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Photosynthate Partitioning into Starch in Soybean Leaves

I. EFFECTS OF PHOTOPERIOD *VERSUS* PHOTOSYNTHETIC PERIOD DURATION

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ABSTRACT

Photosynthesis, photosynthate partitioning into foliar starch, and translocation were investigated in soybean plants (*Glycine max* (L.) Merr. cv. Amsoy 71), grown under different photoperiods and photosynthetic periods to determine the controls of leaf starch accumulation. Starch accumulation rates in soybean leaves were inversely related to the length of the daily photosynthetic period under which the plants were grown. Photosynthetic period and not photoperiod *per se* appears to be the important factor. Plants grown in a 14-hour photosynthetic period partitioned approximately 60% of the daily foliar accumulation into starch whereas 7-hour plants partitioned about 90% of their daily foliar accumulation into starch. The difference in starch accumulation resulted from a change in photosynthate partitioning between starch and leaf residual dry weight. Residual dry weight is defined as leaf dry weight minus the weight of total nonstructural carbohydrates. Differences in photosynthate partitioning into starch were also associated with changes in photosynthetic and translocation rates, as well as with leaf and whole plant morphology. It is concluded that leaf starch accumulation is a programmed process and not simply the result of a limitation in translocation.

Plant growth depends upon the net fixation and transport of carbon from the chloroplast to inter- and intracellular sites of photosynthate demand. However, net photosynthate efflux from the chloroplast during photosynthesis may be 30 to 50% less than the CO_2 fixation rate due to chloroplast starch formation from newly formed sugar phosphates within the chloroplast (3, 8, 12, 22). The result is a linear increase in foliar starch concentration during illumination that may represent 10 to 30% of the laminar dry weight by the end of each diurnal photosynthetic period (6, 8, 16, 20).

Foliar starch metabolism is the subject of an increasing number of physiological and biochemical studies (3, 5, 11, 16, 20) and reviews (13, 14, 22). However, the relationship between plant growth and this large energy reserve, which is unavailable for meristematic growth during the light period, is uncertain. The observations that diurnal declines in foliar CO_2 exchange rates (CER)[1] have been correlated with elevated starch levels (4, 20) support the hypothesis that starch accumulation may be an inefficient process in plant growth.

An understanding of the mechanisms controlling starch synthesis is important in determining the role of chloroplast starch accumulation in plant growth. We hypothesized that foliar starch accumulation in the chloroplast results either from a limitation in the synthesis and translocation of sucrose or from a programmed synthesis that is influenced by the energy demand of the diurnal dark period. If the former is true, the highest starch accumulation rates should occur in plants under a long photosynthetic period. However, if starch synthesis is coupled to the energy demands of the daily dark period, then plants grown in a short photosynthetic period and therefore, a long dark period, would respond with an increase in the rate of starch synthesis. These hypotheses were tested on soybean plants grown in controlled environment chambers.

MATERIALS AND METHODS

Soybean plants (*Glycine max* [L.] Merr. cv. Amsoy 71) were grown from uninoculated seed in black plastic pots (10 × 10 × 15 cm) containing Vermiculite. Four days after emergence, seedlings were thinned to one plant per pot. Air temperature and RH were maintained at constant levels of 27 ± 1 C and 60 ± 2%, respectively, in model M-2 controlled environment chambers (Environmental Growth Chambers, Chagrin Falls, Ohio).[2] The radiant energy for plant growth was supplied by 10 60-w incandescent lamps (2 nE/s·cm^2; about 1 klux) and fluorescent lamps (64 nE/s·cm^2; 45 klux) located above a mylar barrier. The PPFD and photometric measurements were made with a quantum sensor and photometer (model LI-185, Lambda Instr. Corp., Lincoln, Nebr.). Plants were watered daily with a complete nutrient solution (16). Plants under all treatments developed axillary flower buds.

