Contribution of Far-red Photons to Light Compensation Point of Leaf Photosynthesis in Tomato

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Abstract. The light compensation point (LCP) is a key plant photosynthetic parameter and represents the light intensity at which the photosynthetic rate equals the respiration rate, indicating the light level for the null leaf carbon balance. In general, the LCP is calculated from a photosynthetic light response curve (LRC), which characterizes changes in the net photosynthetic rate (P_n) in response to the photosynthetic photon flux density (PPFD; 400–700 nm). However, recent reports highlight a positive contribution of far-red (FR) light (specifically in the range of 700–750 nm) to photosynthesis. FR light is abundant in ecosystems and widely used in indoor crop production, yet its effect on the LCP remains unclear. The objective of this study was to evaluate the effect of FR light (700–750 nm) on the LCP. In this experiment, light conditions with varying FR to extended photosynthetically active radiation [ePAR; 400–750 nm, a revised definition of photosynthetically active radiation (PAR) including FR photons] ratios, representing an abundance of FR light in the light source, were applied during acclimatization and LRC measurements in tomato (*Solanum lycopersicum* cv. Maxxiany). Tomato plants were acclimatized under light conditions with 2% or 44% FR-to-ePAR ratios, with the same extended photosynthetic photon flux density (ePPFD; PPFD for ePAR; 400 $\mu mol \cdot m^{-2} \cdot s^{-1}$) in a growth chamber. P_n was measured under varying PPFD or ePPFD levels of 2% or 44% FR-to-ePAR ratios. The PPFD- and ePPFD-based LCP were calculated using the photosynthetic parameters estimated from the P_n model. Acclimatization under 44% FR light resulted in significantly greater LCPs compared with 2% FR light in both PPFD-based (20.8 ± 4.5 and 18.0 ± 4.5 $\mu mol \cdot m^{-2} \cdot s^{-1}$ for 44% and 2% FR light, respectively) and ePPFD-based (similarly 27.6 ± 3.6 and 23.9 ± 4.0 $\mu mol \cdot m^{-2} \cdot s^{-1}$) measurements. The higher LCPs under 44% FR light suggest the contribution of FR photons to photosynthesis, compensating for its lower PAR levels. This supports that PPFD-based LCPs are likely underestimated when higher FR photons are present in the light source, as the contribution of FR light to photosynthesis is ignored. These findings emphasize the importance of revision of PAR definition to include FR photons (ePAR), which is essential to obtain accurate LCP values, particularly FR-rich light conditions.

The light compensation point (LCP) refers to the light intensity at which photosynthesis and respiration rates are equal. The LCP provides insights into a minimum light intensity required for growth and maintenance (Amthor 1984; Valladares and Niinemets 2008). Thus, studying the LCP is important for understanding plant tolerance to shade (Sterck et al. 2013), which typically involves lower levels of photosynthetically active radiation (PAR; 400–700 nm). Plants acclimatized to shade often exhibit lower LCPs, indicating their adaptation to lower PAR levels for survival and growth (Craine and Reich 2005; Kabir et al. 2023; Valladares and Niinemets 2008).

Light quality under the canopy not only contains reduced levels of PAR, but also a relatively increased fraction of far-red (FR; definition varies, but typically includes photons from 700 to 800 nm) light to PAR than sunlight because of the optical properties of leaves. The increased fraction of FR light under the canopy often induces morphological changes (e.g., elongation of hypocotyl), because FR light is perceived by phytochromes to be a signal (Casal 2012), a key mechanism for plant survival under low PAR levels, which is widely studied in plant ecophysiology. On the other hand, the role of FR photons on photosynthesis has received little attention. This is likely due to the study by McCree (1972), which established the defition of PAR. McCree (1972) measured the photosynthetic efficiency of wavelengths between 350 and 725 nm and reported that FR light has lower photosynthetic efficiency compared to its under PAR.

Recent findings suggest that FR photons contribute to photosynthesis, which have revisited the Emerson effect. Emerson (1957) observed higher photosynthetic rates when both red and far-red light were present simultaneously than the sum of the photosynthetic rates under red and far-red light individually. This finding was named the Emerson effect and, in the 1960s, led to the discovery of two distinct photosystems (photosystems I and II), with photosystems I and II preferentially absorbing FR and red photons, respectively (Ruban 2015). Revisiting this, Zhen and van Iersel (2017) reported that adding FR photons (peak, 735 nm; light intensity, 110 $\mu mol \cdot m^{-2} \cdot s^{-1}$) to red and blue or white light-emitting diode (LED) light (intensity range, 50–700 $\mu mol \cdot m^{-2} \cdot s^{-1}$) significantly increased net photosynthesis (P_n) and the quantum yield of photosystem II in lettuce compared with the same conditions without FR photons. This enhancement in photosynthesis is explained by a balanced excitation between photosystems I and II, resulting in efficient linear electron flow compared with no FR photons in the light source. Follow-up experiments from their group, either adding FR photons to FR-depleted light or filtering FR photons from sunlight, further confirmed the contribution of FR photons to photosynthesis in multiple species, including lettuce, corn, wheat, sorghum, rice, and sunflower (Zhen and Bugbee 2020; Zhen et al. 2022). They ultimately proposed redefining PAR as extended PAR (ePAR; 400–750 nm)

