Bell Pepper (*Capsicum annum* L.) under Colored Shade Nets: Plant Growth and Physiological Responses

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Abstract. Use of colored shade nets has shown benefits in bell pepper and other horticultural crops. There is still, however, limited information on plant growth and physiology of bell pepper crop grown under colored shade nets. The objective was to determine the effects of colored shade nets on plant growth, leaf gas exchange, and leaf pigments of field-grown bell pepper. Experimental design was a randomized complete block with four replications and five shade treatments (black, red, silver, and white nets, and an uncovered control). Mean and maximal air temperature and midday root zone temperature (RZT) were highest in the unshaded treatment. Differences in air temperatures between shade net treatments were smaller compared with the differences in RZT between treatments. Plant fresh weight and stem diameter were reduced in the unshaded treatment, and there were no plant fresh weight and stem diameter differences among shade nets. The incidence of *Phytophthora* blight (caused by *Phytophthora capsici*) was greatest in the unshaded treatment. Leaf stomatal conductance (g_s) and photosystem II efficiency were reduced and leaf temperature increased in unshaded conditions. Leaf net photosynthesis, g_s , internal CO_2 , and PSII efficiency decreased with increasing leaf temperature. Differences in leaf temperature among shade net treatments were because of differences in solar radiation captured by leaves. Leaf total carotenoids were lowest in unshaded conditions and there were no differences in total carotenoids among the shade nets. Chlorophyll *a* concentration and chlorophyll *a/b* ratio was lowest in unshaded conditions. Leaf total phenols, flavonoids, and cupric reducing antioxidant capacity (CUPRAC) values were highest in red net and in unshaded conditions. Trolox equivalent antioxidant capacity (TEAC) values were highest in red net and lowest in silver net. In conclusion, compared with unshaded conditions, shade nets resulted in improved bell pepper plant growth and leaf gas exchange. These responses were due primarily to the reduced leaf and root zone temperatures under shaded conditions, regardless of the color of shade net. The differences in plant growth and function due to color of shade net were inconsistent or minor for most of the plant variables measured.

Bell pepper (*Capsicum annum* L.) yield and quality may be severely impacted under high temperatures, particularly during late

spring and early summer in the southeast United States. High air and root zone temperatures reduce bell pepper yield and increase the incidence of fruit disorders such as blossom-end rot and sunscald (Díaz-Pérez, 2010; Taylor and Locascio, 2004).

Shade nets are used in tropical and subtropical countries for production of horticultural crops (El-Aidy et al., 1993; Ilic et al., 2012; Kittas et al., 2012; Rylski and Spigelman, 1986; Shahak, 2008). Shade nets protect horticultural crops from excessive radiation, wind, hail, and birds. There is limited information on the use of shade nets for vegetable field production in the United States (Boyhan et al., 2008; Roberts and Anderson, 1994; Russo, 1993). Shade nets may influence plant growth by reducing solar radiation intensity and by modifying other microclimatic conditions (Mahmood et al., 2018). Research in Georgia on bell pepper under black shade nets has shown that with increased shade level, total plant leaf area,

individual leaf area, and individual leaf weight increased, whereas number of leaves per plant and specific leaf weight declined (Díaz-Pérez, 2013).

Although black nets are most commonly used, there has been increased interest in colored nets. Colored nets may influence plant growth, yield, and fruit quality because of their ability to modify both light quality and quantity (Arthurs et al., 2013; Fallik, 2009; Ilic et al., 2017). Regardless of net color, shade nets reduce solar radiation with concomitant reductions in air, plant, and soil temperatures. Use of colored shading nets has shown benefits in various horticultural crops, although there is limited information on bell pepper (Stamps, 2009). The objective of our work was to determine the effects of colored shade nets on plant growth, leaf gas exchange, and leaf pigments of field-grown bell pepper.

Materials and Methods

This study was conducted at the Horticulture Farm, University of Georgia (lat. 31.4803° N, long. 83.5211° W), Tifton, GA during the spring seasons of 2015 and 2016. The soil was a Tifton Sandy Loam (a fine, loamy-siliceous, thermic Plinthic Kandicudults) with a pH of 6.5. Before laying mulch with a mulch-laying machine (Kenco Manufacturer, Ruskin, FL), the soil was fertilized with N, P, and K at 50, 22.0, and 41.5 kg·ha⁻¹, respectively, using a 10–10–10 granular fertilizer (Rainbow Plant Food, Montgomery, AL). Fertilizer was incorporated into the soil. Plastic film mulch [black, low-density polyethylene with a slick surface texture, 1.52 m wide and 25 µm thick (Intergro, Clearwater, FL)] was laid. Drip irrigation tape [30 cm emitter spacing and a 12.6 mL·min⁻¹ emitter flow at 0.55 bar of pressure (Aqua traxx; Toro, Abilene, TX)] was placed 5 cm deep in the center of the bed.

