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On the Lack of Morphological Response to Far-red at High and Low Photon Flux in Spinach

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Abstract. **An increasing far-red (FR; 700–750 nm) photon fraction typically triggers shade-avoidant responses such as leaf expansion, but previous work in lettuce has indicated that this occurs only at a higher extended photosynthetic photon flux density (ePPFD; 400–750 nm). We report the interaction between the FR photon fraction and ePPFD in spinach. We grew spinach in growth chambers under ePPFDs of 100, 200, and 500 μmol·m^{-2}·s^{-1}, each with an FR photon fraction of 0.03, 0.10, 0.17, or 0.33. Recent studies have demonstrated the photosynthetic value of FR photons, which makes it important to include these in the definition of photosynthetic photons. We thus substituted FR photons for shorter wavelength photons to keep photosynthetic photons (ePPFD) constant among treatments. As expected, leaf area and dry mass increased with increasing ePPFD; but, surprisingly, there was no effect of an increasing FR photon fraction on leaf area, regardless of ePPFD. These results show that FR photons are equivalent to shorter wavelength photons in spinach; but, unlike lettuce, an increasing FR fraction did not increase leaf area.**

The advent of light-emitting diode (LED) fixtures has facilitated recent photobiological studies. These high-efficiency fixtures enable precise control of spectral quality and quantity. Far-red (FR) photons (700–750 nm) are of particular interest because they are more energetically efficient to produce than red and blue photons. This has led to a body of research that focuses on lettuce because of its clear responses to FR photons.

Spinach (*Spinacia oleracea*) is a widely grown, yet understudied crop in controlled-environment agriculture. Its high nutrient content drives its fresh-market value, which was estimated by the (US Department of Agriculture 2024) to be about $723 million in the United States in 2023. The high chlorophyll content in its comparatively thick leaves makes it distinct from other common leafy greens, such as lettuce. Semenova et al. (2023) found total chlorophyll concentrations in spinach of 2 mg·g^{-1}, whereas Caldwell and Britz (2006) measured chlorophyll concentrations in lettuce of less than 0.6 mg·g^{-1}. This 4-fold greater chlorophyll concentration may lead to unique photobiological responses.

Proietti et al. (2023) reported significantly greater yield and sugar contents when spinach was grown at a photosynthetic photon flux density (PPFD; 400–700 nm) of 800 μmol·m^{-2}·s^{-1} compared with a PPFD of 200 μmol·m^{-2}·s^{-1}. Martínez-Moreno et al. (2024) saw a linear increase in spinach yield from a PPFD of 150 μmol·m^{-2}·s^{-1} to a PPFD of 430 μmol·m^{-2}·s^{-1}. Lőrinc et al. (2019) also reported a significant increase in fresh mass as the PPFD increased from 100 to 300 μmol·m^{-2}·s^{-1}. Nguyen et al. (2021) found that the substitution of green light did not improve spinach growth compared with red and blue light when the PPFD was maintained at 190 μmol·m^{-2}·s^{-1}.

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Photosynthetic Value of FR Photons on Photosynthesis

When FR photons are added to light sources with shorter wavelengths, the quantum yield of photosystem II is improved (Zhen and Van Iersel 2017). Park and Runkle (2017) found that the growth of four flower species was equal even as PPFD decreased, provided that these photons were substituted for FR photons and the extended photosynthetic photon flux density (ePPFD; 400–750 nm) was maintained. Zhen and Bugbee (2020a) studied canopy gas exchange of 14 species and found that FR photons have equivalent efficiency to traditional photosynthetic photons. When they added FR photons to a background of PPFD photons, they demonstrated an increase in canopy photosynthesis that was equivalent to adding the same amount of PPFD photons. In longer term follow-up studies, Zhen and Bugbee (2020b) later substituted PPFD photons for FR photons under electric lights and demonstrated equivalent canopy quantum yield throughout the life cycle of lettuce. Zhen et al. (2022) provided further evidence of the photosynthetic value of FR photons by filtering FR photons from sunlight.

