

Luminescent Quantum Dot Films Increase the Radiation Capture and Yield of Lettuce and Sweet Basil Compared to a Traditional/Neutral-density Greenhouse Glazing

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Keywords. blue light, cryptochromes, luminescent quantum dot films, plant morphology, radiation capture, spectral quality

Abstract. Utilizing quantum dot (QD) luminescent films as a greenhouse covering material is an innovative method of modifying the greenhouse light spectrum. The QD films convert a portion of high-energy ultraviolet and blue photons to lower-energy photons. Previous research has shown that the application of QD films in greenhouses led to improved crop yields of red lettuce and tomatoes. However, the underlying mechanism of the yield increases has not been fully explored. We quantified the effects of solar spectral shifts attributable to QD films on plant morphology, radiation capture, and, subsequently, crop yield. Green and red leaf lettuces and basil were grown in a greenhouse under four treatments: regular-concentration QD film (reg QD film); high-concentration QD film (high QD film); color-neutral polyethylene (PE) film; and control treatment without any films. Compared to the reg QD film, the high QD film converted a higher fraction of blue photons into longer-wavelength photons, resulting in enhanced leaf expansion, stem elongation, and shoot fresh weight of red lettuce and basil compared with those grown under the PE film without spectral modifications. No significant growth differences were observed between the control and high QD film treatments of red lettuce and basil despite a 23% reduction in the average daily light integral (DLI) under the high QD film treatment. Compared to that grown under the control treatment, green lettuce grown under the high QD film treatment had a similar total leaf area but reduced shoot biomass; this was likely associated with reductions in leaf thickness and chlorophyll content. In contrast, the red lettuce showed more pronounced leaf expansion and reduced leaf anthocyanin content under the high QD film, which likely helped to offset the reduction in DLI. Overall, our results indicated that modifying the solar spectrum with QD films as greenhouse covering material could result in improved crop radiation capture and yield in greenhouse production of lettuce and basil. However, the spectral shifts caused by the QD films may affect crop quality attributes, such as anthocyanin levels and the production of other beneficial secondary metabolites. This effect on crop quality should be carefully considered and requires further study.

Received for publication 26 Apr 2024. Accepted for publication 30 Apr 2024.

Published online 21 Jun 2024.

This research was supported by the USDA-NIFA Hatch Project 1026236.

We thank Yilin Zhu, Sangjun Jeong, Michael Legorreta, and Dasom Kim for their assistance with the experimental set-up and data collection. S.Z. is the corresponding author. E-mail: shuyang.zhen@tamu.edu.

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Light is a pivotal environmental factor that affects plant growth and development. Recent advances in light-emitting diode (LED) technology have enabled more precise manipulation of light intensity, spectral quality, and timing of exposure, thus enhancing our understanding of plant photobiological mechanisms and facilitating the development of effective horticultural lighting strategies. Additionally, LEDs can be designed to provide narrow wavebands that target chlorophylls or specific photoreceptors, thereby enhancing photosynthetic efficiency and/or eliciting morphological and

developmental responses (Bantis et al. 2018; Currey and Lopez 2013; Hernandez and Kubota 2012; Massa et al. 2008). Many studies have shown that plant biomass production and the accumulation of beneficial secondary metabolites are dependent on light intensity or photosynthetic photon flux density (PPFD; 400–700 nm), and that both plant yield and quality can be improved through optimizing PPFD for a specific species/cultivar (Dou et al. 2018; Esteban et al. 2014; Fu et al. 2012; Massa et al. 2015; Proietti et al. 2004; Tattini et al. 2014). Regarding light quality, significant research efforts have been performed to characterize plant photosynthetic, morphological, and physiological responses to photons in the photo-biologically active radiation range (280–800 nm), which can be categorized into the following six regions: ultraviolet-B (280–320 nm); ultraviolet-A (320–400 nm); blue (400–500 nm); green (500–600 nm); red (600–700 nm); and far-red (700–800 nm) (Dörr et al. 2020; Zhen et al. 2022).

Plant photoreceptors such as phytochromes and cryptochromes perceive the spectral quality of the light environment and mediate plant responses. Phytochromes can absorb red/far-red photons and trigger shade avoidance responses under conditions with low red/far-red ratios, leading to enhanced stem elongation and/or leaf expansion as adaptations to crowded vegetation environments (Casal et al. 1998; Smith 1982). The morphological responses mediated by phytochromes, especially the enhancement of leaf expansion through the application of far-red light, have been leveraged in controlled-environment agriculture to increase canopy photon capture and biomass production (Meng and Runkle 2019; Park and Runkle 2017; Zhen and Bugbee 2020a).

Cryptochromes comprise another group of photoreceptors that play an important role in regulating plant morphology and secondary metabolism and sense ultraviolet-A and blue light. Active cryptochromes decrease stem elongation and leaf expansion, leading to a more compact plant canopy with reduced photon capture and biomass accumulation (Dou et al. 2018; Hernández and Kubota 2016; Larsen et al. 2020; Meng et al. 2020; Ohashi-Kaneko et al. 2007; Son and Oh 2013; Song et al. 2017). Cryptochromes are activated by blue photons and can be deactivated by green photons (Battle et al. 2020; Bouly et al. 2007; Zhang et al. 2021). Previous studies that used LEDs have demonstrated that an increase in the green photon fraction or a decrease in the blue photon fraction could result in increased leaf expansion and higher yield of a number of species, including lettuce (both green and red leaf cultivars), kale, and tomato (Kusuma et al. 2021; Meng et al. 2019). Kusuma et al. (2021) reported that increasing the percentage of blue photons from 8% to 30% consistently caused substantial reductions in the total leaf area and dry mass of lettuce, cucumber, and tomato under two PPFD levels (200 and 500 $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$), whereas a large increase

in green photon fraction (from 0% to 50%) increased the total leaf area and dry mass of tomato only under a high PPFD of 500 $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ but had few effects on these parameters of lettuce and cucumber. A kinetic model of the cryptochrome photocycle by Procopio et al. (2016) indicated that the activation of cryptochromes by blue light is significantly more efficient (i.e., characterized by a higher quantum yield) than cryptochrome de-activation by green photons. Thus, it is likely that cryptochrome-mediated morphological and physiological responses are more sensitive to changes in the quantity of blue photons than to changes in the quantity of green photons.

