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Effect of Shortened Photosynthetic Period on ^{14}C-Assimilate Translocation and Partitioning in Reproductive Soyeans[1]

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ABSTRACT

Starch accumulation rate in leaves of vegetative soybeans is inversely related to the length of the daily photosynthetic period. However, it is not known whether a similar response would be observed during reproductive growth. Soybeans (*Glycine max* L. Merr. cv Amsoy 71) were grown to three stages of reproductive growth (beginning seed, mid seed-fill, and late seed-fill) under 12-hour daylengths, and then shifted to 6-hour photosynthetic periods (12-hour photoperiods) for 4 days. One and 4 days after treatment, a mid-canopy leaf was pulsed with $^{14}CO_2$, and sampled for radiolabeled starch and water-soluble compounds at 0.5, 1, 3, 9, and 21 hours after labeling.

Plants exposed to the 6-hour photosynthetic periods at the beginning seed stage retained and incorporated significantly more label as starch than did those given 12-hour photosynthetic periods. However, plants exposed to the shortened photosynthetic periods at the late seed-fill stage partitioned less label into starch. Plants exposed at mid seed-fill gave a variable response.

Shortened photosynthetic periods resulted in preferential partitioning of recently fixed carbon to the seed at the expense of the pod wall. The results of these experiments suggest that the increased sink demand present during late reproductive growth may be of greater importance in control of leaf starch accumulation than is the length of the daily photosynthetic period.

The primary products of photosynthesis in higher plants are partitioned between two major metabolic pathways, one leading to starch synthesis within the chloroplast, and the other, to cytoplasmic sucrose synthesis and export. In addition to sucrose synthesis and export, there is also evidence for a sucrose storage pool (5, 8), but little is known about the control of sucrose allocation to either storage or transport. Starch accumulation has been estimated to range from 10 to 20% of the laminar dry weight by the end of each diurnal photosynthetic period (17, 22). This reserve carbohydrate is thought to be unavailable for degradation and export during the day except in the case of low photosynthetic rates (9). In the dark, starch is mobilized to sucrose and translocated from the leaf at rates 25 to 50% of those which occur in the light, presumably until leaf reserves are depleted (2, 10). Recent investigations with vegetative soybeans have indicated that starch accumulation is a tightly regulated process which depends upon the length of the daily photosynthetic period (2-4).

Sink demand has also been implicated in the control of daily starch accumulation. Treatments designed to decrease the source/sink ratio have been largely successful in decreasing starch or total carbohydrate levels within remaining or untreated leaves (13, 21). Nodulated plants have been reported to have lower leaf starch levels and higher activities of SPS[2] than do nonnodulated (nitrate-dependent) plants (11). Leaf starch accumulation has been shown to be negatively correlated with the activity of SPS (16). Presumably, increased sink demand causes a compensatory increase in phloem loading, and a decrease in the size of the sucrose export pool. Removal of sucrose would then allow increased SPS activity, resulting in a preferential diversion of carbon to sucrose synthesis rather than increased starch accumulation. Increased SPS activity has also been associated with increased translocation rates in soybean leaves acclimated to high irradiance (16).

To what extent sink demand and/or daylength influences starch accumulation during reproductive soybean growth is unknown. Reproductive sink demand increases with plant development to a point where half of the recently fixed ^{14}C is found in the beans at maturity (12). Later in seed growth, when current photosynthetic rate is minimal, levels of previously accumulated foliar carbohydrates have been shown to decrease (7, 8, 14). Since a large part of the carbon for seed growth is from concurrent assimilation, increased starch accumulation due to shortened daylength may be counterproductive at this time.

Increased starch accumulation in response to shortened daylength has been shown to occur up through full bloom in determinate soybeans (11). Whether such a response also occurs in later reproductive growth when substantial sink demand exists is unknown.

If daylength is of primary importance in the regulation of assimilate partitioning during reproductive soybean growth, an inherent source limitation may be created when demand exceeds concurrent foliar allocations for export.

