

Remobilization Patterns of C and N in Soybeans with Different Sink-Source Ratios Induced by Various Night Temperatures¹

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ABSTRACT

The effects of increased sink-source ratios, induced by elevating night temperatures, on remobilization of ¹⁴C-assimilates and N within field-grown soybeans (*Glycine max* [L.] Merr.) was investigated from preflowering to maturity. Raising the mean minimum night temperature for the entire growing season from 10 (check, uncontrolled) to 16°C increased seed growth without appreciable effect on final leaf area. Increasing this temperature to 24°C increased seed growth and reduced final leaf area. Leaves, stems, petioles, and pods acted as intermediate storage sites for ¹⁴C assimilates. Only plants with higher night temperatures remobilized some of the stored assimilates during the period of rapid seed growth. Even the seeds in the 24°C plants with the largest sink-source ratios did not utilize all the C-assimilates potentially available for remobilization. Nitrogen was readily remobilized from petioles, stems, and pods of all treatments as early as the beginning of seed development, but from the leaves only during late seed-filling. However, only plants with elevated night temperatures tended to remobilize all of the available N from vegetative tissues and pods. We concluded that a larger portion of stored assimilates may be remobilized to the seed if a strong seed sink can be sustained. It also appeared that with increasing sink-source ratios, N shortage might limit seed yield before a lack of C-assimilates would. A proposed model for soybean assimilate demand, distribution, partitioning, and remobilization is presented.

Contrary to the 'self-destructive' hypothesis developed by Sinclair and DeWit (20), recent evidence suggests that soybean plants are capable of supporting a higher reproductive load from the standpoint of C (2, 3, 8, 16, 22) and N (6, 9, 12, 16, 21) than is usually maintained to maturity. This evidence indicates that some nonstructural photoassimilates are present at maturity in the vegetative parts and pod walls of soybeans which are not converted into seed yield. Pods, stems, leaves, and petioles may serve as intermediate storage sites for C (4, 8, 15, 22) and N (6, 21, 27). Experimental manipulation of the sink-source ratio has demonstrated that these stored assimilates are potentially available for seed demands not met by current photosynthates (3–6, 22, 26).

We recently found that elevated night temperatures enhance soybean seed growth which, in turn, alters dry matter allocation in favor of seeds at the expense of vegetative tissues and pod walls (18). Similar results were reported by Thomas *et al.* (23) who concluded that, until the late seed-filling stage, the main effect of increased reproductive load on assimilate reserves in

vegetative tissues was in limiting the amount of photoassimilates distributed to these tissues rather than in net remobilization from these pools. The objective of the present study was to investigate the effects of increased sink-source ratio on net remobilization of C and N within the soybean canopy throughout reproductive development. We also attempted to model distribution and remobilization of assimilates within soybean plants in response to increased sink-source ratio.

MATERIALS AND METHODS

Plant Materials and Treatment Application. Indeterminate soybean (*Glycine max* [L.] Merr. cv "S09-90") of Maturity Group 0 were grown under field conditions. Treatments included mean minimum night temperatures of $24 \pm 2^\circ\text{C}$ and $16 \pm 1^\circ\text{C}$, and the uncontrolled check (about 10°C) in a randomized block design with four replications. Elevated night temperatures were achieved by enclosing the plots at night in polyethylene-covered chambers and increasing chamber temperature with electric heaters. The chamber covers were removed each morning to provide natural field conditions during the daylight hours. Treatments were applied from 2 weeks after plant emergence until physiological maturity. Detailed cultural practices and experimental procedures have been reported previously (18).

