Effects of Supplemental Light Duration on Greenhouse Sweet Pepper Plants and Fruit Yields

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ABSTRACT. Sweet pepper (*Capsicum annuum* L.) plants were grown under natural or supplemental lighting that extended the photoperiods to 16, 20, or 24 hours. Increasing the photoperiod to 16 and 20 hours increased pepper plant yields, but continuous light (24 hours) decreased yields compared to the 20-hour photoperiod. In a second experiment, plants were exposed to a photoperiod of 14 or 24 hours and either pruned to one fruit every four nodes or not pruned. During the first weeks of treatments, plants grown under continuous light had higher shoot mass (fresh and dry) and yields. After 7 to 8 weeks of treatments, plants under continuous light grew more slowly than plants exposed to a 14-hour photoperiod. At the end of the experiment, shoot mass and yields of plants grown under a 14-hour photoperiod were equal to or higher than plants under continuous light. So, it seems possible to provide continuous lighting for a few weeks to improve growth and yields. Limiting the number of fruit per plant increased shoot mass and decreased yields, but had no effect on the general response of pepper plants to photoperiod treatment. Leaf mineral composition was not affected by photoperiod treatment, indicating that reduced growth and yields under continuous light were not due to unbalanced mineral nutrition. Leaf starch and sugar contents were increased under continuous light. However, fruit pruning treatments did not modify the pattern of starch and sugar accumulation under the different photoperiod treatments. Reduced growth and yields measured under a 24-hour photoperiod are probably explained by starch and sugar accumulation in leaves as a result of leaf limitations rather than a sink limitation.

Many studies have shown that supplemental lighting during winter increases growth and yields of greenhouse vegetables. The effects of supplemental lighting [photosynthetic photon flux (PPF) and photoperiod] on the growth and yields of sweet pepper plants has received little study. Positive results obtained with other greenhouse vegetable crops suggest that supplemental lighting may also be beneficial to peppers. Turcotte et al. (1988) and Demers et al. (1991) observed that supplemental lighting increased growth and yields of pepper plants. Demers et al. (1991) also found that extending the photoperiod up to 20 h increased growth and yields of pepper plants. Costes and Milhet (1970) noted that continuous lighting (a 24-h photoperiod) of pepper plants hastened flowering and fruit setting and increased growth and early yields but not final yields. For pepper plants grown under continuous light, Costes and Milhet (1970) observed some occasional light yellowing and small deformations of leaves but no major problems, while Nilwik (1981) noted chlorosis and loss of leaves. Severe leaf chlorosis and decreased growth and yields were observed on tomato (*Lycopersicon esculentum* Mill.) plants grown under continuous light (Bradley and Janes, 1985; Dorais, 1992; Logendra et al., 1990; Vézina et al., 1991). These authors also noted high starch accumulations in tomato leaves exposed to continuous light and suggested that it may be related to chlorosis development and reductions in growth and yields. Vézina et al. (1991) found that mineral nutrition of tomato plants grown under continuous light was not involved in the development of leaf chloroses and limitations in growth and yields. However, the

effects of photoperiod on mineral nutrition of pepper plants have not been reported.

This study was divided in two parts. The objective of the first experiment was to find the best photoperiod for greenhouse sweet pepper production grown under supplemental lighting. In the second experiment, our objectives were to understand more fully the effects of continuous lighting on growth and yields of sweet pepper plants and to determine if mineral nutrition and photosynthate (starch, sugars) contents in leaves are involved in the development of leaf deformities (and chloroses) as well as growth and yield reductions that occurred under continuous light conditions.

Material and Methods

EXPERIMENT 1. ‘Delphin’ sweet pepper plants were sown in rockwool multicells (Grodan, Denmark) on 13 Oct. at Université Laval (Ste-Foy, Qué., Canada) and transferred to 12-cm pots filled with peat on 1 Nov. On 2 Dec., plants were placed in Allegro peat bags (Les Tourbières Premier Inc., Canada) in a greenhouse covered with a double-layer of polyethylene and exposed to the following treatments: natural light or extended photoperiods of 16, 20, and 24 h. High-pressure sodium (HPS) lamps (400 W, P.L. 780, P.L. Lighting Systems) were used as source of supplemental lighting ($PPF = 110 \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$) to extend photoperiod. Table 1 shows the monthly average of total light energy and contribution of supplemental lighting to total light energy received by plants.