Experimental design was a randomized complete block with four replications and five shade treatments (four colored nets and an unshaded control). Colored nets were black (47% shade), red (42% shade), silver (40% shade), and white (41% shade) (Fig. 1). These values of shade level are as reported by the manufacturer (Green-tek, Janesville, WI) and are within the optimal shade level (30% to 46% shade) for bell pepper (Díaz-Pérez, 2014). Each shade net was placed on a wooden rectangular structure (15 m wide × 6 m long × 5 m high). Experimental design was a randomized complete block with four replications and 10 treatments [5 shade treatments (black, red, silver, and white nets and an unshaded control; Green-tek, Janesville, WI)]. Shade nets reduced solar radiation by about 40%.

Bell pepper ('PS 09979325') transplants were produced in a greenhouse using peat-based medium (All Purpose Mix, Pro-Mix; Quakertown, PA) and polystyrene 200-cell (2.5 × 2.5 cm cell) trays. Plants were established on individual raised beds (formed on 1.8-m centers; 0.76 m wide). The length of

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the field experimental plot was 6 m. Six-week-old transplants were planted on 12 Apr. 2015 and 20 Apr. 2016 in two rows (staggered) per bed, with a 30 cm separation between plants and 36 cm separation between rows (40 plants per plot). About 240 mL of starter fertilizer solution (555 ppm N; 821 ppm P; 0 ppm K) was applied directly to the base of each transplant. Starting three weeks after transplanting, plants were fertilized weekly through the drip system. Total major nutrients applied were 200 kg·ha⁻¹ [nitrogen (N)], 22 kg·ha⁻¹ [phosphorus (P)], and 191 kg·ha⁻¹ [potassium (K)]. The crop was grown following the recommendations of the University of Georgia Extension Service.

Plants were irrigated with an amount of water equivalent to 100% crop evapotranspiration (ET_c), which was calculated by multiplying the reference evapotranspiration (ET_o) by the crop factor (dependent on the crop stage of development). Water was applied when cumulative ET_c was 1.2 mm, which corresponded to about every 2 to 3 d in mature plants (mean ET_o was 5 mm·d⁻¹).

Microenvironment. Air temperature and relative humidity were measured periodically during the season (both in 2015 and 2016) with dataloggers (HOBO, MX2301A; Instru-

mart, Burlington, VT). Data for white treatment were not collected due to a datalogger malfunction. Midday canopy temperature was measured on clear days with an infrared (IR) thermometer on 18 and 25 May, and 3 June 2015 (three measurements per experimental plot). Root zone temperature (8 cm deep) at midday was measured manually with a digital thermometer the same days as canopy temperature. The ET_o and rainfall data were obtained from a nearby University of Georgia weather station (less than 300 m).

Plant growth and chlorophyll index. Plant height and stem diameter were measured weekly for 5 weeks from mid-May to mid-June in three mature plants per plot. Chlorophyll indices (CI) were measured weekly on six leaves per plot using a chlorophyll meter (Chlorophyll Meter SPAD-502; Minolta Co., Ltd., Ramsey, NJ).

Plant diseases. Plants were monitored weekly for presence of *Phytophthora* blight (caused by *Phytophthora capsici*), Southern blight (caused by *Sclerotium rolfsii*), and Tomato spotted wilt [caused by *Tomato spotted wilt virus* (TSWV)]. Etiology of plant diseases was evaluated at the Plant Disease Clinic, University of Georgia, Tifton Campus. Presence of TSWV in symptomatic

plants was confirmed by enzyme-linked immunosorbent assay (ELISA).

Leaf gas exchange and Photosystem II efficiency. Simultaneous measurements of leaf gas exchange (net photosynthesis, *g_s*, internal CO₂ concentration and transpiration), leaf temperature, photosynthetically active radiation (*PAR*), and fluorescence determined as Photosystem II (PSII) efficiency were made with an IR gas analyzer (LI-COR 6400 IRGA with an integrated 6400-40 leaf chamber fluorometer; LI-COR, Inc., Lincoln, NE). PSII efficiency is the fraction of absorbed PSII photons used in photochemistry, and it is measured with a light-adapted leaf (LI-COR, 2003). Water use efficiency was calculated as the ratio between net photosynthesis and transpiration. Air flow rate was set at 300 μmol·m⁻²·s⁻¹ on the reference side. The CO₂ concentration was set at 400 μmol·mol⁻¹ with a CO₂ mixer and a CO₂ tank. Measurements were conducted in developed plants on clear days (unshaded conditions *PAR* > 1900 μmol·m⁻²·s⁻¹) at 1200 to 1500 HR using two developed and fully exposed leaves per plot.

