing red forms of Chl *a*, whose absorption properties are modulated by neighbouring chlorophylls and their surrounding protein environments, widely exist in the antenna and/or core complexes of PSI in algae and higher plants, but the capability and significance of uphill energy transfer to the reaction centre in higher plants is still under debate (Croce & van Amerongen, 2013; Gobets & van Grondelle, 2001; Koehne, Elli, Jennings, Wilhelm, & Trissl, 1999; Rivadossi, Zucchelli, Garlaschi, & Jennings, 1999). Far-red photons are often presumed to be less efficient for energy transfer and trapping in the two photosystems.

Leaf-level photosynthesis under monochromatic light consistently shows that far-red photons are inefficient for photosynthesis. Emerson and Lewis (1943) first observed a sharp decline in the quantum yield of green alga *Chlorella* at wavelengths above 685 nm, where quantum yield at 700 nm dropped to less than half of that at 685 nm. Subsequently, Emerson, Chalmers, and Cederstrand (1957) and Emerson and Rabinowitch (1960) found that the photosynthetic rate is enhanced under simultaneous illumination of far-red ($\lambda > 680$ nm) and shorter wavelengths. This finding contributed to the identification of two photochemical systems with distinct absorption properties in oxygenic photosynthesis (Duysens & Ames, 1962; Hill & Bendall, 1960; Myers, 1971). However, the significance of this synergistic effect on photosynthetic efficiency has received little attention. McCree (1972a) found that enhancement effects were insignificant in four types of white electric lights

(quartz-iodine incandescent, mercury, metalarc, and fluorescent lamps). Later studies on the photosynthetic responses to light have largely focused on fine-tuning the quantum yield spectrum of photosynthesis and each individual photosystem, where the effects of different wavelengths are often perceived as independent and additive (Evans, 1987; Inada, 1976; Laisk, Oja, Eichelmann, & Dall'Osto, 2014; McCree, 1972b).

Recently, a growing body of research indicates that under broad spectrum or combined lights, plants can use far-red photons more efficiently for photosynthesis than previously thought (Hogewoning et al., 2012; Murakami, Matsuda, & Fujiwara, 2018; Zhen & van Iersel, 2017). Hogewoning et al. (2012) observed that the quantum yield for CO₂ fixation in cucumber measured under broad spectral light (wavelength range of 400–725 nm) is 10% to 21% higher, depending on the growth light spectra and intensity, than the weighted sum of the quantum yield determined at 19 wavelengths across the same spectral range. Because the two photosystems operate in series to drive linear electron transport from H₂O to the terminal electron acceptors (usually NADP⁺), excitation of PSI and PSII should be approximately equal to achieve optimal efficiency of photochemistry (Butler, 1978; Allen, 2003). Studies on excitation distribution between the two photosystems have provided compelling evidence that most of the shorter wavelengths from 400 to 680 nm over-excite PSII, whereas longer wavelength far-red photons ($\lambda > 680$ nm) tends to over-excite PSI (Evans, 1987; Hogewoning et al., 2012; Laisk et al., 2014). The synergistic interaction between far-red and shorter wavelengths is thus important for increasing photochemical efficiency. Zhen and van Iersel (2017) found that both photochemical efficiency of PSII (Φ_{PSII} ; the number [moles] of electrons transported per mole of photons absorbed by PSII) and leaf net photosynthetic rate (P_{net}) of lettuce increased when far-red (peak at 735 nm) is added to red/blue or white LED light. Those findings, although limited to leaf-level responses, indicate that far-red photons may significantly contribute to photosynthesis under broad-spectrum light. For instance, sunlight contains ~19% far-red (701–750 nm) relative to PAR (400–700 nm). It is likely that we have been underestimating the true photon flux density that drives photosynthesis by excluding far-red photons from the definition of photosynthetic photon flux density.

The objective of this study was to quantify the value of far-red photons on whole-plant/canopy photosynthesis in diverse species. Specifically, we aimed to: (a) compare the photosynthetic efficiency of far-red photons with shorter wavelength photons, (b) quantify the dose response of far-red on canopy photosynthesis, and (c) determine the effect of wavelength of far-red on canopy photosynthesis.

2 | MATERIALS AND METHODS

2.1 | Plant material and growing conditions

Twelve C₃ species (16 cultivars) and two C₄ species were used, including lettuce (*Lactuca sativa*, green leaf cv. Waldmann's dark green and

red leaf cv. Marshall and cv. Revolution), basil (*Ocimum basilicum*, cv. Italian large leaf), spinach (*Spinacia oleracea*, cv. Bloomsdale), kale (*Brassica napus* var. *pabularia*, cv. Siberian), soybean (*Glycine max*, cv. Hoyt), tomato (*Solanum lycopersicum*, cv. Celebrity), potato (*Solanum tuberosum*, cv. Russet burbank), cucumber (*Cucumis sativus*, cv. Straight eight), sunflower (*Helianthus annuus* cv. Teddy bear), bean (*Phaseolus vulgaris*, cv. Kentucky wonder), wheat (*Triticum aestivum*, cv. Tybalt and cv. Apogee), rice (*Oryza sativa* cv. Ai-Nan-Tsao and cv. Super dwarf), corn (*Zea mays*, cv. Early sunglow), and sorghum (*Sorghum bicolor*, cv. Dwarf grain).

Plants were seeded in 1.7 L containers filled with a soilless medium (50% peat and 50% vermiculite by volume) and grown inside a glass-covered greenhouse with supplemental lighting provided by high pressure sodium (HPS) lamps. The photoperiod was 16 hr day/8 hr night. Plants were irrigated daily with a nutrient solution containing 120 mg L⁻¹ N (21 N-2.2P-16.6 K; Peter's Excel Multi-Purpose 21-5-20, ICL Specialty Fertilizers, Summerville, SC, USA). Groups of plants were seeded every 3 to 4 weeks from 16 January to 21 August 2018, allowing measurements of canopy gas exchange to be made on plants of various sizes. Total daily light integral (DLI, mol m⁻² d⁻¹) was 29 ± 7.3 (mean ± SD). The amount of light plants received from the HPS lamps ranged from 1.9 to 18.2 mol m⁻² d⁻¹, depending on daily and seasonal variations in natural sunlight intensity. As a result, different groups of plants were acclimated to different greenhouse light conditions. Greenhouse temperature was set at 25/20°C day/night and the average daily temperature was 24.5 ± 4.3°C during the growing period. The greenhouse was ventilated for temperature control and was not enriched with CO₂. Average daily relative humidity and vapour pressure deficit were 46.3 ± 11.8% and 1.7 ± 0.8 kPa, respectively. Photosynthetic responses of multiple species to far-red photons were measured in random orders over time, which allowed us to examine the effect of growth environment on the response to far-red photons.

2.2 | Canopy photosynthetic responses to far-red photons

Four to 8 weeks after germination, plants were moved from the greenhouse into a single-chamber (100 L; 36 × 47 × 59 cm; w × l × h) whole-canopy gas exchange system. The design of the system was otherwise similar to the multi-chamber gas exchange system described by van Iersel and Bugbee (2000). Canopy gas exchange was measured under two types of LED lights—cool-white (BIOS lighting, Melbourne, FL, USA) and far-red (Philips, Eindhoven, the Netherlands). The spectral distributions of the LEDs (Figure 1a) were measured using a spectroradiometer (SS-110; Apogee Instruments, Logan, UT, USA). Chamber walls were lined with highly reflective Mylar to eliminate side lighting and increase light uniformity. The reflective walls also help to simulate light environment of a canopy, because they reflect far-red photons similar to neighbouring plants. Chamber air temperature was controlled with resistance heaters and maintained at

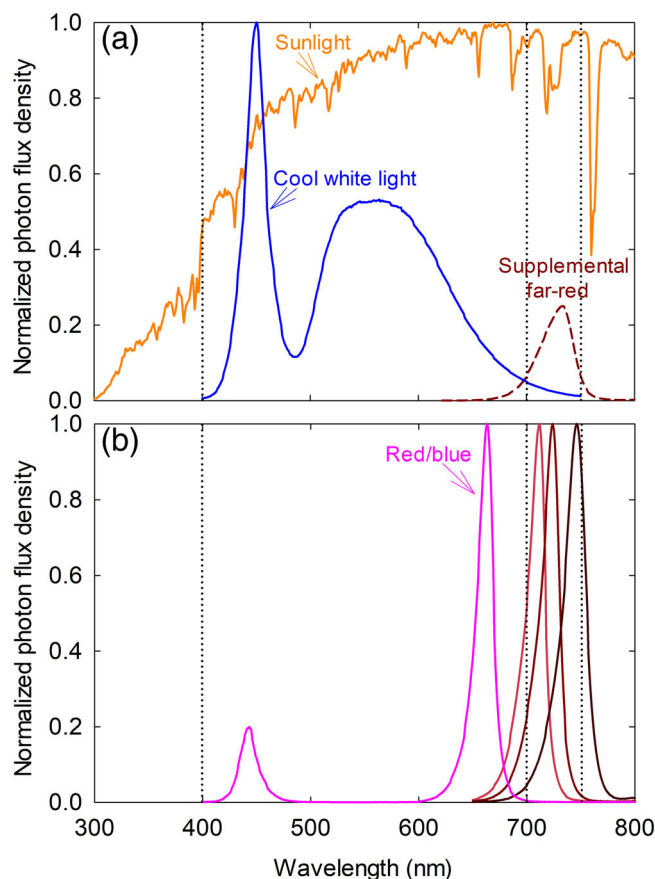


FIGURE 1 Normalized spectral distributions of sunlight, cool-white, red/blue, and far-red light-emitting diodes (LEDs). Far-red LEDs with peak wavelength at 735 nm (a) were used to quantify canopy photosynthetic responses to far-red photons. Another three far-red LEDs with peak wavelengths of 711, 723, and 746 nm, respectively, were used to quantify the effect of wavelength of far-red photons on canopy photosynthesis (b). Dotted vertical lines indicate wavelength at 400, 700, and 750 nm. The traditionally defined photosynthetically active radiation is from 400 to 700 nm, which excludes the longer-wavelength far-red photons (701 to 750 nm)

25 ± 0.1°C, and CO₂ concentration was 600 μmol mol⁻¹. Air flow rate through the chamber ranged from 22.3 to 37.2 mmol s⁻¹ (30 to 50 standard L min⁻¹) depending on the size of plant canopies. To eliminate the mole fraction dilution of CO₂ analysis by water vapour, the pre- and post-chamber air streams sampled by the infrared gas analysers were first passed through nafion dryers (Perma Pure, Lakewood, NJ, USA) and then columns of magnesium perchlorate to completely remove water vapour.

