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# Photoperiodic Regulation of Photosynthate Partitioning in Leaves of *Digitaria decumbens* Stent.

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## ABSTRACT

**In leaves of pangolagrass (*Digitaria decumbens* Stent.), the proportion of photosynthate partitioned into starch adjusts to a change in daylength within 24 hours. After a single 14-hour long day, the relative starch accumulation rate is approximately 50% of that under 7-hour short days. This rapid response was exploited to study the light requirement for the perception of changes in daylength. It was found for short day-grown plants that: (a) 7-hour daylength extensions with dim white light (below the light compensation point for photosynthesis); (b) 7-hour daylength extensions with dim far red light (wavelengths greater than 690 nanomoles); or (c) 0.5-hour night-break irradiations with bright white light were all capable of producing about one-half of the effect of a 7-hour daylength extension with bright light. However, long periods of bright light were not required for a complete effect, since a 7-hour shifted short day (*i.e.* beginning 7 hours later than usual) was as effective as a 14-hour-long day itself. There was also a critical daylength between 11 and 12 hours for the transition between short-day and long-day partitioning patterns. Photoperiod determination depends, at least in part, on a nonphotosynthetic photoreceptor sensitive to both visible and far red irradiation. The duration of the photosynthetic period, as shown in experiments with low-pressure sodium lamps, does not by itself determine the response to daylength.**

In a variety of species, the proportion of photosynthate partitioned into storage carbohydrate (*e.g.* starch) is typically 2- to 3-fold higher in plants grown under SD conditions than in plants grown under LD (4, 6, 7, 23). This increased accumulation of photosynthate in leaves of SD-grown plants is associated with decreased translocation (23). The biochemical bases for daylength effects on partitioning are currently under investigation and may involve changes in a spectrum of enzyme activities including, but not necessarily limited to, sucrose phosphate synthase (12) and ADP-glucose pyrophosphorylase (20). It has been suggested that increased starch accumulation during SD is a 'programmed' response to a presumed requirement for extra carbohydrate during the accompanying long nights (5). Daylength-related differences in partitioning may also affect aspects of growth and development such as shoot/root ratio (5, 11) and flowering (21).

In at least some species, the adaptation of partitioning to daylength is reversible, even after leaf development is complete (7). Thus, plants grown under one daylength regime can be switched to another regime and starch accumulation rates will adjust to the new daylength. In soybeans, this adjustment required about 4 d for a shift between 14 h LD and 7 h SD. The reverse shift (SD to LD) did not result in an adjustment within the same time span. On the other hand, starch accumulation rates in spinach adjusted partially in both directions within 4 d of a daylength shift. A third species, *Digitaria decumbens* Stent., adapted completely within 1 d for shifts in both directions.

The daylength effect on starch accumulation rate in soybeans was ascribed to the duration of the 'photosynthetic' period (5, 8). Thus, LD-grown soybean plants treated for 4 d with 7 h of bright light followed by 7 h of additional dim incandescent light (short photosynthetic period but long photoperiod) still reacted as if adapted to SD. Although photosynthesis and partitioning in a variety of plants are influenced by dim light photoperiod extensions or by alterations in spectral quality (10, 13–15, 17, 18, 26), the soybean plants in this study appeared unable to perceive the added 7 h of dim light. However, the requirement for bright light does not necessarily implicate photosynthesis to the exclusion of other photoreceptor mechanisms. An additional problem is that the dim incandescent light used for daylength extension differed in spectral quality from the main light period and may have affected photoperiod perception (9). Finally, changes in growth and/or metabolism over the 4-d experimental period may have interfered with the determination or expression of the daylength response. This work was therefore initiated to reexamine the light requirement for daylength effects on partitioning in a species, *D. decumbens*, which responds rapidly to alterations in daylength and in which gross changes in leaf growth, development, and net photosynthesis can be excluded (7). A preliminary report of these results has appeared (2).

