Light Environment and Photosynthetic Capacities of Leaves at Different Locations within Eggplant Canopies in a Greenhouse in Ontario, Canada

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Abstract. To effectively manage crop production in a greenhouse, it is essential to understand the natural light environment and physiological responses of the plants to light. This study investigated the dynamics of photosynthetic photon flux densities (PPFD) and light quality within the canopies of greenhouse-grown eggplant (Solanum melongena) and the photosynthetic capacities of leaves at different locations within the canopies. The light environment was quantified at 0.2-m intervals within (intra-canopy) and adjacent to (extra-canopy) the crop canopy on both sunny and cloudy days within a commercial greenhouse located in Leamington, Ontario, Canada. Our results indicated a linear decline in extra-canopy PPFD on both sunny and cloudy days, but an exponential decrease in intra-canopy PPFD. The intra-canopy PPFD decreased by 91% and 76% between 0 m and 0.4 m from the canopy apex on sunny and cloudy days, respectively. The lower canopy (0.6–1.2 m) light spectrum consisted largely of far-red light, equal amounts of red light and green light, with a lower percentage of blue light. Parameters derived from leaf-level light response curves indicated that the light-saturated net carbon exchange rate, light saturation point, and light compensation point decreased as the distance from canopy apex increased, whereas quantum yield was unaffected. Thus, leaves in the lower canopy were less efficient at using high PPFD, but they displayed no deterioration of photosynthetic machinery. Based solely on photosynthetic capabilities, leaves between 0 and 1.0 m from the canopy apex should not be removed to decrease the total plant sink strength.

Winter production of vegetables in greenhouses located in northern latitudes is limited by the amount of solar radiation present, attributable to shorter days and a lower sun angle (Korcynski et al. 2002). The use of supplemental lighting in greenhouses during the winter months has been shown to significantly increase crop yield through the utilization of artificial light to enhance low natural light levels (Hao et al. 2018; Lanoue et al. 2021, 2018b; Olle and Virsile 2013). However, to optimize supplemental light use efficiency, it is important to understand the existing natural light environment. This discussion should incorporate an approach to improve the existing light environment and overall light use efficiency by characterizing light gradients throughout the crop canopy.

Research of the light environment within a greenhouse has mainly focused on leaf-level measurements (Massa et al. 2015; Paradiso et al. 2011; Sun et al. 1998) or was based on computer-generated models that aimed to predict how light can traverse the crop canopy (Pao et al. 2021; Schipper et al. 2023; Wiechers et al. 2011; Zhang et al. 2020). Although commercial vegetable greenhouses attempt to grow plants as uniformly as possible, there is still substantial variability among individual plants. Light variation caused by structural shading also exists, which is difficult to account for using logistical formulas or software (Kittas et al. 1999). There is a lack of research considering real-world plant variations, leaf angles, mutual shading, or reflectance.

Both light photosynthetic photon flux density (PPFD) and spectral quality play important roles in plant activities such as photosynthesis, plant morphology, and overall yield (Zheng and Llewellyn 2022). Therefore, all aspects of transmitted light through the plant canopy are important to note while characterizing the whole-canopy light environment. Although existing literature is focused on how light is altered through transmission of a single leaf (Massa et al. 2015; Paradiso et al. 2011), light transmission was determined in an artificial environment where natural factors like leaf angle, leaf arrangements, or leaf maturity were disregarded.

It is common practice in commercial greenhouses to remove senescing lower canopy leaves because of an increased risk of disease (Thakur et al. 2018). These lower canopy leaves are removed when signs of damage or senescence are apparent. Pruning in greenhouse vegetable crops is also used to balance the source and sink strength of the plant (Gifford and Evans 1981; Smith and Stitt 2007; Wardlaw 1990). Li et al. (2015) found that tomato plants are source-limited during fruiting; therefore, removing sink tissue during this period can benefit net photosynthetic production and fruit yield. Leaves are often considered sources of carbohydrates when fully emerged, but they can also increase sink strength and compete for carbohydrates if they receive irradiances below their light compensation point (Iqbal et al. 2012). Therefore, measurements of light transmission and LCP of leaves throughout the canopy can aid in the development of pruning practices that remove unproductive leaves to balance source–sink strength.

