Spectral Effects of Three Types of White Light-emitting Diodes on Plant Growth and Development: Absolute versus Relative Amounts of Blue Light

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Abstract. **Light-emitting diodes (LEDs) are a rapidly developing technology for plant growth lighting and have become a powerful tool for understanding the spectral effects of light on plants. Several studies have shown that some blue light is necessary for normal growth and development, but the effects of blue light appear to be species-dependent and may interact with other wavelengths of light as well as photosynthetic photon flux (*PPF*). We report the photobiological effects of three types of white LEDs (warm, neutral, and cool, with 11%, 19%, and 28% blue light, respectively) on the growth and development of radish, soybean, and wheat. All species were grown at two *PPF*s (200 and 500 μmol·m^{-2}·s^{-1}) under each LED type, which facilitated testing the effect of absolute (μmol photons per m^{-2}·s^{-1}) and relative (percent of total *PPF*) blue light on plant development. Root and shoot environmental conditions other than light quality were uniformly maintained among six chambers (three lamp types × two *PPF*s). All LEDs had similar phytochrome photoequilibria and red:far red ratios. Blue light did not affect total dry weight (DW) in any species but significantly altered plant development. Overall, the low blue light from warm white LEDs increased stem elongation and leaf expansion, whereas the high blue light from cool white LEDs resulted in more compact plants. For radish and soybean, absolute blue light was a better predictor of stem elongation than relative blue light, but relative blue light better predicted leaf area. Absolute blue light better predicted the percent leaf DW in radish and soybean and percent tiller DW in wheat. The largest percentage differences among light sources occurred in low light (200 μmol·m^{-2}·s^{-1}). These results confirm and extend the results of other studies indicating that light quantity and quality interact to determine plant morphology. The optimal amount of blue light likely changes with plant age because plant communities balance the need for rapid leaf expansion, which is necessary to maximize radiation capture, with prevention of excessive stem elongation. A thorough understanding of this interaction is essential to the development of light sources for optimal plant growth and development.**

The application of LEDs for plant growth lighting has been studied for over two decades (Barta et al., 1992; Bula et al., 1991). Initial studies included only red LEDs because they were the most efficient and emit light that coincides with the maximum absorption of chlorophyll (660 nm). However, it quickly became apparent that some blue light was necessary for normal growth and development of sorghum (Britz and Sager, 1990), soybean (Britz and Sager, 1990; Dougher and Bugbee, 2001a; Wheeler et al., 1991), wheat (Barnes and Bugbee, 1992; Dougher and Bugbee, 2001a; Goins et al., 1997), lettuce (Dougher and Bugbee, 2001a; Hoenecke et al., 1992; Yorio et al., 2001), pepper (Brown et al., 1995), spinach, and radish (Yorio et al., 2001). At the time these studies were conducted, blue LEDs were only 3% to 4% efficient, whereas red LEDs were 15% to 18% efficient (Massa et al., 2006). As such, the goal of these studies was to determine the minimum amount of blue light necessary for normal growth and development (Kim et al., 2005). The efficiency of blue LEDs has since dramatically increased to more than 30%. Because white LEDs are produced by using blue LEDs and phosphors, an increase in the efficiency of blue LEDs has made efficient white LEDs possible (Pimputkar et al., 2009).

Studies on blue light. Wheeler et al. (1991) were the first to propose that the plant developmental response to blue light was dependent on absolute blue light levels (μmol of photons per m^{-2}·s^{-1} between 400 and 500 nm) rather than the relative amount of blue light (percent of total *PPF*). This was a departure from other photobiological responses that are determined by ratios of light rather than absolute amounts (e.g., red:far red ratio and phytochrome photoequilbria). These results were reviewed by Yorio et al. (1998).

Later, Dougher and Bugbee (2001a) examined the effects of blue light on growth and development of lettuce, soybean, and wheat using high-pressure sodium (HPS) and metal halide (MH) lamps filtered to achieve six blue light levels from 0.1% to 26% at 200 and 500 μmol·m^{-2}·s^{-1}. Blue light did not affect total DW, and developmental responses were species-dependent. Lettuce was the most responsive with dramatic decreases in stem length as blue light levels increased. Soybean stem length decreased and leaf area increased up to 6% blue light. Wheat was not significantly affected by blue light. For lettuce, stem length was better predicted by absolute blue light, but for soybean, stem length was better predicted by relative blue light.

Dougher and Bugbee (2001a) plotted stem length against both absolute and relative blue light, but because filtered light sources were used, the results may have been complicated by interactions with other wavelengths of light. In our study, we used three types of white LEDs without filters to determine if other plant growth parameters are better predicted by either absolute or relative blue light.