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to include FR photons as PAR (Zhen et al. 2021).

The photosynthetic activity of FR photons, in addition to a greater fraction of FR photons in light quality under the canopy, raises questions about an accurate estimation of the LCP. The LCP is typically estimated from a photosynthetic light response curve (LRC), which describes P_n as a function of light intensity, and is determined by finding the light intensity at which P_n equals zero. In most cases, light intensities are quantified using photosynthetic photon flux density (PPFD), which is based on the conventional definition of PAR. However, under light conditions with low PAR and high FR intensity, the contribution of FR photons to photosynthesis should not be ignored for accurate LCP estimation. The LCPs measured using PPFD may have been underestimated. To date, we have not found any reports estimating LCPs while including FR photons in the light conditions. Therefore, there is a research gap in understanding the accurate minimum light intensity required for plant growth and maintenance in shade conditions.

We hypothesize that the LCPs under high or low FR light conditions are different because of the synergistic contribution of FR photons to photosynthesis. The objective of our study was to characterize the differences in the LCP with and without FR photons during their acclimatization and LRC measurement. We quantified the photosynthetic LRC of cherry tomato (*Solanum lycopersicum* cv. Maxxiany) under high and low FR light conditions. Tomato is a crop that is most widely grown in a greenhouse, creating a tall canopy in a so-called “high-wire” crop production method. Understanding light levels within the canopy and their influence on crop productivity are important for optimizing productivity in these systems. Furthermore, understanding accurate LCPs with relatively greater FR fractions can provide valuable insights into the development of canopy management or supplemental lighting strategies.

Materials and methods

PLANT MATERIALS. Young seedlings of tomato (cherry-type cv. Maxxiany; Axia Vegetable Seeds, Naaldwijk, Netherlands) grown in a greenhouse were used as the plant material. In the first and second replications, 30 seeds were planted 25 Oct 2023 and 28 Nov 2023 into rockwool plugs (36 mm long × 36 mm wide × 40 mm high; AO PLUG, Grodan, Roermond, Netherlands) covered with vermiculite for germination in a reach-in chamber maintained at 28 °C without light. As soon as radicles emerged, the trays (55 cm long × 28 cm wide × 6 cm high; Heavy-duty 10/20 seed tray, T.O. PLASTICS, Clearwater, MN, USA) holding rockwool plugs were moved into a greenhouse at The Ohio State University Controlled Environment Agriculture Research Complex (Columbus, OH, USA). The greenhouse gutter height, width, and length are 7, 21.7, and 22.2 m, respectively. The greenhouse had an ethylene–tetrafluoroethylene film as roof covering material. The target greenhouse temperatures were 24 °C during the day and 18 °C at night, controlled with a Priva Climate Computer (Priva BV, De Lier, Netherlands) with natural ventilation, fan-and-pad evaporative cooling, rail heating, crop heating, and perimeter heating. Supplemental lighting (Arize Element L1000; General Electric, Boston, MA, USA) was provided when outdoor radiation was less than 400 $W \cdot m^{-2}$, and a photoperiod of 16 h was maintained. The air CO_2 concentration was increased to 1000 $mg \cdot L^{-1}$ using a CO_2 generator (Johnson Gas Appliance Co., Hiawatha, IA, USA) when natural ventilation and fan-and-pad evaporative cooling were not in use. The average daily light integral, air temperature, CO_2 concentration, and vapor pressure deficit (VPD) in the greenhouse were 20.9 ± 1.2 $mol \cdot m^{-2} \cdot d^{-1}$, 21.6 ± 0.6 °C, 497 ± 35 $\mu mol \cdot mol^{-1}$, and 0.93 ± 0.25 kPa for the first experiment, and 19.5 ± 2.4 $mol \cdot m^{-2} \cdot d^{-1}$, 21.3 ± 1.1 °C, 503 ± 90 $\mu mol \cdot mol^{-1}$, and 1.44 ± 0.39 kPa for the second experiment.