Intra-canopy and dynamic lighting strategies are being developed to optimize energy use for crop production. Intra-canopy lighting refers to the use of supplemental lights within the crop canopy, and dynamic lighting strategies involve the use of multiple photon flux densities (PFDDs) and/or spectra that are altered based on environmental conditions to improve crop growth and energy efficiency (Hao et al. 2012; Kalaitzoglou et al. 2019; Kumar et al. 2016; Pinho et al. 2013). Understanding the relationship between the natural light environment and leaf physiological responses can help develop a baseline for these types of lighting strategies; therefore, they can be implemented more efficiently.

To diversify their crop portfolio, Canadian greenhouses are growing new fruit and vegetable crops, such as eggplant (Solanum melongena). However, previous research has mostly targeted tomatoes, cucumbers, and peppers. Therefore, this research intended to add to our limited knowledge of ideal light
conditions for greenhouse eggplant while providing growers with guidance related to the optimization of canopy structure, particularly pertaining to the optimization of light for winter eggplant production.

The objectives of this study were to characterize the intra-canopy and extra-canopy light environment of eggplant in a commercial greenhouse in Ontario, Canada, to characterize leaf photosynthetic capabilities and their responses to light at different locations throughout the plant canopy, and to generate data to provide preliminary scientific guidance for crop management such as de-leafing and intra-canopy lighting.

Materials and Methods

Plant culture. This study was conducted in a commercial glass greenhouse (lat. 42.07°N, long. 82.58°W, elevation 173 m) with a single layer of polyethylene suspended at gutter height (~2.5 m). Eggplant cv. Jaylo seedlings (65 days old) were transplanted on 29 Dec 2021, with a planting density of 4.1 plants/m² into inground trowels filled with a proprietary growing medium consisting of mainly coconut coir and peat. The glasshouse contained six rows of plants with 478 m² of total growing area. The plants were trimmed to two main stems per plant, and sucker branches were pruned to one fruit cluster per branch. Each main stem was supported by twine to a top wire at a height of 2 m from the surface of the growing media. Twine supports were shifted along the top wire, and plants were simultaneously tilted/lowered every 2 weeks to allow for plant stems to grow longer than the 2-m tall top wire. Dead and old leaves were removed every 3 weeks, and all leaves within 0.5 m from the growing media surface were removed on 10 Apr 2022 [102 d after transplanting (DAT)]. Side shoots were pruned just beyond the first cluster of flowers to support one fruit set, and eggplant fruits were harvested every other day when they reached 250 g. The average temperatures within the greenhouse were maintained between 34.4 °C (118 DAT) and 23.4 °C (240 DAT) during the day and 19.7 °C (18.2–23.4 °C) at night. The average greenhouse relative humidity levels were 69.3% (50%–83%) during the day and 74.4% (58%–90%) at night. Greenhouse CO₂ was maintained between 344 and 699 ppm from the growing media surface to number 60% to 70%, and PPFDs of 0, 5, 10, and 15 μmol·m⁻²·s⁻¹ to calculate the LCP and quantum yield (QY), at which LCP is equal to the lowest PPFD required to reach a zero NCER (x-intercept). The QY is equal to the slope of the line (m), which is the molar ratio between the net carbon assimilated and photons absorbed (Φ). Then, A_max, LSP, QY, and LCP were plotted against DFA. The A_max and LSP were fitted with an exponential decay regression Y = Y0·e⁻ᵃ·ξ, whereas Y represents the NCER and PPFD, respectively, and ξ, e, and k represent DFA, Euler’s constant, and growth rate respectively. The LCP was fitted with a linear regression.

