Bell Pepper (*Capsicum annuum* L.) Crop as Affected by Shade Level: Microenvironment, Plant Growth, Leaf Gas Exchange, and Leaf Mineral Nutrient Concentration

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Abstract. Use of shading nets helps ameliorate heat stress of vegetable crops. This study evaluated the effects of shade level on microenvironment, plant growth, leaf gas exchange, and mineral nutrient content of field-grown bell pepper crop. Bell pepper cultivars Camelot, Lafayette, Sirius, and Stiletto were grown at 0%, 30%, 47%, 62%, and 80% shade levels. Photosynthetically active radiation and air, leaf, and root zone temperatures decreased as shade level increased. Despite having increased plant leaf area, there was increased soil water content with increased shade level, indicating reduced soil water use. With increased shade level, the total plant leaf area, individual leaf area, and individual leaf weight increased, whereas leaf number per plant and specific leaf weight decreased. In contrast to non-normalized chlorophyll index (CI) values, CI normalized by specific leaf weight were related to leaf nitrogen (N) and increased with increased shade level. Net photosynthesis and stomatal conductance (g_s) decreased and leaf transpiration increased with increased shade level, particularly above 47% shade level. Leaf concentrations of N, potassium (K), calcium (Ca), magnesium (Mg), manganese (Mn), sulfur (S), aluminum (Al), and boron (B) increased with increased shade level. Relatively few differences in plant growth, leaf gas exchange, and leaf mineral nutrient concentrations were observed among cultivars. In conclusion, morphological changes such as taller plants and thinner and larger leaves likely enhanced light capture under shaded conditions compared with unshaded plants. High shade levels reduced leaf temperature and excessive leaf transpiration but resulted in reduced leaf photosynthesis. Thus, moderate shade levels (30% and 47%) were the most favorable for bell pepper plant growth and function.

Bell pepper (*Capsicum annuum* L.) is an important crop in many parts of the world and is typically grown in open fields on plastic film mulch. In Georgia, bell pepper is grown in the spring and fall on ≈ 1860 ha and has a value of \$50 million. In the spring, bell peppers are typically planted from March to April and harvested from May to early July. Increased temperatures occurring in late

spring and early summer reduce bell pepper yields and increase incidences of fruit physiological disorders such as blossom-end rot and sunscald causing significant loss (Olle and Bender, 2009; Taylor and Locascio, 2004). High temperatures induce flower and fruit abortion in bell pepper (Deli and Tiessen, 1969; Dorland and Went, 1947).

Shading nets are used in tropical and subtropical countries for vegetable production (Allen, 1975; Castellano et al., 2008; El-Aidy et al., 1993; Ilic et al., 2012; Kittas et al., 2012; Ryłski and Spigelman, 1986). Shading nets were used since the early-1900s to the 1960s in the United States for tobacco (*Nicotiana tabacum*) and vegetable production in the northeast and southeast regions (Allen, 1975; Duggar, 1903; Young, 1961). There is, however, little information on use of shading for vegetable production in the southeast United States over the past 40 years (Boyhan et al., 2008; Roberts and Anderson, 1994; Russo, 1993). Studies in Israel report that shading increases plant growth and yield in bell pepper (Ryłski and Spigelman, 1986). Shading also reduces water requirements and

increases irrigation water use efficiency in peppers (Moller and Assouline, 2007). This study evaluated the effects of shade level on the bell pepper crop microenvironment, plant growth, leaf gas exchange, and mineral nutrient content.

