Light Limited Photosynthesis under Energy-Saving Film Decreases Eggplant Yield

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Abstract

Glasshouse films with adjustable light transmittance have the potential to reduce the high energy cost for greenhouse horticulture operations. Whether these films compromise the quantity and quality of light transmission for photosynthesis and crop yield, remains unclear. A "Smart Glass" film ULR-80 (SG) was applied to a high-tech greenhouse horticulture facility and two experimental trials were conducted by growing eggplant () using commercial vertical cultivation and management practices. SG blocked 85% of ultraviolet (UV), 58% of far-red, and 26% of red light, leading to an overall reduction of 19% in photosynthetically active radiation (PAR, 380 - 699 nm) and a 25% reduction in total season fruit yield. There was a 53% (season mean) reduction in short-wave radiation (385 nm to 2105 nm upward; 295 to 2685 nm downward) that generated a net reduction in heat load and water and nutrient consumption that improved energy and resource use efficiency. Eggplant adjusted to the altered SG light environment via decreased maximum light-saturated photosynthetic rates () and lower xanthophyll de-epoxidation state. The shift in light characteristics under SG led to reduced photosynthesis, which may have reduced source (leaf) to sink (fruit) carbon distribution, increased fruit abortion and decreased fruit yield, but did not affect nutritional quality. We conclude that SG increases energy and resource use efficiency, without affecting fruit quality, but the reduction in photosynthesis and eggplant yield is high. The solution is to re-engineer the SG to increase penetration of UV and PAR, while maintaining blockage of glasshouse heat gain.

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Key Points: (min 1 up to 3, each less than 140 characters without acronyms)

- Smart Glass blocks short wave radiation and decreases energy use for cooling, water use, and nutrient consumption.
- Smart Glass reduces photosynthetically active radiation limiting photosynthesis and plants acclimate to low light by altering xanthophylls.
- Smart Glass does not affect overall fruit quality, but a high fruit abortion rate reduces yield possibly through source-sink regulation.

Abstract

Glasshouse films with adjustable light transmittance have the potential to reduce the high energy cost for greenhouse horticulture operations. Whether these films compromise the quantity and quality of light transmission for photosynthesis and crop yield, remains unclear. A "Smart Glass" film ULR-80 (SG) was applied to a high-tech greenhouse horticulture facility and two experimental trials were conducted by growing eggplant (*Solanum melongena*) using commercial vertical cultivation and management practices. SG blocked 85% of ultraviolet (UV), 58% of far-red, and 26% of red light, leading to an overall reduction of 19% in photosynthetically active radiation (PAR, 380 - 699 nm) and a 25% reduction in total season fruit yield. There was a 53% (season mean) reduction in short-wave radiation (385 nm to 2105 nm upward; 295 to 2685 nm downward) that generated a net reduction in heat load and water and nutrient consumption that improved energy and resource use efficiency. Eggplant adjusted to the altered SG light environment via decreased maximum light-saturated photosynthetic rates (A_{max}) and lower xanthophyll de-epoxidation state. The shift in light characteristics under SG led to reduced photosynthesis, which may have reduced source (leaf) to sink (fruit) carbon distribution, increased fruit abortion and decreased fruit yield, but did not affect nutritional quality. We conclude that SG increases energy and resource use efficiency, without affecting fruit quality, but the reduction in photosynthesis and eggplant yield is high. The solution is to re-engineer the SG to increase penetration of UV and PAR, while maintaining blockage of glasshouse heat gain.

Plain Language Summary

Greenhouse horticulture delivers higher outputs than field production, but high energy requirements and costs may be a barrier for many growers. Innovative glass technologies such as 'Smart Glass' (SG) with low thermal transmission will improve the efficiency of greenhouses, with less energy required to maintain optimal growth conditions. SG is designed to block the light wavelengths generating heat and transmit most of the light used by plants for photosynthesis and growth, but the impact on crop productivity and quality is unclear. We demonstrate the benefits (reduced resource use) and disadvantages (lower yield) of eggplant grown in SG. Our findings suggest that the spectral characteristics of current SG should be modified to maintain resource use benefits, while improving yield, for future food production.

1 Introduction

With declining cultivable agricultural land (Roser & Ritchie, 2019) and growing food demand, crop production depends on higher yield through technological advancements and crop improvement. Some of the major challenges of crop production, including limited resources, high cost of energy, and adverse effects of climate change, can be addressed by protected cropping (Rigby, 2019) of horticultural crops in controlled greenhouse environmental conditions. The efficient use of energy in greenhouses has been addressed (Ahamed et al., 2019; Bakker et al., 2008; Cuce et al., 2016; Marucci & Cappuccini, 2016), but few studies have considered the use of innovative glass technologies with selective light transmittance to reduce energy costs and investigate the impacts of altered light environment on plant growth and photosynthesis (Loik et al., 2017). Most of the studies have investigated the impact of artificial light, which may be required for growth and production in a temperate climate zone with low light levels in winter (Goto, 2003; Ouzounis et al., 2015; Park & Runkle, 2018; Yang et al., 2017). However, few studies have tested glazing materials, screens or synthetic films in a natural light environment to reduce the heat load in greenhouses in summer with long periods of hot temperatures and high solar radiation in subtropical and tropical climate zones (Hao & Papadopoulos, 1999; Kwon et al., 2017; Loik et al., 2017). The study by Loik et al., (2017) investigated the use of wavelength-selective photovoltaic systems (WSPVs), which absorbed some of the blue and green wavelengths of the solar spectrum for electricity generation but transmitted remaining wavelengths including most of the red light, on tomato production. They measured the effect of altered light on photosynthesis and yield and suggested further studies on assessing photosynthesis in different crops and climates, in response to altered light environments (Loik et al., 2017).

Plants have access to 49 % of total solar energy within the photosynthetically active spectrum, while 51% of total solar energy is unavailable (Zhu et al., 2010) which can cause cost intensive heat build-up in greenhouses. Energy-efficient designs for high-tech greenhouses are expected to save up to 80% of energy for greenhouse operations (Ahamed et al., 2019; Andersson & Nielsen, 2000; Cuce et al., 2016; Hemming et al., 2011, 2012; Taki et al., 2018). Innovative glass technologies with adjustable light transmittance and semi-transparent photovoltaic glass can greatly reduce energy cost in a commercial greenhouse, and potentially become energy self-sufficient using renewable energy (Loik et al., 2017). Novel glazing and covering materials, such as the commercially available window film ULR-80 ("Smart Glass", SG) with low emissivity, can block the light that mainly contributes to heat, but transmit most of the wavelengths required by plants for photosynthesis and growth. In addition, novel materials with insulation properties trap heat during winter and save energy on heating. SG could significantly contribute to reducing the energy costs in greenhouse operations. Glazing and/or the application of films can change light intensity and spectral quality, thereby having an adverse effect on plant growth, photosynthesis, biomass partitioning, yield and quality (Hao & Papadopoulos, 1999; Loik et al., 2017). Theoretically, blocking radiation not required for photosynthesis can decrease heat build-up in the glasshouse, and hence reduce the energy cost required to maintain cooling in summer. However, this theory of photonics and material science still has not been properly tested in a high-tech greenhouse with a commercial horticultural crop over two seasons.

Plants respond to light intensity, spectral quality, and photoperiod (Babla et al., 2019; Ballaré & Pierik, 2017; Cazzonelli et al., 2020; Poorter et al., 2019). At the leaf level, blue photons are used less efficiently than orange and red photons in photosynthesis (McCree, 1971; Inada, 1976; Bugbee, 2016). The change in spectral quality, especially the ratio of red to far-red light, can affect plant phenology and development of buds, flowers, and fruits (Cerdán & Chory, 2003; Ballaré & Pierik, 2017). Plants cope with light fluctuations via adjustments at the whole organism, cellular, biochemical and molecular levels (Ruban, 2009). The light energy absorbed by pigments in the photosystems is used to drive chemical reactions for photosynthesis, and dissipate excessive light energy from Photosystem II (PSII) via chlorophyll *a* fluorescence and by several other thermal dissipation mechanisms (Baker, 2008; Logan et al., 2007). Photosystems I and II are composed of varying amounts of Chl a, Chl b, β-carotene and xanthophylls (lutein, antheraxanthin, violaxanthin, and neoxanthin) which facilitate quenching of excess PSII energy. Carotenoid pigments play an important function in facilitating photosynthesis and photo-protection, thereby contributing to an optimal carbon balance from source (leaf) to sink (fruit) (Baranski & Cazzonelli, 2016; Demmig-Adams et al., 2014). A reduction in photosynthesis will lower the supply of carbon in source leaves and carbohydrate translocation to sinks such as fruits, thereby affecting fruit set (Aloni et al., 1996; Turner & Wien, 1994). Limitations in photosynthesis can decrease crop yield and quality (Hao & Papadopoulos, 1999), depending on the light environment.

The primary objective of this study was to determine the impact of SG on light quality and quantity, and subsequently on photosynthetic carbon assimilation, leaf biochemistry, yield and nutritional quality of eggplant (*Solanum melongena*) using a high-tech glasshouse facility. We used standard management practices during two greenhouse trials, conducted during high-light and long photoperiod summer growing periods, on a commercial eggplant cultivar (cv Tracey) to assess the efficacy of SG on reducing resource use while minimising negative impacts on crop yield and quality.