## MATERIALS AND METHODS

*Digitaria decumbens* Stent. (pangolagrass), a C-4 forage species (19), was propagated vegetatively in the greenhouse under natural photoperiods. Cuttings were rooted in water, planted in washed river sand, and fertilized periodically with a modified, half-strength Hoagland's solution (20). Active tillering was maintained by frequent trimming. Plants were used without detectable ill effect on the daylength response between 1 and 12 months after sprigging. At least 2 weeks prior to harvesting, plants were transferred to controlled environment chambers (EGC[1], Chagrin Falls, OH) at 27 ± 1°C, 60 to 65% RH, 0.35% $CO_2$, and with 7 h of light (400–600 $\mu$mol $m^{-2}$ $s^{-1}$ PPFD[2], depending on experiment, from CWF+I lamps) and 17 h of dark. These conditions were chosen to duplicate previous work with pangolagrass (6, 7). Plants were cut back at least twice during the initial 2-week

[1] Mention of a trademark or proprietary product does not constitute a guarantee or warranty of the product by the United States Department of Agriculture and does not imply its approval to the exclusion of other products that may also be suitable.

[2] Abbreviations: PPFD, photosynthetic photon flux density; LPS, low pressure sodium; CWF(+I), cool-white fluorescent (plus incandescent).

adaptation to ensure that all harvested leaves developed in the appropriate environment. In some experiments, plants were grown under 14-h LD using LPS lamps and custom growth chambers (3) with comparable conditions except that $CO_2$ was not regulated. Control plants were grown in similar chambers with CWF+I illumination.

Experimental daylength or light quality treatments are described in detail in the text. Unless noted otherwise, they were administered once on the day immediately prior to harvest. CWF lamps were obtained from GTE/Sylvania; plastic filter material was obtained from Rohm & Haas and Westlake Plastics (Lenni, PA) as specified. Spectral irradiance was determined from 350 to 800 nm at 2-nm intervals with scanning spectroradiometers calibrated to NBS-traceable standards (either a Model 740A, Optronics Laboratories, Orlando, FL, or a custom unit). Both units utilize photomultipliers as photodetectors, 2-nm slits, and programmable desk-top calculators to control the collection, correction, storage, and manipulation of data. PPFD was obtained from integrated spectroradiometric measurements or from a calibrated quantum sensor (LI-COR Inc.).

Starch accumulation rates were interpolated from two harvests made 1 and 6 h after the start of light period. Five to six plants were harvested at each time for each treatment. Rates of net photosynthesis were measured with a air seal cuvette and IR gas analyzer system (27) and were also constant after the first h of the light period. Starch and soluble sugar content were assayed in the two most recently expanded leaves on a tiller. After measurement of leaf area (Model LI-3000; LI-COR Inc.), the selected leaves were frozen (70 K), freeze-dried, weighed, ground (60 mesh, Cyclone Sample Mill; UD Corp., Boulder, CO), aliquoted, and extracted either sequentially or in parallel with cold water and takadiastase (Clarase 900; Miles Laboratories, Elkhart, IN) to yield soluble sugar and starch fractions (5). Reducing sugar content, after hydrolysis in 6 N HCl in the case of the soluble sugar fraction, was measured based on ferricyanide reduction (AutoAnalyser II; Technicon Instrument Corp., Tarrytown, NY). For pangolagrass leaves, this procedure gave results similar to one based on methanol-chloroform-$H_2O$ extraction and a coupled enzymic assay of glucose and fructose in the soluble sugar and starch fractions (23).

Table I. *Effect of Daylength on Carbohydrate Accumulation and Retention and on Dry Weight Accretion in Pangolagrass Leaves*

SD-grown plants were given a 7-h daylength extension (CWF+I light, 600 $\mu$mol $m^{-2}$ $s^{-1}$). Leaves were harvested 1 and 6 h into the following light period for determination of specific leaf weight and carbohydrate content. Rates of net photosynthesis (mg $CO_2$ $dm^{-2}h^{-1}$) were measured in the interim and converted into carbohydrate equivalents (5). To determine export, it was assumed that carbohydrate was primarily responsible for the increase in specific leaf weight.

| Parameter | Treatment | |
|---|---|---|
| | SD control | Daylength extension |
| A. Net photosynthesis (mg $CH_2O$ $dm^{-2}h^{-1}$) | 29.24 | 29.92 |
| B. Soluble sugar accumulation (mg $dm^{-2}h^{-1}$) | 0.05 | 0.01 |
| C. Starch accumulation (mg $dm^{-2}h^{-1}$) | 4.98 | 2.47 |
| D. Specific leaf wt accumulation (mg leaf dry wt $dm^{-2}h^{-1}$) | 6.66 | 4.60 |
| E. % of photosynthate exported (1- [D/A]) × 100 | 77.2 | 84.6 |
| F. % of photosynthate retained as starch (C/A) × 100 | 17.0 | 8.3 |

