Plant Physiol. (1987) 85, 592–597
0032-0889/87/85/0592/06/$01.00/0

Regulation of Photosynthetic Carbon Metabolism in Cucumber by Light Intensity and Photosynthetic Period[1]

Received for publication March 20, 1987 and in revised form July 15, 1987

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ABSTRACT

The effects of photosynthetic periods and light intensity on cucumber (*Cucumis sativus* L.) carbon exchange rates and photoassimilate partitioning were determined in relation to the activities of galactinol synthase and sucrose-phosphate synthase. Carbon assimilation and partitioning appeared to be controlled by different mechanisms. Carbon exchange rates were influenced by total photon flux density, but were nearly constant over the entire photoperiod for given photoperiod lengths. Length of the photosynthetic periods did influence photoassimilate partitioning. Assimilate export rate was decreased by more than 60% during the latter part of the short photoperiod treatment. This decrease in export rate was associated with a sharp increase in leaf starch acccumulation rate. Results were consistent with the hypothesis that starch accumulation occurs at the expense of export under short photoperiods. Galactinol synthase activities did not appear to influence the partitioning of photoassimilates between starch and transport carbohydrates. Sucrose phosphate synthase activities correlated highly with sugar formation rates (sucrose, raffinose, stachyose + assimilate export rate, $r = 0.93$, $\alpha = 0.007$). Cucumber leaf sucrose phosphate synthase fluctuated diurnally in a similar pattern to that observed in vegetative soybean plants.

The influence of photoperiod on partitioning of photoassimilates between soluble sugars and starch is of considerable interest in that rates of photoassimilate transport and storage determine the concentrations of carbohydrates available for growth of sink organs (2, 6, 7, 12). Plants may respond to short photoperiods by increasing the rate of leaf starch accumulation (2). Differences in carbon partitioning for cucumber plants grown under short photoperiods/low light intensity and long photoperiods/high light intensity have been measured (1). Although higher rates of starch accumulation were observed under a short photoperiod treatment, the independent effects of photosynthetic photoperiod and light energy over a 24 h period have not been determined.

SPS,[3] a key enzyme in the sucrose biosynthetic pathway, has been implicated in the regulation of carbon partitioning between starch and sucrose in several sucrose translocating species (13, 14, 16). Levels of extractable SPS activity were within the range needed to account for sucrose formation rates; maximum activity varied between species and was negatively correlated with leaf starch concentrations (12). It has been postulated that high SPS activity would permit high rates of sucrose formation (9). Rapid turnover of cytosolic phosphate-esters under these conditions would enhance the exchange of triose phosphates across the chloroplast membrane. The amount of carbon available for starch formation in the chloroplast would be decreased under such conditions and photosynthate diverted toward sucrose formation (9).

Cucumbers (*Cucumis sativus* L.) synthesize the transport carbohydrate, stachyose (19, 20, 26), in three enzymatic steps which are addenda to the sucrose biosynthetic pathway (15). These steps are:

1. UDP-galactose + *myo*-inositol→galactinol + UDP
2. Galactinol + sucrose→raffinose + *myo*-inositol
3. Galactinol + raffinose→stachyose + *myo*-inositol.

Changes in the activity of the enzymes responsible for these reactions may regulate the relative concentration of carbohydrates available for export in cucumber (19, 20). For instance, the first reaction to commit carbon for the production of galactosyl-sugars, catalyzed by Gal-Syn (No. 1), may control carbon partitioning between sucrose and stachyose (8, 19). The role played by SPS in partitioning of photosynthate between chloroplastic starch and export forms of carbohydrate in cucumber is not known. The present study was conducted to examine the effects of short and long photosynthetic periods on cucumber leaf carbohydrate contents and export rates in source leaves, as they relate to the activities of Gal-Syn and SPS.

MATERIALS AND METHODS

Plant Materials. Cucumber seeds (*C. sativus* L.) were sown directly in plastic containers (25 cm deep and 26 cm wide) filled with a substrate composed of gravel and a commercial peat-like mixture (Redi Earth,[4] W.R. Grace Co.). The seeded plastic containers were placed in growth chambers located in the Southeastern Plant Environment Laboratories, North Carolina State University Phytotron, Raleigh, NC. Chamber temperature was maintained at 25 ± ¼°C (4). Containers were watered with deionized water each day until seeds germinated. Seedlings were thinned to one plant per pot. Plants were then irrigated once per day with deionized water and a modified Hoagland solution to ensure adequate moisture and nutrient availability. The nutrient solution contained 5 mM $Ca(NO_3)_2$, 5 mM KNO_3, 1 mM KH_2PO_4,

[1] Paper No. 10962 of the Journal Series of the North Carolina Agricultural Research Service, Raleigh, NC 27695-7601.