2 Materials and Methods

2.1 *Facility description and glass specifications*

The first SG trial was conducted in the state-of-the-art glasshouse facility designed for research and commercial production of horticultural crops at Western Sydney University, NSW, Australia (Figure S1). The 1800 m^2 advanced glasshouse facility established in late 2017 is equipped with Priva software and hardware (Priva, The Netherlands) to monitor and control temperature, humidity, nutrients, CO_2, and irrigation. Glasshouse air temperature is controlled by chilled air blowers, curtains and opening vents. Relative humidity (RH) is controlled using a humidification system, and air temperature is partially controlled using hot water circulation through radiant pipes. We used four 105-m^2 research bays with precise environmental control of atmospheric CO_2, air temperature, RH, and hydroponic nutrient and water delivery. Each research bay included 6 gutters, used to deliver nutrients and water, which support 120-150 plants.

Two research bays were fitted with HD1AR diffuse glass (70% haze; control bays) and two research bays had HD1AR diffuse glass, but were also coated with ULR-80 window film (Solar Gard, Saint-Gobain Performance Plastics, Sydney, Australia). The SG film ULR-80 (Table S1) is a potentially suitable glazing material for greenhouse crop production. It has low thermal emissivity (0.87) which blocks the light that mainly contributes to heat, but transmits most of the wavelengths of light used by plants for growth in the PAR region. According to the manufacturer specifications, SG blocks ~88% light in the infrared (IR) and far-infrared (FIR) region between 780 nm - 2500 nm; and >99% light in the ultraviolet (UV) region between 300 and 400 nm. In addition, SG blocks 43 % of total solar energy with 40% transmission, 54% absorption and 6% reflectance. The two control research bays consist of roof glass (70% diffuse light) and wall glass (5% diffuse light) (Table S1).

2.2 *Plant growth and management*

Solanum melongena (*cv*. Tracey eggplant grafted on tomato *cv*. Kaiser stems) was the first horticulture crop tested under the SG for two experiments (Experiment 1- January 2018 to July 2018 and Experiment 2 - September 2018 to March 2019). For each experiment, six-week-old nursery-grown seedlings were transplanted in Rockwool slabs and transferred into two control hazed glass (Control) and two SG (Treatment) bays. Each bay had 6 gutters (length 10.8 m, width 25 cm, AIS Greenworks, Castle Hill, Sydney, NSW, AUS) with 10 Rockwool slabs (90 × 15 × 10 cm, Grodan, The Netherlands) per gutter. Three plants per slab were planted in the four middle gutters, and two plants per slab were planted in the two side gutters and served as buffer plants. A total of 160 plants were grown in each chamber, but all measurements were performed on the 120 plants grown in the four middle gutters to avoid edge effects. Plants were grown at standard growth conditions under natural light (as described in Table S2 and Figure S2) and were provided non-limiting nutrients and water by the Priva computer-programmed fertigation (nutrients and water) system. Three stems were selected to grow from each plant with weekly pruning and cutting according to commercial practices of eggplant production for vertical protected cultivation. Each stem was considered as an individual plant for replication and all measurements were performed per stem.

2.3 *Light environment measurements*

Light quality and quantity were measured using a portable spectroradiometer (PS300, Apogee Instruments, Inc., Logan, UT, USA) and a PAR sensor (LI-190SZ Quantum Sensor, LI-COR) at the roof level during both experimental trials. Except for the spectroradiometer, all other sensors continually logged data providing output as 5-minute averages. Additional sensors including hobo pendant temp/light data logger (UA-002-08, Instrument Choice, Dry Creek, SA, AUS), PAR (LI-190R-SMV-50 Quantum Sensor, LI-COR), net radiometer (SN-500, Apogee Instruments) and diffuse light sensor (BF5 sunshine sensor, Delta T Devices) were deployed to measure detailed light profiles during the second experimental trial. Three hobo pendant temp/light data loggers (at the base, middle and top positions of the canopy), 5 PAR sensors (at canopy level) and a net radiometer were installed in each chamber. The diffuse light sensors were installed in one control and one SG chamber.

2.4 *Energy and nutrient savings calculations*

The Priva system continuously records energy expenditure on cooling (kW) using water flow, the temperature of the water before entering the chiller, and after exiting the chiller. Each of the research bays was cooled via two 1.2 kW Fan Coil Units (FCUs). Chilled water, from one of the two 75 kW chillers is supplied in a closed loop to each of the two FCUs in each room. The chilled water flows through these two units and is then returned to the 200,000 L storage tank. Priva records the supply and the return temperature of chilled water in each room. The meters do not measure the actual energy in kWh, unlike a meter for electricity, but can be used to calculate an energy value based on three variables: (1) water flowing through the flow meter; (2) temperature of the supply chilled water; and (3) temperature of the return chilled water. It does not record the ON/OFF of the FCUs, but if it reads a significant difference in the temperature of the supply and return, it sends a pulse to Priva. All data are based on the same reading, which allows us to directly use these numbers to determine the energy consumption. The Priva system also continuously records fertilizer and water supply to the irrigation system, and the irrigation water that subsequently enters the drainage system. The net consumption of fertilizer and water is determined using supply and drain values.

2.5 *Plant growth and productivity measurements*

Plant growth and yield parameters were measured periodically in both experimental trials. Replication (n) refers to the total number of plants in two control or two SG chambers. Height was measured 79, 95, 109, 121 and 137 days after planting (DAP) during Experiment 1 (n = 120, 60 stems per chamber) and 111, 125, 140 and 155 DAP in Experiment 2 (n = 24, 12 stems per chamber). Bud, flower and fruit number was measured 164, 171 and 178 DAP during Experiment 1 (n = 72, 36 stems per chamber) and 84, 98, 110, 117, 131 and 146 DAP during Experiment 2 (n = 36, 18 per chamber, respectively). Bud, flower, and fruit development were tracked weekly to test the rate of development of selected tagged buds until plants attained full development to the fruit stage and harvest. Twelve weeks after planting, eggplant fruits (only those between 350 to 450 g, representing commercial harvest mass) were harvested weekly for 18- and 16-weeks during Experiment 1 (n = 360, 180 stems per chamber) and Experiment 2 (n = 240, 120 stems per chamber), respectively. The weight of individual eggplant fruit (between 350 to 450 g) and the number of fruits per stem was recorded. Pruned biomass per chamber was weighed at 5-time points (62, 75, 85, 90 and 96 DAP) in Experiment 2.

2.6 *Leaf gas exchange measurements*

Instantaneous steady-state leaf gas exchange measurements (n > 15) were performed using a portable, open-mode gas exchange system (LI-6400XT, LI-COR, Lincoln, USA). Measurements were performed at 1500 µmol m^{-2} s^{-1} PAR with two CO_2 concentrations (400 µl L^{-1} during Experiment 1 and 500 µl L^{-1} during Experiment 2) and 25°C leaf temperature. The response of A_{sat} to light (Q) (A-Q curve) was measured at 25°C leaf temperature at eight light levels (0, 50, 100, 250, 500, 1000, 1500 and 2000 µmol m^{-2} s^{-1}) in Experiment 1 (n > 8), and 11 steps of light levels (0, 25, 50, 100, 200, 300, 400, 500, 1000, 1500 and 2000 µmol m^{-2} s^{-1}) in Experiment 2 (n > 18). The response of A_{sat} to sub-stomatal CO_2 mole fraction (C_i) (A-C_i response curve) was measured in 8 steps of CO_2 concentrations (50, 100, 230, 330, 420, 650, 1200 and 1800 µl L^{-1}) at 25°C leaf temperature during Experiment 1. Spot measurements at 25°C leaf temperature and 500 µl L^{-1} CO_2 were also performed during Experiment 2 (n > 4) using the clear leaf cuvette under natural light conditions. The light response curve means were fitted using the following equation (Ögren & Evans, 1993; Xu et al., 2019).

$$\mathrm{A} = \frac{(\phi_{max} \cdot I + A_{max}) - \sqrt{(\phi_{max} \cdot I + A_{max})^2 - 4 \cdot \Theta \cdot \phi . I \cdot A_{max}}}{2 \cdot \Theta} - R_d \quad (1)$$

where, *I*=absorbed irradiance, we assumed absorptance = 0.85; *A* = CO_2 assimilation rate at given light; R_d =dark respiration; Φ_{max} = maximum quantum yield of PSII; A_{max} = maximum light-saturated CO_2 assimilation rate; and θ = curvature factor of the light response curve.

