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Trends in Carbohydrate Depletion, Respiratory Carbon Loss, and Assimilate Export from Soybean Leaves at Night[1]

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ABSTRACT

To evaluate assimilate export from soybean (*Glycine max* [L.] Merrill) leaves at night, rates of respiratory CO_2 loss, specific leaf weight loss, starch mobilization, and changes in sucrose concentration were measured during a 10-hour dark period in leaves of pod-bearing 'Amsoy 71' and 'Wells II' plants in a controlled environment. Lateral leaflets were removed at various times between 2200 hours (beginning dark period) and 0800 hours (ending dark period) for dry weight determination and carbohydrate analyses. Respiratory CO_2 loss was measured throughout the 10-hour dark period. Rate of export was estimated from the rate of loss in specific leaf weight and rate of CO_2 efflux. Rate of assimilate export was not constant. Rate of export was relatively low during the beginning of the dark period, peaked during the middle of the dark period, and then decreased to near zero by the end of darkness. Rate of assimilate export was associated with rate of starch mobilization and amount of starch reserves available for export. Leaves of Amsoy 71 had a higher maximum export rate in conjunction with a greater total change in starch concentration than did leaves of Wells II. Sucrose concentration rapidly declined during the first hour of darkness and then remained constant throughout the rest of the night in leaves of both cultivars. Rate of assimilate export was not associated with leaf sucrose concentration.

During vegetative growth in soybean (*Glycine max* [L.] Merrill), leaves are the primary source of assimilates during the day as well as at night (18). With initiation of reproductive growth, leaves provide nearly all of the assimilates deposited into the seed. The photosynthetic contribution of the pod accounts for only about 4% of the carbon imported by the seed (24).

A substantial portion of the carbon assimilated by soybean leaves is partitioned into starch during the day and transported out of the leaf at night (6, 7, 13). Starch accumulation rate is inversely related to the length of the daily photosynthetic period (6, 7). The control mechanism in starch/sucrose formation is located in protoplasts of mesophyll cells (16). Isolated protoplasts from mesophyll cells of species characterized by high accumulation rates of leaf starch partitioned more carbon into starch at the expense of sucrose (16). It can be inferred that plants are physiologically and genetically induced to accumulate reserve carbohydrate in the leaf during the day to maintain assimilate export at night.

It has been suggested (10) that assimilate export at night may be important in the overall carbon economy of soybean seed growth. It was observed (10) that genotypic differences existed in daytime starch concentrations at different CO_2 assimilation rates in soybean. At very low CO_2 assimilation rates the cultivar 'Amsoy 71' was able to maintain an export rate of 27.8 μg carbohydrate m^{-2} leaf area s^{-1} at the expense of starch reserves, whereas in 'Wells II' the export rate continued to decline when CO_2 assimilation rates were reduced. It was suggested that the decline in export rate of Wells II resulted from a limitation in starch mobilization. This suggests that cultivar differences could exist in starch mobilization at night.

The regulation of starch mobilization in leaves is relatively unknown. Likewise, the association between rate of export and rate of starch mobilization at night remains unclear. The purpose of this study was to evaluate nighttime carbon balance in the soybean leaf as related to assimilate export. The general experimental approach was to measure rate of respiratory CO_2 loss and changes in starch and sucrose concentrations and SLW[3] throughout a 10-h dark period. Rate of assimilate export was estimated from the rate of loss in SLW and rate of CO_2 efflux. Two soybean cultivars known to differ in leaf starch accumulation (10) were evaluated during the rapid seed growth stage.

MATERIALS AND METHODS

Plant Culture. Amsoy 71 and Wells II soybean cultivars were grown in a controlled environment room with a 14-h photoperiod, constant 25 ± 1°C temperature, and approximately 50% RH. A mixture of cool-white fluorescent and tungsten-filament incandescent lamps provided a PPFD of 400 μmol m^{-2} s^{-1} (400–700 nm) at the upper level of the canopy and approximately 300 μmol m^{-2} s^{-1} at the level of the leaves selected for analysis. Seeds were planted in 2-L plastic pots containing a fertile greenhouse soil mixture inoculated with *Rhizobium japonicum*. Plants were thinned to one per pot at approximately 2 weeks and watered once daily during vegetative growth and twice daily during reproductive growth with deionized water. Flower initiation at node 6 occurred at approximately 30 d after planting for each variety. Each plant developed 15 to 20 pods. All plants were sampled during the linear phase of seed growth (57 ± 7 d after planting).