[2] This work is a portion of a thesis submitted by N. S. R. in partial fulfillment for the Ph.D. degree.

[3] Abbreviations: SPS, sucrose phosphate synthase; Gal-Syn, galactinol synthase; PPFD, photosynthetic photon flux density ($\mu E \cdot m^{-2} \cdot s^{-1}$); CER, carbon exchange rate (mg $CH_2O \cdot dm^{-2} \cdot h^{-1}$); AER, assimilate export rate (mg $CH_2O \cdot dm^{-2} \cdot h^{-1}$).

[4] Mention of trademark or proprietary product does not constitute a guarantee of the product by the North Carolina Agricultural Research Service nor does it imply approval to the exclusion of other products that may be suitable.

2 mM $MgSO_4$, 4 ppm $ZnCl_2$, 1 ppm boric acid, 0.1 ppm $CuCl_2$, 0.01 ppm Na_2MoO_4.

Plants were grown with an upright morphology by removing laterals and flowers to maintain vegetative plants with similar, single stems. Plants were grown until 11 nodes were produced. Leaves were counted from the growing apex to the first true leaf. Sampling was initiated at this growth stage for plants grown in each treatment.

Light Treatments. The influences of photosynthetic period and light intensity on carbohydrate metabolism were investigated using three light treatments (Fig. 1). The first treatment was a long day (14 h), high intensity photoperiod (LD/HI), while the second was a short day (8 h), high intensity photoperiod (SD/HI). Plants in each of these treatments were exposed to 650 $\mu E \cdot m^{-2} \cdot s^{-1}$ PPFD (at the soil surface) for the duration of their respective photoperiods. To separate the influence of photosynthetic period length from total light energy received, cucumber plants were grown in a third treatment consisting of a long day (14 h) and low intensity photoperiod (LD/LI). Plants in the LD/LI treatment received a PPFD of 380 $\mu E \cdot m^{-2} \cdot s^{-1}$ (at the soil surface). The total light energy received by plants over a 24 h period in the LD/LI and SD/HI treatments was approximately equal. Treatments were initiated at the time containers were placed in the growth chambers. A separate group of seven plants, grown in each of the three treatments, was used for each sampling interval (Fig. 1).

Carbon Exchange Rates. CER was measured with a differential infrared gas analyzer (Anarad model AR-600) by using a 10 cm^2 plexiglass clamp-on cuvette that enclosed the adaxial and abaxial leaf surface. Gas with a CO_2 concentration of about 350 $\mu l \cdot L^{-1}$ was passed over the leaf surface at a rate of 1.5 $L \cdot min^{-1}$. Differences between the concentration of incoming and outgoing gas were measured. Measurements were made at the midpoint of the morning and the midpoint of the afternoon sampling intervals for each treatment (Fig. 1). All measurements were made using source leaves at the seventh node from the apex (19), hereafter referred to as the sample leaf. CER was calculated using the method of Hesketh and Moss (10) and are expressed as mg $CH_2O \cdot dm^{-2} \cdot h^{-1}$.

Assimilate Export Rates. AER from sample leaves was estimated using the general method of Terry and Mortimer (25). Six-leaf discs (1.38 cm^2 each) were removed from source leaves at the beginning and end of each sampling interval during the photoperiod. Leaf discs were taken 1.5 h prior to and 1.5 h after the CER measurements. Leaf discs were freeze-dried and weighed to provide an estimate of the rate of dry weight change per unit area for each sampling interval during the photoperiod.

Determination of Soluble Sugar and Starch. Weighed leaf disc samples were crushed with a glass rod and ground for 1 min in 3 ml of 80% (v/v) ethanol using a Brinkmann Polytron Homogenizer (Brinkman Instruments, Westbury, NY). Samples were held in a boiling water bath for 5 min, cooled, and centrifuged at 1000*g* for 10 min. The supernatant was retained. The pellet was extracted two additional times in 3 ml 80% (v/v) ethanol. Supernatants from each extraction were combined and evaporated to dryness *in vacuo* at 45°C, resolubilized in 0.5 ml distilled water, and stored at −20°C until analyzed.