C Remobilization Study. Four to six plants from each plot were allowed to assimilate ¹⁴CO₂ during the preflowering, early pod development and seed-filling stages. The designated plants were enclosed in a plexiglass chamber (30 × 30 × 60 cm). The labeled CO₂ was generated by injecting 10 ml of 0.6 N lactic acid through a serological stopper into a 50-ml Erlenmeyer flask which contained 3.7 kBq of ¹⁴C in 0.1 M sodium bicarbonate. The ¹⁴CO₂ generated in the flasks was pumped into the chamber through polyethylene tubing. A circulating fan was operating in the chamber during the labeling time. Plants were allowed to assimilate ¹⁴CO₂ for 10 min before the chamber was removed.

Labeled plants were tagged and harvested at 10- to 20-d intervals throughout the growing season. The samples were separated into leaves, petioles, stems, pods, and seeds at harvest and were dried at 60°C for 48 h before being weighed and ground in a Wiley mill to pass through a 2-mm mesh screen. Subsamples of 100 mg were combusted in an automated oxidizer (Packard Tri-carb Sample Oxidizer, model 306). The released CO₂ was captured into 10 ml Oxisorb (New England Nuclear) and 15 ml of Oxiprep (New England Nuclear) scintillation cocktail. Activity was determined by a liquid scintillation counter (Beckman, LS 7500). Each sample was counted for 10 min or 2% of the standard deviation of the mean, whichever occurred earlier. The readings were adjusted automatically for chemical quenching.

The first samples for ¹⁴C activity measurements were taken at least 10 d after labeling. The radioactivity in the various parts of

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the plants was expressed as a PTRR² in the plant. Assuming that in soybeans all ¹⁴C loss through respiration occurs within 7 d after assimilation (15), changes in the percentage of the recovered radioactivity after this period of time would not be caused by the differences in the respiration rates among treatments. Furthermore, variations among treatments for the distribution of assimilates to any plant part during the growth and development would change the concentration of ¹⁴C without affecting the total recovered activity in that same part, or in the whole plant. Thus, changes in the radioactivity in any plant part as a PTRR, can be attributed to the remobilization of ¹⁴C into, or out of, that plant part.

N Remobilization Study. One plant from each plot was harvested biweekly for the entire growing season for N content measurement. The samples were separated into leaves, petioles, stems, pods, and seeds immediately after harvest and were dried at 60°C for 48 h. These samples were then weighed and ground in a Wiley mill to pass through a 2-mm mesh screen. Total N was determined for 30 g of the ground samples, using a micro-Kjeldahl technique.

The data for both studies were analyzed separately for each sampling date as a randomized complete block design. The LSD values were calculated for comparisons among treatments within each date. Significant differences mentioned in this paper are at $P < 0.05$.

RESULTS

Treatment Effects on Sink-Source Ratio. Raising the mean minimum night temperature from 10 (check) to 16°C increased seed weight without affecting the final leaf area; the 24°C treatment increased seed weight and reduced the final leaf area (Table I). Detailed effects of the treatments on dry matter distribution and seed growth were reported elsewhere (18). In general, individual seed growth was the component most responsive to the treatments.

C Remobilization. When labeled during preflowering (45 DAE), the PTRR in the leaves of all treatments generally decreased after an initial increase (Fig. 1a). The decrease was sharper in plants with higher night temperature treatments. This resulted in significantly lower PTRR in the leaves of the 16°C plants compared to the check at 110 DAE (Fig. 1a) indicating that these plants remobilized more assimilates out of their leaves than did the check plants. No significant treatment differences for petiole PTRR were detected (Fig. 1b).

The PTRR in the stems of the check plants gradually increased throughout the sampling period (Fig. 1c). A gradual decline in