Leaf chemical composition. Six leaves per treatment were collected on 29 May and 5 June 2015 and analyzed individually for chemical composition. Carotenoids and chlorophyll (Chl) *a* and *b* were determined in fresh leaves. Leaf tissue was ground in acetone (90% v/v), filtered, and taken to a volume of 50 mL (Ilic et al., 2012; Lichtenthaler, 1987). Pigments concentrations were calculated from the absorbance of the extract at 470, 645, and 663 nm. Total phenols were determined as a measure of total antioxidant capacity following the Follin-Ciocalteu method (Singleton et al., 1999), and data were expressed as gallic acid equivalents. Antioxidant capacity was determined by CUPRAC and TEAC methods (Barros et al., 2007; Castro-Concha et al., 2014). Total flavonoid concentration was determined by the aluminum chloride colorimetric method and expressed in quercetin equivalents (Rawat et al., 2014).

Results and Discussion

Microclimatological factors. Seasonal averages of air temperature and relative humidity for 2015 and 2016 are shown in Tables 1 and 2. In 2015, minimal air temperatures were highest under the black net and lowest in unshaded conditions (Table 1). Mean air temperature was lowest under the black net

Fig. 1. Colored shade nets for bell pepper production (Tifton, GA, Spring 2015 and 2016).

Table 1. Effect of colored shade nets on air and canopy temperature, root zone temperature (RZT), and relative humidity in bell pepper (Tifton, GA, Spring 2015).

Shade	Air temp (°C)			Midday canopy temp. (°C)	Midday RZT (°C)	Relative humidity (%)		
	Minimal	Mean	Maximal			Minimal	Mean	Maximal
Black	22.32 a ^z	27.0 c	33.1 b	27.1 b	34.0 b	49.5 a	69.9 a	87.0 b
Red	22.28 ab	27.1 b	33.1 b	27.0 b	34.9 b	46.8 c	65.9 d	82.8 c
Silver	22.26 b	27.1 b	33.0 c	27.2 b	34.9 b	48.3 b	68.8 b	87.3 a
White	nd ^y	nd	nd	27.6 b	35.2 b	nd	nd	nd
Unshaded	22.17 c	27.2 a	33.9 a	29.4 a	37.1 a	45.7 d	67.6 c	86.9 b
<i>P</i>	<0.0001	<0.0001	<0.0001	<0.001	<0.0001	<0.0001	<0.0001	<0.0001

^zMeans followed by the same letter are not significantly different based on Fisher's protected least significant difference test at 95% confidence.

^ynd = not determined.

Table 2. Effect of colored shade nets on air temperature and relative humidity in bell pepper (Tifton, GA, Spring 2016).

Shade	Air temp (°C)			Relative humidity (%)		
	Minimal	Mean	Maximal	Minimal	Mean	Maximal
Black	20.52 b ^z	26.2 c	31.8 c	43.2 a	62.5 a	82.7 a
Red	20.49 c	26.3 b	32.1 b	39.7 c	58.4 c	79.0 b
Silver	20.56 b	26.4 b	31.9 c	40.9 b	60.5 b	81.9 a
Unshaded	20.66 a	26.6 a	32.6 a	41.3 b	56.0 d	71.5 c
P	<0.0001	<0.0001	<0.0001	<0.0001	<0.0001	<0.0001

^zMeans followed by the same letter are not significantly different based on Fisher's protected least significant difference test at 95% confidence.

Table 3. Effect of colored shade nets on plant growth, leaf chlorophyll index, air temperature, and incidence of soil-borne diseases in bell pepper (Tifton, GA, Spring 2015).

Shade	Ht (cm)	Stem diam (mm)	Chlorophyll index	Incidence soil-borne diseases (%)
Black	39.8 a ^z	10.0 a	66.2 b	26 ab
Red	38.0 a	9.8 a	68.4 ab	25 ab
Silver	41.1 a	10.1 a	69.0 a	29 ab
White	38.0 a	10.5 a	68.9 a	23 b
Unshaded	18.6 b	6.9 b	69.1 a	46 a
P	<0.0001	<0.0001	<0.0001	0.004

^zMeans followed by the same letter are not significantly different based on Fisher's protected least significant difference test at 95% confidence.

Table 4. Effect of colored shade nets on bell pepper plant growth, leaf chlorophyll index, air temperature, and incidence of soil-borne diseases (Tifton, GA, Spring 2016).

