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Differences in the Response of Wheat, Soybean and Lettuce to Reduced Blue Radiation¶

Tracy A. O. Dougher* and Bruce Bugbee
Crop Physiology Laboratory, Department of Plants, Soils and Biometeorology, Utah State University, Logan, UT

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ABSTRACT

Although many fundamental blue light responses have been identified, blue light dose-response curves are not well characterized. We studied the growth and development of soybean, wheat and lettuce plants under high-pressure sodium (HPS) and metal halide (MH) lamps with yellow filters creating five fractions of blue light. The blue light fractions obtained were <0.1, 2 and 6% under HPS lamps, and 6, 12 and 26% under MH lamps. Studies utilizing both lamp types were done at two photosynthetic photon flux levels, 200 and 500 μmol m^{-2} s^{-1} under a 16 h photoperiod. Phytochrome photoequilibria was nearly identical among treatments. The blue light effect on dry mass, stem length, leaf area, specific leaf area and tillering/branching was species dependent. For these parameters, wheat did not respond to blue light, but lettuce was highly sensitive to blue light fraction between 0 and 6% blue. Soybean stem length decreased and leaf area increased up to 6% blue, but total dry mass was unchanged. The blue light fraction determined the stem elongation response in soybean, whereas the absolute amount of blue light determined the stem elongation response in lettuce. The data indicate that lettuce growth and development requires blue light, but soybean and wheat may not.

INTRODUCTION

Electric lamps used for lighting in controlled environments are often chosen on the basis of energy efficiency without regard for spectral quality. Because photons at short wavelengths are more energetically expensive than longer wavelengths, the most cost effective lamps tend to have the least blue light. 'Blue' photons are used less efficiently in photosynthesis than 'red' photons, but some blue light may be necessary for normal plant development (1,2). Red light emitting diodes (LED)† and high-pressure sodium (HPS) lamps are now prevalent in Earth-based research because they are energy efficient lamp types, but they have only 0 and 20%, respectively, of the blue light fraction of sunlight. This raises the question of how much blue light is needed for normal plant growth and development.

Blue light reduces cell expansion (3), therefore, reducing blue light could increase leaf area and stem elongation, which could increase radiation capture and ultimately yield (4,5). Indeed, several studies have shown that reducing blue light can be beneficial. Reduced blue light can increase specific leaf area (SLA) (6,7). Biomass yield under the low blue output of HPS was increased compare to metal halide (MH) in soybean (8), potato (9) and lettuce (10).

Blue light does not appear to alter dry mass accumulation in some species. Tibbitts *et al.* (11) found that lettuce, spinach and mustard had slightly increased leaf area under lamps with less blue light, but there were no consistent changes in dry mass with lamp type. Barnes and Bugbee (12) found that blue light did not affect dry matter accumulation in wheat, but low blue light increased leaf length. Gautier *et al.* (13) found that white clover grown under orange filtered (<0.1% blue) metallic iodure lamps had similar total biomass as plants under unfiltered lamps (23% blue), but nonphotosynthetic thermal radiation was not filtered in this study.

Insufficient blue light, however, can also be detrimental. Wheat tended to have decreased leaf area under lamps with less blue light (11). Soybean stems (14) and lettuce hypocotyls (1) were greatly elongated under lamps with reduced blue light. Pepper biomass decreased when plants were grown under red LED (no blue) compared to plants supplemented with blue light (2). Goins *et al.* (15) found that wheat dry matter accumulation decreased by 53% as blue light fraction decreased from 10 to 0%.

Some of the above-mentioned studies compared lamp types and the authors suggested that differences were due to blue radiation. Three studies added blue fluorescent lamps but the treatments did not have identical nonblue wavelengths (1,2,16). Although several fundamental blue light responses have been identified, blue light dose-response curves

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*To whom correspondence should be addressed at: Crop Physiology Laboratory, Department of Plants, Soils and Biometeorology, Utah State University, 4820 Old Main Hill, Logan, UT 84322-4820, USA. Fax: 435-797-2605; e-mail: tracyaod@cc.usu.edu

†*Abbreviations:* HPS, high-pressure sodium; LED, light emitting diode; LSD, least significant difference; MH, metal halide; PAR, photosynthetically active radiation; PPE, phytochrome photoequilibrium; PPF, photosynthetic photon flux; SLA, specific leaf area; UVA, ultraviolet type A; YPF, yield photon flux.

Table 1. Ratios and amounts of radiation for the six blue light treatments created under HPS (Sylvania Lumalux) and MH (Sylvania Metalarc) lamps*

PPF (μmol m^{-2} s^{-1})	Lamp type	Blue light Fraction (% of total)	Blue light Absolute (μmol m^{-2} s^{-1})	YPF (μmol m^{-2} s^{-1})	PPE (P_{fr}/P_{total})
200	HPS	0.1	0.2	194	0.86
	HPS	1.5	3	192	0.85
	HPS	6	12	190	0.86
	MH	6	12	184	0.84
	MH	12	24	182	0.83
	MH	26	52	177	0.82
500	HPS	0.1	0.5	484	0.86
	HPS	1.5	7.5	480	0.85
	HPS	6	30	474	0.85
	MH	6	30	458	0.85
	MH	12	60	454	0.84
	MH	26	130	441	0.82

*PPF is the photosynthetic photon flux, YPF is the yield photon flux (23) and PPE is the phytochrome photoequilibrium (20).

are not accurately characterized for several reasons: (1) due to lamp limitations, most studies have been conducted at low photosynthetic photon flux (PPF) levels; (2) blue light treatments often do not have either equal nonblue photon levels or equal PPF levels; and (3) the quantity of thermal radiation, and hence leaf and soil warming, has rarely been equalized among treatments. Our objective was to establish blue light dose-response curves at high and low light.