Materials and Methods

The study was conducted at the Horticulture Farm, Univ. of Georgia, Tifton, GA, during the Spring–Summer seasons of 2009 and 2010. The soil was a Tifton Sandy Loam (a fine loamy-siliceous, thermic Plinthic Kandiodults) with a pH of 6.5. Before laying mulch with a mulch-laying machine, the soil was fertilized with N, phosphorus (P), and K at 90, 39.6, and 83 kg-ha⁻¹, respectively, using 10N–10P–10K granular fertilizer. At the same time, plastic film mulch [silver on black, low-density polyethylene with a slick surface texture, 1.52 m wide and 25 μ m thick (RepelGro; ReflecTek Foils, Inc., Lake Zurich, IL)] was laid, drip irrigation tape [20.3-cm emitter spacing and a 8.3-mL-min⁻¹ emitter flow (Ro-Drip; Roberts Irrigation Products, Inc., San Marcos, CA)] was placed 5 cm deep in the center of the bed.

The experimental design was a randomized complete block with four replications and 20 treatments (five shade $\times$ four cultivar combinations). Shading treatments were: 0%, 30%, 47%, 63%, and 80% reduction of photosynthetically active radiation (PAR ; according to the manufacturer). The cultivars were Camelot (Seminis, Oxnard, CA), Lafayette (Siegers Seed Co., Holland MI), Sirius (Siegers Seed Co., Holland MI), and Stiletto (Rogers, Boise, ID).

Bell pepper transplants were produced in a greenhouse using peat-based medium (Pro-Mix, Quakertown, PA) and polystyrene 200-cell (2.5 $\times$ 2.5-cm cell) trays. The length of experimental plot was 3.3 m and plants were established on individual raised beds (6 $\times$ 0.76 m with raised beds formed on 1.8-m centers). Six-week-old bell pepper transplants were planted on 15 Apr. 2009 and 23 Apr. 2010 on two rows per bed with a 30-cm separation between plants and 36-cm separation between rows. Approximately 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 3 weeks after transplanting, plants were fertilized weekly through the drip system.

Shade nets [polypropylene black shade net (Baycor Industrial Fabric, Pendergrass, GA)] were supported with metallic cable and posts forming a pyramidal structure with the highest point at ≈ 2 m along the center of the bed. Shade nets were set 4 weeks after transplanting (12 May 2009 and 21 May 2010). The level of shading was verified by using quantum sensors of a ceptometer (SunFleck Ceptometer; Decagon Devices, Pullman, WA).

Plants were irrigated with an amount of water equivalent to 100% crop evapotranspiration (ETc), which was calculated by multiplying the reference evapotranspiration (ETo) by the crop factor (dependent on the

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crop stage of development). Water was applied when cumulative ET_c was 1.2 mm, which corresponded to every ≈ 2 to 3 d in mature plants (mean ET_o was 5 to 6 mm·d⁻¹). Weather data (air temperature, ET_o, and rainfall) were obtained from a nearby University of Georgia weather station (less than 300 m).

Microenvironment. PAR under each shade treatment was measured at midday (1200 to 1500 HR), on clear days, using a ceptometer

(Decagon Devices, Inc., Pullman, WA) taking two readings per plot. Leaf temperature (T_{leaf}) was measured in each plot with an infrared thermometer gun (Spectrum Technologies, Plainfield, IL). PAR and T_{leaf} measurements were conducted on 6, 11, and 24 June and 3 July 2009; 8, 9, 17, and 24 June, 14 and 29 July, and 6 and 18 Aug. 2010.

Air temperature (T_{air}) was measured with a temperature sensor located inside a

WatchDog data logger (Model 12001 Spectrum Technologies). The data logger was programmed to record readings every hour for each plot containing cv. Camelot. Root-zone temperature (RZT) was measured by determining soil temperature midway between plants within the row at 10 cm below the mulch and the soil surface. Root zone temperature was measured with copper-constantan thermocouples (Model 107; Campbell Scientific,

Fig. 1. Average monthly maximal, minimal, and mean air temperatures and monthly cumulative rainfall during the growing seasons in 2009 and 2010. Weather data obtained from a nearby Univ. of Georgia weather station (less than 300 m), Tifton, GA.

