



Article

A Proof-of-Concept Greenhouse Lighting Control System for Lettuce Using a Real-Time Chlorophyll Fluorescence Biofeedback

Suyun Nam and Rhuanito Soranz Ferrarezi *

Department of Horticulture, University of Georgia, 1111 Miller Plant Sciences Building, Athens, GA 30602, USA

* Correspondence: ferrarezi@uga.edu

Abstract

Supplemental light-emitting diode (LED) lighting is essential for greenhouse crop production when solar radiation is insufficient, but it also contributes substantially to operating costs. Conventional strategies based on fixed photosynthetic photon flux density (PPFD) do not accurately reflect plant photosynthetic status, often leading to inefficient use of light energy. A chlorophyll fluorescence (CF)-based biofeedback system offers a plant-driven approach that dynamically adjusts light output to maintain target photosynthetic parameters. This system has been successfully tested in growth chambers with controlled environmental conditions, but no research has been conducted in greenhouses yet. This study developed and tested a greenhouse-compatible biofeedback lighting system using ‘Casey’ lettuce (*Lactuca sativa*) to evaluate its performance compared with conventional light controls. Two biofeedback control logics were applied: electron transport rate (ETR)-based (target ETR of 85 or 120 $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$) and quantum yield of photosystem II (Φ_{PSII})-based control (target Φ_{PSII} of 0.735), with constant PPFD- and timer-based lighting as reference treatments. Both biofeedback logics maintained their target values, confirming stable performance under dynamic greenhouse conditions. Despite successful real-time light regulation in greenhouse conditions, shoot biomass and energy-use efficiency did not differ among treatments under moderate greenhouse conditions ($p > 0.05$). This study establishes a functional prototype of a real-time physiological biofeedback system for greenhouse supplemental lighting control.

Keywords: controlled environment agriculture; greenhouse lighting; light-emitting diode; lettuce; chlorophyll fluorescence; dynamic light control



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1. Introduction

Artificial lighting plays a key role in greenhouse production, especially when seasonal or weather conditions reduce natural sunlight and limit photosynthetic light availability [1,2]. Photosynthetically active radiation directly influences photosynthesis, and supplemental lighting can enhance crop yield as well as plant morphology, flowering, uniformity, and fruit quality [3,4]. However, electricity for greenhouse supplemental lighting can account for 10–30% of operating costs [5], underscoring the need for precise light management that meets crop requirements while remaining economically viable.

High-pressure sodium (HPS) lamps have long been used for both photoperiodic and photosynthetic purposes, but light-emitting diode (LED) fixtures have become increasingly popular in recent years for their higher energy efficiency and dimmability [6]. Supplemental LED lighting is often regulated by photosynthetic photon flux density (PPFD)-based control,

which adjusts LED output to maintain a target PPFD by providing the additional PPFD required beyond sunlight [7]. A more advanced approach is DLI-based control, which aims to achieve a target daily light integral (DLI) by adjusting both light output and photoperiod over the day. This method utilizes natural sunlight more efficiently by reducing or ending supplemental lighting early when sunlight is abundant or extending the photoperiod when it is insufficient. It provides greater flexibility while optimizing energy use [8]. Both adaptive light strategies improved energy efficiency compared with the on/off regime [9].

While maintaining PPFD or DLI supports consistent growth, more dynamic lighting strategies have been designed based on plant photosynthetic characteristics to improve crop yield and light-use efficiency. For instance, extending the photoperiod while lowering PPFD can deliver the same DLI with greater photosynthetic efficiency. Gradually increasing light intensity over the crop cycle can improve light interception, and providing supplemental light only at the end of production can enhance pigmentation and crop quality within a short period [10–12].

However, photosynthetic efficiency is influenced by light intensity and various environmental factors, as well as their interactions. For example, high light combined with low temperature can induce severe photoinhibition [13], suggesting the need to reduce light intensity under such conditions. Conversely, elevated carbon dioxide (CO₂) increases light-use efficiency, enabling similar photosynthetic rates at lower light levels [14]. Extreme humidity can limit photosynthesis by affecting nutrient uptake and stomatal conductance [15]. These synergistic and antagonistic effects underscore the importance of adjusting supplemental lighting in response to sunlight availability and overall environmental conditions.

Plant-driven climate control strategies have attracted increasing attention for their ability to adjust resource inputs in response to real-time crop physiological status [16,17]. Chlorophyll fluorescence (CF) offers a rapid, non-invasive measurement of photosynthetic responses and is highly responsive to a wide range of abiotic stresses [18,19]. CF parameters, such as electron transport rate (ETR) and the quantum yield of photosystem II (Φ_{PSII}), have been used to develop plant-driven supplemental lighting strategies. One example is targeting daily photochemical integral (DPI) rather than the DLI. DPI represents the total number of electrons transported through photosystem II each day and is more directly linked to plant growth [6]. This approach enables growers to deliver precisely the amount of light energy that plants can use for carbon assimilation, as environmental effects are already reflected in the DPI calculation derived from a regression model relating PPFD to ETR.

Unlike this DPI model-based approach, the “CF-based biofeedback system” directly regulates LED light intensity in real time based on measured photosynthetic responses [20]. In Φ_{PSII} -based control, light intensity is reduced when photosynthetic efficiency declines (e.g., under environmental stress) and increased when plants can utilize higher light intensities. In contrast, ETR-based control adjusts light intensity to maintain a target photosynthetic rate: when Φ_{PSII} decreases, PPFD is increased to compensate, and when Φ_{PSII} is high enough, PPFD is reduced to save energy. This enables more precise, plant-responsive regulation of LED lighting compared with fixed PPFD or DLI-based strategies, although its effectiveness can vary with crop species and environmental conditions [21].

Previous studies have validated the biofeedback systems in climate-controlled chambers, where they dynamically adjusted LED output to capture light acclimation, diurnal patterns, and species-specific responses [20,21]. Under steady indoor conditions with sole source LED lighting, PPFD was increased later in the photoperiod to offset the gradual decline in Φ_{PSII} , and the system maintained PPFD at relatively higher levels for cucumber (*Cucumis sativus*) than for lettuce (*Lactuca sativa*) to compensate for cucumber’s slightly lower Φ_{PSII} . However, it remains uncertain whether such dynamic regulation would perform similarly under greenhouse conditions, where rapidly changing sunlight and

environmental variability alter photosynthetic responses throughout the day, compared to constant lighting [22]. Despite this uncertainty, no trials have yet been conducted in greenhouses using the biofeedback system, and validation remains limited to small-scale and steady indoor settings.

This study had two main objectives: (1) to develop and adapt the CF-based biofeedback lighting system for dynamic greenhouse environments, and (2) to evaluate its performance against conventional lighting control methods with respect to crop yield and energy-use efficiency. It was hypothesized that the CF-based biofeedback lighting system would maintain target ETR and Φ_{PSII} accurately even under fluctuating greenhouse conditions and achieve energy-use efficiency and plant growth comparable to or higher than those under conventional light control.

2. Materials and Methods

2.1. Plant Materials and Growth Conditions

Lettuce ‘Casey’ seeds (Johnny’s Selected Seeds, Waterville, ME, USA) were sown into 72-cell plug trays filled with a peat-perlite soilless substrate (Fafard 1P; SunGro Horticulture, Agawam, MA, USA). The seedlings were cultivated in a walk-in growth chamber equipped with white LED light bars (RAY series with Physiospec indoor spectrum; Fluence Bioengineering, Austin, TX, USA) emitting 39% red, 40% green, 18% blue, and 3% far-red. The PPFD at canopy height was maintained at $250 \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ under a 16 h photoperiod, providing a DLI of $14.4 \text{ mol}\cdot\text{m}^{-2}\cdot\text{d}^{-1}$. An automated ebb-and-flow subirrigation system supplied daily irrigation using a 15N-2.2P-12.4K fertilizer (Jack’s Professional® LX 15-5-15 Ca-Mg; JR Peters, Allentown, PA, USA) at $100 \text{ mg}\cdot\text{L}^{-1}$ N. During the seedling stage, the chamber’s average air temperature, vapor pressure deficit (VPD), and CO_2 concentration were $23.6 \pm 0.2^\circ\text{C}$, $1.01 \pm 0.06 \text{ kPa}$, and $820 \pm 47 \mu\text{mol}\cdot\text{mol}^{-1}$, respectively (mean $\pm$ standard deviation [SD]).