MATERIALS AND METHODS

Lettuce (*Lactuca sativa*, cv. Grand Rapids), soybean (*Glycine max*, cv. Hoyt) and wheat (*Triticum aestivum*, cv. USU-Apogee) were grown in six blue light treatments comprising five blue light fractions (<0.1, 2 and 6% under HPS lamps, 6, 12 and 26% under MH lamps) (Table 1) at PPF levels of 200 and 500 μmol m^{-2} s^{-1} and a 16 h photoperiod. The treatments were applied in a growth room that was divided into six light-tight compartments (80 cm × 90 cm × 145 cm, l × w × h). Each of the six light banks contained two, 1000 W lamps and was filtered with tempered glass and a chilled, circulating water barrier to minimize differences in nonphotosynthetic thermal radiation. Chilled water for the barrier was from a single, shared source, so the temperature difference between water barriers was also minimized. Canary-yellow acetate film (Roscolux #312, Oasis Stage Werks, Salt Lake City, UT) was used to reduce the amount of blue light from HPS or MH lamps (transmission curve, Fig. 1). A comparison of HPS, nonfiltered 6% blue and MH filtered to 6% blue was used to determine if any responses were caused by nonblue wavelengths. Spectral output of the lamps was measured with a spectroradiometer (LI-1800, LICOR, Lincoln, NE). Neutral density fiberglass screening was used when necessary to obtain the desired PPF.

Definition of blue light. Blue light is usually generically defined as radiation from 400 to 500 nm, but this general definition is inadequate for precise photobiological research. We defined blue light as ranging from 320 to 496 nm. Ultraviolet type-A (UVA) wavelengths (320–400 nm) are especially prevalent in MH lamps and are known to be involved in photomorphogenic responses (17–19). Including the UVA wavelengths increases the blue light fraction in HPS lamps only by 5%, but they increase it by 18% in MH lamps. Wavelengths from 496 to 500 nm were not included in the blue fraction because photomorphogenic responses rapidly decrease above about 490 nm (17) and because HPS lamps have a spectral peak from 494 to 502 nm. Including the 496–500 nm wavelengths from HPS lamps would increase the effective blue 25%.

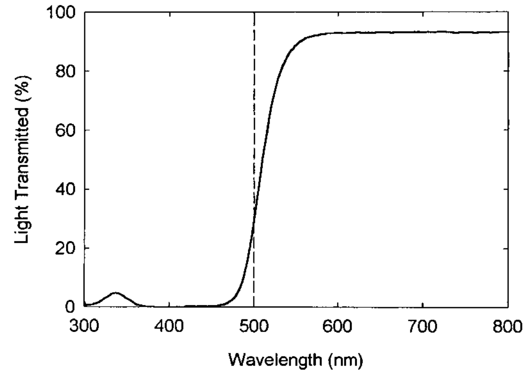

Figure 1. Light transmission curve of canary-yellow cellulose-acetate film (Roscolux #312).

Phytochrome photoequilibrium. Plant morphology and growth are presumed to respond to the balance of active phytochrome to total phytochrome, measured as phytochrome photoequilibrium (PPE) (20,21). Researchers have used PPE, measured at the top of the canopy, to estimate phytochrome status. PPE in these experiments, calculated from spectroradiometric measurements (LI-1800, LI-COR), ranged from 0.82 at the highest blue light fraction to 0.86 at the lowest blue light fraction (Table 1).

Yield photon flux. PPF is the most widely used definition of measurement of photosynthetically active radiation (PAR). PPF weights each photon between 400 and 700 nm equally. In reality, the photosynthetic efficiency of ‘blue’ photons is as much as 30% less than that of ‘red’ photons and the photosynthetic range extends beyond 400–700 nm (22). A more theoretically exact definition of PAR is called the yield photon flux (YPF) (23). YPF weights each photon according to the ‘average leaf’ photosynthetic efficiency curve elucidated by McCree (22). Using the spectroradiometric data and McCree’s weighting factors (22), a YPF was also calculated for each blue light treatment.

Plant culture. Blue light treatments began at planting. Plants were given light 2 h at a PPF of 200 μmol m^{-2} s^{-1} or 1 h at a PPF of 500 μmol m^{-2} s^{-1} for the first 4 days. At the end of 4 days, lettuce and wheat had emerged and soybeans were ready to transplant. Temperature was maintained at 24/22°C day/night during the germination period. Lettuce seeds were sown directly in closed cell foam plugs (Smalley & Co., Salt Lake City, UT) with a diatomaceous earth (Isolite, Size CG-2, Sumitomo Corp., Denver, CO) core. These plugs were kept in a shallow pan of nutrient solution until lettuce emerged and were then transferred to a hydroponic system. Wheat seeds were rolled in moist paper towels and chilled to 4°C (stratified) for 48 h prior to planting into closed cell foam plugs with an Isolite core. Wheat plugs were placed directly in a hydroponic system. Soybean seeds were germinated in 6 cm deep trays of moist Isolite. Seedlings were transplanted into closed cell foam plugs when the hypocotyl was 2–3 cm long and then transferred to a hydroponic system.

Plant growth. For each blue light treatment, six plants of each species were grown in a single aerated hydroponics system (50 L tub, 60 cm × 46 cm × 22 cm, l × w × d). The environment was maintained at 26/22°C day/night ± 0.3/0.2 between sections within a trial. Relative humidity was maintained at 70%. CO_2 was elevated to 1000 μmol mol^{-1} both day and night. All sections were connected to a common air conditioning system *via* a manifold, so CO_2, humidity and temperature differences between sections were minimal.

Measurements and harvest. Chlorophyll measurements were made 2 days before harvest with a nondestructive, clamp-on, chlorophyll meter (SPAD-502, Minolta Corp., Ramsey, NJ), which measures absorbed irradiation at 650 and 940 nm from the intact leaf. Meter readings were in SPAD units, which is based on the ratio of chlorophyll absorbance at 650 nm to nonchlorophyll absorbance at 940 nm. SPAD units are highly correlated with destructive colorimetric chlorophyll measurements (24). Three chlorophyll readings were made and averaged on the middle leaflet of the first trifoliate of soybean, the second true leaf of lettuce (counting up from the cotyledonary leaves) and the second leaf of wheat (Haun Stage 2).

