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**REGULATION OF ASSIMILATE PARTITIONING BY DAYLENGTH AND  
SPECTRAL QUALITY**

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## INTRODUCTION

Photosynthesis is the process by which plants utilize light energy to assimilate and transform carbon dioxide into products that support growth and development. The preceding review provides an excellent summary of photosynthetic mechanisms and diurnal patterns of carbon metabolism with emphasis on the importance of gradual changes in photosynthetically-active radiation at dawn and dusk (Geiger, this volume). In addition to these direct effects of irradiance, there are indirect effects of light period duration and spectral quality on carbohydrate metabolism and assimilate partitioning. Both daylength and spectral quality trigger developmental phenomena such as flowering (e.g., photoperiodism; Deitzer, this volume) and shade avoidance responses (Pausch et al., 1991), but their effects on partitioning of photoassimilates in leaves are less well known. Moreover, the adaptive significance to the plants of such effects is sometimes not clear.

## DAYLENGTH

The light period normally occupies only part of the 24 h cycle, but photosynthesis during the light must support the carbon requirements of the plant during the dark as well. Thus, photosynthetic productivity frequently exceeds the capacity of the plant to transport and/or utilize the products of photosynthesis during the light period alone. Excess capacity is often stored in leaves or other tissues as polymers of glucose or other sugars (e.g., starch, sucrose, fructans). Temporary storage of photosynthate as large molecular weight compounds provides immediate benefits for photosynthesis, since it releases phosphate that would otherwise be sequestered in phosphorylated sugars (potentially inhibiting photosynthesis).

However, carbohydrate storage serves another important purpose. Many plants accumulate large amounts of starch or other carbohydrates in photosynthetic tissues during the light and then breakdown and utilize this material in the dark. This temporal redistribution of photosynthetic products allows plants to support growth and respiration during long dark periods. Mutants unable to accumulate starch are disadvantaged when grown under light-dark cycles as compared to continuous light (Caspar et al., 1985).

Early experiments conducted in greenhouses indicated that plants accumulated a greater proportion of photosynthate as starch under short day conditions (Challa, 1976). Subsequent

experiments were largely performed in controlled environment chambers and documented that similar responses to daylength could be observed in a wide range of species and that plants could adapt to sudden changes in daylength, sometimes within 24 h of the switch (Britz, 1990a). Note that photosynthate partitioning into starch was approximately halved when soybean plants were transferred from a 11.5 h daylength into a 16 h daylength (Table 1; Britz, unpublished data). Partitioning under a 7 h daylength, however, was similar to that under 11.5 h, indicating the transition between short and long-day response was between 11.5 and 16 h. In several well-documented cases, daylength regulation of assimilate partition was demonstrated to result from timing of dark period duration involving circadian rhythms initiated at the transition between light and dark periods (Britz et al., 1987). Detection of the light-dark transition apparently was perceived by non-photosynthetic photoreceptors capable of suppressing rhythms above certain low irradiances (Britz, 1986; Britz, 1991).

**TABLE 1** Effect of Daylength on Carbohydrate Allocation in Soybean

Daylength Treatment*	Leaf Number **	Starch Accumulation (percent of photosynthesis) ***
11.5 h → 7h	TF <sub>3</sub>	34.7
	TF <sub>4</sub>	36.3
11.5 h → 11.5h	TF <sub>3</sub>	35.3
	TF <sub>4</sub>	32.9
11.5 h → 16h	TF <sub>3</sub>	18.7
	TF <sub>4</sub>	19.7

\* Plants were grown (Chatterton and Silviu, 1981) for 24 days at a daylength of 11.5 h (12.5 h dark period) and shifted for 4 days to the indicated daylength prior to measurement. \*\* Third and fourth trifoliolate leaves (TF<sub>3</sub> and TF<sub>4</sub>, respectively). \*\*\* Rates of starch accumulation were determined under growth conditions between 1 and 6 h after lights-on and referenced to rates of intact leaf net photosynthesis expressed as carbohydrate assimilation (Britz, 1990b).

In spite of the early greenhouse work, some researchers (e.g., Geiger et al., 1985) speculated that the daylength response was peculiar to the complex lighting manipulations used in controlled environments (e.g., Britz et al., 1985). However, an extensive series of greenhouse experiments conducted with natural daylight at 12 intervals during a growing season showed that the proportion of assimilate partitioned into starch (TF<sub>4</sub>, 4th trifoliolate) increased steadily under standard measurement conditions as prior daylength shortened between the summer solstice and the autumnal equinox (Britz, 1990b). About one-third of photosynthate was stored as starch at midsummer, but this fraction increased to 80% in early autumn. Temperature in the greenhouse was controlled with a heat pump, so the effect of this variable was minimized. Growth intervals were adjusted so that TF<sub>4</sub> of comparable developmental status (i.e., plastochron), but differing in

daylength history, were obtained for each harvest. In fact, photosynthetic rates of TF4 measured under standard conditions declined only by about 10% at later harvests in the fall.

Increased partitioning into leaf starch was observed under short days at the end of the growing season, in spite of the fact that daily integrals of photosynthetically-active radiation were reduced by 50% and that plants were filling pods at the axil of TF4. These results suggest that daylength effects on assimilate partitioning within a source leaf may take precedence over the demand of nearby sinks. It may also explain why soybean seed development is sometimes found to be sink limited, while leaves may at the same time contain high levels of starch (Streeter and Jeffers, 1979). Clearly, regulation of assimilate partitioning by factors operating at the level of the leaf can be an important component of overall plant productivity.