2.2. Experiment Settings

Three-week-old seedlings were transplanted into 10 cm square containers filled with the same substrate and moved to a glass-covered greenhouse located at the University of Georgia (College of Agricultural and Environmental Sciences, Department of Horticulture, Controlled Environment Agriculture [CEA] Crop Physiology and Production Laboratory), in Athens, GA, USA (lat. $33^\circ 57' 26.676''$ N, long. $83^\circ 22' 36.48''$ W). After 1 week of acclimation, allowing the development of fully expanded leaves suitable for continuous CF measurements, two uniform-sized lettuce plants were selected for each experimental unit. The experiment was conducted on a $9 \text{ m} \times 1.5 \text{ m}$ bench divided into five blocks, each containing four experimental units separated by vertical aluminum panels to prevent light interference. Light treatments were randomized within each block. A 60% shade net was installed to reduce solar radiation and maintain DLI within the desired range.

Two independent experiments were conducted during separate growing periods to evaluate the biofeedback system under different natural light conditions: trial 1 from 7–22 April 2024, and trial 2 from 21 October to 5 November 2024. Therefore, different control targets were evaluated between trials to assess the system performance under a broader range of greenhouse lighting conditions. Daily average, minimum, and maximum values of temperature and VPD during trials 1 and 2 were measured using a temperature and humidity sensor (HMP50; Vaisala, Vantaa, Finland), and the data are shown in (Figure 1). Plants were irrigated daily using an automated ebb-and-flow system with the same nutrient solution used during the seedling stage. Dimmable white LED lights (RAY series with Physiospec Greenhouse spectrum; Fluence Bioengineering, Austin, TX, USA) emitting 37% red, 39% green, 21% blue, and 3% far-red were installed above each experimental unit.

Quantum sensors (SQ-500-SS; Apogee Instruments, Logan, UT, USA) were placed 25 cm below the LED bars in all treatments of the third block to measure combined sunlight and LED light every 10 s. The LEDs provided a maximum supplemental PPFD of approximately $500 \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ at canopy height. All sensors were connected to a datalogger (CR1000; Campbell Scientific, Logan, UT, USA) for data acquisition and LED light control.

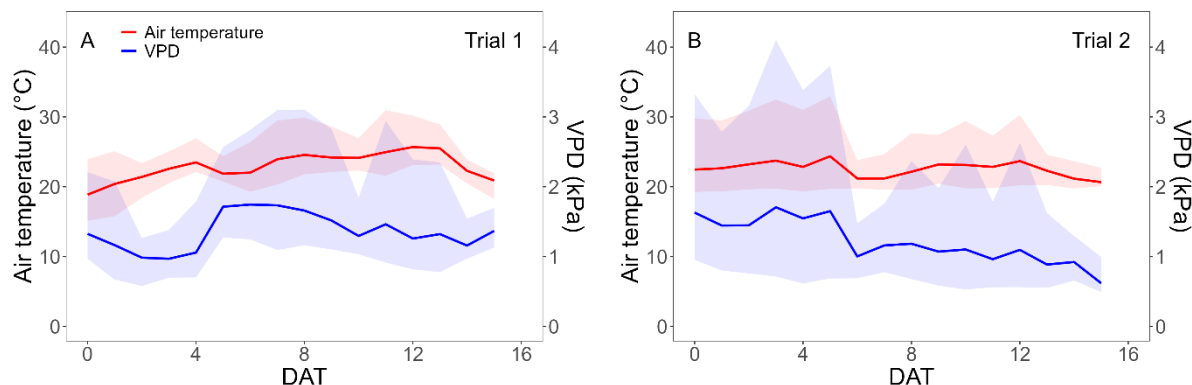


Figure 1. Air temperature and vapor pressure deficit (VPD) recorded during (A) trial 1 (7–22 April 2024) and (B) trial 2 (21 October–5 November 2024). Solid lines represent daily means, and shaded areas indicate the range between daily minimum and maximum values.

2.3. CF Measurements

CF parameters were measured using two pulse–amplitude modulation (PAM) fluorometers (MINI-PAM; Heinz Walz, Effeltrich, Germany) connected to the datalogger via an RS-232 interface for real-time CF monitoring and biofeedback-controlled supplemental LED lighting. Measurement protocols were programmed via proprietary software (LoggerNet version 4.7; Campbell Scientific, Logan, UT, USA) and performed automatically by the datalogger. CF measurements were conducted every 15 min throughout the photoperiod. Additional details on communication between the fluorometers and the datalogger are provided in Nam et al. [21]. The uppermost fully expanded leaf of each plant was used for the measurement, with fluorescence measured at the middle portion of the leaf lamina between secondary veins. Leaves were selected to avoid shading from surrounding foliage and positioned horizontally, such that incoming light was approximately perpendicular to the leaf surface, to ensure representative light exposure (Figure 2). To maintain similar leaf developmental stages during the experiment and to avoid potential photodamage from repeated saturating pulses, the measurement leaf spot was periodically relocated to another uppermost fully expanded leaf on the same plant. The leaf relocation was performed daily at midday in trial 1, whereas in trial 2 it was conducted at the end of each photoperiod to enable tracking of diurnal responses within the same sample.

The CF parameters included ETR, Φ_{PSII} , quantum yield of non-photochemical quenching (Φ_{NPQ}), quantum yield of non-regulated energy dissipation (Φ_{NO}), and maximum quantum efficiency of PSII (F_v/F_m). These were calculated according to the method of Hendrickson et al. [23] using the following equations (Equations (1)–(5)):

$$\Phi_{\text{PSII}} = (F_m' - F_s)/F_m' \quad (1)$$

$$\Phi_{\text{NO}} = F_s/F_m \quad (2)$$

$$\Phi_{\text{NPQ}} = F_s/F_m' - F_s/F_m \quad (3)$$

$$\text{ETR} = \Phi_{\text{PSII}} \times \text{PPFD} \times 0.5 \times 0.84 \quad (4)$$

$$F_v/F_m = (F_m - F_o)/F_m \quad (5)$$

where F_s is the steady-state fluorescence under actinic light, and F_m' is the maximum fluorescence from a light-adapted leaf. F_o and F_m refer to the minimum and maximum fluorescence from a dark-adapted leaf, respectively, both measured daily one hour before sunrise after overnight dark adaptation.

The measuring light intensity and saturating pulse intensity were set to 8 and 10 (out of 12), respectively, with a saturating pulse width of 0.8 s. The measuring light frequency was set to 0.6 kHz (“LOW”) at night and 20 kHz (“HIGH”) during the photoperiod. These settings were chosen to optimize the signal-to-noise ratio, and the actinic effect of the measuring light was negligible under high ambient light from sunlight and supplemental LEDs. Further details are provided in the fluorometer manual [24].