Plants were irrigated as needed with nutrient solution containing 90 $mg \cdot L^{-1}$ N, 47 $mg \cdot L^{-1}$ P, 144 $mg \cdot L^{-1}$ K, 144 $mg \cdot L^{-1}$ Ca, 60 $mg \cdot L^{-1}$ Mg, 116 $mg \cdot L^{-1}$ S, and 89 $mg \cdot L^{-1}$ Cl, in addition to micronutrients. Two weeks after transferring the plants into the greenhouse, each plant was transplanted into a rockwool cube (10 cm long × 10 cm wide × 6.5 cm high; NG2.0, Grodan, Roermond, Netherland) and subirrigated with the same nutrient solution. The plants were grown in the greenhouse until 41 d after germination, during which plants were spaced so they did not shade each other with their leaves.

LIGHT CONDITIONS FOR PHOTOSYNTHETIC ACCLIMATIZATION AND LEAF PHOTOSYNTHESIS MEASUREMENTS. At 43 d after seeding, tomato plants were at a developmental stage with six unfolded leaves. Fifteen uniform plants were selected and moved to two identical plant growth chambers (PGC FLEX; Conviron, Winnipeg, Manitoba, Canada) to provide light environments with two different FR (701–750 nm) levels (8 or 176 $\mu mol \cdot m^{-2} \cdot s^{-1}$) as the acclimatization process, with the same (400–700 nm) or extended PPFD (ePPFD; 400–750 nm) of 400 $\mu mol \cdot m^{-2} \cdot s^{-1}$. The FR-to-ePAR ratios for each treatment were 2% or 44%, respectively (Fig. 1). These ratios were determined based on the measured light quality above and below the canopy in a high-wire tomato production system with a crop height of 3 m and 18 fully expanded leaves within the canopy in our preliminary study (data not shown). The FR and PAR light sources inside the growth chamber were the RAY44 PFRSPEC (Fluence, Austin, TX, USA) and RAY44 Physiospec indoor (Fluence), respectively. The photoperiod of the growth chambers was 16 h. The day and night temperatures of the growth chambers were set as 24 and 18 °C. The CO_2 concentration and VPD in the growth chambers were maintained at 400 $\mu mol \cdot mol^{-1}$ and 1.1 kPa, respectively. Acclimatization was performed for 3 d under the light conditions before measuring leaf-level photosynthetic light responses.

At the beginning of day 4 in the growth chamber, five representative plants were selected from each acclimatization light condition for leaf photosynthesis measurements using a CIRAS-3 portable photosynthesis system (PP Systems, Amesbury, MA, USA). The primary leaflet of the fourth leaf (>13 cm in length, including petiole) was chosen for the measurements. The leaf chamber was uncovered to allow the same light source in the growth chamber (Fig. 1); the transmittance of the leaf chamber was 91%. Each growth chamber was divided into four sections, each with a different number of layers of a black plastic shadecloth (30%, 40%, 50%, and 90% transmission; Be Cool Solutions, Clinton, WI, USA) installed

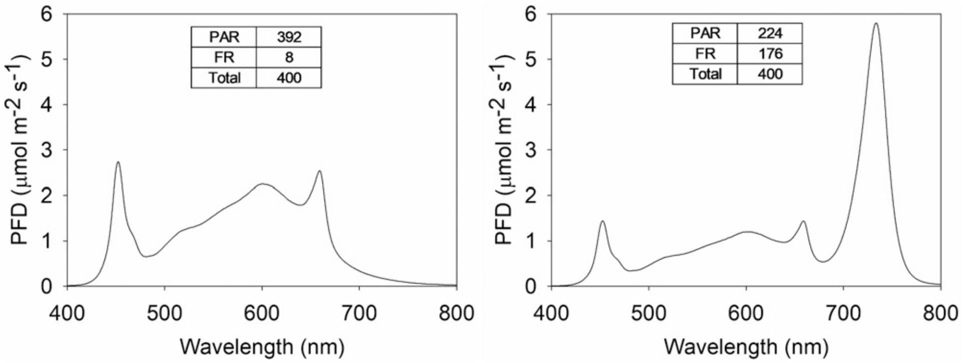

Fig. 1. Spectral distribution of light conditions in each growth chamber. Each chamber had the same total photon flux density (PFD; 400 μmol·m^{-2}·s^{-1}), but different levels of far-red (FR; 701–750 nm) light and photosynthetically active radiation (PAR; 400–700 nm). The table in each graph shows the FR and PAR PFDs (μmol·m^{-2}·s^{-1}) in each chamber, resulting in FR to extended PAR (ePAR; 400–750 nm) ratios of 2% (left) and 44% (right), respectively.

below the light fixtures to adjust to four different PPFD or ePPFD levels. The intensities and spectra of each section within a growth chamber were measured using a spectroradiometer (PS-200; Apogee Instruments, Logan, UT, USA) before and after the leaf photosynthesis measurements (Fig. 2).