2.7 *Spectral analysis of leaves using a spectroradiometer*

Leaf reflectance was collected using an ASD spectroradiometer (FieldSpec 4, Malvern Panalytical Ltd, Malvern, UK) with a spectral range of 350–2500 nm. The sensor has a sampling interval of 1.4 nm and 1.1 nm for 350–1000 nm and 1001–2500 nm regions, respectively. Fully expanded leaves of eggplants were collected from the plant's middle canopy from the four chambers of the glasshouse; measurements were taken with the aid of a leaf clip attached to a plant probe over a 3-hr period (9 am to noon). The leaf clip allows the leaf to touch plant probe and keep the light beam at an angle of 45 degrees. Reflectance spectral values were developed from the conversion of spectra by referencing a 99% Spectralon calibration panel (Labsphere, Inc., North Sutton, NH, USA). A reference measurement of the calibration panel was taken before the first measurement and every 30 minutes onwards. For each leaf, four measurements were taken from six different spots. Spectral index values were estimated for each leaf using the mean of these 24 measurements. Spectral indices, including Water Band Index (WBI) for leaf water content (Peñuelas et al., 1997), modified Normalised Difference Vegetation Index (mNDVI) for chlorophyll content (Fuentes et al., 2001), Photochemical Reflectance Index (PRI) for xanthophyll cycle pigments (Gamon et al., 1992), Red Green ratio (RGR) for anthocyanin content (Fuentes et al., 2001), Structure Intensive Pigment Index (SIPI) for carotenoid to chlorophyll-a ratio (Peñuelas, Baret, et al., 1995), Red Far-Red ratio (RFR) (Mascarini et al., 2006) and Normalised Phaeophytinization Index (NPQI) for chlorophyll degradation (Barnes et al., 1992) were calculated as follows,

$$WBI = \frac{R_{900}}{R_{970}} \tag{2}$$

$$mNDVI = \frac{R_{750} - R_{705}}{R_{750} + R_{705}} \tag{3}$$

$$PRI = \frac{R_{531} - R_{570}}{R_{531} + R_{570}} \tag{4}$$

$$RGR = \frac{\sum_{n=600}^{n=699} R_n}{\sum_{n=500}^{n=599} R_n} \tag{5}$$

$$SIPI = \frac{R_{800} - R_{445}}{R_{800} - R_{680}} \tag{6}$$

$$RFR = \frac{R_{680}}{R_{730}} \qquad (6)$$

$$NPQI = \frac{R_{415} - R_{435}}{R_{415} + R_{435}} \tag{8}$$

2.8 *SPAD measurements and leaf pigment analysis using high-performance liquid chromatography*

One leaf per plant from five different plants per chamber were used for SPAD measurements, and then for pigment analysis using high-performance liquid chromatography (HPLC) and gas chromatography coupled with mass spectrometry (GCMS). Three leaf discs were punched from the top, middle and bottom position of a fully expanded mature leaf using a size 10 (2.54 cm^2 leaf area) cork borer in the morning hours between 10 am to 12 pm. Samples were snap-frozen using liquid nitrogen and kept at -80^{o}C until further analysis. Fresh leaf weight was measured to calculate leaf mass per unit area (LMA) and for quantification of carotenoids and pigments. For both control and treatment, ten biological replicates were collected, frozen in the liquid N_2, and ground to a fine powder with TissueLyser (Qiagen). Carotenoids were extracted under low-light conditions with 500 µL extraction buffer (60% v/v ethyl acetate:40% v/v acetone and 0.1% BHT) and partitioned into the ethyl acetate layer by adding 500 µL of H_2O. The carotenoid-containing organic phase was separated via centrifugation and analyzed by reverse-phase HPLC (Agilent 1200 Series) using GraceSmart-C18 (4-µm, 4.6 × 250-mm column; Alltech) column. HPLC runs were performed as previously described (Alagoz et al., 2020). Pigments were identified based upon their specific retention time (RT) relative to known standards and their spectral characteristics at 440 nm (lutein - L, β-carotene - β, antheraxanthin - A, zeaxanthin - Z, neoxanthin - N, violaxanthin - V, and chlorophylls), and 286 nm (phytoene). Carotenoid quantification was performed as previously described except *cis*-carotene phytoene (Pogson et al., 1996). Phytoene is quantified by using its molar extinction coefficient and molecular weight to convert the peak area in micrograms per gram fresh weight (µg/g FW) as previously described (Britton G et al., 1995). All pigments were quantified at absorption wavelengths with maximum detection. The de-epoxidation state (DPS) of the xanthophyll cycle was calculated as DPS = (A+Z) / (A+Z+V).

2.9 *Leaf metabolite analysis using gas chromatography-mass spectrometry*

One leaf disc (from the middle position per leaf) was used for metabolite profiling using gas chromatography-mass spectrometry (GCMS). Each leaf disc was extracted using methanol/chloroform/water (700/400/800 = 1100 µL aqueous phase) by grinding with sand, followed by phase separation. A 200 µL aliquot of the aqueous phase of the extract was dried, and 50.0 µL 20 µg/mL ribitol was added followed by re-drying for 3 hours. Finally, the extract was derivatized with 40 µL MOX followed by 60 µL MSTFA before analysis by GC-MS as described previously (Lisec et al., 2006). Peaks were aligned and retention indices calculated against alkanes (Kovat's RI). Peak picking, deconvolution and ID were performed with MS-DIAL(Tsugawa et al., 2015) using generic GC-MS parameters, and MSP file for 15,302 entries of metabolites with Kovat's RI. The data matrix was manually edited to verify IDs and remove deconvolution errors Ions with m/z 73 or 147 were not used as quantification ions.

2.10 *Statistics and data analysis*

Data analyses and plotting were performed using R computer software (R Core Team, 2019). The treatment effect was analysed using one-way analysis of variance (ANOVA). The linear model involved testing of each parameter over two treatment conditions, SG and Control glass, using measurements from two SG and two control glass rooms. Replication e.g. n = 10 refers to 10 plants/stems per treatment or 5 plants/stems from each chamber. The homogeneity of variance was tested using Levene's test from the car package. The parameters showing unequal variance (with less than 0.05 probability for Levene's test) were corrected using Welch's t-test for unequal variances using the oneway.test function in R. Other packages were also used, including (but not limited to) lubridate (for effective use of dates in plots), sciplot (for plotting) and doby (for calculating means and standard errors). For GCMS data analysis unpaired T-tests were used for univariate comparisons of metabolite concentrations, with P values corrected to account for the false discovery rate due to multiple comparisons (Benjamini and Hochberg, 1995) using an Excel spreadsheet (Pike, 2011). The significance levels for ANOVA were, $P > 0.05$=ns, $P < 0.05$ = *, $P < 0.01$= ** and $P < 0.001$ = ***.

3 Results

3.1 *SG blocks UV and light wavelengths > 800 nm and significantly reduces PAR*

Spectroradiometer measurements validated manufacturer SG specifications, including blockage of UV and infrared (Table S1 and Figure 1). Although a modest reduction (-5% to -10%) in overall light transmission was expected, a considerable amount of PAR was blocked by SG with higher reduction in red-light (600 nm to 750 nm) relative to blue or green light (Table 1, Figure 1). SG blocked most of the UV (221–279 nm, -85%), and a considerable amount of red (600–699 nm, -26%) and far-red (710–850 nm, -58%), with an overall reduction of -19% PAR integrated from 280–799 nm (Table 1, and Figure 1). Thus, SG changed both the quantity and quality of the light spectrum.

Daily light integral (DLI) measured using a PAR sensor at roof level in each room was significantly reduced (-24% and -28% during Experiments 1 and 2, respectively) under SG relative to control (Table 1 and Figure 1). The reduction in DLI measured at canopy level (-2 % in SG relative to Control) was relatively lower than roof level reduction (-28% in SG relative to Control) in DLI during Experiment 2 (experiment mean). In addition, the proportion of diffuse light measured using a diffuse light sensor was -25% lower in SG relative to Control (Table 1). Short-wave radiation (385 nm to 2105 nm upward; 295 to 2685 nm downward), which mostly contributes to heat generation in the glasshouse, was measured during Experiment 2 using a net radiometer and was reduced by -53% under SG (Table 1, Figure 2). The blocked short-wave radiation consequently reduced energy expenditure on cooling (-8%) by chillers and net fertigation (fertilizer + water) consumption (-18%) under SG relative to Control (Figure 2). In addition, the visible light intensity measured in lux by the hobo pendant temp/light data logger showed significant reduction in daily average light measured at the top (-56%), middle (-70%) and bottom (-67%) of the canopy (Table S3 and Figure 3). Thus, SG blocks most of the heat-generating energy not required by plants, thereby saving energy on cooling and resource use. However, SG also considerably reduces PAR required for photosynthesis and growth.

Table 1 Summary of radiation, light intensity, canopy temperature, leaf gas exchange, and leaf mass area (LMA) measurements: One-way analysis of variance for the Smart Glass effect on radiation (n = 318) during two experiments (Exp) including daily total means for short wave (SW), diffused light, and daily light integral (DLI); light spectrum (n= 18, spectroradiometer measurements at nine locations per chamber) including UV, blue, green, red, PAR and far-red light wavelengths; instantaneous leaf gas exchange (n>15) including light saturated CO_2 assimilation rates (A_{sat}), stomatal conductance (g_s) and intercellular CO_2 concentration (Ci) and photosynthetic water use efficiency ($PWUE$); instantaneous gas exchange at natural growth light (n = 5) including average PAR measured using LI-6400 ($PARi$), CO_2 assimilation rates at growth light (A_{gl}), stomatal conductance and growth light (g_{sgl}) and photosynthetic water use efficiency at growth light ($PWUE_{gl}$); and light response curve modelled parameters (n>18) including maximum light saturated CO_2 assimilation rates (A_{max}), maximum quantum yield (φ_{max}) and curvature factor (Θ).

