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Effect of Photoperiod on Photosynthate Partitioning and Diurnal Rhythms in Sucrose Phosphate Synthase Activity in Leaves of Soybean (*Glycine max* L. [Merr.]) and Tobacco (*Nicotiana tabacum* L.)[1]

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ABSTRACT

Studies were conducted to identify the existence of diurnal rhythms in sucrose phosphate synthase (SPS) activity in leaves of three soybean (*Glycine max* L. [Merr.]) and two tobacco (*Nicotiana tabacum* L.) cultivars and the effect of photoperiod (15 *versus* 7 hours) on carbohydrate partitioning and the rhythm in enzyme activity. Acclimation of all the genotypes tested to a short day (7 hours) photoperiod resulted in increased rates of starch accumulation, whereas rates of translocation, foliar sucrose concentrations, and activities of SPS were decreased relative to plants acclimated to long days (15 hours). Under the long day photoperiod, two of the three soybean cultivars ('Ransom' and 'Jupiter') and one of the two tobacco cultivars ('22NF') studied exhibited a significant diurnal rhythm in SPS activity. With the soybean cultivars, acclimation to short days reduced the activity of SPS (leaf fresh weight basis) and tended to dampen the amplitude of the rhythm. With the tobacco cultivars, photoperiod affected the shape of the SPS-activity rhythm. The mean values for SPS activity (calculated from observations made during the light period) were correlated positively with translocation rates and were correlated negatively with starch accumulation rates. Overall, the results support the postulate that SPS activity is closely associated with starch/sucrose levels in leaves, and that acclimation to changes in photoperiod may be associated with changes in the activity of SPS.

The principal end products of leaf photosynthesis are sucrose and starch. Sucrose is the primary transport form of carbohydrate in many higher plants, whereas starch accumulates in the chloroplast as a temporary storage form of carbohydrate. In the dark, starch reserves can be mobilized to support continued sucrose synthesis and export. One enzyme which may be involved in regulation of partitioning of carbon between starch and sucrose is SPS[2]. SPS is subject to metabolic regulation (1, 7, 10), and furthermore, its maximum activity, as measured in leaf extracts, appears to reflect the capacity of the sucrose biosynthetic pathway. For example, the activity of SPS increases during leaf expansion concurrent with increased rates of sucrose formation and export (9, 16, 21). In fully expanded leaves, SPS activity varies among different genotypes and in general, higher activities of SPS in leaf extracts have been associated with increased partitioning of carbon into sucrose and decreased formation of starch (11–13, 20, 21).

Changes in leaf carbohydrate metabolism in response to altered irradiance and photosynthetic period in experiments with soybean lend support to the postulate that SPS activity may be a major determinant of the rate of formation and translocation of sucrose. Silvius *et al.* (20) established that soybean plants acclimated to high irradiance had higher rates of photosynthesis and translocation, and greater activities of SPS in leaf extracts, than did plants adapted to low irradiance. Importantly, transfer of low-irradiance plants to high irradiance resulted in increased rates of photosynthesis, but translocation rate was not increased. Rather, the rate of starch accumulation was increased. The authors noted that SPS activity in leaves was not increased (at least within 2 d) after transfer to high irradiance. Hence, SPS activity could have placed a biochemical constraint on translocation. Similar conclusions can be drawn from experiments involving changes in photosynthetic period. Transfer of plants from a long (14 h) to short (7 h) photosynthetic period resulted in increased starch accumulation (3–5) and decreased translocation (2, 19). In soybean, transfer to the short photoperiod also was associated with decreased activity of SPS (13), but the activities of other enzymes involved in sucrose formation, such as UDP-glucose pyrophosphorylase and cytoplasmic fructose-1,6-bisphosphatase, were unchanged (Huber and Pharr, unpublished).

In all of these studies, SPS activity was assayed in leaves harvested at a single time during the day, typically toward the end of the photoperiod. Recently, we reported (18) that SPS activity in soybean 'Ransom' leaves varied diurnally. The rhythm persisted under continuous light or dark conditions and thus appeared to be controlled by an endogenous clock (manuscript in preparation). It is not known whether SPS activity varies diurnally in soybean cultivars other than Ransom or in other species such as tobacco. It also is not known if the rhythm in SPS activity is influenced by changes in photoperiod.