the PTRR of the stems of the 16 and 24°C treatments until 75 DAE was followed by a sharp increase on the next sampling date. The decline between 65 and 75 DAE coincided with the beginning of pod development (60–80 DAE), suggesting that some ¹⁴C was remobilized from the stems to the pods in these treatments. The increase in the stem PTRR in these treatments on the following date coincided with the decrease in their leaf PTRR, indicating that the depleted ¹⁴C from the stems was possibly replaced by assimilates remobilized from the leaves. The stem PTRR of the 24°C plants further declined from 90 to 110 DAE and was significantly lower than the other treatments 110 DAE. The decline corresponded with the rapid seed growth stage (90–110 DAE), suggesting that some ¹⁴C assimilated during preflowering was remobilized from stems to developing seeds in the 24°C treatment which had the highest sink-source ratios. This was further supported by the sharp decline in the PTRR of the pods in this treatment during the same period of time (Fig. 1d). The pod PTRR in the 24°C treatment was significantly higher than the other treatments at 90 DAE which was followed by a sharp decrease until 110 DAE. Unlike for the higher night temperature treatments, no decline was observed for the PTRR in the pods of the check plants, suggesting that the seeds of the check plants did not act as strong sinks to remobilize some of the previously fixed ¹⁴C from the pods.

When labeled during early pod development (60 DAE), the leaf PTRRs in the 16 and 24°C plants were consistently lower than the check plants at all sampling dates (Fig. 2a). This suggests that plants receiving higher night temperatures remobilized more of the C-assimilates out of their leaves. A gradual decrease in the PTRR of the leaves and petioles of the check plants (Fig. 2, a and b) was followed by a slow increase in stem and pod PTRR in this treatment (Fig. 2, c and d). There was no indication of ¹⁴C-assimilate remobilization from pods or stems (Fig. 2, c and d) in check plants from 90 to 120 DAE (the seed growth stage). This suggests that current assimilates were sufficient to supply all the assimilate demand by the seeds in this treatment.

The 16°C plants appeared to store the assimilates remobilized out of the leaves in their stems until the beginning of seed growth (Fig. 2c), after which these assimilates were remobilized to the pods (Fig. 2d). This was evidenced by significantly higher PTRR in the stems of this treatment at 90 DAE (Fig. 2c) and in their pods at 105 DAE (Fig. 2d), compared to the check. The PTRR in the pods of the 16°C plants decreased by 120 DAE indicating remobilization of ¹⁴C-assimilates out of the pods.

The ¹⁴C assimilated in the 24°C plants during early pod development seemed to be translocated directly to the pods as evidenced by the significantly higher PTRR in the pods of these plants at 75 DAE, compared to the other treatments (Fig. 2d). A decrease in the PTRR of the 24°C pods, along with that of the

Table I. Percentage Differences from the Check of Leaf Area and Seed Weight for Plants with Elevated Night Temperatures during the Reproductive Development

Mean minimum night temperature treatments were: check (uncontrolled, about 10°C), 16 ± 1°C, and 24 ± 2°C. Treatments were applied from 2 weeks after plant emergence until physiological maturity. The values for leaf area and seed weight on each date were calculated using the equations fit to the average measured values for these traits throughout the growing season as reported by Seddigh and Jolliff (18).

Trait	Mean Minimum Night Temperature Treatment	Days after Emergence													
		37	44	51	58	65	72	79	86	93	100	107	114	121	128
	°C	% differences from check													
Leaf area	16	19	35	36	30	32	32	19	9	-1	-4	-5			
	24	25	57	43	27	25	25	7	-4	-25	-23	-30			
Seed weight	16							696	400	690	133	95	88	51	37
	24							6087	1767	1650	270	136	79	30	23