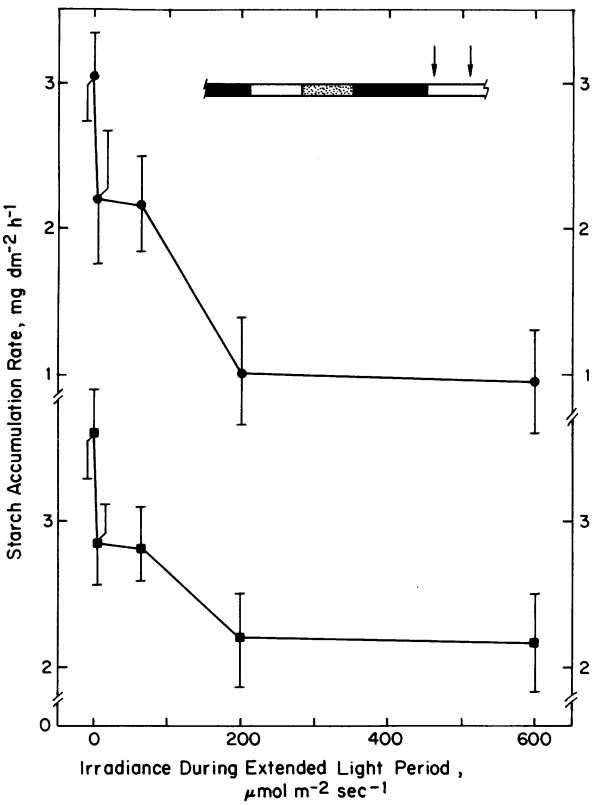


FIG. 1. Effect of irradiance during a single 7-h daylength extension on rates of starch accumulation expressed the following day. SD-grown plants (7-h light period, 600 $\mu$mol $m^{-2}$ $s^{-1}$, open bar) were illuminated with white light at 0 (*i.e.* SD controls), 6, 60, 200, or 600 $\mu$mol $m^{-2}$ $s^{-1}$ for 7 h (stippled bar) starting immediately after the standard light period. Irradiance was adjusted with neutral density screens or with an aluminized Mylar sheet (at the lowest irradiance) so that spectral quality was kept constant. Irradiance was measured in the center of the chambers and was found to decrease up to 25% at the margins. After a 10-h dark period (17 h in the case of the SD controls), all plants were restored to standard irradiance starting at the usual time. Plants were harvested 1 and 6 h into the succeeding light period (vertical arrows). The results from two separate experiments are presented. Bars indicate one SE.

## RESULTS

In comparison to SD controls, a single 7-h daylength extension with bright light had no effect on rates of net photosynthesis and soluble sugar accumulation when measured the following day (Table I, A and B). In neither case was soluble sugar accumulation significantly different from zero. Starch accumulation rate, on the other hand, was reduced approximately 50% by the daylength extension (Table IC). The accumulation of leaf dry weight was also reduced (Table ID). It was calculated that export out of the leaf increased from about 77 to 85% as a result of the daylength extension, assuming (7) that export equals the difference between net photosynthesis (expressed as carbohydrate) and the accumulation of leaf dry weight (mainly carbohydrate). This increase is almost equal to the decrease in the proportion of photosynthate retained as starch (Table IF). These results are essentially identical to those from a similar study of pangolagrass treated with altered daylengths for four cycles (7). Observed rates