Two or four plants of the same species/cultivar were placed inside the chamber, depending on plant size to minimize gaps between plants or excessive overlapping of leaves. Photon flux density of the LED lights at the canopy level was measured daily (mapped at 13 locations across the chamber floor area of 0.17 m²) and adjusted to the target levels for each canopy using a

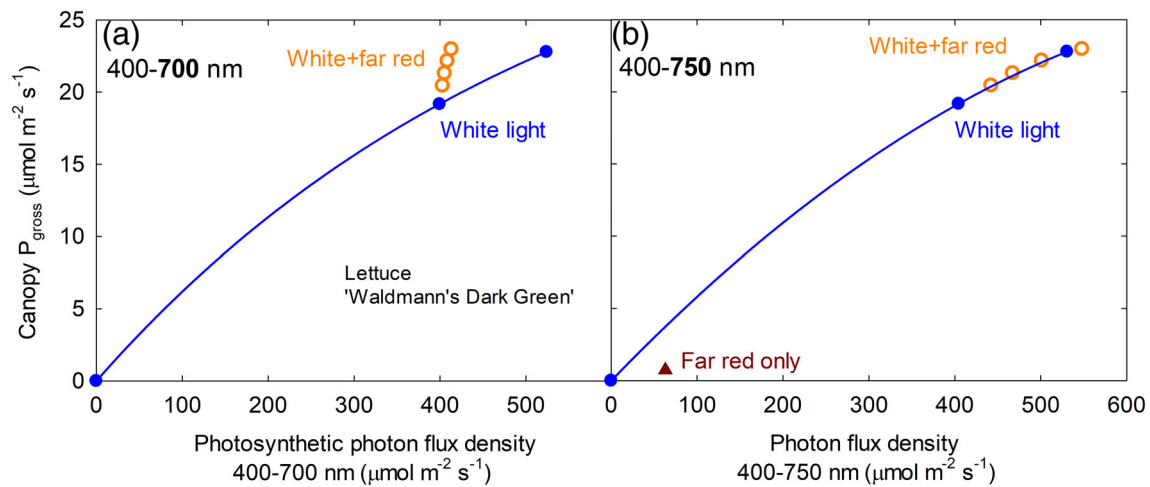


FIGURE 2 Canopy gross photosynthetic rate (P_{gross}) of lettuce cv. Waldmann's dark green as a function of photon flux density integrated over 400–700 nm (a) or 400–750 nm (b). Closed blue symbols represent data points at three intensities of white light (dark, intermediate, and high). Open orange symbols represent different amounts of far-red photons added to the white light of intermediate intensity. Closed dark-red symbols indicate P_{gross} under far-red alone. Symbol colour is consistent in all figures

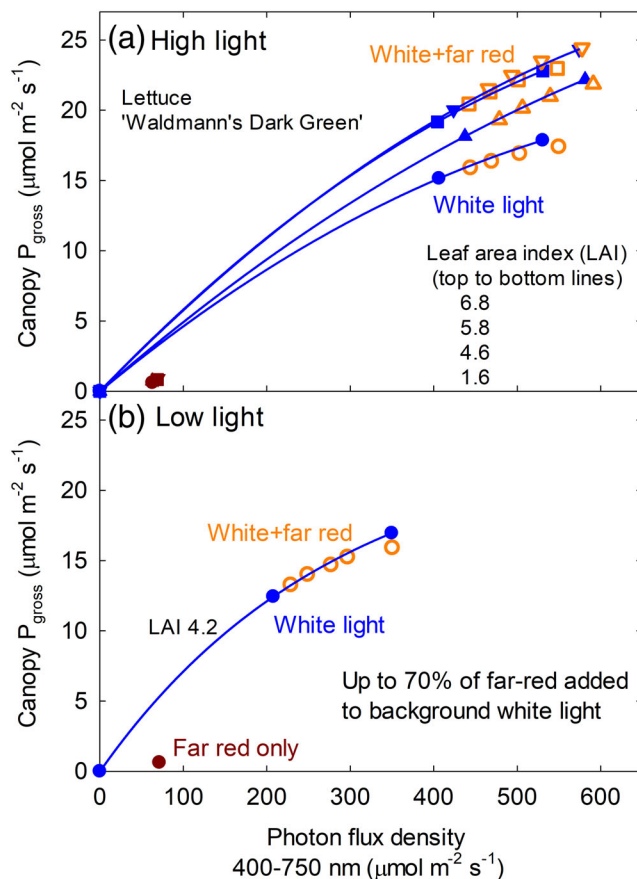


FIGURE 3 The effect of light intensity and canopy size on the responses of canopy gross photosynthesis (P_{gross}) to added far-red photons. Canopy size is indicated by leaf area index (LAI). For clarity, only one set of data under low background white light intensity is presented (b). Two additional replications are included in Figure S1

spectroradiometer (SS-110; Apogee instruments). Light variation on the horizontal plane was typically within 8% of the average light intensity. Plants were given 90 to 120 min to acclimate under a high-intensity white light (e.g., PPFD of $525 \mu\text{mol m}^{-2} \text{s}^{-1}$ in Figure 2). Canopy gas exchange rate ($\mu\text{mol CO}_2 \text{m}^{-2} \text{ground area s}^{-1}$) was monitored in real-time and recorded every second using a datalogger (CR1000; Campbell Scientific, Logan, UT, USA). Then, the white light was dimmed to a lower intensity (e.g., PPFD of $400 \mu\text{mol m}^{-2} \text{s}^{-1}$ in Figure 2) and plants were given 30 to 40 min to acclimate before stabilized net photosynthetic rate (P_{net}) was determined. After that, four levels of far-red were added in increasing order to the white light. The photon flux density of the added far-red (integrated over 701 to 750 nm) typically ranged from 10% to 40% of the background white light (integrated over 400 to 700 nm). For example, in Figure 2, 40 to $140 \mu\text{mol m}^{-2} \text{s}^{-1}$ of far-red photons were added to a background white light of $400 \mu\text{mol m}^{-2} \text{s}^{-1}$. P_{net} was determined 30 min after each increment of far-red photons. After the highest amount of far-red photons was added, the white light and half of the far-red were switched off. Plants were given 30 min before P_{net} under far-red alone was determined. Last, dark respiration (R_{dark} ; negative values) was measured after 30 min of darkness. Canopy gross photosynthesis (P_{gross}) under each light treatment was calculated as: $P_{gross} = P_{net} - R_{dark}$, which assumes that respiration rate was similar in the light and dark. Plants were then destructively harvested, and total leaf area was measured using a leaf area metre (LI-3000; LI-COR, Lincoln, NE, USA). Leaf area index (LAI) was calculated as: $\text{LAI} = \text{total leaf area}/\text{chamber ground area}$. This entire procedure was replicated two to four times for each of the 14 species (18 cultivars) with various canopy sizes.

Additional measurements under low light conditions, that is, up to 70% ($\sim 140 \mu\text{mol m}^{-2} \text{s}^{-1}$) of far-red photons added to a background

white light of $\sim 200 \mu\text{mol m}^{-2} \text{s}^{-1}$, were made on a representative crop lettuce cv. Waldmann's dark green.

To assure that photosynthetic rate remained steady over the course of the measurement period and was not affected by factors other than the light treatment, P_{net} under the high and/or low intensity white light with no added far-red was often remeasured before the dark respiration measurements. Although most species showed steady photosynthesis over time, P_{net} of potato, sunflower, and kale tended to decrease over time. For these species, P_{net} under the background white light was remeasured before each level of far-red photons was added, and the data were normalized based on (a) the photosynthetic rate under white light measured prior to each increment of far-red, and (b) the percent increase in photosynthetic rate after the addition of far-red.

