Plant Physiol. (1990) 94, 448–454
0032-0889/90/94/0448/07/$01.00/0

Received for publication February 23, 1990
Accepted May 2, 1990

Photomorphogenesis and Photoassimilation in Soybean and Sorghum Grown under Broad Spectrum or Blue-Deficient Light Sources[1]

Steven J. Britz and John C. Sager[2]

U.S. Department of Agriculture, Agricultural Research Service, Plant Science Institute, Plant Photobiology Laboratory, Beltsville Agricultural Research Center, Beltsville, Maryland 20705 (S.J.B.), and Smithsonian Institution, Environmental Research Center, Rockville, Maryland 20852 (J.C.S.)

ABSTRACT

The role of blue light in plant growth and development was investigated in soybean (*Glycine max* [L.] Merr. cv Williams) and sorghum (*Sorghum bicolor* [L.] Moench. cv Rio) grown under equal photosynthetic photon fluxes (≈500 micromoles per square meter per second) from broad spectrum daylight fluorescent or blue-deficient, narrow-band (589 nanometers) low pressure sodium (LPS) lamps. Between 14 and 18 days after sowing, it was possible to relate adaptations in photosynthesis and leaf growth to dry matter accumulation. Soybean development under LPS light was similar in several respects to that of shaded plants, consistent with an important role for blue light photoreceptors in regulation of growth response to irradiance. Thus, soybeans from LPS conditions partitioned relatively more growth to leaves and maintained higher average leaf area ratios ($\overline{LAR}$) that compensated lower net assimilation rates ($\overline{NAR}$). Relative growth rates were therefore comparable to plants from daylight fluorescent lamps. Reductions in $\overline{NAR}$ were matched by lower rates of net photosynthesis (A) on an area basis in the major photosynthetic source (first trifoliolate) leaf. Lower A in soybean resulted from reduced leaf dry matter per unit leaf area, but lower A under LPS conditions in sorghum correlated with leaf chlorosis and reduced total nitrogen (not observed in soybean). In spite of a lower A, $\overline{NAR}$ was larger in sorghum from LPS conditions, resulting in significantly greater relative growth rates ($\overline{LAR}$ was approximately equal for both light conditions). Leaf starch accumulation rate was higher for both species and starch content at the end of the dark period was elevated two- and three-fold for sorghum and soybean, respectively, under LPS conditions. Possible relations between starch accumulation, leaf export, and plant growth in response to spectral quality were considered.

Much recent work on effects of spectral quality during photoautotrophic growth has focused on the role of red/far-red ratios and phytochrome (20), but UV and blue light photoreceptors are also important for plant growth and development either independently or in conjunction with phytochrome (6). Although interactions between photosynthesis and photomorphogenetic photoreceptors make it difficult to evaluate the role of shorter wavelengths during broad spectrum illumination, it is possible to determine the photomorphogenetic action of blue and UV radiation against a background of high PPF[3] provided by LPS lamps (23). LPS lamps, direct arc sources emitting mainly at 589 nm, are efficient sources of photosynthetically active radiation that emit relatively low levels of IR radiation and heat (17, 22). Possibly because they lack a blue light component, LPS lamps used alone tend to produce elongated, chlorotic plants with low DM (23, 28, 29).

Red-biased light sources (including LPS lamps) enhance leaf carbohydrate levels (4, 9, 12, 26, 28). Spectral quality effects on photosynthate partitioning may be important to photomorphogenesis, since elevated end-of-day starch levels in leaves are associated with morphological changes such as increased shoot-to-root ratios in soybeans (5, 10). Consequently, the following study was undertaken to investigate the relationship between long-term blue light exposure and plant growth in relation to carbon assimilation, leaf carbohydrate storage, and rates of assimilate export in soybean, a C_3 dicot, and sorghum, a C_4 grass. Both species respond to the balance between red and blue light (28). Moreover, it was possible to select a specific leaf at a well-defined developmental stage for detailed study as a major source of photoassimilates during this time period. DLF and LPS lamps were chosen as broad spectrum and low blue light sources, respectively, and were adjusted to provide approximately equal and relatively high PPF. These studies are relevant to ecological problems such as adaptation to shade and perception of photoperiod (20) as well as to the selection of lamps for controlled environments (24).

MATERIALS AND METHODS

Soybean (*Glycine max* [L.] Merr. cv Williams) and sorghum (*Sorghum bicolor* [L.] Moench. cv Rio) were grown from seed

[1] Dedicated to the memory of Ruth Satter whose enthusiasm for science and life remains a model for all.

[2] Current address: National Aeronautics and Space Administration, Mail Code MD-RES, J. F. Kennedy Space Center, FL 32899.