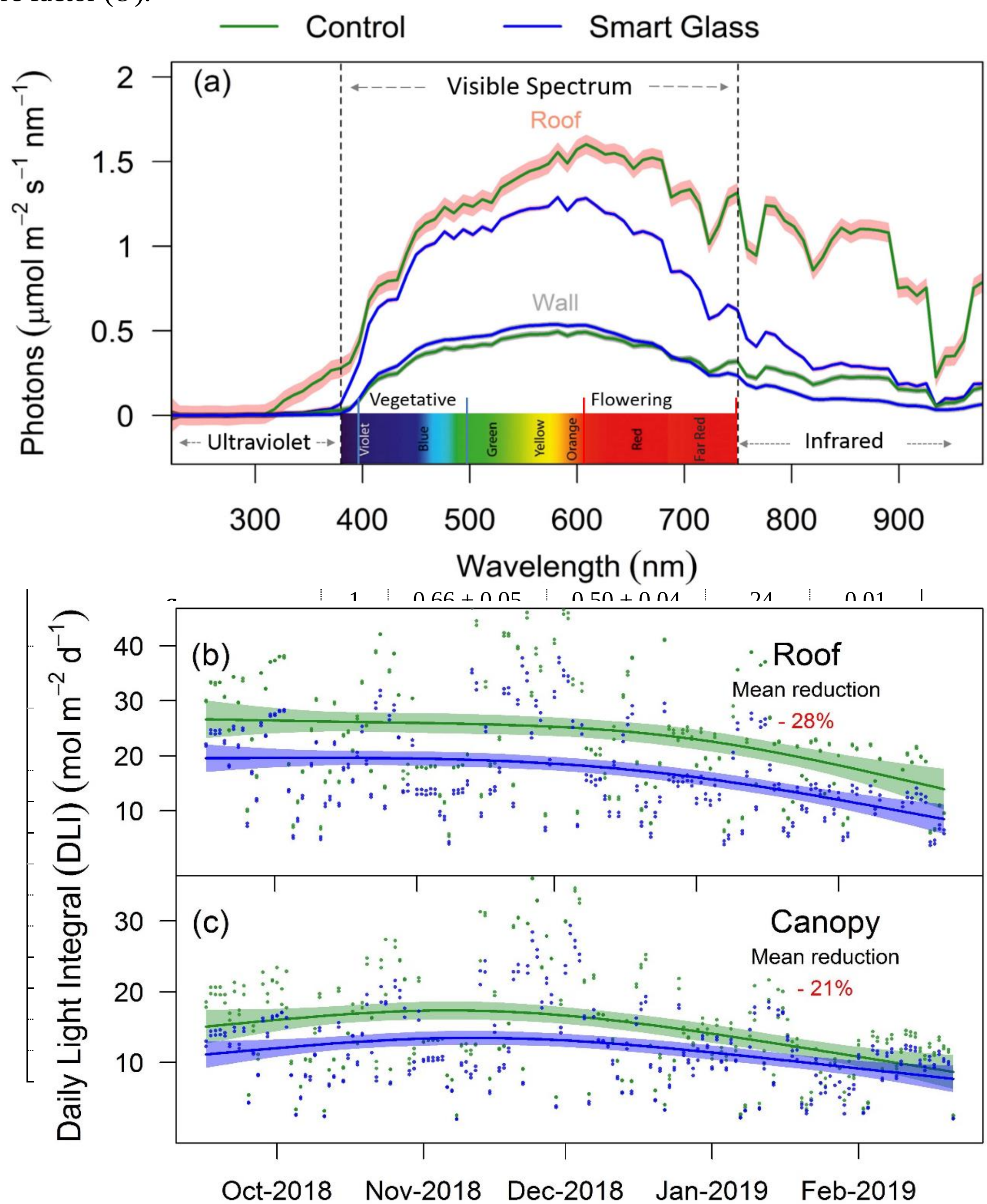

Figure 1 Smart Glass blocks UV and light wavelengths > 800 nm, but also significantly reduces photosynthetically active radiation (PAR) mainly in the red-light region of the spectrum: Smooth plot of photons over wavelength measured using a spectroradiometer at multiple locations (a). Light passing through roof and wall of the glasshouse bay are depicted in peach and grey colors with 95 % confidence intervals, respectively. Lower panel depicts daily light integral (DLI, total daily PAR) measured using PAR sensors at roof level (b) and canopy level (c). Canopy level PAR is the average of five PAR sensors at different locations. Solid line and shaded region depict mean and confidence interval, respectively. Control and Smart Glass rooms are depicted in green and blue, respectively.

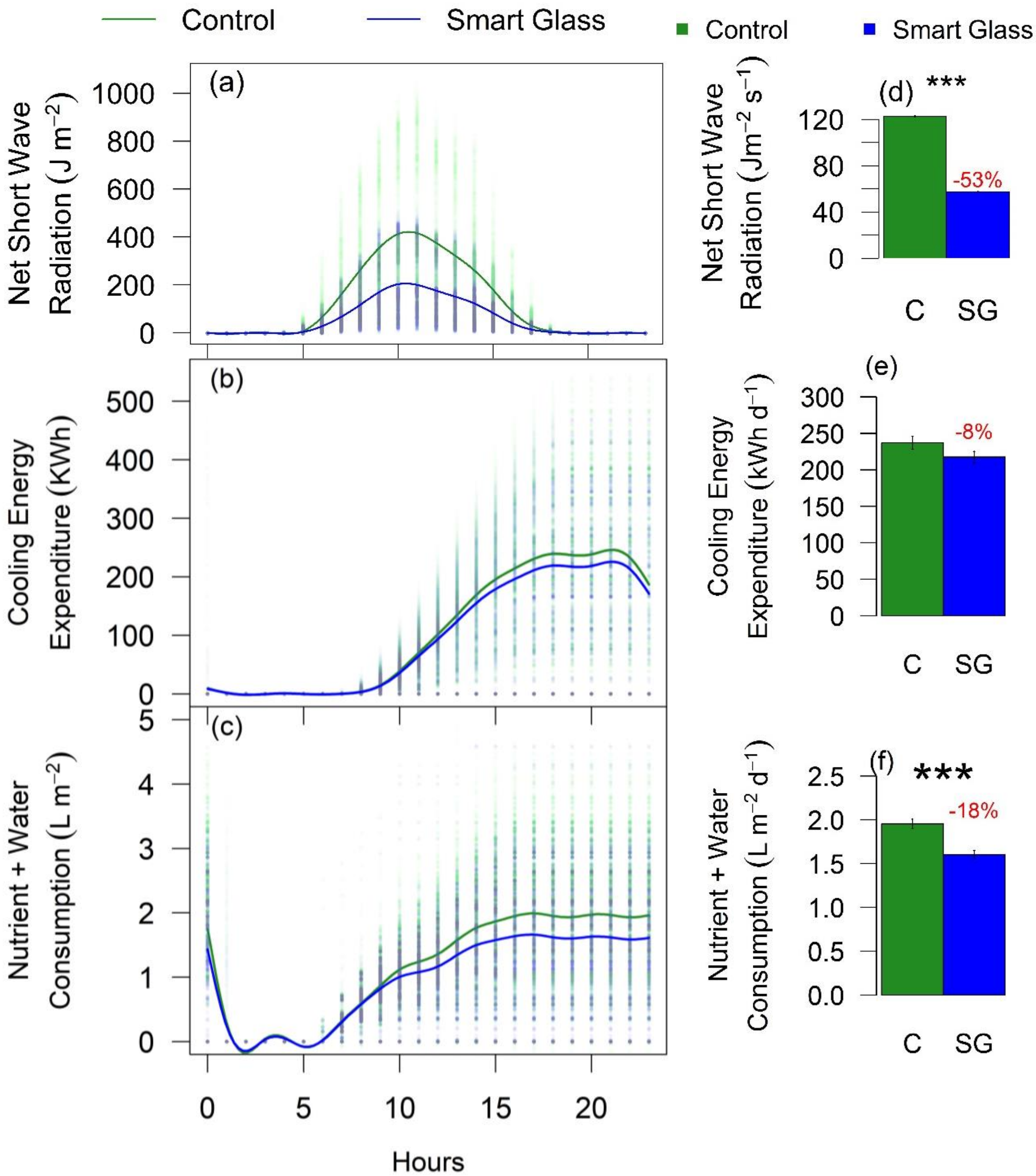

Figure 2 Smart Glass significantly reduced total daily short-wave radiation measured during Experiment 2: Panels a, b and c depict smooth plot of daily net short-wave radiation, cooling energy expenditure and net fertigation consumption, respectively. Solid lines depict the averages with 95% confidence intervals, while the faint data points show daily observations. Panels d, e and f depict bar plot of means for net short-wave radiation, cooling energy expenditure and net fertigation consumption, respectively. Error bars indicate standard error of mean. Control and Smart Glass treatments are depicted in green and blue, respectively.

