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An Experimental Red Fluorescent Film Has Cultivar-specific Effects on Lettuce Yield and Morphology

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Abstract. **Glazing and covering materials used in protected cultivation (PC) are primarily selected based on cost, longevity, heat retention, and light transmission. They can also be engineered to modify transmission of the solar spectrum by the incorporation of fluorescent pigments. Fluorescent pigments typically absorb blue (B; 400–499 nm) and/or green (G; 500–599 nm) photons and emit longer wavelength red (R; 600–699 nm) and, to a lesser extent, far-red (FR; 700–750 nm) photons. However, the incorporation of fluorescent pigments into plastics typically decreases its transmission of photosynthetically active radiation (PAR; 400–700 nm). In small-scale studies, 'Butter Crunch' lettuce (*Lactuca sativa*) shoot fresh mass (SFM) increased by as much as 22% when grown under a red fluorescent (RF) film compared with that grown under an unpigmented film with approximately 25% greater transmission of PAR. The objective of this research was to quantify variation among five lettuce cultivars when grown under a similar experimental RF film in a small-scale and larger-scale greenhouse experiment. Lettuce was grown under an RF film or neutral-density shade that provided a 15% to 24% greater average daily light integral (DLI). The SFM of lettuce increased by up to 45% and yield (SFM per m^2) increased by up to 37% when grown under the RF film, but the magnitude of increase was cultivar-specific. The SFM increase was linearly correlated with the increase in single leaf area but not projected canopy area. This work demonstrates the potential of an RF film to increase the yield of some (but not all) lettuce cultivars compared with neutral-density shade materials. However, further research is necessary to explore potential benefits for other greenhouse crops and changes to crop morphology.**

In the protected cultivation (PC) of specialty crops, the microenvironment is managed to regulate plant growth and development (Reddy 2016; Wittwer and Castilla 1995). This encompasses a variety of agricultural covering materials, including, but not limited to, shade structures, high tunnels, and greenhouses. Covering materials are used to protect crops from unfavorable environmental conditions and are often composed of plastic, fabric, or glass (Wittwer and Castilla 1995). These PC coverings have been engineered to transmit, reflect, absorb, and/or fluoresce solar energy (Hemming 2011). Photoselective materials differentially absorb or reflect portions of the electromagnetic spectrum (Stamps 2009). For example, photoselective coverings that absorb far-red (FR; 700–750 nm) light can inhibit the stem elongation of poinsettia (*Euphorbia pulcherrima*), pea (*Pisum sativum*), and pansy (*Viola ×wittrockiana*) (Clifford et al. 2004; Runkle and Heins 2001). Other photoselective covers absorb red (R; 600–699 nm) or blue B; 400–499 nm) light and alter plant morphology (Lamnatou and Chemisana 2013a; Rajapakse et al. 1999). Materials that absorb ultraviolet (ultraviolet-A and ultraviolet-B; 280–400 nm) radiation can decrease disease pressure and improve plastic lifespan (Edser 2002; Lamnatou and Chemisana 2013b), while others absorb near-infrared (780–3000 nm) radiation and decrease heat transmission to plants and evapotranspiration (Runkle et al. 2002; Sonneveld et al. 2006).

Fluorescent PC coverings absorb high-energy, shorter-wavelength photons and emit photons at longer, less-energetic wavelengths, thus "shifting" the transmission spectrum (Lamnatou and Chemisana 2013a; Pearson et al. 1995). Various approaches are used to shift photons in the ultraviolet, B, or green (G; 500–599 nm) wavebands into longer-wavelength photons, which can improve crop growth in some cases (Edser 2002; Parrish et al. 2021; Raviv 1989; Shen et al. 2021). Most commonly, fluorescent covers increase the photon flux density of R photons but decrease in total photosynthetic photon flux density (PPFD; 400–700 nm). Although these red fluorescent (RF) coverings have increased crop biomass accumulation in some small-scale experiments, questions remain about their efficacy, life span, and economic viability for diverse horticultural crops.

Isolated and purified chlorophyll a (Chl a) and chlorophyll b (Chl b) pigments primarily absorb R light and B light and are the predominant pigments driving photosynthesis (Heldt and Piechulla 2021). At low light intensities, R light can increase instantaneous photosynthesis by as much as 25% more than B light or G light (Bugbee 1994; Inada 1976; McCree 1971). Specifically, R light more efficiently assimilates CO_2 (or evolves O_2) per photon absorbed (i.e., the quantum yield for CO_2 fixation) compared with B or G light. Because of the high efficacy of R light at driving photosynthesis, researchers extrapolated that PC covers that increased R light at the expense of less efficient B light and G light by fluorescence could increase the photosynthetic efficiency of crops and, thus, increase biomass accumulation (Raviv 1989). However, solely focusing on Chl a and Chl b and the quantum yield of R light ignores other important photosynthetic factors. Inada (1976) and McCree (1971) quantified the relative quantum efficiency for a wide range of crops using monochromatic light at low photon flux densities. Extrapolating and applying their curves, most typically the average curve of multiple plant species, to polychromatic light or higher photon flux densities is hypothetical (Bugbee 2016; Hogewoning et al. 2012). Although G light may not be as photosynthetically effective as R light, it has a better ability to penetrate leaves and crop canopies, which can drive photosynthesis lower in mesophyll cells of individual leaves and lower leaves of a plant (Smith et al. 2017). Focusing on Chl a and Chl b also ignores accessory pigments, such as carotenoids, which absorb G light and contribute energy that drives photosynthesis (Ouzounis et al. 2015). Questions remain about the relative efficacy of R light compared with other photosynthetically active wavebands; therefore, further research is needed to determine whether amplified R light, at the expense of less photosynthetically active radiation (PAR), can increase biomass.

The photoreceptor families of phytochrome and cryptochrome photoselectively absorb light and mediate photomorphological responses (Ouzounis et al. 2015). Phytochromes primarily absorb R and FR photons and exist in a dynamic continuum between the active form (Pfr) and inactive form (Pr)

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called phytochrome photoequilibrium (PPE). Inactive Pr primarily absorbs R light and alters its conformation into the Pfr form. Alternatively, active Pfr slowly reverts into inactive Pr in darkness or by absorbing FR light. Therefore, the R:FR of an incident spectrum regulates plant PPE, with a high R:FR creating a high PPE, and vice versa (Sager et al. 1988). The PPE is estimated using the equation [Pr/(Pr+Pfr)], spectral irradiance between 300 to 800 nm, and the absorption spectra of Pr and Pfr (Sager et al. 1988). A low PPE (low R:FR) can promote shade-avoidance responses such as stem and leaf elongation, hyponasty, apical dominance, early flowering, and decreased chlorophyll density (Franklin 2008; Ouzounis et al. 2015). The PC covers that increase the R:FR by reflecting or absorbing FR can reduce shade-avoidance responses and inhibit unwanted extension growth of ornamental crops such as poinsettia and pansy (Clifford et al. 2004; Runkle and Heins 2001). Similarly, increasing the photon flux density of R, but not FR light, as in the case of many fluorescent greenhouse plastics, increases the R:FR and potentially inhibits extension growth.