[3] Abbreviations: PPF, photosynthetic photon flux (μmol m^{-2} s^{-1}); A, net carbon assimilation rate; DLF, daylight fluorescent (lamps); DM, dry matter; LA, leaf area; LAR or $\overline{LAR}$, leaf area ratio, total LA per total DM (dm^2 g^{-1}); L_n, sorghum leaf No., n; LPS, low pressure sodium (lamps); $\overline{NAR}$, net assimilation rate (g dm^{-2} d^{-1}); RDM, residual dry matter (DM minus content of starch and sugar); RGR or $\overline{RGR}$, relative growth rate (g g^{-1} d^{-1}); SLM, specific leaf mass; leaf DM per LA (g dm^{-2}); TF_n, soybean trifoliolate leaf No., n.

in controlled-environment chambers (PGW-36, Conviron[4], Pembina, ND) partitioned into two growing areas with separate canopies for LPS and DLF lamps, but with equivalent environmental conditions (27 ± 1°C, 70 ± 5% RH, 0.5 ± 0.2 m s^{-1} air velocity, and 1000 ± 50 μmol mol^{-1} CO_2 [1]). PPF was 500 ± 50 μmol m^{-2} s^{-1} from both LPS (SOX 180 W, Philips North America, Bloomfield, NJ) and DLF (F48T12/D/VHO, GTE Sylvania, Danvers, MA) lamps set to 14 h light and 10 h dark cycles. Lamp and plant growing spaces were not separated by a barrier.

PPF at the top of the plant canopy was checked every 2 to 3 d with a calibrated quantum sensor (LI-200SB, LI-COR, Lincoln, NE). Lamp banks were moved to accommodate plant growth and lamp degradation. Spectral photon flux for both light treatments was determined from 300 to 800 nm in 2 nm steps with a spectroradiometer, calibrated against a NBS-traceable lamp, and consisting of a miniature receiver coupled by fiber optics to a double monochromator (C-9 System, EG&G, Gamma Scientific, San Diego, CA). Near-IR radiation (800–2800 nm) was measured with an Eppley PSP radiometer and Schott 805 filter (Eppley Laboratories, Newport, RI). Radiation longer than 3000 nm was determined with an Eppley PIR radiometer with coated silicon filter.

Plants were raised in individual cups filled with silica gravel in holding tubs attached to a nutriculture system. The tubs were flooded for 45 min every 4 h. Deionized water was used initially for 3 d followed by a complete nutrient solution (17) for the remainder of the experiment. Planting density was one seed per cup for sorghum and one seed per every other cup for soybean (about 200 and 100 plants per m^2, respectively). Plants were selected for uniformity at 7 to 10 d and reduced to approximately 50 plants per treatment for each experiment.

DM, LA, and plant height were measured from eight plants at each destructive harvest 14 and 18 d after planting. Cotyledons or seeds were not included in DM and petioles or leaf sheaths were not included in LA. Plant height was determined for soybean as the distance between the top of the apical bud and the uppermost portion of the hypocotyl where lateral root initiation had occurred, and for sorghum as the distance between the coleoptile node and the base of the ligule of the most recently collared leaf. Leaves were numbered acropetally in order of appearance. The experiment was performed twice for each species. As determined from two-sided *t*-tests, the replicates were not significantly different so all data were pooled. Standard equations (16) were used to calculate $\overline{NAR}$ and $\overline{LAR}$ for the 4 d interval based on average values. $\overline{RGR}$ was calculated both as the product of $\overline{LAR} \times \overline{NAR}$ (*i.e.* $\overline{RGR}$) and as the slope of the best linear least squares fit to individual values of ln total DM *versus* time (*i.e.* RGR).

Assimilation rate, LA, leaf DM and contents of starch, ethanol-soluble sugars (including sucrose), total N, and Chl were determined 16 d after planting for the most recent, fully expanded leaf. Assimilation rate was measured for an entire soybean leaf blade plus 0.5 to 1 cm of petiole and all but the basal 1 to 2 cm of a sorghum leaf with a differential IRGA and air seal cuvette (4, 5) flushed with breathing gas (0.035% CO_2). Nine leaves were analyzed for each treatment at intervals of 0.5 to 1 h starting 1 to 2 h after lights-on. Rates were constant throughout the light period.

Starch and ethanol-soluble sugars were assayed in leaf samples harvested about 0, 1, 7, and 14 h after the start of the light period (six leaves each time). After LA determination (model LI-3000; LI-COR, Inc.), leaves were grouped in two replicate samples, frozen (−70°C), freeze-dried, weighed, ground (60 mesh; Cyclone Sample Mill; UD Corp., Boulder, CO), aliquoted, extracted twice in hot ethanol (extracts pooled for analysis), and then digested in Clarase 40,000 (Miles Laboratories, Elkhart, IN) to yield soluble-sugar and starch fractions. Reducing sugar content, after hydrolysis of sucrose in 6 N HCl for the soluble fraction, was measured as ferricyanide reduction (AutoAnalyzer II; Technicon Instrument Corp., Tarrytown, NY) using glucose and sucrose as standards for the starch and sugar fractions, respectively.

Chl content was assayed as pheophytin in lyophilized leaf samples collected 1 h into the light period. Aliquots (≈20 mg) were homogenized in 1 N HCl (0.25 mL) and extracted into 80% acetone. Pheophytin *a* and *b*, corrected for Mg, were calculated from absorbance readings at 536 and 666 nm (Aminco DW-2a, Aminco Corp., Silver Spring, MD) using the equations of Vernon (25).

Total N was determined for lyophilized leaf samples collected 7 h into the light period. Aliquots (≈20 mg) were subjected to flash combustion and oxidation in an automated system (model ANA 1500, Erba, Milan, Italy). Soybean leaf samples of known total N content were used as standards.