Light Treatments. Plants were grown in three different light treatments for 28 days after planting (treatments A, B, and C) or, in the case of treatment D, plants were grown as in treatment A for 20 days and then shifted to treatment C for 5 days (Table I). Photosynthetic period and photoperiod were the variables. *Photosynthetic period* is defined as that time interval during which irradiance level was sufficient to sustain net photosynthesis (64 nE/s·cm^2). *Photoperiod* is synonymous with photosynthetic period except in treatment B in which case 7 h of low incandescent irradiation (about 1 nE/s·cm^2) was added to the photosynthetic period. Therefore, plants of treatment B received irradiance levels sufficient to sustain net CO_2 fixation only during the first 7 h of the 14-h photoperiod; 7 h of low irradiance incandescent light was added to a 7-h photosynthetic period to provide a 14-h photoperiod (Table I). Thus, plants in treatments A and B were grown with photosynthetic periods of 14 and 7 h, respectively, without an alteration of the photoperiod. Photosynthetic period and photoperiod were both 7 h in treatment C (Table I). The plants in

[1] Abbreviations: CER: CO_2 exchange rate (mg CO_2/dm^2·h); PPFD: photosynthetic photon flux density; TNC: total nonstructural carbohydrates; SLW: specific leaf weight; CER_A: CH_2O fixation rate (mg CH_2O/dm^2 leaf area·h); CER_w: mg CH_2O/g dry weight·h; A_{max}: area of fully expanded leaf (dm^2).

[2] Mention of a trademark, proprietary product, or vendor does not constitute a guarantee or warranty of the product by the U.S. Department of Agriculture, and does not imply its approval to the exclusion of other products or vendors that may also be suitable.

Table I. *Irradiance Treatments Administered to Soybean Plants During Growth in Controlled Environment Chambers*

Irradiance levels were 64 and about 1 nE/cm^2·s during the photosynthetic period and low irradiance extension, respectively. Plants in treatment D were grown for 20 days as in treatment A, then transferred to conditions of treatment C for 5 days.

Treatment	Photosynthetic Period	+	Low Irradiance Extension	=	Photoperiod	Dark Period	Cycle Duration
					h		
A	14		0		14	10	24
B	7		7		14	10	24
C	7		0		7	17	24
D First 20 days	14		0		14	10	24
Next 5 days	7		0		7	17	24

treatment D were grown for 20 days as in treatment A then transferred to conditions of treatment C for 5 days.

Carbohydrate Analyses. Carbohydrate content of soybean leaf laminae was determined on the third and fourth trifoliolate leaves (T_3 and T_4), numbered acropetally, harvested at intervals throughout the day. The two leaves were combined for analysis. Leaves were excised, leaf areas quickly determined (model LI-3000 portable area meter, LI-COR, Inc., Lincoln, Nebr.), and frozen in liquid N_2. The samples were lyophilized and finely ground (60 mesh) in a Cyclotec tissue grinder (Tecator/Udy, Boulder, Colo.). A 100-mg sample was suspended in 100 ml distilled H_2O at room temperature for 30 min. The resultant water-soluble carbohydrate fraction was quantified (mg/100 mg) by reducing sugar analyses following hydrolysis with 0.6 N HCl. Phosphorylated sugars exhibit reducing power and are therefore measured along with hexoses, hydrolyzed sucrose, and water-soluble starch in the carbohydrate analyses. Another 100-mg sample of leaf tissue was treated with dialyzed takadiastase (17). Per cent TNC (mg/100 mg) was determined colorimetrically by potassium ferricyanide analysis for reducing sugars in the enzyme digest following 0.6 N HCl hydrolysis in an Autoanalyzer II (Technicon Instr. Corp., Tarrytown, N.Y.). Per cent starch was calculated as the difference between TNC and water-soluble carbohydrates.