Fig. 2. Relationships of midday photosynthetically active radiation (PAR), midday leaf temperature (T_{leaf}), mean air temperature (T_{air}), and mean root zone temperature (RZT) with shade level in bell pepper. PAR and T_{leaf} measurements conducted on 6, 11, and 24 June and 3 July 2009; 8, 9, 17, and 24 June, 14 and 29 July, and 6 and 18 Aug. 2010. T_{air} and RZT measured during the period under shade (7 June to 15 Sept. 2009 and 28 May to 9 Aug. 2010), Tifton, GA, Spring of 2009 and 2010.

Fig. 3. Soil water content as function of shade level in bell pepper. Data from cultivars Camelot, Lafayette, Sirius, and Stiletto were pooled, Tifton, GA, Spring of 2009 and 2010.

Logan, UT) connected to a data logger (CR10X; Campbell Scientific) and an AM416 Relay Multiplexer (Campbell Scientific). Air temperature and RZT were measured during the period under shade (7 June to 15 Sept. 2009 and 28 May to 9 Aug. 2010) and were monitored only in cultivar Camelot as a result of a limited number of data loggers available.

Soil water content. Soil water content (volumetric) over the season was measured once every 2 to 3 d (three readings per experimental plot) with a portable time domain reflectometry (TDR) sensor (CS-620; Campbell Scientific). The two metallic 12-cm rods of the TDR sensor were inserted vertically within the row between two plants.

Plant growth. Bell pepper plant height and stem diameter were measured weekly in

Fig. 4. Plant height, plant leaf area, leaf number per plant, individual leaf area and dry weight, stem diameter, specific leaf weight (SLW), and leaf weight ratio (LWR) in bell pepper as a function of shade level. Data from cultivars Camelot, Lafayette, Sirius, and Stiletto were pooled, Tifton, GA, Spring of 2009 and 2010.

three mature plants per plot. Plant leaf area, leaf number per plant, and individual leaf area were measured in two randomly selected mature plants per experimental plot excised at the soil level at the end of the season (30 Aug. 2010). Leaf area was measured with a leaf area meter (LI-3100C; LI-COR, Lincoln, NE). Plant samples were dried at 70 °C for several days until constant weight was obtained and leaf, stem, and vegetative top (leaf + stem) dry weights (DWs) of individual plants determined. For plant growth analysis, specific leaf weight (SLW) and leaf weight ratio (LWR) were calculated from leaf area and DW determinations as follows (Evans, 1972):

- (1) SLW = leaf DW/leaf area
- (2) LWR = leaf DW/vegetative top DW

Leaf chlorophyll index. CIs were determined twice a week over the season on six leaves per plot using a chlorophyll meter (Chlorophyll Meter SPAD-502; Minolta Co., Ltd., Ramsey, NJ).

Leaf gas exchange and photosystem II efficiency. Simultaneous measurements of leaf gas exchange (net photosynthesis, g_s , transpiration, and internal CO_2 concentration) and fluorescence determined as photosystem II (PSII) efficiency were made with an infrared 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 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 $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ on the reference side. The CO_2 concentration was set at 400 $\mu\text{mol}\cdot\text{mol}^{-1}$ with a CO_2 mixer and a CO_2 tank. By setting PAR at the “tracking” option of the LI-6400, the PAR value inside the measurement chamber was similar to that of the plants under each shading treatment. Measurements were conducted in developed plants on clear days (unshaded conditions PAR greater than 1900 $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$) at 1200 to 1500 hr Eastern Standard Time in 2009 (11 and 20 Aug., 8 Sept., and 1 Oct.) and 2010 (28 and 30 July and 12 Aug.) using two developed and fully exposed leaves per experimental plot.

Leaf mineral nutrients. Leaf samples (20 fully developed leaves from new growth) from developed plants were dried at 70 °C for 2 d and analyzed for mineral nutrient concentration at the Univ. of Georgia Agricultural & Environmental Services Laboratories, Athens, GA.