All results were expressed on the basis of RDM (DM minus starch and soluble sugar content) to remove the bias introduced by inclusion of large amounts of nonstructural carbohydrates in DM estimates. Indicated values are averages of triplicate assays for each of the two replicate samples and two replicate experiments for a given harvest or series of harvests. Significance of differences between means was determined from two-sided *t*-tests.

RESULTS

Comparison of Light Sources

Both lamps had similar, low, near-IR and longwave IR integrals (Table I). Shorter wavelength emission from LPS lamps was concentrated at 589 nm with less than 0.17% of the output between 300 and 500 nm, whereas 29% of the output of DLF lamps occurred between 300 to 500 nm (Fig. 1, Table I). In spite of large differences, functional comparability between the two sources was estimated by normalizing lamp spectra against photosynthetic action spectra and by calculating phytochrome photostationary state and cycling rate (18). LPS lamps were estimated to be 15% more efficient for photosynthesis than DLF lamps at equal, limiting PPF (Table I) because emission was concentrated close to the action maximum for photosynthesis. LPS lamps were also estimated to transform phytochrome more completely into Pfr than DLF because extinction coefficients for Pr increase slightly relative to those for Pfr in the vicinity of 600 nm. In fact, calculated photostationary states for LPS and DLF

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

Table I. *Lamp Characteristics*

Spectral data for daylight fluorescent (DLF) and low pressure sodium (LPS) lamps determined at the top of the plant canopy.

Characteristic	DLF	LPS
	$W\ m^{-2}$	
Wavelength range, nm		
400–700	109	100
300–800	114	102
800–2800	13	13
>3000	53	44
	$\mu mol\ m^{-2}\ s^{-1}$	
300–400	11	<1
400–500	140	1
500–600	250	500
600–700	109	3
700–800	16	13
400–700	499	504
300–800	526	517
	relative $\mu mol\ m^{-2}\ s^{-1}$	
Photosynthetic quantum efficiency[a]	432	495
	Pfr/P_{tot}	
Phytochrome photostationary state[a]	0.81	0.91
	Hz	
Phytochrome cycling rate[a]	0.032	0.020

[a] Calculated according to Sager *et al.* (18).

sources (Table I) agreed well with ones measured *in vitro* (18) and *in vivo* (WO Smith, B Lercari, personal communication). Cycling rate under LPS illumination, however, was estimated to be 38% less than under equal PPF of DLF light (Table I).

Plant Growth

Measurements were made on young plants between 14 and 18 d after planting in order to minimize mutual shading and limitations to root growth. Soybean cotyledons had senesced by this time, so their contribution to growth was negligible. In addition, axillary growth was limited.

Both soybean and sorghum grown under LPS lamps were much taller at both 14 and 18 d after planting and weighed less at the first harvest than their counterparts from DLF light (Table II). Although LPS-grown sorghum overcame the initial DM deficit over the 4 d period, soybeans from LPS light continued to weigh significantly less at the second harvest (Table II). About 95% of the total dry matter difference between soybeans from DLF and LPS treatments at the second harvest was attributable to root DM (data not shown). The effect of light treatment on LA in relation to total DM differed between species. Thus, DLF soybeans displayed a large decline in LAR between 14 and 18 d in comparison to plants under LPS. In sorghum, however, the decline in LAR was much larger under LPS illumination.

Growth Kinetics

Changes in total DM and LA relationships suggest dynamic alterations in growth rate and partitioning during the 4 d observation period. RGR for total DM in soybean were