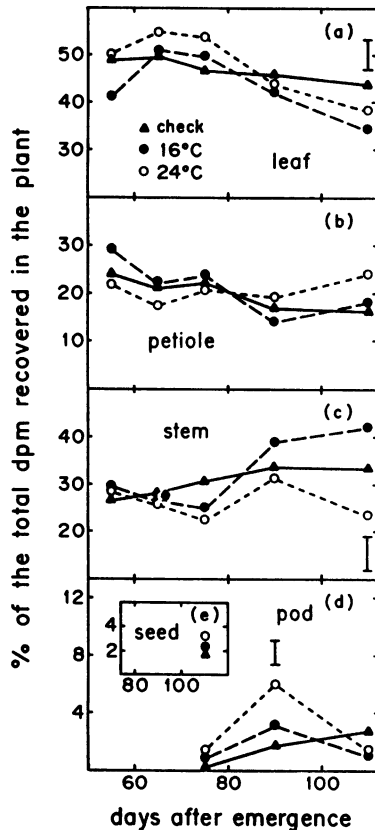


FIG. 1. Effects of night temperature on remobilization of C-assimilates within soybean plants labeled during preflowering (45 DAE). Mean minimum night temperature treatments were: check (uncontrolled, about 10°C), 16 ± 1°C, and 24 ± 2°C. Treatments were applied from 2 weeks after plant emergence until physiological maturity. Whole plants were allowed to assimilate $^{14}\text{CO}_2$ for 10 min. Data are presented as the total dpm recovered in each plant part as the percentage of the total dpm recovered in the whole plant on each sampling date. The data points are means of four replications. The bars represent LSD values at the 0.05 level for comparison between treatment means on a given date.

stems, at the 90 DAE suggests remobilization of ^{14}C into the seeds in this treatment. The PTRR of the stems and pods in the 24°C plants (Fig. 2, c and d) increased again by 105 DAE, apparently because of ^{14}C remobilization out of the leaves and petioles (Fig. 2, a and b). However, the pod PTRR further decreased during the last sampling period (Fig. 2d) which suggests that some of the ^{14}C assimilated during early pod development in this treatment was remobilized to the seeds during late seed-filling. Although plants with higher night temperatures had higher PTRR in their seeds, there was not a significant difference between the PTRR in the seeds of different treatments (Fig. 2e).

When soybeans were labeled during the beginning of the seed-filling stage (75 DAE), plants with higher night temperatures had lower PTRR in their leaves than the check plants at all sampling dates (Fig. 3a). This suggests that the 16 and the 24°C plants initially translocated more ^{14}C assimilated during the beginning of seed-filling out of their leaves than did the check plants. The 24 and 16°C plants also had lower PTRR in their petioles at 100 and 115 DAE, and 100 DAE, respectively (Fig. 3b). The PTRR in the stems of all the treatments were similar until 120 DAE (Fig. 3c) while plants receiving warmer night temperatures had significantly higher PTRR in their pods than the check plants at 85 DAE (Fig. 3d). Thus, it appeared that the 16 and the 24°C plants translocated the majority of the ^{14}C assimilated during the beginning of seed-filling from their leaves to their pods.

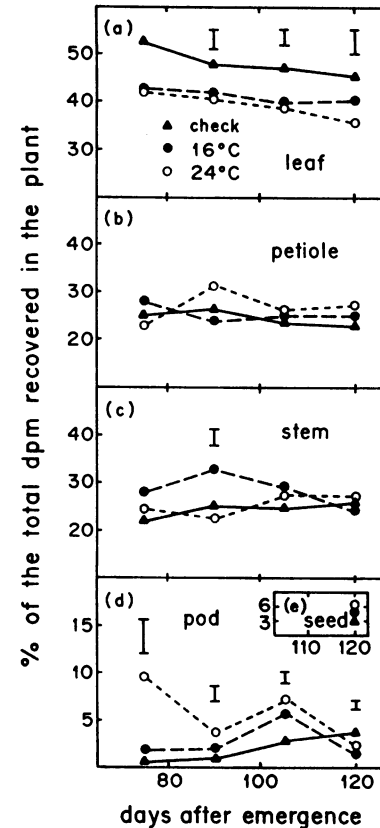


FIG. 2. Effects of night temperature on remobilization of C-assimilates within soybean plants labeled during early pod development (60 DAE). Treatment descriptions, data presentation, and statistical analysis were as in Figure 1.