The objective of this study was to determine whether the presence of reproductive structures has more influence over starch/WSC partitioning than does the length of the daily photosynthetic period.

MATERIALS AND METHODS

Plant Culture. Soybeans (*Glycine max* L. Merr. cv Amsoy 71) were grown in plant growth chambers (Conviron model E15) with a 12-h light duration up until treatment. A combination of

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[2] Abbreviations: SPS, sucrose phosphate synthetase; WSC, water-soluble compounds; TNC, total nonstructural carbohydrates; CER, CO_2 exchange rate (mg CO_2 dm^{-2} h^{-1}); PPFD, photosynthetic photon flux density; CER_A, CH_2O fixation rate (mg CH_2O dm^{-2} h^{-1}); CER_W, mg CH_2O g^{-1} dry wt h^{-1}.

incandescent and fluorescent lamps provided a PPFD of 500 μE m^{-2} s^{-1} at the top of the canopy. Temperature was 26°C during the light period and 21°C during the dark period. The growth medium was a 5:4:2 mixture of soil:sand:zorb-all (IMC Chemicals, Des Plaines, IL) in 12.5- × 12.5-cm plastic pots. At the time of planting, seeds were inoculated with *Rhizobium japonicum*, USDA strain 140. Plants were thinned to one plant per pot at the unifoliolate leaf stage (VI [6]). Branches were removed as soon as they formed to ensure uniform plants for sampling. Sufficient one-fifth strength Hoagland solution was provided hourly to provide leaching of excess nutrients. Completely randomized designs were used in these studies with five replications per treatment and sampling time.

Light Treatment. At three dates (51, 63, and 79 d after planting) when the plants were at growth stages R5 (beginning seed), R6 (mid seed-fill), and R6 (late seed-fill), respectively, they were shifted to shortened photosynthetic periods (6 h; 0800–1400), but normal photoperiods (12 h; 0800–2000). Irradiance levels during the first 6 h were the same as those of the controls, followed by 6 h of low irradiance incandescent irradiation (about 10 μE m^{-2} s^{-1}) to provide a 12-h photoperiod. Temperature during the low irradiance period was maintained at 26°C. These conditions were maintained for a period of 4 d for each growth stage, during which time the sampling took place.

Carbon Assimilation and Translocation. All measurements described were conducted at 1 and 4 days after imposition of the shortened photosynthetic periods. During the middle of the photosynthetic period, CER at 350 μl l^{-1} CO_2 was measured on an attached leaf in the middle of the canopy at *in situ* light intensity using an infrared gas analyzer (Beckman model 865) as described elsewhere (14). Leaf temperatures were measured simultaneously with CER using Chromel-Alumel thermocouples appressed to the abaxial leaf surface. Carbon exchange rate was expressed as mg CO_2 dm^{-2} h^{-1} or as mg of CH_2O as described by Chatterton and Silvius (3).

To monitor the partitioning of recently fixed carbon to starch, WSC, and residual material, plants were pulsed with $^{14}CO_2$ and sampled at regular intervals for the next 9 to 21 h. At 1000, the tenth trifoliolate leaf from the base of the plant was sealed in a 27- × 28-cm clear plastic bag (Ziploc, Dow Chemical). Attached beneath this bag and opening into it was a 20-ml polyethylene scintillation vial preloaded with 1 ml 1 N lactic acid. The area around the petiole was sealed with florist's adhesive, and 0.5 ml 0.1 N NaOH containing 1.9×10^5 Bq $NaH^{14}CO_3$ (Research Products Int. Corp.; 2.1×10^9 Bq $mmol^{-1}$) was injected into the scintillation vial via a serum stopper. After 15 min, 1 ml 2 N KOH was injected into the vial to neutralize the reaction. Following another 15-min period, the pulsing bag was removed and one leaf disc (2.3 cm^2) was immediately removed from each leaflet of the trifoliolate. In the first two stages of reproductive growth (55 and 63 days after planting), leaf discs were removed at 0.5, 1, 3, and 9 h after labeling. The samples were taken sequentially from opposite sides of the midrid and basipetal to the previous sample. The leaf discs were immediately frozen in liquid N_2, transported to the laboratory, and freeze-dried. Based on an average of the leaf areas from each growth stage, the removal of three leaf discs at each time after labeling represented a removal of 3.4% of the total area of the trifoliolate leaf. The entire plant was then harvested at the end of the 9-h chase for subsequent measurements of plant parameters and movement of label to the pods in the axil of the labeled leaf. During late reproductive growth (79 d after planting), a 21-h sampling time was added, and plant harvest was conducted at the end of this 21-h chase period.