Cryptochromes primarily absorb ultraviolet light and B light and inhibit stem and leaf elongation and promote anthocyanin biosynthesis (Kusuma et al. 2021; Li and Yang 2007; Ouzounis et al. 2015). Low-intensity B light, indicative of vegetative shading, can induce shade-avoidance responses such as greater stem elongation, reduced branching, and increased leaf area (Franklin 2008). Increasing stem elongation and leaf area has been correlated with increasing dry mass accumulation of lettuce and tomato using light-emitting diodes (LEDs) in growth chambers without sunlight (Kusuma et al. 2021). While controlling the light environment is more difficult in a PC system than in an indoor space, a photoselective PC material that decreased transmission of B light increased stem elongation of the floriculture crops pansy, lobelia (*Lobelia* ×*speciosa*), campanula (*Campanula carpatica*), and coreopsis (*Coreopsis* ×*grandiflora*) compared with a neutral-density (ND) shade material inside a greenhouse (Runkle and Heins 2001). Because RF PC materials reduce the transmission of B light, it could be postulated that plants will have longer stems and greater leaf area, thus increasing crop biomass accumulation though greater light interception.

Red pigmentation is a desirable quality attribute of some horticultural crops, including red-leaf lettuce cultivars. In part, leaf pigmentation is regulated by the photon distribution and PPFD (Meng et al. 2020; Steyn et al. 2002). Generally, increasing the proportion of B, ultraviolet-A, and ultraviolet-B photons in a spectrum or increasing the PPFD increases leaf chlorophyll and anthocyanin concentrations in a dose-dependent manner (Meng et al. 2020; Snowden et al. 2016). Increased red pigmentation (i.e., increased anthocyanin concentration) in leaves acts as a defense mechanism against photoinhibition, which can occur when plants are grown under stressful conditions such as a high PPFD (Steyn et al. 2002). In theory, RF covers that decrease the flux of transmitted B photons and PPFD should cause lettuce to develop leaves with lower anthocyanin concentrations, which could detract from overall crop quality.

There is growing interest in the technological advancement of PC coverings that alter the solar spectrum to increase plant growth. Recently, an experimental RF plastic film that down-converted some B and G photons into R photons was developed that increased the shoot fresh mass (SFM) of indoor-grown lettuce (*Lactuca sativa*) by 19% to 22% and greenhouse-grown lettuce by 22% to 30% compared with a nonpigmented control with 20% to 25% greater transmitted PPFD (Shen et al. 2021). Despite promising results by Shen et al. (2021), more research is needed to determine crop-specific and cultivar-specific responses to RF films. We grew five lettuce cultivars under an experimental RF film used by Shen et al. (2021) and compared growth responses to those under a ND PC covering. We postulated that the RF film would: 1) increase lettuce biomass accumulation because R light more efficiently drives photosynthesis than B light or G light (at least on an instantaneous basis); 2) decrease red pigmentation of red-leaf lettuce because of decreased transmission of B light; and 3) increase the leaf size of lettuce because of the decrease in transmitted B light.

Materials and Methods

Expt. 1. Small greenhouse chambers

Lettuce seedling culture. ‘Rex’ and ‘Cherokee’ lettuce seeds (Johnny’s Selected Seeds, Winslow, ME, USA) were sown in Rockwool cubes (AO 25/40; Grodan, Milton, Ontario, Canada) in a 23 °C controlled environment growth room at an ambient CO_2 concentration. Seedlings germinated under an 18-h photoperiod with a PPFD of 180 $\mu mol \cdot m^{-2} \cdot s^{-1}$ from 2700 K warm-white LEDs (PHYTOFY RL; OSRAM, Beverley, MA, USA) as controlled by proprietary PHYTOFY control software. Seedlings received irrigation as needed using deionized water and hydroponic water-soluble 12N–4P–16K RO fertilizer (Hydro FeED; JR Peters, Inc., Allentown, PA, USA) and magnesium sulfate (Pennington Seed Inc., Madison, GA, USA) that provided the following nutrients (in $mg \cdot L^{-1}$): 125 nitrogen (N), 42 phosphours (P), 167 potassium (K), 73 calcium (Ca), 49 magnesium (Mg), 39 sulfur (S), 1.7 iron (Fe), 0.52 manganese (Mn), 0.56 zinc (Zn), 0.13 boron (B), 0.47 copper (Cu), and 0.13 molybdenum (Mo). The fertilizer solution pH and electrical conductivity (EC) were measured after the formulation of a stock solution with a handheld meter (HI9814; Hanna Instruments, Woonsocket, RI, USA) and adjusted to a pH of 5.8 and EC of 1.2 $mS \cdot cm^{-1}$. Transparent plastic humidity domes covered the germinating seedlings for the first 4 d (until radical emergence). Seedlings for replications 1 and 2 grew for 10 d, until seedlings had two true leaves and were ready for transplant.

Chamber coverings and design. The experimental RF film was a 210-μm-thick polymethyl methacrylate plastic that contained a fluorescent plastic additive (Lumogen F Red 305; BASF, Ludwigshafen, Germany) which down-converted B and G photons into R and FR photons (Shen et al. 2021). The fluorescent pigment had a peak absorption at 576 nm and peak emission at 617 nm. The ND material was identical to the RF film but did not include a fluorescent plastic additive. Both films were covered with microstructures to increase total light transmission that consequently increased light diffusion (increase photon scattering). The full preparation of the RF and ND films was described by Shen et al. (2021).

Four chambers were fabricated with 1.3-cm-diameter polyvinyl chloride pipe and four opaque 1.3-cm-thick insulation sheets and placed on aluminum benches inside a glass-glazed research greenhouse (42.7°N lat.) (Fig. 1A). Each chamber was 107 cm wide × 236 cm long × 51 cm tall, with a total volume of 1.3 m^3. A single piece of transparent 64-mm-thick clear acrylic sheeting functioned as the roof of each chamber. The experimental RF film covers comprised individual 24-cm × 15-cm pieces that were taped onto the underside of the acrylic sheet roof with black electrical tape. Each south-facing wall had a 6-$m^3 \cdot min^{-1}$ fan (Axial 1751; AC Infinity Inc., City of Industry, CA, USA) that exchanged the air volume in each chamber 4.6 times per minute to improve temperature uniformity inside each chamber. To improve light uniformity and minimize shadows cast by the chamber walls, only a 112-cm × 55-cm area (0.62 m^2) in the middle of each chamber was used to grow plants. Additionally, chamber interior walls were painted with flat white paint to improve light scattering within chambers. Air temperature and instantaneous PPFD in each chamber were measured by a shielded and aspirated type E thermocouple (Omega Engineering, Inc., Stamford, CT, USA) and a quantum sensor (LI-190SA; LI-COR, Inc., Lincoln, NE, USA; or SQ-500; Apogee Instruments, Inc., Logan, UT, USA). Environmental conditions inside each chamber were measured every 1 min and averaged hourly with a datalogger (CR-1000; Campbell Scientific, Inc., Logan, UT, USA) and multiplexer (AM16/32B; Campbell Scientific, Inc.). Two chambers were covered with an ND or RF film.