The present study was undertaken to obtain more information about the diurnal rhythm in SPS activity and additional details about the biochemical basis for control of export of assimilates and increased starch formation under short day photoperiods. The specific objectives of this study were to compare the effects

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[2] Abbreviations: SPS, sucrose-phosphate synthase; CER, carbon dioxide exchange rate (mg CO_2 or $CH_2O/dm^2 \cdot h$).

of photoperiod (LD *versus* SD) on (a) photosynthate partitioning in leaves and (b) the diurnal rhythm in SPS activity in leaves. The photoperiod experiments were conducted with three soybean and two tobacco cultivars that differed in photoperiod requirements for floral induction.

MATERIALS AND METHODS

Plant Material and Experimental Protocol. Selection of the cultivars used in the present study was based on different photoperiod requirements for floral induction. The soybean cultivars and the growth habits chosen were 'Maple Presto' (maturity group OO; indeterminate), 'Ransom' (group VII, determinate), and 'Jupiter' (group X, determinate). As maturity group increases, flowering is initiated by a shorter day, but plants of group OO, such as Maple Presto may be essentially photoperiod insensitive as is the case with cv 'McCall' (D. Egli, personal communication). Two tobacco cultivars were also studied. Cultivar 'NC 2326' is basically photoperiod insensitive, and flowers in the field in response to stress conditions (*e.g.* low temperatures, nutrient deficiency). However, cv 'NC 22NF' is an isogenic line derived from NC 2326 that is photoperiod sensitive (E. A. Wernsman, personal communication).

Soybean seeds were planted, and tobacco seedlings were transplanted, into pots containing a soil mixture (8). The plants were grown for a 3-week period in a greenhouse and then transferred into growth chambers in the Southeastern Plant Environment Laboratories (Phytotron). Plants were maintained under cyclical 15-h light:9-h dark (LD) or 7-h light:17-h dark (SD) conditions for 4 d prior to the experimental period. Photosynthetic photon flux density at the surface of the pots was about 700 $\mu E \cdot m^{-2} \cdot s^{-1}$. Chamber air temperatures were maintained at 26°C throughout the experiment. Nutrient solution (8) was supplied twice daily. The pots were flushed with deionized H_2O prior to the second application of nutrient solution.

The experiments were conducted on the 4th d after the plants were transferred to the LD or SD regimes. Specific leaf weight (g fresh weight/dm^2) for SD plants was reduced only about 7% relative to leaves of LD plants when the study was conducted. Three plants were sampled at about 3-h intervals over the 24-h light-dark cycle. At each harvest, leaf discs (4.4 cm^2) were taken and stored on dry ice prior to lyophilization (for leaf dry weight) and carbohydrate analysis. The leaf was then excised, weighed, and sliced into segments and immediately frozen at −80°C for later enzyme analysis. During the light period, CERs were measured between harvests.

Carbon Assimilation and Translocation. Photosynthetic rates were measured using a Beckman model 865 differential IR CO_2 analyzer[3] equipped with a clamp-on Plexiglas cuvette enclosing the upper and lower surfaces of a 10-cm^2 area of the appropriate leaf. Air at the same temperature and CO_2 concentration of the ambient air was passed through the cuvette for 30 to 45 s at a flow rate of 1.5 l/min. Differences between CO_2 concentration in incoming and exhaust air streams were monitored and used to calculate CERs. CERs, measured as mg CO_2 assimilated/$dm^2 \cdot h$, were converted to mg CH_2O formed/$dm^2 \cdot h$ by multiplying the CO_2 exchange rate by 0.68. CERs were relatively constant during the light period, and mean values are presented. Assimilate export was measured by the method of Terry and Mortimer (22), based on the difference between assimilate production and leaf dry weight changes. Mean rates of dry weight accumulation and starch accumulation during the light period were obtained by linear regression of values from harvests taken at different times.