Extraction and Analysis Procedure. The three freeze dried leaf discs from each sampling time were placed in 50-ml polyethylene centrifuge tubes. The tissue was then homogenized (Brinkman Polytron, model PT 10 20 350D with PTV-2 generator) in 10 ml distilled H_2O for 30 s at 9000 rpm. The homogenate was centrifuged (IEC, model K) in a horizontal rotor for 15 min at 1650*g* and the supernatant decanted into 25-ml volumetric flasks. The residue was resuspended in 10 ml of distilled H_2O and recentrifuged another 10 min at 1650*g* . The supernatant was decanted, combined with the original extract, and brought up to 25 ml with distilled H_2O. Five -ml aliquots were removed and combined with 15 ml of Aquisol-2 (New England Nuclear) and subjected to liquid scintillation spectroscopy. This fraction was designed ^{14}C-labeled WSC.

Each pellet remaining from the second WSC centrifugation was combined with 6 ml distilled H_2O and transferred to a 25-ml Erlenmeyer flask. After adding 1.5 ml of ethanol, the mixture was boiled for 1 to 2 min, and then allowed to cool to room temperature. To this mixture was added 3 ml of a sodium acetate buffer solution (pH 4.45), and 3 ml of a 0.5% α-amylase solution (Clarase 40,000; Miles Laboratories, Inc.). The mixture was then incubated at 38°C for 44 h to allow complete enzymic degradation of the starches. After incubation, the extracts were filtered through Whatman No. 1 filter paper into volumetric flasks and brought up to 25 ml with distilled H_2O. Five-ml aliquots were removed and combined with 15 ml of Aquisol-2 and subjected to liquid scintillation spectroscopy. This fraction was designated ^{14}C-labeled starch.

The filter paper used in the starch filtration was dried and pelletized. The filter paper plus residue was then combusted in a tissue oxidizer and the $^{14}CO_2$ released was absorbed in 9 ml of Carbosorb II and 13 ml of Permafluor V. This fraction was counted directly and designated ^{14}C-residual material.

Pods at the pulsed node were harvested separately, dried, and divided into pod walls and seeds. These separate fractions were ground in a cyclone sample mill (Udy Analyzer Co, Boulder, Co) and subsamples were removed and weighed. These subsamples were combusted using a tissue oxidizer (Packard model 306), and the released $^{14}CO_2$ was absorbed in 6 ml of Carbosorb II (Packard instrument Co.) and 16 ml of Permafluor V (Packard Instrument Co.) and counted on a liquid scintillation spectrometer (Beckman, model LS-8000).

Radiolabeled ^{14}C accumulated in the pod walls and seeds was expressed both in terms of the the total amount translocated to the pods in the axil of the labeled leaf, and as the sink strength of each of the individual fractions. Sink strength was calculated by dividing the amount of radioactivity found in either the seed or pod wall fraction by the sum of the radioactivity found in both and then multiplying this number by 100. The partitioning of label into starch, WSC, and residual material within the leaf was expressed as a percentage of the total ^{14}C activity present in these three fractions at 0.5 h.

Plant Parameters. Measurements taken from plant harvests at 1 and 4 d after treatment in each experiment consisted of the following: (a) at 51 and 63 d after planting (beginning and mid seed-fill)—total number of pods, number of pods at the axil of the labeled leaf, leaf area of the labeled leaf, and pod wall and seed dry weights from the pods at the labeled leaf axil; (b) at 70 d after planting (late seed-fill)—all of the above, plus total dry weight measurements of the leaf blade, pod wall + seed, and stem + petiole fractions.