Leaf Dry Matter and Carbohydrate Analyses. At approximately 1400 to 1600 h during the day two mature trifoliolate leaves per plant, located between the sixth and tenth nodes, were selected randomly and tagged according to nodal position. The PPFD for each lateral leaflet to be sampled was carefully measured with a LI-COR model LI-1905B quantum sensor without disturbing leaflet orientation in the canopy. Leaf samples for determination of SLW and carbohydrate concentrations were

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[3] Abbreviations: SLW, specific leaf weight (laminar weight per unit laminar area); PPFD, photosynthetic photon flux density; CH_2O, carbohydrate; Fru 2,6-P_2, fructose 2,6-bisphosphate.

obtained by removing one randomly selected lateral leaflet from each selected leaf immediately prior to initiation of the dark period at 2200 h and then removing the opposite lateral leaflet at a specified time during the dark period. Sampling during the dark period was done under dim, nonphotosynthetic, green light. Areas of lateral leaflets were determined using a leaf area meter (Hayashi Denko model AAM-5 or LI-COR model LI-3000). Leaflets were then quickly submerged in liquid N_2 and stored at −29°C until freeze-dried. After freeze-drying, leaflets were weighed and then ground to pass a 1-mm screen in a Tecator/Udy sample mill. A subsample from each of these individual ground samples was used to determine sucrose and starch concentration.

Sucrose extraction was carried out by placing individual subsamples of 50 mg into 50-ml plastic centrifuge tubes with 6 ml of 80% (v/v) ethanol and shaking in a water bath for 18 h at 40°C. Extracts were heated to evaporate the ethanol to a volume of approximately 1 ml and then contents were diluted to 7 ml with deionized water. Chl was removed by adding 2.0 ml chloroform, vortexing well, and centrifuging the chloroform-water mixture for 10 min at 6000*g*. To determine sucrose concentration, two separate 0.5 − ml aliquots were removed from the upper clear phase. One aliquot received 0.5 ml deionized water and the other aliquot received 0.5-ml of 0.1 mg ml^{-1} invertase (EC 3.2.1.26, Sigma) solution. Glucose concentration of each 1.0-ml aliquot was determined with a glucose oxidase (EC 1.1.3.4, Worthington Diagnostics) enzyme system (Statzyme). Sucrose concentration was determined from the difference between total glucose upon addition of invertase and free glucose.

The residue from the ethanol extraction was dried overnight at 55°C and then gelatinized in 10 ml of deionized water for 2 h in a boiling water bath. Upon removal, 5 ml of 0.1 M acetate buffer (pH 4.5) containing 25 mg amyloglucosidase (EC 3.2.1.3, Sigma) was added. Starch concentrations were determined as previously reported (10).

Respiratory CO_2 Efflux Measurements. Respiratory CO_2 efflux rates during the 10-h dark period (2200–0800 h) were measured on randomly selected trifoliolate leaves located between the sixth and tenth nodes. For each cultivar, continuous measurements of CO_2 efflux were recorded at 2- to 4-min intervals during the dark period for approximately seven individual leaves that had received a PPFD of approximately 265 μmol m^{-2} s^{-1} during the day prior to sampling. Measurements of CO_2 efflux were made on individual trifoliolate leaves using an acrylic chamber containing an effective circulating fan. Air containing about 450 μl CO_2 L^{-1} was supplied to the chamber from a compressed air cylinder at a flow rate of approximately 194 μl s^{-1}. Relative humidity was maintained at approximately 50% by forcing part of air stream through water prior to entering the chamber. Respiratory CO_2 efflux was measured as the difference between exiting and entering CO_2 concentrations using an Esterline Angus model 743 differential infrared gas analyzer. The dew points of entering and exiting air were measured with two General Eastern model 1201 dew point hygrometers. Leaf temperature was monitored using a thermocouple pressed to the underside of the leaf. A circulating water bath was used to maintain leaf temperature in the chamber at 25 ± 1°C. The mean of four observations for CO_2 efflux, leaf temperature, and entering and exiting dew points were recorded on an Omnidata Polycorder model 516 at 2- to 4-min intervals throughout the dark period.

Estimation of Assimilate Export Rate. Estimation of export rate was made using the method of Terry and Mortimer (28). The rate of export E was determined using the relationship, $E = D - R$, where D is the rate of decrease in SLW and R the rate of respiratory loss. It was assumed that the dry matter changes in the leaf were due to carbohydrate-type compounds. In calculating export rate, CO_2 efflux rates were converted to equivalent CH_2O. This was done by multiplying the CO_2 efflux rate by 0.68, the molar ratio of the two forms of carbon.