Experimental design was a randomized complete block with treatments repeated three times (18 plants per experimental unit). Analyses of variance and multiple comparison tests (Waller-Duncan) (SAS statistic software, SAS Institute, Cary, N.C.) were used to determine the differences between treatments.

Red ripe fruit were harvested weekly from 3 Mar. until 16 July. Fruit >100 g and with no blemishes (bottom end rot, deformity, etc.) were classified as marketable. Pepper plants were trained to

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Table 1. Monthly average for total light energy ($\text{mol}\cdot\text{m}^{-2}\cdot\text{d}^{-1}$) received by plants at Université Laval (Ste-Foy, Québec) and at Cornell University (Ithaca, N.Y.).

Month	Ste-foy				Ithaca	
	Natural light	Supplemental lighting			Supplemental lighting	
		16 h	20 h	24 h	14 h	24 h
December	5.9	12.1 (51) ²	13.7 (57)	15.3 (62)	---	---
January	8.1	14.0 (42)	15.6 (48)	17.2 (53)	25.7 (60)	37.2 (72)
February	12.1	17.6 (31)	19.2 (37)	20.8 (42)	28.6 (45)	40.1 (61)
March	17.8	22.4 (20)	23.9 (26)	25.5 (30)	34.7 (30)	46.2 (47)
April	22.6	26.4 (15)	28.0 (19)	29.6 (24)	36.9 (21)	48.4 (39)
May	25.6	28.9 (12)	30.5 (16)	32.1 (20)	42.4 (15)	53.9 (33)
June	27.4	29.7 (8)	31.3 (13)	32.9 (17)	---	---
July	27.3	29.3 (7)	30.9 (12)	32.5 (16)	---	---

²For supplemental lighting treatments, total light energy = natural light energy + supplemental light energy. Values in parenthesis represent the proportion (%) of the total light energy provided by supplemental lighting (supplemental light energy/natural light energy + supplemental light energy).

keep two main stems. Secondary stems were pruned weekly at the fourth node. No fruit were allowed to develop on secondary stems. Plant density was 3.3 plant/m². Plants were placed in double rows (oriented north to south) 1.5 m. apart (30 cm between single rows within double row) and were irrigated daily with a complete nutrient solution ($\text{EC} = 2.0$ to $2.8 \text{ mS}\cdot\text{cm}^{-1}$, $\text{pH} = 5.5$ to 6.0) using a drip-irrigation system. Heating was set to maintain a minimal temperature of 17°C during the night and 22°C during the day. Ventilation was set at 25°C (low) and 28°C (high). Lamps usually remained on during the day but were automatically turned off when temperature reached 28°C (high-speed ventilation). Greenhouse atmosphere was enriched to $1000 \mu\text{mol}\cdot\text{mol}^{-1}$ of CO_2 using a pure liquid source. Carbon dioxide enrichment was controlled by a infrared gas analyzer (Priva Computers).

EXPERIMENT 2. 'Delphin' sweet pepper plants were sown in rockwool multicells on 25 Nov. at Cornell University (Ithaca, N.Y.), transplanted into rockwool cubes ($7.5 \times 7.5 \text{ cm}$) on 15 Dec., and placed on Allegro peat bags in a glasshouse on 17 Jan. Starting on 29 Jan., plants were exposed to extended photoperiods of either 14 or 24 h. Metal halide lamps (400 W, GTE-Sylvania) were used as source of supplemental light ($\text{PPF} = 350 \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$) to extend the photoperiod. Table 1 shows the monthly average of total light energy and contribution of supplemental lighting to total light energy received by plants. For each photoperiod treatment, half of the plants were pruned to keep one fruit every four nodes on the main stems while the other plants were allowed to bear as many fruit as they could (no fruit removed).