2.3 | Single leaf gas exchange responses to far-red photons

Leaf-level gas exchange responses to far-red photons were quantified to validate data obtained on whole canopies. Measurements were made on uppermost fully expanded leaves of lettuce cv. Marshall using a portable photosynthesis system with a $3 \times 3\text{-cm}$

clear-top chamber (LI-6800; LI-COR, Lincoln, NE). A cool white and two far-red LED fixtures, as described above, were used as light sources. Light transmission (%) through the clear-top chamber was measured using a spectroradiometer (SS-110; Apogee Instruments) and multiplied by the output spectra of the LED lights to calculate light intensity at leaf surface. The clear-top chamber transmitted light uniformly from 400 to 750 nm. Leaves were first acclimated to a white light of $400 \mu\text{mol m}^{-2} \text{s}^{-1}$ ($\pm 1\%$) for about 90 min until leaf P_{net} and stomatal conductance (g_s) reached a steady state. Then, $60 \mu\text{mol m}^{-2} \text{s}^{-1}$ of far-red photons (701–750 nm; 15% of white photon flux density) were added to the white light, and leaves were given about 60 min for P_{net} and g_s to stabilize. The far-red LED was then switched off, and leaves were given another 60 min under white light of $400 \mu\text{mol m}^{-2} \text{s}^{-1}$ to assure that P_{net} and g_s remained constant as previously measured. After that, the white light intensity was increased to $460 \mu\text{mol m}^{-2} \text{s}^{-1}$, and plants were again given about 60 min to acclimate. Gas exchange data were recorded every 30 s throughout the measurement period. The CO_2 concentration within the leaf cuvette (C_a) was $400 \mu\text{mol mol}^{-1}$, and leaf vapour pressure deficit was maintained at 1.0 kPa. Flow rate was $800 \mu\text{mol s}^{-1}$. This entire procedure was repeated four times with four different plants.

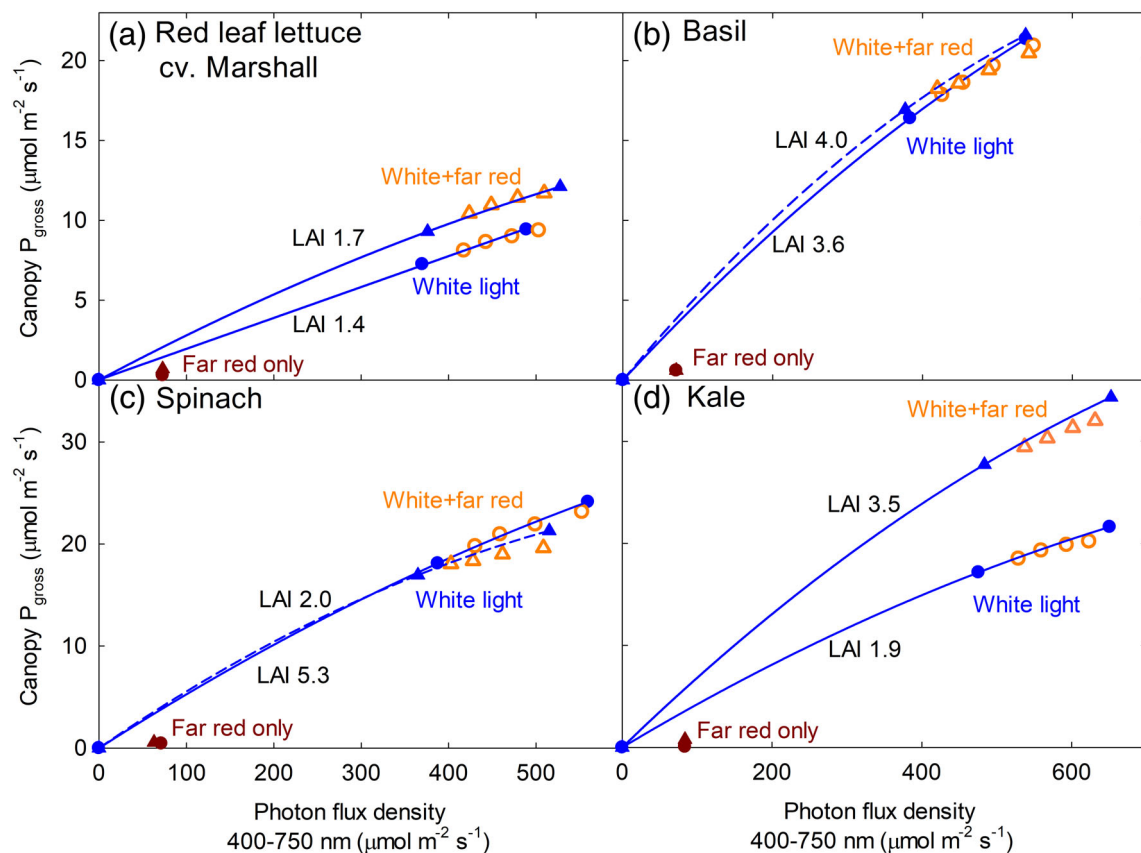


FIGURE 4 Canopy gross photosynthesis (P_{gross}) in response to the addition of far-red photons to a background of white light for four leafy green vegetable species. LAI stands for leaf area index. See Figure 2 for symbol legend

2.4 | Effect of wavelengths of far-red on canopy photosynthesis

Three far-red LEDs (LumiLeds, San Jose, CA, USA) with peak wavelengths of 711, 723, and 746 nm, respectively, were used to quantify the effect of wavelength of far-red photons on canopy photosynthesis (see Figure 1b for spectrum). A background of red/blue light ($510 \pm 7 \mu\text{mol m}^{-2} \text{s}^{-1}$; 16% blue and 84% red, with peaks at 443 nm and 663 nm; Figure 1b) was provided by red and blue LEDs (Fluence Bioengineering, Austin, TX, USA). Twelve uniformly sized mature lettuce plants (cv. Waldmann's dark green) were moved into a three-chamber gas exchange system (four plants per chamber). The system details and chamber conditions were similar to the single-chamber gas exchange system described above. In addition to the background red/blue light, plants in each chamber received equal amount of total photons ($50 \mu\text{mol m}^{-2} \text{s}^{-1}$) provided by one of the three far-red LEDs. This counts for all the photons emitted by the far-red LEDs, including those of wavelength shorter than 700 nm or greater than 750 nm.

Plants were first given 90 to 120 min under the background red/blue light. Canopy photosynthesis of a given chamber was measured every second for 60 s, and then the tubing that connected the chamber to the infrared gas analyser was purged for 45 s before the next chamber was sampled. Far-red LEDs were then switched on for about

45 min until P_{net} had stabilized. The background red/blue light was switched off, and P_{net} under far-red alone was determined after about 30 min. After that, far-red was turned off and R_{dark} was determined after 30 min of darkness.

2.5 | Leaf light absorbance

To quantify the effects of far-red on absorbed photon basis, leaf light absorbance was determined on the leaves used for single leaf gas exchange measurements using a spectroradiometer (PS300; Apogee Instruments), similar to the method of Nelson and Bugbee (2015). Leaf absorption of red/blue and far-red photons were quantified by multiplying the leaf absorbance spectrum by the spectral output of the LED lights. Additionally, leaf light absorbance was determined for several representative species used for canopy gas exchange study.

2.6 | Statistical analysis

Light response curves under background white (or red/blue) light were fitted using regression (linear and exponential rise to maximum) in Statistical Analysis Systems (SAS Institute, Cary, NC, USA). Each

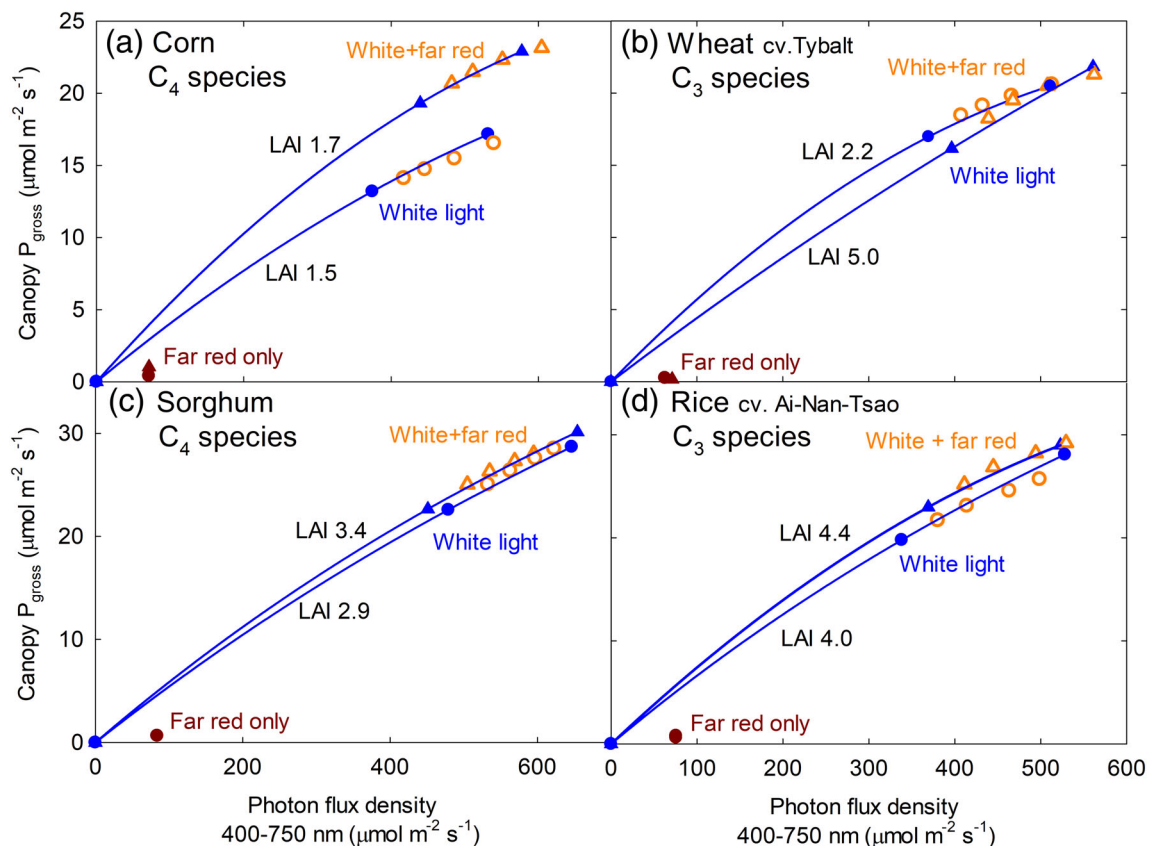


FIGURE 5 Canopy gross photosynthesis (P_{gross}) in response to the addition of far-red photons to a background of white light for four monocotyledon species, including two C_4 crops and two C_3 crops. LAI stands for leaf area index. See Figure 2 for symbol legend