The SLW (mg/dm^2) of the experimental leaves was calculated from the lyophilized dry weight divided by leaf area at harvest. Conversion of per cent TNC (mg/100 mg) to mg/dm^2 was accomplished via the following relationship:

$$\text{mg TNC/dm}^2 = \frac{\%\ \text{TNC} \times \text{SLW}}{100}$$

Residual dry weight of leaves, representing protein, cellulose, and other components of the residue following takadiastase treatment, was calculated by subtracting mg TNC/dm^2 from SLW. Diurnal rates of TNC and residual accumulation were obtained from mathematically determined slopes of regression lines. Relative growth rates (RGR, g/g·day) were calculated as follows:

$$\text{RGR} = \frac{\ln W_2 - \ln W_1}{t_2 - t_1}$$

where W_1 and W_2 are dry weights of plant parts harvested at two different times, t_1 and t_2. All reported values for SLW, TNC, and water-soluble carbohydrates are means of six replicate determinations, each from separate plants.

Carbon Assimilation and Translocation. The CER for attached leaf T_3 was measured under growth conditions in acrylic plastic chambers using an adaptation of the air-seal technique (25). Four leaf chambers were connected in parallel to a flow-through IR gas analysis system. The CER for T_3 leaves was measured during the photosynthetic period on each of four plants, and the mean diurnal CER determined. Leaf T_3 was fully expanded as ascertained from periodic measurements of leaf area using comparable plants.

In order to express CER and rates of carbohydrate accumulation in the same units, mg of CO_2 fixed was converted to mg of CH_2O since the chemical composition of the leaf is approximated by this empirical formula. Thus, CER_A (mg CH_2O/dm^2·h) equals CER (mg CO_2/dm^2·h) × 0.68, where 0.68 represents the molar ratio of the two forms of carbon. CER_W (mg CH_2O/g·h) equals CER_A × l/SLW (g/dm^2). Translocation rates (mg/dm^2·h) were calculated by subtracting foliar accumulation rates from CER_A. The foliar accumulation rate is the sum of residual and TNC accumulation rates.

RESULTS

The results presented are representative of those obtained from experiments repeated in time. The third trifoliolate leaf (T_3) of soybean plants grown under a 14-h photosynthetic period (treatment A) had higher CER_A (Table II) than plants grown under a 7-h photosynthetic period (treatment B). However, the CER_W of 7-h plants was significantly higher than that of 14-h plants (Table II). Leaf area of the fully expanded leaves of 14-h plants was not significantly greater than that of 7-h plants.

Diurnal starch accumulation rates of leaves T_3 and T_4 were altered by the length of the photosynthetic period under which the soybean plants were grown (Fig. 1). This difference is apparent when rates are expressed either on a leaf dry weight basis (mg/100 mg·h) or on a leaf area basis (mg/dm^2·h). Foliar starch accumulation rates in the 7-h photosynthetic period were much higher than those in the 14-h photosynthetic period in spite of the lower CER_A of 7-h plants (Fig. 1 and Table II). Starch content of the leaves at the end of the 7-h photosynthetic period was about 15% of the laminar dry weight compared to about 10% in the 14-h treatment (Fig. 1). In all treatments starch was depleted during the dark period to about 1 to 3% of laminar dry weight (2–6 mg/dm^2) by the beginning of the subsequent photoperiod (Fig. 1). Water-soluble carbohydrates, primarily sucrose and monosaccharides, attained higher concentrations in leaves T_3 and T_4 of 7-h plants than in corresponding leaves of 14-h plants grown under the same PPFD (Fig. 2).

Plants grown in a 7-h photosynthetic period followed by a 17-h dark period (Table I, treatment C) had the same starch accumulation rates as plants grown in a 7-h photosynthetic period followed by 7 h of low irradiance incandescent light and 10-h dark (treatment B). Foliar starch percentages of treatment C at hours 1 and 6 are indicated by the stars in Figure 1.

The CER_A and translocation rates of leaf T_3 differed in plants grown under 14-h and 7-h photosynthetic periods (Table III). Nevertheless, the differences in rates of starch accumulation (Fig. 1) and in soluble carbohydrate levels (Fig. 2) resulted from differences in photosynthate partitioning between TNC (starch plus soluble carbohydrates) and residual components within the leaf (Table III). Leaves T_3 and T_4 of 14-h photosynthetic period

Table II. *Carbon Assimilation Rates (Leaf T_3), Specific Leaf Weights, and Leaf Areas (Leaves T_3 and T_4) as a Function of Length of Photosynthetic Period*

Plants were grown for 25 days, and gas exchange measurements were conducted under conditions of treatments A and B (Table I).