Stachyose, raffinose, galactinol, and sucrose levels were ascertained using HPLC. The system consisted of a Waters 6000A pump (Millipore, Waters Chromatography Division), a Waters Sugar-Pak I column, and a Waters 401 refractive index detector connected to a strip chart recorder. Distilled water at a flow rate of 0.5 ml/min was used as the solvent. The column temperature was maintained at 75°C and was preceded by a Waters Bondpak C_{18}/Corasil guard and a set of anion and cation cartridges (Bio-Rad Laboratories, deashing guards). All guards were operated at an ambient temperature of 22°C. Twenty μl of sample were injected. Sugars were identified and quantified on the basis of retention time and peak heights of sugar standards.

The leaf residue remaining after ethanolic extraction was resuspended in 1 ml 0.2 M KOH and boiled for 30 min. Samples were cooled and adjusted to about pH 5.50 by adding 2 ml of 1 M acetic acid. Amyloglucosidase (Sigma Chemical), which had been dialyzed against 50 mM Na-acetate buffer (pH 4.5), was used to digest the gelatinized starch to glucose by incubating preparations in a 55°C water bath for 60 min. The reaction was terminated by placing samples in a boiling water bath.

The released glucose was detected enzymically. An aliquot of sample was incubated for 30 min at 22°C in 0.5 ml of a reaction mixture containing 200 mM Hepes-NaOH buffer (pH 8.0), 10 mM $MgCl_2$, 10 mM DDT, 2 mM ATP, 2 mM $NADP^+$, 2 units hexokinase (Sigma Chemical, type VI from Bakers Yeast), and 2 units glucose 6-P dehydrogenase (Sigma Chemical, type V from Bakers Yeast). The reduction of $NADP^+$ by glucose 6-P dehydrogenase was determined spectrophotometrically at 340 nm using a Lambda 3 Spectrophotometer (Perkin-Elmer Corp., Oak Brook, IL). Glucose concentrations were determined by comparisons to glucose standards.

Extraction and Assay of Enzymes. SPS activity was measured using the method described by Huber and Israel (14) with minor

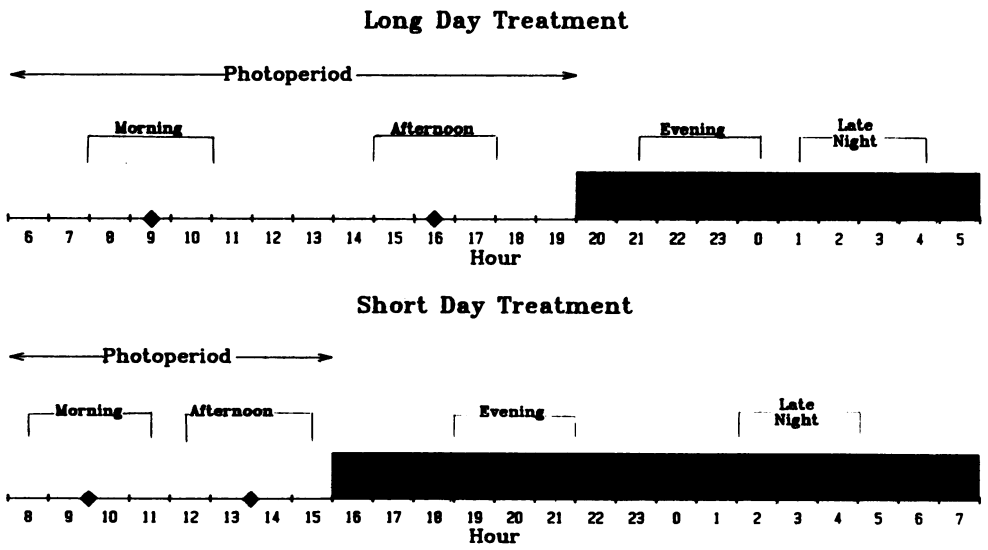

FIG. 1. Photoperiod treatments and sampling intervals. Photoperiod and PPFD for each treatment are: 8 h/650 $\mu E \cdot m^{-2} \cdot s^{-1}$ (SD/HI), 14 h/380 $\mu E \cdot m^{-2} \cdot s^{-1}$ (LD/LI), and 14 h/650 $\mu E \cdot m^{-2} \cdot s^{-1}$ (LD/HI). Sampling intervals include: Morning, Afternoon, Evening, Late Night. Identical sampling intervals were used for SD/HI, LD/HI and LD/LI treatments. (♦), Midpoint in photoperiod sampling intervals. Separate groups of seven plants were used for the four sampling intervals within each 24 h period.

