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Interactive Effects of Photon Flux Density and Carbon Dioxide Concentration on Energy-use Efficiency for Indoor Baby-greens Production

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Abstract. **In effort to improve resource-use efficiency of indoor specialty-crop production, this study examined potential interactive effects of a range of photosynthetic photon flux densities (PPFDs) and carbon dioxide (CO_2) concentrations on growth and quality attributes of densely seeded baby-stage red lettuce (*Lactuca sativa* cv. Rouxai). Growth PPFDs tested included 200, 300, 400, and 500 $\mu mol \cdot m^{-2} \cdot s^{-1}$. Growth CO_2 concentrations tested included 400, 800, 1200, and 1600 $\mu mol \cdot mol^{-1}$. Growth parameters including shoot fresh mass, shoot dry mass, and leaf area were measured after a 17-day cropping cycle. Quality attributes such as red pigmentation and chlorophyll concentration were quantified nondestructively. Energy consumption for lighting (kWh) was measured over the entire cropping cycle for each experimental treatment, and energy-use efficiency (EUE) was calculated as a function of shoot fresh mass produced per kWh of electricity expended for lighting. Results indicated significant PPFD × CO_2 interaction effects for all measured productivity parameters except chlorophyll concentration. CO_2 was the less-limiting factor, with crop-productivity responses maximizing at 1200 $\mu mol \cdot mol^{-1}$. PPFD was the more-limiting factor, with no evidence of light saturation at any PPFD/CO_2 combination tested. Although both PPFD and CO_2 influenced pigmentation, chlorophyll concentration was more strongly affected by PPFD. EUE was highest at the lowest PPFD tested across all CO_2 concentrations and declined with increasing PPFD. In addition to establishing a PPFD × CO_2 profile for baby-stage lettuce production, our findings suggest that from the industry standards of 800 $\mu mol \cdot mol^{-1}$ CO_2 and 200 $\mu mol \cdot m^{-2} \cdot s^{-1}$ PPFD, increasing PPFD further can lead to four to nine more cropping cycles per year, which possibly could offset increased electricity costs, particularly with premium market pricing for baby-stage lettuce. The choice of PPFD dictating CO_2 concentration to achieve production goals may be determined by incorporating the findings of this study into comprehensive cost-benefit analyses.**

Vertical farming (VF) is a highly technical indoor crop-production system in which plants are cultivated in vertically stacked layers under sole-source lighting typically provided by light-emitting-diodes (LEDs). As the most recent advancement in controlled-environment agriculture (CEA), VF is expected to play a significant role in future agricultural production chains. Key advantages of VF include year-round local production, substantially higher yield per unit growing area, and improved water-use efficiency (Cai et al. 2025; Graamans et al. 2018). However, the VF industry faces economic challenges, primarily due to fragile profitability driven by high capital and operational expenses (Ahamed et al. 2023; Arcasi et al. 2024; Warner et al. 2023). Electrical energy consumed constitutes 30% to 40% of total operational costs (Avgoustaki and Xydis 2020; Kozai and Niu 2020; Kozai et al. 2019), with LED lighting accounting for 80% of that energy cost (Kozai 2022; Yokoyama 2019). According to a recent industry report, improving EUE is a top priority for VF stakeholders (Global CEA Census Report 2024), highlighting the need to minimize energy costs associated with sole-source lighting.

Various studies have evaluated methods to improve EUE of sole-source lighting in VF. Using a modeling approach, Avgoustaki and Xydis (2021) demonstrated that intermittent lighting could reduce electric lighting costs 16% to 26% compared with continuous lighting. Similarly, findings of a modeling and experimentation study by Kaiser et al. (2024) showed that dynamic lighting patterns changing in response to daily changes in electrical cost could help save energy in VF without reducing biomass production. LEDs for sole-source lighting also can allow flexible light quality, through which EUE can be improved. For example, substituting lower-energy far-red for red and blue wavelengths has been suggested to help improve EUE of lettuce production in VF (Carotti et al. 2024). Although research targeted to improve EUE is ongoing, overall energy consumption remains high. The estimated energy consumption for indoor-grown lettuce is anticipated to decrease with improvements in equipment efficiency and operational controls (Miserocchi and Franco 2025), which cannot be considered a short-term goal.

High energy costs have prompted VF growers to produce rapidly turning baby-stage crops that include young plants of many different species grown under relatively low PPFDs, typically ranging from 150 to 300 $\mu mol \cdot m^{-2} \cdot s^{-1}$ of photosynthetically active radiation (PAR) (400 to 700 nm), trending toward the lower end of that PPFD range (Dou and Niu 2020). Tender and flavorful baby greens require only a fraction the production time of mature leafy greens (Medina et al. 2012). They have a competitive market price as well, and are sought-after products among consumers due to their high nutritional value (Carrasco et al. 2024; Moghimi and Asiabanpour 2023). Therefore, quick-turning baby-stage leafies have become a staple product of VF (Wong et al. 2020), which helps growers minimize electrical bills in their quest for profitability (Graham 2024). In addition, because baby greens are densely seeded, they quickly close their foliar canopy to overhead lighting and, thus, minimize energy inefficiencies that otherwise occur in VFs when photons fall on empty spaces between growing plants (Sheibani et al. 2023).

Research evaluating lighting requirements for baby-greens production is limited. Zauli et al. (2024) found that baby kale grown under a low PPFD for extended photoperiods accumulated more biomass than when grown under high PPFD for shorter photoperiods. Similarly, Pennisi et al. (2020) reported that young lettuce and basil plants responded positively to a PPFD increase from 100 to 250 $\mu mol \cdot m^{-2} \cdot s^{-1}$, but found diminishing returns of growth when using 300 $\mu mol \cdot m^{-2} \cdot s^{-1}$. Significant knowledge gaps exist regarding characterization of EUE for baby greens.