Manipulating the light environment is more challenging in greenhouses, especially in terms of spectral quality, than in indoor farms that use electric lighting. In greenhouses, light intensity is typically controlled using shade cloths to reduce light levels and supplemental light sources to increase light levels. High-pressure sodium fixtures have been the traditional choice for greenhouse supplemental lighting, but they have relatively low photon efficacy (micromoles of photon output per joule of input energy) and lack the ability to control light spectra (Nelson and Bugbee 2014). More energy-efficient LEDs are increasingly being used in greenhouses. Compared with monochromatic or broad-spectrum LEDs with fixed spectral outputs, multispectral tunable LEDs are less commonly used for greenhouse lighting because of their high costs. Moreover, modifying greenhouse light spectral quality with LEDs may be less effective under backgrounds of natural sunlight (Hebert et al. 2022).

Several studies have examined the utility of spectral conversion/shifting films for altering solar spectral quality to improve photosynthetic efficiency and crop growth without the consumption of energy (El-Bashir et al. 2016; Hebert et al. 2022; Kang et al. 2023; Parrish et al. 2021; Shen et al. 2021; Shoji et al. 2022; Yoon et al. 2020). Spectral conversion films can be engineered using various materials, such as fluorescent dyes (Arbeloa et al. 2007), quantum dots (QDs) (Parrish et al. 2021), and photonic structures (Shen et al. 2021), with each providing distinct spectral-shifting characteristics. Previous research on spectral conversion films for agricultural applications mainly focused on films designed to convert ultraviolet radiation into blue light, or to convert green light to red light (Kang et al. 2023; Parrish et al. 2021; Shen et al. 2021). Yield increases have been reported for a wide range of crops grown under various types of spectral conversion films, including lettuce, Chinese cabbage, cucumber, kale, and tomato, compared with those grown under neutral-density polyethylene (PE) films (Hemming et al. 2006; Kang et al. 2023; Nishimura et al. 2012; Novoplansky et al. 1990; Shen et al. 2021; Yoon et al. 2020).

Among the spectral conversion film options, films incorporated with $\text{CuInS}_2/\text{ZnS}$ (CIS/ZnS) QDs have recently emerged and have been applied to greenhouse crop production.

A primary advantage of using CIS/ZnS QD films is a large spectral shift within the visible light spectrum that features the conversion of a portion of ultraviolet and blue photons to green, red, and far-red photons. This spectral shift can affect cryptochrome and phytochrome activities and alter plant morphology. Additionally, the conversion of ultraviolet and blue photons to green and red photons could improve photosynthetic efficiency (Liu and van Iersel 2021; McCree 1971; Tera-shima et al. 2009), potentially contributing to increased plant biomass production. Parrish et al. (2021) grew 'Outregeous' red leaf lettuce under electric light provided by metal halide lamps converted through two types of CIS/ZnS QD films (peak emission centered at 600 and 660 nm) or a PE film without spectral shifts. They found that red lettuce showed improved fresh biomass, dry biomass, and total leaf area under both types of QD films compared with those grown under the PE film with similar light intensity (Parrish et al. 2021). It is important to note that metal halide light differs substantially in spectral quality compared with natural sunlight. Hebert et al. (2022) reported that tomato 'Merlice' grown under the CIS/ZnS QD film treatment inside a greenhouse showed a faster growth rate, higher saleable production yield, and lower fruit waste than that grown under a control treatment without light-modifying films (Hebert et al. 2022). However, the underlying mechanism of the observed yield increases has not been fully explored.

The objective of this study was to quantify the effects of CIS/ZnS QD films on the morphology, pigmentation, and biomass production of greenhouse-grown leafy vegetables and herbs (specifically, green and red leaf lettuces and sweet basil). We hypothesized that the spectral shifts caused by the QD film, especially the reduction in the blue light fraction, may result in improved plant biomass production by enhancing leaf expansion and radiation capture. We used films containing CIS/ZnS QDs at two different concentrations and compared plant responses under the QD films to those under PE film and a control treatment without the application of spectral conversion films. The results of this study offer insight into the potential benefits of using QD films in greenhouse crop production.

Materials and Methods

Plant materials and greenhouse environmental conditions. Green butterhead lettuce (*Lactuca sativa* 'Rex'), red romaine lettuce (*L. sativa* 'Outregeous'), and sweet basil (*Ocimum basilicum* 'Genovese') were used during this study. Seeds (obtained from Johnny's Selected Seeds, Fairfield, ME, USA) were directly sown in 1.8-L containers filled with a soilless substrate (85% peat and 15% perlite by volume; ASB Greenworld, Pointe-Sapin, New Brunswick, Canada) in a polycarbonate-covered greenhouse. These three crops were selected because of their

economic importance, different growth habits, and contrasting leaf color (red and green). Ten days after sowing seeds, seedlings were thinned to one plant per container, and uniform plants of each species/cultivar were transferred to light spectral treatments in the same greenhouse (see experimental details). Plants were fertigated daily with a water-soluble fertilizer applied at 100 $\text{mg}\cdot\text{L}^{-1}$ N (20N–8.7P–16.6K; 20–20–20 Peter's Professional General Purpose; ICL Specialty Fertilizer, Summerville, SC, USA) throughout the experiment. During the growing period (6 Mar 2022 to 9 Apr 2022), the average daily temperature, relative humidity, and vapor pressure deficit in the greenhouse were $23.3 \pm 2.1^\circ\text{C}$, $52.6\% \pm 17.2\%$, and 1.5 ± 0.4 kPa, respectively.