Materials and Methods

Plant material and cultural conditions. Radish (*Raphanus sativus*, cv. Cherry Belle), soybean (*Glycine max*, cv. Hoyt), and wheat (*Triticum aestivum*, cv. Perigee) seeds were pre-germinated for 24, 36, and 48 h, respectively, and subsequently transplanted to root modules measuring 15 × 18 × 9 cm (length × weight × height; 2430 cm^3). For the radish and soybean experiments, nine seeds were planted in each root module and for the wheat experiment, 12 seed were planted in each root module. All root modules were filled with soilless media (one peat:one vermiculite by volume), watered to excess with a complete, dilute fertilizer solution (0.01N–0.001P–0.008K; Scotts® Peat-Lite, 21-5-20), and allowed to passively drain. Five grams of slow-release fertilizer (16N–2.6P–11.2K; Polyon® 1 to 2 month release, 16-6-13) were mixed uniformly into each root module to maintain leachate electrical conductivity measurements between 100 and 150 mS·m^{-1} (1.0 and 1.5 mmhos·cm^{-1}). After planting, each root module was randomly placed within one of six growth chambers, which measured 18 × 20 × 26 cm (9360 cm^3) for the 200 μmol·m^{-2}·s^{-1} treatments and 20 × 23 × 30 cm (13,800 cm^3) for the 500 μmol·m^{-2}·s^{-1} treatments (Fig. 1). The inside of all chambers was lined with

high-reflectance Mylar®. Type-E thermocouples connected to a data logger (Model CR10T; Campbell Scientific, Logan, UT) were used to continuously monitor temperature. In each growth chamber, one thermocouple was used and was adjusted upward as plants grew, remaining directly above the plant canopy. Temperatures averaged 23.0 and 24.3 °C in the low-light and high-light treatments, respectively. Temperature differences among chambers were less than 0.5 °C. To avoid partial shading of the plants, the thermocouples were not shielded; had they been shielded, our measurements indicate that recorded temperatures would have been reduced by ≈0.5 °C. Radish, wheat, and soybean seedlings began to emerge 1, 2, and 5 d after planting, respectively. All growth chambers were ventilated and exposed to the same room conditions with an average daytime CO_2 concentration of ≈450 μmol·mol^{-1} (ppm) measured using a CO_2 probe (Model GMP222; Vaisala Inc., Finland) and average relative humidity (RH) of 30% measured using a RH probe (Model HMP110; Vaisala Inc.). Dilute fertilizer solution was applied as needed to maintain ample root-zone moisture.

Light treatments. Warm, neutral, and cool white LEDs (Multicomp; Newark, Gaffney, SC) were used. Measurements of *PPF*, yield photon flux (YPF), phytochrome photoequilibrium (PPE), relative (percent of total *PPF*) amounts of blue (400 to 500 nm), green (500 to 600 nm), and red (600 to 700 nm) light, and the absolute (μmol photons per m^{-2}·s^{-1}) amount of blue light for all LED treatments in each growth chamber were made using a spectroradiometer (Model PS-200; Apogee Instruments, Logan, UT; Table 1). The spectral output of each LED type at both *PPF*s is shown in Figure 2. Red to far red ratio was measured using a red:far red sensor (SKR110; Skye Instruments, U.K.), which measures the red light from 630 to 665 nm and far red from 715 to 740 nm (Table 1). During the experiment, *PPF* was measured using a quantum sensor (LI-188B; LI-COR, Lincoln, NE) calibrated for each treatment against the spectroradiometer. *PPF* was maintained constant relative to the top of the plant canopy by adjusting the distance between the light source and the canopy. Variability of *PPF* within each growth chamber was less than 5% and root modules in each chamber were rotated 180° every 3 d. The photoperiod was 16 h during the day and 8 h during the night.

Definition of blue light. Many previous studies have used light sources with ultraviolet radiation from either cool white fluorescent or green fluorescent lamps (Kim et al., 2004a, 2004b; Yorio et al., 2001) or MH or HPS lamps (Brown et al., 1995; Dougher and Bugbee, 2001a, 2001b; Schuerger et al., 1997). Because ultraviolet-A radiation is often considered to be as effective as blue light for inducing some photomorphogenic responses, blue light has frequently been defined to include ultraviolet-A radiation (e.g., 320 to 500 nm). The LEDs in this study contained limited ultraviolet-A radiation so we defined blue light as 400 to 500 nm.