Another critical factor affecting crop productivity is carbon dioxide (CO_2) concentration, as VFs filled with dense vegetation require a steady supply of CO_2 to sustain crop growth in the light. Growth of indoor plants slows when CO_2 becomes limiting due to photosynthetic drawdown of CO_2, insufficient CO_2 injection, or limitations of air turnover or distribution (Zhang and Kacira 2022). For this reason, CO_2 concentration in VFs typically is maintained at 800 to 1000 μmol·mol^{-1} (Kozai 2013, 2018). In general, crops benefit from double-ambient CO_2, even during early stages of crop development (Sheibani et al. 2024). In a study by Chen et al. (2021), lettuce plants responded positively to elevated CO_2 concentrations of 800 or 1600 μmol·mol^{-1} from days 5 to 30 after transplanting. In that study, at a PPFD of 150 μmol·m^{-2}·s^{-1}, CO_2 concentrations of 800 or 1600 μmol·mol^{-1} resulted in 29% and 41% higher light-use efficiency, respectively, compared with ambient CO_2 (Chen et al. 2021). Holley et al. (2022) reported an increase in lettuce biomass as CO_2 increased from 400 to 1600 μmol·mol^{-1}, although the greatest increment in growth occurred in the transition from 400 to 800 μmol·mol^{-1}, followed by diminishing returns at higher CO_2 concentrations.

For optimization of production recipes, determining combined effects of environmental inputs is essential. Optimization level of parameters varies with species as well as length of cropping cycle.

In effort to optimize production of baby greens in VF, potential interactive effects of environmental factors must be addressed, as increasing PPFD will likely cause more rapid photosynthetic drawdown of CO_2. Thus, preferred PPFD levels also will require maintenance of nonlimiting CO_2 concentrations. Knight and Mitchell (1988) found that CO_2 enrichment increased leaf number and shoot fresh and dry mass of lettuce under moderate and high PPFDs. Lettuce seedlings responded positively to higher PPFD and CO_2 enrichment, and at 300 μmol·m^{-2}·s^{-1} of PPFD, dry mass was 100% higher when ambient CO_2 concentration was doubled (Kitaya et al. 1998). These studies (Kitaya at al. 1998; Knight and Mitchell 1988) were conducted before the LED era for plant lighting, and before EUE was a major economic concern. Studies conducted by Huber and Hernández (2019a, 2019b) showed that higher CO_2 concentrations can offset lower DLIs when propagating seedlings in VF. However, as shown by Walters and Lopez (2022), different species have distinctive responses to CO_2 concentration at the seedling stage.

In this study, we aimed to investigate various PPFD levels at different CO_2 concentrations to determine if light saturation occurred for any combinations based on endpoint growth analysis. If higher PPFDs than are traditionally used in the industry cause a plateau in crop-growth response, growing crops at those light levels may not be economically feasible. However, if higher-tested PPFDs still lead to increased crop responses without significantly diminishing EUE returns, it may be feasible to use enhanced PPFDs that can potentially drive more crop turns per year in VF.

With growing concern about EUE under sole-source lighting and high carbon footprint of VF, determining optimal combinations of PPFD and CO_2 concentration for best crop response is essential. Thus, the current investigation explores potential interactions between PPFD × CO_2 concentration for a popular red oakleaf lettuce cultivar whose yield, pigmentation, and EUE are sensitive at the baby stage of crop development (Sheibani et al. 2023, 2024). The findings of this study will provide insight into achieving a balance between energy use and crop productivity, contributing to the sustainability and profitability of VF systems.

Materials and Methods

Experimental design. In the current study, CO_2 was the main independent variable, and split-plot was the experimental design. CO_2 was injected into the entire growth chamber, making it the main plot with four simultaneous PPFD treatments as subplots. Two replicates of all treatment combinations with subplots were conducted over time. The first replicate included CO_2 concentrations of 400, 800, 1200, and 1600 μmol·mol^{-1}, followed by a second replicate with the same CO_2 concentrations.

Environmental settings. Experiments were conducted in a single walk-in growth chamber (EGC, Chagrin Falls, OH, USA), with experimental replications conducted over time. Air temperature was set to 23/21 ± 2 °C during light/dark periods, respectively. Relative humidity was maintained at 70% ± 5%. CO_2 injection/maintenance began on day 8 after sowing seeds, when the first set of true leaves had emerged. The CO_2 set point was 400, 800, 1200, or 1600 μmol·mol^{-1} during the photoperiod and 400 μmol·mol^{-1} during the dark period. Although 400 μmol·mol^{-1} was the near-ambient setpoint, 800 μmol·mol^{-1} is the industry standard; 1200 and 1600 μmol·mol^{-1} are elevated CO_2 concentrations that were maintained for treatment comparisons.

Sole-source-lighting-system adjustments. Four height-adjustable LED fixtures (Biomass Production System for Education; ORBITEC/Sierra Space Corporation, Madison, WI, USA) were mounted on wire-mesh benches in the walk-in growth chamber. Each fixture included three channels of blue, green, and red wavebands with peak emission wavelengths of 448 nm, 530 nm, and 627 nm, respectively. Photoperiod was adjusted to 16 h from 0600 HR to 2200 HR daily. The vertical distance between photon-emitting surface and cropping surface was set to 15 cm (5.9 inches). Using a spectroradiometer (LI-180 Spectrometer, LI-COR Bioscience, Lincoln, NE, USA), target PPFD and spectral composition were determined as the average of four corner points and one central point under each fixture. At each given CO_2 concentration, PPFD was set to 200 μmol·m^{-2}·s^{-1} during the first 4 d after sowing seeds, with a spectral composition of 82% red, 9% blue, and 9% green. On day 4, using the same spectral composition, PPFD treatments of 200, 300, 400, and 500 μmol·m^{-2}·s^{-1} were randomly assigned to the four LED fixtures. Each fixture was equipped with a power/energy meter (Poniie, PN-2000, accuracy-class 1.0 with 0.01 W, 0.01 V, and 0.001A resolution), and cumulative energy consumption (kWh) was recorded daily and at the end of the cropping cycle.