Plants were harvested prior to canopy closure to minimize the complicating changes in spectral quality caused by canopy closure. Lettuce and soybean were harvested 18 and 17 days after transplanting, respectively. Wheat was harvested 21 days after planting. Fresh mass, leaf area, branch or tiller number and stem length were taken immediately upon harvest. Shoots longer than 1 cm, originating from an apical junction, were counted as a branch (or tiller). Stem length was measured as the main branch length, including the hypocotyl. Plant material was dried for 48 h at 80°C and dry mass determined. SLA was calculated as total leaf area divided by dry mass of the leaves. Carbon partitioning to each plant part was calculated as dry mass of plant part divided by the total dry mass.

Statistical analysis. All six blue light treatments were evaluated at one time under a single PPF level and each PPF level (200 *vs* 500) was replicated twice in time. Differences between blue light fractions were tested using analysis of variance using a split-plot design with lamp type as the main plot. General linear mean procedure was utilized for lettuce because one replicate trial was missing at 12% blue and PPF of 500 μmol m^{-2} s^{-1}, due to aeration problems. Mean comparisons were made using least significant difference (LSD) at $\alpha = 0.05$ (SAS Institute, Cary, NC). Regression lines, fit using Sigma Plot (4.0, SPSS Inc., Chicago, IL) are plotted to emphasize the statistically significant means and trends. Regression analysis (Sigma Plot 4.0) alone was used to compare relative and absolute blue light. In the graphs, each point is an average of six plants and duplicated data points at each blue light fraction represent replicate trials in time.

RESULTS

Sensitivity to lamp type with constant blue light fraction

We expected the means to be similar in the two 6% blue treatments (filtered MH *vs* unfiltered HPS) since other wavelengths are not thought to affect the blue light response. As expected, the responses for wheat and soybean were not significantly different between HPS and MH at 6% blue (Figs. 2 and 3), suggesting that their blue light responses are not affected by the remaining spectral composition. Wheat and soybean blue light effects were thus considered to be continuous between lamp types over the five blue light fractions, and the means at the 6% blue light fractions were combined for regression analysis.

In contrast to wheat and soybean, lettuce growth was significantly altered by lamp type. Dry mass, leaf area, SLA and chlorophyll concentration of lettuce were significantly different for plants grown under 6% HPS blue and 6% MH blue (Figs. 4a–d, 6c,f and 7c). This indicates that caution must be used in claiming a blue light response when other parts of the spectrum vary (see ''Discussion'' in companion paper [25]). Blue light effects on lettuce chlorophyll concentration, dry mass accumulation, leaf area and SLA were graphed separately for each lamp type, but other parameters were not significantly different between lamp types and blue light fraction responses were considered continuous.

Dry mass accumulation and partitioning

Although increasing blue light fraction tended to decrease wheat dry mass, the effect was not statistically significant (Fig. 2a–d). Wheat carbon partitioning was similar under all blue light treatments (Fig. 2e–g). Because plants were harvested only 17 days into the life cycle, the small differences we observed could become larger as the plants matured.

Soybean leaf and total dry mass did not respond to changes in blue light fraction (Fig. 3a,d). Stem dry mass decreased with increasing blue light fraction (Fig. 3b). According to the LSD test, root dry mass was significantly less at high (26%) and low (0%) blue light fraction than midrange blue light treatments (2, 6 and 12%) (Fig. 3c). Increased carbon partitioning to stems at lower blue light fraction was mostly at the expense of the roots (Fig. 3e,f).

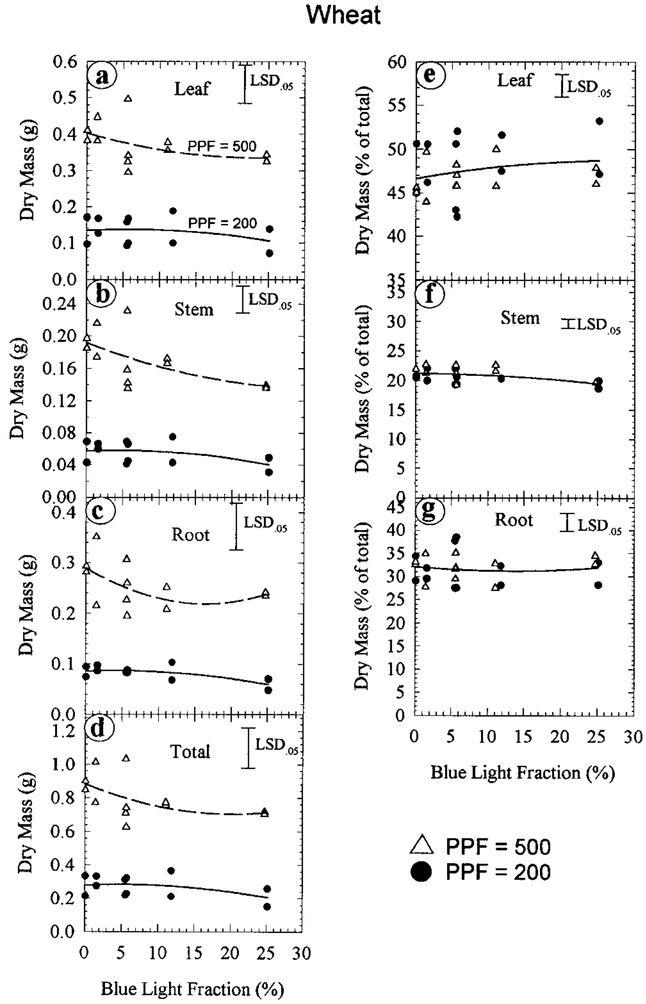

Figure 2. Effect of blue light fraction on wheat leaf, stem, root and total dry mass and dry mass as a percent of total. Each point is an average of six plants. Replicate data points at each blue light fraction represent replicate trials in time. Error bars represent the LSD at the $\alpha = 0.05$ level between blue light fractions within a PPF.