A portable spectroradiometer (LI-180 Spectrometer; LI-COR, Inc.) was used to measure light transmission through films at canopy height on a cloudless day at solar noon on 7 Nov 2019. The total photon flux density) of extended PAR (400–750 nm) transmitted through the ND and RF experimental films are displayed in Table 1 and Fig. 1B. The ND film evenly reduced the photon flux density at each nanometer while the RF film absorbed most of the B light and G light and fluoresced it as R light and FR light at a peak wavelength of 648 nm.

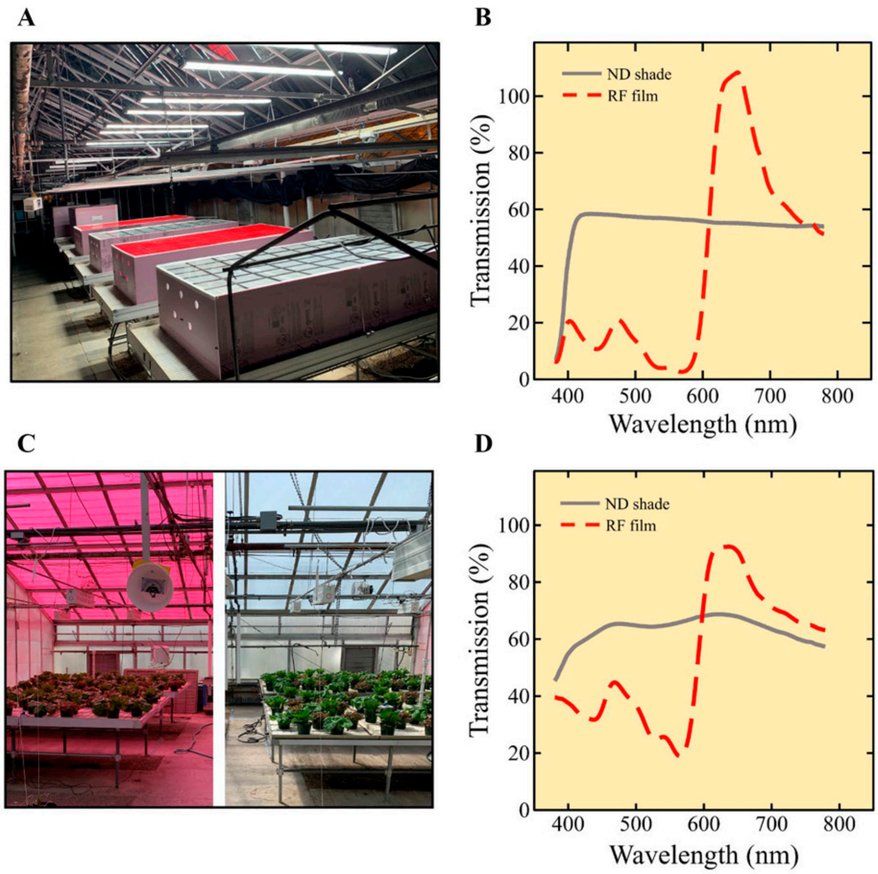

Fig. 1. Experimental setup for the small chamber trial (Expt. 1) (**A** and **B**) and greenhouse trial (Expt. 2) (**C** and **D**). In Expt. 1, two chambers were covered with a neutral-density (ND) shade or red fluorescent (RF) film. In Expt. 2, one greenhouse was covered with whitewash and an identical greenhouse was covered with the RF film. Transmission spectra in (**B**) and (**D**) were measured at solar noon.

Compared with the ND film, the RF film decreased the transmission of B and G photons by 73% and 88%, respectively, while it increased the transmission of R and FR photons by 58% and 44%, respectively.

Greenhouse environment. Temperature and supplemental lighting were controlled by a greenhouse environmental control system (Integro 725; Priva, De Lier, the Netherlands) with setpoints at 19 °C and a 16-h photoperiod. Steam heating, roof vents, and exhaust fans regulated air temperature. Supplemental lighting was provided from luminaires (ILM-PG-180-2-300W-ED-FS-60; Rofianda Trading BV, Tilburg, the Netherlands) containing SunLike LEDs (STW9C2SB-S; Seoul Semiconductor Co., Gyeonggi-do, South Korea) that emitted a PAR spectrum similar to sunlight. The LEDs provided an average PPFD of 190 ± 15 $\mu mol \cdot m^{-2} \cdot s^{-1}$ at the chamber roof surface and operated from 0600 HR to 1000 HR in the morning and 1800 HR to 2200 HR in the evening each day.

Table 1. Transmission characteristics of protected cultivation covering materials measured with a spectroradiometer inside a glass-glazed greenhouse at solar noon.

	Expt. 1		Expt. 2	
	Covering material			
Transmission characteristic	ND[iv]	RF[v]	ND	RF
TPFD ($\mu mol \cdot m^{-2} \cdot s^{-1}$; 400–750 nm)[i]	696	543	1041	878
Blue (% of TPFD; 400–499 nm)	22	8	23	16
Green (% of TPFD; 500–599 nm)	30	5	31	17
Red (% of TPFD; 600–699 nm)	32	65	32	48
Far red (% of TPFD; 700–750 nm)	16	23	15	19
PPE[ii]	0.72	0.76	0.73	0.74
iPPE[iii]	0.40	0.45	0.42	0.42

[i] Average total photon flux density (TPFD; 400–750 nm) was measured at canopy height at solar noon.
[ii] Phytochrome photoequilibrium (PPE) calculated according to Sager et al. (1988).
[iii] Internal phytochrome photoequilibrium (iPPE) calculated according to Kusuma and Bugbee (2021).
[iv] A neutral-density (ND) covering material that did not alter solar spectrum.
[v] A red fluorescent (RF) covering material that down-converted blue and green photons into red and far-red photons.

Plant culture. 'Cherokee' and 'Rex' lettuce seedlings were transplanted into each of four experimental chambers inside the greenhouse on 6 Oct 2019 and 13 Nov 2019 for replication 1 and 2, respectively. Both cultivars were transplanted into a Delta 6.5 Rockwool hydroponic substrate (Grodan) and placed on plastic trays at a density of 310 cm^2 per plant. Plants received sub-irrigation with fertilizer as described previously but at (in $mg \cdot L^{-1}$) 150 N, 50 P, 200 K, 88 Ca, 58 Mg, 47 S, 2.1 Fe, 0.63 Mn, 0.68 Zn, 0.15 B, 0.56 Cu, and 0.15 Mo. Irrigation pH and EC were measured at irrigation events with a handheld meter (HI9814; Hanna Instruments), with averages of 5.7 ± 0.1 and 1.4 ± 0.2 $mS \cdot cm^{-1}$, respectively. Lettuce plants grew in each chamber for 30 d until destructive measurements on 5 Nov 2019 and 13 Dec 2019 for replication 1 and 2, respectively.