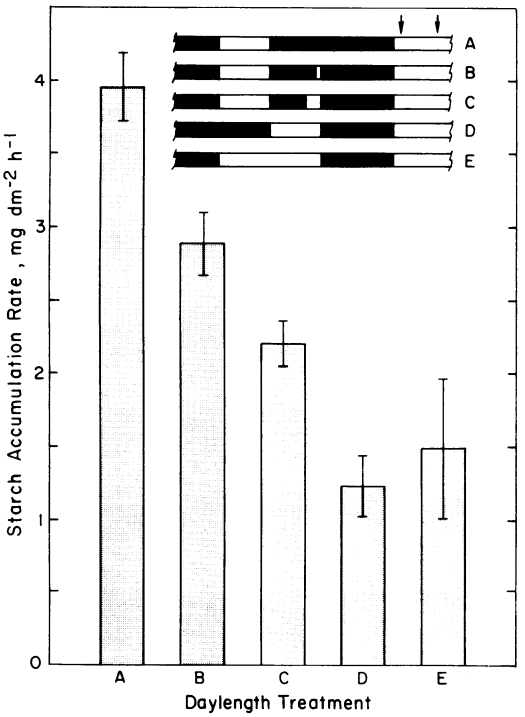


FIG. 2. Effect of different illumination schedules on rates of starch accumulation expressed the following day. SD-grown plants were given the following experimental treatments (see inset bar diagrams): A, standard 7-h SD; B, 0.5-h night interruption starting 6.5 h into the dark period; C, 2-h night interruption starting 5 h into the dark period; D, 'shifted' 7-h SD starting 7 h later than usual; E, 14-h LD. Starch content was determined 1 and 6 h into the succeeding light period (vertical arrows). All illuminations were at 600 $\mu$mol $m^{-2}$ $s^{-1}$ with standard spectral quality. Bars indicate one SE.

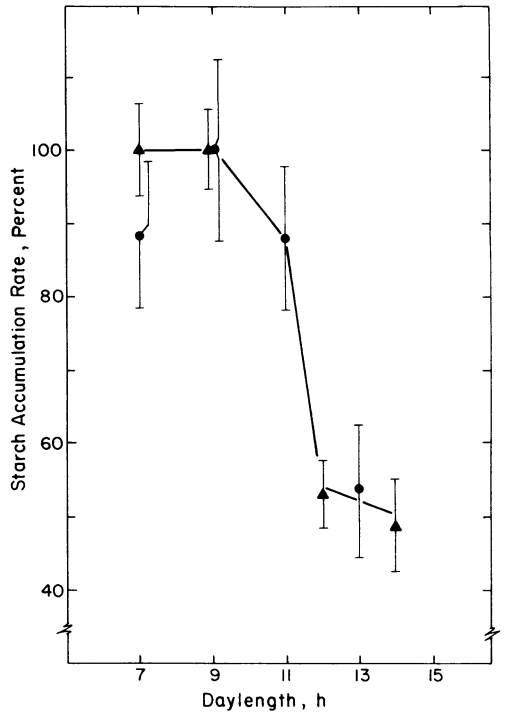


FIG. 3. Effect of daylength on rates of starch accumulation. SD-grown plants were given daylength extensions of from 0 to 7 h at full irradiance (600 $\mu$mol $m^{-2}$ $s^{-1}$) and standard spectral quality and then harvested the next day. Data from two experiments are normalized to 100% at a daylength of 9 h. Bars indicate one SE.

of net photosynthesis and soluble sugar accumulation were not affected by any of the experimental treatments reported below.

To investigate the irradiance dependence of the daylength response, 7 h white-light photoperiod extensions were given to 7 h SD-grown plants. Neutral density filters were used to maintain identical spectral quality. Starch accumulation was determined during the subsequent light period at full irradiance (Fig. 1). Though the differences between the SD controls and the lowest irradiance are not statistically significant, two separate experiments are figured to demonstrate the reproducibility of the results. The results suggest that two reactions with differing sensitivity to light are involved in the response to daylength. A relatively light-sensitive intermediate reaction accounts for about one-half of the total LD-induced reduction in the starch accumulation rate. The threshold for this reaction is unknown, but it appears to be saturated by 6 $\mu$mol $m^{-2}$ $s^{-1}$ (1% of the growth chamber irradiance and less than one-half of the light compensation point for net photosynthesis [15 $\mu$mol $m^{-2}$ $s^{-1}$] as determined in separate experiments). Net carbon fixation is therefore not required for a daylength effect on partitioning. A second, less light-sensitive reaction completed the LD effect and was saturated by 200 $\mu$mol $m^{-2}$ $s^{-1}$. The effect of still higher irradiances has not been tested, although photosynthesis in these plants is not saturated at 600 $\mu$mol $m^{-2}$ $s^{-1}$. A similar, biphasic response to irradiance during the latter half of a day was observed for the starch accumulation rate of plants adapted to LD conditions (data not shown). In consideration of possible spectral quality effects, a daylength extension experiment was also performed with dim incandescent light (25 $\mu$mol $m^{-2}$ $s^{-1}$ PPFD). A 37% decrease in the rate of starch accumulation was observed in response to this treatment, unlike the results for soybean (5) but like the results for comparable PPFD of mainly CWF irradiation (Fig. 1).