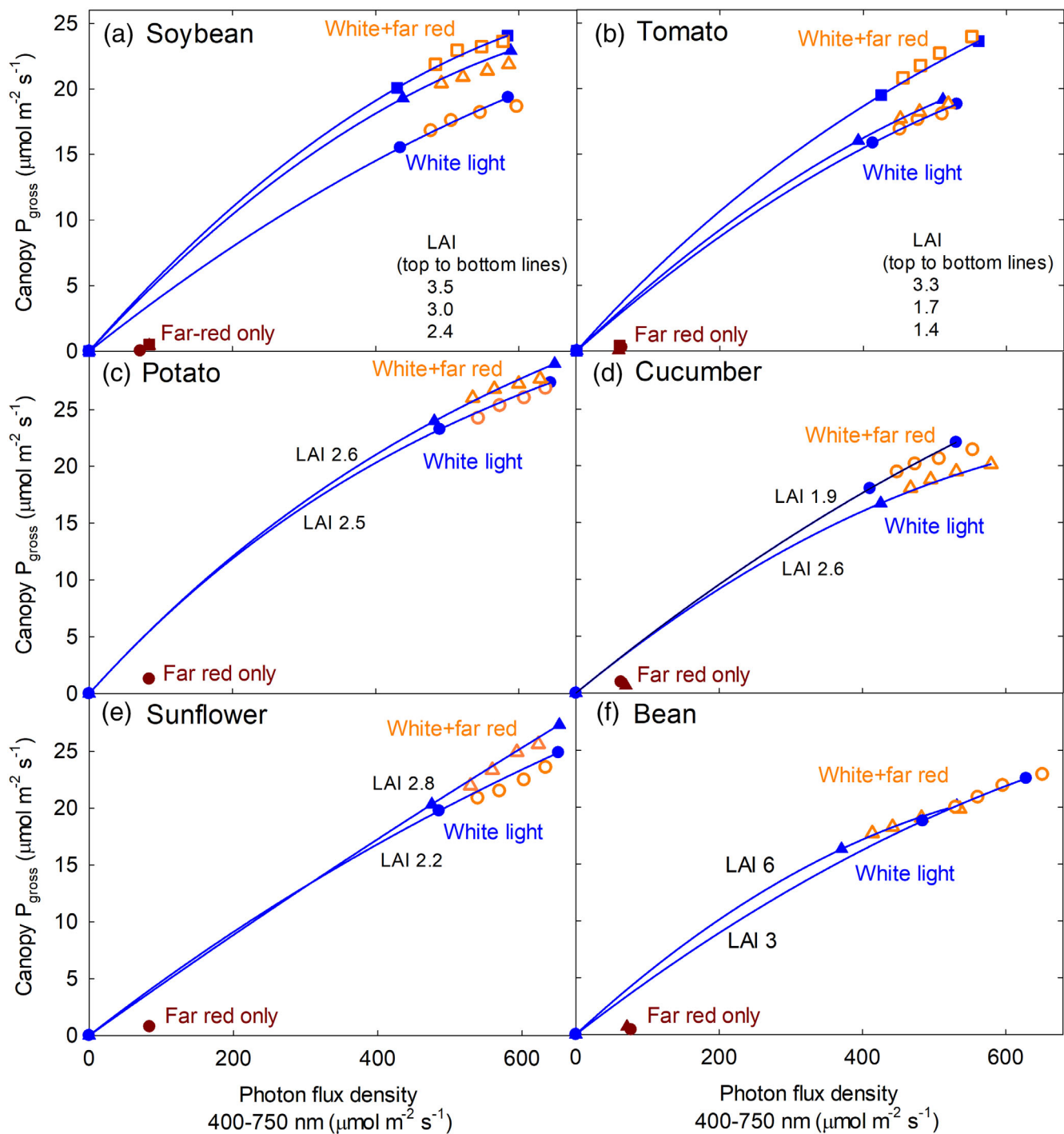


FIGURE 6 Canopy gross photosynthesis (P_{gross}) in response to the addition of far-red photons to a background of white light for six fruiting vegetable/crop species. LAI stands for leaf area index. See Figure 2 for symbol legend

curve was fitted using a single set of measurements. Replication curves of the same species/cultivar were obtained from new groups of plants (often with dissimilar LAI). Gas exchange rates upon adding different levels of far-red were compared with the predicted values under equal photon fluxes of white or red/blue light based on the fitted light response curves. Data were analysed using ANOVA in SAS, with mean separation performed using Fisher's protected least significant difference (LSD, $p = .05$).

3 | RESULTS

3.1 | Canopy photosynthetic responses to far-red photons

Canopy P_{gross} of lettuce cv. Waldmann's dark green increased nonlinearly with increasing PPFD of white light (Figure 2a), exhibiting a typical light response curve of photosynthetic carbon fixation.

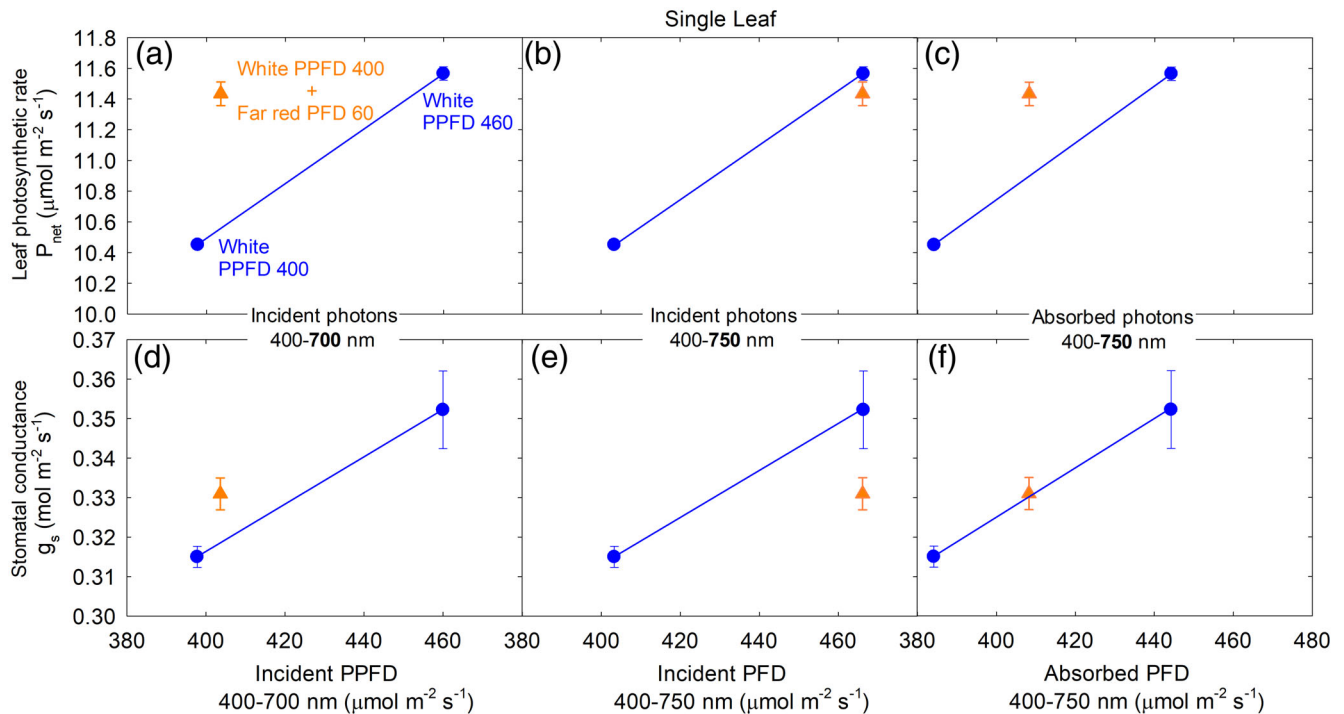


FIGURE 7 Single leaf net photosynthesis (P_{net} ; a–c) and stomatal conductance (g_s ; d–f) under white light or a mix of white and far-red photons. The number following each type of light in the symbol legend indicates photon flux density in $\mu\text{mol m}^{-2} \text{s}^{-1}$. Same data were plotted against three different x-axes: incident photosynthetic photon flux density integrated over 400–700 nm (a,d), incident photon flux density integrated over 400–750 nm (b,e), or absorbed photon flux density integrated over 400–750 nm (c,f). Lettuce cv. Marshall was used for data collection. Data points represent means from four replicates with error bars representing standard error ($n = 4$)