Plant data collection. During destructive plant measurements, SFM was measured with a digital scale (GR-200; A&D Store, Inc., Wood Dale, IL, USA). Then, shoots were dried in a drying oven (Blue M; Blue M Ovens, New Columbia, PA, USA; or SMO28-2; Sheldon Manufacturing, Inc., Cornelius, OR, USA) for 4 d at 60 °C and weighed using a digital scale (GX-1000; A&D Store, Inc.). Relative chlorophyll content [Soil Plant Analysis Development (SPAD) index] was averaged from three measurements per plant and measured with a handheld chlorophyll meter (MC-100; Apogee Instruments, Inc.). The CIELAB color was averaged from three measurements per plant with a handheld colorimeter (Chroma Meter CR-400 or BC-10 Plus; Konica Minolta Sensing America, Inc., Ramsey, NJ, USA). The International Commission on Illumination Laboratory color space values L^*, a^*, and b^* correspond to lightness from black (0) to white (100), green (−) to red (+), and blue (−) to yellow (+), respectively. The projected canopy area (PCA; cm^2) was measured using top-down photos and ImageJ software (Rasband 2023). Lettuce yield was calculated by dividing SFM by PCA and converted to units of $kg \cdot m^{-2}$. Specific leaf area of the most recent fully expanded leaf was calculated by dividing its area measured with a leaf area meter (LI-3000; LI-COR) by its dry mass (g). Radiation use efficiency was calculated by dividing shoot dry mass by the total intercepted light integral (400–700 nm; $mol \cdot m^{-2}$). The total intercepted light integral was calculated by multiplying total light integral ($mol \cdot m^{-2}$ photon) in each treatment by the PCA of each plant. Tipburn severity index was calculated as $\{[(S*5)+(M*3)+(L*1)]*100\}/P*5$, where S is the number of plants with severe tip burn, M is the number of plants with moderate tipburn, L is the number of plants with minor tipburn, and P is the total number of plants (Frantz et al. 2004).

Experimental design and data analysis. The experiment was a randomized complete block design with two replications over time. Each block contained two chambers, with one roofed with either the ND or RF film. Each chamber was randomly assigned 10 'Cherokee' and 10 'Rex' lettuce plants, for a total of 80 plants per replication (20 plants per chamber per replication), resulting in a total of 40.

Data were pooled because there were no significant ($P > 0.05$) treatment × replication or treatment × block interactions for any growth parameters measured. Data were analyzed using R software (R Core Team 2023) using an analysis of variance (ANOVA) and Students *t* test at $\alpha = 0.05$. Highly influential outliers were evaluated and removed when they exceeded Cook's distance = 0.5. A linear regression analysis of the average percentage change in lettuce SFM as a function of percentage change in single leaf area of lettuce grown under an ND shade or an RF film was conducted.

Expt. 2. Greenhouse trial

Lettuce seedling culture. 'Rouxai', 'Dragoon', and 'Butter Crunch' lettuce seeds (Johnny's Selected Seeds) were germinated in Rockwool cubes (same as in Expt. 1) in a 23 °C controlled environment growth room at ambient CO_2 concentration. Seedlings were grown using the same nutrient solution, photoperiod, PPFD, and humidity domes as in Expt. 1. However, a different warm-white LED (RAY22; Fluence, Austin, TX, USA) was used for germination. Seedlings grew for 8 d, from 10 Mar 2022 to 18 Mar 2022, until they had two true leaves and were ready for transplant.

Greenhouse trial setup. The south-facing glass roof of two 7.9-m × 8.6-m greenhouse sections were covered with either an external application of ND whitewash (ReduSol; Lumiforte, Baarle-Nassau, the Netherlands) or an experimental fluorescent film adhered to the interior glass glazing with an area of 7.9 m × 5.9 m (Fig. 1C). Whitewash was applied to the control greenhouse in Expt. 2; therefore, the difference in transmitted PPFD was more similar to Expt. 1. The east-facing and west-facing walls of each greenhouse were painted white to minimize the amount of light not entering through the south-facing roof. Inside each greenhouse, air temperature and instantaneous PPFD were measured at plant height by two shielded and aspirated thermocouples (Type E; Omega Engineering, Inc.) and two quantum sensors (SQ-500; Apogee Instruments, Inc.). Environmental conditions inside were measured every 1 min and averaged hourly with a datalogger (CR-1000; Campbell Scientific, Inc.) and multiplexer (AM16/32B; Campbell Scientific, Inc.).

Greenhouse treatments. The light spectrum inside each greenhouse section was measured at bench height with a spectroradiometer (LI-180 Spectrometer; LI-COR, Inc.) on a cloudless day at solar noon on 9 Mar 2022 (Table 1 and Fig. 1C). Compared with Expt. 1, the maximum transmitted total photon flux density was higher in both the ND and RF greenhouses, and the RF greenhouse light environment had greater fractions of B and G photons, lower fractions of R and FR photons, and a peak wavelength of 640 nm. Relative to the ND greenhouse, the RF film decreased the transmission of B and G photons by 40% and 54%, respectively, while it increased the transmission of R and FR photons by 26% and 11%, respectively. The greenhouse air temperature was controlled by an environmental control system (Integro 725; Priva) with a constant air temperature setpoint of 20 °C. Steam heating, roof vents, and exhaust fans regulated air temperature.

Mature lettuce culture. Lettuce 'Rouxai', 'Dragoon', and 'Butter Crunch' seedlings were randomly selected and transplanted into one of the two greenhouse treatments on 18 Mar 2022. Each greenhouse contained four 1.83-m × 3.15-m benches. Plants were placed on each bench at a density of 0.12 m^2 per plant. Lettuce seedlings were transplanted into 15.2-cm round pots filled with a Suremix peat-based soilless substrate (Michigan Grower Products, Inc., Galesburg, MI, USA) and irrigated as needed with a solution consisting of reverse-osmosis water supplemented with 13N–1.3P–12.5K MSU Orchid RO Water Special water-soluble fertilizer (GreenCare Fertilizers, Inc., Kankakee, IL, USA) that contained (in $mg \cdot L^{-1}$) 125 N, 13 P, 120 K, 77 Ca, 19 Mg, 1.7 Fe, 0.4 Cu, 0.4 Zn, 0.8 Mn, 0.2 B, and 0.2 Mo. Lettuce plants grew for 35 d until destructive measurements were taken on 22 Apr 2022.

Experimental design, data collection, and analysis. Expt. 2 was organized as a completely randomized design. Each greenhouse was randomly assigned the ND or RF film treatment and randomly assigned 'Rouxai', 'Dragoon', and 'Butter Crunch' lettuce seedlings. Data collection and analysis were the same as described in Expt. 1, and were analyzed separately for each lettuce cultivar. Twenty-five plants per lettuce cultivar were selected for data collection ($n = 25$). Data from Expt. 2 were compared with data from Expt. 1 because both used the same RF film and an ND control with greater transmission of PAR.