Carbohydrate Analyses. Lyophilized leaf discs were extracted with hot 80% ethanol until the tissue was free of pigment. The supernatant was enzymically analyzed for sucrose and hexoses by the method of Jones *et al.* (14). The particulate fraction, containing starch, was suspended in 1.0 ml of 0.2 N KOH and placed in boiling water for 30 min. After cooling, the pH of the mixture was adjusted to about pH 5.5 with 200 μl of 1.0 N acetic acid. To each sample, 1.0 ml of dialyzed amyloglucosidase solution (from *Aspergillus oryzae* [Sigma], 35 units/ml in 50 mM Na-acetate buffer, pH 4.5) was added, and the tubes were incubated at 55°C for 15 min. After digestion, the tubes were placed in boiling water for 1 min, centrifuged, and the glucose in the supernatant was analyzed enzymically using hexokinase and glucose-6-P dehydrogenase.

Extraction and Assay of SPS. The frozen leaf tissue was ground with a Polytron high speed homogenizer in a medium (8.0 ml of medium/g fresh weight) containing 50 mM Hepes-NaOH (pH 7.2), 5 mM $MgCl_2$, 1 mM EDTA, 2.5 mM DTT, 2% PEG-20 (w/v), and 1% BSA (w/v). The brei was then filtered through eight layers of cheesecloth, and cells were disrupted by passage through a French pressure cell (330 kg/cm^2). Debris was pelleted by centrifugation at 38,000*g* for 10 min and enzyme assays were conducted on the supernatant fluid.

Sucrose-P synthase was assayed by measurement of fructose-6-P-dependent formation of sucrose (+sucrose-P) from UDP-glucose (13). The assay mixture (70 μl) contained 7.5 mM UDP-glucose, 7.5 mM fructose-6-P, 15 mM $MgCl_2$, 50 mM Hepes-NaOH (pH 7.5), and an aliquot of leaf extract. Mixtures were incubated at 25°C, and reactions were terminated after 10 min by addition of 70 μl of 1 N NaOH. Unreacted fructose-6-P (or fructose) was destroyed by placing the tubes in boiling water for 10 min. After cooling, 0.25 ml of 0.1% (v/v) resorcinol in 95% ethanol and 0.75 ml of 30% HCl were added, and the tubes incubated at 80°C for 8 min (17). The tubes were allowed to cool, and the A_{520} was measured.

RESULTS

Effect of Photoperiod on Soybean Cultivars. Three soybean cultivars were grown in a greenhouse and then transferred to growth chambers with either a LD (15 h) or SD (7h) photoperiod. As shown in Table I, photoperiod had little or no effect on CER, but SD plants had higher starch accumulation rates, and lower translocation rates compared to LD plants. The higher translocation rates of the LD plants were associated with higher leaf sucrose concentrations (measured at 1500 h) relative to SD plants.

The effects of photoperiod on photosynthate partitioning in leaves documented in Table I have been reported previously in soybean 'Amsoy 71' (2) and in several other species (3, 4, 19). However, in previous studies, leaves of SD plants had higher sucrose concentrations compared to leaves of LD plants (2, 19). In the present study, leaves of LD and SD plants had similar sucrose concentrations at the beginning of the photoperiod, but thereafter, the concentration of sucrose in leaves of LD plants continued to increase whereas in leaves of SD plants, sucrose concentration tended to plateau at a lower concentration. Typical results for Ransom are shown in Figure 1. Thus, for comparisons between photoperiod treatments, leaf sucrose concentrations at 1500 h (*i.e.* end of SD photoperiod) were used (Table I).

Previously, we reported (13) that acclimation of soybean plants to a SD photoperiod was associated with decreased activities of SPS in leaves harvested at the end of the SD photoperiod. Because SPS activity varies diurnally in soybean leaves (18), it was necessary to determine the effect of photoperiod on the diurnal rhythm in enzyme activity.

Diurnal changes in SPS activity in leaves of three soybean

[3] Mention of a trademark or proprietary product does not constitute a guarantee or warranty of the product by the United States Department of Agriculture and does not imply its approval to the exclusion of other products that may also be suitable.

Table I. *Effect of Photosynthetic Period on Carbon Assimilation, Starch Accumulation Rate, and Translocation in Three Soybean Cultivars*

Rates are means from three replicate observations made at three (SD) or six (LD) time points during the light period.