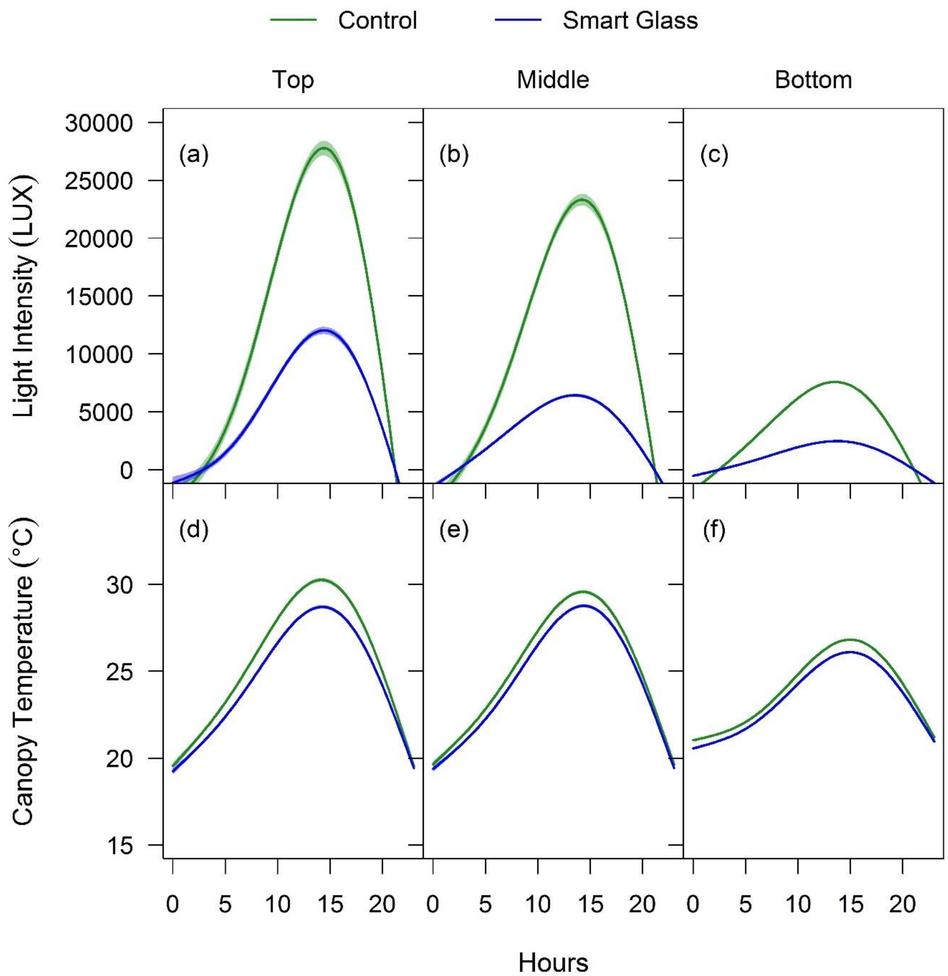

Figure 3 Daily averages of light intensity and canopy temperature measured during Experiment 2: Smooth plot of daily averages light intensity in lux (a, b and c) and canopy temperature (d, e and f). Solid lines represent the growth averages, while the shaded region depicts 95 % confidence intervals. Control and Smart Glass treatments are depicted in green and blue, respectively.

3.2 *SG reduces eggplant photosynthesis due to light limitation*

The impact of an altered light environment on photosynthesis was investigated by measuring instantaneous leaf gas exchange and light response curves. Altered light quality and quantity, including reduction in PAR, decreased light-saturated CO_2 assimilation rates (A_{sat}) (-12% and -18 % in Experiment 1 and 2, respectively). However, stomatal conductance (g_s) decreased (-24%) only in Experiment 1 (Table 1 and Figure 4).

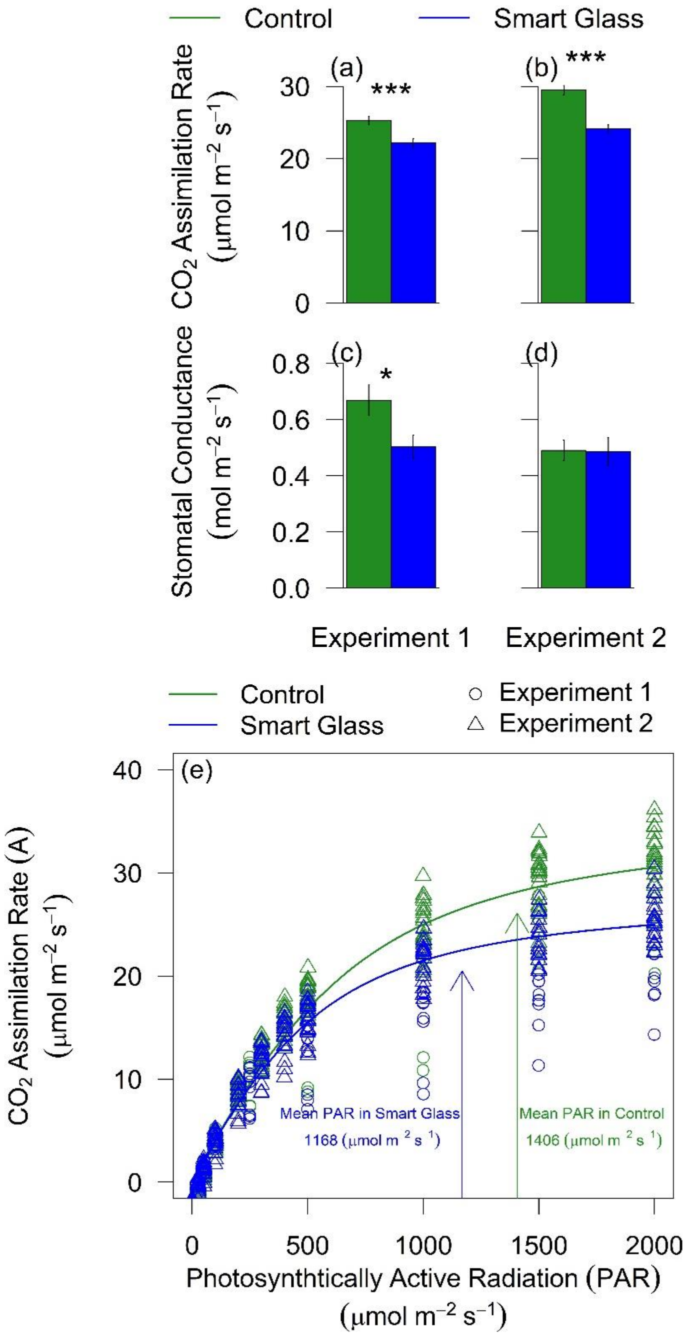

Figure 4 Smart Glass decreased photosynthesis in both experiments due to reduced photosynthetically active radiation (PAR): Bar plot of means for light-saturated CO_2 assimilation rates (A_{sat}) (a, b) and stomatal conductance (g_s) (c, d) measured at 1500 PAR (µmol m^{-2} s^{-1}). The error bars indicate standard error (SE) of the mean. Lower panel (e) depicts light response of photosynthesis. Circles and triangles represent Experiment 1 and 2, respectively. Control and Smart Glass are depicted in green and blue, respectively. Light response curves were fit using equation 1. Where, I = irradiance, A = CO_2 assimilation rate at given light, Φ_{max} = maximum quantum yield of PSII, A_{max} = maximum light-saturated CO_2 assimilation rate and θ = curvature factor of the light response curve.

In Experiment 2, instantaneous leaf gas exchange measured at natural growth light levels (1406 and 1168 μmol m^{-2} s^{-1} mean PAR in control and SG, respectively) showed reductions in CO_2 assimilation rates (A) (-21%) and g_s (-18%) under SG (Table 1 and Figure 4). Leaf level photosynthetic water use efficiency (PWUE) did not differ, either during light-saturated or ambient growth light conditions (Table 1). In addition, average daily canopy temperature measured at the top, middle and bottom position of the canopy was reduced by 0.5 to 0.9 °C under SG during Experiment 2 (Table 1 and Figure 3).

Based on AQ curves, photosynthetic rates were generally reduced under SG at higher light intensities in both experiments. Maximum light-saturated CO_2 assimilation rates (A_{max}) (-22%) were significantly reduced under SG in Experiment 2, while maximum quantum yield (Φ_{max}) and curvature factor (θ) were similar under both control and SG (Table 1 and Figure 4). The dark respiration (R_d) measured during light response curves was decreased by 14% under SG relative to control (Table 1). Therefore, reductions in PAR under SG caused light limitation and decreased photosynthesis, particularly at higher light levels, suggesting adaptive changes in the photosynthetic apparatus without changes in the photosynthetic efficiency.