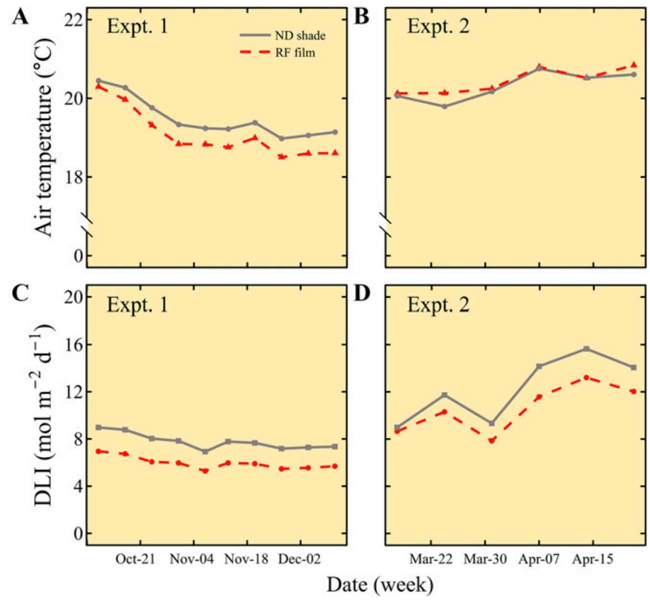

Fig. 2. Average weekly air temperature (**A** and **B**) and daily light integral (DLI; 400–700 nm) (**C** and **D**) inside small chambers (Expt. 1) and greenhouses (Expt. 2) covered with a neutral-density (ND) or red fluorescent (RF) film.

Results

Environmental conditions under the treatments

The average air temperatures inside the ND and RF film treatments were 19.6 °C and 19.1 °C in Expt. 1 (Fig. 2A) and 20.3 °C and 20.4 °C in Expt. 2 (Fig. 2B), respectively. The average daily light integrals (DLIs) inside the ND and RF treatments were 7.9 and 6.0 $mol \cdot m^{-2} \cdot d^{-1}$ in Expt. 1 (a 24% difference between treatments) (Fig. 2C) and 11.4 and 9.7 $mol \cdot m^{-2} \cdot d^{-1}$ in Expt. 2 (a 15% difference between treatments) (Fig. 2D).

RF film increased leaf area

Figure 3 displays a representative plant from each lettuce cultivar grown in the two experiments under the ND or experimental RF film. Figure 4 displays a comparison of lettuce grown under an RF film or an ND shade with 15% to 24% greater average DLIs at canopy height. Regardless of cultivar, the average single-leaf area was 6% to 25% greater under the RF film compared with the ND and higher-light environment (Table 2; Fig. 4A). The RF film increased the PCA of 'Rex', 'Cherokee', and 'Rouxai' lettuce by 12% to 17%, but 'Butter Crunch' PCA decreased by 23% relative to the ND material (Fig. 4B). Similarly, the specific leaf area of 'Rex', 'Cherokee', and 'Rouxai' increased by 11% to 24% under the RF film, but the specific leaf area decreased by 15% to 19% for 'Dragoon' and 'Butter Crunch' (Fig. 4C).

Biomass accumulation differed among cultivars

The RF films had varying effects on SFM within and between experiments. In Expt. 1,

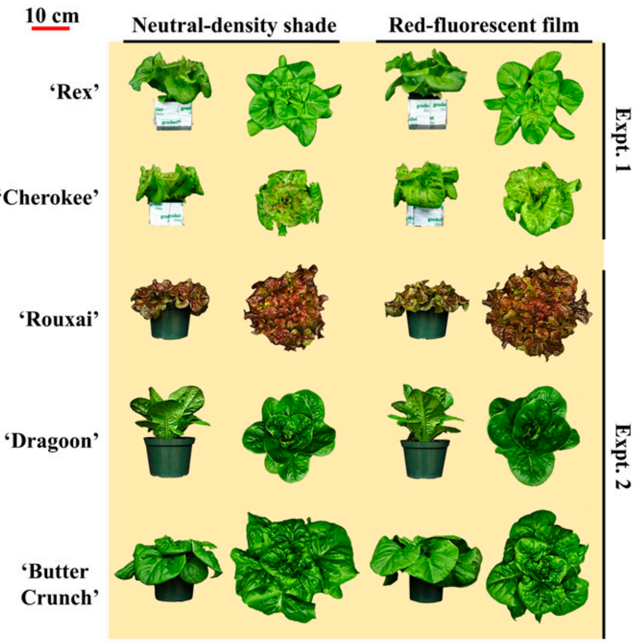

Fig. 3. Representative plants of lettuce grown under a neutral-density shade (ND) or red-fluorescent (RF) film. 'Cherokee' and 'Rex' were grown for 30 d after germination, and 'Rouxai', 'Dragoon', and 'Butter Crunch' were grown for 35 d.

the SFM of 'Rex' lettuce decreased by 7%, but it increased by 7% in 'Cherokee' under the RF film (Table 2; Fig. 4D). In Expt. 2, the SFM of 'Rouxai' and 'Dragoon' under the RF film increased by 45% and 15%, but the 'Butter Crunch' SFM was not significantly different between treatments. The yield ($kg \cdot m^{-2}$) of lettuce decreased under the RF film by 9% to 19% in Expt. 1, and it increased by 10% to 37% in Expt. 2 relative to the ND shade (Fig. 4E). The radiation use efficiency increased by 9% to 49% for 'Cherokee', 'Rouxai', 'Dragoon', and 'Butter Crunch' compared with the ND materials (Fig. 4F).

Leaf coloration responses were inconsistent

The differences in pigmentation of lettuce leaves were inconsistent across experiments and cultivars (Table 2). Specifically, the SPAD index values of 'Rex', 'Rouxai', and 'Butter Crunch' were similar, while those of 'Cherokee' and 'Dragoon' under the RF film decreased by 11% and 13%, respectively. Under the RF film, the L^* value (where greater values indicate lighter leaves) of 'Cherokee', 'Rouxai', and 'Dragoon' increased by 4% to 7%. The a^* value (where