Solar spectral modification treatments with QD films. To characterize the responses of plant growth, morphology, and pigmentation to greenhouse solar spectral quality modifications, the following three types of films were examined during this study: regular-concentration CIS/ZnS QD film (reg QD film; UbiQD, Los Alamos, NM, USA); high-concentration CIS/ZnS QD film (high QD film; UbiQD); and PE film (to create a diffuse light environment with mildly reduced light intensity similar to that under the QD films). A control treatment without any light-modifying films was included as a fourth treatment (control). Nine cuboid structures (length $\times$ width $\times$ height: $1.5 \text{ m} \times 1.2 \text{ m} \times 0.9 \text{ m}$) were constructed using polyvinyl chloride (PVC) pipes to create the three types of film treatments (i.e., reg QD film, high QD film, and PE film; three structures per film type). The top of each PVC structure was completely covered with film, with three sides partially covered from the top (leaving uncovered openings 30 cm in height from the greenhouse benches) and the northwest-facing side open for air ventilation. The PVC structures were placed at least 2 m apart to minimize the shadows cast among spectral treatments. To quantify the spectral shifts of light passing through the films, we measured the light intensity and spectral distribution at 30 locations within the bench area (1.8 m^2) enclosed by each PVC/film structure. The measurements were obtained on a sunny day around solar noon using a spectroradiometer (PS300; Apogee Instruments, Logan, UT, USA) placed 20 cm above the bench top. Each light measurement under a PVC/film structure was paired with a measurement obtained within seconds under unfiltered greenhouse sunlight, and the spectroradiometer remained in the same location while the PVC/film structure was removed. The proportions of ultraviolet-A (320–400 nm), blue (401–500 nm), green (501–600 nm), red (601–700 nm), and far-red (701–800 nm) wavebands of light filtered through each type of film and unfiltered greenhouse sunlight were determined by dividing the photon flux density within each waveband by the total photon flux density integrated from 320 to 800 nm (Fig. 1; Table 1). The phytochrome photostationary state (PSS) in each

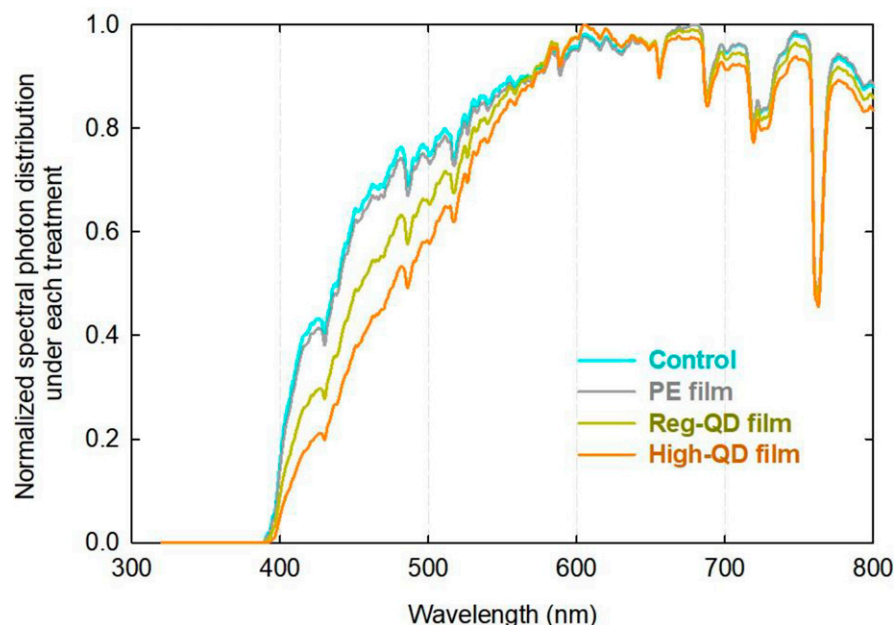


Fig. 1. Normalized spectral photon distributions under four spectral treatments. Unfiltered greenhouse sunlight was the control treatment. Additionally, light was filtered through the following three types of film: regular-concentration quantum dot film (reg QD film), high-concentration quantum dot film (high QD film), and polyethylene (PE) film.

treatment was calculated according to the method described by Sager et al. (1988).

Experimental setup. The four treatments were arranged in a randomized complete block design with three blocks (Supplemental Fig. 1). Eight uniform plants of each species/cultivar were placed under each treatment area (eight plants per treatment $\times$ three species/cultivar = 24 experimental plants per treatment). A total of 15 additional plants (five plants per species/cultivar) were placed along the edges as bordering plants in each treatment. A total of 156 plants per species/cultivar were grown in this study, including 96 experimental plants (eight plants per treatment $\times$ four treatments $\times$ three blocks) and 60 bordering plants (five plants per treatment $\times$ four treatments $\times$ three blocks).

Twelve quantum sensors (SQ-500; Apogee Instruments, Logan, UT) and 12 type-J thermocouples were connected to a datalogger

(CR1000X; Campbell Scientific, Logan, UT, USA) and placed slightly above plant height at the center of plant canopies under each of the 12 experimental units (four treatments $\times$ three blocks) to measure PPFD and air temperature every 30 s (Table 1). The daily light integral (DLI; total amount of 400–700 nm photosynthetic photons received per square meter of area per day) was calculated from the PPFD measurements.

Growth parameters. Each crop was harvested separately on three consecutive days 19 to 21 d after the start of treatments. ‘Rex’ lettuce was harvested first, followed by ‘Outredgeous’ lettuce and basil. The following growth parameters of each experimental plant were measured: number of leaves; total leaf area (using a leaf area meter; model LI-3100C; LI-COR, Lincoln, NE, USA); shoot fresh weight; and shoot dry weight (after fully dehydrated for 5 d at 80 °C in a drying

oven). The leaf mass per area (LMA) was calculated by dividing the leaf dry weight by the total leaf area ($\text{g}\cdot\text{m}^{-2}$). The leaf chlorophyll contents ($\mu\text{mol}\cdot\text{m}^{-2}$) of green leaf lettuce and basil of mature leaves were measured three times per plant and averaged (MC-100 chlorophyll meter; Apogee Instruments, Logan, UT, USA). The plant height of basil was also measured, and leaves and stems were separated to determine the fresh and dry weights.

Projected leaf area. A digital camera was installed 140 cm above the plant height to obtain top-down photos of ‘Rex’ and ‘Outredgeous’ lettuce plants at the end of the experiment. Each plant was placed at the center of a 60 cm $\times$ 60 cm whiteboard (background). Photos of ‘Rex’ lettuce (with green leaves) were analyzed to determine the projected leaf area using an open-source Python program (available at <https://github.com/jakobottar/green-pixel-analysis>). The Python program calculates the ratio of green pixels (plant tissues) to the total pixel count of the background area. The projected leaf area was calculated by multiplying the background area (3600 cm^2) by the fraction of the green pixels (Klassen et al. 2004).