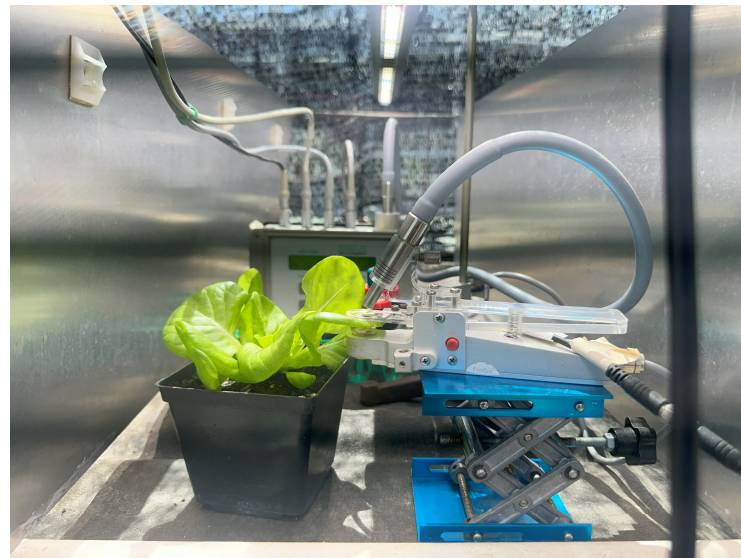


Figure 2. Experimental unit of the biofeedback treatment showing chlorophyll fluorescence measurement on lettuce (*Lactuca sativa*). A quantum sensor was placed adjacent to the measured leaf and fluorometer at the same height, aligned with the light-emitting diode (LED) bar to ensure equal irradiance.

2.4. Biofeedback Supplemental Light Control

Two biofeedback logics were implemented in the datalogger to control the supplemental lighting based on either ETR or Φ_{PSII} . Real-time CF measurements were obtained every 15 min, and the datalogger calculated the updated target PPFD ($PPFD_t$) based on the current PPFD ($PPFD_c$) and the ratio of the target CF value to the current CF value. For the ETR-based logic, $PPFD_t$ was calculated as:

$$PPFD_t = PPFD_c \times (ETR_t / ETR_c) \quad (6)$$

Here, ETR_t is a target ETR value, and ETR_c is the current ETR value. The equation assumes a linear relationship between ETR and PPFD, allowing light intensity to increase or decrease proportionally depending on whether ETR_c falls below or exceeds ETR_t . For the Φ_{PSII} -based logic, $PPFD_t$ was computed as:

$$PPFD_t = PPFD_c \times (\Phi_{PSII,c} / \Phi_{PSII,t}) \quad (7)$$

$\Phi_{PSII,t}$ is a target Φ_{PSII} value, and $\Phi_{PSII,c}$ is the current Φ_{PSII} value. This equation reflects the general decrease in Φ_{PSII} with increasing PPFD, such that when $\Phi_{PSII,c}$ exceeds $\Phi_{PSII,t}$, supplemental light intensity increases, while when $\Phi_{PSII,c}$ falls below $\Phi_{PSII,t}$, supplemental light intensity decreases.

During the first 30 min of the photoperiod, a fixed PPFD of 275 in trial 1 and 420 $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ in trial 2 was uniformly applied to all biofeedback-controlled treatments as an initial light condition. The initial period allowed Φ_{PSII} to stabilize before initiating dynamic light control, thereby preventing unstable fluctuations in light intensity caused by transient Φ_{PSII} responses, as demonstrated previously [21].

The datalogger was connected to an analog output module (SDM-AO4A, Campbell Scientific, Logan, UT, USA) to control the intensity of supplemental lighting. The module sent 0–10 V direct current dimming signals to the LED drivers, each of which powered one of the supplemental light treatments in all five blocks. The dimming signal was determined based on the third block and applied uniformly across all blocks. Although some spatial variation in sunlight among blocks may occur, this configuration reflects a centralized control approach in which supplemental lighting is regulated based on measurements from a limited number of sensors, as commonly practiced in greenhouse production. The dimming signals were updated every 10 s based on the following equation:

$$\text{New dimming signal} = \text{Old dimming signal} \times (\text{PPFD}_t / \text{PPFD}_c) \quad (8)$$

Here, PPFD_t is the target PPFD, which is reset every 15 min based on each CF measurement, while PPFD_c is the instantaneous PPFD measured every 10 s. Although CF is measured less frequently, this approach enabled rapid and continuous adjustment of LED output based on real-time sunlight irradiance throughout each 15 min cycle.

To avoid potential flickering at low dimming levels, a minimum dimming signal of 0.8 V (corresponding to 8% of full output in the 0–10 V control range) was enforced. This ensured that the supplemental LED lights remained continuously on during the photoperiod, even when high natural sunlight resulted in reduced dimming output. This approach also prevented frequent switching and minimized potential effects of inrush current on electricity use.

2.5. Harvest and Energy Use Parameters

All plants were harvested 15 days after the initiation of supplemental light treatments. Shoot fresh weight was recorded, and shoot dry weight was measured after drying at 80 °C for 72 h. Leaf chlorophyll contents were measured on the uppermost fully expanded leaves using a handheld meter (CCM-200 plus; Opti-Sciences, Hudson, NH, USA). Total leaf area was measured using a leaf area meter (LI-3100; LI-COR, Lincoln, NE, USA). A linear relationship between dimming signals and power consumption was determined using a power meter (P4400; P3 International Corporation, New York, NY, USA). Power consumption was measured at dimming signals ranging from 0 to 10 V in 1 V increments, with five replicates at each level. Linear regression resulted in the following equation: Power consumption (W) = $8.106 \times \text{dimming signal (V)}$ ($R^2 = 0.99$). This equation was used to estimate total electricity use for LED lighting accumulated over the experiment, and energy-use efficiency ($\text{g DW}\cdot\text{kWh}^{-1}$) was calculated as shoot dry weight divided by total electricity use.

2.6. Experimental Design and Statistical Analysis

In trial 1, four supplemental light treatments were arranged in a randomized complete block design (RCBD) with five blocks. The treatments were: (1) ETR-based control with a ETR_t of 85 $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ (ETR 85), (2) Φ_{PSII} -based control with a $\Phi_{\text{PSII},t}$ of 0.735 (Φ_{PSII} 0.735), (3) constant PPFD of 275 $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ (PPFD 275), and (4) timer-based PPFD of 400 $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ from 6:00 to 10:00 and from 17:00 to 21:00 (Add 400).

The constant PPFD and timer-based treatments were included as reference lighting strategies for comparison with the biofeedback controls. In the constant PPFD treatment,

supplemental lighting was adjusted to maintain the target PPFD when natural sunlight was below the setpoint, while total PPFD could exceed the target under high sunlight conditions. In contrast, in the timer-based treatment, a fixed LED output was added to ambient sunlight during low-sunlight hours without light level adjustment. All target values were selected based on preliminary testing to ensure that all treatments delivered comparable DLIs, allowing direct comparison of lighting strategies under similar light conditions.

In trial 2, only the ETR-based biofeedback logic was further tested because it demonstrated more stable supplemental lighting regulation in trial 1, whereas the Φ_{PSII} -based control resulted in larger fluctuations in light intensity. Two treatments were evaluated: ETR_t of 120 $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ (ETR 120) and a constant PPFD of 420 $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ (PPFD 420), using the same RCBD layout. This simplified treatment structure in trial 2 allowed direct comparison between the most stable biofeedback strategy identified in trial 1 and a conventional greenhouse lighting control approach.

Target values for ETR (85 and 120 $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$) and Φ_{PSII} (0.735) were initially informed by PPFD response ranges reported in Nam et al. [21]. Because that study was conducted in a growth chamber using a different lettuce cultivar, additional preliminary tests were conducted under greenhouse conditions to identify target levels that produced comparable PPFD ranges. The photoperiods were 15 h (6:00–21:00 h) and 12 h (07:00–19:00 h) in trials 1 and 2, respectively, and were selected to approximate the natural daylength during each experimental period while avoiding excessively extended photoperiods.

All statistical analyses were performed in R (v4.5.0; R Foundation for Statistical Computing, Vienna, Austria). For final growth and energy-use parameters, linear mixed-effects models were applied with lighting treatment as a fixed effect and block as a random effect. One-way analysis of variance (ANOVA) was used to test treatment effects, and Tukey's Honestly Significant Difference (HSD) test was performed for pairwise comparisons at a 95% confidence level.