Plant material and substrate. Red Oakleaf lettuce cv. Rouxai (Rijk Zwaan, De Lier, Netherlands) was used as the test model crop for this study. Plants were grown in 36-cell trays (CN-IKN-606, Greenhouse Megastore, Danville, IL, USA) placed within a propagation tray (25.4 × 50.8 cm) filled with a 50:50 (v/v) coco coir/perlite substrate at a planting density of 279 plants/m^2. Translucent domes were placed over trays to promote uniform germination immediately after sowing seeds. Two layers of wicking fiber (Cap-Mat II, Hummert International, Earth City, MO, USA) were placed in the bottom of the trays to ensure uniform nutrient-solution delivery to each cell. Initially, trays were overhead-irrigated with 1500 mL of tap water, ensuring adequate, uniform substrate hydration. A commercial fertilizer solution containing macro and micro elements (Fancy Lettuce, AmHydro, Arcata, CA, USA) was dissolved in reverse osmosis water to reach an electrical conductivity (EC) of 1.2 to 1.4 mS·cm^{-1} and a pH of 5.6 to 5.8, measured with a portable EC/pH meter (HI 9813-6 pH/EC/TDS/C, Hanna Instrument Gro-Chek, Woonsocket, RI, USA). Bottom fertigation with upward capillary wicking started on day 4 after sowing seeds, at which time domes were removed. Four hundred milliliters of fertilizer solution were then added to one corner of each tray every other day. Foliar canopy closure coincided with harvest 17 d after sowing seeds. Nine plants from each treatment were randomly selected for nondestructive image analyses of pigmentation and chlorophyll concentration. The largest leaf of each plant was clamped for chlorophyll measurement (MC-100 Chlorophyll Concentration Meter, Apogee Instruments, Logan, UT, USA). Overhead photographic images were used for pigmentation analysis using "png" package within R-studio statistical software (R Foundation, Vienna, Austria) to calculate L*a*b values defined by the International Commission on Illumination. The greater the a* value, the redder the leaf,

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whereas the smaller the a* value, the greener the leaf. The same methodology was used by Kelly and Runkle (2023a, 2023b).

Shoot fresh mass of individual plants was measured immediately upon harvest (PL602E, Mettler-Toledo, Columbus, OH, USA). Leaf area was subsequently measured using a leaf area meter (LI-3100C, LI-COR Bioscience), after which individual plant tissues were bagged and oven-dried for 4 d (Isotemp 180L oven; Thermo Fisher Scientific, Waltham, MA, USA) before shoot dry mass was measured.

Statistical analysis. Growth data within a given CO_2 concentration were pooled for each PPFD tested. Using statistical software (version 9.4, SAS Institute Inc., Cary, NC, USA), data were subjected to linear-mixed effect model analysis. *P* values were determined using least square means, and $\alpha < 0.05$ was used to determine differences between means, where appropriate.

EUE calculations. Although measured parameters were expressed on a "per-plant" basis, EUE was expressed as total shoot fresh mass produced in a given tray under each PPFD tested. Cumulative energy (kWh) associated with the LED lighting system for that tray was recorded over the entire cropping cycle, and EUE was calculated based on the following formula:

$$\text{Energy use efficiency} = \frac{\text{Total shoot fresh mass (g)}}{\text{Cumulative energy expended for LED lighting (kWh)}}$$

Cropping cycle estimation.

$$\text{Cropping cycle at higher PPFD} = \frac{\text{Cropping cycle at lower PPFD}}{\text{Biomass differential between higher and lower PPFDs}}$$

Results

Plants grown at CO_2 concentrations of 800, 1200, or 1600 $\mu mol{\cdot}mol^{-1}$ across all PPFDs tested had higher shoot fresh and dry mass than did plants for CO_2 at the near-ambient setpoint of 400 $\mu mol{\cdot}mol^{-1}$ (Fig. 1A and B).

Response to PPFD and CO_2 concentration: shoot fresh mass. Within each CO_2 concentration tested, increasing PPFD increased shoot fresh/dry mass, indicating that PPFD was limiting to crop productivity within the range tested. At 400 $\mu mol{\cdot}mol^{-1}$ CO_2, the highest PPFD of 500 $\mu mol{\cdot}m^{-2}{\cdot}s^{-1}$ yielded 73%, 45%, and 14% higher shoot fresh mass than did 200, 300, and 400 $\mu mol{\cdot}m^{-2}{\cdot}s^{-1}$, respectively (Fig. 1A). At 800 $\mu mol{\cdot}mol^{-1}$ CO_2, growth increased robustly between PPFDs of 200, 300, and 400 $\mu mol{\cdot}m^{-2}{\cdot}s^{-1}$, but began to taper off between 400 and 500 $\mu mol{\cdot}m^{-2}{\cdot}s^{-1}$. No significant difference was noted in shoot fresh mass between PPFDs of 400 and 500 $\mu mol{\cdot}m^{-2}{\cdot}s^{-1}$, although shoot fresh mass was 41% and 19% higher under the highest PPFD compared with 200 and 300 $\mu mol{\cdot}m^{-2}{\cdot}s^{-1}$, respectively (Fig. 1A). Unlike 800 $\mu mol{\cdot}mol^{-1}$ CO_2, at 1200 or 1600 $\mu mol{\cdot}mol^{-1}$ CO_2, shoot fresh mass at 500 $\mu mol{\cdot}m^{-2}{\cdot}s^{-1}$ was 17% and 13% higher than at 400 $\mu mol{\cdot}m^{-2}{\cdot}s^{-1}$, respectively (Fig. 1A). At 1200 $\mu mol{\cdot}mol^{-1}$ CO_2, shoot fresh mass was 36%, 22%, and 17% higher when 500 $\mu mol{\cdot}m^{-2}{\cdot}s^{-1}$ was used compared with 200, 300, and 400 $\mu mol{\cdot}m^{-2}{\cdot}s^{-1}$, respectively. A similar pattern was measured at 1600 $\mu mol{\cdot}mol^{-1}$ CO_2, at which shoot fresh mass was 31%, 24%, and 13% higher for plants grown under the highest PPFD of 500 $\mu mol{\cdot}m^{-2}{\cdot}s^{-1}$, compared with 200, 300, and 400 $\mu mol{\cdot}m^{-2}{\cdot}s^{-1}$, respectively (Fig. 1A). Overall, among all 16 combinations tested, the highest shoot fresh mass occurred under the combination of 1200 $\mu mol{\cdot}mol^{-1}$ of CO_2 and 500 $\mu mol{\cdot}m^{-2}{\cdot}s^{-1}$ of PPFD (Fig. 1A).