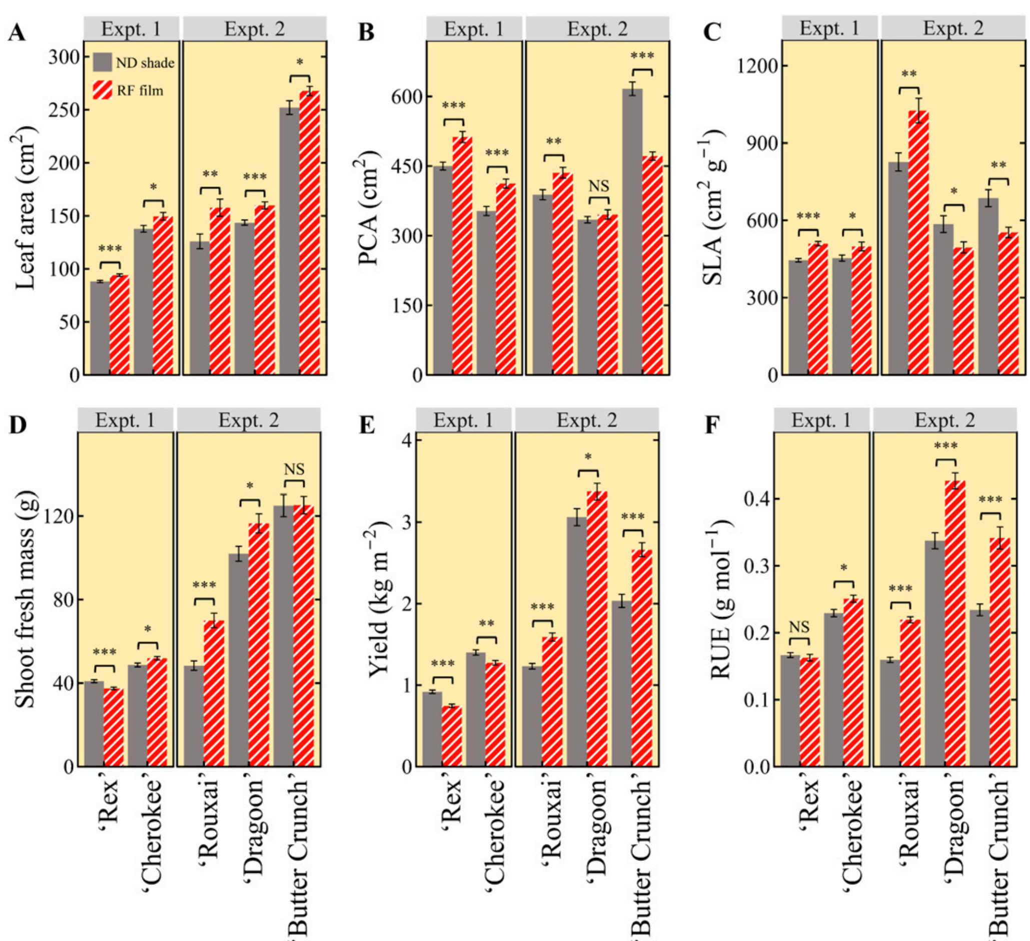

Fig. 4. Growth parameters of lettuce grown under a neutral-density (ND) shade or red fluorescent (RF) film. Values represent means ± standard error. Projected canopy area (PCA), specific leaf area (SLA), and radiation use efficiency (RUE) were calculated as described. 'Cherokee' and 'Rex' were grown for 30 d after germination (n = 40), and 'Rouxai', 'Dragoon', and 'Butter Crunch' (n = 25) were grown for 35 d. Asterisks indicate significant differences between treatments for each cultivar. $P < 0.05$, $P < 0.01$, and $P < 0.001$ are designated by *, **, and ***, respectively.

Table 2. Growth response of lettuce grown under different protected cultivation covering materials. 'Cherokee' and 'Rex' were grown for 30 d after germination (n = 40), and 'Rouxai', 'Dragoon', and 'Butter Crunch' (n = 25) were grown for 35 d.

Lettuce cultivar	Covering material	Growth parameter					
		Shoot dry mass (g)	SPAD index	L^*	a^*	b^*	Tipburn index[vi]
Rex	ND[i]	1.89 a[iii]	24.6 a	46.7 a	−22.0 b	31.5 a	0
	RF[ii]	1.67 b	23.6 a	46.2 a	−20.7 a	28.9 b	0
Cherokee	ND	1.94 a	26.1 a	44.5 b	−17.6 a	27.6 b	0
	RF	2.02 a	23.2 b	47.5 a	−20.0 b	31.5 a	0
Rouxai	ND	2.56 b	19.3 a	31.0 b	2.31 a	9.92 a	0
	RF	3.36 a	19.6 a	32.4 a	1.57 a	7.06 b	0
Dragoon	ND	4.61 b	41.9 a	38.4 b	−8.33 a	16.5 b	23.3
	RF	5.12 a	36.4 b	40.0 a	−8.90 b	18.5 a	34.2
Butter Crunch	ND	5.90 a	33.7 a	39.4 a	−8.81 a	18.5 b	0.8
	RF	5.60 a	32.3 a	39.9 a	−9.36 b	20.0 a	3.3

[i] A neutral-density (ND) covering material that did not alter solar spectrum.

[ii] A red fluorescent (RF) covering material that down-converted blue (400–499 nm) and green (500–599 nm) photons into red (600–699 nm) and far-red (700–750 nm) photons.

[iii] Mean separation letters within each column and for each lettuce cultivar are significantly different by Tukey's honestly significant difference test at $P < 0.05$.

[iv] The tipburn index was calculated as described by Frantz et al. (2004), with increasing tipburn index values indicating a greater percentage of plants with tipburn and greater tipburn severity.

lower values indicate greener leaves and greater values indicate redder leaves) of 'Rex' increased by 6%, while that of 'Cherokee', 'Dragoon', and 'Butter Crunch' decreased by 6% to 14%. However, the b^* value (where lower values indicate bluer leaves and greater values indicate yellower leaves) decreased by 8% to 29% for 'Rex' and 'Rouxai', but it increased by 8% to 14% for 'Cherokee', 'Dragoon', and 'Butter Crunch'.

The RF film increased tipburn in some cultivars

Marginal leaf necrosis (tipburn) was not present in either lettuce cultivar in Expt. 1 (Table 2). However, in Expt. 2, tipburn incidence and severity (quantified by the tipburn index) increased by 10.9 and 2.5 in 'Dragoon' and 'Butter Crunch' when grown under the RF film, respectively.

Discussion

A comparison of studies that use RF materials is difficult because of several experimental differences, including the following: 1) varying concentrations of fluorescent pigments, which affect the transmitted PPFD; 2) differences in the types of fluorescent pigments used, leading to variations in the transmitted photon distribution; 3) variances in control and monitoring of environmental conditions; and 4) significant variation in the crops and cultivars studied (Hemming et al. 2006; Hidaka et al. 2008; Kang et al. 2023, 2024; Loik et al. 2017; Minich et al. 2011; Nishimura et al. 2012; Parrish et al. 2021; Rodríguez et al. 2003; Shen et al. 2021). A majority of studies of fluorescent PC covers used plastics containing fluorescent pigments that primarily absorbed B and G photons and fluoresced R photons (Hemming et al. 2006; Hidaka et al. 2008; Kang et al. 2023; Loik et al. 2017; Minich et al. 2011; Rodríguez et al. 2003). Similar to the RF film used in the current work, these materials increased the proportion of R light but decreased the overall transmission of PAR. Fewer studies have used plastics containing fluorescent pigments that primarily absorbed ultraviolet and fluoresced R photons (Kang et al. 2024; Parrish et al. 2021). In theory, plastics containing ultraviolet-absorbing fluorescent pigments can potentially have a higher transmitted PPFD than pigments that absorb B and G photons because photons in the ultraviolet waveband are either not used or used inefficiently for photosynthesis.

Under optimal laboratory conditions, the light-extracting microstructures for a different batch of the same experimental RF film extracted 89% of the internally generated light (Shen et al. 2021). Without the light-extracting microstructures, only 25% of the internally generated light was extracted, indicating the microstructures significantly increased the total number of fluoresced photons reaching plants. With an 89% extraction efficiency, it could be inferred that the percentage transmission difference between the RF and ND films used in Expt. 1 would be 10% to 15% rather than the 24% difference measured. In previous plant experiments under conditions not optimized for light transmission, the difference in transmission between unpigmented and pigmented plastic was 21% to 28% (Shen et al. 2021), similar to that reported here. These differences in light extraction (i.e., light transmission) could be attributed to the use of light sources that varied between studies (i.e., LEDs, sunlight, or a combination of the two), different angles of light incidence from varying chamber geometries used in the experiments, and/or differences between the manufactured batches of the films.