Statistical analysis. Data were analyzed using the General Linear Model and Regression Procedures from SAS (SAS Version 9.3; SAS Inst. Inc., Cary, NC). Data means were separated by Fisher’s protected least significant difference test at 95% confidence. Percentages were transformed to arcsine values before analysis. For clarity, non-transformed percentage means were used for presentation in tables and figures. Data from all years were

pooled if no year $\times$ treatment interactions were found.

Results and Discussion

Microenvironment. Maximal, minimal, and mean air temperatures and rainfall during the growing seasons in 2009 and 2010 are shown in Figure 1. Midday PAR , midday T_{leaf} , mean T_{air} , and mean RZT decreased with increased shading levels (Fig. 2). Mean PAR values were similar over the season in both years (data not shown). Mean T_{air} was 0.5 °C lower, midday T_{leaf} was 2.7 °C lower, and RZT was 2.6 °C lower at 80% shading compared with unshaded conditions. PAR and T_{leaf} were not different among cultivars (data not shown).

Our results are consistent with previous reports that show that shading reduces solar radiation, T_{air} , RZT, and T_{leaf} (Allen, 1975; Kittas et al., 2009; Smith et al., 1984; Valli et al., 1965; Zhang, 2006). In Israel, a 30% black shading screen was found to reduce solar radiation and wind speed but did not significantly alter maximum daily air temperature and vapor pressure deficit compared with open field conditions (Moller and Assouline, 2007). The optimal T_{air} range for pepper is 20 to 25 °C (Rubatzky and Yamaguchi, 1999; Wien, 1997), whereas the optimal RZT range under field conditions is 25 to 27.5 °C (Díaz-Pérez, 2010). High values of seasonal T_{air} , midday T_{leaf} , and seasonal RZT (Fig. 2) suggest that bell pepper plants were under heat stress, particularly those that were unshaded. Root zone temperature under plastic mulch affects plant growth and yield in several vegetable crops (Díaz-Pérez et al., 2008). Root zone temperature is affected by the amount of heat retained by the plastic mulch, which is determined by the optical properties of the mulch (Lamont, 2005). Root

zone temperature increases with increased solar radiation and decreases with increased shading as that caused by plant canopy cover (Díaz-Pérez et al., 2005). In some circumstances, like when there is poor ventilation inside the shade house, shading nets may increase T_{air} (Castellano et al., 2008). In this study, however, the relatively small shading structures used allowed for air circulation that probably reduced presence of T_{air} gradients under shade.

Soil water content. Soil water content increased with increased shade levels in all cultivars (Fig. 3). Possibly, shading reduced evaporative demand and caused reduced transpiration, resulting in decreased soil water uptake by bell pepper (Allen, 1975; Kittas et al., 2009; Moller et al., 2004; Valli et al., 1965). In unmulched soil, shading could also reduce soil evaporation. A 30% black shading net reduced solar radiation, wind speed, and water requirements and increased irrigation water use efficiency in bell pepper (Moller and Assouline, 2007). Similarly, in greenhouse-grown tomato (*Solanum lycopersicum* L.), crop water use decreased and water use efficiency increased with shade level (Gent, 2008).

Plant growth. Plant height, plant leaf area, individual leaf area, individual leaf DW, and LWR (fraction of total aboveground biomass allocated to leaves) increased with increased shade level, whereas number of leaves per plant and SLW (leaf weight per unit leaf area; it is an estimator of leaf thickness) decreased with increased shade level (Fig. 4). Leaf, stem, and vegetative top dry weights were not significantly different among shade levels. Among cultivars, individual leaf DW was highest ($P < 0.05$) for ‘Stiletto’ (236 mg/leaf) followed by ‘Sirius’ (189 mg/leaf), ‘Lafayette’ (188 mg/leaf), and ‘Camelot’ (212 mg/leaf). Leaf weight ratio was highest ($P < 0.05$) for

Fig. 5. Chlorophyll indices (CIs) and normalized CI (CI divided by their respective specific leaf weight) as function of shade level in bell pepper. Data from cultivars Camelot, Lafayette, Sirius, and Stiletto were pooled, Tifton, GA, Spring of 2009 and 2010.