Although lettuce dry mass was significantly different for the two 6% blue treatments (6% HPS *vs* 6% MH) and, therefore, could not be analyzed as a continuous variable, there was a trend for increasing dry mass with increasing blue light fraction under each lamp type (Fig. 4a–d). More carbon was partitioned to the stem at low blue at the expense of the leaves (Fig. 4e,f). Both stem and leaf carbon partitioning changed drastically between 0 and 2% blue. Leaf carbon partitioning recovered by 2% blue, but carbon partitioning to the stem was still significantly higher at 2% blue than 6% blue or above. Some of the carbon partitioning compensation came from the roots, but the change in percent root dry mass with blue light fraction was not statistically significant.

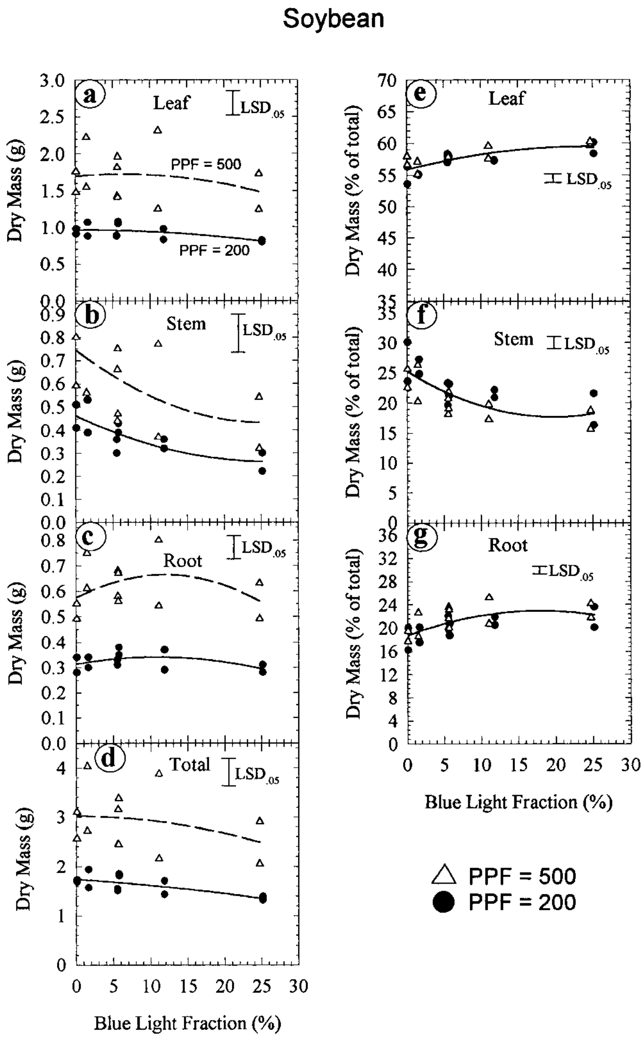

Figure 3. Effect of blue light fraction on soybean leaf, stem, root and total dry mass (g) and dry mass as a percent of total. Each point is an average of six plants. Replicate data points at each blue light fraction represent replicate trials in time. Error bars represent the LSD at the α = 0.05 level between blue light fractions within a PPF.

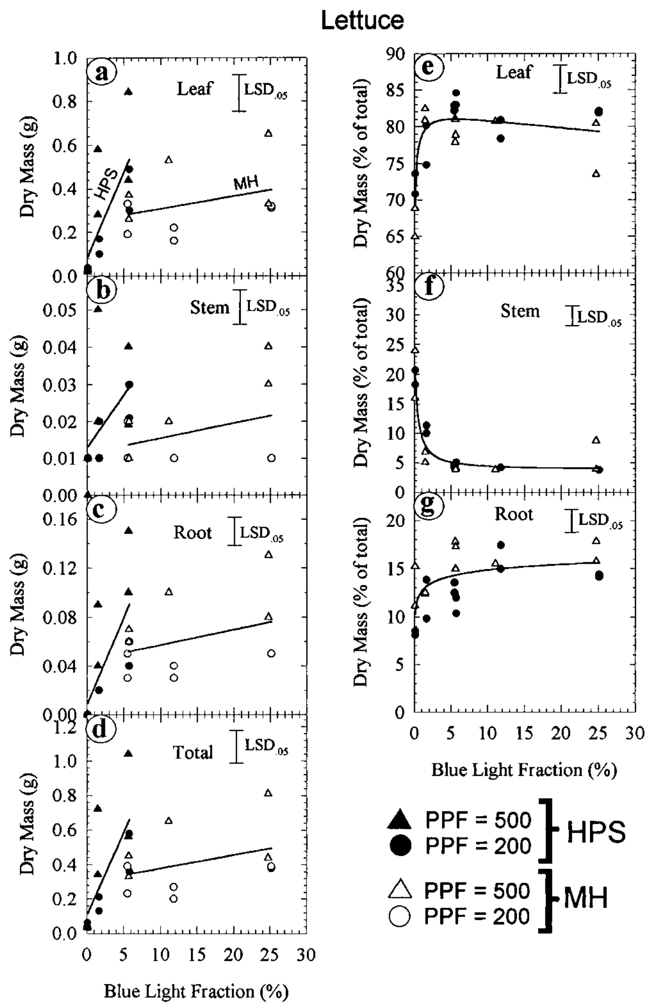

Figure 4. Effect of blue light fraction on lettuce leaf, stem, root and total dry mass (g) and dry mass as a percent of total. Each point is an average of six plants. Replicate data points at each blue light fraction represent replicate trials in time. Error bars represent the LSD at the α = 0.05 level between blue light fractions.