Cultivar	Day length	CER	Starch Accumulation	Export	Leaf Sucrose Concentration[a]
	h	*mg $CH_2O/dm^2 \cdot h$*			*mg/g fresh wt*
Maple Presto	15	19.7	2.80	16.2	2.20
	7	19.4	3.83	15.0	1.30
Ransom	15	22.0	3.38	17.7	3.15
	7	19.1	4.58	13.3	1.95
Jupiter	15	20.6	2.70	17.1	2.50
	7	20.0	4.33	14.4	1.80

[a] Sucrose content at 1500 h.

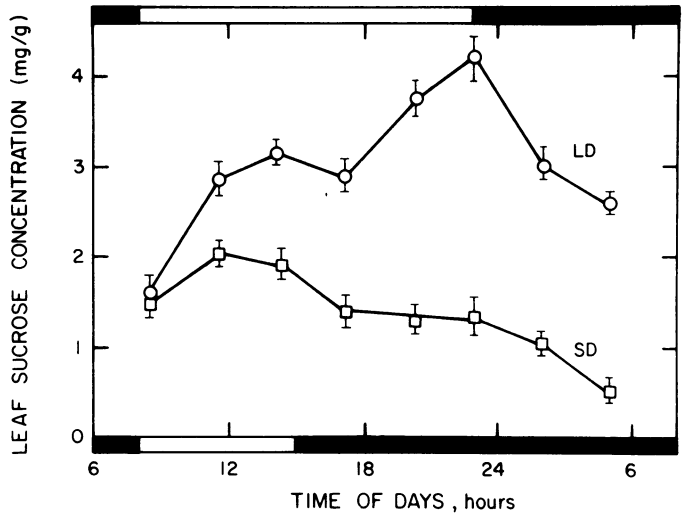

FIG. 1. Diurnal variation in sucrose concentration in leaves of soybean Ransom plants adapted to LD or SD photoperiods. The light-dark cycles are indicated by the bars at the top (LD) and bottom (SD) of the figure.

cultivars acclimated to LD or SD photoperiods are shown in Figure 2. The diurnal rhythms in SPS activity in leaves of Ransom (Fig. 2A) and Jupiter (Fig. 2B) tended to be qualitatively similar under the LD photoperiod. With these genotypes, SPS activity reached maximum levels toward the end of the photoperiod and again toward the end of the dark period. The effect of the SD photoperiod was to reduce the mean SPS activity and dampen the amplitude of the rhythm. In leaves of SD plants, a rhythm in SPS activity was still observed in Ransom but not in Jupiter (Fig. 2, A and B). In contrast, diurnal variation in SPS activity was less apparent in leaves of Maple Presto in LD or SD plants (Fig. 2C). Nevertheless, leaves of SD plants again had consistently lower SPS activities compared to leaves of LD plants.

To compare SPS activities in leaves of the three cultivars in the light, mean values were calculated from observations during the light period and are presented in Table II. With each cultivar, SPS activity was substantially reduced in leaves of SD plants compared to LD plants. It was of interest to compare mean values for SPS activity in leaves (Table II) with mean daily rates of starch accumulation and translocation (Table I). Because photosynthetic rates were similar in all treatments, absolute rates of the different processes can be compared. In general, starch accumulation rate was correlated negatively with export rate (Fig. 3A). Thus, increased partitioning of carbon into starch in