3. Results and Discussion

3.1. Adaptation of the Biofeedback System for the Greenhouse

Several modifications were required to adapt the previously developed indoor biofeedback system to greenhouse conditions [20,21]. The first adjustments focused on the fluorometer settings. The measuring light intensity was set to level “8”, the same as the device preset. Although the default measuring light frequency is 0.6 kHz, a higher frequency of 20 kHz was used during the photoperiod since a higher measuring light frequency was required to improve signal detection under high ambient irradiance in the greenhouse. Increasing measuring light intensity or frequency amplifies the fluorescence signal, but may cause an actinic effect or an increase in leaf temperature [24]. At the standard 12 mm distance between a fiber-optic and leaf surface, the combination of intensity level 8 with 0.6 or 20 kHz corresponds to approximately 0.15 and 5 $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ PPFD, respectively. However, those PPFD levels and thermal effects were negligible under the high greenhouse ambient irradiance during the experiment. The datalogger program was therefore designed to automatically switch to 20 kHz when ambient PPFD exceeded 100 $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$, while maintaining 0.6 kHz at night. This approach optimized the signal-to-noise ratio under fluctuating greenhouse conditions.

Another consideration was the potential interference between the PAM-measuring light and the modulation frequency of the photosynthetic LEDs. Commercial horticultural LEDs commonly use pulse-width modulation (PWM) dimming, with modulation frequencies ranging from 100 Hz to 50 kHz [25]. When the PWM frequency is close to the PAM modulation frequency, aliasing effects can distort fluorescence signals.

In this study, analog-dimming LEDs operating at 120 Hz were used, which eliminated potential overlap with the MINI-PAM's high modulation frequencies of 20 kHz during the photoperiod. However, relatively newer PAM models such as MINI-PAM II operate at much lower modulation frequencies (5–25 Hz under normal conditions and 100 Hz during saturating pulses) [26]. In such cases, aliasing could occur if the LED system operates at lower, overlapping frequency. Therefore, reliable CF measurements require verifying the specifications of both the PAM fluorometer version and the LED fixtures to avoid potential aliasing artifacts.

The saturating pulse intensity was set to level “10”, slightly higher than the default value of “8”. This was necessary because plants that are acclimated to high light levels in the greenhouse may require stronger pulses to fully close PSII reaction centers. However, both the intensity and duration of the saturating pulse should be carefully optimized, as repeated F_m' measurements with excessively strong and prolonged pulses may cause irreversible photodamage [21]. Pulse duration was kept at the default of 0.8 s. The average values of F_v/F_m during the experiments were 0.847 ± 0.003 , 0.853 ± 0.004 , and 0.820 ± 0.008 for the ETR 85, Φ_{PSII} 0.735, and ETR 120 treatments, respectively (mean $\pm$ SD). These values are above 0.82 and within the typical range for healthy, non-stressed plants, suggesting that photodamage was minimal [19]. In addition, the measured leaves were replaced daily to avoid cumulative stress from repeated CF measurements. Based on these results, the saturating pulse intensity and duration used in this study appear appropriate under greenhouse conditions with regular leaf replacement applied.

Photochemical quenching (e.g., qP, qL) could not be determined in this study because its calculation requires F_o' , the light-adapted minimum fluorescence measured using a brief dark interval followed by far-red illumination to fully open PSII reaction centers. Such conditions are challenging to implement in the field or greenhouse conditions under natural sunlight [19]. Traditionally, F_o' was also required to calculate Φ_{NPQ} and Φ_{NO} according to Kramer et al. [27]. To overcome this limitation, an alternative approach based on the “lake model” was applied, which assumes interconnected light harvesting antennae and provides a more realistic representation of energy distribution for higher plants [23]. This calculation (Equations (2) and (3)) does not require F_o' measurements and can be readily implemented in dataloggers. Importantly, using Φ_{NPQ} and Φ_{NO} could open opportunities for future biofeedback strategies, such as minimizing Φ_{NO} while allowing photoprotective Φ_{NPQ} , rather than relying solely on Φ_{PSII} , thereby improving both energy-use efficiency and plant stress management [28].

3.2. Biofeedback System Performance Under Greenhouse Conditions

In trial 1, the average ETR of the ETR 85 treatment was $86.6 \mu\text{mol} \cdot \text{m}^{-2} \cdot \text{s}^{-1}$ (Table 1), with 80% of data points falling within $\pm 5\%$ of the target (Figure 3A). The slightly higher average to the setpoint (Figure 4A) resulted from midday fluctuation in sunlight (Figure 5A), which induced transient peaks in PPFD (Figure 6A) and corresponding ETR above the target. In the PPFD 275 treatment, similar spikes occurred when natural sunlight alone exceeded the PPFD setpoint despite minimal supplemental lighting input (Figure 6D). These values should be regarded not as inaccurate control of the biofeedback system but as an unavoidable outcome of fluctuating sunlight in greenhouse conditions. The PPFD and DLI variability under ETR 85 were comparable to those of PPFD 275 (Figures 5 and 7), demonstrating stable regulation of supplemental lighting by the ETR-based biofeedback logic under fluctuating sunlight. The Add 400 treatment showed apparent day-to-day variations in DLI, because a fixed amount of supplemental light ($11.5 \text{ mol} \cdot \text{m}^{-2} \cdot \text{day}^{-1}$) was simply added to natural sunlight (Figure 7). In contrast, the ETR 85 and PPFD

275 treatments maintained consistent levels, avoiding both under- and over-supply of light energy, thereby ensuring proper crop growth and efficient energy use [9].

The average Φ_{PSII} of the Φ_{PSII} 0.735 treatment was 0.722, slightly below the target, largely because occasional midday sunlight spikes reduced Φ_{PSII} (Table 1). Only 45% of data points fell within $\pm 1\%$ of the target Φ_{PSII} value (Figure 3E), showing relatively higher variability (Figure 4E). PPFD adjustments were also considerably more dynamic than in the ETR 85 treatment (Figure 6B). This pattern may be associated with daily replacement of the fluorometer measurement spot during the day. Even when measurements were taken from the same plant, newly selected leaves may have differed in their light prehistory and microclimate [19], leading to abrupt PPFD shifts until Φ_{PSII} stabilized to the target value. This leaf replacement protocol was applied equally to both Φ_{PSII} - and ETR-based treatments. However, ETR-based control was less sensitive to such changes because PPFD is incorporated into the ETR calculation, buffering the effects of fluctuations in Φ_{PSII} . To reduce these disturbances and avoid interfering with light adjustment, it is preferable to change measurement spots before or after the photoperiod. The Φ_{PSII} 0.735 treatment showed slightly higher Φ_{NPQ} compared to ETR 85 (Table 1), likely reflecting the need for stronger photoprotective responses under fluctuating PPFD [28,29]. Non-photochemical quenching (NPQ) responds rapidly to high irradiance but relaxes more slowly when irradiance decreases, potentially leading to an “overprotected” PSII and reduced photosynthetic efficiency [30]. This suggests that even when similar amounts of light are provided, supplemental lighting may be used less efficiently for photosynthesis depending on the control parameter.