3.3 *Eggplant leaves grown under SG have an altered xanthophyll composition*

The composition and abundance of carotenoid pigments was quantified in top canopy leaves from control and SG grown plants. Downregulation of photosynthesis and A_{max} in low light conditions in SG was correlated with an altered pigment composition and spectral indices. There was a significant reduction in specific xanthophyll pigments (A, Z, V and N), yet no change in lutein or β-carotene. Altered light under SG significantly reduced pool sizes of A (-26%), Z (-45%) and V (-18%). de-epoxidation state (DPS) was consequently lowered (-14%) in leaves from plants grown under SG. In addition, the photochemical reflectance index (PRI) was significantly increased (+8%) under SG, which is inversely proportional to the DPS (Gamon et al., 1992; Peñuelas, Filella, et al., 1995) (Table 2 and Figure 5). A lower structure intensive pigment index (SIPI), a measure of carotenoid to chlorophyll *a* ratio (Peñuelas, Baret, et al., 1995) was consistent with a lower carotenoid / chlorophyll ratio quantified by HPLC (-0.3% and -8%) in SG relative to Control leaves. There was a reduction in mNDVI (-2%) and SPAD values (-6%) that suggest that leaf chlorophyll content was slightly lower in SG grown plants. However, HPLC data showed no significant difference in chlorophyll content when measured per unit fresh weight (Table 2). Rather, a lower leaf water content evident from reduced WBI (-1%) (Peñuelas et al., 1993) and LMA (-9%), indicated that chlorophyll content was reduced per unit leaf area, but not per unit fresh weight (Table 2 and Figure 5). It is worth noting that the spectral indices and physical measurements do not usually commensurate with each other, given the different way they are measured and that the indices are 'indicators' rather than direct estimates. Untargeted GCMS of polar metabolites resolved >200 features in leaves (Table S6). After FDR correction, peaks areas (i.e. concentration) of 13 metabolites differed significantly between SG and control (FDR-corrected t-test). However, all of the significantly different metabolites were present at low concentrations and in no cases were fold-differences large. Therefore, leaves from plants grown under SG acclimated with an altered xanthophyll composition and DPS without altering metabolite, total carotenoid or chlorophyll levels (Table 2 and Figure 5).

Table 2 Summary of reflectance-based spectral indices, SPAD measurements, leaf mass per area (LMA) and pigment analysis using HPLC: Summary of statistical analysis using one-way analysis of variance (ANOVA) for the Smart Glass effect on spectral indices (n = 20), leaf pigment parameters, SPAD measurements and LMA (n = 10).

Parameter (mean)	**Exp**	**Treatment**		**Change (%)**	**P - Value**
		Control	**Smart Glass**		
Spectral Index parameters					
Leaf water content (WBI)	1	1.0456 ±0.0005	1.0364 ± 0.001	-1	1.4×10^{-8}
Chlorophyll Content (mNDVI)	1	0.640 ± 0.002	0.625 ± 0.004	-2	0.002
Xanthophyll Cycle (PRI)	1	0.0437 ± 0.0003	0.0475±0.0005	+8	9.3×10^{-7}
Carotenoid/Chl-a (SIPI)	1	1.0142 ± 0.0003	1.011 ± 0.0002	-0.3	1.9×10^{-7}
Red Green Ratio (RGR)	1	0.671 ± 0.002	0.631 ± 0.004	-6	2.9×10^{-9}
Chlorophyll degradation (NPQI)	1	0.010 ± 0.001	0.021 ± 0.001	+50	2.8×10^{-6}
Red-Far-red Ratio (RFR)	1	0.0901 ± 0.0004	0.088 ± 0.0003	-2	0.001
Chlorophyll and carotenoid absolute levels measured by HPLC					
Chlorophyll a (µg/gfw)	2	1543 ± 37	1569 ± 29	+1	0.5
Chlorophyll b (µg/gfw)	2	624 ± 17	642 ± 14	+3	0.4
Phytoene (µg/gfw)		137 ± 12	69 ± 6	-49	0.0001
Β-Carotene (µg/gfw)	2	105 ± 2	101 ± 2	-4	0.1
Lutein (µg/gfw)	2	190 ± 4	194 ± 5	+2	0.5
Neoxanthin (µg/gfw)	2	54 ± 1	44 ± 1	-18	0.0005
Xanthophyll cycle pigments using HPLC					
Violaxanthin (µg/gfw)	2	73 ± 2	60 ± 2	-18	0.0009
Antheraxanthin(µg/gfw)	2	3.5 ± 0.1	2.6 ± 0.1	-26	0.0004
Zeaxanthin (µg/gfw)	2	2.2 ± 0.1	1.2 ± 0.1	-45	3.6×10^{-5}
De-epoxidation (DPS)	2	0.073 ± 0.003	0.063 ± 0.002	-14	0.03
Tot Carotenoid (µg/gfw)	2	430 ± 8	404 ± 11	-6	0.09
Tot Chlorophyll (µg/gfw)	2	2168 ± 54	2212 ± 44	+2	0.5
Xanthophyll/Chlorophyll	2	0.0365 ±0.0009	0.0291 ± 0.0007	-20	1.1×10^{-5}
Carotenoid/Chlorophyll	2	0.198 ±0.003	0.182 ± 0.002	-8	0.0007
SPAD Values at different leaf positions					
Leaf - Top	2	56.1 ± 0.7	52.6 ± 1.1	-6	0.02
Leaf - Middle	2	56.7 ± 0.9	53.8 ± 1.1	-5	0.06
Leaf - Bottom	2	57.4 ± 0.9	52.9 ± 1.2	-7	0.01
Leaf mass area (LMA) using leaf fresh weight per unit area					
Leaf-Top (mg/cm^2)	2	19.4 ± 0.3	17.9 ± 0.4	-7	0.01
Leaf-Middle (mg/cm^2)	2	20.5 ± 0.5	18.4 ± 0.4	-10	0.007
Leaf-Bottom (mg/cm^2)	2	20.4 ± 0.6	17.8 ± 0.4	-12	0.003

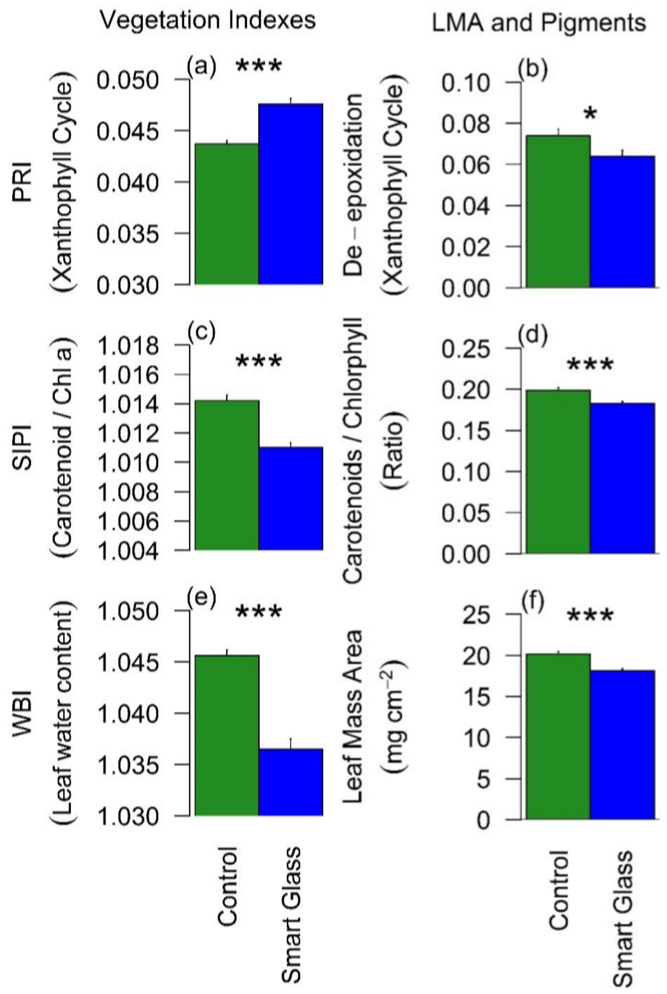

Figure 5 Plants acclimated to low light under SG by reducing carotenoids and xanthophyll cycle pigments: Bar plot of means for photochemical reflectance index (PRI) inversely related to xanthophyll cycle pigments Antheraxanthin (A), Zeaxanthin (Z) and Violaxanthin (V) (a), de-epoxidation (DPS= (A + Z) / (A + Z +V)) state of xanthophyll cycle pigments measured using HPLC (b), structure intensive pigment index (SIPI) proportional to carotenoid/chlorophyll a ratio (c), carotenoid/chlorophyll ratio measured using HPLC (d), water band index (WBI) related to leaf water content (e) and leaf mass per area (f). The error bars indicate standard error (SE) of the mean. Control and Smart Glass rooms are depicted in green and blue, respectively.

3.4 *SG does not affect morphological features or fruit quality, but a high fruit abortion rate reduces yield*

Plant morphological traits including height, bud, flower and fruit number were analysed in response to altered light environment under SG. Plants grown under SG had similar height, number of flowers, and number of buds (Table 3). However, mean fruit number (-28%, p-value < 0.001 and -23%, p-value < 0.001) and fruit weight (-32%, p-value < 0.001 and -24%, p-value < 0.001) were significantly reduced leading to decreased productivity under SG relative to the control (Table 3 and Figure 6).

Table 3: Summary of plant morphology, yield and fruit quality parameters: Summary of statistical analysis using one-way analysis of variance (ANOVA) for the Smart Glass effect on plant height (n>24), bud/flower/fruit number (n>36), pruned total biomass (per chamber), yield (experiment total), fruit weight (n>240) and fruit quality parameters (n= 6-10).