Shade	Stem diam (mm)	Top fresh wt (g)	Chlorophyll index	Incidence soil-borne disease (%)	
				Southern blight	Phytophthora blight
Black	11.9 ab ^z	373 ab	60.4 b	13.1	1.9 b
Red	12.0 ab	393 ab	60.7 b	15.6	1.3 b
Silver	12.8 a	431 a	60.7 b	14.7	0.3 b
White	12.0 ab	446 a	61.4 b	13.4	2.2 b
Unshaded	11.2 b	291 b	62.8 a	18.8	13.9 a
P	<0.0001	0.008	<0.0001	0.288	0.0005

^zMeans followed by the same letter are not significantly different based on Fisher's protected least significant difference test at 95% confidence.

and highest in unshaded conditions. Maximal air temperature was lowest under the silver net and highest under unshaded conditions. Midday RZTs were highest in the unshaded treatment, and there were no RZT differences between shading nets (Table 1). Root zone temperature increased with increasing *PAR* ($r^2 = 0.936$) under the shade net treatments, while air temperature was unrelated to *PAR*. Minimal, mean, and maximal relative humidity was among the lowest under the red net and in unshaded conditions. In 2016, minimal air temperatures were lowest under the red net and highest in unshaded conditions (Table 2). Mean air temperature was lowest under the black net and highest in unshaded conditions, while maximal air temperature was lowest under the black and silver nets and had highest values in the unshaded treatment. Minimal relative humidity was lowest under the red net and highest under the black net. Mean relative humidity was lowest in unshaded conditions and highest under the black net. Maximal relative humidity was lowest under unshaded conditions and highest under the black net.

Shade nets affect the quality and quantity of solar radiation received by the crop as well as the air and soil temperature under the net. In the present study, the differences in air temperatures between shade net treatments were smaller compared with the differences in RZT. In a study in Florida using shadehouse structures with full cov-

ering, daily maximum air temperatures were higher inside shadehouses with red, blue, and pearl nets compared with black nets or uncovered conditions (Arthurs et al., 2013). In the present study in which shade structures were rectangular prisms and the net covered only the upper portion of the structure, maximal air temperature was lowest under the silver net and highest under unshaded conditions. In a study in Hungary using colored shade nets over pepper, air temperature showed relatively little changes in response to colored shade nets, and air temperature decreased with increasing shade level (Ombódi et al., 2015). The reduction of solar radiation (*PAR*, IR, and longwave radiation) under shade nets probably contributed to the reduced air temperatures and reduced RZTs under shaded conditions, compared with unshaded conditions. Reduced air and leaf temperature under shade nets resulted in diminished plant transpiration due to reduced evaporative demand, compared with the unshaded treatment.

Plant growth and chlorophyll index. In 2015, plant height and stem diameter were reduced in the unshaded treatment (Table 3), and there were no differences in plant height and stem diameter among shade nets. Chlorophyll index was reduced under the black net. In 2016, stem diameter and top fresh weight were reduced in unshaded conditions (Table 4). Chlorophyll index was the highest

in unshaded conditions, while there were no differences in chlorophyll indexes among shade nets.

Light is essential for photosynthesis in plants, but it may also influence plant growth and development through the action of several photoreceptors such as phytochromes (Smith, 2000). Red nets have been found to reduce the red/far-red ratio resulting in enhanced vegetative growth in various crops (Oren-Shamir et al., 2001; Shahak, 2008). In this study, shade nets modified light quantity (i.e., *PAR*) received by bell pepper plants; the effect of shade net treatments on light quality was not measured. Black nets and colored nets have been reported to influence plant growth of bell pepper and other vegetables (Díaz-Pérez, 2013; Ilic et al., 2017; Ombódi et al., 2015; Shahak, 2008). In greenhouse-grown eggplant, plant height, leaf number, total leaf area, individual leaf area, and plant fresh weight were increased under shading compared with an open field (Aied et al., 2017).

Plant diseases. In 2015, the incidence of soil-borne diseases (unidentified diseases) was increased in unshaded conditions (Table 3). In 2016, the incidence of southern blight was unaffected by shade treatments, while the incidence of Phytophthora blight was increased in unshaded conditions (Table 4). The incidence of Tomato spotted wilt incidence was small and similar among shade treatments (mean = 0.51%).

Table 5. Effect of colored shade nets on leaf net photosynthesis (P_{net}), stomatal conductance (g_s), internal CO_2 , photosystem II (PSII) efficiency, photosynthetic water use efficiency (WUE), photosynthetically active radiation (PAR), and leaf temperature (T_{leaf}) in bell pepper (Tifton, GA, Spring 2015).

Shade	Net photosynthesis ($\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$)	g_s ($\text{mmol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$)	Internal CO_2 ($\mu\text{mol}\cdot\text{mol}^{-1}$)	PSII efficiency ^y	WUE	PAR ($\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$)	T_{leaf} ($^{\circ}\text{C}$)
Black	28.4 ab ^z	756 ab	306.8 a	0.260 a	1.68	985 d	31.8 b
Red	28.0 ab	769 ab	304.6 a	0.231 a	1.67	1064 c	31.8 b
Silver	29.1 a	820 a	307.9 a	0.242 a	1.66	1102 bc	31.9 b
White	26.5 bc	613 bc	290.9 ab	0.234 a	1.75	1135 b	33.2 a
Unshaded	25.1 c	515 c	280.2 b	0.161 b	1.74	1851 a	34.2 a
<i>P</i>	0.0004	<0.0001	0.0011	<0.0001	0.057	<0.0001	<0.0001

^zMeans followed by the same letter are not significantly different based on Fisher's protected least significant difference test at 95% confidence.