Stem length

Wheat stem length decreased by only 11% as blue light fraction increased from 0 to 26%, and this response was not statistically significant (Fig. 5a). Soybean stem length decreased only 7% as blue light increased from 0 to 2%, but a further increase to 6% blue decreased stem length by 44% (Fig. 5b). Overall, increasing blue light fraction from 0 to 26% decreased soybean stem length 67%. Lettuce stem length decreased 72% between 0 and 2% blue and a further 13% from 2 to 6% blue (Fig. 5c). Overall, lettuce stem length decreased 88% from 0 to 26% blue.

Leaf area and SLA

Wheat leaf area and SLA were constant under all blue light treatments (Fig. 6a,d). Soybean leaf area was statistically highest between 2 and 12% blue and decreased at extreme low (0%) and high (26%) blue (Fig. 6b). Soybean SLA (dry mass basis) was not significantly affected by the blue light fraction (Fig. 6e), which is contrary to the findings of Britz and Sager (6) (dry mass basis).

Both leaf area and SLA of lettuce were affected by lamp type and could not be drawn as a continuous response curve for blue light fraction. However, under HPS lamps, there was a dramatic increase in leaf area from 0 to 6% blue at 200 μmol m^{-2} s^{-1} and from 0 to 2% at 500 μmol m^{-2} s^{-1} (Fig. 6c). There was little response to blue light fraction under the MH treatments (6–26% blue). SLA decreased with increasing blue light fraction under each lamp type (Fig. 6f). There was a 54% decrease in SLA between 0 and 2% blue. The mean SLA of 152 m^2 kg^{-1} at 0% blue is extremely high, reflecting the thin, translucent, leaves.

Chlorophyll concentration

Wheat chlorophyll concentration was not affected by blue light fraction (Fig. 7a). Soybean chlorophyll concentration increased 13% between 0 and 2% blue, but was constant from 2 to 26% blue (Fig. 7b). As noted above, lettuce chlorophyll concentration was significantly different between the

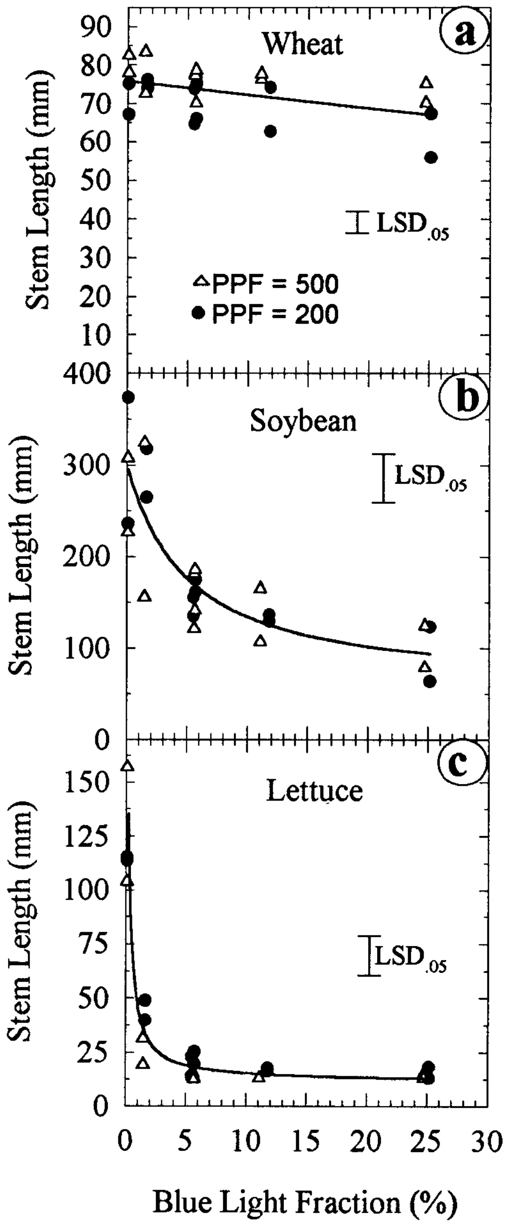

Figure 5. Effect of blue light fraction on: (a) wheat; (b) soybean; and (c) lettuce stem length. Each point is an average of six plants. Replicate data points at each blue light fraction represent replicate trials in time. Error bars represent the LSD at the α = 0.05 level between blue light fractions.

two 6% blues. However, lettuce chlorophyll concentration increased significantly under each lamp type with increasing blue light fraction (Fig. 7c).

Tillering or branching

Wheat tiller number tended to decrease with increasing blue light fraction, but differences were not significant (Fig. 8). Soybean branch numbers were statistically different, but means ranged only from 5.25 to 5.95, which is probably not physiologically important to light interception and canopy closure.