Parameter	Photosynthetic Period	
	14 h	7 h (+7 h low)
	Treatment A	*Treatment B*
CH_2O synthesis		
CER_A (mg/dm^2·h)	19.89a[1]	16.39b
CER_W (mg/g·h)	59.20b	81.95a
Leaf area (dm^2)	2.80a	2.41a
Specific leaf weight (mg/dm^2)	336a	200b

[1] Means within horizontal rows followed by the same letter are not significantly different at $P \leq 5\%$ (F-test).

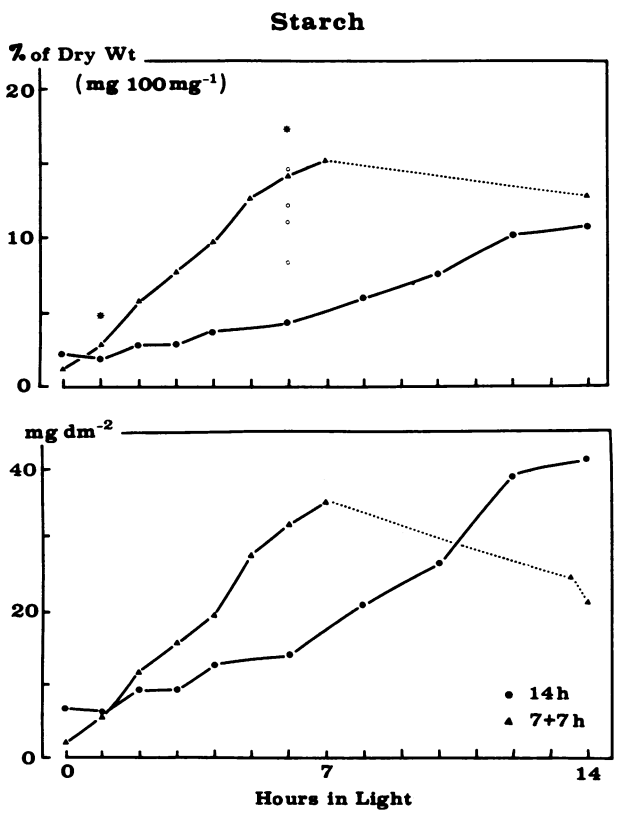

FIG. 1. Starch content (per cent of leaf dry weight and mg starch/dm^2 leaf area) of trifoliolate leaves T_3 and T_4 of soybean plants grown for 28 days under either a 14-h (●, treatment A), or a 7-h (▲, treatment B) photosynthetic period. Stars (*, treatment C) represent starch content of leaves T_3 and T_4 of plants grown in treatment B (▲) but with 17 h of darkness instead of 7 h of low irradiance incandescent plus 10 h of dark following the 7-h photosynthetic period. (○): Increasing starch content in leaves T_2 and T_3 of plants on 4 consecutive days following a shift from a 14-h to a 7-h photosynthetic period, treatment D. Starch content increased from day 1 following a shift from a 14-h to a 7-h photosynthetic period (bottom ○) through day 4 (uppermost ○).

plants partitioned approximately 60% of the total foliar accumulation into TNC and the remainder into residual components. However, corresponding leaves of 7-h photosynthetic period plants partitioned about 90% of the total foliar accumulation into TNC (Table III) in spite of their lower CER_A.

Lowering the irradiance under which plants were grown from 64 to 32 nE/s·cm^2 did not obscure the effects of photosynthetic period duration on photosynthate partitioning and translocation (unpublished data). This was true in spite of an approximately 30% reduction in CER_A.