Statistical Analysis. A completely randomized design was used and analysis of the data was done using the least squares method of multiple regression. Due to canopy position and natural shading, sucrose and starch concentrations and SLW among leaflets were affected by differences in PPFD. To remove the influence of PPFD on all measured parameters except dark respiration, a multiple regression model involving time and light was developed for each parameter and used to adjust all values to a mean PPFD of 265 μmol m^{-2} s^{-1} before doing further statistical analyses.

Statistical analyses were conducted to determine the statistical significance of linear and quadratic relationships over time and significant differences between cultivars. This was accomplished by employing full least squares analyses using indicator variables on the combined data and testing cultivar differences in the individual β-coefficients in a stepwise regression procedure. Where cultivar differences were nonsignificant at $P<0.05$, common β-coefficients were used.

Analyses involving nonlinear regression models were employed when statistically significant curvature was present. In all cases where a nonlinear equation was actually employed, the sum of squares for the error term was smaller than that for the linear regression model. Since r and R^2 values were not available in the computer output from the nonlinear program, Pearson correlation coefficients between the observed Y and the predicted Y from the nonlinear regression ($r_{y\cdot\hat{y}}$) are provided. Significance of the Pearson correlation coefficient was determined by testing the hypothesis $r=0$.

RESULTS

The presence of statistically significant curvature in starch concentration and SLW trends during the dark period in both cultivars indicated that the linear model

$$y = \beta_0 + \beta_1 x$$

would not accurately describe either of these trends. Plots of regression lines of the second-order polynomial

$$y = \beta_0 + \beta_1 x + \beta_2 x^2$$

with the starch and SLW data for each cultivar indicated that this model was not able to describe the observed leveling off of starch concentration and SLW during the latter part of the dark period. This also was true of the nonlinear monomolecular model

$$y = a + be^{-kx}.$$

The Gompertz model

$$y = \exp(a - be^{-kx})$$

was modified to

$$y = A_0 + \exp(a - be^{-k(10-x)})$$

and was chosen as the nonlinear model that would more accurately describe trends in SLW and starch concentration. A substitution of $(10-x)$ in the exponent was necessary to get a maximum y value at 0 h and a minimum y value at 10 h of the dark period. The variable A_0 was added to the model as an estimate of the minimum value of y. After comparing linear and nonlinear models for sucrose concentration during the dark period, it was apparent that the monomolecular model would more accurately describe the trends in sucrose concentration. Mathematical and statistical aspects of the above regression models are discussed by Causton and Venus (4).

Concentration of sucrose in leaflets of both cultivars decreased rapidly during the first hour of darkness and then remained nearly constant throughout the rest of the dark period (Fig. 1). At the

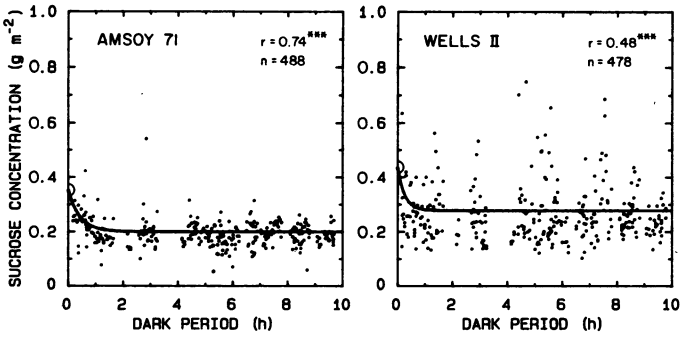

FIG. 1. Trends in sucrose concentration during a 10-h dark period in leaves of Amsoy 71 and Wells II soybean. r Value is the Pearson correlation between observed Y and predicted Y from the monomolecular regression; ***, significant at $P<0.001$; n is the total number of leaf samples. The open symbol represents the mean of approximately 150 observations at time 0 that were included in the regression, but are not shown.