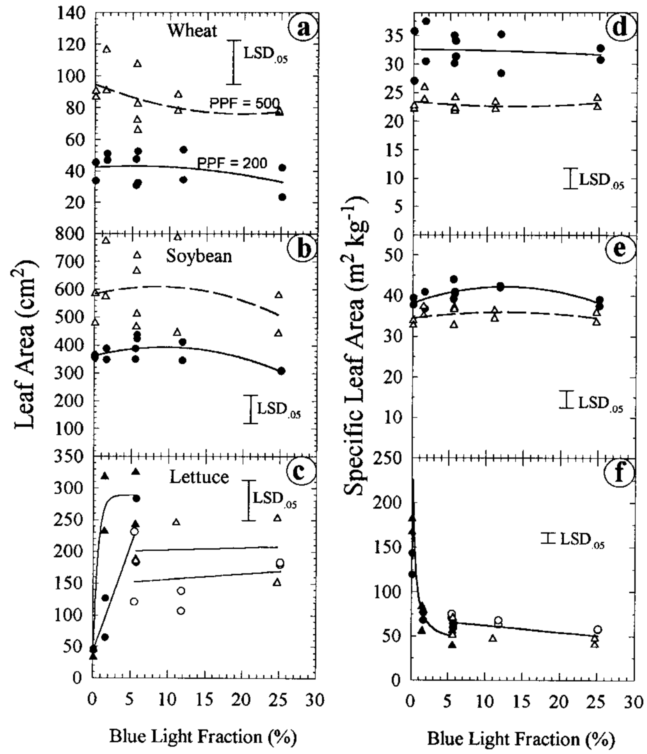

Figure 6. Effect of blue light fraction on wheat, soybean and lettuce; leaf area and specific leaf area. Each point is an average of six plants. Replicate data points at each blue light fraction represent replicate trials in time. Error bars represent the LSD at the α = 0.05 level between blue light fractions within a PPF.

DISCUSSION

Species differences

Graphing each species as a percent of maximum response highlights the major differences of each species' relative response to blue light (Fig. 9a,b). These differences in species response to blue light may be associated with differences in plant morphology. Although other plant classifications, such as monocot *vs* dicot, might explain the differences in species response, plant morphology directly affects the light environment within the plant. Therefore, a plant morphology classification may explain the differences in species response. Wheat, whose meristematic leaves and stems are sheltered from direct light by upper leaves and leaf sheathes (erectophile morphology, common to grasses and most monocots, but not all monocots), showed no response to blue light. Both lettuce and soybean, whose meristematic cells in expanding leaves and stems are 'exposed' (planophile morphology, common to dicots and a few monocots), responded to blue light fraction. Interestingly, the relative response of lettuce stem length and leaf area to low blue was more pronounced than it was in soybean (Fig. 9a,b).

Planophile species have consistently shown a response to blue light (1,2,9,11), but results for the erectophile species are mixed. Ryegrass leaf area and shoot length did not respond to red- *vs* blue-biased lamps, but sorghum did respond (26). The sorghum response suggests that some erectophile species are blue light sensitive, but Warrington and Mitchell (26) only tested lamp type and not blue light response. Direct

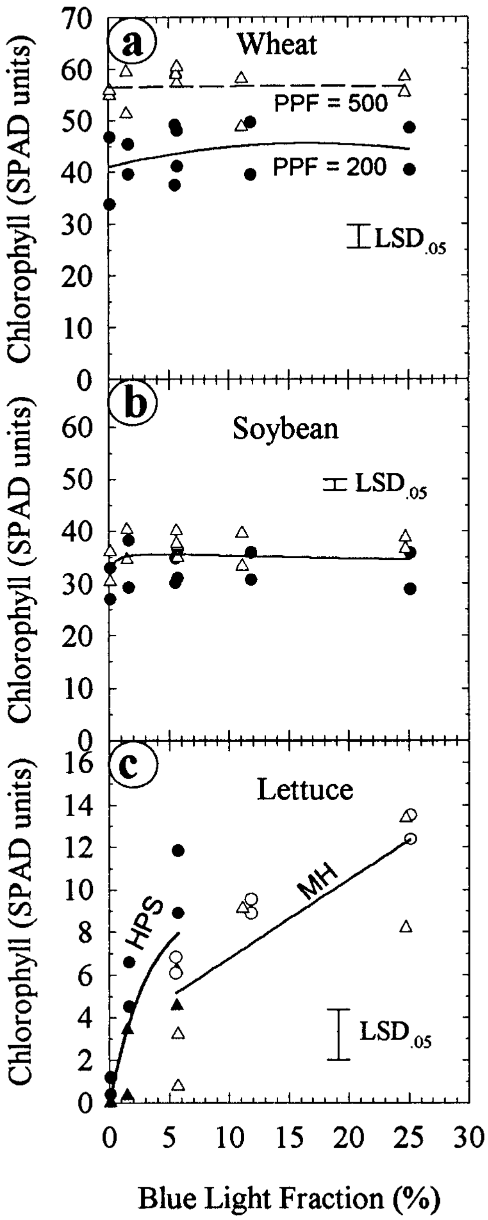

Figure 7. Effect of blue light fraction on: (a) wheat; (b) soybean; and (c) lettuce chlorophyll concentration (SPAD units, fresh weight basis). Each point is an average of six plants. Replicate data points at each blue light fraction represent replicate trials in time. Error bars represent the LSD at the α = 0.05 level between blue light fractions (within a PPF for wheat).

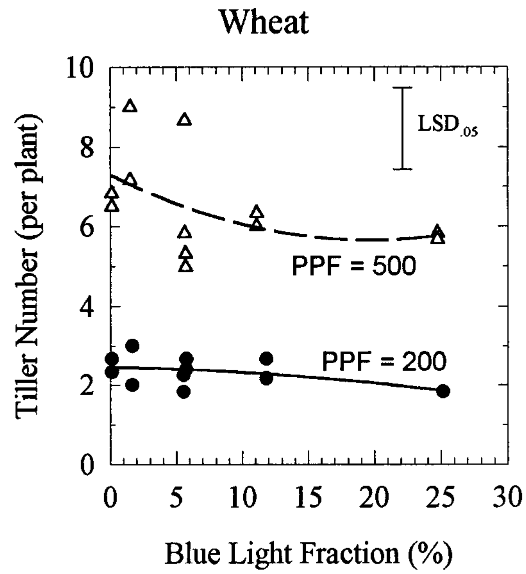

Figure 8. Effect of blue light fraction on wheat tiller number. Each point is an average of six plants. Replicate data points at each blue light fraction represent replicate trials in time. Error bars represent the LSD at the α = 0.05 level between blue light fractions within a PPF.