Effects of FR Photons on Morphology

FR photons alter plant morphology through photoreceptors called phytochromes (Voitsekhovskaja 2019). FR light influences internodal and petiole length, leaf and petiole hyponasty, plant height, and biomass, especially in shaded environments (Tan et al. 2022; Zhen et al. 2021). Increasing FR photons often signal a shaded environment, which can increase stem elongation and leaf expansion to capture more light and help plants compete with neighbors for photon capture (Demotes-Mainard et al. 2016). Recent studies have demonstrated the effects of FR photons on leaf expansion in lettuce (Carotti et al. 2024; Legendre and Van Iersel 2021; Liu and Van Iersel 2022), but the effects of FR photons on spinach morphology are poorly characterized.

FR Photon Interactions with Light Intensity

Kusuma and Bugbee (2023) investigated the effects of increasing ePPFD and FR fraction in lettuce (*Lactuca sativa*) and cucumber (*Cucumis sativis*). They found that in lettuce, increasing the FR fraction led to greater leaf area and dry mass at a high ePPFD, but not at a low ePPFD. In cucumber, increasing the FR fraction resulted in a greater leaf area and biomass across all ePPFDs from 100 to 500 μmol·m^{-2}·s^{-1}, indicating the effect of FR photons was species dependent.

The effect of FR photons has not been widely studied in spinach. A single article suggested no difference in the leaf area or dry mass of spinach when the FR fraction was increased from about 0.08 to 0.45, but the ePPFD was not held constant (Lőrinc et al. 2019). Those researchers did find a greater specific leaf area (SLA) in plants receiving the higher FR fraction, but these effects could have been the result of a change in ePPFD.

Our objective was to determine the effect of FR fraction on the morphology and growth of spinach at three ePPFDs. We hypothesized that spinach would behave similarly to lettuce by increasing leaf area and dry mass with increasing FR fraction at high ePPFDs, but not at low ePPFDs.

Materials and Methods

Cultural and environmental conditions. To facilitate quantifying leaf area, flat-leaf spinach (*Spinacia oleracea* cv. Melody hybrid) was used in all studies. Spinach seed germination benefits from a unique seed pretreatment (Katzman et al. 2001). Seeds were soaked in 500 mL of 0.5% sodium hypochlorite (a 10% solution of 5% commercial bleach) for 4 h while being stirred continuously with a magnetic stir bar. After soaking, the seeds were rinsed with reverse-osmosis (RO) water and aerated vigorously in 500 mL of RO water at a rate of 1 $L \cdot min^{-1}$ for 15 h. The seeds were then transferred onto germination paper soaked in a 0.3% hydrogen peroxide for 2 d at 23 °C until radicle emergence from the pericarp (Langenfeld and Bugbee 2022). The seeds and paper were kept sealed in a clear plastic germination box during germination. Lower germination temperatures may have increased germination uniformity in untreated seeds, but our pretreatment method improved uniformity, so seeds were germinated at room temperature.

Eight germinated seeds were planted into each of 12 acrylic containers, measuring 20 cm long by 18 cm wide by 13 cm deep, and filled with soilless media. The mixture was composed of 75% peatmoss (Premier Pro-Moss TBK; Premier Horticulture, Inc., Quakertown, PA, USA), 13% vermiculite (horticultural coarse vermiculite; Perlite Vermiculite Packaging Industries, North Bloomfield, OH, USA), and 12% rice hulls (PBH Nature's Media Amendment; Riceland Foods, Inc., Stuttgart, AR, USA) by volume. A wetting agent (AquaGro® 2000 G; Aquatrols, Paulsboro, NJ, USA) was added at a concentration of 1 $g \cdot L^{-1}$ of peat to help increase wetting ability. Hydrated lime (calcium hydroxide) was added at a concentration of 1.5 $g \cdot L^{-1}$ of peat to increase the pH to 6. Plants were thinned to four per chamber within the first 2 d after planting to maintain uniformity among chambers and to minimize crowding. Nonuniform seedlings were removed to promote the growth of representative plants.