### SPECTRAL QUALITY

It has been known for some time that spectral quality affects plant tissue composition. In particular, carbohydrate levels are higher, while protein and amino acids are lower, in plants raised under red-biased as compared to blue-biased spectra (e.g., Warrington and Mitchell, 1976). It is important to determine if photosynthate partitioning contributes to morphological and physiological adaptation to altered spectral quality (e.g., canopy shade). A crucial question is whether spectral quality affects photosynthate partitioning directly at the level of source leaf metabolism or indirectly as a result of photomorphogenetic effects on the strength of developing sinks. For example, high starch content in the first leaf of cucumber was shown to correlate well with the growth of the developing third leaf as controlled by blue light and/or ultraviolet-B radiation (Britz and Adamse, 1994). It seems likely that starch content in the first leaf was an indicator of sink demand.

Soybeans raised under relatively high photosynthetically-active radiation from blue-deficient low pressure sodium (LPS) lamps manifested many of the characteristics of shade plants (Britz and Sager, 1990). The leaves contained baseline (i.e., end-of-night) starch levels three fold higher than plants raised under broad spectrum fluorescent light. Moreover, 35% more photosynthate was partitioned into starch and sugar during the first half of the light period, apparently causing a decline in export from 52 to 37% of photosynthate (Table 2; Britz and Sager, 1990). Some of the retained carbon may have been used to support leaf growth at the expense of root growth (Table 2). High ratios of total leaf area to total dry matter compensated reduced photosynthesis on an area basis and maintained similar total Relative Growth Rates under the two different spectral quality conditions (Table 2). Note that net photosynthesis (total leaf basis!) was equal for first trifoliolate leaves measured under growth conditions for the two different light qualities even though the area of leaves from blue-deficient conditions was much greater. These data confirm the importance of generating high leaf area and suggest that changes in source leaf partitioning may be a form of resource rationing that maintains high photosynthesis under perceived shade conditions.

**TABLE 2** Photoassimilation, Export and Growth Parameters in Soybean

Parameter	Broad Spectrum Fluorescent Lamps	Blue-deficient Low Pressure Sodium Lamps
<u>First Trifoliolate Leaf*</u>		
Leaf Area (dm <sup>2</sup> )	0.559 b***	0.656 a
Net Photosynthesis (mg-C leaf <sup>1</sup> h <sup>-1</sup> )	3.46 a	3.47 a
Starch + Soluble Sugar Accumulation (percent of net photosynthesis)	34	46
Export (percent of net photosynthesis)	52	37
<u>Relative Growth Rates**</u>		
Total Dry Matter (g g <sup>-1</sup> d <sup>-1</sup> )	0.226 ab	0.218 b
Leaf Dry Matter (g g <sup>-1</sup> d <sup>-1</sup> )	0.195 b	0.212 b
Stem Dry Matter (g g <sup>-1</sup> d <sup>-1</sup> )	0.252 a	0.230 ab
Root Dry Matter (g g <sup>-1</sup> d <sup>-1</sup> )	0.253 a	0.208 b
Leaf Area (dm <sup>2</sup> dm <sup>-2</sup> d <sup>-1</sup> )	0.157 c	0.202 b
<u>Leaf Area Ratio (dm<sup>2</sup> g<sup>-1</sup>)</u>		
14 days	2.09 a	2.19 a
18 days	1.59 b	2.07 a

\*Determined 16 days after planting.

\*\*Determined 14 to 18 days after planting.

\*\*\*Values followed by different letters are significantly different at the 5% confidence level.

More detailed experiments with younger soybean seedlings (8 to 10 days after planting) revealed significant reductions in the partitioning of <sup>14</sup>C-labelled photosynthate to the roots of plants transferred from blue-sufficient to blue-deficient lighting (Verkleij and Britz, unpublished data). Alterations in translocation preceded discernible changes in the partitioning of growth to the root but were accompanied by only small changes in primary leaf assimilate accumulation, raising questions about the cause-and-effect relationship between leaf carbohydrate storage and growth patterns. Under these conditions, high levels of leaf starch were shown to result from small and gradual increases in the proportion of photosynthate stored as starch during the light coupled with small reductions in the amount of starch broken down in the dark.

## CONCLUSIONS

The effects of daylength and spectral quality on assimilate partitioning and leaf carbohydrate content should be considered when conducting controlled environment experiments or comparing results between studies obtained under different lighting conditions. Changes in partitioning may indicate alterations to photoregulatory processes within the source leaf rather than disruptions in sink strength. Moreover, it may be possible to use photoregulatory responses of assimilate partitioning to probe mechanisms of growth and development involving translocation of carbon or adaptation to environmental factors such as elevated CO<sub>2</sub>. It may also be possible to steer assimilate partitioning for the benefit of controlled environment agriculture using energy-efficient manipulations such as daylength extensions with dim irradiances, end-of-day alterations in light quality, or shifting plants between different spectral qualities as a part of phasic control of growth and development. Note that high starch levels measured on a one-time basis provide little information, since it is the proportion of photosynthate stored as starch that is meaningful. Large differences in starch content can result from small changes in partitioning integrated over several days. Rate information is required.

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