'Lafayette' (0.446) followed by 'Stiletto' (0.426), 'Sirius' (0.403), and 'Camelot' (0.397). Leaf, stem, and vegetative top DWs, stem diameter, plant leaf area, leaf number per plant, individual leaf area, and SLW were similar among cultivars. There were no shade-by-cultivar interactions for any of the plant growth variables.

Under low light, plants undergo morphological changes to maximize light use. Plants adapted to shade have greater foliar surface and specific leaf area, thinner leaves, and taller stems compared with plants adapted to strong light (Larcher, 1995). Our results agree with studies showing that shaded peppers have longer internodes, larger leaves, greater whole-plant leaf area, and thinner leaves (i.e., lower SLW) (Duggar, 1903; Kittas et al., 2009; Young, 1961). Results are also consistent with a bell pepper study under high-light field conditions in Israel, in which plant height, number of nodes, and leaf area increased with increased shade level (Rylski and Spiegelman, 1986). Changes in bell pepper plant growth [augmented leaf biomass, leaf area, and plant height at the expense of fruit biomass (unpublished data)] habit and increased LWR with increased shading indicate that plants underwent modifications in the allocation of assimilates, resulting in maximized light interception under shaded conditions.

Under shaded conditions, plants had thinner leaves, as indicated by their lower SLW values. A 40% shade level in tomato reduced SLW by 24% compared with unshaded plants (Bertin and Gary, 1998). Similarly, in pepper, the 47% shade level resulted in a 19% reduction in SLW. The energetic cost for the plant to produce a given leaf area is lower when shaded (Larcher, 1995). Stems in shaded plants were thinner and presumably less lignified than those under higher light conditions, although stem biomass was unaffected. Stem diameter is related to upper plant DW, leaf area, and the ability of plants to transport water from the soil to leaves (Larcher, 1995). Increased plant leaf area with increased shading was associated with a reduced number of leaves per plant. In several species, specific leaf area (inverse of SLW) and chlorophyll concentration increase with increased shading (Björkman, 1981).

Leaf chlorophyll index. Chlorophyll indices decreased with increased shading levels (Fig. 5) and were not correlated with leaf N concentration. Chlorophyll indices were highest ($P < 0.0001$) in 'Camelot' (mean =

60.7) followed by 'Lafayette' (mean = 59.8) and 'Stiletto' (mean = 59.5) and lowest in 'Sirius' (mean = 58.4). In general, leaves adapted to low light have larger chloroplast size and greater chlorophyll content per chloroplast than leaves adapted to strong light (Larcher, 1995). Chlorophyll indices have been used as indirect estimators of chlorophyll and leaf N concentrations (Liu

et al., 2006; Madeira and de Varennes, 2005; Tremblay et al., 2011). Our results that CI were not correlated with leaf N contradicts numerous reports (Liu et al., 2006; Madeira and de Varennes, 2005; Tremblay et al., 2011). Possibly, the low correlation between CI and leaf N was the result of reduced leaf thickness as a result of shading treatments (Li et al., 2011; Peng et al., 1993).

Fig. 6. Net photosynthesis, internal CO_2 concentration, transpiration, stomatal conductance (g_s), water use efficiency (WUE), and photosystem II (PSII) efficiency in bell pepper as affected by shade level. Data from cultivars Camelot, Lafayette, Sirius, and Stiletto were pooled, Tifton, GA, Spring of 2009 and 2010.