In the current study, the experimental RF film had an inconsistent effect on lettuce SFM. Depending on the experiment and lettuce cultivar, the experimental RF film decreased lettuce SFM per plant by 7% or increased it by up to 45% (Fig. 4D). Likewise, past studies of RF materials reported varying effects on crop biomass accumulation (Hemming et al. 2006; Hidaka et al. 2008; Kang et al. 2023; Loik et al. 2017; Minich et al. 2011; Rodríguez et al. 2003). In these studies, growth metrics under RF materials were similar to, or greater than, an ND control with a greater transmission of PAR. For example, lettuce SFM was similar or increased by approximately 30%, cabbage (*Brassica rapa* spp. *pekinensis*) shoot dry mass increased by 33%, strawberry (*Fragaria* ×*ananassa*) yield was similar or increased by 60%, radish (*Raphanus raphanistrum*) root mass increased by 50%, and tomato fruit number or size was similar or slightly decreased. Although many crops have been evaluated under RF materials, the lack of repetition for any one crop or cultivar makes it difficult to determine consistent effects on biomass accumulation. Further research would benefit from more consistent crop selection and the inclusion of an ND treatment with PAR photon transmission equal to the RF material. This would allow for a clearer understanding of which crops benefit primarily from shading, and which could further benefit from an altered solar spectrum.

In some circumstances, comparing plant growth under the RF film to a greenhouse that allows maximum transmission of PAR (i.e., without shading) may be a more appropriate comparison for commercial greenhouse crop production, especially under light-limiting conditions. For example, lettuce grown in the winter or early spring, when the average DLI inside a greenhouse is less than the recommended 14 to 17 $mol \cdot m^{-2} \cdot d^{-1}$ (Albright et al. 2000; Faust and Logan 2018), would likely have greater biomass with higher light transmission. Without the application of whitewash in Expt. 2, the average DLI would have been approximately 30% higher; therefore, the average DLI would have increased from 11.4 $mol \cdot m^{-2} \cdot d^{-1}$ to approximately 15 $mol \cdot m^{-2} \cdot d^{-1}$. It can be inferred that the SFM of each lettuce cultivar grown in Expt. 2 would have been approximately 25% greater without the whitewash (Kelly et al. 2020). As a consequence, 'Rouxai' SFM would have been approximately 10% greater under the RF film than in a nonshaded greenhouse (with a higher DLI), whereas the SFM of 'Dragoon' and 'Butter Crunch' would have decreased by 10% and 20% under the RF film, respectively. This suggests that the RF film can be useful for some, but not all, lettuce cultivars when compared with a nonshaded greenhouse.

In this study, regardless of the experiment or lettuce cultivar, the most consistent morphological acclimation response under the RF film was increased single leaf area (Fig. 4A). Similarly, single leaf area of lettuce, cabbage, and two cultivars of cucumber (*Cucumis sativus*) increased under an RF material relative to an ND control (Kang et al. 2023; Minich et al. 2011; Nishimura et al. 2012; Rodríguez et al. 2003). However, this response was not consistent in other studies, suggesting that species-specific and cultivar-specific responses to RF films. For instance, the single leaf area of 'Longifolia' romaine lettuce, radish, and strawberry grown under an RF film was similar to that under an ND control (Hemming et al. 2006; Hidaka et al. 2008; Kang et al. 2023).

Stem and leaf elongation in various plant species can be inhibited by B light; these species include arabidopsis (*Arabidopsis thaliana*), wheat (*Triticum aestivum*), soybean (*Glycine max*), cucumber, lettuce, poinsettia, pansy, lobelia, campanula, and coreopsis (Clifford et al. 2004; Dougher and Bugbee 2001; Hernández and Kubota 2016; Meng et al. 2020; Runkle and Heins 2001). Attenuating the PPFD or fraction of B light typically increases extension growth. This growth response is mediated through cryptochromes, phototropins, or both, and it increases the competitiveness of a plant to intercept PAR photons (Franklin 2008). The experimental RF film in this study decreased B light transmission by 40% to 58%, which likely suppressed the inhibition of lettuce extension growth and increased single leaf area. Therefore, increases in plant extension growth in this study and others is likely caused, at least in part, by decreases in transmitted B light under films with fluorescent additives.

Shoot architecture (i.e., the spatial arrangement of aboveground organs) characteristics such as leaf area, number of branches, and stem length influence photon interception and, consequently, biomass accumulation (Fageria et al. 2006). There are positive correlations between increased lettuce leaf area, plant diameter, or PCA and increased dry mass accumulation (Kim et al. 2004; Li and Kubota 2009; Park and Runkle 2017; Snowden et al. 2016; Wang et al. 2016). In those experiments, decreasing B light, or its ratio with other wavebands, increased leaf area, which increased whole-plant net assimilation and shoot dry mass. Similarly, in the current study, increased biomass accumulation was positively correlated with increased single leaf area (Fig. 6A). While, rather than single or total leaf area, PCA could be a better metric for relating light interception with plant growth because it does not quantify overlapping leaf area. While an increase in SFM was correlated with increased single leaf area, it was not correlated with PCA (Fig. 6B). In the most extreme case, 'Butter Crunch' single leaf area increased under the RF film in Expt. 2, but PCA decreased.

The lack of consistency between increased single leaf area and PCA of SFM of 'Butter Crunch' could, in part, be explained by the following: 1) top-down photography that ignored plant architecture attributes such as leaf angle; 2) differences in light diffusion between the ND and RF greenhouses during Expt. 2; and 3) variance in growth habit compared with other cultivars (e.g., head-forming vs. loose-leaf). First, leaf angle can affect photosynthetic efficiency. More vertical maize (*Zea mays*) and rice (*Oryza sativa*) leaves had less photoinhibition and greater grain yields than plants with more horizontal leaves (Mantilla-Perez and Salas Fernandez 2017). Assuming all other factors are equal, as the angle between stem and leaf decreases (i.e., with a more vertical leaf) top-down photographs would increasingly underestimate leaf surface area and, thus, light interception. Improved plant architecture measurement techniques such as three-dimensional modeling could improve our estimates of light interception for studies that evaluate RF materials. Second, the degree of light diffusion varied between Expt. 1 and Expt. 2; light diffusion was constant in Expt. 1; however, in Expt. 2, there was greater light scattering in the RF greenhouse (as evidenced by shadowing) compared with the whitewashed greenhouse. The diffuseness of light can influence plant morphology and whole-plant photosynthesis (Hemming et al. 2008; Li and Yang 2015). While increased light scattering is a common feature of RF materials, research has not attempted to decouple the complex interaction of light quality, quantity, and diffuseness created by RF materials. Third, including a broader range of lettuce cultivars with varying head-forming types could provide better insight into how RF materials influence single leaf area and plant architecture. For example, Rouxai is a loose-leaf red cultivar and showed the greatest SFM increase among all cultivars tested. However, because no other loose-leaf cultivars were included and Rouxai also had red leaves, it remains unclear whether green loose-leaf cultivars would respond in a similar way. Expanding the range of cultivars to include both green and red leaves across different head types would help clarify these effects.