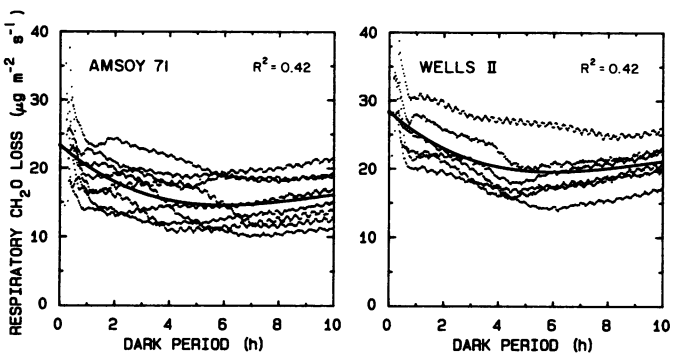

FIG. 2. Rate of respiratory CH_2O loss from leaves of Amsoy 71 and Wells II soybean during a 10-h dark period. For each cultivar, measurements of CO_2 efflux were recorded at 2- to 4-min intervals during the dark period for approximately seven individual leaves receiving a PPFD of approximately 265 μmol m^{-2} s^{-1} during the day prior to the dark period. Second order polynomial regression model.

beginning of the 10-h dark period sucrose concentration was 0.349 g m^{-2} in Amsoy 71 leaflets and 0.433 g m^{-2} in Wells II leaflets. During the first hour of the dark period, however, sucrose concentration in Amsoy 71 and Wells II leaflets decreased to 0.214 and 0.280 g m^{-2}, respectively, and remained at approximately these levels throughout the remaining 9 h of darkness.

Rate of respiratory CH_2O loss was greater in Wells II leaves than in Amsoy 71 leaves throughout the dark period (Fig. 2). Rate of respiratory CH_2O loss was greatest at the beginning of the dark period. Initial rates of loss were 23.5 and 27.4 μg CH_2O m^{-2} s^{-1} in leaves of Amsoy 71 and Wells II, respectively. Respiratory CH_2O loss gradually decreased until 5 h into the dark period and then increased slightly during the remainder of the dark period.

Concentration of starch was 6.32 g m^{-2} in Amsoy 71 leaves and 5.02 g m^{-2} in Wells II leaves at the beginning of the dark period and decreased to 3.02 and 2.43 g m^{-2}, respectively, by the end of the dark period (Fig. 3). Total decrease in starch concentration during the 10-h dark period was 3.31 and 2.59 g m^{-2} in leaves of Amsoy 71 and Wells II, respectively.

Rate of starch mobilization in both cultivars was relatively low during the first 2 h and then increased to a maximum 6 to 7 h into the dark period (Fig. 4). During the last 2 to 3 h of the dark period rate of starch mobilization gradually decreased as the concentration of starch reached a base level prior to the next 14-h photoperiod (Fig. 3).

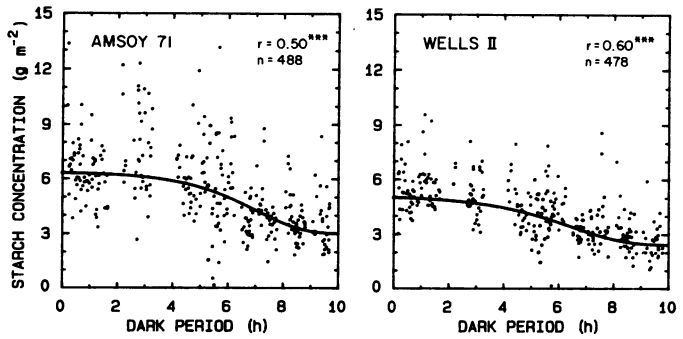

FIG. 3. Trends in starch concentration during a 10-h dark period in leaves of Amsoy 71 and Wells II soybean. r Value is the Pearson correlation between observed Y and predicted Y from the Gompertz regression; ***, significant at $P<0.001$; n is the total number of leaf samples of which approximately 150 were taken at time 0 for each cultivar and included in the regression but are not shown.

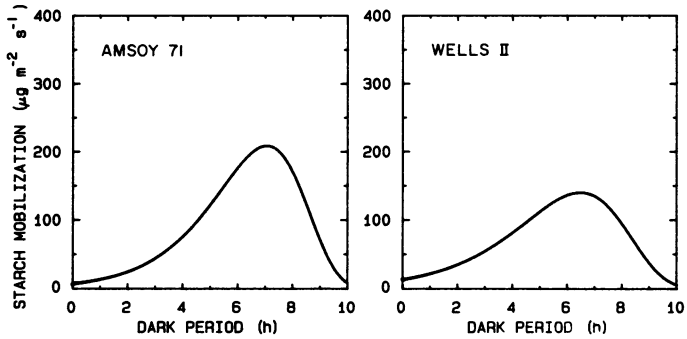

FIG. 4. Rate of starch mobilization from leaves of Amsoy 71 and Wells II soybean during a 10-h dark period. Rates of starch mobilization were determined from the first derivative of equations used in Figure 3 and presented as positive values.