Experimental design was a split plot with photoperiod treatments as the main factor and fruit pruning as the sub-treatments (nine plants per experimental unit). Treatments were repeated twice. Analyses of variance and contrasts were used to determine the differences between treatments. Red ripe fruit were harvested weekly (starting on 26 Mar.) and weighed, and their position (node number) on the plant was noted. No CO_2 enrichment was used during this experiment. Other experimental conditions (plant density, irrigation, etc.) were identical to those in Expt. 1.

One-third of the plants were destructively sampled at 5-week intervals after the beginning of treatments (5 Mar., 9 Apr., and 14 May) and the following parameters measured on each plant: plant height, number of nodes, fresh and dry mass of leaves and stem, and mass and position (node number) of fruit left on plants. Dry mass was measured after drying at 70°C during 48 h. The 20 upper leaves (10 on each main stem) were separately sampled; their fresh and dry mass and leaf area (portable planimeter LI-3000; LI-COR, Lincoln, Nebr.) were measured and their specific fresh mass (fresh

mass/leaf area) and specific dry mass (dry mass/leaf area) were calculated. The harvest index (fruit harvested + fruit left on plant/whole plant fresh mass + fruit harvested + fruit left on plant) was also calculated.

On each sampling date, subsamples of the fifth and tenth leaves from the apex of the plant were taken for mineral analyses. Total nitrogen concentrations were determined using the Kjeldahl method (colorimeter Technicon; TRAACS 800). Other element concentrations were determined with an inductively coupled plasma atomic emission spectrophotometer (model 61E; Thermo Jarrell-Ash, Boston). Also, on week 8 (26 Mar.) and 12 (23 Apr.), samples of the fifth leaf were taken at the beginning (0800 HR) and the end of the day (1800 HR) for starch and sugar content analyses. Leaf samples were cold ground, homogenized in ethanol, heated in boiling water, and centrifuged, and pellet (starch) and supernatant (soluble sugars) were separated (Ozbun et al., 1973). Glucose and the resulting glucose from the enzymatic degradation of sucrose (with invertase and gluco-isomerase) and fructose (with gluco-isomerase) were determined by coupling the oxidation of glucose to the reduction of NADP⁺ with hexokinase and Glc-6-P dehydrogenase and reading absorbance at 340 nm (Galtier et al., 1995). Starch was resuspended and hydrolyzed overnight at 37°C using amyloglucosidase and α -amylase (Robinson et al., 1988). Glucose resulting from the hydrolysis of starch was determined as described above.

Results

EXPERIMENT 1. After 10 weeks of treatment, we noted some leaf deformations (wrinkles) but no chlorosis on plants grown under continuous light. Costes and Milhet (1970) also observed leaf deformations on pepper plants under continuous light. Contrary to Nilwik (1981), no leaf chlorosis nor leaf loss was observed. Light leaf deformations also happened occasionally on plants receiving 20 h of light but not on plants grown under the 16-h photoperiod and natural light.

Pepper plants grown under extended photoperiod treatments had significantly higher early yields (marketable and total) (3 Mar. to 5 May) than those under natural light (Table 2). Also, plants grown under the 20-h photoperiod had significantly higher yields than plants maintained under 16- and 24-h photoperiod. No difference was noted between yields of plants grown under the 16- and 24-h photoperiods. Differences between treatments in the number of fruit harvested were generally the same as for yields (Table 2). Number of fruit and yields measured between weeks 11 and 20 (12

Table 2. Yields of pepper plants grown under different photoperiods (Ste-Foy, Québec).