Although the 24°C plants had significantly lower PTRR in their leaves than the check at 80 and 100 DAE, apparently because of higher initial ^{14}C translocation out of their leaves, they further remobilized more ^{14}C -assimilates from their leaves by 115 DAE (Fig. 3a) during the time when seed demand for assimilates was high. This is further evidenced by significantly higher PTRR in the seeds of the 24°C plants compared to the other treatments at 115 DAE (Fig. 3e). Additional remobilization occurred from the stems of the 24°C plants between 115 and 135 DAE (Fig. 3c), apparently to support the seed demand for C-assimilates during the late seed growth stage.

The pod PTRR in the 16°C plants declined between 100 and 115 DAE (Fig. 3d). This coincided with the period of rapid seed growth and suggests that some C-assimilates were remobilized from pods to the seeds in this treatment. However, no apparent remobilization was observed out of the leaves, petioles, and stems of the 16°C plants after 100 DAE (Fig. 3, a-c). This implies that the assimilate demand by the seeds of the 16°C treatment was satisfied by current supplies of this material and some remobilization from pods. The PTRR did not seem to decrease considerably in leaf, petiole, stem, or pod of the check plants after 100 DAE (Fig. 3, a-d), indicating that all the C-assimilate demand by the seeds of this treatment was supplied by the current photosynthates and remobilization of these materials was not required.

The PTRR remained high in the leaf, petiole, and stem of the check and 16°C treatments, relative to those in the 24°C plants, suggesting that some potentially available C-assimilates were not utilized by the seeds of these treatments. Furthermore, the PTRR remained high in the pods of all treatments at maturity (Fig. 3d), which indicates that even the intense sink-source ratio induced

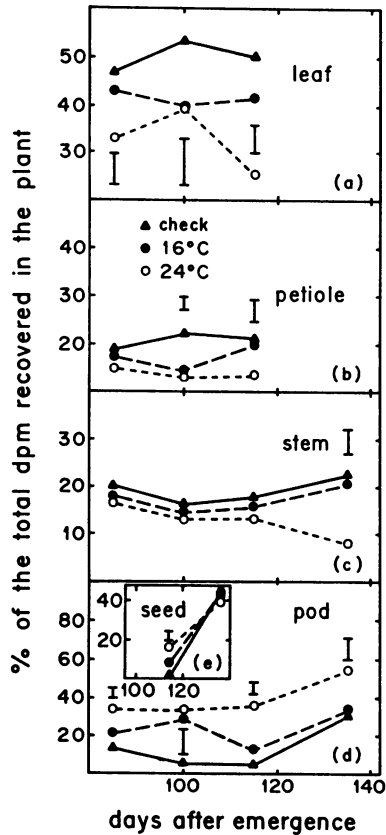


FIG. 3. Effects of night temperature on remobilization of C-assimilates within soybean plants labeled during early seed-filling (75 DAE). Treatment descriptions, data presentation, and statistical analysis were as in Figure 1.

by the 24°C treatment was insufficient to result in utilization of all the available C-assimilates. Moreover, it appeared that C-assimilates for seed development were withdrawn preferentially from pods, stems, petioles, and leaves. However, since C-assimilates are replaced by the adjacent source as they are depleted, pods are likely to be the last plant part exhausted of assimilates.

N Remobilization. Plants with higher night temperatures generally had lower N concentration in leaf, petiole, stem, and pod, than the check plants (Fig. 4, a-d). The seed N concentrations were similar among treatments at maturity, although plants with higher night temperature treatments tended to have higher N concentration in their seed during the earlier measurements (Fig. 4e). The N concentrations in all plant parts reported here are consistent with the literature (9, 21, 27).

Nitrogen appeared to readily remobilize from petioles and pods as early as the beginning of seed growth, but from the leaves and stems only during rapid seed-filling (Fig. 4). The N concentration in the stems continued to increase until rapid seed-filling, supporting other reports (1, 5) that stems may play an important role for storage of excess N until it is utilized by the rapidly growing seeds. The N concentration in leaves, petioles, stems, and pods of the check plants at maturity were significantly higher than the other treatments (Fig. 4, a-d). This indicates that the seeds of the check plants did not utilize all the potentially available N. Similar results have been reported for different soybean varieties under field conditions (27).