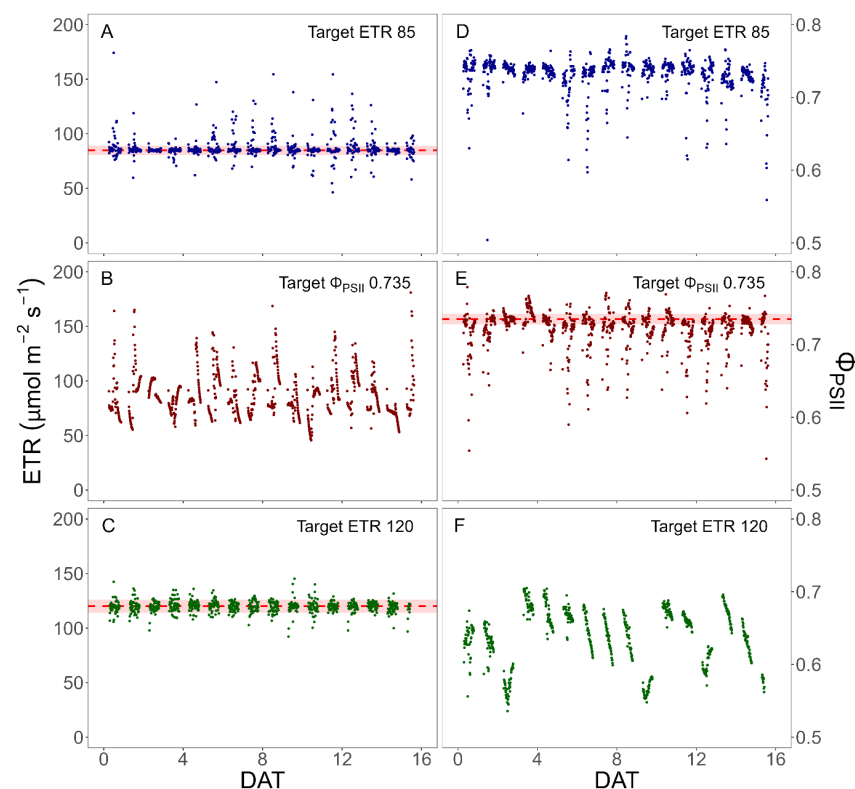


Figure 3. Electron transport rate (ETR) (A–C) and quantum yield of photosystem II (Φ_{PSII}) (D–F) under three biofeedback treatments over 16 days after treatment (DAT). Dashed lines indicate the target values (ETR 85 $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$, Φ_{PSII} 0.735, or ETR 120 $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$), and red shaded areas represent the acceptable target ranges, defined as $\pm 5\%$ for ETR and $\pm 1\%$ for Φ_{PSII} . Panels (A,B,D,E) show results from trial 1, and panels (C,F) show results from trial 2.

Table 1. Light and chlorophyll fluorescence parameters averaged over 16 days in trial 1 and 2. Parameters include daily light integral (DLI), photosynthetic photon flux density (PPFD), electron transport rate (ETR), quantum yield of photosystem II (Φ_{PSII}), quantum yield of non-photochemical quenching (Φ_{NPQ}), and quantum yield of non-regulated energy dissipation (Φ_{NO}).

Trial	Treatments	DLI ($\text{mol} \cdot \text{m}^{-2} \cdot \text{day}^{-1}$)	PPFD ($\mu\text{mol} \cdot \text{m}^{-2} \cdot \text{s}^{-1}$)	ETR ($\mu\text{mol} \cdot \text{m}^{-2} \cdot \text{s}^{-1}$)	Φ_{PSII}	Φ_{NPQ}	Φ_{NO}
1	ETR 85	15.1 ± 0.3	283.0 ± 24.1	86.6 ± 9.2	0.732 ± 0.024	0.078 ± 0.015	0.188 ± 0.017
	Φ_{PSII} 0.735	15.2 ± 1.4	286.2 ± 65.4	86.9 ± 19.7	0.722 ± 0.026	0.090 ± 0.019	0.185 ± 0.019
	PPFD 275	15.2 ± 0.4	284.6 ± 28.3				
	Add 400	15.0 ± 1.3	279.2 ± 155.6				
2	ETR 120	19.3 ± 1.1	447.1 ± 29.8	119.8 ± 5.4	0.639 ± 0.039	0.107 ± 0.017	0.255 ± 0.031
	PPFD 420	18.2 ± 0.2	420.0 ± 1.5				

Values are means $\pm$ standard deviations. For DLI, $n = 15$. For other parameters, $n = 939$ for trial 1 and $n = 733$ for trial 2.

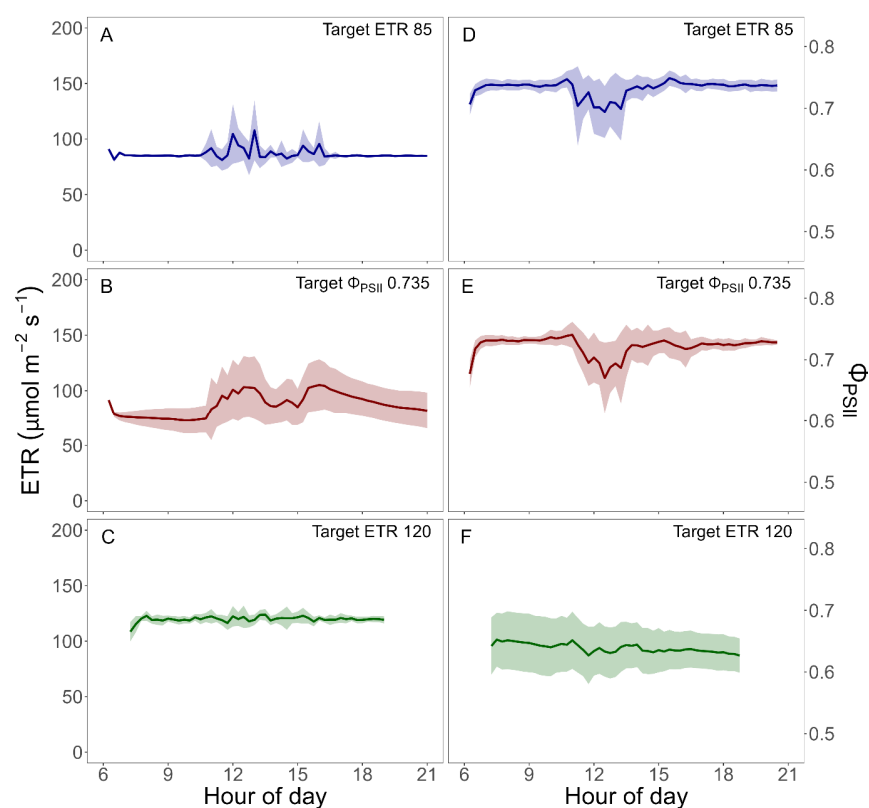


Figure 4. Diurnal patterns of electron transport rate (ETR) (A–C) and quantum yield of photosystem II (Φ_{PSII}) (D–F) under three biofeedback treatments, summarized across 16 days. Data were aggregated across days at each time of day (15 min resolution), with solid lines representing the mean ETR and shaded areas indicating ± 1 standard deviation (SD). (A,D): target electron transport rate (ETR) of $85 \mu\text{mol} \cdot \text{m}^{-2} \cdot \text{s}^{-1}$, (B,E): target Φ_{PSII} of 0.735, and (C,F): target ETR of $120 \mu\text{mol} \cdot \text{m}^{-2} \cdot \text{s}^{-1}$. Panels (A,B,D,E) show results from trial 1, and panels (C,F) show results from trial 2.

DLI of the Φ_{PSII} 0.735 treatment fluctuated across days independently of natural sunlight availability, in contrast to the consistent DLI levels of ETR 85 and PPFD 275 (Figure 7). This highlights the inherently dynamic nature of Φ_{PSII} -based logic, which regulates supplemental light input upward under favorable conditions and downward under stressful conditions [21,31]. However, average PPFD and DLI over the entire cultivation period were similar among the three light treatments; ETR 85, Φ_{PSII} 0.735, and PPFD 275 (Table 1). The target values applied in this study were determined based on lettuce ‘Casey’ grown under the specific greenhouse conditions and should not be expected to produce identical

PPFD or DLI under different species, cultivars, or environmental conditions. For example, high-light-acclimated plants upregulate photosynthetic machinery and have higher Φ_{PSII} and ETR, whereas shade-adapted species such as pothos maintain relatively lower Φ_{PSII} and ETR even after acclimating to high light [32,33]. Consequently, shade species would yield higher PPFD under ETR-based control to compensate for their lower Φ_{PSII} values, and there will be lower PPFD under Φ_{PSII} -based control to avoid excess light stress, with the opposite responses expected from sun-acclimated plants or crops. Therefore, appropriate target values for either Φ_{PSII} - or ETR-based control should be determined empirically for each crop and growth environment through preliminary testing.