To determine the time course of plant adaptation to a shortened photosynthetic period, soybean plants were grown under a 14-h photosynthetic period until 21 days after planting and then transferred to a 7-h photosynthetic period (Table I, treatment D). Leaves T_2 and T_3 (fully expanded) were harvested only at hours 1 and 6 following the beginning of the photosynthetic period; therefore, the calculation of starch and residual accumulation rates by regression analysis was not possible. However, starch percentages in leaves at the 6th h on 4 consecutive days after the transfer clearly indicate that metabolic adjustments were triggered by the change in photosynthetic period (Fig. 1, ○). On the 4th day, the starch accumulation rate was the same as that of leaves that had developed under a 7-h photosynthetic period. Lower rates of photosynthate partitioning into residual components accompanied the increase in foliar starch accumulation in plants transferred to the 7-h photosynthetic period.

Dry matter partitioning between shoots and roots of soybean plants was altered during the 4-day period following transfer to the 7-h photosynthetic period. Relative shoot growth rate was unaltered in spite of a 50% reduction in daily photosynthetic period (Table IV). Shoot growth was apparently maintained by a reduced translocation of assimilates to the roots, as evidenced by the sharp reduction in relative root growth rate and the resultant increase in the shoot to root ratio (Table IV).

DISCUSSION

CO_2 exchange rates and photosynthate partitioning into starch, residual dry weight, and translocation were altered when plants were grown under a short compared to a long photosynthetic period even though photoperiod was held constant (7). Our results permit certain deductions regarding the relationship of CER to leaf morphology and carbohydrate accumulation and the relationships among starch synthesis, translocation, and plant growth strategies.

CER and Leaf Morphology. Leaves of plants grown under a 7-h photosynthetic period were thinner, but photosynthetically more efficient per unit of dry weight than those of plants grown in the 14-h photosynthetic period. Reduced SLW of 7-h leaves resulted from a sharp reduction in photosynthate allocation to residual components of leaves suggesting that, under a short photosynthetic period, the soybean plant curtails photosynthate allocations to leaf components that do not contribute to CER.

Previous ontogenetic studies of soybean leaves revealed an inverse relationship between SLW and CER_W during leaf devel-

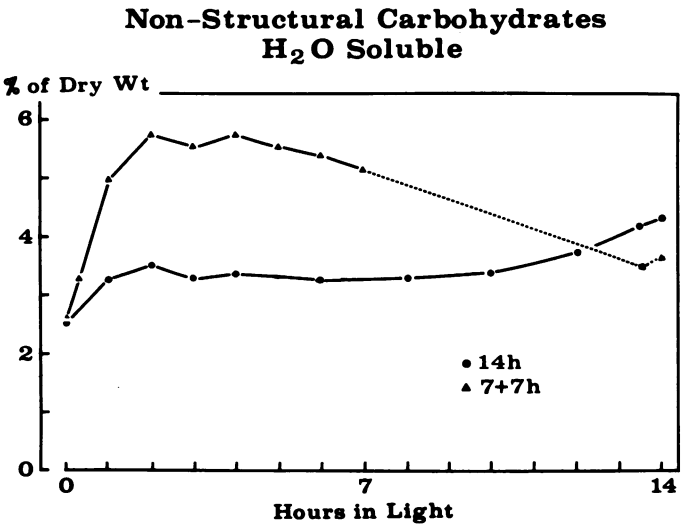

FIG. 2. Water-soluble sugar content of trifoliolate leaves 3 and 4 of soybean plants grown as indicated in the legend of Figure 1.

Table III. *Carbon Assimilation, Accumulation, and Translocation Rates in Soybean Leaves Grown under Photosynthetic Periods of 7 and 14 h with a Photoperiod of 14 h in Both Treatments*

Foliar accumulation and translocation rates were calculated from CO_2 exchange measurements (leaf T_3) and TNC (starch and sugars) analyses (leaves T_3 and T_4) as described under "Materials and Methods."