Containers were placed in 12 chambers (length, 20 cm; width, 23 cm; height, 30 cm) that were in a larger common room to improve uniformity of temperature, humidity, and CO_2 among chambers. Each chamber had white walls and two fans (one inflow and one outflow) to provide an ample air exchange of approximately one exchange per minute with the common room. This airflow provided an air velocity of ~0.5 $m \cdot s^{-1}$ at the top of the canopy and a uniform temperature of 23 ± 0.5 °C among chambers. The CO_2 concentration within the chambers was not controlled, but was uniform among chambers at the CO_2 of the room, which was about 500 ppm. The vapor pressure deficit was uniform among chambers at 1.3 ± 0.2 kPa. Plants were watered as needed with nutrient solution that contained 120 $mg \cdot L^{-1}$ N (72 $mg \cdot L^{-1}$ nitrate-N, 42 $mg \cdot L^{-1}$ ammonium-N, and 6 $mg \cdot L^{-1}$ urea-N), 31 $mg \cdot L^{-1}$ P, 177 $mg \cdot L^{-1}$ K, 45 $mg \cdot L^{-1}$ Ca, 19 $mg \cdot L^{-1}$ Mg, 25 $mg \cdot L^{-1}$ S, 17 $mg \cdot L^{-1}$ Si, 0.9 $mg \cdot L^{-1}$ Fe, 0.3 $mg \cdot L^{-1}$ Mn, 0.4 $mg \cdot L^{-1}$ Zn, 0.41 $mg \cdot L^{-1}$ B, 0.85 $mg \cdot L^{-1}$ Cu, and 0.06 $mg \cdot L^{-1}$ Mo.

Lighting systems and spectral treatments. Systems and chambers were previously used and described by Kusuma and Bugbee (2023). There were three ePPFD intensities (100, 200, and 500 $\mu mol \cdot m^{-2} \cdot s^{-1}$) with four FR fractions (0.03, 0.10, 0.17, and 0.33 by substitution). We defined the FR fraction as the density of photons from 700 to 750 nm divided by the density of photons from 400 to 750 nm. The photoperiod for each chamber was 16/8 h light/dark, resulting in an extended daily light integral (400–750 nm) of 5.8, 11.5, and 28.8 $mol \cdot m^{-2} \cdot d^{-1}$.

Treatments were developed using white (2700 and 6500 K), red (658 nm) and FR (726 nm) LEDs (Lumileds LLC, San Jose, CA, USA) to provide ~20% blue, ~40% green, and ~40% red photons as a proportion of ePPFD in the 0.03 FR fraction treatment. We increased the FR fraction by adding FR LEDs and dimming the white LEDs. This decreased the fraction of the blue, green, and red photons, but we maintained the red-to-blue ratio (Supplemental Table 1). Spectral distributions were measured using a spectroradiometer (PS-300; Apogee Instruments, Logan, UT, USA) at the height of the substrate in the container (Fig. 1). Containers were rotated 180° every 3 d to improve light uniformity.

Measurements. Plants were harvested 24 d after emergence. Leaf area (leaves plus petioles) was measured using a leaf area meter (LI-3000; LI-COR, Lincoln, NE, USA). The fresh mass of each plant was measured, and tissue was then dried at 80 °C for 48 h in a drying oven. The SLA was calculated by dividing the fresh leaf area of each plant (in square centimeters) by the dry mass of each plant (in grams). Measurements from the four plants in each chamber were averaged together. We normalized measurements to the 0.03 FR fraction treatment within each ePPFD block to examine the FR effect in the absence of ePPFD. The photon conversion efficacy (PCE) was calculated by dividing the dry mass per plant by the chamber area per plant (assumed to be one fourth of the chamber area, or 0.0112 m^2). This value was then multiplied by the growth time (24 d) and divided by the ePPFD (in moles) to calculate PCE in grams of dry biomass per moles of photons.

Statistical analysis. The study was replicated six times. Every treatment (chamber) was the mean of four plants. We used a linear regression model (lm) in R (ver. 4.0.5; R Foundation for Statistical Computing, Vienna, Austria) to analyze significance among FR fraction levels within each ePPFD level. The ePPFD and FR interaction was analyzed using analysis of variance in R by treating each as a categorical variable. Statistical significance was determined at the $\alpha = 0.05$ level.

Results

Plants grown at an ePPFD of 500 $\mu mol \cdot m^{-2} \cdot s^{-1}$ had visually darker leaves that were visually more cupped around the edges than plants grown at the lower ePPFDs of 100 or 200 $\mu mol \cdot m^{-2} \cdot s^{-1}$ (Fig. 2). Although there was a visual difference in leaf area among plants with increasing ePPFD, there was no visual difference among FR treatments within an ePPFD level.