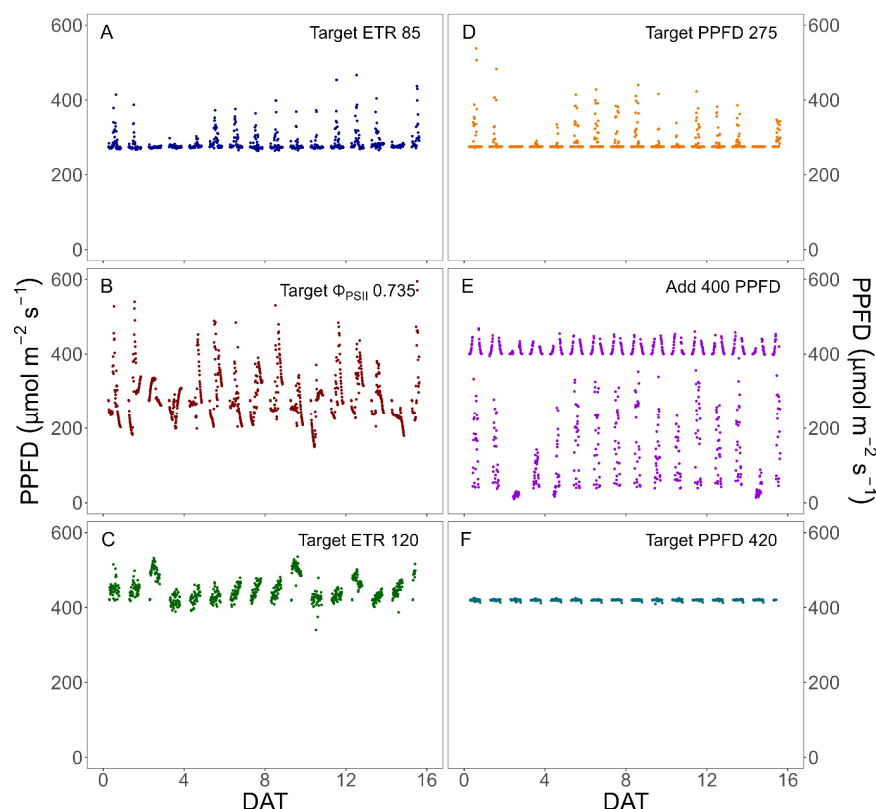


Figure 5. Photosynthetic photon flux density (PPFD) under three biofeedback and three reference treatments over 16 days after treatment (DAT). (A) target electron transport rate (ETR) of $85 \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$; (B) target Φ_{PSII} of 0.735; (C) target ETR of $120 \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$. Reference controls included maintaining PPFD at 275 (D) or $420 \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ (F) by adjusting LEDs in response to sunlight and adding $400 \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ supplemental light for 4 h at the beginning and end of the photoperiod (E). Panels (A,B,D,E) show results from trial 1, and panels (C,F) show results from trial 2.

3.3. Dynamic Regulation of PPFD Under High ETR Target

The ETR 120 treatment averaged $119.8 \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ (Table 1), with 82% of data points within $\pm 5\%$ of the target (Figure 3C). Trial 2 was conducted under lower sunlight availability than trial 1, and the higher ETR setpoint further reduced the occurrence of light overshoots (Figure 6C). As a result, the achieved ETR was closer to the target, with a smaller standard deviation than in the ETR 85 treatment in trial 1 (Figure 4C). The corresponding PPFD of the ETR 120 treatment averaged $447.1 \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ over trial 2 (Table 1). Φ_{PSII} values of the ETR 120 treatment were lower and more variable than in ETR 85 and Φ_{PSII} 0.735 treatments (Figure 3D–F), and corresponding supplemental light was dynamically adjusted to compensate for those changes in Φ_{PSII} , resulting in day-to-day variation in DLI (Figures 5C and 7).

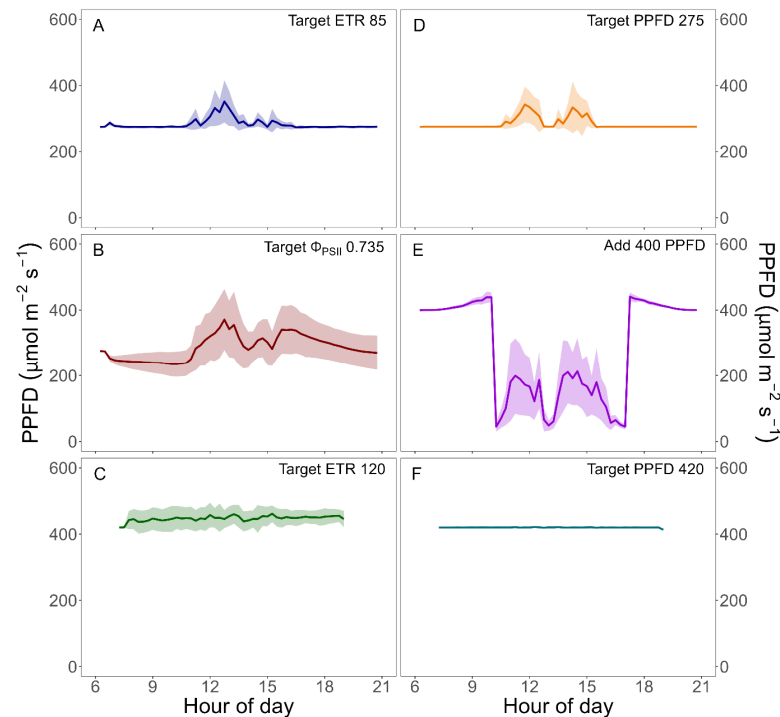


Figure 6. Diurnal patterns of photosynthetic photon flux density (PPFD) under three biofeedback and three reference treatments, summarized across 16 days. Data were aggregated across days at each time of day (15 min resolution), with solid lines representing the mean PPFD and shaded areas indicating ± 1 standard deviation (SD). (A) target electron transport rate (ETR) of $85 \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$; (B) target Φ_{PSII} of 0.735; (C) target ETR of $120 \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$. Reference controls included maintaining PPFD at 275 (D) or $420 \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ (F) by adjusting LEDs in response to sunlight, and adding $400 \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ supplemental light for 4 h at the beginning and end of the photoperiod (E). Panels (A,B,D,E) show results from trial 1, and panels (C,F) show results from trial 2.

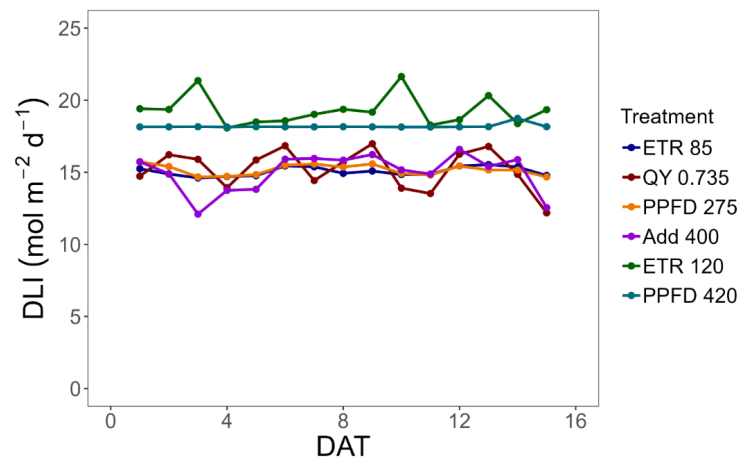


Figure 7. Daily light integral (DLI) over 16 days after treatment (DAT) under six supplemental LED lighting treatments in trial 1 and 2.