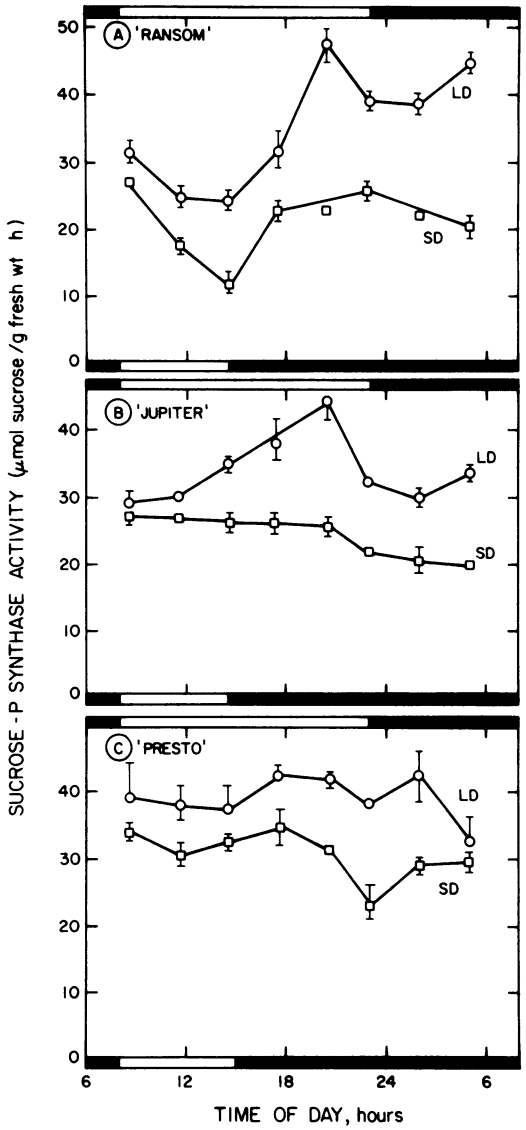

FIG. 2. Effect of photoperiod (LD *versus* SD) on diurnal variation in SPS activity in soybean cultivars: A, Ransom; B, Jupiter; and C, Maple Presto.

Table II. *Mean SPS Activities during the Light Period in Leaves of the Soybean Cultivars as Affected by Photoperiod*

Cultivar	Mean SPS Activity	
	LD	SD
	μmol sucrose/g fresh wt·h	
Ransom	33.3	19.3
Jupiter	34.7	29.6
Maple Presto	38.8	32.1

leaves of SD plants occurred presumably at the expense of sucrose formation and, hence, translocation *in vivo*. Export rate was correlated positively with the mean SPS activity in leaf extracts (Fig. 3B); thus, starch accumulation and SPS activity were correlated negatively (Fig. 3C). Because specific leaf weight was not significantly different in leaves of SD and LD plants, the relationships shown in Figure 3 would not be substantially altered if SPS activity was expressed on a leaf area basis.

Effect of Photoperiod on Tobacco Cultivars. Two tobacco

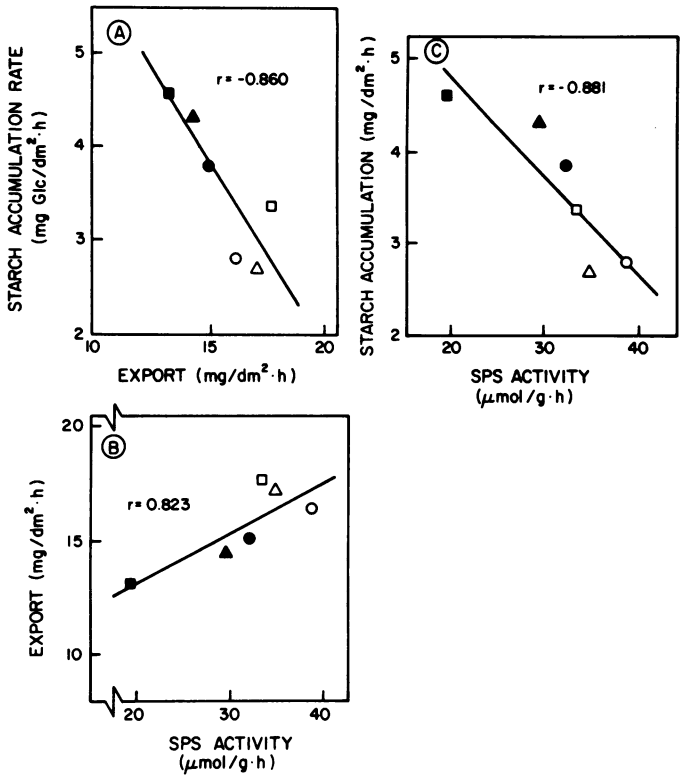

FIG. 3. Correlations between photosynthate partitioning and SPS activity in leaves of soybean plants adapted to LD (○, △, □) or SD (●, ▲, ■) photoperiods. Cultivars: Ransom (□, ■); Jupiter (△, ▲); Maple Presto (○, ●). Correlations are significant at the 5% level.