Response to PPFD and CO_2 concentration: shoot dry mass. At 400 $\mu mol{\cdot}mol^{-1}$ CO_2, shoot dry mass of young lettuce plants grown

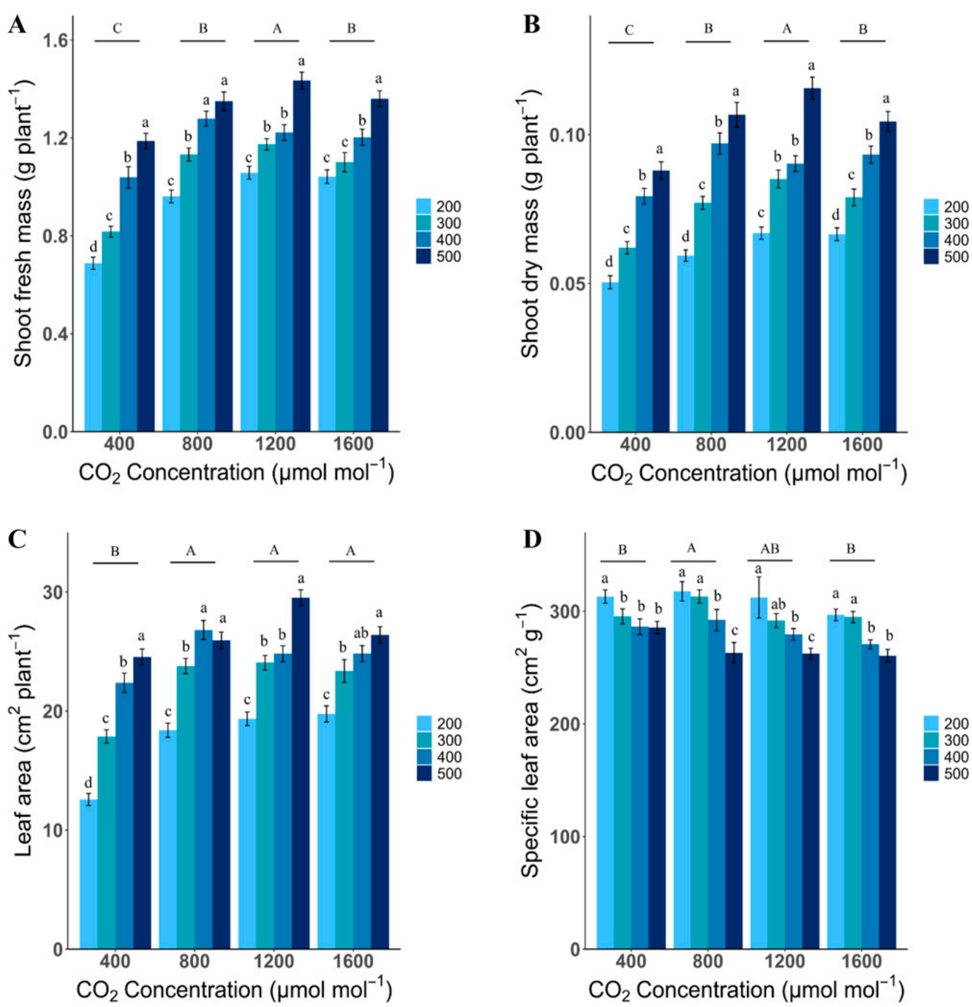

Fig. 1. Shoot fresh mass (**A**), shoot dry mass (**B**), leaf area (**C**), and specific leaf area (**D**) of lettuce 'Rouxai' at baby stage under four photosynthetic photon flux densities (in $\mu mol{\cdot}m^{-2}{\cdot}s^{-1}$) treatments of 200, 300, 400, or 500, and four CO_2 concentrations (in $\mu mol{\cdot}mol^{-1}$) of 400, 800, 1200, or 1600. Each bar represents the mean ± *SE* (n = 72). Different upper-case letters above each bar grouping represent significant differences between CO_2 treatments. The interaction effect was significant for shoot fresh mass, shoot dry mass, leaf area, and specific leaf area.

under 500 μmol·m^{-2}·s^{-1} was 74%, 45%, and 10% higher than that achieved at 200, 300, and 400 μmol·m^{-2}·s^{-1}, respectively (Fig. 1B). Likewise, at 800 μmol·mol^{-1} CO_2, shoot dry mass at 500 μmol·m^{-2}·s^{-1} was 18%, 13%, and 10% higher than at 200, 300, and 400 μmol·m^{-2}·s^{-1}, respectively (Fig. 1B). A slightly different trend was measured at 1200 μmol·mol^{-1} CO_2, for which shoot dry mass was similar for 300 and 400 μmol·m^{-2}·s^{-1}. Shoot dry mass at 500 μmol·m^{-2}·s^{-1} was 74%, 35%, and 28% higher than that at 200, 300, and 400 μmol·m^{-2}·s^{-1}, respectively (Fig. 2B). At 1600 μmol·mol^{-1}, shoot dry mass under 500 μmol·m^{-2}·s^{-1} was 58%, 33%, and 12% higher than at 200, 300, and 400 μmol·m^{-2}·s^{-1}, respectively (Fig. 1B). Similar to fresh mass, the highest shoot dry mass occurred at the combination of 1200 μmol·mol^{-1} CO_2 and PPFD of 500 μmol·m^{-2}·s^{-1} among all 16 combinations tested.