^yPhotosystem II (PSII) efficiency. It is the fraction of absorbed PSII photons that are used in photochemistry and is used as an indicator of plant stress.

Table 6. Effect of colored shade nets on leaf net photosynthesis (P_{net}), stomatal conductance (g_s), internal CO_2 , photosystem II (PSII) efficiency, photosynthetic water use efficiency (WUE), photosynthetically active radiation (PAR), and leaf temperature (T_{leaf}) in bell pepper (Tifton, GA, Spring 2016).

Shade	P_{net} ($\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$)	g_s ($\text{mmol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$)	Internal CO_2 ($\mu\text{mol}\cdot\text{mol}^{-1}$)	PSII efficiency ^y	WUE	PAR ($\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$)	T_{leaf} ($^{\circ}\text{C}$)
Black	25.7 ^z	539 ab	293.7 ab	0.23 ab	1.65 b	1051 c	32.48 bc
Red	28.0	665 a	301.9 a	0.21 b	1.65 b	1204 b	31.60 c
Silver	26.9	544 ab	287.5 ab	0.23 ab	1.78 ab	1200 b	32.31 bc
White	23.9	421 b	277.1 bc	0.25 a	1.81 ab	1066 c	33.06 ab
Unshaded	24.7	417 b	266.6 c	0.15 c	1.87 a	1991 a	33.77 a
<i>P</i>	0.273	0.002	0.001	<0.0001	0.014	<0.0001	0.0002

^zMeans followed by the same letter are not significantly different based on Fisher's protected least significant difference test at 95% confidence.

^yPhotosystem II (PSII) efficiency. It is the fraction of absorbed PSII photons that are used in photochemistry and is used as an indicator of plant stress.

Fig. 2. Leaf net photosynthesis, stomatal conductance, internal CO_2 concentration, and photosystem II efficiency as influenced by midday leaf temperatures in bell pepper plants under colored shade nets (Tifton, GA, Spring 2015 and 2016).

Light level may affect soil microbial populations under natural and field conditions. The densities of *Pythium* spp. have been found to decrease under forest canopy gaps (Reinhart et al., 2010). Incidence of

Phytophthora blight has been reported to decrease with increased shade level in bell pepper (Díaz-Pérez, 2014). In the present study, it is unclear whether the influence of shade on incidence of Phytophthora blight

was due to a direct effect of light level on the pathogen, the host, or their interaction with the environment.

The influences of shade nets on plant diseases are little understood. In pepper, under colored shade nets, leaf coverage by powdery mildew (*Leveillula taurica*) was found to augment with increasing shade level; black, blue-silver, green, and red nets were associated with reduced powdery mildew levels (Elad et al., 2007). Interestingly, the incidences of southern blight and Tomato spotted wilt in the present study were unaffected by shade treatments, indicating that bell pepper plant diseases may respond differently to shade conditions (i.e., light quantity and quality). Shade nets probably provided some relief from plant water stress to infected plants having restricted capacity for water uptake and transport due to an impaired vascular system (Aguirreolea et al., 1995).

Gas exchange. In 2015, leaf net photosynthesis and g_s were highest under silver net and lowest in unshaded conditions (Table 5). Internal CO_2 concentration and PSII efficiency were lowest in unshaded conditions. The WUE was not significantly different among treatments. The PAR ranged from 1851 $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ in the unshaded treatment to 985 $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ in the black net treatment. Leaf temperature was highest in the white net and unshaded treatments. In 2016, net photosynthesis was unaffected by shade net treatments (Table 6). Stomatal conductance and internal CO_2 were highest under the red net and among the lowest under unshaded conditions and the white net. The PSII efficiency was highest under the white net and lowest in unshaded conditions. The WUE was increased in unshaded conditions. The PAR ranged from 1991 $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ in the unshaded treatment to 1051 $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$

Fig. 3. Relationship between leaf net photosynthesis and stomatal conductance in bell pepper plants under colored shade nets (Tifton, GA, Spring 2015 and 2016).

Fig. 4. Leaf photosystem II efficiency as influenced by photosynthetically active radiation (*PAR*) in bell pepper plants under colored shade nets (Tifton, GA, Spring 2015 and 2016).

in the black treatment. Leaf temperature was highest in the unshaded treatment and lowest under the red net.

Mean leaf temperature at midday increased with increasing *PAR* under the nets ($r^2 = 0.596$; $P = 0.009$). However, when data from unshaded conditions were not considered in the statistical analysis, leaf temperature showed no relationship with *PAR* under the nets, indicating that leaf temperature had no relationship with the differences in *PAR* among mulches. Leaf net photosynthesis, g_s , internal CO_2 , and PS II efficiency decreased with increasing values of leaf temperature (Fig. 2). Leaf net photosynthesis increased with increasing rates of leaf g_s (Fig. 3). Photosystem II efficiency decreased with increasing *PAR* values (Fig. 4). Among shade nets, there was no relationship between internal CO_2 and *PAR*.