Considering the transmittance of the leaf chamber in the portable photosynthesis system and the measured total photon flux density (PFD) levels from the spectroradiometer, the ePPFD levels used for leaf photosynthesis measurements were 0, 11.8, 28.2, 51.9, and 64.6 μmol·m^{-2}·s^{-1} under the 2% FR light quality, and 0, 11.8, 34.6, 61.9, and 89.2 μmol·m^{-2}·s^{-1} under the 44% FR light quality. For the same light conditions, PPFD levels were 0, 11.6, 27.6, 50.9, and 63.3 μmol·m^{-2}·s^{-1} for 2% FR and 0, 6.6, 19.4, 34.7, and 49.9 μmol·m^{-2}·s^{-1} for 44% FR, respectively. The plants were exposed to each light intensity at least 15 min to measure the P_n, starting from higher to lower PPFD or ePPFD levels. During the P_n measurements, the leaflet was not shaded by any leaves above in each section of the growth chamber. For measuring dark respiration (R_d), plants were exposed to a dark condition for at least 30 min. The light quality during the acclimatization and leaf photosynthesis measurements is summarized in Table 1.

Fig. 2. A setup for leaf photosynthesis measurement using a portable photosynthesis system in a growth chamber and light measurement by a spectroradiometer.

Data analysis. The measured P_n under varying PFDs (quantified either as PPFD or ePPFD) were fitted into a common P_n model [$P_n = A_{max} \times (1 - \exp(-IS \times PFD) - R_d)$], where A_{max}, IS, and R_d are maximum photosynthetic rate, initial slope, and dark respiration, respectively. The nonlinear regression analysis was conducted for estimating the model parameters using the nls function in R software (ver. 4.2.2; R Foundation for Statistical Computing, Vienna, Austria). Based on each P_n model, the LCP was found as the PPFD or ePPFD at $P_n = 0$. With light qualities during acclimatization and leaf photosynthesis measurement as the main effect, two-way analysis of variance was performed using R software (ver. 4.2.2, R Foundation for Statistical Computing). The mean separation of these parameters was achieved with Tukey's honestly significant difference test using the agricolae package in R.

Results and discussion

The P_n increased as the light intensity (PPFD or ePPFD) increased (Supplemental Figs. 1–4) and fit well in the P_n model for all cases ($R^2 > 0.94$). The LCPs ranged from 10.9 to 27.4 μmol·m^{-2}·s^{-1} and 17.6 to 36.4 μmol·m^{-2}·s^{-1} when PPFD or ePPFD, respectively, was used for the P_n model. The LCP levels in our experiment are similar to those reported for tomato (13.0–36 μmol·m^{-2}·s^{-1}) (Gómez and Mitchell 2016; Nederhoff and Vegter 1994; Xiaoying et al. 2012). Regardless of the main effect, the LCP was greater when the ePPFD was used for the P_n model. The higher LCP with

Table 1. Light quality conditions during acclimatization and leaf photosynthesis measurement in terms of far-red (701–750 nm) to extended photosynthetically active radiation (400–750) ratios.

Light treatments: acclimatization → photosynthesis measurement (% FR)	Light quality during acclimatization over 3 d (% FR)	Light quality during leaf photosynthesis measurement
2 → 2	2	2
44 → 2	44	2
2 → 44	2	44
44 → 44	44	44

FR = far-red.

Table 2. Summary of two-way analysis of variation with mean ± standard deviation of the light compensation point as influenced by differences in far-red (701–750 nm) to extended photosynthetically active radiation (400–750 nm) ratios during the acclimatization and photosynthetic light response curve measurements (n = 20).[i]

Factor	FR-to-ePAR ratio	R_d ($\mu mol \cdot m^{-2} \cdot s^{-1}$)	PAR-based LCP ($\mu mol \cdot m^{-2} \cdot s^{-1}$)	ePAR-based LCP ($\mu mol \cdot m^{-2} \cdot s^{-1}$)
Light quality during ACC	2% FR	0.92 ± 0.16 b[ii]	18.0 ± 4.5 b	23.9 ± 4.0 b
	44% FR	1.10 ± 0.12 a	20.8 ± 4.5 a	27.6 ± 3.6 a
Light quality during LRC	2% FR	1.00 ± 0.14 a	23.2 ± 2.9 a	23.7 ± 3.0 b
	44% FR	1.02 ± 0.19 a	15.6 ± 2.4 b	27.8 ± 4.3 a
Significance	—	ACC*** and LRC^{NS}	ACC*** and LRC***	ACC** and LRC***

[i] The light compensation points (LCPs) were estimated from either photosynthetically active radiation (PAR; 400–700 nm) or extended photosynthetically active radiation (ePAR)-based light response curves (LRCs).