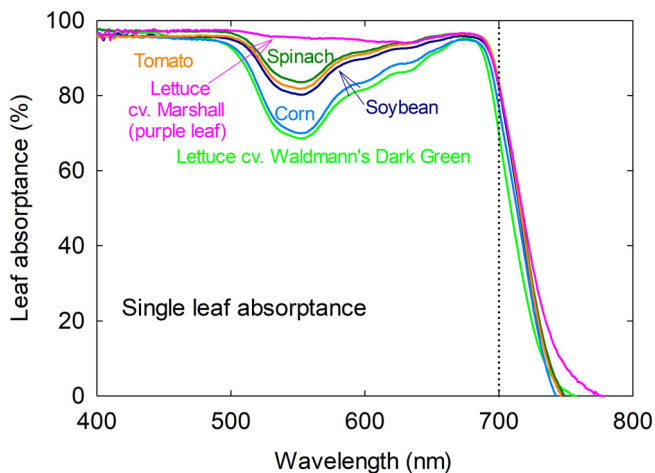


FIGURE 8 Leaf light absorbance of six representative species. Dotted vertical line indicates wavelength at 700 nm. Measurements of lettuce cv. Marshall were made on the same leaves that were used to quantify the responses of leaf gas exchange to added far-red photons (see data in Figure 7)

Adding 40 to $140 \mu\text{mol m}^{-2} \text{s}^{-1}$ (10% to 35%) of far-red photons (integrated over 701–750 nm) to a background white light of $400 \mu\text{mol m}^{-2} \text{s}^{-1}$ (400–700 nm) increased canopy P_{gross} by 6.7% to 20% (Figure 2a). In comparison, increasing the white light intensity by 10% to 35% from a $PPFD$ of $400 \mu\text{mol m}^{-2} \text{s}^{-1}$ similarly resulted in

6.7% to 21% increase in canopy P_{gross} , indicating that the added far-red photons were as effective as short wavelength photons. Because 8.7% of the photons from the far-red LEDs were below 700 nm, there were 1% to 3% increases in $PPFD$ with the addition of far-red photons. The magnitude of increase in canopy P_{gross} upon adding far-red was substantially greater than that in $PPFD$, resulting in poor correlation between P_{gross} and $PPFD$ (Figure 2a). In contrast, canopy P_{gross} correlated strongly with photon flux density integrated over 400–750 nm (Figure 2b). P_{gross} under a mixture of white and far-red photons was equal to P_{gross} under white light of the same total photon flux density. Far-red photons alone, however, were inefficient for canopy photosynthesis as evidenced by the low P_{gross} under far-red photons. At the same photon flux density ($70 \mu\text{mol m}^{-2} \text{s}^{-1}$), canopy P_{gross} under white light (interpolated from the fitted regression curves) was more than five times greater than that under far-red (Figure 2b).

3.2 | LAI, high/low background light, and far-red intensity

Similar effect of far-red photons on canopy P_{gross} of lettuce cv. Waldmann's dark green was observed in canopies of various LAI, where up to 40% of far-red photons were added to a background white light of $\sim 400 \mu\text{mol m}^{-2} \text{s}^{-1}$ (Figure 3a).

TABLE 1 Enhancement of canopy photosynthesis by different wavelengths of far-red

| Peak far-red wavelength | Absorbed photon flux ($\mu\text{mol m}^{-2} \text{s}^{-1}$) | Canopy P_{gross} under far-red alone ($\mu\text{mol m}^{-2} \text{s}^{-1}$) | Increase in canopy P_{gross} upon adding far-red to background light | Enhancement (ΔP_{gross}) |
|-------------------------|---|--|---|---|
| 711 nm | 29.4 | 1.1 ± 0.1 | 1.7 ± 0.2 | 0.59 ± 0.07 |
| 723 nm | 17.6 | 0.45 ± 0.08 | 1.2 ± 0.2 | 0.75 ± 0.1 |
| 746 nm | 4.6 | 0.05 ± 0.03 | 0.5 ± 0.1 | 0.45 ± 0.07 |

Note: Equal amount of incident photons ($50 \mu\text{mol m}^{-2} \text{s}^{-1}$) from one of three far-red LEDs (peak at 711, 723, or 746 nm) were added to a background red/blue light of $510 \mu\text{mol m}^{-2} \text{s}^{-1}$. Enhancement of canopy gross photosynthesis (P_{gross} ; $\mu\text{mol m}^{-2} \text{s}^{-1}$) was calculated as the increase in canopy P_{gross} upon adding far-red to background light subtracted by canopy P_{gross} under far-red alone. Canopy P_{gross} under background red/blue light without far-red was $24.4 \pm 0.6 \mu\text{mol m}^{-2} \text{s}^{-1}$. Data represent mean \pm SE ($n = 4$).

The response was consistent under low light conditions (background white light of $200 \mu\text{mol m}^{-2} \text{s}^{-1}$), up to about 40% of added far-red photons (Figures 3b and S1). Canopy P_{gross} with more than 40% of added far-red photons, however, gradually became lower than that under white light of the same total photon flux; P_{gross} with 70% added far-red (i.e., $140 \mu\text{mol m}^{-2} \text{s}^{-1}$ far-red plus $200 \mu\text{mol m}^{-2} \text{s}^{-1}$ white) was on average 7% lower than that under white light of $340 \mu\text{mol m}^{-2} \text{s}^{-1}$ (Figures 3b and S1).

3.3 | Species effects

The effect of far-red photons was consistent among 14 species, including leafy green vegetables (Figure 4), monocotyledon C_3 and C_4 species (Figure 5), and fruiting vegetable/crop species (Figure 6). Adding far-red photons caused similar increase in canopy photosynthesis as adding white light. Canopy P_{gross} under only far-red photons was low in all species (Figures 4–6).

3.4 | Single leaf gas exchange responses to far-red photons

Both P_{net} and g_s of lettuce cv Marshall increased upon adding far-red to a background white light (Figure 7). Leaf P_{net} under a mixture of white ($400 \mu\text{mol m}^{-2} \text{s}^{-1}$) and far-red photons ($60 \mu\text{mol m}^{-2} \text{s}^{-1}$) was statistically equal to that under $460 \mu\text{mol m}^{-2} \text{s}^{-1}$ of white light (Figure 7b), which was consistent with the photosynthetic responses to far-red at canopy level (Figure 4a). Compared with the traditional photosynthetic photon flux density (400 to 700 nm), integrating photon flux density from 400 to 750 nm better explained the effect of far-red photons on leaf P_{net} (Figure 7a,b).

Due to the poor leaf absorption of far-red photons (Figure 8), only 34.2% of the incident far-red photons (701–750 nm) were absorbed, whereas 95.9% of the incident white photons (400–700 nm) were absorbed. Given the same amount of absorbed far-red or white photons, the added far-red caused greater increase in P_{net} than white photons (Figure 7c).

Unlike P_{net} , which increased by the same extent when equal amount of incident far-red or white photons were added, leaf g_s

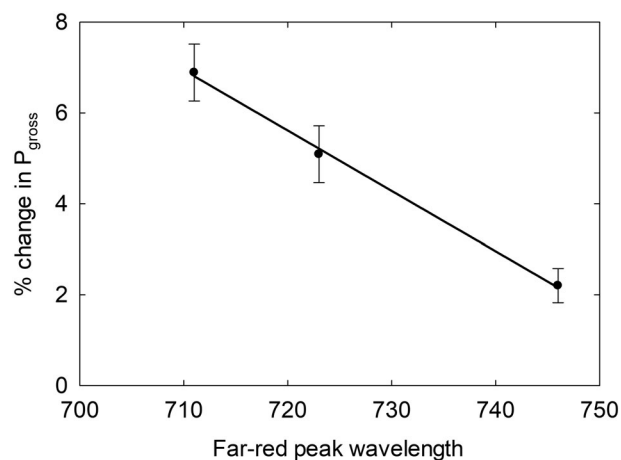


FIGURE 9 The effect of different wavelengths of far-red photons on canopy photosynthesis of lettuce cv. Waldmann's dark green. Percent increase in canopy gross photosynthesis (P_{gross}) was quantified by adding 10% of far-red to a background of red/blue light of $510 \mu\text{mol m}^{-2} \text{s}^{-1}$. Data points represent means from four replicates with vertical error bars representing standard error ($n = 4$)

showed a much smaller increase with the addition of far-red photons (Figure 7e). As a result, intercellular CO_2 concentration (C_i) tended to be lower with the addition of far-red (Figure S2). Given the same amount of absorbed far-red or white photons, however, the added far-red caused similar increase in leaf g_s compared with white photons (Figure 7f).