Table 1. Leaf gas exchange variables and photosynthesis II (PSII) efficiency in bell pepper as affected by cultivar, Tifton, GA, Spring–Summer of 2009 and 2010.^a

Cultivar	Net photosynthesis ($\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$)	Internal CO_2 ($\mu\text{mol}\cdot\text{mol}^{-1}$)	g_s ($\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$)	Transpiration ($\text{mmol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$)	Water use efficiency ($\mu\text{mol}\cdot\text{mmol}^{-1}$)	PSII efficiency ($\mu\text{mol}\cdot\text{mmol}^{-1}$)
Camelot	21.2 a ^y	287 ab	0.610	9.66	2.37	0.314
Lafayette	19.8 b	283 b	0.565	9.28	2.39	0.304
Sirius	19.5 b	288 ab	0.625	9.52	2.36	0.315
Stiletto	20.3 ab	293 a	0.613	9.56	2.33	0.323
Significance	***x	*	NS	NS	NS	NS

^aLeaf gas exchange measurements (n = two plants/experimental plot) conducted on 11 and 20 Aug., 8 Sept., and 1 Oct. 2009 and 28 and 30 July and 12 Aug. 2010.

^yMeans followed by the same letter in a column are not significantly different based on Fisher's protected least significant difference test ($P \leq 0.05$).

*NS, *, ***Nonsignificant or significant at $P < 0.05$, and 0.001, respectively.

g_s = stomatal conductance.

Chlorophyll indices were normalized by dividing them by their respective SLW. Normalized CI increased with increased shade level (Fig. 4) and increased quadratically with leaf N concentration ($r^2 = 0.867$; $P = 0.001$). Our results are consistent with those of Peng et al. (1993) in rice (*Oryza sativa* L.) and indicated that CI in bell pepper leaves should be normalized by SLW when comparing leaves differing in thickness such as leaves from different developmental stages or leaves grown in dissimilar light environments. Another possible cause for the low correlation between CI and leaf N is that values greater than 50 may be less accurate for the chlorophyll meter used. Possibly, the reduced accuracy is related to increased leaf thickness. In woody ornamentals with thick leaves, the Chlorophyll Meter SPAD-502 (Minolta Co., Ltd., Ramsey, NJ) also gave CI that were unrelated with leaf N concentration (Ruter, personal communication).

Leaf gas exchange. 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 (Fig. 6). Net photosynthesis and g_s were relatively unaffected at 30% to 47% shade level or lower. There was a linear relationship between net photosynthesis and g_s ($y = 8.72x + 11.6$; $r^2 = 0.362$; $P < 0.0001$). Net photosynthesis was highest in ‘Camelot’ and lowest in ‘Lafayette’ and ‘Sirius’ and internal CO_2 concentration was highest in ‘Stiletto’ and lowest in ‘Lafayette’ (Table 1). Stomatal conductance, transpiration, water use efficiency, and PSII efficiency were similar among cultivars. There were no date $\times$ shade interactions.

Moderate shading levels resulted in reduced leaf temperature and leaf transpiration without reducing net photosynthesis. This reduced leaf transpiration was likely attributed to reduced evaporative demand and probably explains the increased soil water content and reduced plant water uptake under shaded conditions. The linear relationship between net photosynthesis and g_s suggests that stomatal control of photosynthesis was substantial under shade. The increased internal CO_2 concentration with increased shade level also suggests, however, that there were also non-stomatal factors such as mesophyll or biochemical factors, limiting net photosynthesis (Assmann, 1988).

To our knowledge, there are no reports on leaf gas exchange in bell pepper as affected by shade levels under field conditions. The ecophysiological literature has numerous

reports on differences in functional characteristics between sun and shade leaves. In general, sun leaves have greater photosystem activity, speed of electron transport, quantum yield, carboxylation efficiency, and photosynthetic capacity compared with shade leaves (Larcher, 1995). In soybean (*Glycine*

max L.), under shade cloth, g_s and water use efficiency of shaded leaves were higher than for unshaded leaves (Allen, 1975). In lemon [*Citrus limon* (L.) Burm. Fil. cv. Verna] trees, canopy conductance and photosynthesis were unaffected by shading; however, daily transpiration was reduced in shaded plants, which

Fig. 7. Leaf mineral nutrient composition of mature bell pepper as affected by shade level. Data from cultivars Camelot, Lafayette, Sirius, and Stiletto were pooled, Tifton, GA, Spring of 2009 and 2010.