Harvest period and photoperiod (h)	Marketable fruit		Total fruit		Mean fruit
	Yield (kg·m ⁻²)	No. (no/m ²)	Yield (kg·m ⁻²)	No. (no/m ²)	mass (g)
3 March until 5 May (weeks 1 to 10) (early yields)					
Natural	3.7 a ^c	28.4 a	4.2 a	36.3 a	129.0 a
16	5.2 b	34.4 b	6.0 b	43.7 b	150.4 c
20	6.1 c	42.6 c	7.0 c	52.0 c	143.8 bc
24	4.6 b	32.9 ab	5.6 b	44.9 b	139.0 ab
12 May to 16 July (weeks 11 to 20) (late yields)					
Natural	3.7 a	26.5 a	4.3 a	32.6 a	139.8 a
16	4.1 a	27.3 a	4.8 a	34.1 a	149.8 b
20	5.0 b	34.7 b	5.9 b	44.7 b	143.8 ab
24	4.2 a	29.9 a	4.9 a	37.8 a	141.4 ab
3 March to 16 July (weeks 1 to 20) (total yields)					
Natural	7.4 a	54.9 a	8.5 a	68.9 a	134.2 a
16	9.3 b	61.7 b	10.8 b	77.8 b	150.2 b
20	11.1 c	77.3 c	12.9 c	96.7 c	143.8 ab
24	8.8 b	62.8 b	10.5 b	82.7 b	140.1 ab

^aFor each column and harvest period, values followed by different letters are significantly different at $P = 0.05$ (Waller-Duncan multiple comparison test).

May to 16 July) were only significantly higher under the 20-h photoperiod than the other photoperiods (Table 2). Differences between treatments for final yields (3 Mar. to 16 July) were identical to those for early yields. At the end of the experiment (16 July), plants cultivated under extended photoperiod treatments bore more immature fruit than plants grown under natural light (data not shown).

In general, during the first 10 weeks of harvest (3 Mar. to 5 May), supplemental lighting increased the average fruit mass compared to natural light (Table 2). The highest average fruit mass was obtained at the 16-h photoperiod, while longer photoperiods (20 and 24 h) progressively decreased average fruit mass. Our results confirm those of Costes and Milhet (1970), who observed that continuous light resulted in average fruit mass lower than that obtained with a 15-h photoperiod. During harvest weeks 11 to 20 (12 May to 16 July), only fruit harvested on plants grown under the 16-h photoperiod had a significantly higher average mass than fruit harvested from the natural light treatment. No difference was observed for the percentage of marketable fruit (82% to 87%) obtained under the different photoperiod treatments (data not shown).

EXPERIMENT 2. As in Expt. 1, pepper plants grown under continuous light showed some leaf deformations (wrinkles) (after

12 weeks of treatments) but no chlorosis, while plants receiving 14 h of light did not show any leaf deformations or chlorosis.

Significant interactions between photoperiod treatments and sampling dates were observed with most of the parameters measured (Tables 3 and 4). Using simple effect contrasts, we determined the differences between photoperiods within each sampling date. After 5 weeks of treatments (5 Mar.), leaf and whole-plant fresh and dry mass as well as dry matter percentage of leaves had increased significantly as a result of 24 h light (Table 4). Plant height, number of nodes, internode length, and leaf area were not different between photoperiods at week 5 (5 Mar.) (Table 3). By weeks 10 (9 Apr.) and 15 (14 May), plant height and internode length were greater for the 14-h photoperiod treatment, while the number of nodes was higher under the 24-h photoperiod. In addition, the earlier advantage in leaf and whole-plant dry mass and leaf dry matter percentage had disappeared (no difference between the 14- and 24-h photoperiod treatments), while leaf and whole-plant fresh mass became higher under the 14-h photoperiod (Table 4). Specific mass (fresh and dry) and dry matter content of the first 20 upper leaves (data not shown) as well as whole-plant dry matter percentage (Table 4) remained significantly higher under continuous light for the total duration of the experiment.

Table 3. Photoperiod effects on growth and development of pepper plants (Ithaca, N.Y.).