Leaf gas exchange responses in the present study were probably highly influenced by leaf temperature. Differences in leaf temperature among shade net treatments are because of differences in solar radiation captured by leaves. Little IR is absorbed by leaves at wavelengths below 2000 nm, but more than 97% of solar radiation is absorbed at wavelengths above 7000 nm (Larcher, 1995).

Photosynthesis can be controlled by stomatal and nonstomatal factors (Jones, 1992). Occurrence of high leaf temperature was probably associated with high solar radiation and plant water stress due to low leaf transpiration and low g_s . The linear relationship between net photosynthesis and g_s in the present study indicates that there was a large stomatal control of photosynthesis under the various *PAR* levels. In a field study on bell pepper under different shade levels, net photosynthesis, transpiration, g_s , and water use efficiency decreased quadratically and internal CO_2 concentration and PSII efficiency increased quadratically with increased shade level. The authors concluded that leaf gas exchange responses were also highly dependent on stomatal factors (Díaz-Pérez, 2013). In a study on lemon trees (*Citrus limon*), shaded trees had reduced transpiration (sap flow), reduced trunk shrinkage, reduced leaf water potential, and increased water-use efficiency, indicating that shaded trees showed decreased water stress compared with unshaded trees (Alarcon et al., 2006).

Table 7. Effect of colored shade nets on leaf chemical composition in bell pepper (Tifton, GA, Spring 2015).

Shade	Carotenoids (mg·L ⁻¹)	Chl <i>a</i> ^y (mg·L ⁻¹)	Chl <i>b</i> ^y (mg·L ⁻¹)	Chl <i>a/b</i>	CUPRAC ^x (μM)	TEAC ^w (μM)	Total phenols [gallic acid equiv. (mg·L ⁻¹)]	Flavonoids [Quercetin equiv. (mg·mL ⁻¹)]
Black	1.10 ab ^z	4.47 bc	2.00	2.28	8153 c	13606 d	714 c	456 b
Red	1.19 a	4.84 a	2.13	2.28	10093 a	23425 a	1016 a	798 a
Silver	1.17 a	4.79 a	2.10	2.30	8867 b	11372 e	794 b	472 b
White	1.18 a	4.71 ab	2.04	2.33	8174 c	19615 c	720 c	491 b
Unshaded	1.06 b	4.31 c	1.90	2.35	9981 a	22008 b	1017 a	767 a
<i>P</i>	0.025	0.0015	0.143	0.170	<0.0001	<0.0001	<0.0001	<0.0001

^zMeans followed by the same letter are not significantly different based on Fisher's protected least significant difference test at 95% confidence.

^yChl *a* = Chlorophyll *a*; Chl *b* = Chlorophyll *b*.

^xCUPRAC = cupric reducing antioxidant capacity.

^wTEAC = trolox equivalent antioxidant capacity.

Leaf chemical composition. Leaf total carotenoids were lowest in unshaded conditions and there were no differences in total carotenoids among the shade nets (Table 7). Chlorophyll *a* concentrations were highest in plants under the red and silver nets and lowest in unshaded conditions. Chlorophyll *b* concentration was unaffected by the shade net treatments. There was positive correlation between chlorophyll *a* and *b* ($r^2 = 0.948$), while there were no relationships between chlorophyll index with either chlorophyll *a* or *b*. The chlorophyll *a/b* ratio ranged from 2.28 (for plants under the black and red nets) and 2.35 (unshaded plants) and was unaffected by shade net treatments.

Leaf CUPRAC values were highest in the red net treatment and unshaded treatment, while lowest under the black and white nets. TEAC values were highest in the red net treatment and lowest in the black net. Total phenols and flavonoids were highest in the red net treatment and in unshaded conditions. Total phenols were reduced in the black and white net treatments.

Leaves contain a diverse group of bioactive secondary plant products that perform diverse functions, including a regulatory effect on other plants, microorganisms, or animals (Larcher, 1995). The concentration and composition of secondary compounds may change in response to environmental conditions. Pigments including Chl *a*, Chl *b*, and carotenoids are involved in photosynthesis and indicate nutritional status. Shaded leaves typically have higher chlorophyll (Chl *a* and *b*) concentrations than unshaded leaves. Leaf chlorophyll concentration increases to maximize photosynthesis under light-limiting conditions (Björkman, 1981). Pepper leaves under black and blue shade nets were found to have higher chlorophyll concentrations compared with leaves under red, pearl, and white nets and unshaded control (Ilic et al., 2017).