Anthocyanin content index. The top-down photos of ‘Outredgeous’ lettuce (with red leaves) were analyzed using a Python program for the projected leaf area and using the normalized difference anthocyanin index (NDAI), which is an image-based index developed by Kim and van Iersel (2023), to estimate the anthocyanin concentration. The NDAI is determined based on the optical properties of anthocyanins, which show high absorbance in the green and low absorbance in the red region of the spectrum. The Python program separates the plant objects from the background and extracts the pixel intensity of the green and red color channels from the red-green-blue images to calculate the NDAI as $(I_{\text{red}} - I_{\text{green}})/(I_{\text{red}} + I_{\text{green}})$, where I is the pixel intensity (see Fig. 2 for an example of a red-green-blue image of an ‘Outredgeous’ lettuce plant canopy, NDAI image, and its corresponding histogram).

Statistical analysis. This experiment contained four light spectral treatments arranged

Table 1. Proportion of different wavebands in unfiltered greenhouse sunlight and light transmitted through three types of films.

Treatment	Proportion of each waveband (%) transmitted by each treatment								Environmental data under each treatment	
	Ultraviolet-A (320–400 nm)	Blue (401–500 nm)	Green (501–600 nm)	Red (601–700 nm)	Far-red (701–800 nm)	B:R ratio	R:FR ratio	PSS (Sager et al. 1988)	DLI ($\text{mol}\cdot\text{m}^{-2}\cdot\text{d}^{-1}$)	Air temperature (°C)
Control (no film)	0.21	17.26	26.36	29.25	26.93	0.59	1.09	0.72	24.3 $\pm$ 6.6 a	23.5 $\pm$ 1.9 NS
PE film	0.19	16.89	26.29	29.44	27.19	0.57	1.08	0.72	20.2 $\pm$ 5.3 b	23.5 $\pm$ 1.9 NS
Reg QD film	0.11	14.07	27.03	30.93	27.85	0.45	1.11	0.72	21.2 $\pm$ 5.8 b	23.3 $\pm$ 2.0 NS
High QD film	0.05	11.64	27.36	32.29	28.67	0.36	1.13	0.73	18.9 $\pm$ 5.0 b	23.4 $\pm$ 1.9 NS

Values of each waveband proportion were averaged among 30 measurements obtained under each treatment [unfiltered greenhouse sunlight (control), polyethylene (PE) film, regular-concentration quantum dot film (reg QD film), and high-concentration quantum dot film (high QD film)] using a spectroradiometer. The daily light integral (DLI) and temperature inside each treatment were measured by a quantum sensor and a type-J thermocouple installed at the center of each treatment (three blocks). Data points of the environmental data represent the mean $\pm$ SD over a 21-d treatment period. The phytochrome photostationary state (PSS) was calculated according to the method described by Sager et al. (1988). Different letters indicate significant treatment differences at $P < 0.05$.

B = blue; FR = far-red; NS = not significant; R = red.

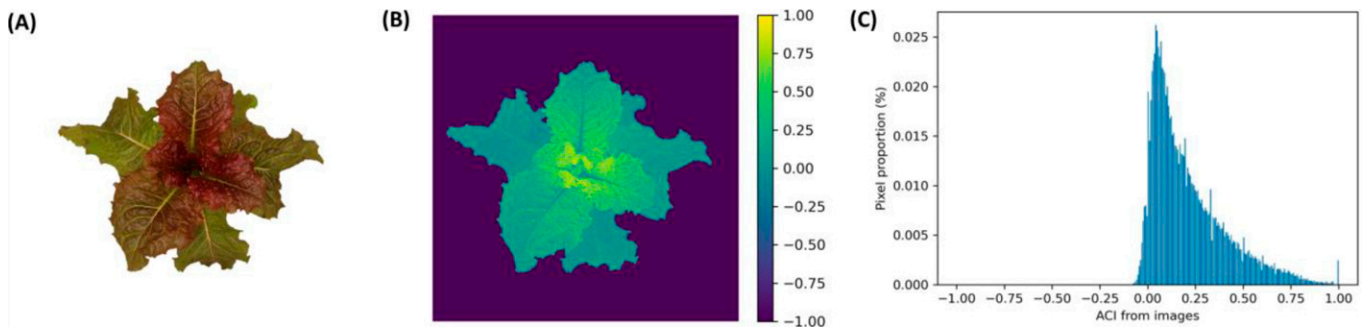


Fig. 2. A red-green-blue (RGB) image of an 'Outredgeous' lettuce plant canopy (A). Image of the normalized difference anthocyanin index (NDAI) (B) and its corresponding histogram (C). The NDAI was analyzed using the Python program developed by Kim and van Iersel (2023). The program extracts the pixel intensity of the green and red channels from the RGB images to calculate NDAI as follows: $(I_{\text{red}} - I_{\text{green}})/(I_{\text{red}} + I_{\text{green}})$, where I is the pixel intensity.

in a randomized complete block design with three blocks (i.e., three repetitions of each treatment). Data from each of the three species/cultivar were analyzed separately using an analysis of variance (Statistical Analysis Systems; SAS Institute, Cary, NC, USA). Mean separation was performed using Tukey's honestly significant difference test to compare means among treatments, with statistical significance set at $P < 0.05$.

Results

Modifications of environmental conditions by the films

Light spectral quality and phytochrome PSS. Significant light spectral shifts were observed under the two types of QD films (Fig. 1; Table 1). Compared with the control treatment, both the QD films resulted in partial conversion of ultraviolet-A and blue light into green, red, and far-red radiation. Under the high QD film treatment, the fraction of blue light relatively decreased by 33% (from 17.26% to 11.64% of the total photon flux density within 320 to 800 nm). In contrast, the fractions of green, red, and far-red relatively increased by 4%, 10%, and 6%, respectively, compared with the control. In the reg QD film treatment, the blue light fraction relatively decreased by 18%, whereas the green, red, and far-red radiation fractions relatively increased by 3%, 6%, and 3%, respectively (Fig. 1; Table 1). The greenhouse polycarbonate covering material poorly transmitted ultraviolet radiation (ultraviolet-A was only 0.21% of the total photon flux density in the control treatment), and the QD films efficiently converted 45% to 76% of ultraviolet-A radiation transmitted into the greenhouse. Compared with the control treatment, the PE film did not significantly alter the light spectral quality. Nonetheless, compared with those of the control and PE film treatments, the spectral shifts of the QD films did not cause significant changes in the phytochrome PSS, which was estimated following the work of Sager et al. (1988) (Table 1).