modifications. Leaf extracts were prepared by homogenizing (Brinkman Polytron Homogenizer, Brinkman Instruments, Westbury, NY) 2 g fresh weight of shredded leaves 0°C for 1 min in 10 ml 50 mM Hepes-NaOH buffer (pH 7.5), 10 mM $MgCl_2$, 1 mM EDTA, 1% polyethylene glycol-20, 0.25% BSA (Sigma Chemical) and 5 mM DTT. The homogenate was filtered through cheesecloth, centrifuged at 32,000*g* for 10 min, and the supernatant was assayed for SPS activity. Activity was determined on the basis of fructose 6-P-dependent formation of sucrose (+sucrose-phosphate) from UDP-glucose. A total reaction volume of 70 μl contained 25 mM UDP-glucose, 8 mM fructose 6-P, 5 mM $MgCl_2$, 50 mM Hepes-NaOH buffer (pH 7.5), and leaf extract. Reactions were incubated at 25°C for 40 min and terminated by addition of 70 μl 1 N NaOH. Unreacted fructose 6-P and fructose were destroyed by placing tubes in a boiling water bath for 10 min. Once cooled, 0.25 ml of 1% resorcinol in 95% (v/v) ethanol and 0.75 ml 30% (v/v) HCL were added. Tubes were placed in an 80°C water bath for 8 min, removed and cooled to room temperature. SPS activity was determined spectrophotometrically at 520 nm by measuring formation of sucrose-P and sucrose. Rates of sucrose formation were based on detected sucrose concentrations in comparison to sucrose standards.

Gal Syn activity was determined using extracts from 1 g leaf tissue prepared as described above in a grind medium containing 50 mM Hepes-NaOH buffer (pH 7.0) and 10 mM DTT. Gal Syn activity was determined utilizing an isotopic assay described by Handley *et al.* (8).

Statistical Analysis. Means and standard errors were determined from samples of seven plants. Possible relationships between carbohydrate partitioning parameters, such as dry weight accumulation rates *versus* starch accumulation rates, were examined using two-way correlation analysis. Correlations were conducted across all treatments using mean values ($n = 6$).

RESULTS

Photosynthesis and Carbohydrate Partitioning. Light intensity altered the rate of carbon dioxide fixation in cucumber source leaves (Table I). CER under low PPFD was about half the rate measured under the two high intensity treatments irrespective of photoperiod length. CER varied little between morning and afternoon sampling intervals in the SD/HI and LD/LI treatments. CER was slightly lower during the afternoon interval as compared to the morning sampling interval in the LD/HI treatment.

In contrast, length of the photosynthetic period altered partitioning of photoassimilate in cucumber source leaves (Table I). Although a decrease in AER from morning to afternoon was observed in all three treatments, plants grown under SD/HI conditions exhibited the sharpest decline. Export rates were decreased by 60% during the afternoon sampling interval in source leaves of plants grown under an 8 h photosynthetic period. Lower AER during the afternoon sampling interval for SD plants was associated with approximately 50% of the total fixed carbon being incorporated into starch. AER across all treatments was negatively correlated with leaf dry weight accumulation ($r = -0.88$, $\alpha = 0.0001$). Increased leaf dry weight during the photoperiod was positively correlated with starch accumulation ($r = 0.95$, $\alpha = 0.004$). These results support the supposition that dry weight increase in cucumber source leaves was at least partially due to starch accumulation at the expense of export.