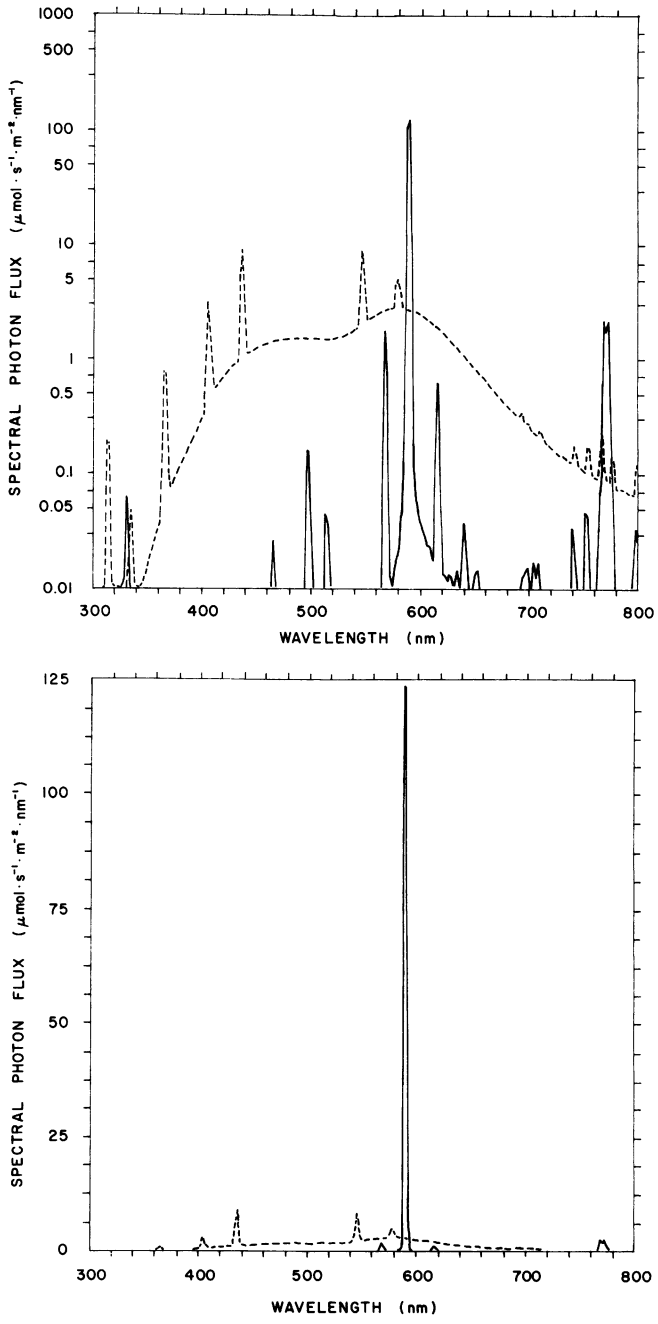

Figure 1. Upper panel: Log spectral photon flux determined at 2 nm intervals between 300 and 800 nm for low pressure sodium (*solid line*) and daylight fluorescent (*dashed line*) lamps. The integrals between 400 and 700 nm were approximately equal (500 $\mu mol\ s^{-1}\ m^{-2}$) for each lamp type. Lower panel: Linear presentation of the same data.

Table II. *Plant Growth*

Total plant height, total dry matter, and leaf area ratio 14 and 18 d after planting for soybean and sorghum grown under daylight fluorescent (DLF) or low pressure sodium (LPS) illumination. Values are averages calculated from two pooled replicate experiments. Within a horizontal row, values with different letters are significantly different at the 95% confidence level.

Growth Parameter	Time Elapsed after Planting (d)			
	14		18	
	DLF	LPS	DLF	LPS
Soybean				
Plant height (cm)	10.7d	26.7b	14.6c	35.9a
Dry matter (g)	0.637c	0.559d	1.572a	1.337b
Leaf area ratio ($dm^2\ g^{-1}$)	2.087a	2.192a	1.592b	2.074a
Sorghum				
Plant height (cm)	7.3c	10.1b	10.2b	14.8a
Dry matter (g)	0.237b	0.166c	0.735a	0.652a
Leaf area ratio ($dm^2\ g^{-1}$)	2.499b	2.761a	2.297c	2.316c

approximately equal for both light treatments whether calculated as the product of $\overline{LAR}$ and $\overline{NAR}$ or directly from slope of ln DM (Table III, Fig. 2). However, equivalent growth under different lamp types was achieved in different ways for soybean and sorghum. RGR for leaf DM and LA in soybean from DLF conditions were significantly lower between 14 and 18 d after sowing than those for stem and root DM (Fig. 2). These differences were reflected as significant decreases between days 14 and 18 in the percentage of DM in the leaves (data not shown) as well as in LAR (Table II) and indicate decreased partitioning of resources to leaves. In contrast, soybean plants from LPS conditions maintained approximately equal RGR for leaf, shoot and root DM accretion and for LA expansion (Fig. 2). As a result, relative leaf DM (data not shown) and LAR (Table II) remained constant for the duration of the experiment. Differences in partitioning to the leaves were important, since comparatively large $\overline{LAR}$ compensated for reductions in $\overline{NAR}$ with the result that RGR for total dry matter, calculated by either method, were about the same under both light conditions (Table III).

RGR for DM accretion in sorghum (whole plant, leaves, stem and roots) were significantly greater under LPS illumination (Fig. 2; Table III) and appeared to result from increased $\overline{NAR}$, since $\overline{LAR}$ were comparable (Table III). As with soybean, there was good correspondence between RGR calculated either directly or as the product of $\overline{LAR}$ and $\overline{NAR}$.

Assimilation Rate, Chl, Total N, and Carbohydrate Content

Alterations in $\overline{NAR}$ indicate that changes in A may accompany adaptation of soybean and sorghum to blue light-deficient LPS conditions. Consequently, whole-leaf CO_2 exchange rates were determined at the midpoint of the experiment, 16 d after sowing, for the most recent, fully expanded leaves, TF_1 in soybean, and L_5 or L_6 in sorghum. TF_1 at this time had reached 95% of full expansion under both light sources, accounting for about one-third of total LA in both cases. The rate of leaf initiation in sorghum, unlike in soybeans, was affected by light quality. Thus, L_5 of LPS plants and L_6 in DLF plants reached full expansion (appearance of the ligule above the subtending leaf sheath) by 16 d after planting. L_5 and L_6 comprised almost one-half and one-third of total LA for plants from LPS and DLF conditions, respectively. The selected leaves represented the major source of assimilates for the period 14 to 16 d after sowing. In fact, the contribution of the selected leaves to whole plant assimilation was probably greater than suggested by LA, since total LA included both developing and older leaves with lower rates of A. L_5 and L_6 were assumed to be compaable based on date of initiation (chronological age), LA and SLM (see below).