Parameter (mean)	**Exp**	**Treatment**		**Change (%)**	**P - Value**
		Control	**Smart Glass**		
Productivity and Development Parameters					
Mean Height (cm $stem^{-1}$)	1	236 ± 2	234 ± 2	-1	0.6
	2	276 ± 3	279 ± 4	+1	0.6
Mean Bud Number (n $stem^{-1}$)	1	6.4 ± 0.2	6.4 ± 0.3	0	0.9
	2	6.2 ± 0.2	6.2 ± 0.2	0	0.9
Mean Flower Number (n $stem^{-1}$)	1	0.6 ± 0.1	0.6 ± 0.1	0	ns
	2	1.6 ± 0.1	1.7 ± 0.1	+5	0.3
Mean Fruit Number (g $stem^{-1}$)	1	0.39 ± 0.01	0.28 ± 0.01	-28	2.2×10^{-16}
	2	0.53 ± 0.01	0.41 ± 0.01	-23	1.1×10^{-13}
Mean Fruit Weight (g $stem^{-1}$)	1	155 ± 2	105 ± 2	-32	2.2×10^{-16}
	2	192 ± 4	145 ± 3	-24	2.2×10^{-16}
Total Yield (kg/m^{-2}/year)	1+2	41.3	31.8	-23	NA
Pruned Biomass (kg)	2	6.3	5.2	-17	NA
Eggplant Fruit Quality Parameters					
Mineral (ash) (g 100 g^{-1})	1	0.43 ± 0.01	0.39 ± 0.01	-9	0.02
	2	0.35 ± 0.01	0.25 ± 0.01	-28	3.5×10^{-7}
pH	1	5.46 ± 0.02	5.53 ± 0.02	+1	0.03
	2	5.09 ± 0.02	5.04 ± 0.02	-1	0.1
Titratable Acidity (mq NaOH kg^{-1})	1	9.6 ± 0.4	9.3 ± 0.6	-3	0
	2	9.9 ± 0.4	9.4 ± 0.2	-5	0.3
Moisture (%)	1	93.9 ± 0.2	94.4 ± 0.2	+1	0.2
	2	94.7 ± 0.2	95.3 ± 0.1	+1	0.07
Total Soluble Solids (Brix)	1	3.6 ± 0.1	3.1 ± 0.1	-12	0.02
	2	2.91 ± 0.07	2.65 ± 0.05	-8	0.07
Glucose (g 100 g^{-1})	1	1.02 ± 0.01	1.09 ± 0.01	+6	0.004
Fructose (g 100 g^{-1})	1	1.07 ± 0.01	1.13 ± 0.01	+5	0.01
Sucrose (g 100 g^{-1})	1	0.17 ± 0.01	0.24 ± 0.02	+29	0.03
Total Sugars (g 100 g^{-1})	1	2.27 ± 0.03	2.47 ± 0.04	+8	0.002
Fat (%)	1	0.072 ± 0.008	0.059 ± 0.005	-18	0.1
N (%)	1	0.112 ± 0.004	0.107 ± 0.002	-4	0.3
Protein (%)	1	0.702 ± 0.026	0.674 ± 0.013	-4	0.3

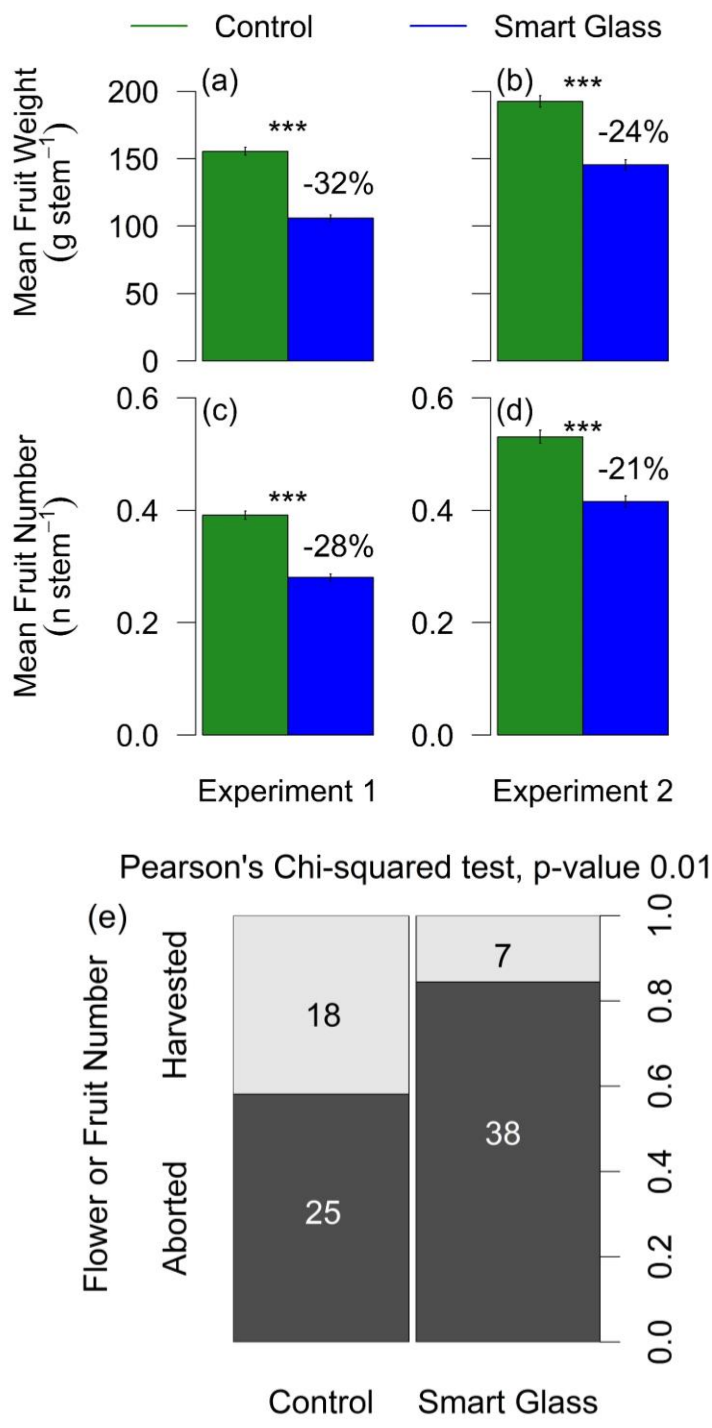

Figure 6 Smart Glass significantly reduced fruit number in both experiments due to fruit abortion: Bar plot of means for fruit weight (a, b) and fruit number (c, d) in experiment 1 and 2. The error bars indicate standard error (SE) of the mean. Control and Smart Glass rooms are depicted in green and blue, respectively. Lower panel (e) depicts number of flowers aborted or developed into harvestable fruit during Experiment 2. Variation in abortion rate was dependent on Smart Glass according to Pearson's chi squared test (p value 0.01).

A reduction in fruit number was attributed to increased abortion of flowers or fertilized young fruits (Chi-square test, p-value <0.01) under SG (Figure 6). In addition, the biomass harvested after pruning was lower (-17%) under SG relative to control (Table 3).

Fruit quality parameters, including pH, titratable acidity, moisture, total soluble solids (brix), mineral content (ash), elemental composition (AGVITA, Table S4), metabolites (GCMS, Table S5), sugar content (HPLC), fat (ANKOM) and nitrogen (DUMAS) content were assessed. None of the > 400 metabolites resolved by untargeted GC-MS differed significantly between SG and control (FDR-corrected t-test). We found increases in total sugars (+8%), sucrose (+29%), Fe (+28%) and decreases in mineral content (-9% and -28% in Experiment 1 and 2, respectively), but otherwise parameters were unchanged (Tables 3 and S3). In summary, SG did not affect eggplant morphological traits, but increased abortion rate in fertilised young fruits, thereby decreasing fruit yield without major changes in fruit quality.

4. Discussion

SG film ULR-80 blocked 85% of UV (221–279 nm), 26% of red (600–699 nm) and 58% far-red (710–850 nm) light with an overall reduction of 19% PAR (280 - 799 nm) and 53% reduction (season mean) in short wave radiation (385 nm to 2105 nm upward; 295 to 2685 nm downward) measured using spectroradiometer. This consequently reduced energy expenditure for cooling and water and nutrient consumption. However, SG also reduced mean season PAR (DLI: -24% and -28% in Experiment 1 and 2, respectively) leading to reductions in photosynthesis and hence productivity (mean fruit weight: -32 and -24% in Experiment 1 and 2, respectively), and generally did not affect fruit quality except for significantly increasing the sweetness of the fruits. Growth under SG reduced A_{max} and the xanthophyll cycle pigments (A, V and Z) and DPS, thereby highlighting that SG grown plants may have partially acclimated to low light conditions. Novel glazing materials with low thermal emissivity can be applied to greenhouses to reduce energy expenditure and resource use (water and nutrients), but specifically SG film ULR-80 will require spectral compositional modification to maximise PAR transmission to avoid compromising plant productivity.