The lack of correlation between SFM and PCA suggests there are potential mechanisms related to photosynthetic rate or capacity that could have caused increased lettuce SFM under our RF film. In previous studies, RF materials influenced single-leaf photosynthesis in a species-dependent manner. Some pepper (*Capsicum annuum*) and strawberry cultivars had greater single-leaf photosynthetic capacity when grown under an RF material relative to an ND control (Loik et al. 2017; Yoon et al. 2020). However, photosynthetic capacity did not increase for crops such as tomato (*Lycopersicon esculentum*), cucumber, basil (*Ocimum basilicum*), or several *Citrus* spp. under RF films relative to ND controls with a higher average PPFD (Loik et al. 2017). Considering these conflicting responses, some crops morphologically and photosynthetically acclimate more than others under RF materials. Developing a better understanding of the magnitude of crop acclimation under RF materials and how responses may depend on other environmental factors (e.g., DLI and air temperature) would advance the commercial application and further development of RF greenhouse technologies.

A decrease in the proportion of B light in a spectrum, the PPFD, or both generally decreased SPAD index values of lettuce leaves (Meng et al. 2020; Snowden et al. 2016). Although the RF film in this study decreased the transmitted B photon flux density and PPFD, its effect on SPAD index varied among cultivars. Findings from other studies that used RF films support cultivar-specific responses. For example, 'Rex' lettuce had a lower SPAD index under an RF film compared with an ND control (Kang et al. 2024), whereas the SPAD index of a romaine-type lettuce was similar under the two treatments (Kang et al. 2023). Collectively, lettuce plants grown under RF films had a similar or slightly reduced SPAD index compared with that of those under ND materials with a higher B light fraction and PAR photon transmission.

Ideally, RF materials would not inhibit the biosynthesis of anthocyanins that give increased value to some horticultural crops, such as red-leaf lettuce, despite decreasing the transmission of B light. In a previous study, decreasing the B photon flux density and PPFD decreased the anthocyanin concentration of red-leaf lettuce 'Rouxai' (Kelly and Runkle 2023). The RF film had an inconsistent effect on leaf redness (a proxy for anthocyanin concentration); the a^* of 'Cherokee' deceased but that of 'Rouxai' did not. Despite 'Cherokee' having lower a^* values under the RF film, this was difficult to perceive with a visual assessment and, thus, is likely not commercially relevant (Figs. 3 and 5). In another study, the anthocyanin index of 'Outredgeous' lettuce progressively decreased when grown under RF films with an increasing fluorescent effect and lower transmission of B light (Kang et al. 2024). Few studies have investigated how RF films influence anthocyanin concentration; therefore, more research is needed to determine cultivar-specific responses.

Marginal necrosis (leaf tipburn) is a common physiological disorder of lettuce that is caused by insufficient translocation of calcium to the apical meristem (Frantz et al. 2004). The percentage of plants with tipburn and its severity typically increase in environments with a high PPFD, high temperature, low vapor-pressure deficit, and insufficient air velocity around the shoot apical meristem. In theory, the experimental RF film used in the current study should have reduced the incidence of lettuce tipburn relative to the ND shade with an approximately 20% greater average DLI. On the contrary, tipburn incidence

Average lettuce leaf color

	Neutral-density shade	Red-fluorescent film
'Rex'	#5C7837	#5A753B
'Cherokee'	#5C723A	#627A3A
'Rouxai'	#52473A	#534A40
'Dragoon'	#575C3E	#5B623F
'Butter Crunch'	#5B623F	#5B623D

Fig. 5. The average lettuce leaf color measured in the CIELAB color space was converted to hexadecimals. The value inside each colored bar corresponds to the color hexadecimal code.

increased in 'Dragoon' and 'Butter Crunch' grown under the RF film compared with that of those grown under the ND shade. An increased tipburn index could be related to increased leaf expansion rate under the RF film. Alternatively, lettuce tipburn can increase when transpiration rates are low. Transpiration rate is controlled through the opening and closing of stomata with guard cells, which are regulated primarily by B and R light (Matthews et al. 2020; Sharkey and Raschke 1981). The B light-induced stomatal opening begins at a very low photon flux density (≈5–10 $\mu mol \cdot m^{-2} \cdot s^{-1}$) and is approximately 10-times more effective than R light for opening stomata (Sharkey and Raschke 1981). Additionally, the magnitude of stomatal conductance depends on the flux of B light, whereby decreasing the flux of B photons attenuates conductance (Sharkey and Raschke 1981). Thus, RF films that decrease the flux of B photons may increase the incidence of tipburn, in part, by limiting transpiration and the translocation of calcium to the actively growing shoot apical meristem. However, few studies directly evaluated tipburn and light quality; therefore, this assumption cannot be validated. While RF materials can increase lettuce crop yield, their implementation may be limited if these materials also increase physiological disorders. To prevent tip burn, the implementation of RF materials may necessitate altering crop cultural practices such as harvesting lettuce earlier before tipburn symptoms develop, increasing air velocity around shoot apical meristems, or adjusting what cultivars are grown under these films because tipburn sensitivity varies among cultivars (Ertle and Kubota 2022).

Incorporating fluorescent pigments into agricultural plastics started in the early 1990s. However, the implementation of RF greenhouse plastics has remained challenging for several reasons, including the following: 1) increased cost of pigmented plastics compared with nonpigmented plastics; 2) unpredictable effects on crop morphology and yield; 3) increasing the concentration of fluorescent pigments decreases the transmitted PPFD; 4) transmitted photon distributions vary among films; and 5) fluorescent pigments can photo-oxidize rapidly and become nonfunctional if not designed properly (El-Bashir et al. 2016; Kang et al. 2023; Stallknecht and Runkle 2003; Park and Runkle 2023). While the commercial implementation has been limited thus far, RF PC covers have the potential to increase the yield of at least some crops, including lettuce, but further research is warranted to determine the economic feasibility of incorporating this technology in various locations.

Conclusion

In summary, an experimental RF film converted a significant portion of B and G photons into R and FR photons but decreased the total transmitted PPFD compared with an ND control. Based on this study with lettuce, the RF film increased the yield of lettuce (by up to 37%) compared with plants grown under an ND control with a 15% to 24% higher transmitted PPFD. However, the mechanism in which the RF films increase lettuce yield was undetermined. The RF films have potential as a greenhouse covering or shading material when they are stable and economical, and when a reduction in PPFD and a change in plant morphology (such as greater extension growth or leaf area) are acceptable or desirable.

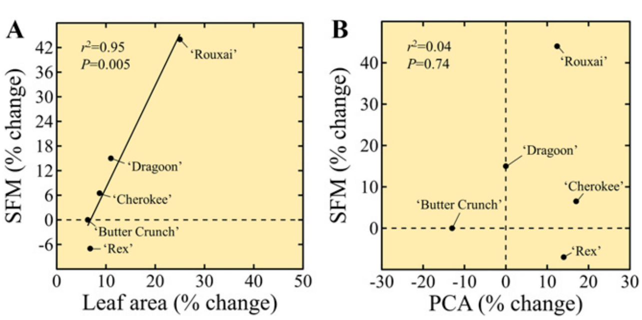

Fig. 6. The correlation between the average percentage change in lettuce shoot fresh mass (SFM) as a function of percentage change in single leaf area (**A**) or projected canopy area (PCA) (**B**) of lettuce grown under a neutral-density shade or red fluorescent film.

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