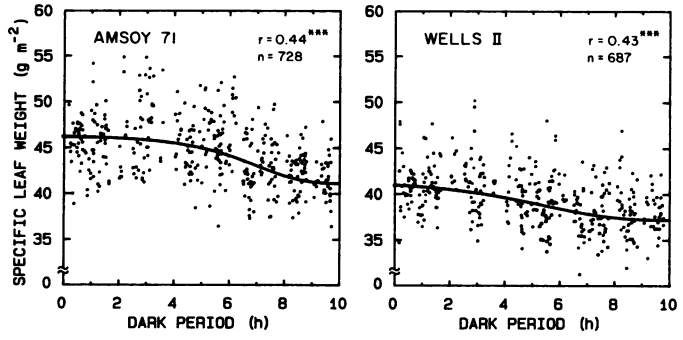

FIG. 5. Trends in specific leaf weight during a 10-h dark period in leaves of Amsoy 71 and Wells II soybean. r Value is the Pearson correlation between observed Y and predicted Y from the Gompertz regression; ***, significant at $P<0.001$; n is the total number of leaf samples of which approximately 150 were taken at time 0 for each cultivar and included in the regression but are not shown.

Specific leaf weight of Amsoy 71 and Wells II leaves was 46.2 and 41.0 g m^{-2}, respectively, at the initiation of the dark period and decreased to 41.1 and 37.2 g m^{-2}, respectively, by the end of the dark period (Fig. 5). Total decrease in SLW during the 10-h dark period was 5.1 and 3.8 g m^{-2} for Amsoy 71 and Wells II, respectively. Rate of loss in SLW was relatively low initially, gradually increased to a maximum at 6 to 7 h into the dark period,

and then decreased during the remaining 3 to 4 h of darkness (Fig. 5).

Rate of assimilate export from Amsoy 71 leaves (Fig. 6) increased to a peak of 304 $\mu g\ m^{-2}\ s^{-1}$ at 7 h and then declined to near zero by the end of the dark period. Rate of assimilate export from Wells II leaves (Fig. 6) followed a pattern similar to that of Amsoy 71. Export rate from Wells II leaves, however, increased more gradually during the first 4 h, reached a lower maximum of 152 $\mu g\ m^{-2}\ s^{-1}$ approximately 1.5 h earlier in the dark period, and declined more gradually before reaching an export rate close to zero by the end of the dark period.

DISCUSSION

Rate of assimilate export was not constant, but rather peaked during the middle of the dark period (Fig. 6). Diurnal trends in carbon export have been reported for mature leaves of soybean (17, 23) and cotton (*Gossypium hirsutum* L.) (14). Huber *et al.* (17) reported that export rate from leaves of soybean increased to a maximum of approximately 600 $\mu g\ CH_2O\ m^{-2}\ s^{-1}$ at midday and then decreased to near zero at the end of the day. Maximum rates of export from cotton leaves during the dark period occurred 4 h after the start of the dark period (14).

Rate of assimilate export was closely associated with rate of starch mobilization throughout the dark period in both cultivars (Figs. 4 and 6). The trend in starch mobilization during the dark period (Fig. 4) is similar to those reported for mature leaves of cotton (14) and pepper (*Capsicum annuum*) (25).

Cultivar differences in total amount of starch mobilized and amount of SLW loss were reflected in the magnitude of peak rates of export during the middle of the dark period. Amsoy 71 had a higher maximum export rate in conjunction with a greater total change in starch concentration and SLW than did Wells II. Rate of export was associated with the rate of starch mobilization and with the amount of starch reserves available for export. Daytime export rates from leaves of tomato (*Lycopersicon esculentum*) (15) and soybean (10) at very limited carbohydrate production rates have been reported to be maintained at the expense of starch reserves. Fader and Koller (10) observed that Amsoy 71 plants had nearly a 3-fold greater leaf starch concentration and an export rate nearly twice that of Wells II at a carbohydrate production rate near zero. They postulated that Amsoy 71 was better able to mobilize starch reserves and maintain a minimum export rate dependent on the rate of starch breakdown; whereas, low leaf starch concentration in Wells II limited starch breakdown and consequently, the amount of carbon available for export. Thus, it appears that rate of export is dependent on the rate of starch mobilization and on the amount of starch reserves available for export during the dark period as well as at limited carbohydrate production rates (10) during the day.