Daily light integral. The average DLI was highest under the control treatment ($24.3 \pm 6.5 \text{ mol} \cdot \text{m}^{-2} \cdot \text{d}^{-1}$; mean $\pm$ SD), followed by the reg QD film treatment ($21.2 \pm 5.7 \text{ mol} \cdot \text{m}^{-2} \cdot \text{d}^{-1}$), PE film ($20.2 \pm 5.3 \text{ mol} \cdot \text{m}^{-2} \cdot \text{d}^{-1}$), and high

QD Film ($18.9 \pm 5.0 \text{ mol} \cdot \text{m}^{-2} \cdot \text{d}^{-1}$) (Table 1). Compared with that of the control treatment, the average DLIs under the reg QD film, PE film, and high QD film treatments were reduced by $\sim 13\%$, 17% , and 23% , respectively. There were no significant differences in the DLIs among the three treatment blocks.

Air temperature. The films did not significantly affect air temperature (including daily maximum, minimum, and average temperatures), and the average daily temperatures of the four treatments during the experiments were between 23.3 and 23.5°C (Table 1). However, there was a significant block effect on air temperature, with the highest temperature in block 1 ($23.9 \pm 0.27^\circ\text{C}$; farthest from the cooling pad of the greenhouse fan-and-pad cooling system), followed by block 2 ($23.6 \pm 0.25^\circ\text{C}$) and block 3 ($22.8 \pm 0.60^\circ\text{C}$; closest to the cooling pad) (see Supplemental Fig. 1 for the block arrangement).

Biomass production and plant morphology

Shoot fresh weights and dry weights of the control treatment were significantly higher than those of the PE film and reg QD film treatments for both lettuce cultivars, most likely because of the reductions in the DLIs with the PE film and reg QD film treatments (Fig. 3A and 3B). However, there were no significant differences in the shoot fresh weight, shoot dry weight, and total leaf area between the control and high QD film treatments for 'Outredgeous' red lettuce (Fig. 3A–C) despite a 23% reduction in the average DLI of the high QD film treatment compared with that of the control. The total leaf area of both lettuce cultivars tended to be reduced with the PE film and reg QD film compared with that associated with the high QD film and control treatments. The LMA was consistently lower with the three types of film treatments than with the control (Fig. 3D).

Among the three types of film treatments, the high QD treatment yielded significantly higher shoot fresh weight (by 9% to 10%), shoot dry weight (by 8% to 10%), and total leaf area (by 7% to 8%) of 'Outredgeous' red lettuce than the PE film and reg QD film treatments (Fig. 3A–C). For 'Rex' green lettuce, the total leaf area under the high QD film treatment was higher (by 9%) than that of the reg QD film treatment (Fig. 3C). However, no significant differences in the shoot fresh

weight, shoot dry weight, and leaf mass per area were detected among the three film treatments (Fig. 3D). The projected ground area of both lettuce cultivars showed trends similar to that of the total leaf area (Supplemental Fig. 2).

Regarding basil, both the reg QD film and high QD film treatments resulted in shoot fresh weight, shoot dry weight (leaves + stems), and total leaf area similar to those of the control treatment, whereas the PE film treatment resulted in significant reductions in those parameters compared to those of the control treatment (Fig. 3A–C). The LMA of basil grown under the control treatment was significantly higher than that of basil grown under the QD film treatments; however, there was no significant difference between the control and PE film treatments (Fig. 3D). The leaf fresh weight and leaf dry weight of basil under the control treatment were higher than those of basil grown under the PE film and reg QD film treatments; however, there were no significant differences between the control and high QD film treatments (Fig. 4A and 4B). Stem fresh weight and stem dry weight of basil were highest under the high QD film treatment (Fig. 4C and 4D). Basil plants grown under high QD film had similar heights as those grown under the reg QD film, but they were taller than those grown under PE film and control treatments (Fig. 4E). Plants grown under the PE film treatment had fewer leaves than those grown under the control and QD film treatments (Fig. 4F).

Pigmentation analysis

The leaf chlorophyll contents of both 'Rex' lettuce and basil were highest with the control treatment and reduced with the PE film and QD film treatments (Fig. 5). 'Outredgeous' red romaine lettuce had a higher accumulation of anthocyanin when grown under the control treatment, followed by the PE film, reg QD film, and high QD film treatments.

Discussion

Effects of light environment modifications by the QD films on plant morphology and biomass accumulation. The light environment (including light intensity and spectral quality) and temperature are crucial environmental factors that affect plant growth and development