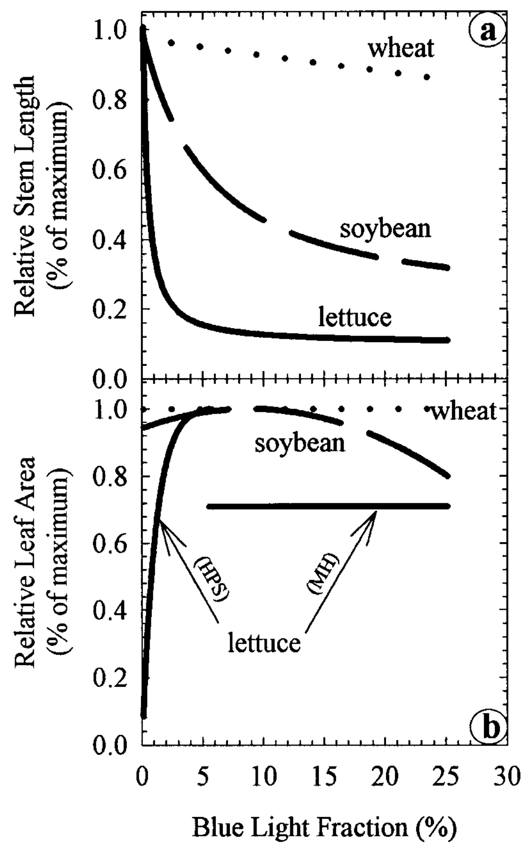

Figure 9. Effect of blue light fraction on the relative: (a) stem length; and (b) leaf area of wheat, soybean and lettuce. Lines are regressions of means of both PPF levels.

investigation of blue light response in sorghum and other grass (erectophile) species is needed to test if a generalization can be made between erectophile and planophile plants.

Inconsistencies with other research

Although Barnes and Bugbee (12) saw a longer wheat leaf length with low blue, only the longest fully extended leaf was measured and there was no significant difference in dry matter accumulation. Also, in contrast to our findings, Barnes and Bugbee (12) found that tillering increased 25% between 1 and 25% blue and Goins *et al.* (15) found no increase in tillering between 0 and 0.85% blue, but a 71%

increase between 0.85 and 8.5% blue. The difference between our tillering data and that of Barnes and Bugbee (12) may be genetic differences between cultivars, as their experiments utilized 'Fielder', an extremely high-tillering cultivar compared to 'USU-Apogee'. Goins *et al.* (15) used a low-tillering cultivar, but tillering differences were also evident. The apparent discrepancy between Goins *et al.* (15) and our data may be due to the short-duration of our experiments, which may have not allowed time for all blue light effects to be fully manifested. However, similar to our immature wheat results, Barnes and Bugbee (12) found mature wheat dry mass was not significantly different between 1% blue (filtered MH) and 25% blue (MH) light. Goins *et al.* (15) did see a statistically significant reduction in mature wheat shoot dry matter between 31% blue (fluorescent) and 0.85% blue (red LED plus blue fluorescent), but grain yield was not affected.

Another reason for the discrepancy in tillering results may be due to differences in thermal radiation within experiments. Goins *et al.* (15) used a Plexiglas barrier over the blue fluorescent lights and red LED has a low thermal emittance, so small thermal radiation differences existed between treatments. Barnes and Bugbee (12) used the same chilled water bath system as in our experiments, so thermal radiation differences between treatments were not likely.

It is important to point out that our lowest blue treatment was not truly zero blue and our lamp sources contained far red. However, the PPE of red LED is 0.88, similar to our treatments. Therefore, interactions with phytochrome are probably not responsible for the difference seen between our 0.1% blue and red LED.

The results for soybean and lettuce were mostly consistent with previous reports, especially under our $<0.1\%$ blue treatment compared to red LED (0% blue) (1). Soybean SLA did not respond to increasing blue light as seen previously in a comparison of daylight fluorescent and blue-deficient low-pressure sodium (6), but Britz and Sager did not separate lamp and plant growth space, so the thermal radiation environment was very different.

Consideration of YPF

In our experiments, PPF was equivalent between blue light treatments, but YPF declined by as much as 10% as blue light fraction increased from 0 to 26% blue (Table 1). Considering that photosynthetic efficiency has a direct effect on dry mass, caution must be used when comparing treatments at an equal PPF and claiming blue light effects on dry mass accumulation. Because YPF correlates with the variation in total dry mass for our experiment, there is likely no blue light effect on dry mass.

YPF differences do not explain the difference in dry mass between the two 6% blue treatments in lettuce. Indeed, 6% blue MH has a 3% lower YPF than the 6% blue HPS. With a 3% difference in YPF, only a 3% difference in dry mass could be expected, but the total dry mass between the two treatments differed by 56%.

It is important to note that accurate measurements of YPF can only be made with a spectroradiometer. Under these and many other lamp types, PPF sensors and commercial YPF sensors can have substantial errors (23).

Morphology and carbon partitioning

Although total dry mass is explained better by YPF than by PPF for all species, soybean dry mass partitioning is attributable to the morphological changes caused by altering the blue light fraction. The increase in stem mass at low blue came at the expense of the roots and, to a lesser extent, the leaves. Although shifts in carbon partitioning did not affect total biomass yield, they may affect seed yield. Small differences in early growth can cause large differences in yield, especially when dry mass accumulation is affected (4,5).

Consideration of PPE

PPE estimates the balance of active and inactive phytochromes from response curves of the purified phytochrome *in vitro.* However, the *in vivo* role of chlorophyll altering the radiation absorbed, and thus PPE, is still unknown because the phytochrome response *in vivo* with chlorophyll present has not yet been measured (20). Nonetheless, many plant morphological responses are attributable to changes in the balance of red and far-red light as measured by PPE (20,21). These morphological differences are typically observed when comparing a PPE of 0.71 (sunlight) with a much lower PPE of 0.3–0.5 (shade). In our study, the PPE ranged only from 0.82 to 0.86, both typical of direct sunlight. Therefore, while phytochrome response cannot entirely be ruled out, the magnitude of the responses observed were likely too large to be elicited by such a small change in PPE.