4.1 *SG blocks radiation and decreases energy use for cooling, water use, and nutrient consumption*

According to manufacturer specifications, SG film (ULR-80) was anticipated to block UV and mostly higher wavelengths of light with marginal reductions (-5 to -10%) in light transmission. However, SG blocked a considerable amount of PAR at the canopy level (-25%, season mean), leading to a light limitation for plant growth and photosynthesis. Significant reductions (-53%, season mean) in short wave radiation under SG blocked radiation contributing to heat, ultimately decreasing energy used by chillers for cooling (-8%) and irrigation (water + nutrient) consumption (-18%). A previous study with tomatoes reported energy saving up to 25-33% using glass with an anti-reflection coating with some near-infrared (NIR) reflective properties (Hemming et al., 2011). Another study with tomatoes grown under wavelength-selective photovoltaic systems (WSPVs) found small water savings due to reduced (-25%) stomatal conductance (Loik et al., 2017). WSPVs absorbed some of the blue and green wavelengths of the solar spectrum for electricity generation, but transmitted remaining wavelengths including most of the red light (Loik et al., 2017). In contrast, SG reduced the intensity of light mainly in the red-light region of the visible light spectrum, which suggested differences in the quality of light in our study relative to Loik et al. (2017). The reduction in water and nutrient consumption of the eggplant crop in our study can be attributed to a reduction in radiation load, as well as decreased photosynthesis and productivity. The electrical power used by chillers is an indirect measurement of energy use (kWh) calculated using water flow and temperatures, before and after cooling. Hence, the actual total energy savings could be different, and a detailed, certified accounting of energy usage is required in future investigations.

4.2 *Plants acclimated to low light by reducing A_{max} and xanthophyll composition*

SG changed light quantity and quality and this was reflected in the responses of photosynthetic activity and pigments. Light limited reduction in photosynthetic rates is consistent with tomatoes (-20%) grown under WSPVs when measured at higher light levels (Loik et al., 2017). Interestingly, photosynthetic light saturation was observed at ~500 μmol m^{-2} s^{-1} in tomato (Loik et al., 2017) relative to ~1000 μmol m^{-2} s^{-1} in eggplants (current study) which can be due to differences in growth CO_2, temperature (Xin et al., 2019) and species. Stomatal conductance was decreased by SG in one of the two eggplant experiments. Loik et al., (2017) also found a higher reduction in g_s than A_{sat} which was linked to reduced blue light under WSPVs which plays an important role in stomatal functioning. Light intensity and quality both affect stomata (O'Carrigan et al., 2014) and in dynamic light environments, stomata have been found to respond more slowly than photosynthesis, resulting in non-coordination between A and g_s (McAusland et al., 2016). Reduced stomatal conductance, similar to reduced photosynthesis, is partly in response to lower light intensity under SG. However, altered light quality, particularly vastly reduced red and far-red light, may have modified the stomatal response in Experiment 2 and further work is required to understand the impact of SG on light quality and stomata.

In the current study, A_{sat} and A_{max} were reduced without significant changes in Φ_{max} and θ, suggesting that the photosynthetic apparatus acclimated in response to reduced light intensity (Evans & Poorter, 2001). Acclimation was generally uniform across light-dependent and light-independent reactions of photosynthesis, including photosynthetic efficiency and the electron or photon cost of CO_2 fixation, which aligns with unchanged total chlorophyll or carotenoid content. In contrast, chlorophyll a/b ratios and electron transport components decreased at lower light levels in spinach and pea (Evans, 1987; Terashima & Evans, 1988) which can be attributed to the stronger light treatment (>70% lower light for spinach and >80% lower light for pea) compared to relatively modest light treatment (~26 % lower light for eggplant) in our study. Unchanged total chlorophyll and carotenoid content suggests that the light treatment in our study was not strong enough to induce changes in total pigment levels, but the shifted light environment could alter pigment composition associated with light capture and photo protection.

Carotenoid pigments such as the xanthophylls facilitate non-photochemical quenching (NPQ) and light capture (Demmig-Adams et al., 2014; Niyogi, 1999). Selective synthesis and degradation of chloroplast components during acclimation have been shown to modulate the composition and function of the photosynthetic apparatus (Bailey et al., 2001). Under high light, violaxanthin undergoes de-epoxidation (DPS) via an antheraxanthin intermediate back to zeaxanthin in the thylakoid pigment bed to help dissipate excess light-induced excitation energy as heat and minimise photo-oxidative stress (Demmig-Adams et al., 2014; Demmig-Adams & Adams, 2006; Havaux et al., 2004; Marin et al., 1996). The DPS was lower (~0.07) in eggplant leaves due to the markedly low abundance of A and Z, keeping consistent with tomato (F. Ding et al., 2017) and rice leaves (Yin et al., 2010), in comparison to eucalyptus tree leaves that have a considerably higher DPS (~0.7) and similar abundances of V, A and Z (Dhami et al., 2020). Lower light levels are linked to lower DPS values, which can rise during the midday in response to higher light levels (L. Ding et al., 2006). Our results suggest a limited capacity for eggplant to use the xanthophyll cycle for photo-protection, perhaps relying instead on the production of antioxidants (Logan et al., 2006). Spectral indices (e.g., SIPI and PRI) provide additional evidence to support the lower DPS and these indices have been successfully used for quantifying biophysical characteristics of agricultural crops (Peñuelas, Baret, et al., 1995; Peñuelas, Filella, et al., 1995; Thenkabail et al., 2000). Plants grown under SG appear to have acclimated by lowering their xanthophyll composition, without affecting lutein, β-carotene or chlorophyll levels. This is consistent with the recent meta-analysis on plant responses to light (Poorter et al., 2019), where the xanthophyll to chlorophyll ratio correlates with the quantity of light. Lower DPS and zeaxanthin levels under SG also suggest plants may have reduced NPQ based on the curvilinear relationship between Zeaxanthin and NPQ (Cheng et al., 2003). However, photosynthesis was limited by electron transport rate under WSPVs, yet no differences were found in NPQ (Loik et al., 2017). Taken together, a reduction in A_{max} was associated with a reduction in xanthophyll composition and DPS in SG leaves, thereby revealing a reduced photosynthetic capacity for plants acclimated to the SG environment.

4.3 *Reduced photosynthesis and high abortion rate under SG decreases yield without changing fruit quality*

In crop plants, the average yield is generally reduced by 0.8 to 1% for every 1% reduction in light intensity (Marcelis et al., 2006). In accordance, we found that light limited (~-26% DLI) photosynthesis under SG reduced fruit yield (~ -28%) without significantly affecting fruit quality and plant morphological traits, including plant height, bud number, and flower number. One of the few changes in fruit quality (e.g. 29% increase in sucrose content) was a positive impact of SG, while the decrease in mineral (-9% and -28% in experiment 1 and 2 respectively) content was a negative impact. The reduction in fruit yield was driven by reduced fruit number due to a high flower abortion rate under SG relative to control. A very high rate of flower abortion (56.2% in cv Emi and 93.4% in cv Long Negro) has been reported for eggplant cultivars (Passam & Khah, 1992). However, a previous study found a decrease in flowers, flower buds, fresh fruit weight and fruit growth period under reduced light intensity in eggplants (Uzun, 2007). One cultivar of tomato (*cv*. Clarence) grown under WSPVs also showed a significant decrease in fruit number and mass due to lower light and photosynthesis (Loik et al., 2017). Poorter et al., (2019) also showed a strong relationship between light intensity and fruit number. The yield reduction in our study could be related to the control of carbon from source to sink. Limited availability of carbon due to reduced photosynthesis may have triggered plants to decrease the number of fruits developed to full maturation, which was evident from high abortion rates in SG. Source-sink regulation is known to control fruit load depending on the availability of photosynthate for translocation during fruit development (Marcelis et al., 2004), which allows plants to produce fewer, but fully developed and better quality fruits (Pallas et al., 2013). Fruit set is related to assimilate supply (source strength) in pepper and low light decreased fruit set due to lower capacity to accumulate sugars and starch during the day (Aloni et al., 1996). Turner & Wien, (1994) suggested that the low light stress-induced abscission in pepper associated with reduced assimilate partitioning to flower buds could be related to the high assimilate consumption in the maintenance of expanded leaves. However, light quality was also altered in SG, which may have induced fruit abortion and decreased yield (Cerdán & Chory, 2003). Hence, further investigation is required to understand if light quality, light quantity or both are driving the reduction in fruit yield.

5 Conclusions

SG blocked UV and light wavelengths > 780 nm, but also a significant proportion of PAR mainly in the red-light region of the spectrum, contributing to decreased energy, water and nutrient consumption. Reductions in PAR reduced photosynthesis in leaves from SG grown plants, which was associated with a decrease in yield due mainly to higher fruit abortion rates, without affecting fruit quality. SG did not affect morphological features, including plant height, floral bud number or the number of open flowers. Further investigation into whether light quality and /or quantity primarily reduce fruit yield will shed light on how to engineer a new generation of SG for protected cropping industries. It should be noted that SG is likely to have different effects in a crop-specific manner; e.g., vegetative crops such as leafy vegetables may have a different response because leaves, and not reproductive structures, are harvested for yield. Thus, additional SG trials with different crop types are required to identify the most appropriate SG characteristics for use with a wide variety of crop plants. Overall, this research shows that novel glass technologies can provide significant energy savings for commercial vegetable greenhouses and may benefit growers who seek to develop sustainable food production with lower resource use in the future.

Acknowledgments, Samples, and Data

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