Response to PPFD and CO_2 concentration: leaf area. Leaf area typically increased with increasing PPFD within each CO_2 concentration tested (Fig. 1C). For instance, at 400 μmol·mol^{-1} CO_2, plants grown under a PPFD of 500 μmol·m^{-2}·s^{-1} had 95%, 37%, and 10% larger leaves compared with 200, 300, and 400 μmol·m^{-2}·s^{-1}, respectively (Fig. 1C), whereas at 800 μmol·mol^{-1} CO_2, no significant difference occurred for leaf area between 400 and 500 μmol·m^{-2}·s^{-1}. Plants grown at 500 μmol·m^{-2}·s^{-1} had 41% and 9% larger leaves than those under 200 and 300 μmol·m^{-2}·s^{-1}, respectively (Fig. 1C). At 1200 μmol·mol^{-1} CO_2, plants grown at a PPFD of 500 μmol·m^{-2}·s^{-1} had 53% larger leaves than those grown under 200 μmol·m^{-2}·s^{-1}, whereas leaf area for PPFDs of 300 and 400 μmol·m^{-2}·s^{-1} trended in-between those extremes (Fig. 1C). Similarly, at 1600 μmol·mol^{-1} CO_2, plants grown under a PPFD of 200 μmol·m^{-2}·s^{-1} had 34% smaller leaves compared with at 500 μmol·m^{-2}·s^{-1}, whereas 300 and 400 μmol·m^{-2}·s^{-1} trended in-between (Fig. 1C).

Response to PPFD and CO_2 concentration: specific leaf area. Specific leaf area followed slightly different trends across tested CO_2 concentrations. Higher values of specific leaf area indicating degree of leaf thinness occurred at the lowest PPFD of 200 μmol·m^{-2}·s^{-1}, whereas trends were slightly different at each given CO_2 concentration. For example, at 400 μmol·mol^{-1} CO_2, the thinnest leaves occurred for plants grown under 200 μmol·m^{-2}·s^{-1}, whereas no significant differences occurred among all other tested PPFDs (Fig. 1D). At the elevated 800, 1200, and 1600 μmol·mol^{-1} CO_2 concentrations, leaf thinness was similar for plants grown under 200 and 300 μmol·m^{-2}·s^{-1}, and significantly lower from higher PPFDs of 400 and 500 μmol·m^{-2}·s^{-1} (Fig. 1D).

Response to PPFD and CO_2 concentration: pigmentation development. Consistent with growth parameters, the highest value of a* occurred at 1200 μmol·mol^{-1} CO_2 and 500 μmol·m^{-2}·s^{-1} PPFD. Plants grown at the lowest PPFD of 200 μmol·m^{-2}·s^{-1} had the least pigmentation, whereas young lettuce plants grown at 500 μmol·m^{-2}·s^{-1} PPFD had the most pigmentation across all CO_2 concentrations (Fig. 2A). No significant differences in pigmentation were measured for plants grown under PPFDs of 400 and 500 μmol·m^{-2}·s^{-1} across CO_2 concentrations, whereas the difference was significant between PPFDs of 300 and 200 μmol·m^{-2}·s^{-1} (Fig. 2A).

Response to PPFD and CO_2 concentration: chlorophyll concentration. Both CO_2 concentration and PPFD were significant as main effects (*P* values = 0.034 and <0.0001, respectively). However, the CO_2 × PPFD interaction was not significant, suggesting that chlorophyll concentration was a function of increasing PPFD (Fig. 2B). The highest chlorophyll concentration occurred at the highest CO_2 concentration of 1600 μmol·mol^{-1} and the highest PPFD of 500 μmol·m^{-2}·s^{-1} (Fig. 2B), whereas the lowest chlorophyll concentration occurred at the lowest PPFD of 200 μmol·m^{-2}·s^{-1}, with PPFDs of 300 and 400 trending in-between the two extremes (Fig. 2B).

Energy-use efficiency. Cumulative energy for LED lighting recorded for 17-d cropping cycles was 19, 24, 29, and 36 kWh for PPFDs of 200, 300, 400, and 500 μmol·m^{-2}·s^{-1}, respectively. An EUE of 1.82 g kWh^{-1} was found for the industry-standard combination of 200 μmol·m^{-2}·s^{-1} PPFD × 800 μmol·mol^{-1} CO_2. However, under PPFDs of 300, 400, or 500 μmol·m^{-2}·s^{-1} at the same 800 μmol·mol^{-1} CO_2 concentration, EUE declined to 1.69, 1.58, and 1.35 g kWh^{-1}, respectively. At an even higher CO_2 concentration of 1200 μmol·mol^{-1}, EUE at 200 μmol·m^{-2}·s^{-1} PAR was 2.00 g kWh^{-1}, but declined to 1.76, 1.51, and 1.43 g kWh^{-1} at the same increasing PPFDs. Thus, within a given CO_2 concentration, increasing PPFD was accompanied by progressively diminishing returns for gains in crop biomass. At the near-ambient CO_2 concentration of 400 μmol·mol^{-1}, the degree of diminishment was less steep with an average slope of −0.04, while the average slope was −0.156, −0.19, and −0.20 at CO_2 concentrations of 800, 1200, and 1600 μmol·mol^{-1}, respectively (Fig. 3).