Statistical Analysis. Significant differences between means within each growth stage and sampling time were detected using two sample *t* tests, with the probability given at the end of each table. Comparisons of the profiles of ^{14}C-labeled starch, WSC, and residual retention between the treatments were also accomplished using two sample *t* tests ($P \leq 0.05$) at each interval after labeling.

Table I. *Rates of Carbon Exchange and Carbohydrate Synthesis from Leaves of Amsoy 71 Soybeans*

The leaves were exposed to shortened photosynthetic periods at three stages of reproductive growth (R5, beginning seed; early R6, mid seed-fill; later R6, late seed-fill) expressed as a mean of five plants.

Time after planting	Length of Treatment	Photosynthetic Period	CER	CER_A	CER_W
d		*h*	$mg \cdot CO_2 \cdot dm^{-2} \cdot h^{-1}$	$mg\ CH_2O \cdot dm^{-2} \cdot h^{-1}$	$mg\ CH_2O \cdot g^{-1}$ dry $wt \cdot h^{-1}$
51 (stage R5)	1	12	25.8 NS	17.6 NS	28.0 NS
		6	25.7	17.5	28.4
55	4	12	27.9 NS	19.0 NS	28.4[a]
		6	31.7	21.6	34.6
63 (early R6)	1	12	20.9 NS	14.2 NS	22.4 NS
		6	21.5	14.6	24.8
67	4	12	20.8[a]	14.2[a]	21.2[b]
		6	25.4	17.3	27.8
79 (late R6)	1	12	21.0 NS	14.3 NS	22.6 NS
		6	23.7	16.1	26.9
82	4	12	24.2[b]	16.4[b]	22.1[c]
		6	30.5	20.8	31.2

[a] Significant at the 1% level.
[b] Significant at the 5% level.
[c] Significant at the 10% level.

Table II. *Starch/WSC Ratios Calculated from the Amount of Radioactivity Incorporated into Each Fraction as a Per Cent of the Total ^{14}C found in Labeled Starch, WCS, and Residual Material at 0.5 Hour*

From the leaves of Amsoy 71 soybeans in response to shortened photosynthetic periods at three stages of reproductive growth (R5, beginning seed; early R6, mid seed-fill; late R6, late seed-fill).

Time after Planting	Length of Treatment	Photoperiod	Starch/WSC	Difference
d		*h*		%
51 (stage R5)	1	12	0.31[a]	
		6	0.46	+48
55	4	12	0.41[a]	
		6	0.60	+46
63 (early R6)	1	12	0.42[a]	
		6	0.56	+33
67	4	12	0.77[a]	
		6	0.90	+17
79 (late R6)	1	12	0.54[b]	
		6	0.42	−22
83	4	12	0.56[b]	
		6	0.47	−16

[a] Average of the four sampling times during the 8-h sampling period.
[b] Average of the five sampling times during the 24-h sampling period.

RESULTS

On the 1st d after imposition of the shortened photosynthetic periods, rates of carbon exchange and carbohydrate synthesis were not significantly altered at any stage of reproductive growth (Table I). After 4 d of treatment, both CER_A and CER_W were significantly increased in those plants exposed to 6-h photosynthetic periods at all stages of reproductive growth, except CER_A at stage R5. The magnitude of the increase also changed with advancing plant development. The increase in CER_W ranged from 22% at beginning seed, to 41% at late seed-fill. The same comparison for CER_A encompasses a 6 to 26% range.

No significant differences due to the shortened photosynthetic period were found in any of the measured parameters of vegetative or reproductive growth at any growth stage (data not shown).