The average mass weight per plant increased from 2.20 to 7.78 g as the ePPFD increased from 100 to 500 $\mu mol \cdot m^{-2} \cdot s^{-1}$ (Supplemental Table 2). The average dry mass per plant increased from 0.15 to 0.90 g as the ePPFD increased from 100 to 500 $\mu mol \cdot m^{-2} \cdot s^{-1}$, but there was no significant change in dry mass with increasing FR fraction at any ePPFD (Fig. 3). The percent dry mass also increased with increased ePPFD, but there was no difference among FR fractions (Supplemental Table 2).

The leaf area increased as the ePPFD increased from 100 to 500 $\mu mol \cdot m^{-2} \cdot s^{-1}$, but increasing the FR photon fraction had no effect on leaf area at any ePPFD. The SLA decreased as the ePPFD increased. There was a significant increase in SLA with increasing FR fractions at ePPFDs of 100 and 200 $\mu mol \cdot m^{-2} \cdot s^{-1}$ ($P < 0.05$), but not at 500 $\mu mol \cdot m^{-2} \cdot s^{-1}$. There was no significant interaction between ePPFD and

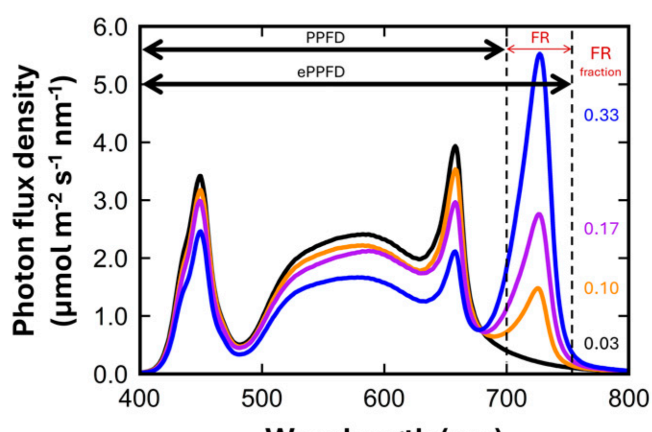

Fig. 1. The spectral photon distribution for four fractions of far-red (FR) light [0.03 (black), 0.10 (orange), 0.17 (purple), and 0.33 (blue)] substituted to achieve an extended photosynthetic photon flux density (ePPFD; 400–750 nm) of 500 $\mu mol \cdot m^{-2} \cdot s^{-1}$. The spectral ratios among chambers with lower ePPFDs were within 5% (Supplemental Table 1).

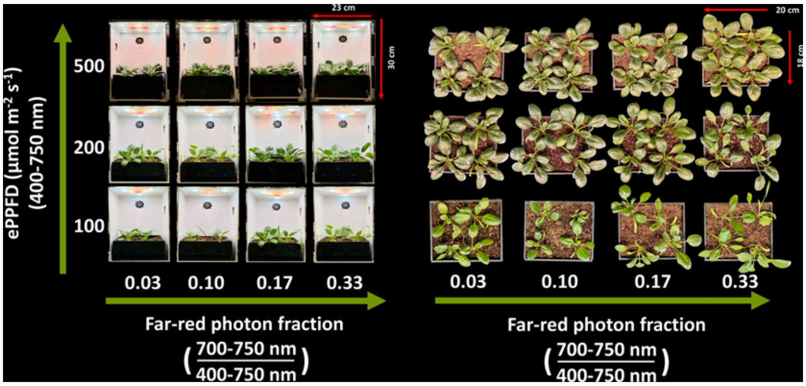

Fig. 2. Representative photos showing side and top views of the morphological effects in spinach (*Spinacia oleracea*) with increasing extended photosynthetic photon flux density (ePPFD; 400–750 nm) and far-red fraction (700 to 750 nm).

FR fraction with any of the parameters except SLA (Supplemental Table 3).

The PCE was greatest at 200 $\mu mol \cdot m^{-2} \cdot s^{-1}$, followed by 500 and then 100 $\mu mol \cdot m^{-2} \cdot s^{-1}$ ePPFDs (Fig. 4). There was no significant difference in PCE among FR fractions at any ePPFD.