Table III. *Effect of Photoperiod on Photosynthate Partitioning and Mean SPS Activities in Leaves of Two Tobacco Cultivars*

Rates are means from three replicate observations made at three (SD) or six (LD) time points during the light period.

Cultivar	Day length	CER	Starch Accumulation	Export	Leaf Sucrose Concn.[a]	Mean SPS Activity
	h	*mg CH_2O/dm².h*			*mg/g*	*μmol/g·h*
2326	15	18.0	2.4	14.4	2.4	16.1
	7	16.7	4.1	10.4	1.3	8.8
22NF	15	17.2	2.3	13.9	2.3	13.7
	7	17.3	4.1	11.6	1.3	8.7

[a] Content at 1500 h.

cultivars, which differ in photoperiodic sensitivity of floral induction, were tested for effects of photoperiod on carbon partitioning in leaves. The effect of photoperiod on photosynthate partitioning in tobacco has not been reported previously. In general, the tobacco cultivars responded to the SD photoperiod as did the soybean cultivars. Leaves of plants acclimated for 4 d to the SD photoperiod had increased rates of starch accumulation, decreased rates of translocation, and lower leaf sucrose concentrations, compared to leaves of LD plants (Table III). In addition, the mean activity of SPS during the light period was lower in leaves of SD plants. Therefore, as with soybean (Fig. 3), changes in the activity of SPS with SD were correlated positively with export and sucrose concentration, but negatively correlated with accumulation of starch.

Diurnal variation in SPS activities in leaves of tobacco plants acclimated to LD and SD photoperiods are shown in Figure 4. In leaves of LD plants, a distinct rhythm was evident in '22NF' (Fig. 4A) whereas there was markedly less variation evident with '2326' (Fig. 4B). However, with both cultivars, leaves of SD plants exhibited a pronounced diurnal rhythm and the activity of SPS was lower during the light period (Fig. 4, C and D). In the dark, activity of SPS increased such that activities were similar in leaves of LD and SD plants.

DISCUSSION

An essential component of the response of carbon partitioning to changes in photoperiod appears to be changes in SPS activity. With all the genotypes tested in the present study, leaves of SD plants had lower activities of SPS and lower leaf sucrose concentrations during the photoperiod as compared to leaves of LD plants. It is generally recognized that although leaf sucrose may be compartmented in different pools in the leaf (15), total leaf sucrose concentration is one of the principal determinants of translocation rate (6). The results obtained in the present study are certainly consistent with this postulate. In addition, the mean activity of SPS during the light period was correlated positively with translocation rate and negatively with starch accumulation rate. Although the results do not establish that the reduction in SPS activity caused the increase in starch accumulation (and decrease in translocation), the consistent association between SPS activity and carbon partitioning suggests that the two are closely related.

In the present study, mean rates of starch accumulation and translocation for the entire light period were calculated in the different treatments, and compared with the mean activity of SPS during the light period. When the activity of SPS changes during the light period, it might be expected that partitioning of carbon would also change during the course of the day. The sampling protocol used in the present study was not adequate to ascertain whether export rate changed during the day. However, in a recent study with field-grown soybean 'Bragg' plants, a substantial increase in SPS activity during the light period was indeed found to be correlated with changes in translocation rate (manuscript in preparation). Thus, future studies need to consider that changes may occur in translocation and photosynthate partitioning, as well as in SPS activity, during the light period.

Selection of the cultivars used in the present study was based on different photoperiod requirements for floral induction. With all five genotypes tested, leaves of SD plants had similar photosynthetic rates, but increased rates of starch accumulation and decreased rates of translocation relative to LD plants. Thus, it can be concluded that the effect of photoperiod on photosynthate partitioning is not related to the photoperiod requirements for floral induction.