Further experiments were undertaken to determine the effect of different durations of light. Interruption of the dark period with 0.5- or 2-h light treatments (full irradiance, standard spectral quality) starting 6.5 and 5 h, respectively, into the dark period caused reductions in the starch accumulation rate of SD-grown plants observed the following day (Fig. 2). The 2-h treatment was more effective than the 0.5-h treatment, but neither irradiation was as effective as a full 7-h daylength extension (*i.e.* a 14-h LD). However, it is not known if the optimum night break times were used. In any case, a full 14 h of light was not required for the complete LD response, since a 7 h 'shifted' SD treatment (Fig. 2D) in which the light was given during the latter half of the day worked as well as the full 14 h.

The dependence of starch accumulation rate on the duration of illumination was also explored by the use of one-time-only full irradiance daylength extensions of 0, 2, 4, 5, 6, or 7 h given to SD-grown plants (Fig. 3). The rate of starch accumulation dropped sharply between the 4- and 5-h treatments, corresponding to daylengths of 11 and 12 h, respectively.

The spectral quality requirement of single 7-h daylength extensions was investigated with four different broad wavelength bands isolated from cool-white fluorescent lamps with acrylic filters. All treatments (except for one of the blue light replicates) caused significant reductions in the starch accumulation rate measured on the day subsequent to treatment (Table II). Although the results were comparable to the effects of intermediate CWF light irradiances (6 to 60 $\mu$mol $m^{-2}$ $s^{-1}$), none of the spectral treatments was as effective as high-irradiance CWF light. The red light source was also tested at 15 $\mu$mol $m^{-2}$ $s^{-1}$ and was found to have a similar partial effect on partitioning (data not shown), indicative that the action of red light was saturated at these irradiances.

Table II. *Effect of Spectral Quality during Daylength Extensions*

Single 7-h daylength extensions with high irradiance CWF light or with dim light of different spectral qualities were given to SD-grown plants beginning at the end of the normal light period. Starch accumulation rate was determined the next day under standard high irradiance white light conditions and expressed as a percentage of the 7-h SD controls.

| | Light Treatment | | | | |
|---|---|---|---|---|---|
| | Blue[a,b] | Green[a,c] | Red[a,d] | Far Red[a,e] | CWF |
| Wavelength of maximum irradiance (nm)[f] | 475 | 545 | 637 | 745 | 579 |
| Bandwidth (nm)[f,g] | 395–545 | 490–595 | 585–>800 | 690–>800 | |
| Photon fluence rate ($\mu$mol $m^{-2}$ $s^{-1}$)[h] | | | | | |
| 350–700 nm | 39.8 | 36.3 | 42.2 | 0.06 | 460 |
| 700–800 nm | 0 | 0 | 9.6 | 4.7 | 11.7 |
| Starch accumulation rate (% of SD control) | | | | | |
| Experiment 1 | 74.7[i] | 60.9[i] | 67.5[i] | | 61.2[i] |
| Experiment 2 | 91.8 | 72.3[i] | 71.8[i] | | 40.1[i] |
| Experiment 3 | | | 80.4[i] | 73.1[i] | 47.2[i] |
| Average | 83.3 | 66.6 | 73.2 | 73.1 | 49.5 |

[a] F96T12/CW/VHO lamps. [b] One 3-mm Rohm & Haas No. 2424 acrylic filter plus 13-mm 7.8% $CuSO_4$ (w/v, technical grade). [c] One each 3-mm Rohm & Haas No. 2092 and 2208 acrylic filters plus $CuSO_4$ as above. [d] One each 3-mm Rohm & Haas No. 2423 and 2422 acrylic filters. [e] One 5-mm Westlake Plastics FRT acrylic filter. [f] Determined from spectroradiometric data expressed in $w \cdot m^{-2}$; values from Hg line regions excluded from calculations. [g] Defined as wavelength range where irradiance is greater than 1% of maximum as determined above. [h] Integrated over the wavelength range indicated after conversion to mol. [i] Treatments significantly different from SD control at 95% confidence (2-sided Student's *t* test).