3.5 | Effect of wavelengths of far-red on canopy photosynthesis

Responses of canopy photosynthesis to far-red wavelengths were quantified by adding $50 \mu\text{mol m}^{-2} \text{s}^{-1}$ of photons from one of three far-red LEDs (peak at 711, 723, or 746 nm) to a background red/blue light of $510 \mu\text{mol m}^{-2} \text{s}^{-1}$. Shorter wavelength far-red photons, alone or applied simultaneously with the background light, produced higher rate of photosynthesis than longer wavelength far-red photons (Table 1). Percent increase in canopy P_{gross} upon adding far-red decreased linearly with increasing wavelength of the added far-red

photons (Figure 9). Far-red photons with peak at 723 nm caused the greatest enhancement of canopy photosynthesis, calculated as canopy $P_{\text{gross}}(\text{white} + \text{far-red}) - P_{\text{gross}}(\text{white}) - P_{\text{gross}}(\text{far-red})$, followed by photons with peak at 711 nm. Far-red photons with peak at 746 nm were not effective in driving photosynthesis when applied alone, and induced the smallest enhancement effect when applied with background red/blue light (Table 1).

4 | DISCUSSION

Photons above 700 nm are generally considered to have minimal photosynthetic activity. This view is based on the low action/quantum yield of photosynthesis under monochromatic far-red light (Emerson & Lewis, 1943; Inada, 1976; McCree, 1972b). Recent studies have revisited the Emerson enhancement effect and demonstrated the significance of the synergistic interaction between far-red and shorter wavelengths on leaf photosynthesis (Hogewoning et al., 2012; Kono et al., 2020; Murakami et al., 2018; Zhen & van Iersel, 2017). It remained unclear, however, if the photosynthetic efficiency of far-red photons at single leaf or canopy level is comparable with traditionally defined photosynthetic photons. Our comprehensive gas exchange measurements allow rigorous assessment of the photosynthetic value of far-red photons.

4.1 | Efficiency of far-red for canopy P_{gross} compared with 400–700 nm photons

Although far-red photons (701–750 nm) alone had low photosynthetic efficiency, adding them to a background of white light caused canopy P_{gross} to increase significantly (Figures 2–6). This is consistent with previous findings on leaf-level photosynthetic responses to far-red (Zhen & van Iersel, 2017). It is especially noteworthy that adding far-red photons (up to 40% of background PPFD) caused similar increases in canopy P_{gross} as adding white photons of the same amounts (Figures 2–6; also see Figure 7 to compare with single leaf response). This indicates that, on incident photon basis, the added far-red photons were as effective for canopy photosynthesis as white photons.

On absorbed photon basis, the added far-red photons have higher quantum yield (expressed as the increase in canopy P_{gross} per unit increase in absorbed photon) than the added white photons, because light absorption of a leaf or plant canopy is higher in the shorter wavelength region than in the far-red region (Holmes & Smith, 1977; Kasperbauer, 1971). For instance, 85% of the incident cool white LED light was absorbed by a single layer of leaf of lettuce cv Waldmann's dark greens, but only 21% of the incident far-red photons (701–750 nm) were absorbed (Figure 8). The higher effectiveness of absorbed far-red photons reflects their distinct mechanism for enhancing photosynthesis: Although the added white photons increase the total number of photosynthetic photons, the added far-red photons increase photosynthesis by improving photochemical efficiency.

We included far-red photons from 701 to 750 nm. Zhen, Haidekker, and van Iersel (2018) indicated that far-red photons of wavelength above 752 nm are not effective in enhancing photochemical efficiency as they are no longer used by PSI due to low photon energy and absorption. Using laser diodes to obtain extremely narrow-wavebands (FWHM of 2–3 nm), they also found that photochemical efficiency started to increase when photons above 686 nm and up to 731 nm were added to a background short wavelength light. Limited by the availability of laser diodes, the effect of photons within 731 to 752 nm on photochemical efficiency were not determined, and it was speculated that the upper wavelength limit of photons that enhance photochemistry falls in between the 731–752 nm range (Zhen et al., 2018). By including photons up to 750 nm in the integration of far-red photon flux, we are likely making a more conservative estimate (i.e., an underestimation) of the photosynthetic efficiency of the far-red photons.

4.2 | Far-red dose-response

The effect of far-red on canopy photosynthesis is dose-dependent (i.e., there was little further increase in canopy P_{gross} when more than ~40% of far-red photons were added to background shorter wavelength white light; Figures 3 and S1). This response is expected because the effect of far-red on photosynthesis is achieved through synergistic interaction with shorter wavelength photons that over-excite PSII. As efficient photochemical reactions require balanced excitation between the two photosystems, the addition of far-red photons can restore the excitation balance between the two photosystems and improve photochemical efficiency. However, only a certain amount of far-red is needed to balance the excitation between the two photosystems; further increasing far-red results in little increase in photochemical efficiency or photosynthetic rate, as far-red photons by themselves are inefficient for linear electron transport (Zhen & van Iersel, 2017).

Because the enhancement effect is dependent on the ratio of far-red to background short wavelength photon flux, the top layer (or top two layers) of the canopy, which is highly efficient at absorbing short wavelength photons, is arguably most important for the synergistic enhancement of canopy photosynthesis when combining far-red and shorter wavelength photons. Even though far-red photons can penetrate deeper into the inner canopy, they most likely contribute little to canopy photosynthesis when shorter wavelength photons are limited or absent.

4.3 | Far-red stimulated cyclic electron transport on C_3 and C_4 photosynthesis

The effect of far-red on canopy photosynthesis was similar among the diverse species used in this study, regardless of photosynthetic pathway, light adaptation or acclimation, canopy size and architecture, leaf anatomical structure (e.g., thickness), and pigment compositions

(e.g., chlorophyll and anthocyanin content). This indicates that the mechanism by which far-red enhances photochemical efficiency and photosynthesis is common among higher plants.

C₄ species such as corn and sorghum require extra ATP to concentrate CO₂ in bundle sheath cells and a higher ratio of ATP to NADPH for carbon assimilation compared with C₃ species. Cyclic electron transport (CEF) around PSI, which generates ATP without the production of NADPH, is thought to play a central role in supplying the extra ATP required in C₄ photosynthesis (Amthor, 2010; Takabayashi, Kishine, Asada, Endo, & Sato, 2005; Yamori & Shikanai, 2016). Sagun, Badger, Chow, and Ghannoum (2019) quantified partitioning of absorbed white light (provided by a halogen lamp that emits a large amount of far-red photons) to PSI under low irradiances (50–300 $\mu\text{mol m}^{-2} \text{s}^{-1}$) and high CO₂ partial pressure (4%) of a range of species, including C₃ and C₄ grasses. They found that even though light acclimation and irradiance intensities affected light partitioning to PSI and PSII, C₄ species distributed a higher fraction of absorbed light to PSI compared with C₃ species (Sagun et al., 2019). This may suggest a more prominent role of cyclic electron transport in C₄ species.

The functional importance of cyclic electron transport has also been shown in C₃ species in order to meet the required ATP:NADPH ratio for the Calvin-Benson cycle; in addition, CEF serves as a photoprotective mechanism under abiotic stress conditions (Heber & Walker, 1992; Johnson, 2011; Rochaix, 2011; Rumeau, Peltier, & Cournac, 2007). Far-red stimulates CEF around PSI, which is likely essential for efficient photosynthesis in both C₃ and C₄ species (Finazzi & Johnson, 2016; Kono, Yamori, Suzuki, & Terashima, 2017). In addition, far-red was shown to be a key factor in PSI protection against photoinhibition by keeping the pool of P700 more oxidized and driving CEF, especially under fluctuating light (Kono et al., 2017; Yamori, 2016).

4.4 | Wavelength-dependency of far-red on canopy photosynthesis

The photosynthetic efficiency of far-red photons and their effectiveness at enhancing photosynthesis is also dependent on the wavelength of photons. Shorter wavelength photons, alone or applied simultaneously with the background light, supported higher rate of photosynthesis than longer wavelength photons (Table 1; Figure 9). However, the enhancement of photosynthesis, calculated as the increase in canopy P_{gross} upon adding far-red to background light subtracted by canopy P_{gross} under far-red alone, tended to be greater with the 723-nm-peak far-red LEDs. The possible causes for this wavelength-dependency of photosynthetic response to far-red include: (a) the photon absorption efficiency decreases with increasing wavelength (Table 1 and Figure 8) and (b) enhancement of photochemical efficiency by far-red is wavelength-dependent (Zhen, Haidekker & van Iersel, 2018).

Specifically, the far-red LEDs with shorter peak wavelength emitted a greater amount of photons below 700 nm. About 28.8% of the

photons emitted by the 711 nm-centred LEDs were below 700 nm, compared with 11% by the 723-centred LEDs and only 1.5% by the 746-nm-centred LEDs. Those shorter wavelength photons were more efficiently absorbed and used for photosynthesis when applied alone, but they were less efficient at enhancing photochemical efficiency compared with longer wavelength photons (Zhen et al., 2018). Photons from 703 to 731 nm tended to be more efficient at increasing photochemical efficiency than photons below 703 nm or above 731 nm (Zhen et al., 2018).

The 746-nm-centred far-red LEDs, which emitted 24.1% of its photons above 750 nm, were ineffective for photosynthesis when applied alone and caused the smallest photosynthetic enhancement. This was partly attributable to its poor photon absorption: only 9% of incident photons from the 746 nm-peak LEDs were absorbed, compared with the 57% leaf absorption of the incident photons from the 711-centred LEDs. This result is consistent with the finding by Zhen et al. (2018) that photons above 752 nm were not effective at enhancing photochemical efficiency.