Weeks after start and date	Photoperiod (h)	Plant		Internode length (cm)	First 20 upper leaves		
		ht (cm)	No. of nodes		Area (dm ²)	Fresh mass (g)	Dry mass (g)
5 (5 March)	14	64.4 ^{NS}	21.2 ^{NS}	3.0 ^{NS}	1.18 ^{NS}	46.3*	5.37**
	24	63.8	22.0	2.9	1.27	52.5	6.73
10 (9 April)	14	98.4***	28.6 ^{NS}	3.4***	1.65***	64.9**	7.79 ^{NS}
	24	86.5	29.5	2.9	1.34	56.5	8.14
15 (14 May)	14	123.2***	35.1***	3.5***	1.26***	51.6*	7.99 ^{NS}
	24	111.6	38.8	2.9	1.02	45.5	7.59
Anova							
Photoperiod		***	***	***	***	NS	NS
Date		**	***	NS	NS	NS	NS
Photoperiod × date		**	***	***	***	***	*

NS, *, **, *** Nonsignificant or significant at $P = 0.05$, 0.01, or 0.001, respectively.

Table 4. Photoperiod effects on vegetative growth of pepper plants (Ithaca, N.Y.).

Weeks after start and date	Photoperiod (h)	All leaves			Whole plant		
		Fresh mass (g)	Dry mass (g)	Dry matter (%)	Fresh mass (g)	Dry mass (g)	Dry matter (%)
5 (5 March)	14	221.8*	26.6*	12.0*	366.4*	45.1*	12.3
	24	253.1	33.5	13.2	420.8	56.0	13.3
10 (9 April)	14	420.4 ^{NS}	54.3 ^{NS}	12.9***	675.8 ^{NS}	92.0 ^{NS}	13.6
	24	431.0	65.7	15.2	673.8	104.9	15.5
15 (14 May)	14	755.8*	116.9 ^{NS}	15.5 ^{NS}	1197.5*	195.0 ^{NS}	16.3
	24	722.9	116.5	16.1	1140.1	193.6	17.0
Anova							
Photoperiod		NS	*	***	NS	NS	*
Date		**	**	*	**	**	NS
Photoperiod × date		**	*	**	**	*	NS

NS, *, **, *** Nonsignificant or significant at $P = 0.05$, 0.01 , or 0.001 , respectively.

Total (cumulative) yields of pepper plants grown under continuous light were higher than plants receiving 14 h of light (Table 5). However, this is probably due to the fact that yields tended to be higher (difference not significant) under continuous light during the first period of harvest (weeks 8 to 10, 26 Mar. to 9 April) but not during the second period of harvest (weeks 11 to 15, 16 Apr. to 14 May). Total fruit (harvested and on plant) and harvest index were significantly higher under continuous light after 5 and 10 weeks (5 Mar. and 9 Apr., respectively) of treatments, but not at the end of experiment (14 May) (Table 5).

For most parameters measured, we observed significant differences between fruit-pruned and nonpruned plants (data not shown). Fruit load reduction (pruned plants) resulted in a displacement of total growth from reproductive to vegetative. Fruit-pruned plants were taller and had bigger and denser stems and larger, heavier, and denser leaves, but had lower yields. Pepper plants under both photoperiods were similarly affected by fruit-pruning treatment (no interaction between photoperiod and fruit pruning treatments). In addition, fruit-pruning treatment had no effect on the date of appearance or severity of leaf deformations.

Leaf mineral composition (N, Ca, Mg, and Fe) of pepper plants was not affected by photoperiod (Table 6) (other elements analyzed were Mn, B, Zn, Cu, and Mo, data not shown). Only leaf K content was significantly lower under continuous light than under the 14-h photoperiod. Also, leaf P content of plants grown under

the 14-h photoperiod was significantly higher, but only at week 5 (5 Mar.). However, leaf K and P content under both photoperiods were within recommended levels (Turcotte and Gosselin, 1987) for a sweet pepper crop.