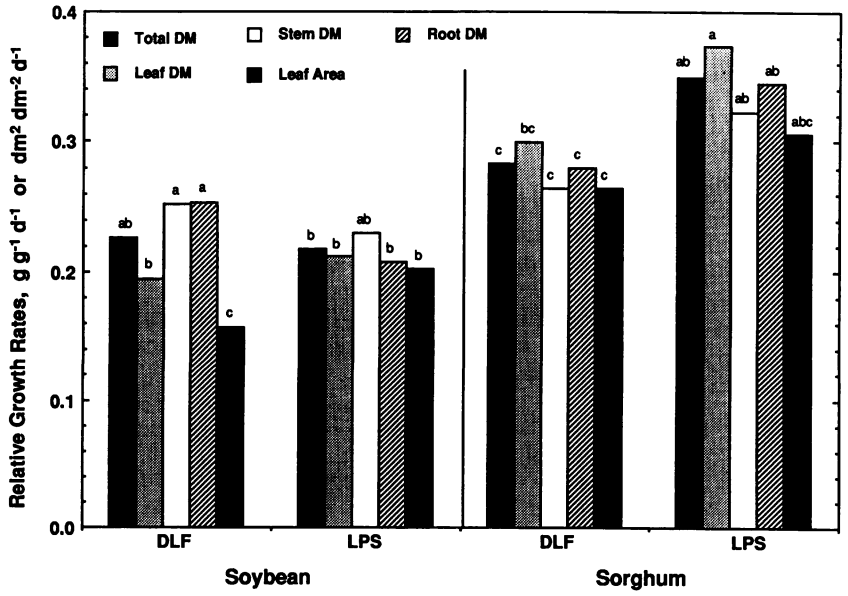

Figure 2. Relative growth rates for total dry matter, leaf dry matter, stem dry matter, root dry matter, and total leaf area of soybean and sorghum plants between 14 and 18 d after planting. Plants were grown from seed under either DLF or LPS lamps. For a given species, values represented by columns topped with different letters are significantly different at the 95% confidence level.

Table III. *Plant Growth Kinetics*

Average leaf area ratio ($\overline{LAR}$), net assimilation rate ($\overline{NAR}$), and relative growth rate ($\overline{RGR}$), for total dry matter (DM) between 14 and 18 d after planting for soybean and sorghum grown under daylight fluorescent (DLF) or low pressure sodium (LPS) illumination. $\overline{LAR}$, $\overline{NAR}$, and $\overline{RGR}$ were determined from average values and were not subjected to statistical analysis. RGR values with different letters are significantly different at the 95% confidence level.

Growth Parameters	Soybean		Sorghum	
	DLF	LPS	DLF	LPS
$\overline{LAR}$ ($dm^2\ g^{-1}$)	1.73	2.10	2.33	2.40
$\overline{NAR}$ ($g\ dm^{-2}\ d^{-1}$)	0.127	0.103	0.120	0.138
Total DM $\overline{RGR}$[a] ($g\ g^{-1}\ d^{-1}$)	0.219	0.216	0.280	0.332
Total DM RGR[b] ($g\ g^{-1}\ d^{-1}$)	0.226c	0.218c	0.283b	0.349a

[a] Calculated as $\overline{LAR} \times \overline{NAR}$. [b] Regression coefficients for linear least squares fitted to individual values of ln (Total DM) versus time (days).

Assimilation rates were about 15% lower under LPS illumination for both soybean and sorghum when based on LA (Table IV). Most important from the standpoint of whole plant assimilation, increased LA under LPS conditions (Table V) compensated for this reduction such that A on a whole leaf basis was equal for both species and light treatments (Table IV). Several other alterations in source leaves were noted. SLM was significantly less under LPS conditions (Table V), consistent with the formation of broader, thinner leaves (13). The effect was more pronounced for soybean leaves. In addition, leaf Chl contents were lower under LPS conditions, particularly for sorghum (Table V). Consequently, A calculated with respect to RDM or total Chl for TF_1 were on average significantly greater (20 and 33%, respectively) under LPS light (Table IV). Assimilation rate based on total Chl was 27% greater for sorghum under LPS light (Table IV), but A remained lower on an RDM basis (Table IV).

Chlorosis of sorghum leaves was associated with a significant 13% reduction in total N (Table V). The much smaller reduction in Chl in soybean leaves (9%) was not accompanied by a loss in total N. In addition, no differences in the ratio of Chl *a* to Chl *b* were observed with respect to light treatment for either species.

The most dramatic alterations in leaf composition in response to LPS treatment were noted for starch which was 167% and 72% greater on a RDM basis at the start of the light period for soybean and sorghum, respectively (Table V). The content of ethanol-soluble sugars was similar under both light conditions, indicating that high starch content in LPS was not related to a general back-up of carbohydrates in the light. Note that total N and Chl content in leaves of soybean plants grown under LPS conditions would have appeared greatly reduced relative to plants from DLF conditions if expressed on a simple DM basis because of the large differences in starch content.