The regulation of starch mobilization is relatively unknown. Fru 2,6-P_2 recently has been established as a regulatory metabolite in photosynthate partitioning (3, 9, 27). An increase in starch synthesis during the day has been associated with an increase in leaf Fru 2,6-P_2 concentration (26). If Fru 2,6-P_2 is involved in regulating the flow of carbon from the chloroplast (starch reserves) to the cytoplasm (fructose-1,6-diphosphate) during the dark period, a reduction in Fru 2,6-P_2 concentration should coincide with an increase in starch mobilization. Huber *et al.* (17) reported that the concentration of Fru 2,6-P_2 in leaves of soybean was high during the first 3 to 4 h of the dark period, but then declined at an increasing rate during the remaining hours of darkness. This decline in Fru 2,6-P_2 concentration coincides with the decline in starch concentration observed in the present study (Fig. 3). It is possible that the rate of starch mobilization also may involve diurnal changes in the ratio of amylopectin to amylose (5), amylolytic activity (20), or compartmental changes within the leaf (12).

Rate of assimilate export during darkness (Fig. 6) was not closely associated with leaf sucrose concentration in either cultivar (Fig. 1). There have been, however, several reports (10, 13, 15) of positive correlations between daytime export rate and leaf sucrose concentration. Since leaf sucrose concentration remained constant (Fig. 1) while rate of starch mobilization changed (Fig. 4), the flux of carbon through the sucrose pool apparently changed according to the rate of starch mobilization. Sucrose phosphate synthase, an enzyme suggested to be the rate-limiting step in sucrose synthesis, has been reported to be positively correlated with rate of export during the day (14, 17) but not during the night (14, 21–23). The activity of enzymes involved in sucrose metabolism and the mechanisms involved in sucrose loading and phloem transport apparently were sufficient to support rapid sucrose synthesis and export during the periods of maximum starch mobilization observed in the present study.

Fader and Koller (10) reported a greater increase in export rate per unit increase in whole-leaf sucrose concentration during the day in leaves of Wells II than in Amsoy 71. They suggested this difference may be due to Wells II partitioning a greater proportion of sucrose into an exportable pool (11, 19) than did Amsoy 71. The loss of 0.153 g m^{-2} in sucrose during the first hour of darkness in leaves of Wells II compared to 0.135 g m^{-2} in leaves of Amsoy 71 (Fig. 1) also may be indicative of a greater sucrose pool that is readily available for export. In addition, the greater concentration of sucrose maintained during the dark period in leaves of Wells II (0.277 g m^{-2}) compared to Amsoy 71 (0.199 g m^{-2}) could be indicative of a greater sucrose pool that is not readily available for export. It is clear, however, that the association between concentration of leaf sucrose and export rate observed during the day for these two cultivars (10) is not present during the dark period.

Rate of assimilate export (Fig. 6) was not closely associated with respiratory CH_2O loss (Fig. 2). Throughout the dark period, Wells II had a higher respiratory CH_2O loss and maintained a greater concentration of sucrose than did Amsoy 71. Positive correlations between carbohydrate concentration and respiration rate have been reported (1, 2, 8). Rapid decline in sucrose concentration during the first hour in leaves of both cultivars was sufficient to support observed respiratory CH_2O losses ranging from 20 to 30 $\mu g\ m^{-2}\ s^{-1}$. The increase in respiratory CH_2O loss during the latter half of the dark period while sucrose concentration was constant suggests that some factor in addition to the concentration of sucrose was affecting the rate of respiratory CH_2O loss.

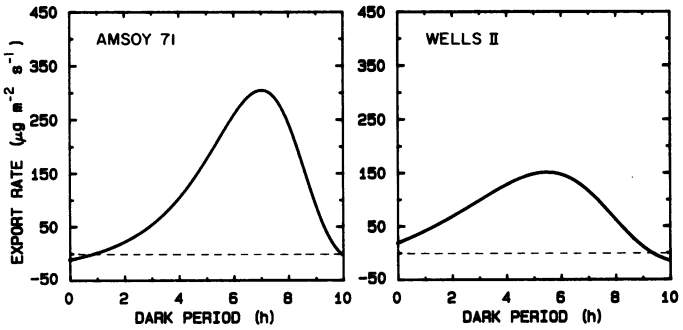

FIG. 6. Rate of assimilate export from leaves of Amsoy 71 and Wells II soybean during a 10-h dark period. Rate of export was estimated from the rate of loss in specific leaf weight and rate of CO_2 efflux.

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