Discussion

Consistent with the results of previous studies, increasing the ePPFD from 100 to 500 $\mu mol \cdot m^{-2} \cdot s^{-1}$ increased dry mass in spinach. Lőrinc et al. (2019), Proietti et al. (2023), and Martínez-Moreno et al. (2024) all demonstrated yield increases in spinach with increasing PPFD ranging from 100 to 800 $\mu mol \cdot m^{-2} \cdot s^{-1}$.

In contrast to studies in lettuce and cucumbers, we saw no change in the dry mass or leaf area of spinach with increasing substitution of FR photons (constant ePPFD across FR fraction treatments). These results confirm that FR photons have equivalent photosynthetic capacity as shorter wavelength photons, but there was no benefit of FR on leaf expansion. There was a statistically significant increase in SLA with increasing FR fraction at the two lower ePPFDs (100 and 200 $\mu mol \cdot m^{-2} \cdot s^{-1}$), but it was not significant at 500 $\mu mol \cdot m^{-2} \cdot s^{-1}$ ($P = 0.066$). The 25% increase in SLA (thinner leaves) without an increase in total leaf area indicates that the FR fraction likely increased petiole elongation, especially at the lower ePPFD.

Zhen and Bugbee (2020b) saw a 30% increase in lettuce growth when substituting shorter wavelength photons for an FR fraction of 0.15 over an ePPFD of 350 $\mu mol \cdot m^{-2} \cdot s^{-1}$. They associated this with increased photon capture resulting from increased leaf area. Kusuma and Bugbee (2023) found that increasing the FR fraction increased the leaf area in lettuce at higher ePPFDs, and increased the leaf area in cucumber at all ePPFDs. The leaf area in our study did not increase with increasing FR fraction, so there was no increase in photon capture.

The value of FR photons in photosynthesis is becoming increasingly evident even in sunlight. Zhen et al. (2022) measured leaf net photosynthetic rate before and after applying an FR filter to sunlight and found a 41% decrease in corn and 61% decrease in sunflower when FR photons were removed from sunlight. The FR photons contributed 81% to 93% of the ePPFD when plants were shaded, which suggests their effect on photosynthesis was substantial at low light levels.

Plant responses to shade are classified as shade avoidant and/or shade tolerant (Xu et al. 2021). Shade-avoidant plants are typically more sensitive to low light and respond by increasing stem and petiole elongation to maximize light interception by growing vertically upward (Henry and Aarssen 1997; Legris et al. 2019). In contrast, shade-tolerant plants respond by increasing leaf expansion (Bloor and Grubb 2004). These contrasting responses can result from how shade-tolerant species optimize their light capture through decreasing dark respiration rates to increase carbon gain (Xu et al. 2021).

Using previous definitions and the results of our study, spinach can be classified as a shade-avoidant species. We observed lighter green leaves at lower ePPFDs, which is consistent with decreased chlorophyll concentrations and thinner leaves. This correlates with the increasing SLA we observed with decreasing ePPFD. We also observed increasing apical dominance (a more vertical leaf angle), but no change in leaf area with increasing FR fraction, which mimics shaded conditions. We attempted to measure leaf angle in one trial, but the small top-heavy plants made these measurements difficult and inconclusive, so they were not measured in other trials.

Spinach growth might not be enhanced by increasing the FR fraction, but the inclusion of these longer wavelength photons increases energy efficiency, which decreases production costs without reducing yield. There was no effect of FR on PCE, but there was an effect of ePPFD. Not surprisingly, the PCE was