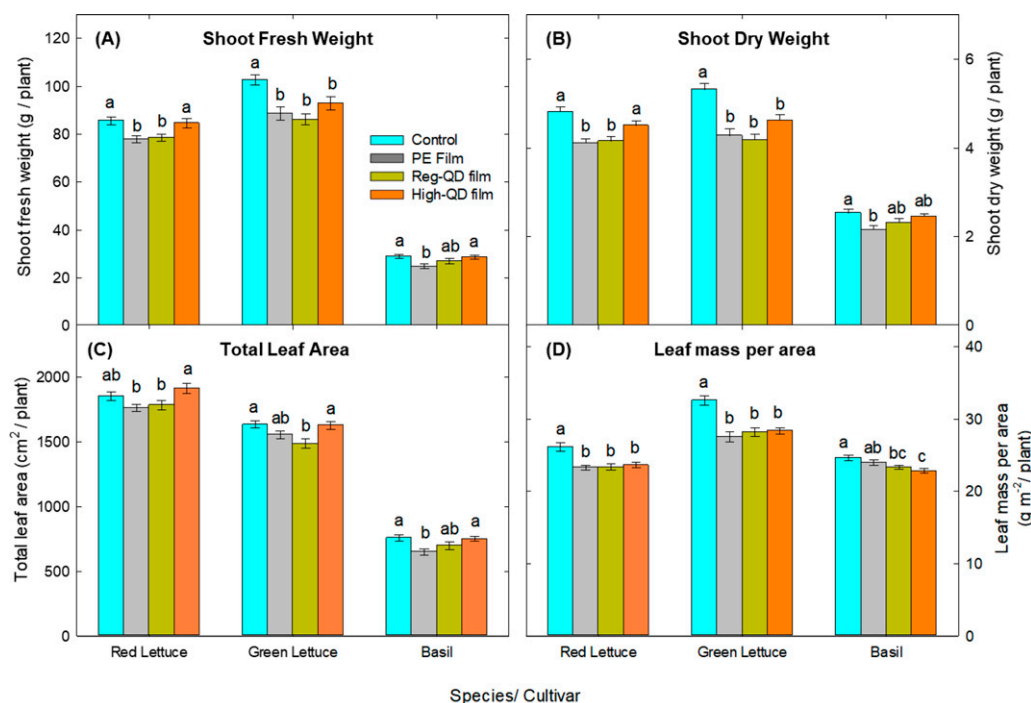


Fig. 3. Shoot fresh weight (A), shoot dry weight (B), total leaf area (C), and leaf mass per area (D) of ‘Outregeous’ red romaine lettuce, ‘Rex’ green butterhead lettuce, and ‘Genovese’ sweet basil grown under four treatments [unfiltered greenhouse sunlight (control), polyethylene (PE) film, regular-concentration quantum dot film (reg QD film), and high-concentration quantum dot film (high QD film)]. Data points represent the mean $\pm$ SE (n = 24; eight plants per treatment $\times$ three blocks). Different letters indicate significant treatment differences within each crop at $P < 0.05$ according to Tukey’s honestly significant difference (HSD) test.

(Bayat et al. 2018; Hatfield and Prueger 2015). We found that both the average DLI and light spectral distribution varied among the four treatments (Fig. 1; Table 1). Specifically, the DLIs under the reg QD film, PE film, and high QD film treatments were reduced by 13% to 23% compared with that of the control, and there were no significant differences in the DLIs among the three film treatments. This is consistent with the findings of previous studies that reported that spectral conversion films cause reductions in light intensity (Hebert et al. 2022; Parrish et al. 2021; Salvador et al. 2008). Although the PE film only reduced light intensity without affecting the light spectral distribution, the QD films converted a portion of blue photons into green, red, and far-red photons, with a greater degree of spectral shift under the high QD film treatment (Fig. 1; Table 1). Despite the modifications of the light environment by the QD and PE films, air temperatures were similar across all four treatments (Table 1).

The reduction in the DLI under the PE film treatment without solar spectral modifications led to reduced shoot biomass production in all three crops compared with the control (Figs. 3A and 3B). This was expected because the photosynthetic rate and biomass production generally decrease as the DLI decreases (Dou et al. 2018; Huber et al. 2021; Modarelli et al. 2022; Sutulienė et al. 2022). In contrast with the responses under the PE film treatment, although the DLI under the high QD treatment was 23% lower than that under the control treatment (Table 1), shoot fresh weight, shoot dry weight, and total leaf

area of red lettuce and basil grown under the high QD film treatment were similar to those grown under the control treatment (Fig. 3). This was most likely attributable to the greater spectral shift under the high QD film (i.e., a decrease in the proportion of ultraviolet-A and blue photons and a simultaneous increase in the green, red, and far-red regions) (Fig. 1). Hebert et al. (2022) reported that tomatoes grown under similar QD films showed a 10% increase in the vegetative growth rate, a 36% reduction in unmarketable fruit waste (because of fruit cracking), and a 5.7% increase in yield per unit production area despite a 14% decrease in the DLI compared with that of the control treatment without the QD film.

All three crops grown under the control treatment exhibited the highest LMA, indicating greater leaf thickness (Fig. 3D). Formisano et al. (2021) reported that higher light intensity resulted in several physiological and morphological adaptations, including increased leaf thickness and a more compact canopy. Another study reported that increasing the proportion of blue photons from 8% to 30% resulted in an increased LMA of cucumber and tomato under a high PPFD treatment of 500 $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ (Gommers et al. 2013). During our study, no significant differences in the LMA were detected in either lettuce cultivar among the PE film, reg QD film, and high QD film treatments, despite a lower blue light fraction under the QD film treatments. The LMA of basil plants grown under the PE film treatment was significantly higher than that of those grown under the high QD film treatment. This significant difference in

LMA of basil suggests that basil has greater sensitivity to spectral shifts caused by QD films.

Even though the solar spectrum was also shifted from blue to longer wavelength regions under the reg QD film treatment, the magnitude of the spectral shift was much smaller than that under the high QD film. As a result, no significant growth differences were observed in all three crops grown under the reg QD film treatment compared with those grown under the PE film treatment, and reductions in the total biomass and leaf area compared with those of the control treatment were observed. Because the PE film, reg QD film, and high QD film reduced the DLI by similar amounts, these results suggested that the effects of QD films on plant growth and morphology are dependent on the magnitude of the light spectral shift. Unlike that under the high QD film treatment, the magnitude of the spectral shift under the reg QD film treatment was not sufficient to compensate for the reduction in the DLI during this experiment.

Spectral shifts under QD films regulate cryptochrome-mediated plant responses. Light spectral quality is perceived by photoreceptors, such as phytochromes and cryptochromes, and regulates a wide range of plant responses mediated by these photoreceptors. Despite significant spectral shifts under the reg and high QD film treatments (compared with those under the control and PE film treatments), the PSS remained consistent across all four treatments. However, we observed distinct differences in plant growth and morphology among the

Sweet basil 'Genovese'