Distinct diurnal patterns of Φ_{PSII} were observed in the ETR 120 treatment (Figure 8A–C), with values either remaining stable, gradually decreasing, or declining followed by recovery later in the day. The corresponding PPFD responses exhibited inverse patterns, showing three distinct trends: remaining stable, gradually increasing, and peaking before declining (Figure 8D–F). Even when Φ_{PSII} was relatively stable, PPFD still ranged widely between $400\text{--}450 \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ during a day (Figure 8D), whereas PPFD 420 maintained a tightly consistent intensity (Figure 6F). Similar trends have been reported previously, where higher

ETR setpoints led to greater variation in Φ_{PSII} and PPFD across replications in lettuce and cucumber [21]. These results suggest that ETR-based control does not necessarily provide a constant PPFD but instead varies light intensity in response to real-time changes in Φ_{PSII} , particularly under higher ETR setpoints. Such variability likely arises because photosynthetic processes cannot adjust instantly to rapid light fluctuations. The kinetics of NPQ, stomatal conductance, and the utilization of adenosine triphosphate (ATP) and nicotinamide adenine dinucleotide phosphate (NADPH) are inherently delayed and often asymmetric, so short-term changes in PPFD are not immediately matched by changes in Φ_{PSII} [34–36]. In addition, cumulative environmental stress during a day may reduce photosynthetic efficiency in the midday and afternoon [37]. Taken together, the combination of a high ETR setpoint and dynamic greenhouse conditions led to more variable supplemental light regulation in the ETR 120 treatment than in the ETR 85 treatment (Figure 5A,C).

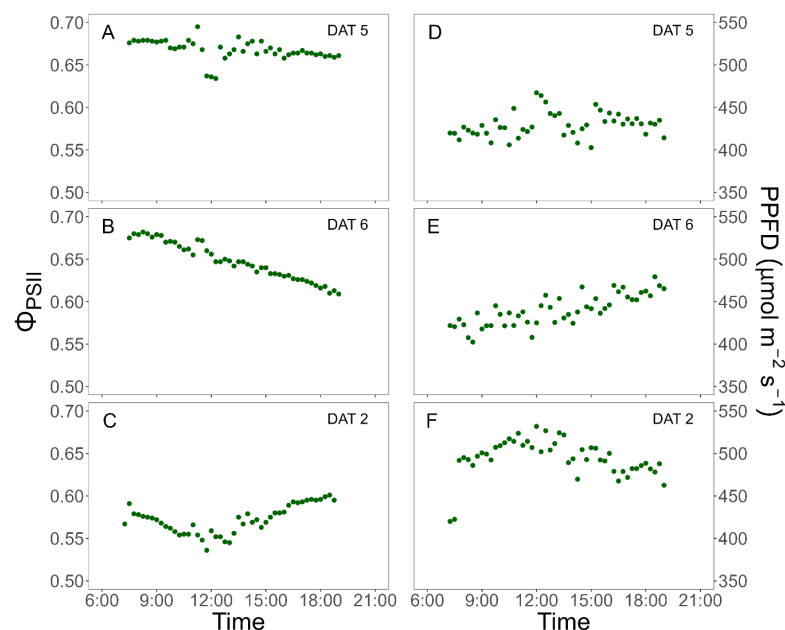


Figure 8. Quantum yield of photosystem II (Φ_{PSII}) on representative days after treatment (DAT) (A–C) and the corresponding photosynthetic photon flux density (PPFD) for those days (D–F). Single-day profiles are shown to illustrate diurnal patterns not readily visible in the 16-day overview. All panels show results from trial 2.

3.4. ETR- and Φ_{PSII} -Based Biofeedback Logic

In ETR-based biofeedback control, PPFD is adjusted according to the ratio of the target to the current ETR (Equation (6)), assuming a linear relationship between ETR and PPFD. This approach has been used successfully in climate-controlled chambers [20,31]. Table 2 shows an example dataset from the ETR 85 treatment in trial 1 on 17 April. At 10:00 and 16:00 h, when sunlight was low, ETR_c was already close to the ETR_t , and only small PPFD adjustments were needed. Around midday, fluctuating sunlight caused abrupt deviations in $PPFD_c$, most likely due to cloud movement. This led to sharp shifts in the ETR_t/ETR_c ratio. Even so, the calculated $PPFD_t$ remained stable within a narrow range (270–290 $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$). ETR increases with increasing PPFD and approaches saturation at higher light levels, reflecting photosynthetic limitations such as upregulated NPQ and reduced CO_2 availability [38]. However, the ETR-based logic, based on a linear relationship between ETR and PPFD, successfully maintained consistent light control with frequent and iterative adjustments despite fluctuations in sunlight, demonstrating the practical utility of the linear approximation for greenhouse lighting control. Nevertheless, the performance of this approach under greater variability in solar radiation remains to be evaluated.

Table 2. Example dataset illustrating electron transport rate (ETR)-based biofeedback control.

Time	PPFD _c	ETR _c	ETR _t	ETR _t /ETR _c	PPFD _t
...					
10:00	269	85.4	85	0.995	270
10:15	270	85.0	85	1.000	270
10:30	271	85.2	85	0.998	270
...					
12:30	278	85.0	85	1.000	278
12:45	208	61.5	85	1.382	288
13:00	427	131.0	85	0.649	277
13:15	213	66.0	85	1.287	275
13:30	275	83.5	85	1.018	280
...					
16:00	272	84.8	85	1.010	272
16:15	273	84.5	85	1.007	274
16:30	271	84.8	85	1.014	272
...					

Time: measurement time (hh:mm); PPFD_c: current PPFD at the time of measurement ($\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$); ETR_c: current ETR at the time of measurement ($\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$); ETR_t: target ETR ($\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$); ETR_t/ETR_c: ratio of target to current ETR; PPFD_t: target PPFD calculated by the ETR-based biofeedback logic ($\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$); "...": indicates omitted intermediate time points.

In Φ_{PSII} -based control, PPFD is adjusted based on the ratio of current to target Φ_{PSII} (Equation (7)), reflecting the general decrease in Φ_{PSII} with increasing PPFD. Table 3 shows an example dataset illustrating Φ_{PSII} -based biofeedback control. In the morning and late afternoon, $\Phi_{\text{PSII},t}$ was stably achieved with only minor PPFD adjustments, similar to ETR-based control. Around midday, however, fluctuating sunlight led to abrupt increases in PPFD_c, resulting in transient deviations in $\Phi_{\text{PSII},c}$ relative to $\Phi_{\text{PSII},t}$. For instance, at 12:30 h, PPFD_c was $365 \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ while $\Phi_{\text{PSII},c}$ remained relatively high (0.737), close to the target value. Consequently, PPFD_t was kept at a similarly high level ($366 \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$), resulting in a decline in Φ_{PSII} at 12:45 and sustained elevated supplemental light levels. However, following iterative corrections lowered PPFD_t and restored Φ_{PSII} close to the target value by 13:30 h.

Table 3. Example dataset illustrating quantum yield of photosystem II (Φ_{PSII})-based biofeedback control.

Time	PPFD _c	$\Phi_{\text{PSII},c}$	$\Phi_{\text{PSII},t}$	$\Phi_{\text{PSII},c}/\Phi_{\text{PSII},t}$	PPFD _t
...					
10:00	228	0.729	0.735	0.992	228
10:15	227	0.733	0.735	0.997	226
10:30	227	0.731	0.735	0.995	226
...					
12:30	365	0.737	0.735	1.003	366
12:45	356	0.685	0.735	0.932	332
13:00	341	0.662	0.735	0.901	307
13:15	297	0.690	0.735	0.939	279
13:30	279	0.730	0.735	0.993	277
...					
16:00	293	0.742	0.735	1.010	296
16:15	296	0.740	0.735	1.007	298
16:30	296	0.745	0.735	1.014	300
...					

Time: measurement time (hh:mm); PPFD_c: current PPFD at the time of measurement ($\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$); $\Phi_{\text{PSII},c}$: current Φ_{PSII} at the time of measurement; $\Phi_{\text{PSII},t}$: target Φ_{PSII} ; $\Phi_{\text{PSII},c}/\Phi_{\text{PSII},t}$: ratio of current to target Φ_{PSII} ; PPFD_t: target PPFD calculated by the inverse model without intercept based on PPFD_c; "...": indicates omitted intermediate time points.