Rates	Photosynthetic Period	
	14 h	7 h (+7 h low)
	mg/dm^2·h (%)	
CH_2O synthesis	19.89 (100)	16.39 (100)
Foliar accumulation		
TNC (starch and sugars)	3.20 (16)	5.28 (32)
Residual	2.30 (12)	0.57 (04)
Total	5.50 (28)	5.85 (36)
Translocation	14.39 (72)	10.54 (64)

Table IV. *Comparison of Dry Weight Accumulation and Partitioning Patterns of Control Plants (14-h Photosynthetic Period) with Plants Shifted to a 7-h Photosynthetic Period*

Beginning at 21 days after planting, half of the plants were given a 7-h daily photosynthetic period, the others remained under a 14-h photosynthetic period. Harvests were made 1 h after the beginning of the photosynthetic period.

Dry Weight Distribution	Photosynthetic Period	
	14 h (control)	7 h
Day 22		
Shoot dry weight (g)	2.21a[1]	1.72a
Root dry weight (g)	0.69a	0.54a
Shoot/root ratio	3.20a	3.18a
Day 25		
Shoot dry weight (g)	3.54a	2.78b
Root dry weight (g)	1.26a	0.76b
Shoot/root ratio	2.81b	3.66a
RGR[2] (g/g·day):		
Shoot	0.16	0.16
Root	0.20	0.12

[1] Means within horizontal rows followed by the same letter are not significantly different at $P \leq 5\%$ (F-test). Those followed by different letters are significantly different at $P \leq 1\%$.

[2] Rate of change in dry weight from day 22 to day 25.

opment (16). The SLW continued to increase beyond A_{max} but the additional dry matter input, which included additional Chl and soluble protein, was not accompanied by increases in photosynthetic output.

CER and Foliar Carbohydrate Accumulation. Diurnal declines in CER have been correlated with plastid starch accumulation in soybean (20) and other species (3–5, 14). This correlation has been interpreted as evidence for the existence of a feedback inhibition of photosynthesis. Although diurnal mean CER_A was less, CER_W was greater in leaves of plants grown under the 7-h photosynthetic period in spite of their higher starch percentages than in leaves of 14-h plants. Therefore, our CER_W data do not support the hypothesis that starch accumulation causes a feedback inhibition of CER.

Control of Starch Synthesis. Carbohydrate accumulation in leaves has been ascribed to a large photosynthate supply and limited photosynthate demand (5, 14, 18, 24). For example, inhibition of corn leaf expansion by low temperatures resulted in carbohydrate accumulations in both source and sink leaves because leaf expansion was inhibited to a greater extent than CER (1). Conversely, increased photosynthate demands following induction of tillering in pangola plants (*Digitaria decumbens* Stent.) were associated with reduced chloroplast starch accumulation (5). Although it is apparent from the above reports that starch accumulation is influenced by photosynthate demand, little is known about the mechanism that controls the proportion of photosynthate retained within the chloroplast under steady-state growth conditions. Challa (3) recently reported higher rates of starch accumulation in cucumber (*Cucumis sativus* L.) leaves when plants received an 8-h *versus* a 14-h photosynthetic period. However, he (3) did not attempt to separate the effects of different irradiance levels from those of different photosynthetic periods.

Our results provide some insights into the mechanisms for control of foliar starch synthesis in the light. First, we have shown that the rate of starch accumulation in fully expanded soybean leaves is a function of the duration of the daily photosynthetic period but is unaffected by a classical photoperiod treatment. Although the phenomenon is not a classical photoperiod response, it may be a high irradiance reaction (9, 21). However, the length of the daily period when net photosynthesis does not occur may also affect the starch accumulation rate.

Second, rates of foliar TNC accumulation, representing primarily starch accumulation, were not necessarily proportional to CER_A. If starch accumulation simply results from the retention within the chloroplast of a relatively constant proportion of the total carbon fixed, then shortening the photosynthetic period and reducing CER_A should decrease starch accumulation rates. However, our results indicate that while CER_A was reduced by shortening the photosynthetic period, the TNC accumulation rates increased 65% (Fig. 1 and Table III). This suggests that starch accumulation is controlled independently of CO_2 fixation rate *per se*. Furthermore, starch accumulation is not simply a result of translocation potential being insufficient to keep pace with CER.