Carbohydrate Status and Enzyme Activity. Soluble sugar concentrations in cucumber source leaves during the photoperiod were calculated by averaging the concentrations from leaf disc samples collected at the beginning and end of each sampling interval. Stachyose, raffinose, and galactinol concentrations were slightly increased in the afternoon sampling interval in all three treatments (data not shown). In contrast, significant increases in leaf sucrose concentations occurred during the afternoon photoperiod for all the treatments (Fig. 2) Although previous studies with soybean plants (5) have reported that such increases in sucrose were associated with higher AER, this relationship was not observed in source leaves of cucumber plants (Table I). AER was lower during the afternoon when sucrose concentrations increased in cucumber source leaves in all three treatments.

High SPS activities were generally associated with high CER and AER (Table I). AER and accumulation rates of sucrose, raffinose, and stachyose were combined (sugar formation rate) in order to examine their association with SPS activity. Sugar formation rates were positively correlated with SPS activity ($r = 0.93$, $\alpha = 0.007$) across all treatments (Fig. 3). SPS activity, expressed as mg sucrose$\cdot dm^{-2} \cdot h^{-1}$, was lower *in vitro* than required to account for the amount of carbon flux through calculated sugar formation rates (Fig. 3). If the assumption is made that stachyose represents 100% of AER, the extractable SPS activities account for only about 45% of the sucrosyl moiety represented in cucumber sugar formation rates. Although SPS activities in the present study were within the range of previously measured SPS values in cucumber source leaves (18, 20), they may not represent SPS activity *in situ*. Conversely, it is possible that amino acids or organic acids may constiture a substantial fraction for the translocate from source leavces to sink tisssues. Amino acids and organic acids account for at least 14% of the

Table I. *Influence of Light Treatments on Cucumber Leaf Carbon Exchange Rate, Carbohydrate Partitioning, and Activities of Galactinol Synthase (Gal-Syn) and Sucrose Phosphate Synthase (SPS) during the Photoperiod*

Each datum represents the mean and standard error of seven plants.

Light Treatment	CER (0.68)[a]	AER[b]	Starch Accumulation	SPS Activity	Gal-Syn Activity
		$mg \cdot dm^{-2} \cdot h^{-1}$		$\mu mol \cdot dm^{-2} \cdot h^{-1}$	
Morning					
SD/HI	20.8 ± 0.6	11.5 ± 1.3	5.9 ± 0.5	7.3 ± 1.3	84.4 ± 10.3
LD/LI	11.6 ± 0.5	6.0 ± 1.9	2.2 ± 0.4	4.6 ± 1.0	70.0 ± 4.6
LD/HI	26.2 ± 0.8	17.3 ± 3.2	4.1 ± 1.1	11.6 ± 1.1	156.2 ± 10.0
Afternoon					
SD/HI	20.9 ± 0.2	4.3 ± 2.9	10.1 ± 1.2	4.9 ± 1.4	137.4 ± 5.9
LD/LI	10.5 ± 0.7	4.4 ± 1.0	2.2 ± 0.4	5.9 ± 1.1	78.4 ± 10.4
LD/HI	23.1 ± 1.1	12.8 ± 3.7	3.9 ± 1.0	13.2 ± 1.4	95.1 ± 8.2

[a] Carbon exchange rates (CER) were measured on source leaves located at the seventh node from the growing apex. [b] Assimilate export rate (AER) and starch accumulation rate were estimated from leaf discs collected 1.5 h before and after CER measurements for morning and afternoon sampling intervals.