Relative *vs* absolute blue light

Blue light can be described in two ways, the absolute amount of blue light or the fraction of blue light relative to the PAR. Little research has been done to clarify which definition best describes physiological responses. Hoenecke *et al.* (1) found that lettuce hypocotyl extension responded to absolute rather than to relative blue light. Similarly, Wheeler *et al.* (14) suggested that soybean stem elongation was responsive to absolute rather than to relative blue light. We conducted studies using two PPF levels so we could quantify relative *vs* absolute blue light effects (Table 1). If absolute blue light determines plant response, the blue light fraction response curves at the two PPF levels should overlap when graphed on an absolute blue light axis.

Indeed, our data for lettuce stem length agree with those of Hoenecke *et al.* (1), where a regression of the data fits better when graphed on an absolute blue light axis (Fig. 10a,c). Soybean stem length, on the other hand, regresses better with a relative blue light axis (Fig. 10b,d). This apparent discrepancy in the soybean data may lie with the fact that Wheeler *et al.* (14) only tested 6–26% blue where stem length is less sensitive to blue light.

All wheat parameters we studied were unresponsive to blue light, so comparisons between relative and absolute blue light responses are not meaningful. With lettuce, we were also unable to evaluate the effects of relative *vs* absolute blue light in parameters other than stem length because of the complicating lamp type interaction. For soybean dry mass, leaf area and SLA, there is a response to the blue light fraction, but the responses are different at the two PPF (Figs. 3 and 6b,e). However, graphing the data as absolute blue

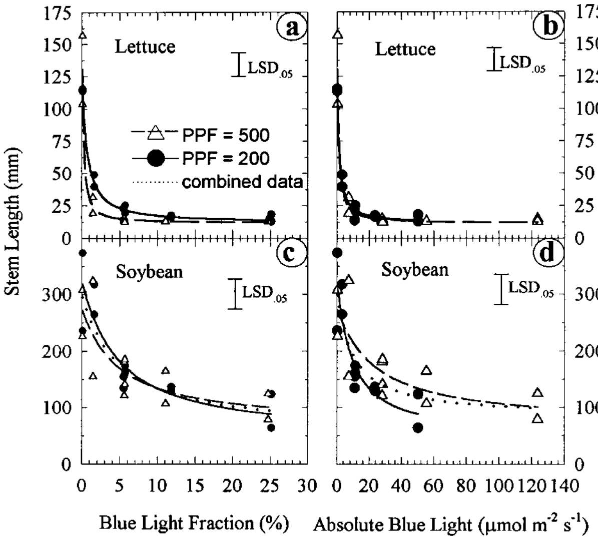

Figure 10. A comparison of blue light fraction and absolute blue light to describe: (a,b) lettuce; and (c,d) soybean stem length response to blue light. Error bars represent the LSD at the $\alpha = 0.05$ level between blue light fractions within a PPF.

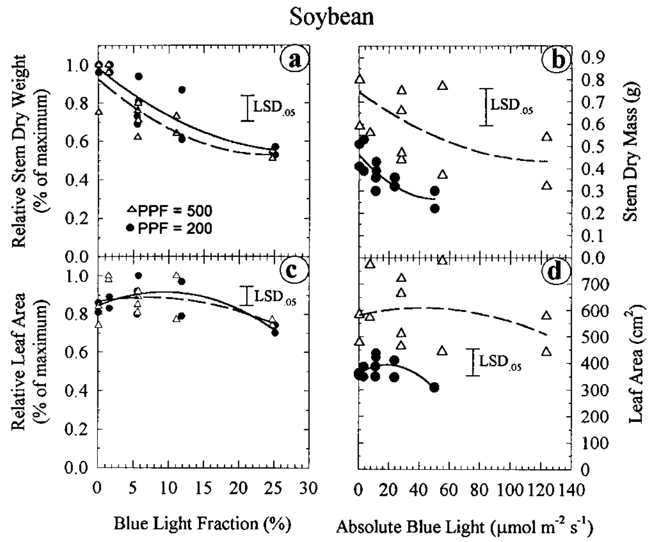

Figure 11. A comparison of blue light fraction and absolute blue light to describe soybean: (a) relative stem dry mass; (b) stem dry mass; (c) relative leaf area; and (d) leaf area. Error bars represent the LSD at the $\alpha = 0.05$ level between blue light fractions within a PPF.

light does not cause the two PPF levels to overlap (Fig. 11b,d). The stem length and leaf area responses do overlap for blue light fraction when graphed as a percent of maximum (Fig. 11a,c). This also holds true for leaf, root and total dry mass and SLA. This suggests that although the percent of maximum response can be predicted by blue light fraction, the absolute magnitude of the response is determined by PPF.

CONCLUSIONS

Blue light effects were species dependent. Wheat was unresponsive to blue light fraction. Soybean was slightly responsive with leaf area maximized at midrange blue light fractions (2–12%), stem length minimized at 26% blue, but no blue light effect on total dry mass. Lettuce was highly responsive to blue light fraction with maximum stem elongation and minimum leaf expansion at low blue light fractions (0–2%). Lettuce was also sensitive to other wavelengths.

For Earth-based controlled environment production and space-based life support systems, the goal is to maximize productivity while minimizing plant height and energy consumption. Minimizing blue light in lamps increases energy efficiency. Blue light was not required for maximum productivity of soybean and wheat dry mass and leaf area. However, a higher blue light fraction is required to reduce soybean stem elongation. Lettuce dry mass and leaf area, on the other hand, increased dramatically when as little as 2% blue was added, which also suppressed excessive stem elongation. This research indicates that lamps with a high fraction of blue photons (>6%), such as MH, are not only energetically wasteful compared to reduced blue lamps, but can reduce plant growth.

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