Although Φ_{PSII} generally decreases with increasing PPFD, its response may lag behind rapid fluctuations in light intensity due to relatively slow mechanisms such as NPQ dynamics and stomatal behavior [39,40]. As a result, Φ_{PSII} -based control, which relies directly on instantaneous photochemical efficiency, exhibited greater variability in PPFD adjustments compared to ETR-based control under fluctuating greenhouse conditions. These results suggest that relying solely on Φ_{PSII} for light regulation may lead to less stable control, especially when photosynthetic responses are not synchronized with rapid changes in incident light.

3.5. Lettuce Growth Responses and Energy-Use Efficiency

In trial 1, shoot fresh and dry weight did not differ significantly among treatments (Table 4). Total leaf area was slightly smaller, and leaf chlorophyll content was higher at PPFD 275, whereas the Add 400 treatment showed the opposite trend, with biofeedback treatments displaying intermediate responses. However, these differences were minor and did not indicate distinct treatment effects. Regarding lighting energy use, the Φ_{PSII} 0.735 treatment consumed the most energy over the experiment, followed by the ETR 85 and reference controls, but overall energy-use efficiency remained statistically similar among treatments. Similarly, in trial 2, no significant differences were found in either growth parameters or energy-use efficiency.

Table 4. Growth and energy use parameters measured 16 days after the treatments.

Trials	Treatments	Shoot Fresh Weight (g)	Shoot Dry Weight (g)	Total Leaf Area (cm ²)	Leaf Chlorophyll Content (CCI)	Total Electricity Use (kWh)	Energy-Use Efficiency (g DW·kWh ^{−1})
1	ETR 85	122 ± 7	6.38 ± 0.28	1969 ± 60 ab	13.4 ± 0.2 ab	9.81	0.651 ± 0.029
	Φ_{PSII} 0.735	128 ± 4	6.76 ± 0.17	1945 ± 56 ab	13.6 ± 0.3 ab	10.23	0.661 ± 0.017
	PPFD 275	115 ± 3	6.26 ± 0.12	1786 ± 57 b	14.5 ± 0.6 a	9.09	0.689 ± 0.013
	Add 400	123 ± 4	6.51 ± 0.18	2068 ± 39 a	12.5 ± 0.8 b	9.08	0.717 ± 0.020
	<i>p</i> -values	0.24	0.32	0.0025	0.028		0.095
2	ETR 120	147 ± 13	7.2 ± 0.4	2459 ± 119		12.16	0.594 ± 0.038
	PPFD 420	141 ± 13	6.8 ± 0.4	2380 ± 119		10.89	0.622 ± 0.038
	<i>p</i> -values	0.69	0.39	0.64			0.54

Values are means ± standard errors. $n = 5$ for trial 1 and $n = 4$ for trial 2. Different letters within each column indicate significant differences at $\alpha = 0.05$, according to Tukey's HSD test.

In contrast to the present results, a comparable study conducted in a climate-controlled chamber on basil (*Ocimum basilicum*) reported higher biomass and energy-use efficiency under CF-based feedback lighting compared with constant PPFD [41]. Under constant 380 $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ PPFD for 18 h, Φ_{PSII} declined from 0.65 to 0.45 during the later part of each photoperiod. The authors attributed this decline primarily to photosynthate accumulation and reduced sink capacity in leaves [42], leading the feedback controller to reduce LED intensity as photosynthetic demand decreased. However, the observed decline in Φ_{PSII} may not solely reflect diurnal physiological responses. The controller reached the target Φ_{PSII} late in the photoperiod, suggesting a slow system response, and frequent saturating pulses (every 5 min) may also have induced photoinhibition [21]. Thus, it remains unclear whether the reduced light intensity reflected plant regulation or artifacts of the control system itself.

In this study, the absence of differences in growth and energy-use efficiency across the biofeedback and reference light control methods likely reflected the relatively steady environmental conditions. Under such conditions, plant photosynthetic demand likely remained relatively stable throughout the photoperiod. The benefits of the biofeedback lighting may become more evident under environments with greater temporal variability or

extreme greenhouse environments, such as strong diurnal changes in temperature. Under these conditions, photosynthetic capacity may vary over time, allowing dynamic light regulation to better align light supply with real-time plant demand compared with constant PPFD strategy.

Crop characteristics may also influence the effectiveness of the biofeedback lighting. Species with higher light requirements may respond differently to dynamic light regulation than shade-adapted crops. For example, Nam et al. [21] reported that lettuce and cucumber showed different PPFD adjustment patterns under the same biofeedback target levels, reflecting crop-specific photosynthetic responses. Comparative studies across crops with contrasting light requirements could therefore further reveal the advantages of dynamic, plant-driven light regulation in greenhouses.

Although growth and energy use did not differ here, this study demonstrates the feasibility of implementing a CF-based biofeedback prototype in greenhouses and provides a foundation for future refinements under more variable or stress-prone environments and across diverse crops. Future research may explore a broader range of control target levels and alternative CF parameters for biofeedback control to further optimize plant-driven lighting strategies.

4. Conclusions

The first proof-of-concept application of a chlorophyll fluorescence-based biofeedback system under greenhouse conditions was demonstrated for regulating supplemental LED lighting. The system, originally developed for indoor environments, was successfully adapted to dynamic greenhouse conditions with fluctuating sunlight and heterogeneous microclimates. Both ETR- and Φ_{PSII} -based logics maintained target photosynthetic responses under variable greenhouse conditions. Across two trials, lettuce growth and light energy-use efficiency did not differ significantly among the biofeedback and reference controls. Nevertheless, these results demonstrate the feasibility of chlorophyll fluorescence-based biofeedback lighting control in greenhouses and provide a foundation for further validation under more variable environments and across diverse crops. More broadly, this work highlights the use of real-time plant physiological responses for plant-centered greenhouse control.

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Abbreviations

The following abbreviations are used in this manuscript:

HPS	High-pressure sodium
LED	Light-emitting diode
PPFD	Photosynthetic photon flux density
DLI	Daily light integral
CO ₂	Carbon dioxide
CF	Chlorophyll fluorescence
ETR	Electron transport rate
PSII	Photosystem II
Φ_{PSII}	Quantum yield of photosystem II
DPI	Daily photochemical integral
VPD	Vapor pressure deficit
SD	Standard deviation
CEA	Controlled environment agriculture
PAM	Pulse–amplitude modulation
Φ_{NPQ}	Non-photochemical quenching
Φ_{NO}	Non-regulated energy dissipation
F_v/F_m	Maximum quantum efficiency of PSII
F_s	Steady-state fluorescence under actinic light
F_m'	Maximum fluorescence from a light-adapted leaf
F_o	Minimum fluorescence from a dark-adapted leaf
F_m	Maximum fluorescence from a dark-adapted leaf
PPFD _t	Target PPFD
PPFD _c	Current PPFD
ETR _t	Target ETR
ETR _c	Current ETR
$\Phi_{PSII,t}$	Target Φ_{PSII}
$\Phi_{PSII,c}$	Current Φ_{PSII}
RCBD	Randomized complete block design
ETR 85	ETR-based control with a ETR _t of 85 $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$
$\Phi_{PSII} 0.735$	Φ_{PSII} -based control with a $\Phi_{PSII,t}$ of 0.735
PPFD 275	Constant PPFD of 275 $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$
Add 400	Timer-based PPFD of 400 $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ from 6:00 to 10:00 and from 17:00 to 21:00
ETR 120	ETR-based control with a ETR _t of 120 $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$
PPFD 420	Constant PPFD of 420 $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$
ANOVA	Analysis of variance
HSD	Honestly significant difference
PWM	Pulse-width modulation
NPQ	Non-photochemical quenching
ATP	Adenosine triphosphate
NADPH	Nicotinamide adenine dinucleotide phosphate

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