Statistical analysis. The trial was designed as a factorial with two fixed factors: DFA and the ambient light condition. Outliers within each DFA interval and ambient light condition were assessed and removed using the interquartile range exclusive method in Excel (Microsoft Office version 16.66.1; Microsoft, Redmond, WA, USA). All data were checked for normality, homogeneity, and heteroskedasticity using RStudio (RStudio version 1.4.1717; Boston, MA, USA). The number of leaves and soil plant analysis development (SPAD) values were statistically analyzed using RStudio by an analysis of variance, followed by an estimated marginal means fixed effects model with a Tukey adjustment to test for significant differences between all DFA values (α = 0.05). Regression lines were generated for the parameters of PPFD, light spectrum, and photosynthetic capacity using graphing software (Pvision version 9.5; GraphPad Software, San Diego, CA, USA) and plotted when significant (P < 0.05) (Supplemental Table 1).

Results

Photosynthetic photon flux density. The spatial distribution of PPFD trends remained consistent throughout the growth of eggplant plants. Figure 1 displays a representative distribution of PPFD throughout the crop canopy measured at 105 and 106 DAT. Both extra-canopy and intra-canopy PPFDs decreased as DFA increased. Extra-canopy PPFDs followed a linear regression in relation to DFA, whereas intra-canopy PPFDs followed an exponential regression. The greatest decrease in intra-canopy PPFD was between 0 and 0.2 m DFA under both sunny and cloudy conditions. Intra-canopy light reached a minimum PPFD at a DFA of 0.4 to 0.6 m.

Light spectrum. The spectral distribution of intra-canopy light followed a similar trend throughout eggplant growth under both sunny and cloudy conditions. Although the spectral
Photosynthetic capacity assessment. The parameters derived from leaf light response curves (Supplemental Fig. 3) assisted in the assessment of photosynthetic capacity of individual leaves within the eggplant canopy. These parameters demonstrated similar trends throughout the growth of eggplant and are represented in Fig. 3. The A_max, LSP, and LCP decreased as DFA increased, whereas QY was not significantly affected by DFA.

Plant morphology and leaf chlorophyll. Plant morphology patterns generally remained constant as the plants grew and developed. Significantly more leaves resided at the median DFA within the plant canopy. The highest densities of leaves were observed at a DFA of 0.2 to 0.4 m after the first two measurements (Fig. 4A, B), and between 0.4 and 0.6 m in the last readings (Fig. 4C). The leaf chlorophyll content decreased as DFA increased (Fig. 4D–F). The greatest SPAD readings were found between 0 and 0.2 m in the initial measurements (Fig. 4D), and between 0 and 0.4 m in the latter readings (Fig. 4E, F). Generally, SPAD readings remained higher at a lower DFA, especially during the latter readings. Leaf temperature was not significantly different at any DFA (data not shown), with means of 26.1 ± 0.2°C, 19.3 ± 3.2°C, and 23.9 ± 4.0°C at the time of each measurement.

Discussion

Light environment. Photosynthesis is largely influenced by the light that a plant’s leaves are exposed to; acclimation to long-term light history shapes the photosynthetic capacity and respiration rate, thus setting the boundaries to which photosynthetic mechanisms can respond to different light intensities in the short term. Furthermore, the current light exposure determines the current photosynthetic rate. Because of Canada’s northern latitude, light is often the defining factor that determines the greenhouse crop yield during winter months; this statement is also applicable to many countries in northern latitudes (Korczynski et al. 2002). Therefore, quantifying how light interacts with crop canopies can be fundamental to improving winter crop growth and production among these regions.

Few studies have attempted to quantify how much light is present throughout herbaceous plant canopies within a greenhouse environment (Kaiser et al. 2019; Kasperbauer 1971). Light absorption has often been characterized through single leaves (Balegh and Biddulph 1970; Inada 1976; Maas and Dunlap 1989; Paradiso et al. 2011), but the leaf level results should not be used to predict the whole-plant level of light transmission (Paradiso et al. 2011). Although previous studies have modeled plant canopies through predictive computer generations (i.e., ray tracing and three-dimensional modeling) (de Visser et al. 2014; Diëman et al. 2019; Hintz et al. 2019; Kim et al. 2020; Schipper et al. 2023), it is difficult to accurately model the true light environment because of the complex and variable nature of canopy structures’ interactions with light. Therefore, the physical data collected throughout this study could be used in conjunction with predictive computer-generated models to further understand plant–light interactions.