It is apparent from the results presented herein that differences in amplitude and timing of peaks in the diurnal rhythm of SPS activity exist among species and cultivars, and that photoperiod can influence certain properties of the rhythm in a given genotype. Under the LD photoperiod, some of the cultivars exhibited a more distinct rhythm in SPS activity (soybean Ransom and Jupiter; tobacco 22NF) than did others (soybean Maple Presto and tobacco 2326). Thus, the effect of the SD photoperiod (*i.e.* lower activities of SPS during the photoperiod) was not dependent upon the presence of a diurnal rhythm in enzyme activity. However, in some cases, the SD photoperiod affected the diurnal variation in SPS activity. This was most pronounced with the tobacco cultivars (Fig. 4), where the changes in SPS activity under the SD photoperiod were closely aligned with the light-dark transition. Alignment of the rhythm with the light-dark transition was not observed in leaves of LD plants. Another point of interest is that of the five genotypes tested, the three that are most photoperiod sensitive for floral induction (soybean Ransom and Jupiter and tobacco 22NF) were the genotypes that had a pronounced diurnal rhythm in SPS activity under the LD pho-

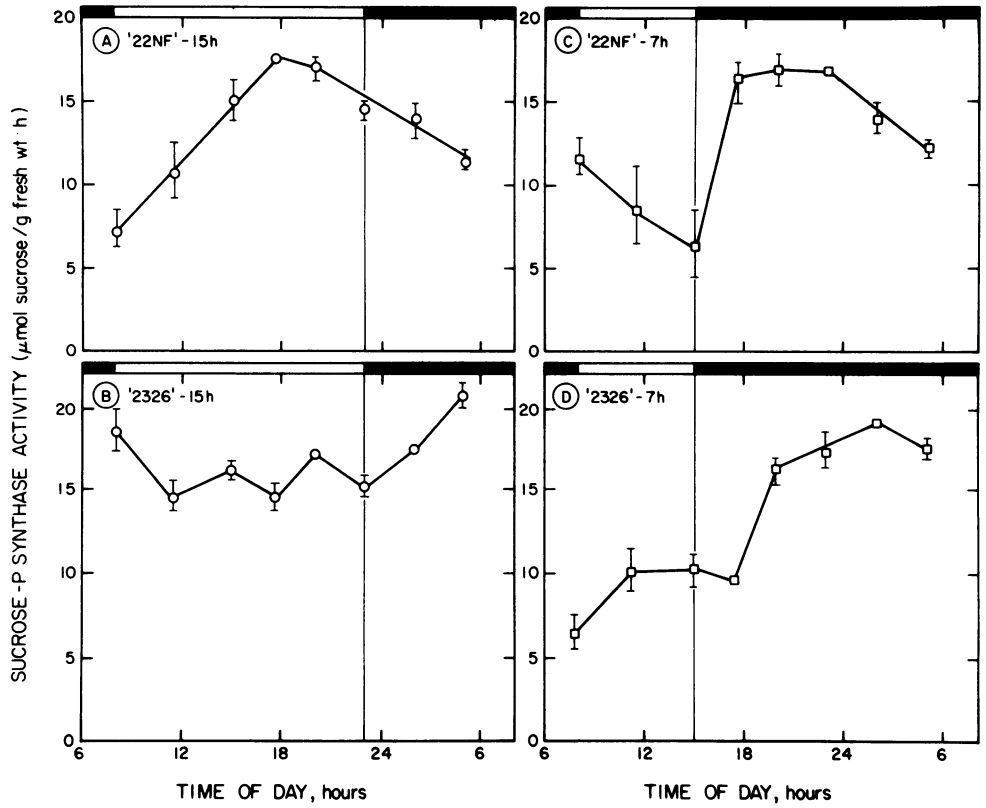

FIG. 4. Effect of photoperiod (LD *versus* SD) on diurnal variation in SPS activity in tobacco cv 22NF (A, C) and cv 2326 (B, D).

toperiod. The two genotypes that are almost photoperiod insensitive (soybean Maple Presto and tobacco 2326) exhibited little, if any, diurnal variation in SPS activity (under LD). Thus, it is interesting to speculate that some relation may exist between these two parameters, or that floral induction and SPS activity are regulated by some common element.

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