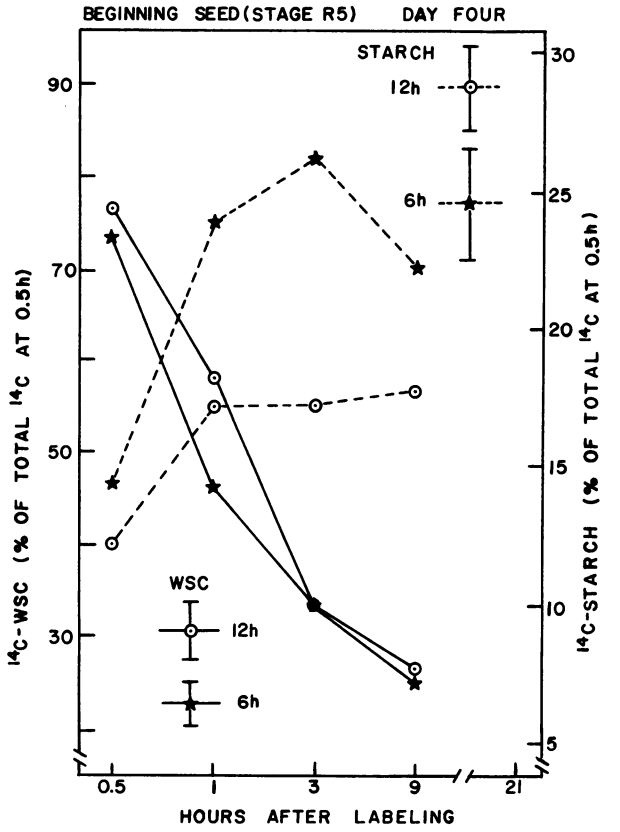

FIG. 1. The effect of 4 d of shortened photosynthetic periods on the retention and partitioning of label as starch or WSC in a mid-canopy leaf of Amsoy 71 soybeans at the beginning seed stage. Each data point represents the mean of five replicates ± SE.

No significant differences were observed in total Bqs present at 0.5 h for any of the treatments (data not shown). This may seem surprising when considering the differences observed in carbon exchange or carbohydrate synthesis, but may be due to treatment differences in translocation occurring before the discs

were removed at 0.5 h. However, since no differences were observed in the total radioactivity present at 0.5 h, and since the amount of translocation of ^{14}C to the pod (in 30 min) was assumed to be insignificant as compared to that in the total chase, comparisons based on the total radioactivity present at 0.5 h were considered valid despite the lack of correlation with CER.

Differences in assimilate partitioning were observed at 1 and 4 d at the beginning seed (R5) stage, and at day 1 during mid seed-fill (early R6) (Table II). At the R5 stage, the plants exposed to 6-h photosynthetic periods for 1 d incorporated and retained significantly less label as WSC, and an increased amount of label as starch, although this increase was not significant (data not shown). Because of this simultaneous decrease in WSC, and increase in starch accumulation, the starch/WSC ratio was increased 48% for the 6-h plants at this time (Table II). After four 6-h photosynthetic periods, plants at R5 showed no significant differences in the profile of WSC retention, but starch accumulation was significantly increased (Fig. 1). This increase in starch accumulation resulted in a 46% increase in the starch/WSC ratio for the 6-h plants (Table II). No significant differences were observed in the residual profiles for either treatment or sampling time at the beginning seed stage (R5) (data not shown). During this growth stage, shortened photosynthetic periods seemed to induce an increase in starch accumulation similar to that previously observed in vegetative and flowering soybeans (3, 4, 11).

Later in reproductive development, at the mid seed-fill stage (early R6), a similar but less pronounced increase in starch accumulation occurred due to 6-h photosynthetic periods (Table II). After one 6-h photosynthetic period, significantly more label was incorporated and retained as starch (Fig. 2) and as residual