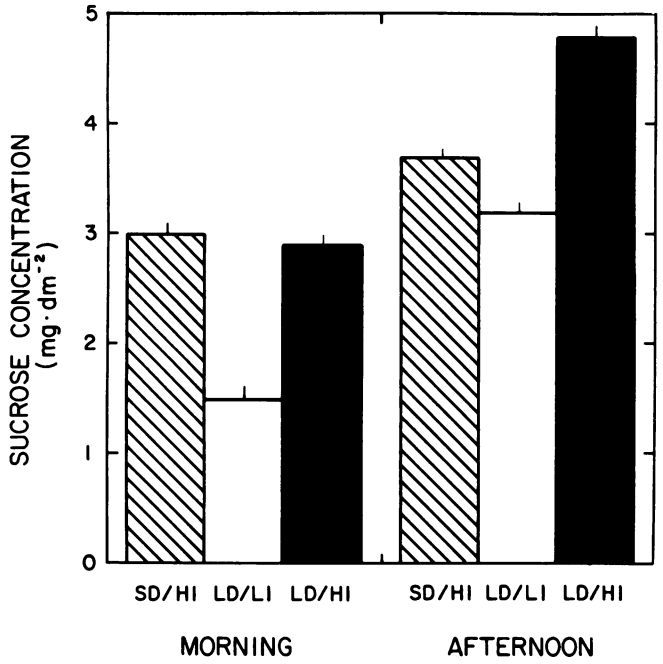

FIG. 2. Influence of three light treatments on sucrose concentrations during the photoperiod. Values for concentrations found in leaf discs collected at the beginning and end of the 3 h morning and afternoon sampling intervals were averaged. Data represent the mean values for seven plants with standard errors. See Figure 1 for treatment definitions.

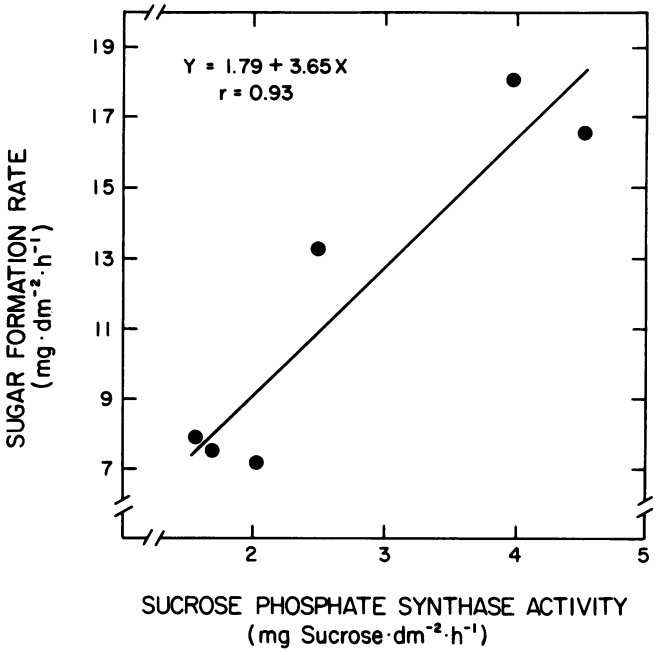

FIG. 3. Relation between sugar formation rate and SPS activity in cucumber source leaves during the photoperiod ($n = 6$). Sugar formation rate calculated by combining AER and accumulation rates for sucrose, raffinose, and stachyose.

^{14}C-photoassimilates exported from soybean source leaves (11). The contribution of amino acids and/or organic acids to estimates of cucurbit AER has been as high as 50% (21).

Cucumber source leaves from plants grown under LD/LI had substantially lower starch mobilization rates throughout the night sampling intervals, as compared to cucumber plants grown under high PPFD (Table II). Starch mobilization rates in source leaves

Table II. *Influence of Three Light Treatments on Starch Mobilization and Activities of Sucrose Phosphate Synthase (SPS) and Galactinol Synthase (Gal-Syn) during the Dark Period*

Each datum represents the mean and standard error of seven plants.

Light Treatment	Starch Mobilization[a]	SPS Activity	Gal-Syn Activity
	$mg \cdot dm^{-2} \cdot h^{-1}$	$\mu mol \cdot dm^{-2} \cdot h^{-1}$	
Early night			
SD/HI	3.9 ± 0.9	10.0 ± 1.2	72.8 ± 13.2
LD/LI	1.1 ± 0.4	9.2 ± 0.8	68.8 ± 10.2
LD/HI	3.9 ± 0.9	21.7 ± 2.1	116.4 ± 8.3
Late night			
SD/HI	2.2 ± 0.1	8.5 ± 1.0	103.9 ± 16.1
LD/LI	0.7 ± 0.4	5.5 ± 1.1	54.8 ± 10.6
LD/HI	3.8 ± 0.7	11.8 ± 1.2	114.5 ± 20.8

[a] Changes in starch concentrations were calculated from leaf discs collected at the beginning and end of 3 h intervals in the middle of the early and late night sampling intervals.