4.5 | Far-red effects on stomatal conductance

It is possible that far-red enhances photosynthesis through stomatal regulation. Holmes, Sager, and Klein (1986) observed that far-red radiation alone was ineffective in opening the stomata of *P. vulgaris*, whereas the addition of far-red to a background of white light caused a marked increase in leaf steady-state stomatal conductance that was associated with an increase in leaf photosynthetic rate. Because plants often adjust their stomatal conductance in proportion to the needs of photosynthetic tissues for CO₂ (Wong, Cowan, & Farquhar, 1979, 1985), it is unclear whether an increase in stomatal conductance from adding far-red is the cause or the result of the increase in photosynthetic rate. We found that adding same amount incident far-red or white photons caused similar increase in leaf P_{net} , but the increase in g_s was significantly smaller with the addition of far-red (Figure 7b,e). It thus becomes evident that far-red does not stimulate stomatal opening compared with white photons, and the effect of far-red on photosynthesis is probably not associated with stomatal opening. Instead, the stomatal response to far-red is most likely a response to the increase in photosynthetic rate.

4.6 | Chl *d* and *f* and genetic engineering of far-red utilizing crops—A feasible solution to improve crop yield?

Due to the common belief that far-red photons cannot be used for photosynthesis, genetic engineering of crop plants to harness far-red photons for photosynthesis has been put forward as a potential method to increase crop yield (Ho, Shen, Canniffe, Zhao, & Bryant, 2016; Wolf & Blankenship, 2019). Red-shifted forms of chlorophylls *d* and *f* (Chl *d* and *f*) that are modified in their chemical structures and absorb and utilize longer wavelength far-red photons (700 to 750 nm)

for photochemistry have been discovered in a number of oxygenic photosynthetic cyanobacteria (Chen et al., 2010; Miyashita et al., 1996). These cyanobacteria are typically adapted or acclimated to far-red-enriched environments. Among all the known chlorophylls, Chl *f* has the longest wavelength absorption maximum (Chen et al., 2010). It was recently reported that the primary electron donor of PSI in a Chl *f*-containing cyanobacterium is shifted from P700 to P745, and the primary electron donor of PSII is shifted from P680 to P727, significantly extending the upper wavelength threshold for oxygenic photosynthesis (Nürnberg et al., 2018). Red shifts in reaction centre absorption also occur in cyanobacteria that primarily use Chl *d* for both light harvesting and photochemical redox reactions (Hu et al., 1998; Loughlin, Lin, & Chen, 2013; Tomo et al., 2007). Enhanced oxygen evolution under far-red was observed in cyanobacterium *Leptolyngbya* (strain JSC-1) that synthesized Chl *d* and *f* (in addition to Chl *a*) and remodelled its photosynthetic apparatus in response to far-red illumination (Gan et al., 2014).

To date, no Chl *d* or *f*-containing algae or higher plants have been identified. Potentially, the introduction of Chl *d* and *f*, along with modification of reaction centre proteins, presents an exciting opportunity to utilize far-red photons. The feasibility of this approach is yet to be determined. Meanwhile, previous studies and our present results indicate that under broad spectrum or combined lights, plants are already able to use far-red photons (700 to 750 nm) efficiently for photosynthesis through synergistic enhancement of photosynthetic efficiency. This is particularly relevant to crop production under partial or full electric light in controlled environment facilities (e.g., greenhouses and indoor vertical farms) because most of the currently used LED grow lights do not emit any (or only contain insufficient amount of) far-red photons. The exact value of far-red on photosynthesis, however, may depend on the spectral composition of short wavelength photons (e.g., a combination of red and blue photons versus a broad spectrum white LED light). This is because the spectral composition of photons in the PAR region may affect the degree of excitation energy distribution imbalance between PSII and PSI—a prerequisite for enhancement of photosynthesis to occur when combining far-red and shorter wavelength photons (Zhen & van Iersel, 2017). Laisk et al. (2014) reported that PSII was over-excited at most of the wavelengths within 400–680 nm, except for at 400–450 nm, and 510, 620, and 680 nm where PSI and PSII had similar quantum yield for electron transport. It is thus reasonable to speculate that the PAR region of the sunlight overexcites PSII, and the presence of abundant far-red in sunlight most likely improves photosynthetic efficiency by helping to restore excitation balance between PSI and PSII. Studies using our current definition of PAR may undercount photosynthetic photon flux and thus over-estimate quantum yield under sunlight.

Nonetheless, far-red only enhances photosynthesis in the presence of sufficient amount of shorter wavelength photons. Far-red photons that reach the inner canopy are most likely not used for photosynthesis. Genetic engineering of crops that can efficiently utilize far-red for photosynthesis in the absence of shorter wavelength photons could increase canopy photosynthesis and yield.

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REFERENCES

- Allen, J. F. (2003). State transitions—A question of balance. *Science*, 299, 1530–1532.
- Amthor, J. S. (2010). From sunlight to phytomass: On the potential efficiency of converting solar radiation to phyto-energy. *New Phytologist*, 188, 939–959.
- Barber, J., & Archer, M. D. (2001). P680, the primary electron donor of photosystem II. *Journal of Photochemistry and Photobiology A: Chemistry*, 142, 97–106.
- Björn, L. O., Papageorgiou, G. C., Blankenship, R. E., & Govindjee. (2009). A viewpoint: Why chlorophyll *a*? *Photosynthesis Research*, 99, 85–98.
- Blankenship, R. E., & Chen, M. (2013). Spectrum expansion and antenna reduction can enhance photosynthesis for energy production. *Current Opinion in Chemical Biology*, 17, 457–461.
- Bugbee, B., & Monje, O. (1992). The limits of crop productivity. *Bioscience*, 42, 494–502.
- Butler, W. L. (1978). Energy distribution in the photochemical apparatus of photosynthesis. *Annual Review of Plant Physiology*, 29, 345–378.
- Chen, M., & Blankenship, R. E. (2011). Expanding the solar spectrum used by photosynthesis. *Trends in Plant Science*, 16, 427–431.
- Chen, M., Schliep, M., Willows, R. D., Cai, Z., Neilan, B. A., & Scheer, H. (2010). A red-shifted chlorophyll. *Science*, 329, 1318–1319.
- Croce, R., & van Amerongen, H. (2013). Light-harvesting in photosystem I. *Photosynthesis Research*, 116, 153–166.
- Duysens, L. N. M., & Ames, J. (1962). Function and identification of two photochemical systems in photosynthesis. *Biochimica et Biophysica Acta*, 64, 243–260.
- Emerson, R., Chalmers, R., & Cederstrand, C. (1957). Some factors influencing the long-wave limit of photosynthesis. *Proceeding of the National Academy of Science USA*, 43, 133–143.
- Emerson, R., & Lewis, C. M. (1943). The dependence of the quantum yield of chlorella photosynthesis on wave length of light. *American Journal of Botany*, 30, 165–178.
- Emerson, R., & Rabinowitch, E. (1960). Red drop and role of auxiliary pigments in photosynthesis. *Plant Physiology*, 35, 477–485.
- Evans, J. R. (1987). The dependence of quantum yield on wavelength and growth irradiance. *Australian Journal of Plant Physiology*, 14, 69–79.
- Finazzi, G., & Johnson, G. N. (2016). Cyclic electron flow: Facts and hypotheses. *Photosynthesis Research*, 129, 227–230.
- Gan, F., Zhang, S., Rockwell, N. C., Martin, S. S., Lagarias, J. C., & Bryant, D. A. (2014). Extensive remodeling of a cyanobacterial photosynthetic apparatus in far red light. *Science*, 345, 1312–1317.
- Gifford, R. M., Thorne, J. H., Hitz, W. D., & Giaquinta, R. T. (1984). Crop productivity and photoassimilate partitioning. *Science*, 225, 801–808.
- Gobets, B., & van Grondelle, R. (2001). Energy transfer and trapping in photosystem I. 2001. *Biochimica et Biophysica Acta*, 1507, 80–99.
- Hanson, M. R., Lin, M. T., Carmo-silva, A. E., & Parry, M. A. J. (2016). Towards engineering carboxysomes into C3 plants. *The Plant Journal*, 87, 38–50.