In higher plants, Chl *a* is more important for photosynthesis than Chl *b*. In the present study, the chlorophyll *a/b* ratio was unaffected by the shade net treatments. The chlorophyll *a/b* ratio typically decreases with solar radiation, from a ratio of 3.2 to 4 in sun-exposed leaves, to a ratio of 2.5 to 2.9 in shade leaves (Lichtenthaler, 1987).

There is limited information on how shade nets modify light quality and how these modifications influence leaf chemical composition and other plant responses (Kotilainen et al., 2018). Carotenoids protect the chlorophyll molecules from photo-oxidation under excessive solar radiation. In this study, however, carotenoid concentration was reduced under unshaded conditions, suggesting that photooxidation was minimal under unshaded conditions. In tea plant (*Camellia sinensis* L.), Chl *a* and *b* and carotenoids increased with increasing nitrogen fertilization rate (Wang et al., 2019). The decreased concentration of Chl *a* under shade nets is consistent with other reports indicating that plants increase chlorophyll

concentration to maximize photosynthesis under light-limiting conditions (Björkman, 1981; Larcher, 1995). In the medicinal plant Van Haldi (*Hedychium spicatum*), phenolics concentrations and antioxidant activities in the rhizomes varied with growth stage and time of the year (Rawat et al., 2014).

In conclusion, compared with unshaded conditions, shade nets resulted in improved bell pepper plant growth and leaf gas exchange. These responses were due primarily to the reduced leaf and root zone temperatures under shaded conditions, regardless of the color of shade net. The differences in plant growth and function due to color of shade net were inconsistent or minor for most plant variables.