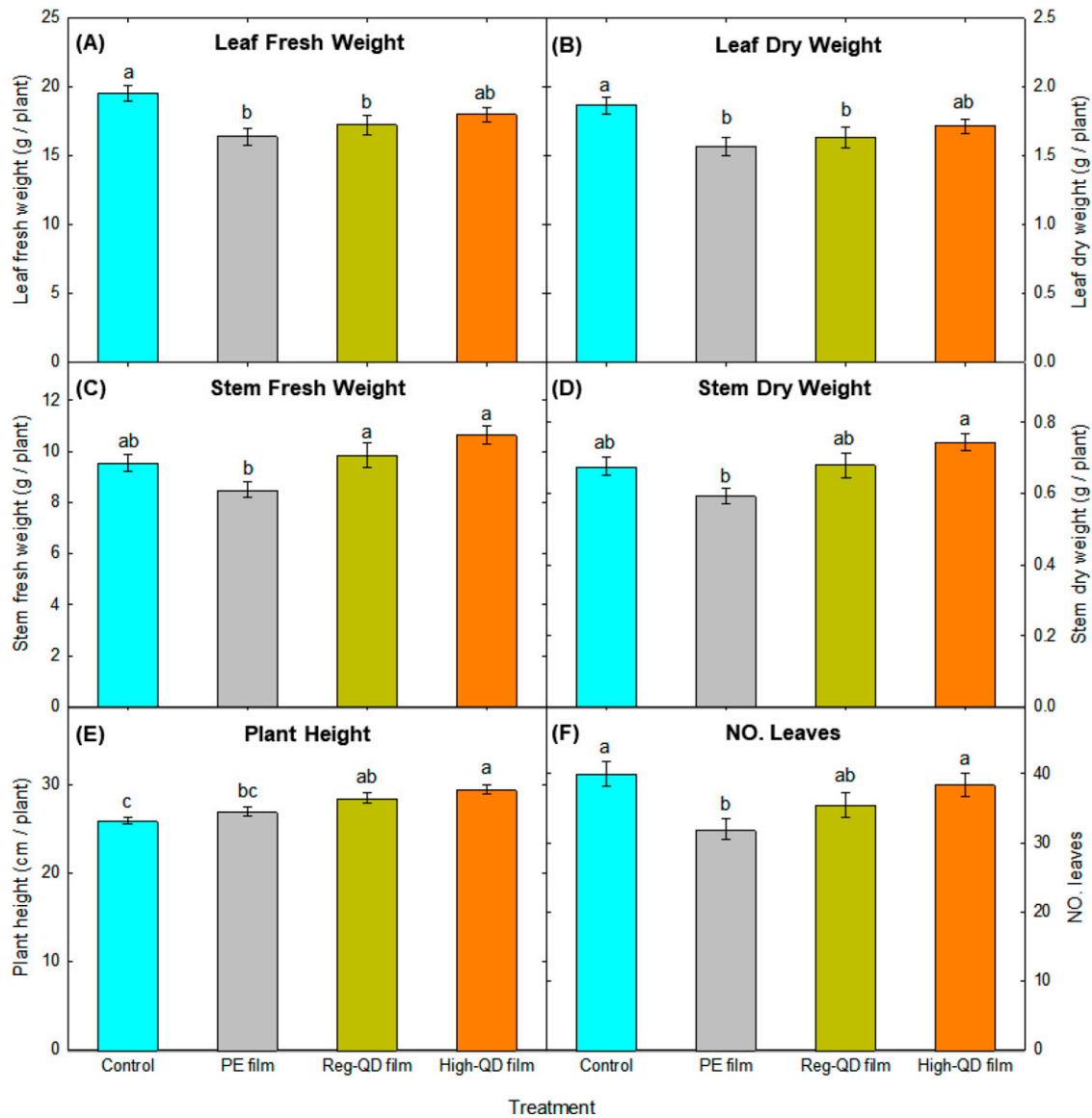


Fig. 4. Leaf fresh weight (A), leaf dry weight (B), stem fresh weight (C), stem dry weight (D), plant height (E), and number of leaves (F) of 'Genovese' sweet basil grown under four treatments [unfiltered greenhouse sunlight (control), polyethylene (PE) film, regular-concentration quantum dot film (reg QD film), and high-concentration quantum dot film (high QD film)]. Data points represent the mean $\pm$ SE ($n = 24$; eight plants per treatment $\times$ three blocks). Different letters indicate significant treatment differences at $P < 0.05$ according to Tukey's honestly significant difference (HSD) test.

treatments for all three crops. For basil plants grown under the high QD film treatment, significant increases in the plant height, stem fresh weight, stem dry weight, number of leaves, and total leaf area compared with those associated with the PE film treatment were detected (Figs. 3C and 4C–F). Because the DLI and PSS were similar under the PE film and QD film, this morphological change in basil was most likely attributable to cryptochrome deactivation because the blue light fraction within the 320- to 800-nm spectral range decreased from 16.9% under the PE film to 11.6% under the high QD film (Table 1). Prior studies reported that shade avoidance responses, which are primarily triggered by green and far-red photons, can induce increased stem elongation and leaf expansion and enhance light capture at the plant canopy level (Kim et al. 2004; Meng and

Runkle 2019; Pierik and de Wit 2013; Robson et al. 1993; Smith et al. 2017; Zhen and Bugbee 2020a,b). Although basil grown under high QD film exhibited typical symptoms of the shade avoidance responses, and although green and far-red light were relatively enriched under the high QD film, the ratio of red to far-red light and PSS remained similar among all four treatments because the fraction of red light also increased along with that of far-red light under the QD films. Therefore, the increased stem elongation and leaf expansion of basil under the high QD film were likely not caused by the effects of phytochromes; instead, they were likely caused by cryptochrome deactivation. Ultraviolet-A and blue photons are widely known to activate cryptochromes, leading to a decrease in hypocotyl (and stem) elongation and leaf area, resulting in more compact

plants (Meng et al. 2020; Ohashi-Kaneko et al. 2007; Son and Oh 2013).

Green photons, which stimulate the shade avoidance responses, can deactivate cryptochromes (Battle et al. 2020; Bouly et al. 2007; Kusuma et al. 2021; Müller and Ahmad 2011). During a short-term experiment, Bouly et al. (2007) reported that wild-type *Arabidopsis* seedlings exposed to blue photons (445 nm) for only 48 h showed reduced hypocotyl lengths and higher anthocyanin concentrations compared with those of seedlings grown under a mixture of blue and green photons. Meng et al. (2019) showed that decreasing blue photons from 60 to 0 $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ while simultaneously increasing green photon flux from 0 to 60 $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ (i.e., substituting green for blue photons) resulted in more leaf expansion and higher biomass production in green

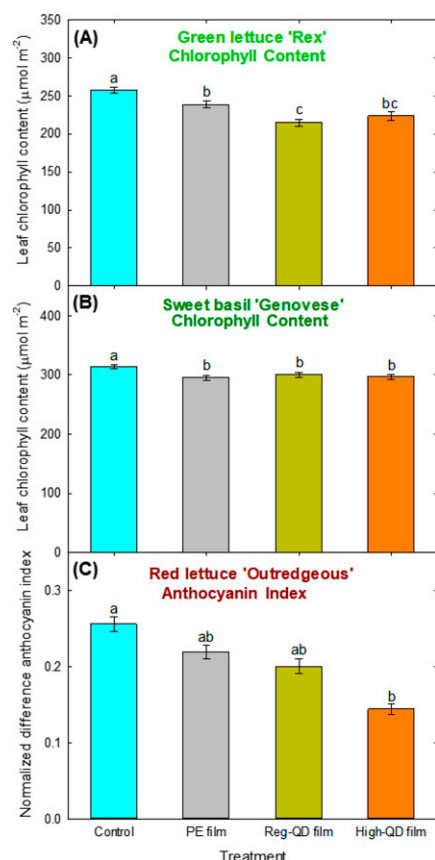


Fig. 5. Leaf chlorophyll content of 'Rex' green lettuce (A) and 'Genovese' sweet basil (B) and normalized difference anthocyanin index (NDAI) of 'Outregeous' red lettuce (C) grown under four treatments [unfiltered greenhouse sunlight (control), polyethylene film (PE film), regular-concentration QD film (reg QD film), and high-concentration QD film (high QD film)]. Data points represent the mean $\pm$ SE ($n = 24$; eight plants per treatment $\times$ three blocks). Different letters indicate significant treatment differences at $P < 0.05$ according to Tukey's honestly significant difference (HSD) test.