Cropping-cycle estimation.

$$\text{The annual number of cropping cycles at a PPFD of } 200 = \frac{365}{17} \approx 21$$

At the industry-standard CO_2 concentration of 800 μmol·mol^{-1}, shoot fresh mass of a baby-stage crop grown at a PPFD of 500 μmol·m^{-2}·s^{-1} was 1.4-fold higher than that of a crop grown at 200 μmol·m^{-2}·s^{-1}. The feasibility of shortening a cropping cycle at higher PPFD can be estimated:

$$\text{cropping cycle at PPFD of 500} = \frac{\text{cropping cycle at PPFD of 200}}{1.4} = \frac{17}{1.4} = 12\,(\text{days})$$

Thus,

$$\text{Annual number of cropping cycles at PPFD of } 500 = \frac{365}{12} \approx 30$$

Shoot fresh mass of plants grown at a PPFD of 400 μmol·m^{-2}·s^{-1} was 1.32-fold

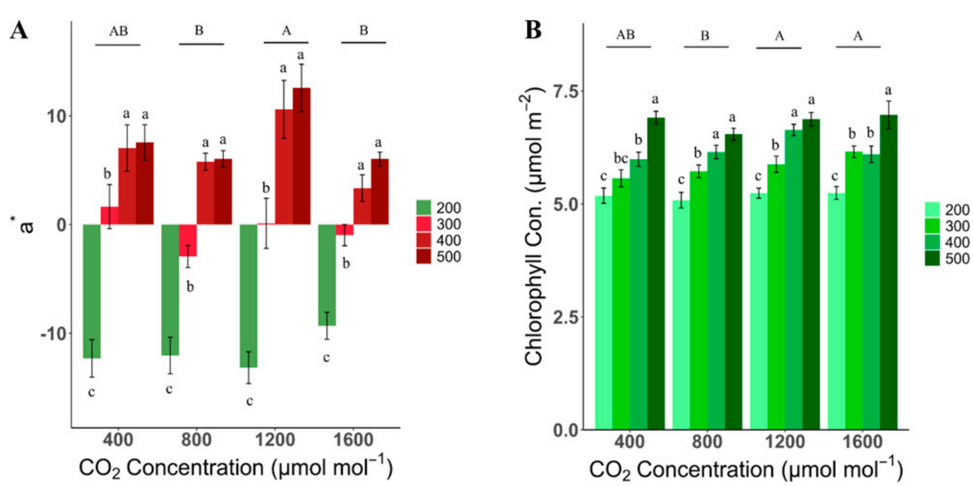

Fig. 2. Foliar color coordinates [a* for greenness-redness (negative-positive)] (**A**), and chlorophyll concentration (in μmol·m^{-2}) (**B**) of lettuce 'Rouxai' at baby stage under four photosynthetic photon flux densities (in μmol·m^{-2}·s^{-1}) treatments (200, 300, 400, and 500), and four CO_2 concentrations (in μmol·mol^{-1}) of 400, 800, 1200, and 1600. Each bar represents the mean ± *SE* (n = 18). The significance above each graph represents the difference between CO_2 treatments. The interaction effect was significant for foliar color coordinate, and non-significant for chlorophyll concentration.

higher than that at 200 $\mu mol \cdot m^{-2} \cdot s^{-1}$. Thus,

$$\text{Cropping cycle at PPFD of 400} = \frac{\text{cropping cycle at PPFD of 200}}{1.32} = \frac{17}{1.32} = 12.8\ (\text{days})$$

Thus,

$$\text{Annual number of cropping cycles at PPFD of } 400 = \frac{365}{12.8} \approx 28$$

Shoot fresh mass produced at a PPFD of 300 $\mu mol \cdot m^{-2} \cdot s^{-1}$ was 1.17-fold higher than that at 200 $\mu mol \cdot m^{-2} \cdot s^{-1}$. Cropping cycle at PPFD of 300 =

$$\frac{\text{cropping cycle at PPFD of 200}}{1.17} = \frac{17}{1.17} = 14.5\ (\text{days})$$

Thus,

$$\text{Annual number of cropping cycles at PPFD of } 300 = \frac{365}{14.5} = 25$$

Discussion

There were significant PPFD × CO_2 interaction effects for almost all measured productivity parameters, suggesting that the effect of each main factor on growth and biomass accumulation depends on the level of the other factor. Shoot fresh and dry mass as indicators of productivity were highest at 1200 $\mu mol \cdot mol^{-1}$ CO_2, with CO_2 limiting those parameters at 400 and 800 $\mu mol \cdot mol^{-1}$ (Fig. 1A and B). Carbon dioxide was supra-optimal at 1600 $\mu mol \cdot mol^{-1}$, with shoot mass and leaf area beginning to decline. CO_2 was the least limiting main factor in this study since the interaction profile indicated that maximum shoot biomass occurred at 1200 $\mu mol \cdot mol^{-1}$ CO_2 (Fig. 1A and B). The effect of CO_2 concentration varies with species, cultivar, developmental stage, and the PPFD at which plants are grown. In a study by Wheeler et al. (2024), dry mass was highest when 'Outredgeous' lettuce was grown at 1500 $\mu mol \cdot mol^{-1}$ CO_2, whereas the highest dry mass of 'Dragon' lettuce occurred at 3000 $\mu mol \cdot mol^{-1}$ CO_2, and 6000 $\mu mol \cdot mol^{-1}$ CO_2 was supra-optimal for both cultivars. Holley et al. (2022) found that shoot fresh and dry mass of 'Rouxai' lettuce responded positively to elevated CO_2, with the largest growth increment occurring between 400 and 800 $\mu mol \cdot mol^{-1}$, but no significant differences occurred between 800, 1200, and 1600 $\mu mol \cdot mol^{-1}$. Plants were grown under a limiting PPFD of 250 $\mu mol \cdot m^{-2} \cdot s^{-1}$ in that study, which likely explains why plants were not responsive to higher CO_2. Similarly, when lettuce plants were grown at a low PPFD of 150 $\mu mol \cdot m^{-2} \cdot s^{-1}$, fresh and dry mass increased when ambient CO_2 was doubled, but no significant differences were reported when CO_2 was further increased to 1600 $\mu mol \cdot mol^{-1}$ (Chen et al. 2021).