Photosynthate Partitioning and Leaf Export

Rates of starch accumulation based on RDM were significantly greater for soybean and sorghum leaves grown and measured under LPS illumination (Table VI) and may account in part for differences in starch at the start of the light period. However, accumulation in leaves of soluble sugars including sucrose was not significantly different. Relative net leaf export (Table VI), expressed as a percentage of A, was calculated from the difference between A (determined as carbohydrate and constant during the light) and total SLM accumulation during the photoperiod (8). Approximately 20% less photosynthate was exported from soybean leaves grown under LPS light, about three-quarters of which could be accounted for by increased starch accumulation (Table VI). Note that starch accumulation and export were determined by independent methods. Estimated export was higher for sorghum and did not vary with light treatments (Table VI). Small differences in partitioning into starch with respect to light treatment were thus not correlated with discernible differences in leaf export.

DISCUSSION

Although LPS and DLF light sources were comparable with respect to standardized tests of photosynthesis and phytochrome action (Table I), initial growth of soybean and sorghum under LPS conditions was inhibited relative to broad spectrum DLF illumination as indicated by significantly lower DM 14 d after planting (Table II). However, various morphological or physiological adaptations apparently halted or reversed the early inhibition, since total DM RGR for the subsequent 4 d period (Fig. 2, Table III) were either equal for the two light treatments (soybean) or greater under LPS light (sorghum). In soybean, these adaptations appeared to involve a shift in DM allocation such that leaf growth equaled that of the stem and root. Leaf expansion was also maintained at a greater rate resulting in larger $\overline{LAR}$ under LPS conditions essential to compensate reduced $\overline{NAR}$. The importance of compensatory adjustments of LA was demonstrated by A, lower under LPS illumination on a LA basis but equal for both light treatments on a whole leaf basis. The significance of LA maintenance has been noted previously (14, 15).

In contrast to soybean, alterations in DM partitioning between root and shoot of sorghum were small, LAR was more constant, and leaf DM RGR were equivalent to that for stem and root. Overall increases in RGR for the whole plant and individual parts were associated with increased $\overline{NAR}$.

Table IV. *Leaf Photosynthetic Rates*

Net CO_2 exchange was determined 16 d after sowing in the most recently expanded leaf of soybean and sorghum grown under daylight fluorescent (DLF) or low pressure sodium (LPS) illumination. Values within a row with different letters are significantly different at the 95% confidence level.

Rate	Soybean		Sorghum	
	DLF[a]	LPS[a]	DLF[b]	LPS[c]
mg C $dm^{-2}\ h^{-1}$	6.19c	5.27d	10.23a	8.69b
mg C $leaf^{-1}\ h^{-1}$	3.46a	3.47a	3.48a	3.40a
mg C·g $RDM^{-1}\ h^{-1}$	24.4d	29.3c	58.0a	53.5b
mg C·mg $Chl^{-1}\ h^{-1}$	2.12d	2.82c	3.73b	4.74a

[a] TF_1. [b] L_6. [c] L_5.

Table V. *Leaf Characteristics*

Area, specific leaf mass (SLM), total Chl (Chl *a* + Chl *b*), Chl *a*/Chl *b*, total leaf nitrogen (total N), starch, and soluble sugars (including sucrose) were determined 16 d after planting for the most recently expanded leaf of soybean and sorghum grown under daylight fluorescent (DLF) or low pressure sodium (LPS) illumination. For a given species, values within a horizontal row with different letters are significantly different at the 95% confidence level.

Characteristic	Soybean		Sorghum	
	DLF[a]	LPS[a]	DLF[b]	LPS[c]
Leaf area[d] (dm^2)	0.559b	0.656a	0.340d	0.390c
SLM[d] (g RDM dm^{-2})	0.254a	0.179b	0.177b	0.162c
Chl *a* + Chl *b*[e] (μg [mg RDM]$^{-1}$)	11.5b	10.5c	15.5a	11.3b
Chl *a*/Chl *b*	2.9a	3.0a	3.2a	3.4a
Total N[f] (μg [mg RDM]$^{-1}$)	59.7a	59.9a	61.4a	53.4b
Starch[g] (μg [mg RDM]$^{-1}$)	61b	163a	87b	150a
Soluble sugars[g] (μg [mg RDM]$^{-1}$)	24b	29b	44a	52

[a] TF_1. [b] L_6. [c] L_5. [d] Values averaged for entire light period. [e] Sampled 1 h into the light period. [f] Sampled 7 h into the light period. [g] Sampled at the onset of the light period.

$\overline{NAR}$ is a whole plant parameter integrated over one or more days taking into account A, respiration and factors such as canopy architecture and light penetration. In spite of these potential complications, a 15% reduction in A on a LA basis under LPS illumination was reflected in similar reductions in $\overline{NAR}$ for soybean. The situation in sorghum, however, was quite different. $\overline{NAR}$ was 17% higher for LPS-grown plants whereas A was 15% lower. Resolution of the discrepancy will require more detailed studies considering possible complications in the relation between A and $\overline{NAR}$ (*e.g.* changes in A over the 4 d measurement period, contribution from other leaves, dark respiration). Note, $\overline{NAR}$ for sorghum was a smaller percentage of daily A than in soybean.