Although the plants with higher night temperature treatments remobilized greater proportions of the available N in their vegetative tissues and pod walls (Fig. 4, a-d), the check plants contributed a higher proportion of the seed N through remobilization (Table II). This is because of both lower total seed N in

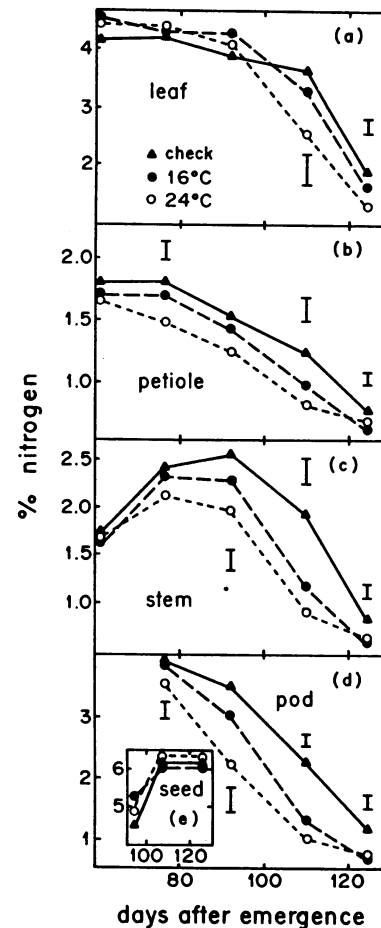


FIG. 4. Effects of night temperature on N concentration in different plant parts as a function of DAE. Treatment descriptions and statistical analysis were as in Figure 1.

the check plants (Table II) as well as higher total dry matter production in these plants (18). This agrees with previous reports (9, 27) that the proportion of seed N contributed through remobilization is related to the amount of potentially redistributable N available in the vegetative plant parts and pod walls at the beginning of seed-fill. This in turn depends on the total dry matter accumulated in these plant parts.

DISCUSSION

The results of the present study agree with the increasing literature reporting that soybeans are capable of supporting a higher reproductive load from the standpoint of both C and N assimilates. Stems and pods seemed to act as major intermediate storage sites for C-assimilates, which is consistent with the literature (4, 5, 22). However, the present data indicate that C-assimilates may also be remobilized from leaves if the seed can exert sufficient demand for these assimilates. In contrast to some previous reports (15, 22) our results also suggest that C assimilated during preflowering and early pod formation may be remobilized during the rapid seed growth stage if the current assimilates, and the assimilates stored at the beginning of seed fill, cannot support all the seed demand for these materials. Although N appeared to readily remobilize from vegetative parts and pods in all the treatments, only plants with greater sink-source ratios tended to remobilize N to its lower limits as reported by Streeter (21). These results emphasize that C and N may be remobilized from the vegetative tissue and pod walls more efficiently if seed demand for assimilates is increased through im-

Table II. *Effects of Night Temperature on N Remobilization within Soybean Plants*

Treatment descriptions are as in Table I. The seed N remobilized from other plant parts was calculated by subtracting the highest measured total amount of N in each plant part from its total at maturity. The data are the means of four replications.

Mean Minimum Night Temperature Treatments	Seed N					
	Remobilized from other plant parts				Total	Total from remobilization
	Leaf	Petiole	Stem	Pod		
°C	$g\ m^{-2}$					%
10 (check)	6.45	0.65	3.32	3.65	27.99	50.26
16	7.24	0.61	2.43**	4.63	41.45**	35.97**
24	6.50	0.42	1.93**	3.18	36.55*	32.91**

** and * refer to significant differences from the check within each column at the 0.05 and 0.01 levels of probability, respectively, as compared by LSD.

provement of seed sink strength. Our results also tended to support the 'nearest source' concept (22) that the assimilates are withdrawn by the seeds preferentially from the closest source.