Baby lettuce crop response to PPFD in the present study was pronounced, indicating that it had not yet plateaued within the CO_2 concentration range tested (Fig. 1A and B). Effort to determine the light-saturation level of more developed lettuce stages has been made by Fu et al. (2012), indicating that biomass increased as PPFD increased from 100 to 400 $\mu mol \cdot m^{-2} \cdot s^{-1}$, with diminishing increments of growth occurring between 400 and 600 $\mu mol \cdot m^{-2} \cdot s^{-1}$, followed by an actual reduction in biomass at 800 $\mu mol \cdot m^{-2} \cdot s^{-1}$ (Fu et al. 2012). Assuming those experiments were conducted under near-ambient CO_2, it was not surprising that PPFD saturation occurred at 400 $\mu mol \cdot m^{-2} \cdot s^{-1}$. Mature lettuce responded positively to increasing PPFDs up to 250 $\mu mol \cdot m^{-2} \cdot s^{-1}$, but growth reduction began to occur at 300 $\mu mol \cdot m^{-2} \cdot s^{-1}$ when CO_2 was maintained at only 450 $\mu mol \cdot mol^{-1}$ (Pennisi et al. 2020).

In a study by Knight and Mitchell (1988), 'Waldmann's Green' lettuce growth was responsive to 1500 $\mu mol \cdot mol^{-1}$ CO_2 in the presence of a PPFD of 450 $\mu mol \cdot m^{-2} \cdot s^{-1}$, but higher increments of CO_2 up to 2000 $\mu mol \cdot mol^{-1}$ did not result in higher biomass accumulation. Such findings suggest that at a given PPFD, there is an optimum CO_2 level, above which higher CO_2 increments do not contribute further to biomass accumulation and can begin to inhibit it. Similarly, findings by Esmaili et al. (2020) suggest that at a PPFD of 300 $\mu mol \cdot m^{-2} \cdot s^{-1}$, 1200 $\mu mol \cdot mol^{-1}$ CO_2 was optimal to achieve highest biomass, but 1600 $\mu mol \cdot mol^{-1}$ CO_2 did not further enhance biomass accumulation. Effects of PPFD and CO_2 concentration on lettuce as a candidate salad crop for the International Space Station were investigated by Richards et al. (2004). At 400 or 1200 $\mu mol \cdot mol^{-1}$ CO_2, there was a linear increase in lettuce yield when PPFD increased from 150 to 300 $\mu mol \cdot m^{-2} \cdot s^{-1}$, but yield plateaued when PPFD was increased to 450 $\mu mol \cdot m^{-2} \cdot s^{-1}$. Mature lettuce plants did not benefit from higher PPFD as tip burn caused lower biomass accumulation at a higher PPFD of 450 $\mu mol \cdot m^{-2} \cdot s^{-1}$ (Richards et al. 2004). Lettuce-seedling growth and morphology were investigated at different combinations of PPFD, photoperiod, and CO_2 by Kitaya et al. (1998), in which a longer photoperiod and/or higher CO_2 concentration compensated for low PPFD during a 3-week cropping cycle.

Leaf area also was affected by the combined effects of CO_2 and PPFD in the current study. Within each CO_2 concentration tested, leaf area increased at each higher PPFD (Fig. 1C). Higher total leaf area could be the result of more leaf expansion, higher leaf number, or both. Mitchell et al. (1997) found that CO_2 enrichment increased leaf number of 'Waldmann's green' leaf lettuce. The present study concluded that leaf area of plants grown at elevated CO_2 concentrations of 800, 1200, or 1600 $\mu mol \cdot mol^{-1}$ was higher than when grown at 400 $\mu mol \cdot mol^{-1}$, likely as a result of one or two more leaves forming per plant, which contributed to the higher biomass.

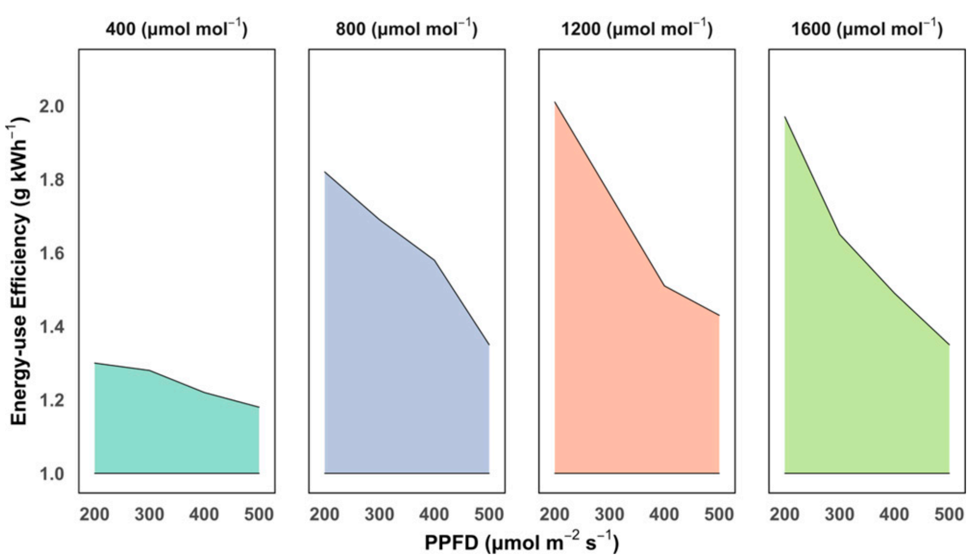

Fig. 3. Energy use efficiency (grams fresh mass per kWh of energy) at four CO_2 concentrations ($\mu mol \cdot mol^{-1}$) of 400, 800, 1200, and 1600, and four photosynthetic photon flux densities ($\mu mol \cdot m^{-2} \cdot s^{-1}$) of 200, 300, 400, and 500.