Third, rates of photosynthate translocation from fully expanded soybean leaves increased with an increase in the length of the photosynthetic period. Our results do not rule out the possibility that translocation from the leaves of 7-h photosynthetic period plants is rate-limiting, and therefore at least partly responsible for starch accumulation. Greater starch accumulation under a 7-h photosynthetic period was associated with decreased synthesis of residual components but did not affect total foliar accumulation when compared with plants grown in a longer photosynthetic period (Table III). Therefore, a major difference in photosynthate partitioning existed in the amount of photosynthate allocated to starch *versus* residual components in soybean leaves grown under 7- and 14-h photosynthetic periods in controlled environments.

Influences of Photosynthetic Period on Leaf and Whole-Plant Development. Additional data are necessary for further characterization of the mechanisms of photosynthate partitioning within the fully expanded soybean leaf; however, the adaptive significance of the phenomenon is evident. When an environmental factor such as light or water becomes limiting, detrimental effects of the less favorable condition may be minimized by alterations in photosynthate partitioning. For example, soybean root growth is favored over shoot growth when vegetative plants are exposed to low soil moisture (15). The resultant growth favors acquisition of water during unfavorable soil conditions and reduces evaporative losses. In contrast, a shortened photosynthetic period favored shoot growth over root growth (Table IV). The soybean plants responded to a short photosynthetic period by diverting relatively more photosynthate into the light-capturing shoot. Within the shoot itself more efficient energy utilization (increased CER_W) resulted from decreased photosynthate partitioning into residual components of leaves. An increased proportion of the carbon fixed by plants grown in a short photosynthetic period was retained within the chloroplast during the day as starch, and translocated out of the leaf during darkness. The fact that shoot growth was favored over root growth under the shortened photosynthetic period suggests that photosynthates were translocated preferentially to growth centers of the shoot.

Various other plant responses have been associated with the length of the photosynthetic period. Garner *et al.* (10) reported an increase in foliar soluble sugars of short day *Cosmos bipinnatus* and long day radish under short day and long day conditions, respectively. Similarly, Tsybul'ko (19) noted a foliar accumulation of assimilates in short day *Perilla* and long day *Brassica* under inductive photoperiods. He concluded that long day plants translocated most of their assimilates during the day, whereas short day plants translocated more during the night (19). In a review article, Wardlaw (23) concluded that the dominant effect of daylength is the transformation from vegetative to floral development and that the greater translocation of assimilates in long day plants under long days and short day plants under short days results from these developmental changes. Bodson *et al.* (2) concluded that although photosynthate partitioning and translocation influenced floral induction in the long day plant *Sinapis alba*; additional determining factors may operate. In the present experiments, floral induc-

tion occurred under all treatments regardless of photoperiod or photosynthetic period; however, photosynthate partitioning responses differed. We conclude that the change in partitioning with a change in photosynthetic period is independent of the vegetative to floral transformation.

Our results demonstrate that daily partitioning of photosynthates in soybean leaves among starch synthesis, residual dry weight accumulation, and translocation to sites outside the leaf are modified by the duration of the daily photosynthetic period. However, partitioning remained unchanged when photoperiod was varied with photosynthetic period held constant. Leaves receiving a short daily photosynthetic period accumulated much more foliar starch and conversely less residual dry weight during photosynthesis than leaves receiving a long photosynthetic period. Results of the present study suggest that: *(a)* a potentially inefficient partitioning of carbon occurs in a fully expanded soybean leaf grown in a 14-h photosynthetic period; *(b)* length of the daily photosynthetic period influences the partitioning of carbon within soybean leaves. Indeed starch synthesis seems to be a programmed process and possibly regulated by the same photomorphogenetic controls that determine leaf thickness and whole plant morphology. Any model designed to account for the photosynthetic period-dependent shift in photosynthate partitioning should consider: starch synthesis within the chloroplast; photosynthate efflux from the chloroplast into the cytoplasm; synthesis of cellulose, protein, and other residual components of leaf cells; and the synthesis and extracellular translocation of sucrose.

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