In addition to the genetic capacity for seed growth and the availability of photoassimilates, soybean seed yield can be limited by external factors such as photoperiods (3, 6), night temperatures (18, 23), and perceived light (13), which directly affect seed growth. However, most previous work has implicated photoassimilate production as the major limitation to soybean seed growth. Consequently, much attention has been given to finding ways to prevent early senescence and prolong seed growth duration.

Contrary to the self-destructive hypothesis (20), increasing remobilization of C and N from vegetative tissues to the seeds may not necessarily result in earlier senescence, while reducing the demand for assimilates might actually decrease the rate of photosynthesis (5, 14, 26). Furthermore, increased carbohydrate supply to the roots will not increase N_2 fixation in the absence of a strong seed sink (1, 25) whereas a strong sink may enhance N_2 fixation (25). Photosynthetic activity and senescence of soybean leaves late in the season is independent of leaf N content (5, 14, 26). The results of our experiments also indicated that plants with the highest sink-source ratio had the highest photosynthetic rate during the rapid seed-fill (19) while their leaf N contents were the lowest (present data). These results imply that increasing seed sink strength could improve not only the efficiency of remobilization of C and N assimilates from reserves to the seeds, but it may also result in an increase in the production of these assimilates. Additionally, the results of the present study agree with Nelson *et al.* (16) that under conditions of high sink-source ratios, N might become limiting earlier than C.

Reproductive Sink Strength and Assimilate Allocation; a Proposed Model. The following conceptual model was developed in an attempt to describe the relationship between sink-source ratios and distribution, partitioning, and remobilization of assimilates within the soybean canopy. The model suggests some of the reasons for the controversies among researchers on the effects of altering sink-source ratios.

(a) Plants first respond to the reproductive sink demand for assimilates by altering the distribution patterns in favor of the added sinks (2, 11, 23), which would have no apparent effect on the export rates of assimilates out of the leaves. This response may play a more important role in plants with indeterminate growth habit and may also be more apparent in long-term experiments (18).

(b) Plants then respond to added sink demand for assimilates by altering the partitioning of current assimilates within source leaves in favor of export, which results in lowering the proportion of assimilates allocated for storage in these leaves (14, 26). This may also result in an increase in the rate of CO_2 fixation in these

leaves (10). The increased CO_2 fixation may not be apparent if the extra demand for assimilates can be satisfied by altering the distribution patterns within the plant. However, changes in the partitioning of assimilates seem to be the first mechanism through which plants respond to added sink in the short term (7) before they alter the distribution patterns.

(c) Remobilization of assimilates will then occur only if changes in the distribution or partitioning patterns of assimilates cannot supply the added sink demand. It appears that plants will first remobilize the stored assimilates in the mesophyll cells (12) which is not expected to impair physiological function of the leaves. Furthermore, a decrease in the stored assimilates associated with higher demands for these materials may result in an increase in the rate of CO_2 fixation (24), whereas an increase in the content of stored assimilates indicates an excess production of these materials and does not necessarily reduce the rate of assimilation (17).

(d) Only under extremely high sink-source ratios would the functional assimilates likely be degraded for further remobilization of C and N to supply even further demand by the reproductive sink. This would damage the physiological function of the plant, causing early senescence and limited productivity.

The model suggests that under conventional production practices, soybean seed yield is more likely limited by seed sink strength than, as commonly assumed, by the availability of photoassimilates for seed growth. More efficient mobilization of C and N from the stored reserves to the seed is possible if a strong seed sink can be sustained. The potential for increased seed production in commercially grown soybeans may be achieved by genetic manipulation of plants if the external factors which directly regulate seed growth, and the mechanism through which these factors exert their influence, were known. Furthermore, redistribution is more efficient than assimilation, even if the same levels of seed production were achieved.

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