For both sampling dates [26 Mar. (week 8) and 23 Apr. (week 12)], continuous light compared to the 14-h photoperiod treatment significantly increased starch, sucrose, and hexose (glucose, and fructose) content in pepper leaves when samples were taken at 0800 HR (data not shown). For samples taken at 1800 HR, the difference in starch content between the two photoperiods was smaller than at 0800 HR but remained significantly higher under continuous light, while no difference was observed for sucrose and hexose content (Table 7, data on 23 Apr., week 12). Our results were similar to data obtained from tomato plants by Logendra et al. (1990), Vézina et al. (1991), and Dorais (1992), who noted increased leaf starch content (and increased sugars in some case) under continuous light. Reducing fruit load (pruned plants) did not modify sucrose and hexose content (samples taken at 0800 and 1800 HR on both dates) and starch content (samples taken at 0800 and 1800 HR on 26 Mar., week 8). On 23 Apr. (week 12), starch content (at 0800 and 1800 HR) was significantly lower in fruit-pruned plants. In addition, starch and sugar accumulation in leaves of pepper plant grown under the two photoperiod treatments was not influenced by fruit-pruning treatment (no interaction between photoperiod and fruit pruning treatment).

Table 5. Photoperiod effects on yields of pepper plants (Ithaca, N.Y.).

Weeks after start and date	Photoperiod (h)	Yield by harvest period		Total		Harvest index
		(kg/plant)	(kg/plant)	yield ^z (kg/plant)	fruit ^y (kg/plant)	
5 (5 March)	14	---	---	---	0.23*	0.37*
	24	---	---	---	0.34	0.43
10 (9 April)	14	0.13	0.13	0.13	0.65**	0.48**
	24	0.24	0.24	0.24	0.80	0.54
15 (14 May)	14	0.75	0.88	0.88	1.72 ^{NS}	0.59 ^{NS}
	24	0.73	0.97	0.97	1.69	0.60
Anova						
Photoperiods		NS	*	***	***	***
Date		**	***	***	***	**
Photoperiod × date		NS	NS	*	*	**

^zTotal or cumulative yield = harvested fruit only (beginning of experiment until sampling date).

^yTotal fruit = fruit harvested + fruit on plants (beginning of experiment until sampling date).

NS, *, **, *** Nonsignificant or significant at $P = 0.05$, 0.01 , or 0.001 , respectively.

Table 6. Leaf mineral composition of pepper plants grown under different photoperiods (Ithaca, N.Y.).

Weeks after start and date	Photoperiod (h)	N (%)	P (%)	K (%)	Ca (%)	Mg (%)	Fe (mg·kg ⁻¹)
5 (5 March)	14	4.64	0.48**	5.91	3.29	1.06	206.5
	24	4.59	0.42	5.62	3.34	1.05	229.4
10 (9 April)	14	4.55	0.43 ns	7.25	3.00	0.99	101.8
	24	4.48	0.39	6.41	2.95	0.97	98.2
15 (14 May)	14	4.53	0.38 ns	5.86	2.77	1.09	83.3
	24	4.67	0.42	5.46	2.44	0.97	74.5
Means	14	4.58	0.44	6.40	3.05	1.04	130.5
	24	4.57	0.41	5.88	2.97	1.00	134.0
Recommended level ²		3.5–4.2	0.39	5.1–5.9	2.8–3.2	0.5–0.75	112
Anova							
Photoperiod		NS	*	*	NS	NS	NS
Date		NS	NS	*	*	NS	**
Photoperiod × date		NS	*	NS	NS	NS	NS

²Turcotte and Gosselin. 1987.NS, *, **, ***Nonsignificant or significant at *P* = 0.05, 0.01, or 0.001, respectively.

Discussion

EXPERIMENT 1. Our results show that supplemental lighting increased yields of sweet pepper plants, especially during spring (March and April), and that the best photoperiod is 20 h. The increased yields were mainly due to an increase in the number of fruit harvested, but also to some increase in the average fruit mass. Exposing plants to continuous light caused negative effects such as decreased yields and leaf deformations. During weeks 11 to 20 (12 May to 16 July), the increased natural light level and lower use of supplemental lighting reduced the difference between photoperiod treatments in total light energy received by plants. For example, plants under continuous light received 160% more light energy in December, 44% in March, and 19% in July than plants under natural light only. This small difference in total light energy between photoperiod treatments probably explain why, during weeks 11 to 20 (12 May to 16 July), no difference was observed in the average fruit mass between natural light treatment and extended photoperiod treatments of 20 and 24 h as well as in yields between the natural light treatment and extended photoperiods of 16 and 24 h.