Each leaf in the eggplant canopy can experience a wide range of PPFDs, which rapidly vary throughout the day and have pronounced effects on leaf-level photosynthesis (van Westreenen et al. 2023). In general, leaves at the top of the canopy with a lower DFA received more direct extra-canopy light with minor shading, whereas leaves lower in the canopy experienced mostly intra-canopy light that was transmitted or reflected, with few sites of direct light. Therefore, a leaf at a particular DFA may receive a PPFD anywhere between the measured intra-canopy and extra-canopy PPFDs, but leaves lower in the canopy often received a greater proportion of intra-canopy light. Under cloudy conditions, intra-canopy PPFD in the lower canopy closely followed the extra-canopy PPFD, whereas the extra-canopy PPFD on sunny days is much higher than the intra-canopy PPFD. This increased variability on sunny days is most likely caused by the increase in a strong mutual shading effect; as natural light increases, a larger discrepancy between intra-canopy PPFD and extra-canopy PPFD is expected.

The eggplant canopy structure exhibited the highest density of leaves between 0.2 and 0.6 m. This elevated leaf density increased mutual leaf shading and likely explains why the intra-canopy PPFD decreased by more than 80% at DFA values more than 0.4 m. The eggplants may also acclimatize for this decreased PPFD in the lower canopy because we observed significantly lower chlorophyll...
Fig. 2. Spectral ratio of blue light (400–499 nm), green light (500–599 nm), red light (600–699 nm), and far-red light (700–780 nm) relative to the total photosynthetic photon flux density (PPFD) (400–780 nm). Measurements were obtained at 0.2-m vertical intervals within (intra-canopy) the Solanum melongena cv. Jaylo canopy. Measurements were obtained on a cloudy day [13 Apr 2021; 105 days after transplanting (DAT)] (A) and a sunny day (14 Apr 2021; 106 DAT) (B). The data points represent the means of replicates (n = 15), and the bars represent ±SE. A line indicates significant regression (P < 0.05).

Concentrations at DFA values more than 0.4 to 0.8 m.

Because light-emitting diode supplemental lighting is generally used in greenhouses to compensate for the low natural PPFD during winter, growers and light manufacturers must consider which specific wavelengths or combination of wavelengths are best for their crop and environment. Single leaf studies that evaluated photosynthetically active radiation (PAR) absorption in green leaves have determined that red light and blue light are well-absorbed, whereas the absorption of green light is considerably lower (Dielman et al. 2019; Hogewoning et al. 2012; Inada 1976; McCree 1971; Paradiso et al. 2011). Although green light is not absorbed as readily as other wavelengths at the leaf level, it is not valid to assume that green light is in abundance within the lower canopy. Our results indicated no significant difference in green light transmission relative to blue and red wavelengths (Fig. 2). This differs from the results of Smith et al. (2017), who found higher green light ratios relative to blue light and red light within and outside bean canopies.

Intra-canopy lighting strategies are often used within vegetable crop greenhouses to improve the lower canopy light environment. Intra-canopy lighting promotes a more uniform light environment that can benefit crop biomass and fruit production (Kumar et al. 2016; Schipper et al. 2023; Trouwborst et al. 2011b). Our data demonstrate the greatest decline in intra-canopy PPFD from a DFA of 0 to 0.6 m, whereas no significant decline in the QY was recorded (Figs. 1 and 3C). This portion of the plant canopy (0.4–0.6 m) also had the greatest density of leaves (Fig. 4A–C). Therefore, intra-canopy lighting positioned at a DFA of 0.6 m may be an optimal position to improve light capture and uniformity because this region of the canopy includes the most drastic decrease in PPFD while containing the greatest leaf density.