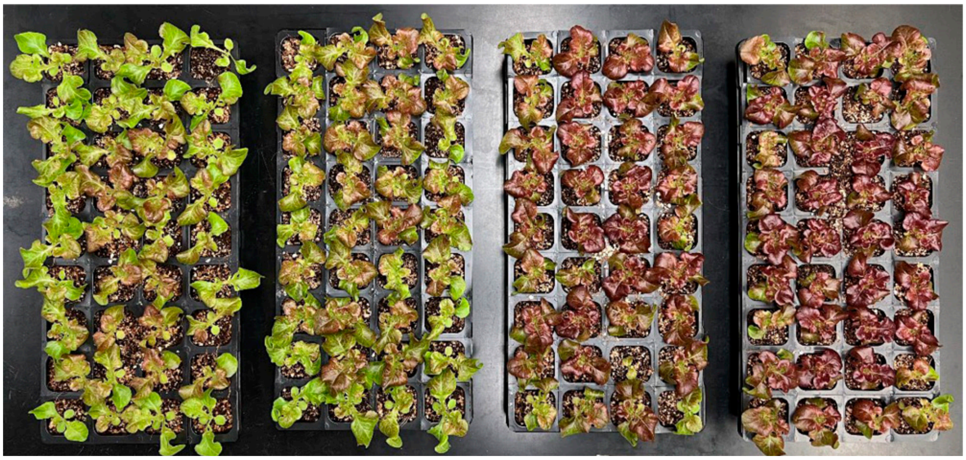

Fig. 4. Red oakleaf lettuce 'Rouxai' after a 17-d cropping cycle, grown at PPFDs of 200, 300, 400, and 500 $\mu mol \cdot m^{-2} \cdot s^{-1}$ (left to right) and 800 $\mu mol \cdot mol^{-1}$ CO_2 for 13 d of that cycle.

Leaf-blade shape changed in the current study with increasing PPFD. Petioles were longest at lower PPFDs (Fig. 4). Thicker leaves also formed at higher PPFDs, as confirmed by reductions in specific leaf area (SLA) (Fig. 1D). Ghorbanzadeh et al. (2021) also found that higher PPFDs resulted in lower SLA of lettuce.

Pigmentation, as a quality and marketability attribute of red leaf lettuce, increased at each higher PPFD tested (Figs. 2A and 4). For each CO_2 concentration, plants grown at 200 $\mu mol \cdot m^{-2} \cdot s^{-1}$ had the lowest pigmentation, whereas 400 and 500 $\mu mol \cdot m^{-2} \cdot s^{-1}$ always had the highest. Pigmentation development in 'Rouxai' directly corresponds with PPFD, as reported by Sheibani et al. (2023). Chlorophyll content also is affected by PPFD (Pennisi et al. 2020), as well as by CO_2 concentration (Holley et al. 2022; Wheeler et al. 2024). In the current study, leaf chlorophyll concentration was the only parameter unaffected by PPFD × CO_2, although CO_2 as a main effect was significant (P value = 0.034). The effect of PPFD also was highly significant (P value <0.0001). In another study (Das et al. 2024), total chlorophyll concentration of lettuce plants increased as light increased from 60 to 400 $\mu mol \cdot m^{-2} \cdot s^{-1}$, both at transplant and harvest stages.

As expected, EUE decreased as PPFD increased, which aligns with the principle of diminishing returns with increasing inputs. The cumulative energy expended to produce a baby-stage crop in a tray was 19, 24, 29, and 36 kWh at PPFDs of 200, 300, 400, and 500 $\mu mol \cdot m^{-2} \cdot s^{-1}$ over a 17-d cropping cycle (including the first 4 d at 200 $\mu mol \cdot m^{-2} \cdot s^{-1}$ for all treatments). The increments of energy reflected increasing energy cost of higher PPFDs, likely due in part to LED "current droop" with increasing light intensity (Oh et al. 2019; Piprek 2010), as well as approach to saturation of crop photosynthesis. Similar patterns of diminishing returns were noted across all CO_2 concentrations tested. At the low-limiting CO_2 concentration of 400 $\mu mol \cdot mol^{-1}$, increasing increments of PPFD contributed less to biomass accumulation compared with that at elevated CO_2, but caused EUE to decrease at a slower rate. Quantum yield (g biomass/mol of photons) of lettuce also decreased as daily light integral ($mol \cdot m^{-2} \cdot d^{-1}$) increased (Richards et al. 2004). However, the rate of decrease was less at 400 compared with that at 1200 $\mu mol \cdot mol^{-1}$ CO_2 because CO_2 also was more limiting at that concentration.

From an industry standpoint, this investigation addressed whether extra increments of yield obtained using higher PPFDs justified the extra electrical increments consumed, and whether use of higher PPFDs could potentially result in more cropping cycles per year. At a CO_2 concentration of 800 $\mu mol \cdot mol^{-1}$, four, seven, and nine more cropping cycles are feasible on an annual basis if PPFD is increased to 300, 400, or 500 from a baseline of 200 $\mu mol \cdot m^{-2} \cdot s^{-1}$, respectively.

Conclusions

Indoor baby 'Rouxai' lettuce crops responded positively to both PPFD and CO_2 over the ranges tested in this study However, PPFD was a limiting factor for biomass accumulation, even at the highest CO_2 concentration tested, whereas CO_2 concentration gave maximum crop response at 1200 $\mu mol \cdot mol^{-1}$. The significance of interactive effects of PPFD × CO_2 highlight the importance of multifactor optimization. The highest shoot fresh and dry mass occurred under the combination of 1200 $\mu mol \cdot mol^{-1}$ CO_2 and PPFD of 500 $\mu mol \cdot m^{-2} \cdot s^{-1}$, which may or may not be the best economic choice for industry. Guided by the crop-productivity and EUE findings of this study, comprehensive cost-benefit analyses should help to determine the most affordable choice of PPFD for baby-lettuce production in VF for each marketing situation.

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