EXPERIMENT 2. We observed that, for the first 5 weeks, pepper plants grew better under continuous light than under a 14-h photoperiod, indicating that pepper plants effectively used the

extra light energy provided by continuous lighting. However, at the end of the experiment, plants grown under the 14-h photoperiod had developed the same amount of fruit and had a total growth equal to or higher than plants under continuous light. This indicates that growth and fruit production rates of plants receiving continuous light were decreased after the first 5 weeks. During that period, the difference between photoperiod treatments in total light energy received by plants was decreased by increasing natural light level and lower use of supplemental lighting. Continuous light provided 45% more light energy in February and 27% more in May than the 14-h photoperiod. This should have resulted in similar growth and fruit production rates of plants under the two photoperiods. In such a case, the differences (higher growth and yields under continuous light) observed after 5 weeks of treatments should have remained. Therefore, the decreased growth and fruit production rates can only be explained by the fact that continuous light negatively affected sweet pepper plants.

Our work shows that it may be possible to provide continuous lighting for a few weeks to improve growth and yields during months with the lowest natural light levels (December and January) and then decreasing the photoperiod to 20 h. However, this practice should be investigated to determine if using continuous light for a few weeks may cause residual negative effects on growth and yields of sweet pepper plants.

Table 7. Effects of photoperiod and fruit pruning on leaf starch and sugar content (mg/g fresh mass) of pepper plants (samples taken on 23 Apr., week 12 at 18 h) (Ithaca, N.Y.).

Photoperiod (h)	Fruit pruning	Starch	Sucrose	Glucose	Fructose
14	Pruned	7.33	1.69	0.88	0.43
	Control	8.30	1.76	0.81	0.43
24	Pruned	7.84	1.84	0.91	0.46
	Control	8.56	1.75	0.84	0.49
Average	14 h	7.82	1.72	0.84	0.43
	24 h	8.20	1.80	0.87	0.48
	Pruned	7.59	1.77	0.90	0.45
	Control	8.43	1.76	0.83	0.46
Anova					
Photoperiod		**	NS	NS	NS
Fruit pruning		***	NS	NS	NS
Photoperiod × fruit pruning		NS	NS	NS	NS

NS, *, **, ***Nonsignificant or significant at *P* = 0.05, 0.01, or 0.001, respectively.

Our results for leaf mineral contents indicate that the fertilization program used in this experiment was adequate for a greenhouse sweet pepper crop and that growth and yield decreases observed under continuous light were probably not related to mineral nutrition problems.

Fruit-pruned plants had greater vegetative growth than plants that were not pruned. Also, in general, no difference was noted in leaf starch and soluble sugars contents between fruit-pruning treatments. This suggests that, for fruit-pruned plants under both photoperiods, carbon assimilates that were not used for fruit production were used instead for increased vegetative growth.

Extending the photoperiod to 24 h increased leaf starch accumulation (and soluble sugars contents at certain periods of the day). The fact that the pattern of starch and sugar accumulation in leaves under both photoperiods was not influenced by fruit-pruning treatments suggests that increased starch and sugar content under continuous light is not caused by limiting sink strength. Furthermore, fruit-pruning treatments did not affect the severity or date of appearance of leaf deformations. Therefore, if starch and sugar accumulation is involved in the development of the negative effects, such as decreased growth and yields and leaf deformations, caused by continuous light on pepper plants, it is most likely that this accumulation is the result of a limitation within the leaf, probably the carbon metabolism. Such a limitation of the leaf carbon metabolism is possibly the sucrose-phosphate synthase (SPS) enzyme. This enzyme is responsible for synthesis of sucrose, which is the main export sugar, and its activity level can influence carbon partitioning. For example, Galtier et al. (1995) and Galtier et al. (1993) found that transgenic tomato plants overexpressing the SPS enzyme had decreased leaf starch contents and increased leaf sucrose content, photosynthesis rate, and shoot to root ratio compared to untransformed plants.

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