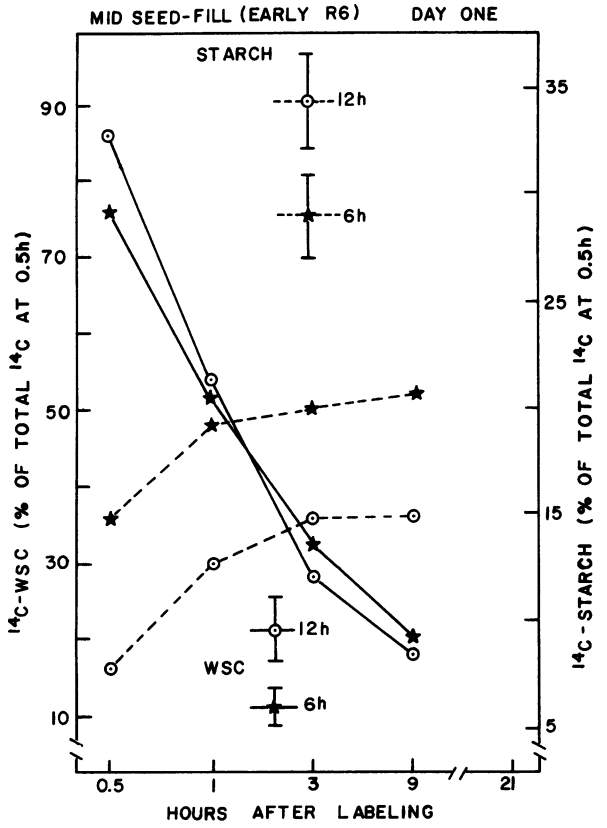

FIG. 2. The effect of 1 d of shortened photosynthetic period on the retention and partitioning of label as starch or WSC in a mid-canopy leaf of Amsoy 71 soybeans at mid seed-fill. Each data point represents the mean of five replicates ± SE.

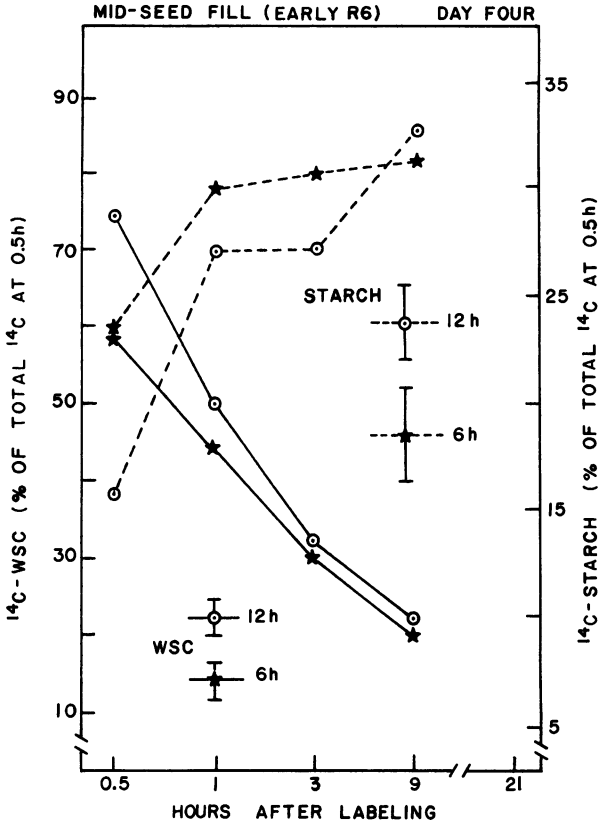

FIG. 3. The effect of 4 d of shortened photosynthetic periods on the retention and partitioning of label as starch or WSC in a mid-canopy leaf of Amsoy 71 soybeans at mid seed-fill. Each data point represents the mean of five replicates ± SE.

material (data not shown), while very little effect was found on WSC (except at 0.5 h) (Fig. 2). After 4 d of treatment, significantly less WSC and more starch was found for the 6-h plants at 0.5 h, with no significant differences occurring thereafter (Fig. 3). The changes in starch accumulation from day 1 to day 4 were reflected in the corresponding starch/WSC ratios (Table II). The increase in the ratio for those plants exposed to shortened photosynthetic periods declined from 33% to 17% when the treatment was applied at mid seed-fill.