Effects of spectral quality on A have been noted in other studies. Barley, swiss chard, cucumber and kidney bean grown under red radiation all had lower A on a leaf area basis than did plants grown under blue light (11, 27). The differences were not explained. Thus, it is interesting that similar reductions in A on an area basis (≈15%) in soybean and sorghum appear related to different factors, a large reduction in RDM per unit LA in soybean and Chl deficiency in sorghum (Table V). Fe-deficiency has been suggested as a cause of chlorosis under LPS treatment (2). However, A remained approximately constant based on Chl in leaves of sugar beet rendered chlorotic by Fe-stress (21), unlike A in soybean and sorghum. In fact, increased A on a Chl basis in leaves of LPS light-grown soybean and sorghum was about double that predicted by the spectral analysis (Table I). It is not clear if changes in A represent actual modifications in photochemical or metabolic efficiency of photosynthesis in response to spectral quality (19) or, alternatively, reductions in nonessential, light-harvesting Chl under LPS conditions. Note that A on a whole leaf basis (the unit of significance for the plant) was not affected by light quality (Table IV).

A major purpose of this study was to relate photomorphogenetic differences under LPS and DLF illumination to photosynthesis and partitioning. An increased content of starch under LPS conditions was observed for both species at least partly as a result of altered photosynthate partitioning. But, in neither soybean nor sorghum was increased starch associated with decreased growth, possibly because net changes in starch accumulation over 24 h were a small percentage of the total assimilate. However, reduced export during the light period in soybean was correlated with increased partitioning into starch.

Blue light has been reported to increase the activity of phosphoenolpyruvate carboxylase and nitrate reductase from cells and leaves of higher plants and may thereby stimulate the synthesis of amino acids and proteins (7, 29). Although relatively small increases in carbohydrate content in leaves of sorghum grown under LPS light were associated with decreased total leaf N, total N was not altered in TF_1 of soybean in response to LPS treatments even though large differences in starch content were observed.

Plants grown under LPS light were similar in many respects (28, 29) to plants grown under red or red-biased light sources (*e.g.* taller stems, decreased root:shoot ratio, increased individual leaf areas, lower SLM [thinner leaves], increased LAR [soybean], fewer total leaves [sorghum], increased leaf carbohydrate, and decreased total Chl), indicating that calculated reductions in phytochrome cycling rate under LPS light relative to DLF (Table I) or red light (18) were not important for growth regulation. However, morphological characteristics of plants from LPS and red light were comparable to etiolated or shaded plants (3), suggesting that blue light photoreceptors may play a role in the adaptation of soybean to vegetation shade. The application of blue-deficient light sources is therefore relevant to the study of agronomic problems such as canopy closure and intercropping and provides, in addition, a means to study regulation of photosynthetic carbon metabolism in relation to plant growth.

Table VI. *Photosynthate Partitioning into Stored Leaf Carbohydrates and Relative Leaf Export During the Light Period*

Rates of accumulation of starch and soluble sugars (including sucrose) were determined 16 d after planting in the most recently expanded leaf of soybean and sorghum grown under daylight fluorescent (DLF) or low pressure sodium (LPS) illumination from harvests approximately 1 h and 7 h into the light period. Values within a horizontal row with different letters are significantly different at the 95% confidence level. The proportion of assimilate exported was estimated as the difference between average values of net photosynthesis (A) expressed as carbohydrate and specific leaf mass accumulation rate in the most recently expanded leaf.

Allocation	Soybean		Sorghum	
	DLF[a]	LPS[a]	DLF[b]	LPS[c]
	mg-C g-RDM^{-1} h^{-1}			
Starch	8.5b	13.6a	2.4d	4.8c
Soluble sugars	0.2b	0.7b	2.8a	3.4a
	% of A			
Relative export	61	48	79	78

[a] TF_1. [b] L_6. [c] L_5.

ACKNOWLEDGMENTS

We thank Dr. C. Sloger and Mr. L. Nash of the Nitrogen Fixation and Soybean Genetics Laboratory, Beltsville Agricultural Research Center for assistance in determination of total N, Mr. J. L. Edwards of the Smithsonian Environmental Research Center for performing spectral measurements, and Mr. D. R. Lee and Mr. W. E. Hungerford of the Plant Photobiology Laboratory for photosynthetic and carbohydrate determinations, respectively. Dr. W. J. Kenworthy of the Agronomy Department, Univ. Maryland, College Park, MD, and Dr. A. G. Gillaspie of the Plant Pathology Laboratory, Beltsville Agricultural Research Center supplied soybean and sorghum seeds respectively. This work was supported by U.S. Department of Agriculture CRIS No. 1275-23000-002.