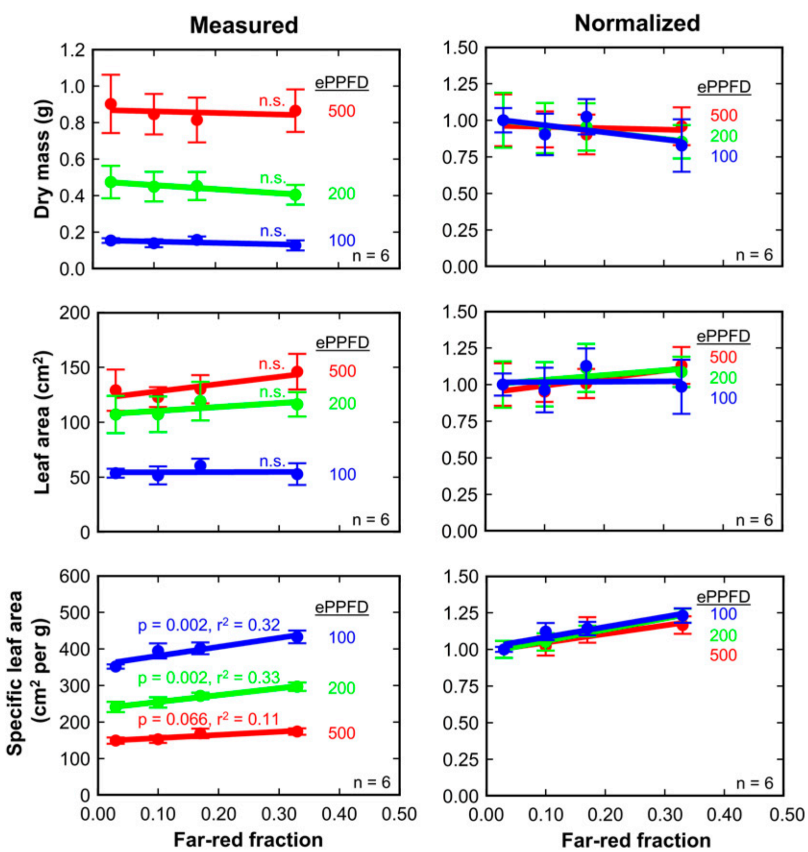

Fig. 3. The effect of the far-red (FR) fraction on the measured (**left panels**) and normalized (**right panels**) dry mass, leaf area, and specific leaf area of spinach (*Spinacia oleracea*) grown for 24 d at an extended photosynthetic photon flux density (ePPFD; 400–750 nm) of 100, 200, or 500 $\mu mol \cdot m^{-2} \cdot s^{-1}$ with increasing fractions of substituted FR photons. Data were normalized to the 0.03 FR fraction treatment for each ePPFD. Error bars represent the standard error of the mean, n = 6, and n.s. indicates no significant difference among FR fractions.

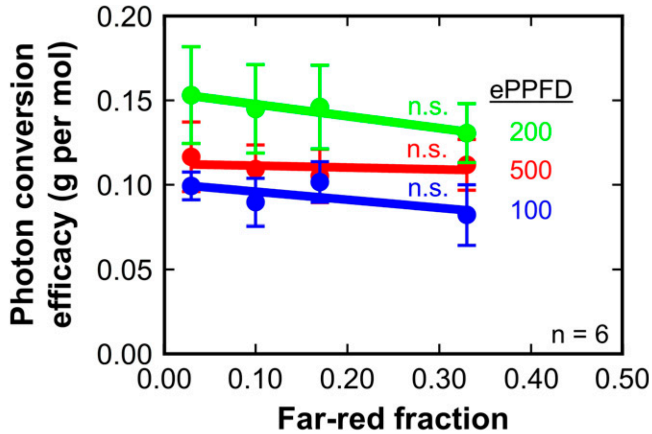

Fig. 4. The effect of the far-red (FR) fraction on photon conversion efficacy (PCE) of spinach (*Spinacia oleracea*). Plants were grown for 24 d at an extended photosynthetic photon flux density (ePPFD; 400–750 nm) of 100, 200, or 500 μmol·m^{-2}·s^{-1}. The PCE was determined by dividing the shoot dry mass in grams per square meter per day by the extended daily light integral (400–750 nm) in moles per square meter per day. Error bars represent the standard error of the mean, n = 6, and n.s. indicates no significant difference among FR fractions.

greatest at an ePPFD of 200 μmol·m^{-2}·s^{-1}, which indicates that photons are used less efficiently at an ePPFD of 500 μmol·m^{-2}·s^{-1}. This higher photon flux could have led to the increased leaf cupping we observed at the highest ePPFD. The most energetically efficient ePPFD for spinach grown appears to be between 200 and 500 μmol·m^{-2}·s^{-1}.

Conclusion

As expected, increasing the ePPFD from 100 to 500 μmol·m^{-2}·s^{-1} increased spinach growth. In contrast to studies in lettuce and cucumber, increasing the FR fraction did not increase leaf area. Although higher ePPFDs increased growth, the PCE was maximized at 200 μmol·m^{-2}·s^{-1}. Understanding interactions among spectral quality and ePPFD is critical to crop optimization in controlled-environment agriculture.

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