At late seed-fill (late R6), 79 d after planting, shortened photosynthetic periods resulted in decreased starch accumulation at both 1 and 4 d after treatment. The starch profiles for day 1 are given in Figure 4. The data for day 4 (not shown) were very similar to those for day 1. The WSC profiles were almost identical for the two treatments at both sampling times, thus the starch/WSC ratios were decreased by the shortened photosynthetic periods (Table II). This response indicates that some influence other than daylength was exerting control over photosynthetic starch/WSC partitioning during late reproductive growth.

The nature of this unknown influence may be defined more clearly if the treatment effects on ^{14}C translocation are examined in relation to advancing reproductive development. At the beginning of seed-fill (R5), the effect of the shortened photosynthetic period on radioactivity in pod walls was nil after 1 d of treatment, but there was a 31% decrease after 4 d of treatment (Table III). A similar treatment effect was found to occur during both sampling times at mid seed-fill (early R6). In this instance, there was 33% less total radioactivity observed in the pod walls of the 6-h plants at day 1 and 46% less at day 4 (Table III). In terms of sink strength, no effect was observed at day 1, but after four 6-h shortened photosynthetic periods, the percentage of label trans-

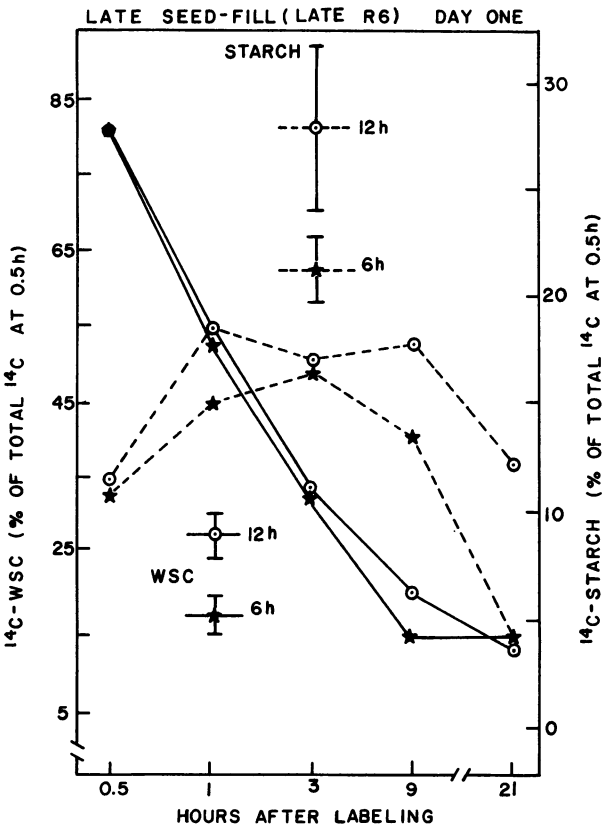

FIG. 4. The effect of 1 d of shortened photosynthetic period on the retention and partitioning of label as starch or WSC in a mid-canopy leaf of Amsoy 71 soybeans at late seed-fill. Each data point represents the mean of five replicates ± SE.

located was preferentially shifted in favor of the seed by 7.4% (Table III). Shortened photosynthetic periods also resulted in a preferential partitioning of label to occur at late seed-fill (late R6). The 6-h plants accumulated 16.1% and 6.7% more label in the seeds than in the pods on d 1 and 4, respectively.

DISCUSSION

The importance of current assimilation during late seed growth has been documented (12, 15, 18). Highly significant ($P \leq 0.001$) increases in CER_A and CER_W in response to shortened photosynthetic periods during late seed-fill presumably result from the high priority given to seed growth during this period. Increased carbon assimilation during acclimation to 6-h photosynthetic periods would then satisfy the requirements for both the energy demand of the nonphotosynthetic period, and the sink demand of the reproductive structures.