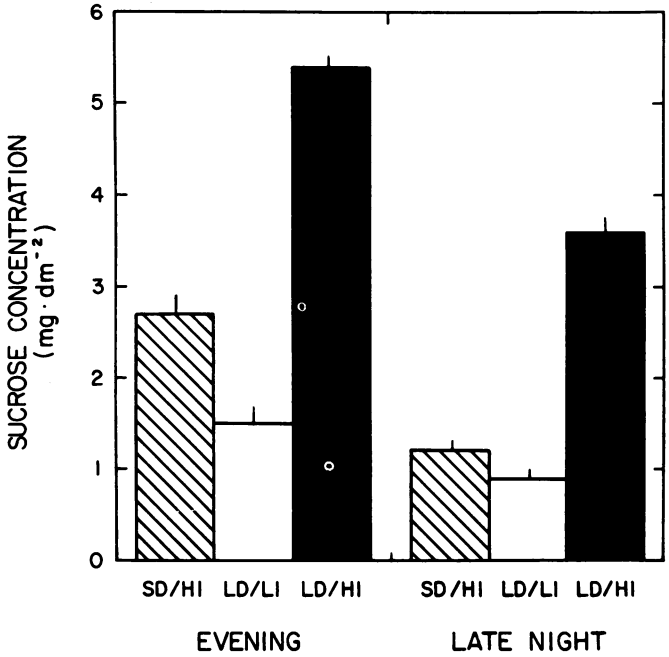

FIG. 4. Influence of three light treatments on sucrose concentrations during the night period. Values for concentrations found in leaf discs collected at the beginning and end of early night and late night sampling intervals were averaged. Data represents the mean values for seven plants with standard error. See Figure 1 for treatment definitions.

of plants grown under the two high PPFD treatments were the same during the early night sampling interval (Table II). During the late night interval starch mobilization declined in leaves of cucumber plants grown under the short photoperiod treatment. The decrease in starch mobilization during the late night sampling interval for plants grown under an 8 h photoperiod represent a depletion of starch reserves in source leaves during an extended night period. Plants in the SD/HI treatment contained substantially less starch per unit area at the end of the late night sampling interval (2.69 ± 0.51) than plants in either the LD/LI or LD/HI treatments (5.66± 1.42, 6.77 ± 1.52 $mg \cdot dm^{-2}$, respectively).

Soluble sugar concentrations in cucumber source leaves during the night interval were calculated in the same manner as photoperiod samples. Concentrations of stachyose, reffinose, and galactinol were relatively constant over both sampling intervals (data not shown). Sucrose concentrations decreased in cucumber

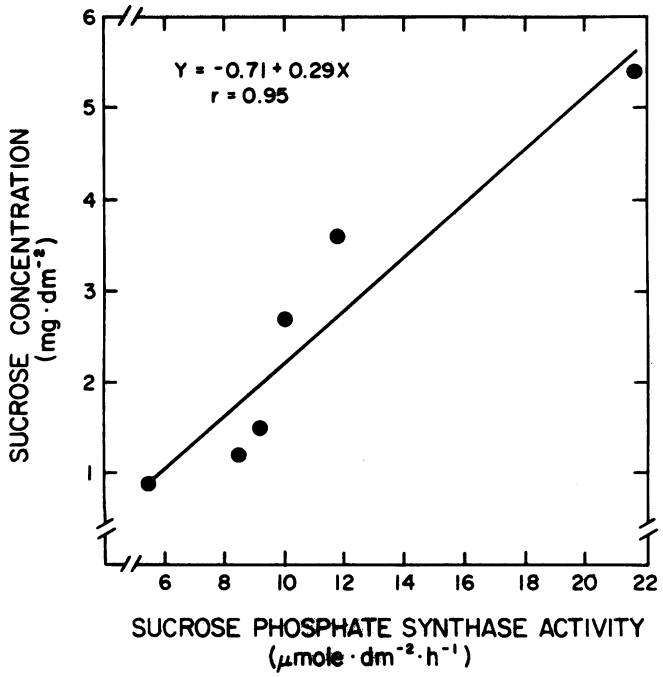

FIG. 5. Relation between sucrose concentration and SPS activity in cucumber source leaves during the night period ($n = 6$). Sucrose concentration determined as described in Figure 4.

source leaves over the night period (Fig. 4). SPS activity was positively correlated with leaf sucrose concentrations ($r = 0.95$, $\alpha = 0.0001$) across all treatments during the night period (Fig. 5). SPS activity in source leaves of cucumber plants exhibited a similar diurnal pattern to that of vegetative soybean plants (17, 22). Highest SPS activities of the entire 24 h period occurred during the early night sampling interval (Table II).