- Heber, U., & Walker, D. (1992). Concerning a dual function of coupled cyclic electron transport in leaves. *Plant Physiology*, 100, 1621–1626.
- Hill, R., & Bendall, F. (1960). Function of the two cytochrome components in chloroplasts: A working hypothesis. *Nature*, 186, 136–137.
- Ho, M.-Y., Shen, G., Canniffe, D. P., Zhao, C., & Bryant, D. A. (2016). Light-dependent chlorophyll f synthase is a highly divergent paralog of PsbA of photosystem II. *Science*, 353, aaf9178.
- Hogewoning, S. W., Wientjes, E., Douwstra, P., Trouwborst, G., van Ieperen, W., Croce, R., & Harbinson, J. (2012). Photosynthetic quantum yield dynamics: From photosystems to leaves. *Plant Cell*, 24, 1921–1935.
- Holmes, M. G., Sager, J. C., & Klein, W. H. (1986). Sensitivity to far-red radiation in stomata of *Phaseolus vulgaris* L: Rhythmic effects on conductance and photosynthesis. *Planta*, 168, 516–522.
- Holmes, M. G., & Smith, H. (1977). The function of phytochrome in the natural environment-II. The influence of vegetation canopies on the spectral energy distribution of natural daylight. *Photochemistry and Photobiology*, 25, 539–545.
- Hu, Q., Miyashita, H., Iwasaki, I., Kurano, N., Miyachi, S., Iwaki, M., & Itoh, S. (1998). A photosystem I reaction center driven by chlorophyll d in oxygenic photosynthesis. *Proceeding of the National Academy of Science USA*, 95, 13319–13323.
- Inada, K. (1976). Action spectra for photosynthesis in higher plants. *Plant & Cell Physiology*, 17, 355–365.
- Johnson, G. N. (2011). Physiology of PSI cyclic electron transport in higher plants. *Biochimica et Biophysica Acta*, 1807, 384–389.
- Kasperbauer, M. J. (1971). Spectral distribution of light in a tobacco canopy and effects of end-of-day light quality on growth and development. *Plant Physiology*, 47, 775–778.
- Kirst, H., Shen, Y., Vamvaka, E., Betterle, N., Xu, D., Warek, U., ... Melis, A. (2018). Downregulation of the *CpSRP43* gene expression confers a truncated light-harvesting antenna (TLA) and enhances biomass and leaf-to-stem ratio in *Nicotiana tabacum* canopies. *Planta*, 248, 139–154.
- Koehne, B., Elli, G., Jennings, R. C., Wilhelm, C., & Trissl, H. W. (1999). Spectroscopic and molecular characterization of a long wavelength absorbing antenna of *Ostreobium* sp. *Biochimica et Biophysica Acta*, 1412, 94–107.
- Kok, B. (1961). Partial purification and determination of oxidation reduction potential of the photosynthetic chlorophyll complex absorbing at 700 m μ . *Biochimica et Biophysica Acta*, 48, 527–533.
- Kono, M., Kawaguchi, H., Mizusawa, N., Yamori, W., Suzuki, Y., & Terashima, I. (2020). Far-red light accelerates photosynthesis in the low-light phases of fluctuating light. *Plant & Cell Physiology*, 61, 192–202. <https://doi.org/10.1093/pcp/pcz191>
- Kono, M., Yamori, W., Suzuki, Y., & Terashima, I. (2017). Photoprotection of PSI by far-red light against the fluctuating light-induced photo-inhibition in *Arabidopsis thaliana* and field-grown plants. *Plant & Cell Physiology*, 58, 35–45.
- Kromdijk, J., Glowacka, K., Leonelli, L., Gabilly, S. T., Iwai, M., Niyogi, K. K., & Long, S. P. (2016). Improving photosynthesis and crop productivity by accelerating recovery from photoprotection. *Science*, 354, 857–861.
- Kubis, A., & Bar-Even, A. (2019). Synthetic biology approaches for improving photosynthesis. *Journal of Experimental Botany*, 70, 1425–1433.
- Laik, A., Oja, V., Eichelmann, H., & Dall'Osto, L. (2014). Action spectra of photosystems II and I and quantum yield of photosynthesis in leaves in state 1. *Biochimica et Biophysica Acta*, 1837, 315–325.
- Long, S. P., Zhu, X.-G., Naidu, S. L., & Ort, D. R. (2006). Can improvement in photosynthesis increase crop yields? *Plant, Cell and Environment*, 29, 315–330.
- Loughlin, P., Lin, Y., & Chen, M. (2013). Chlorophyll d and *Acaryochloris marina*: Current status. *Photosynthesis Research*, 116, 277–293.
- McCree, K. J. (1972a). Significance of enhancement for calculation based on the action spectrum for photosynthesis. *Plant Physiology*, 49, 704–706.
- McCree, K. J. (1972b). The action spectrum, absorptance and quantum yield of photosynthesis in crop plants. *Agricultural Meteorology*, 9, 191–216.
- Melis, A. (2009). Solar energy conversion efficiency in photosynthesis: Minimizing the chlorophyll antennae to maximize efficiency. *Plant Science*, 177, 272–280.
- Miyashita, H., Ikemoto, H., Kurano, N., Adachi, K., Chihara, M., & Miyachi, S. (1996). Chlorophyll d as a major pigment. *Nature*, 383, 402.
- Murakami, K., Matsuda, R., & Fujiwara, K. (2018). A mathematical model of photosynthetic electron transport in response to the light spectrum based on excitation energy distributed to photosystems. *Plant & Cell Physiology*, 59, 1643–1651.
- Myers, J. (1971). Enhancement studies in photosynthesis. *Annual Review of Plant Physiology*, 22, 289–312.
- Nelson, J. A., & Bugbee, B. (2015). Analysis of environmental effects on leaf temperature under sunlight, high pressure sodium and light emitting diodes. *PLoS One*, 10, e0138930.
- Nürnberg, D. J., Morton, J., Santabarbara, S., Telfer, A., Joliot, P., Antonaru, L. A., ... Rutherford, A. W. (2018). Photochemistry beyond the red limit in chlorophyll f-containing photosystems. *Science*, 360, 1210–1213.
- Ort, D. R., Merchant, S. S., Alric, J., Barkan, A., Blankenship, R. E., Bock, R., ... Zhu, X. G. (2015). Redesigning photosynthesis to sustainably meet global food and bioenergy demand. *Proceeding of the National Academy of Science USA*, 112, 8529–8536.
- Rivadossi, A., Zucchelli, G., Garlaschi, F. M., & Jennings, R. C. (1999). The importance of PS I chlorophyll red forms in light-harvesting by leaves. *Photosynthesis Research*, 60, 209–215.
- Rochaix, J. D. (2011). Regulation of photosynthetic electron transport. *Biochimica et Biophysica Acta*, 1807, 878–886.
- Rumeau, D., Peltier, G., & Cournac, L. (2007). Chlororespiration and cyclic electron flow around PSI during photosynthesis and plant stress response. *Plant, Cell and Environment*, 30, 1041–1051.
- Sagun, J. V., Badger, M. R., Chow, W. S., & Ghannoum, O. (2019). Cyclic electron flow and light partitioning between the two photosystems in leaves of plants with different functional types. *Photosynthesis Research*, 142, 321–334.
- Schuler, M. L., Mantegazza, O., & Weber, A. P. M. (2016). Engineering C_4 photosynthesis into C_3 chassis in the synthetic biology age. *The Plant Journal*, 87, 51–65.
- South, P. F., Cavanagh, A. P., Liu, H. W., & Ort, D. R. (2019). Synthetic glycolate metabolism pathways stimulate crop growth and productivity in the field. *Science*, 363, eaat9077.
- Takabayashi, A., Kishine, M., Asada, K., Endo, T., & Sato, F. (2005). Differential use of two cyclic electron flows around photosystem I for driving CO_2 -concentration mechanism in C_4 photosynthesis. *Proceeding of the National Academy of Science USA*, 102, 16898–16903.
- Tomo, T., Okubo, T., Akimoto, S., Yokono, M., Miyashita, H., Tsuchiya, T., ... Mimuro, M. (2007). Identification of the special pair of photosystem II in a chlorophyll d-dominated cyanobacterium. *Proceeding of the National Academy of Science USA*, 104, 7283–7288.
- van Iersel, M. W., & Bugbee, B. (2000). A multiple chamber, semi-continuous, crop carbon dioxide exchange system: Design, calibration, and data interpretation. *Journal of American Society for Horticultural Science*, 125, 86–92.
- Wolf, B. M., & Blankenship, R. E. (2019). Far-red acclimation in diverse oxygenic photosynthetic organisms. *Photosynthesis Research*, 142, 349–359. <https://doi.org/10.1007/s11120-019-00653-6>
- Wong, S. C., Cowan, I. R., & Farquhar, G. D. (1979). Stomatal conductance correlates with photosynthetic capacity. *Nature*, 282, 424–426.
- Wong, S. C., Cowan, I. R., & Farquhar, G. D. (1985). Leaf conductance in relation to rate of CO_2 assimilation. I. Influence of nitrogen nutrition, phosphorus nutrition, photon flux density, and ambient partial pressure of CO_2 during ontogeny. *Plant Physiology*, 78, 821–825.

- Yamori, W. (2016). Photosynthetic response to fluctuating environments and photoprotective strategies under abiotic stress. *Journal of Plant Research*, 129, 379–395.
- Yamori, W., & Shikanai, T. (2016). Physiological functions of cyclic electron transport around photosystem I in sustaining photosynthesis and plant growth. *Annual Review of Plant Biology*, 67, 81–106.
- Zhen, S., Haidekker, M., & van Iersel, M. W. (2018). Far-red light enhances photochemical efficiency in a wavelength-dependent manner. *Physiologia Plantarum*, 167, 21–33. <https://doi.org/10.1111/ppl.12834>
- Zhen, S., & van Iersel, M. W. (2017). Far-red light is needed for efficient photochemistry and photosynthesis. *Journal of Plant Physiology*, 209, 115–122.
- Zhu, X. G., Long, S. P., & Ort, D. R. (2010). Improving photosynthetic efficiency for greater yield. *Annual Review of Plant Biology*, 61, 235–261.

SUPPORTING INFORMATION

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