Literature Cited

- Aguirreolea, J., J. Irigoyen, M. Sanchezdiaz, and J. Salaverri. 1995. Physiological alterations in pepper during wilt induced by *Phytophthora capsici* and soil water deficit. *Plant Pathol.* 44:587–596.
- Aied, K.Y., Z. Wahab, R.H. Kamaruddin, and A.R. Shaari. 2017. Growth response of eggplant (*Solanum melongena* L.) to shading and cultivation inside a greenhouse in a tropical region. *Intl. J. Sci. Res.* 8:89–101.
- Alarcon, J.J., M.F. Ortuno, E. Nicolas, A. Navarro, and A. Torrecillas. 2006. Improving water-use efficiency of young lemon trees by shading with aluminised-plastic nets. *Agr. Water Manage.* 82:387–398.
- Arthurs, S.P., R.H. Stamps, and F.F. Giglia. 2013. Environmental modification inside photoselective shadehouses. *HortScience* 48:975–979.
- Barros, L., P. Baptista, and I.C.F.R. Ferreira. 2007. Effect of *Lactarius piperatus* fruiting body maturity stage on antioxidant activity measured by several biochemical assays. *Food Chem. Toxicol.* 45:1731–1737.
- Björkman, O. 1981. Response to different quantum flux densities, p. 57–107. In: O.L. Lange, P.S. Nobel, C.B. Osmond, and H. Ziegler (eds.). *Physiological Plant Ecology. Responses to the Physical Environment*. Springer-Verlag, Berlin.
- Boyhan, G., J. Díaz-Pérez, C. Riner, R. Hill, and D. Thigpen. 2008. Evaluation of bell pepper and tomato varieties with and without shade. *HortScience* 43:1256.
- Castro-Concha, L.A., J. Tuyub-Che, A. Moo-Mukul, F.A. Vazquez-Flota, and M.L. Miranda-Ham. 2014. Antioxidant capacity and total phenolic content in fruit tissues from accessions of *Capsicum chinense* Jacq. (Habanero pepper) at different stages of ripening. *Sci. World J.* 2014:809073.
- Díaz-Pérez, J.C. 2010. Bell pepper (*Capsicum annum* L.) grown on plastic film mulches: Effects on crop microenvironment, physiological attributes, and fruit yield. *HortScience* 45:1196–1204.
- Díaz-Pérez, J.C. 2013. Bell pepper (*Capsicum annum* L.) crop as affected by shade level: Microenvironment, plant growth, leaf gas exchange, and leaf mineral nutrient concentration. *HortScience* 48:175–182.
- Díaz-Pérez, J.C. 2014. Bell pepper (*Capsicum annum* L.) crop as affected by shade level: Fruit yield, quality, postharvest attributes, and incidence of *Phytophthora blight* (caused by *Phytophthora capsici* Leon.). *HortScience* 49:891–900.
- El-Aidy, F., M. El-Afry, and F. Ibraheim. 1993. Effect of shade and fertilizer levels and their interaction on fruit yield of sweet pepper. *Acta Agron. Hung.* 42:59–67.
- Elad, Y., Y. Messika, M. Brand, D.R. David, and A. Szejnberg. 2007. Effect of colored shade nets on pepper powdery mildew (*Leveillula taurica*). *Phytoparasitica* 35:285–299.
- Fallik, E. 2009. Can colored shade nets maintain sweet pepper quality during storage and marketing? *Acta Hort.* 830:37–44.
- Ilic, Z.S., L. Milenkovic, L. Stanojevic, D. Cvetkovic, and E. Fallik. 2012. Effects of the modification of light intensity by color shade nets on yield and quality of tomato fruits. *Scientia Hort.* 139:90–95.
- Ilic, Z.S., L. Milenkovic, L. Sunic, S. Barac, J. Mastilovic, Z. Kevresan, and E. Fallik. 2017. Effect of shading by coloured nets on yield and fruit quality of sweet pepper. *Zemdirbyste-Agriculture* 104:53–62.
- Jones, H.G. 1992. *Plants and microclimate*. Cambridge University Press, Cambridge.
- Kittas, C., N. Katsoulas, N. Rigakis, T. Bartzanas, and E. Kitta. 2012. Effects on microclimate, crop production and quality of a tomato crop grown under shade nets. *J. Hort. Sci. Biotechnol.* 87:7–12.
- Kotilainen, T., T.M. Robson, and R. Hernández. 2018. Light quality characterization under climate screens and shade nets for controlled-environment agriculture. *PLoS One* 13:e0199628.
- Larcher, W. 1995. *Physiological plant ecology. Ecophysiological and stress physiology of functional groups*. Springer, Berlin.
- LI-COR. 2003. Using the LI-6400. *Portable Photosynthesis System. Book 5. Leaf Chamber Fluorometer*. LI-COR Biosciences, Inc., Lincoln, NE.
- Lichtenthaler, H.K. 1987. Chlorophylls and carotenoids—Pigments of photosynthetic membranes. *Methods Enzymol.* 148:350–382.
- Mahmood, A., Y.G. Hu, J. Tanny, and E.A. Asante. 2018. Effects of shading and insect-proof screens on crop microclimate and production: A review of recent advances. *Scientia Hort.* 241:241–251.
- Ombódi, A., Z. Pék, P. Szuvandzsiev, Z. Tóthné Taskovics, A. Kóházi-Kis, A. Kovács, H. Ledóné Darázsi, and L. Helyes. 2015. Effects of external coloured shade nets on sweet peppers cultivated in walk-in plastic tunnels. *Not. Bot. Horti Agrobot. Cluj-Napoca* 43:398–403.
- Oren-Shamir, M., E.E. Gussakovsky, E. Shpiegel, A. Nissim-Levi, K. Ratner, R. Ovadia, Y.E. Giller, and Y. Shahak. 2001. Coloured shade nets can improve the yield and quality of green decorative branches of *Pittosporum variegatum*. *J. Hort. Sci. Biotechnol.* 76:353–361.
- Rawat, S., I.D. Bhatt, R.S. Rawal, and S.K. Nandi. 2014. Effect of developmental stage on total phenolics composition and antioxidant activities in *Hedychium spicatum* Buch.-Ham. ex. D. Don. *J. Hort. Sci. Biotechnol.* 89:557–563.
- Reinhart, K.O., A.A. Royo, S.A. Kageyama, and K. Clay. 2010. Canopy gaps decrease microbial densities and disease risk for a shade-intolerant tree species. *Acta Oecol. Intl. J. Ecol.* 36:530–536.
- Roberts, B.W. and J.A. Anderson. 1994. Canopy shade and soil mulch affect yield and solar injury of bell pepper. *HortScience* 29:258–260.
- Russo, V.M. 1993. Shading of tomato plants inconsistently affects fruit yield. *HortScience* 28:1133.

- Rylski, I. and M. Spigelman. 1986. Effect of shading on plant development, yield and fruit quality of sweet pepper grown under conditions of high temperature and radiation. *Scientia Hort.* 29:31–35.
- Shahak, Y. 2008. Photo-selective netting for improved performance of horticultural crops. A review of ornamental and vegetable studies carried out in Israel. *Acta Hort.* 770:161–168.
- Singleton, V.L., R. Orthofer, and R.M. Lamuela-Raventos. 1999. Analysis of total phenols and other oxidation substrates and antioxidants by means of Folin-Ciocalteu reagent. *Methods Enzymol.* 299:152–178.
- Smith, H. 2000. Phytochromes and light signal perception by plants—An emerging synthesis. *Nature* 407:585–591.
- Stamps, R.H. 2009. Use of colored shade netting in horticulture. *HortScience* 44:239–241.
- Taylor, M.D. and S.J. Locascio. 2004. Blossom-end rot: A calcium deficiency. *J. Plant Nutr.* 27:123–139.
- Wang, Y.J., X. Hu, G. Jin, Z.W. Hou, J.M. Ning, and Z.Z. Zhang. 2019. Rapid prediction of chlorophylls and carotenoids content in tea leaves under different levels of nitrogen application based on hyperspectral imaging. *J. Sci. Food Agr.* 99:1997–2004.