and red lettuces and kale during long-term crop cultivation under LEDs. In this study, we observed a slight increase in green photons but a significant decrease in the blue photon fraction under the high QD film treatment. Despite having a significantly lower DLI under the high QD film treatment, plant biomass was comparable to that under the control treatment, especially that of red leaf lettuce and basil (Fig. 3). This was likely attributable to enhanced leaf expansion and radiation capture because the total leaf area was highest under the high QD film treatment in all crops. Our findings of red and green lettuces and basil indicated that the reduced DLI under the high QD film treatment may be offset by the spectral shift that promotes cryptochrome deactivation.

Pigmentation was affected by both light intensity and spectral quality. We observed the highest chlorophyll and anthocyanin contents in the control treatment with unconverted greenhouse sunlight (Fig. 4), which might have resulted from the combined effects of the higher DLI and higher blue photon

fraction compared with those of the PE and QD film treatments. The chlorophyll content tends to increase under higher light intensity; for example, Snowden et al. (2016) found that a higher light intensity of $500 \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ resulted in an increased chlorophyll concentration in seven species/cultivars, including green lettuce, compared with that associated with a lower light intensity of $200 \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$.

Under high blue light, active cryptochromes inhibit leaf expansion and stem extension but promote pigments, including chlorophylls and anthocyanins (Bouly et al. 2007; Kusuma et al. 2021; Park and Runkle 2023; Snowden et al. 2016). A reduction in the blue light fraction under the QD films likely led to reduced cryptochrome activities. Among PE and both QD film treatments (which had similar DLIs), green leaf lettuce grown under the reg QD film and high QD film treatments (with reduced blue light fractions) tended to have reduced leaf chlorophyll contents compared with those of plants grown under the PE film (Fig. 5A). The leaf chlorophyll contents of green and red leaf lettuces and kale grown under LEDs decreased as blue photons decreased from 60 to $0 \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ (Meng et al. 2019). Similarly, Hogewoning et al. (2010) reported that the leaf area-based chlorophyll content in cucumber decreased with the decreasing blue light fraction (from 50% to 0%) under a red background light. Even though these previous studies were conducted in climate-controlled growth rooms using LEDs rather than in a greenhouse, the trends of the chlorophyll responses mirrored the responses of green lettuce to spectral shifts under QD films. No significant differences in the chlorophyll contents were observed in sweet basil grown under the PE, reg QD film, and high QD film treatments (Fig. 5B), which indicated varying sensitivity to blue light among species.

The anthocyanin index in red leaf lettuce exhibited a pattern similar to that of the responses of the chlorophyll content. In red leaf lettuce, the anthocyanin index was highest in the control group, followed by the PE film, reg QD film, and high QD film treatment groups (Fig. 5C). Our findings aligned with those of a previous study that used a Laboratory color space analysis as an indicator of anthocyanin accumulation and found that 'Rouxai' red lettuce exhibited reduced anthocyanin accumulation as the blue photons decreased from 60 to $0 \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ (Meng et al. 2019). Other studies reported that blue light promotes anthocyanin production by stimulating cryptochromes (Giliberto et al. 2005; Li and Kubota 2009; Meng et al. 2004). Meng et al. (2004) found that blue photons promoted the gene expression of chalcone synthase and dihydroflavonol-4-reductase, which are key regulators of the anthocyanin pathway. Both the lower DLI and reduced blue photon fraction under the high QD film treatment may result in reduced activation of cryptochromes compared with that of the control treatment. A reduction in the anthocyanin content in plants grown under QD films should be considered because higher anthocyanin accumulation in red leaf

lettuce and other red-colored leafy vegetables is generally desirable.

Implications for the development of novel greenhouse glazing materials. Our results suggested that a sufficient magnitude of spectral red shift can overcome DLI loss and lead to leaf expansion and yield increases. However, the DLI loss of the QD film itself (and that of the control PE film) is clearly responsible for the initial yield loss observed with the PE film and reg QD film during this study. For the greenhouse industry, direct incorporation of QDs into the façade materials of greenhouses would lead to minimal intensity loss if applied as an added layer in an extruded PE cover, rather than being applied as an additional internal layer within an existing greenhouse. This may lead to the realization of the benefit of spectral red shifting without the DLI loss. Additionally, QDs could potentially be applied as an inner layer of a glass, acrylic, or polycarbonate greenhouse glazing.

Conclusion

Overall, we found that spectral shifts caused by QD films (i.e., a reduction in the blue light fraction and increases in green, red, and far-red fractions) promoted leaf expansion and stem elongation of red and green lettuces and basil. The morphological changes induced under the high QD film resulted in improved radiation capture and plant yield compared with those of plants grown under PE film with similar light intensity but without spectral shifts. However, all three films (PE film, reg QD film, and high QD film) resulted in a reduction in light intensity. This reduction in light intensity under the PE film and reg QD film decreased plant yield compared with that under the control (i.e., unfiltered greenhouse sunlight). In contrast, the high QD film resulted in plant yield comparable to that of the control despite a 23% reduction in DLI under the high QD film. This likely indicates that the stimulative effects of the spectral shift by the high QD film compensated for the reduction in the DLI. This experiment was conducted with films located within the greenhouse, which resulted in light interacting with two layers of material (i.e., the greenhouse covering material and the treatment QD film). By directly integrating QDs in the greenhouse covering material (e.g., PE films), increased crop yield and morphological improvements may be expected because of the spectral shift and increased ultraviolet light availability attributable to the QDs without reductions in the DLI.

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