Table 2. Leaf mineral nutrient concentrations in four cultivars of mature bell pepper plants grown in the field, Tifton, GA, Spring–Summer of 2009 and 2010.²

	N	P	K	Ca	Mg	S	Al	B	Cu	Fe	Mn	Mo	Na	Ni	Zn
	(%)						($\mu\text{g}\cdot\text{g}^{-1}$)								
Camelot	4.67 a ²	0.30 a	4.81 ab	1.06 a	0.28 c	0.49 b	50	34 a	89	160	263	2.6	36	2.8	94 a
Lafayette	4.64 a	0.31 a	4.85 a	1.06 a	0.34 a	0.52 a	47	32 ab	87	156	233	2.5	36	2.8	82 b
Sirius	4.78 a	0.29 a	4.90 a	0.88 b	0.30 b	0.51 ab	46	35 a	91	160	236	2.6	39	2.6	79 bc
Stiletto	4.49 b	0.26 b	4.62 b	0.99 a	0.26 c	0.49 b	50	29 b	90	156	234	2.5	36	2.4	72 c
Significance	***y	****	*	****	****	*	NS	**	NS	NS	NS	NS	NS	NS	****

²Means separated within columns using Fisher's protected least significant difference test ($P \leq 0.05$).

³NS, ****, ***, **, *Nonsignificant or significant at $P \leq 0.0001$, $P \leq 0.001$, $P \leq 0.01$, or $P \leq 0.05$, respectively.

displayed an increased water use efficiency compared with exposed trees (Alarcon et al., 2006). The reduced transpiration and maintenance of photosynthesis in shaded plants compared with exposed trees indicated that use of screen structures in semiarid environments could help reduce plant water stress and increase water use efficiency (Barradas et al., 2005).

Leaf mineral nutrients. Leaf concentrations of N, K, Ca, Mg, S, Al, B, and Mn increased with increased shading levels for the majority of nutrients, although the concentrations changed little below 30% shade for K, Ca, and Mg or 47% shade for N (Fig. 7). Mineral nutrients, however, varied in degree of increase with shading ranging from as low as 7% in P to 75% in Mn. Leaf concentrations of P, copper, iron, Mn, molybdenum, sodium, nickel, and zinc (Zn) did not show either linear or quadratic relationships with shade level. Among cultivars, 'Stiletto' had the lowest leaf concentrations of N, P, K, Mg, B, and Zn (Table 2). There were few differences among cultivars for the other mineral nutrients. The differences in concentrations among cultivars were relatively small for most mineral nutrients.

There are a limited number of studies on mineral nutrient uptake and accumulation by vegetable crops as affected by shading. The increased foliar nutrient concentrations observed in our study in response to shading are consistent with reports on tomato showing that shading increases foliar concentration of N, P, and K (Liu et al., 2003), plant N concentration and dry mass partitioning to roots (de Groot et al., 2002), and N and K uptake (Gent, 2008). Increased foliar N concentration in shaded plants has been associated with increased leaf chlorophyll concentration, a plant response intended to increase light capture under shaded conditions (de Groot et al., 2002).

Shading possibly resulted in increased mineral nutrient concentrations in shaded leaves by modifying temperature conditions. Reductions in T_{air} and RZT associated with shading allowed for amelioration of heat stress that might have resulted in increased mineral nutrient uptake. Previous studies in tomato in solution culture indicated that the optimal temperature for uptake of the majority of mineral nutrients and plant growth responses is 25 °C (Tindall et al., 1990). It may be that heat stress amelioration by shading benefited bell pepper plant growth indirectly by modifying the crop thermal environment so as to be more favorable for mineral nutrient uptake.

In conclusion, morphological changes such as taller plants and thinner and larger leaves likely enhanced light capture under shaded conditions compared with unshaded plants. High shade levels reduced leaf temperature and excessive leaf transpiration but resulted in reduced leaf photosynthesis. Thus, moderate shade levels (30% and 47%) were the most favorable for bell pepper plant growth and function.

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