[ii] NS, **, *** Nonsignificant or significant at $P < 0.01$ or 0.001, respectively. The analysis of variance showed no significant effect of replication or interaction between the two main factors.

ACC = acclimatization; FR = far-red; R_d = dark respiration.

ePPFD is a result of the inclusion of FR light, as PAR increases ePPFD levels in the LRCs, which alters the initial slope in the exponential equation and, consequently, the LCP (Walters and Reich 2000). Recent studies have reported a positive or equal contribution of FR photons to photosynthesis (Zhen and Bugbee 2020). Zhen and Bugbee (2020) demonstrated that canopy photosynthesis in lettuce was equivalent when comparing different FR ratios under the same ePPFD level, including photons from the ePAR spectrum, created by white and FR LEDs. In addition, they observed reduced net and gross photosynthesis in *Zea mays* and *Helianthus annuus* when FR photons were filtered from sunlight (Zhen et al. 2022). The contribution of FR photons to photosynthesis is associated with balancing the excitation between photosystems I and II. FR photons enhance the excitation of photosystem I, leading to a synergistic effect with the overexcitation of photosystem II (Ruban 2015; Zhen and van Iersel 2017).

The effects of FR ratios during acclimatization and photosynthesis measurement on the LCPs are shown in Table 2. Acclimatization under 44% FR light resulted in significantly higher LCPs for both PAR ranges compared with those acclimatized under 2% FR light. The high FR-to-ePAR ratio also increased R_d significantly, which is likely the reason why the LCPs were greater when acclimatized under a high FR ratio. In contrast, a typical shade response is known to occur under high FR and low PAR conditions, which generally lowers the LCP to maximize the net C gain during photosynthesis under the limited-light condition (Craine and Reich 2005; Kabir et al. 2023; Sterck et al. 2013; Wang et al. 2023). A decreasing R_d was also observed when plants were acclimatized under low PPFD levels without FR photons (Frantz and Bugbee 2005; Nemali and van Iersel 2004). The increase in the R_d and LCP observed for plants acclimatized under high FR photons in our experiments could not be explained with these typical low-light or FR-light responses.

The effect of FR photon ratios during P_n (LRC) measurements differed between PAR-based and ePAR-based LCPs. The ePAR-based LCP was 17.3% higher under the 44% FR treatment compared with the 2% FR treatment. The difference in the LCPs between the 44% and 2% FR treatments is likely explained by the contribution of FR photons on photosynthesis following the effect of higher FR light during acclimation in our study, similar to that observed by Zhen and Bugbee (2020). In contrast, in the PAR-based LRCs, the 2% FR treatment resulted in a 48.7% higher LCP than that obtained under the 44% FR treatment. The higher LCP from the 44% FR treatment can be attributed to the exclusion of FR photons from the definition of PAR. The change in the LCPs by different PAR definitions indicates that the LCPs measured with PPFD can significantly underestimate the light level that compensates the photosynthesis, especially when a significant proportion of the light is FR.

The contrasting trends of LCPs derived from PAR- and ePAR-based LCPs suggest the importance of defining PAR accurately, especially in light environments containing both PAR and FR photons. Our findings indicate that excluding FR photons from PAR can lead to significant misinterpretations of photosynthetic characteristics as well as light interception under given light conditions. Modern greenhouses are often equipped with high-power electrical lighting with little or no FR photons, which creates a wide range of FR ratios depending on the incident solar radiation. Zhen et al. (2021) proposed revising the definition of PAR to include FR photons based on their findings showing an equal contribution of FR photons to photosynthesis, when FR photons are present simultaneously with PAR photons. Of interest, they proposed that the equal contribution of FR photons to photosynthesis is likely valid only up to a 30% FR fraction in the ePPFD levels, whereas our FR ratio was 44%, similar to the level observed under a dense tomato plant canopy. It is unclear whether an additional increase in photosynthesis occurred with FR-to-ePAR ratios greater than 30%. Given the role of FR light in photosynthesis, considering both PAR and FR photons in the definition of PAR would allow a more accurate assessment of plant responses to light. Our study supports this perspective by demonstrating the importance of including FR photons in PAR when evaluating photosynthetic parameters like the R_d and LCP.

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