The increase in leaf starch accumulation which occurred at beginning seed-fill due to shortened photosynthetic period occurred more rapidly than previously reported (4, 11). At 1 d after treatment, increases in the starch/WSC ratio occurred at beginning seed and mid seed-fill (Table III). The fact that the increase in starch accumulation was maintained 4 d after treatment at the beginning seed stage indicates that these plants were behaving much like their vegetative counterparts (2–4, 11). The decreased starch/WSC ratio observed at day 4 at mid seed-fill suggests that these plants were in a transition stage. This transition was also indicated by the preferential partitioning of label in favor of the seed at the expense of the pod wall. The ^{14}C translocation and partitioning data from the growth stages prior to and after mid seed-fill suggest that reproductive sink demand was beginning to exert more influence than was the length of the daily photosynthetic period at this stage.

There appears to be no question as to the influence of the reproductive sink over photosynthetic starch/WSC partitioning during late seed-fill. At this stage of growth, the starch/WSC ratio of the plants exposed to 6-h photosynthetic periods was decreased below that of the control at both 1 and 4 d after treatment was imposed (Table II). There was a trend for less starch to be accumulated and retained in the 6-h plants at both day 1 (Fig. 3) and day 4 (data not shown) during late seed-fill. Significantly less starch was found 21 h after the $^{14}CO_2$ pulse at both sampling times (Fig. 3). This difference was probably due to mobilization and translocation of label to the reproductive sink during the dark period. The significance of this difference was that the level of labeled starch found in 6-h plants at the end of the dark period was less than that of the controls. This result suggests that at least in this variety of soybean, a more efficient

Table III. *Effect of Shortened Photosynthetic Period on the Accumulated Radioactivity and Sink Strengths of the Pod Walls and Seeds of Amsoy 71 Soybeans after Exposure of the Subtending Leaf to $^{14}CO_2$. The data are expressed as a mean of five plants.*

Time after Planting	Length of Treatment	Photosynthetic Period	Total Activity		Sink Strength	
			Pod wall	Seed	Pod wall	Seed
d		*h*	*Bq (× 10^5)*		*% of total Bqs found in pod wall and seed*	
51 (stage R5)	1	12	1.52 NS			
		6	1.62			
55	4	12	2.56[a]			
		6	1.76			
63 (stage R6)	1	12	3.02[a]	4.54 NS	40.4 NS	59.6 NS
		6	2.03	3.09	40.0	60.0
67	4	12	2.26[b]	2.87 NS	44.5[a]	55.5[a]
		6	1.21	2.08	37.1	62.9
79 (late R6)	1	12	0.63 NS	1.73[a]	25.4[c]	74.6[c]
		6	0.47	5.15	9.3	90.7
83	4	12	0.49 NS	2.30 NS	19.6[a]	80.4[a]
		6	0.52	3.65	12.9	87.1

[a] Significant at the 10% level.
[b] Significant at the 1% level.
[c] Significant at the 5% level.

process of mobilization is possible, with a greater amount of stored reserves utilized for translocation to the seed.

The preferential partitioning of label from the pod wall to the seed due to treatment has been reported previously. Streeter and Jeffers (19) have shown decreased levels of TNC in the pod walls of soybeans supporting increased reproductive loads during seed-fill. Work conducted previously in our lab has shown less radiolabeled assimilate (as a percent of the total ^{14}C at 0.5 h) in the pod walls of soybeans supporting increased reproductive loads during late seed growth (1). The possibility that pod walls may contribute to seed-fill via mobilization was reported by Thorne (20), but the process was shown to be cultivar dependent. The process of redistribution from the pod wall was shown not to be of great importance to final seed yield in the same variety which was used in our study—Amsoy 71. The data for total Bqs and sink strength indicated less accumulation by the pod wall due to shortened photosynthetic period in these experiments. Since the seed is the sink of primary importance during mid to late reproductive growth, it appears that the plant is responding to decreased source activity by steepening the sucrose concentration gradient from the source leaf. In this manner, the pod wall may effectively enhance the partitioning of assimilate to the seed in cases where the source/sink ratio has been decreased (*i.e.*, increased reproductive loads, or shortened photosynthetic periods). These data also indicate that the accumulation of ^{14}C-assimilate by the seed may be accelerated by shortened daylength in a manner analogous to the increased starch accumulation observed in leaves of vegetative soybeans treated in a similar manner.

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