Table III. *Effect of LPS Illumination on Photosynthate Partitioning into Pangolagrass Leaf Starch*

Plants were raised on 14-h LD under either broad spectrum (CWF+I) or narrow band (LPS) illumination at the indicated photon fluence rates (250–840 nm). The PPFD for each treatment was 92.4% of these values; 91.8% of the 250- to 840-nm photon fluence rate was within 541 to 613 nm for the LPS lamps, while 47.% was within this range for the CWF+I lamps.

| | Light Treatment | |
|---|---|---|
| | CWF + I | LPS |
| Photon fluence rate 250–840 nm ($\mu$mol $m^{-2}$ $s^{-1}$) | 410 | 440 |
| Net photosynthesis (mg $CH_2O$ $dm^{-2}h^{-1}$) | 20.9 ± 0.4 | 22.2 ± 0.3 |
| Soluble sugar accumulation (mg $dm^{-2}h^{-1}$) | 0.11 ± 0.11 | 0.09 ± 0.14 |
| Starch accumulation (mg $dm^{-2}h^{-1}$) | 2.27 ± 0.37 | 4.94 ± 0.73 |
| Starch accumulation (% of Pn) | 10.9 | 22.3 |

Direct attempts to demonstrate phytochrome involvement in the daylength response were inconclusive because 30-min 'pulses' of dim (10 $\mu$mol $m^{-2}$ $s^{-1}$) red or far red light were ineffective when given as dark period interruptions.

A complete daylength shift requires fairly high irradiances which raises the possibility that the duration of photosynthesis may be involved with the mechanism of daylength perception. This was examined with LPS light-grown plants. Amber, almost monochromatic LPS irradiation (589 nm) is theoretically well-matched to photosynthetic action spectra (22), but generally results in aberrant-looking plants because of the lack of photomorphogenetically-active wavelengths (24). When grown under LPS lamps for 14 h LD, pangolagrass plants had rates of photosynthesis comparable to broad spectrum control plants but their rates of starch accumulation were much higher (Table III). As a result, photosynthate partitioning into starch was similar to that for SD plants. LPS plants actually accumulated dry weight faster, so the increase in starch is unlikely to be caused by sink limitation.

## DISCUSSION

The daylength effect on partitioning in pangolagrass is photoperiodic, since it depends more on the timing of illumination than on the total amount. This conclusion is supported by the effect of a 'shifted' short day (Fig. 2D), the existence of an apparent critical daylength (Fig. 3), and a rhythmic dependence of partitioning on prior dark periods (1). Although the full LD effect in pangolagrass required relatively bright light, other photoperiodic responses are also known to require high fluence rates, some over extended durations (25).

The influence on partitioning of low irradiances (Fig. 1) and of far red light (Table II) suggest the involvement of a nonphotosynthetic photoreceptor in the perception of photoperiod. It is certainly clear that a long duration with a 'high' photosynthetic rate is insufficient by itself to trigger a LD response (Table III). The LPS lamp data also indicate that the photoreceptor is not sensitive to 589-nm light alone. However, a more specific description of the spectral sensitivity is difficult because the broad band wavelength treatments used in this study (Table II) are probably all above saturation for the intermediate irradiance effect. It is therefore not clear which part of the spectrum is most

effective. Moreover, it is not known whether the effect of red light is the result of the far red component (700–800 nm) also produced by this source, or whether the effect of far red light is the result of the low level of red light passing the far red cut-on filter. Similar concerns for spectral overlap pertain to the blue and green treatments, although neither of these latter sources has detectable levels of far red radiation. The action of both short (blue or green) and long wavelengths (red or far red) is similar to some of the so-called 'high irradiance responses' of plant photomorphogenesis which have action maxima around 710 nm as well as in the visible spectrum (16).

No direct information is available concerning the spectral sensitivity of the complete LD effect (observed at white light irradiances >60 $\mu$mol $m^{-2}$ $s^{-1}$), but it is notable that the CWF source has double the action of the red source (Table II) even though it has only 20% more power at wavelengths greater than 635 nm. Since the intermediate effect of the red source is already saturated, it is likely that either an additional photoreceptor is operating at shorter wavelengths or the fluence rate response curve for the onset of the full daylength effect is very sharp. The LPS lamp data do not rule out an interaction between photosynthesis and an additional photoreceptor at high irradiances. Further spectral studies including narrow band illumination over a range of fluence rates and durations are obviously required. But, an interpretation of such studies will first require an understanding of the interaction of light with underlying rhythms (1).

Additional experiments will be undertaken to localize the photoreceptor for the daylength response and to determine the relative contribution of source and sink to its regulation. With regard to the latter question, it will probably be necessary to measure the effect of daylength on rates of translocation, mobile pool sizes, and phloem concentration. However, it has also been reported that daylength-induced differences in carbohydrate partitioning into starch persist in isolated chloroplasts (20), suggestive that the response (though not necessarily the daylength sensing mechanism) can be localized to the chloroplast.

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