Photosynthesis and leaf location. Productivity of fruiting crops relies on the plant’s ability to photosynthesize and translocate photosynthetic assimilates to actively growing fruit (Iqbal et al. 2012; Lanoue et al. 2018a). When focusing solely on crop photosynthesis and fruit growth, achieving a steady yield is possible only through the continuous preservation of a balanced sink–source strength (Marcelis et al. 2004). Therefore, it is important for growers to identify the source–sink strength of their crop. Artificial adjustment to this relationship can be achieved through plant pruning or introduction of intra-canopy lighting to regulate source/sink homeostasis, growth, and yield.

Generally, a leaf that receives a PPFD below its LCP facilitates net negative carbon production; therefore, it should be pruned to remove a competing, nonmarketable sink tissue. Based on this, our data suggest that no leaves should be pruned because the PPFD remained above the LCP at each DFA. However, this could be attributable to the greenhouse’s existing pruning practice that involved removing the lower 0.5 m of leaves after 102 DAT. It is also important to note that plant organs may provide benefits to the plant in addition to photosynthetic products. Leaves act as sources of mobile nutrients for the development of sink tissue. Thus, pruning leaves should not solely rely on photosynthetic efficiency; other factors including nutrient storage, airflow restriction, and impact on increased disease susceptibility should also be considered.

We observed a decline in A_{max} and LSP values as DFA increased (Fig. 3), meaning that leaves lower in the plant canopy have a lower capacity for photosynthesis at elevated PPFDs. Eggplants were grown unidirectionally, with all side shoots and suckers pruned; therefore, it is viable to correlate DFA to leaf age. With this correlation, our results were similar to those of Besford (1993), who also found a decreased capacity for photosynthesis in older tomato leaves. However, the decrease in photosynthetic capacity cannot be explained solely based on leaf age because older leaves with a greater DFA also received a lower PPFD relative to the top of the canopy. Burkey and Wells (1991), Petersen et al. (2010), and Trouwborst et al. (2011a) provided evidence that leaf senescence and decreased photosynthetic capacity are more closely related to light conditions and demonstrated how a poor light environment initiates senescence. In a practical setting, it is likely that both leaf age and a poor light environment [lower PPFD levels deep within the canopy] (Fig. 1) caused by mutual shading within the plant canopy led to the reduced photosynthetic capacity and SPAD values (Figs. 3 and 4D–F) observed during this study.

Despite the decline in PPFDs relative to the DFA, the QY was unaffected by the DFA, and leaves with a greater DFA expressed a lower LCP (Fig. 3). Thus, leaves in the lower canopy may have a lower capacity for producing assimilates for the plant, but they photosynthesize as efficiently as higher
canopy leaves at lower PPFDs. This does not indicate breakdown of the photosynthetic machinery; instead, it indicates an inefficiency to use higher PPFDs. Because the average PPFD decreased drastically at a DFA of more than 0.2 m (Fig. 1), it may be possible to increase overall plant productivity by improving the light environment within this portion of the plant canopy. Therefore, we believe that improving the light environment within this region would provide increased whole-plant productivity by improving the light environment within this portion of the plant canopy. Therefore, we believe that improving the light environment within this region would provide increased whole-plant photosynthesis, leading to increased growth and yield.

Conclusion

Overall, this study presented the dynamics of PPFDs and light quality throughout greenhouse-grown eggplant canopies. We provided evidence that does not support the notion that green light exists in a higher concentration within the lower plant canopy compared with other photosynthetically active radiation wavelengths. We observed a steep decline in the PPFD from a DFA of 0 to 0.4 m; however, the leaves between 0 and 1.0 m exhibited no difference in QY. Thus, providing supplemental light to this region may improve whole-plant photosynthesis. Based solely on photosynthetic capabilities, we can also advise against removing healthy leaves within the lower canopy because these leaves never received PPFDs below their LCP. Future research should consider quantifying the intra-canopy light environment of greenhouse crops with the addition of supplemental light and assessing how supplemental light impacts photosynthetic capabilities throughout the canopy.

References Cited