LITERATURE CITED

1. ASAE Guidelines for Measuring and Reporting Environmental Parameters for Plant Experiments in Growth Chambers (1986) American Society of Agricultural Engineers Year Book, St Joseph MI, pp 407–411
2. **Bennett JH, Lee EH, Krizek DT, Olsen RA, Brown JC** (1982) Photochemical reduction of iron. II. Plant related factors. J Plant Nutr **5:** 335–344
3. **Blackman GE, Wilson GL** (1954) Physiological and ecological studies in the analysis of plant environment. IX. Adaptive changes in vegetative growth and development of *Helianthus annuus* induced by an alteration in light level. Ann Bot **18:** 71–94
4. **Britz SJ, Hungerford WE, Lee DR** (1985) Photoperiodic regulation of photosynthate partitioning in leaves of *Digitaria decumbens*. Plant Physiol **78:** 710–714
5. **Chatterton NJ, Silvius JE** (1979) Photosynthate partitioning into starch in soybean leaves. I. Effects of photoperiod versus photosynthetic period duration. Plant Physiol **64:** 749–753
6. **Gaba V, Black M** (1987) Photoreceptor interaction in plant photomorphogenesis: the limits of experimental techniques and their interpretations. Photochem Photobiol **45:** 151–156
7. **Gnanam A, Habib Mohamed A, Seetha R** (1980) Comparative studies on the effect of ammonia and blue light on the regulation of photosynthetic carbon metabolism in higher plants. *In* H Senger, ed, The Blue Light Syndrome. Springer, Berlin, pp 433–443
8. **Ho LC** (1976) The relationship between the rates of carbon transport and of photosynthesis in tomato leaves. J Exp Bot **27:** 87–97
9. **Holzapfel A, Wild A, Zerbe R** (1983) Effects of kinetin and different light qualities on the content of carbohydrates. Biochem Physiol Pflanzen **178:** 297–306
10. **Huber SC** (1983) Relation between starch formation and dry-weight partitioning between the shoot and root. Can J Bot **6:** 2709–2716
11. **Ko B** (1982) Optical characteristics and spectral dependence of photosynthesis of crop leaves developed under different light qualities (Japanese). Environ Cont Biol **20:** 1–7
12. **Leong T-Y, Goodchild DJ, Anderson JM** (1985) Effect of light quality on the composition, function, and structure of photosynthetic thylakoid membranes of *Asplenium australasicum* (Sm.) Hook. Plant Physiol **78:** 561–567
13. **Mirecki RM, Teramura AH** (1984) Effects of ultraviolet-B irradiance on soybean. V. The dependence of plant sensitivity on the photosynthetic photon flux density during and after leaf expansion. Plant Physiol **74:** 475–480
14. **Mooney HA, Küppers M, Koch G, Gorham J, Chu C, Winner WE** (1988) Compensating effects to growth of carbon partitioning changes in response to SO_2-induced photosynthetic reduction in radish. Oecologia **75:** 502–506
15. **Potter JR, Jones JW** (1977) Leaf area partitioning as an important factor in growth. Plant Physiol **59:** 10–14
16. **Radford PJ** (1967) Growth analysis formulae—their use and abuse. Crop Sci **7:** 171–175
17. **Sager JC, Edwards JL, Klein WH** (1982) Light energy utilization efficiency for photosynthesis. Trans ASAE **25:** 1737–1746
18. **Sager JC, Smith WO, Edwards JL, Cyr KL** (1988) Photosynthetic efficiency and phytochrome photoequilibria determination using spectral data. Trans ASAE **31:** 1882–1887
19. **Senger H, Bauer B** (1987) The influence of light quality on adaptation and function of the photosynthetic apparatus. Photochem Photobiol **45:** 939–946
20. **Smith H** (1982) Light quality, photoperception, and plant strategy. Annu Rev Plant Physiol **33:** 481–518
21. **Terry N** (1983) Limiting factors in photosynthesis. IV. Iron stress-mediated changes in light-harvesting and electron transport capacity and its effects on photosynthesis *in vivo*. Plant Physiol **71:** 855–860
22. **Thimijan RW, Heins RD** (1983) Photometric, radiometric, and quantum light units of measure: a review of procedures for interconversion. HortScience **18:** 818–822
23. **Thomas B, Dickinson HG** (1979) Evidence for two photoreceptors controlling growth in de-etiolated seedlings. Planta **146:** 545–550
24. **Tibbits TW, Morgan DC, Warrington IJ** (1983) Growth of lettuce, spinach, mustard, and wheat plants under four combinations of high-pressure sodium, metal halide, and tungsten halogen lamps at equal PPFD. J Am Soc Hort Sci **108:** 622–630
25. **Vernon LP** (1960) Spectrophotometric determination of chlorophylls and pheophytins in plant extracts. Anal Chem **32:** 1144–1150
26. **Voskresenskaya NP** (1972) Blue light and carbon metabolism. Annu Rev Plant Physiol **23:** 219–234
27. **Voskresenskaya NP, Kumakov AV, Drozdova IS** (1984) Photosynthetic CO_2 exchange of the barley leaf and age changes of it in plants grown under light of different spectral composition. Sov Plant Physiol **31:** 180–186
28. **Warrington IJ, Mitchell KJ** (1976) The influence of blue- and red-biased light spectra on the growth and development of plants. Agric Meteorol **16:** 247–262
29. **Wild A, Holzapfel A** (1980) The effect of blue and red light on the content of chlorophyll, cytochrome *f*, soluble reducing sugars, soluble proteins and the nitrate reductase activity during growth of the primary leaves of *Sinapis alba*. *In* H Senger, ed, The Blue Light Syndrome. Springer, Berlin, pp 444–451