Large variations in Gal-Syn activity were observed between the three light treatments (Tables I and II). Highest Gal Syn activity occurred in source leaves of plants grown under high PPFD, irrespective of photoperiod length. Gal-Syn activity was consistently greater than SPS activity in cucumber source leaves and exhibited variable diurnal changes in activity. However, Gal-Syn activity was not significantly correlated with either photoassimilate export ($r = 0.54$. $\alpha = 0.27$) or AER and formation rates of galactinol, raffinose, and stachyose ($r = 0.33$, $\alpha = 0.26$) during the photoperiod. Starch mobilization during the night period was not associated with changes in Gal-Syn activity ($r = 0.66$ $\alpha = 0.16$).

DISCUSSION

Carbon fixation rates in photosynthetically active tissue may vary with changes in PPFD (7). The results of the present study indicate that PPFD had a greater influence than photoperiod length on CER of cucumber source leaves. The magnitude of carbon fixation varied dramatically between source leaves under high and low light intensities, with maximum rates occurring under high levels of PPFD (Table I). These results are consistent with previous studies that implicated PPFD as a primary stimulus for differences in CER (2, 3, 24).

Increased starch accumulation appears to be a genetically programmed response to an extended night period (2). Although higher rates of starch accumulation in response to short photoperiod has been reported previously for cucumber, differences due to the independent influences of PPFD and photoperiod length were not ascertained (1). In this study, duration of the photosynthetic period influenced partitioning between starch and transport carbohydrates. Cucumber plants exposed to both high PPFD and short photosynthetic photoperiods had higher starch accumulation rates than plants grown under long photoperiods with high or low PPFD. Short photoperiod stimulated an increase in starch accumulation and a corresponding decrease in AER in comparison to plants grown under LD/HI (Table I).

Cucumber plants grown under winter or spring photoperiods mobilized starch at the same rates for the majority of their respective night periods (1). Up to 70% of the photosynthetic carbohydrate reserves in cucumber leaves may be lost during night respiration when cucumber plants are grown under 8 and 14 h photoperiods (1). In the present study plants grown under an 8 h photoperiod nearly depleted their carbohydrate reserves 3 h prior to the beginning of the next photoperiod. This drain on stored carbohydrate could represent genetically controlled processes (respiration and rate of starch mobilization) that require higher starch accumulation during the day when cucumber plants are grown under short photoperiods.

Gal-Syn activity has been associated with raffinose saccharide formation on a developmental basis in cucumber leaves and maturing soybeans seeds (8, 19, 23). Evidence from the present experiment indicates that cucumber source leaves respond to higher rates of photosynthesis with increased Gal-Syn activity (Table I). Marked differences in activity occurred under high PPFD conditions, yet elevated activity was not associated with higher assimilate export or galactosyl sugar formation during the photoperiod and night period.

The role of SPS in regulating the partitioning of carbon between transport and storage carbohydrates in stachyose translocating plants is not clear. SPS activity has been measured in cucumber source leaves of different ages under ambient and enriched CO_2 conditions (18). Under both CO_2 conditions extractable SPS activity declined with plant age. Results of the present study suggest that SPS activity may in part regulate photoassimilate carbon partitioning in cucumber. SPS activity was highly correlated with sugar formation rates (export rate plus the accumulation rate of sucrose, raffinose, and stachyose). Under conditions of high starch accumulation and lower AER extractable SPS activity decreased under short photoperiods. Additionally, SPS activity showed diurnal variation in cucumber source leaves similar to those observed in vegetative soybean plants (17, 22). Although the metabolic consequences of diurnal variations in SPS activity are not fully understood, such fluctuations are of interest due to an association with carbon assimilation and export. Further investigations of the diurnal patterns of SPS and the other enzymes involved in the biosynthesis of stachyose must be conducted before the control of carbon partitioning in cucumber source leaves is fully known.

Acknowledgments—The authors thank Dr. S. C. Huber for use of an Anarad gas analyzer and helpful advice on SPS enzyme assays; Millipore, Waters Chromatography Division, Milford, MA for HLPC equipment furnished through an equipment grant; and Mrs. H. N. Sox and Ms. E. J. Mitcham-Butler for technical assistance.

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