Fig. 1. Experimental set-up showing growth chambers, LED arrays, root modules, and thermocouples. The crop shown is radish on the day of harvest. Note the differences in plant form across treatments, which are arranged (left to right) warm, neutral, and cool white LEDs. LED = light-emitting diode.

Table 1. Spectral characteristics of warm, neutral, and cool white LEDs at two photosynthetic photon fluxes (200 and 500 μmol·m^{-2}·s^{-1}).[z]

						Parameter			
	PPF	YPF	YPF/PPF	PPE	R:FR	Amount blue	Percent of total *PPF*		
LED type	(μmol·m^{-2}·s^{-1})		ratio	P_{fr}/P_{total}	ratio	(μmol·m^{-2}·s^{-1})	Blue	Green	Red
Warm	200	180	0.90	0.84	5.10	22.6	11.3	42.8	45.9
Neutral	200	176	0.88	0.84	5.60	38.2	19.1	47.9	33.0
Cool	200	172	0.86	0.83	6.10	55.6	27.8	49.0	23.2
Warm	500	455	0.91	0.84	4.71	49.0	9.80	41.3	48.9
Neutral	500	440	0.88	0.84	5.11	89.5	17.9	46.6	35.5
Cool	500	430	0.86	0.83	5.73	125.0	25.0	49.6	25.4

[z]For a discussion on the difference between photosynthetic photon flux (*PPF*) and yield photon flux (YPF), see Barnes et al. (1993). Yield photon flux (YPF) and phytochrome photoequilibrium (PPE) were determined according to Sager et al. (1988).
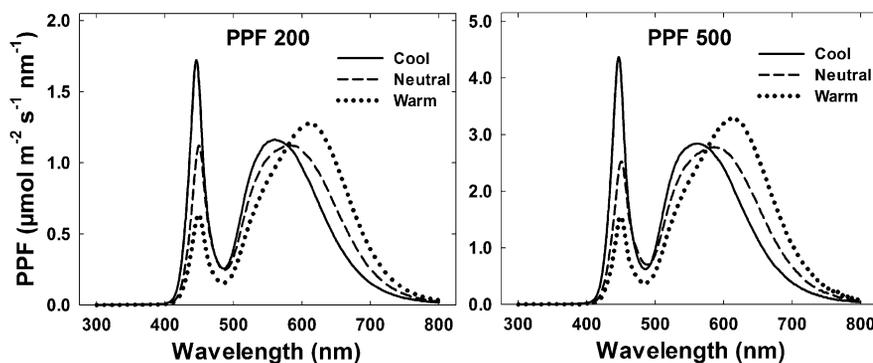LED = light-emitting diode.

Fig. 2. Spectral distribution of warm, neutral, and cool white LEDs at 200 and 500 μmol·m^{-2}·s^{-1}. Both spectra are shown because overdriving the LEDs to achieve 500 μmol·m^{-2}·s^{-1} caused a slight spectral shift in all three LED types. LED = light-emitting diode.

Plant measurements. To minimize the effects of canopy closure in the radish and soybean experiment, four of the original nine plants were thinned at 9 and 10 d after emergence (DAE), respectively; no plants were thinned in the wheat experiment. For radish and soybean, leaf chlorophyll concentration index (CCI) of the first set of true leaves was measured with a portable chlorophyll meter (CCM-200; Opti-Sciences Inc., Hudson, NH). Experiments were ended and the plants were harvested at canopy closure 14, 17, and 22 DAE for radish, soybean, and wheat, respectively. For radish and soybean, total leaf area was measured after harvest. The number and length of branches per plant per treatment were measured in soybean and the number of tillers per plant was determined for wheat. For all three species, separated stems and leaves (or tillers in wheat) were dried for 48 h at 80 °C and their DW was measured. Root weights were not measured.

Statistical analysis. There was one replicate study for each species. The number of plants used to calculate the mean are specified in each figure caption. Data were plotted against both the absolute and the relative amount of blue light. Sigma Plot (Version 12.0; SPSS Inc., Chicago, IL) was used to fit regression lines to each data plot. Following the methods used by Dougher and Bugbee (2001a), both graphs were visually compared and the best fit curve was selected as the most likely indicator for the observed photomorphogenic response.

Results and Discussion

Overall, blue light significantly altered development in soybean and radish, whereas wheat was minimally responsive. Each developmental parameter responded differently to the absolute and relative amount of blue light. This study was conceptually similar to Dougher and Bugbee (2001a) but provided a more detailed and comprehensive analysis of developmental parameters and includes an additional species, radish. It also provides potentially cleaner results because filters were not required to achieve specific blue light levels.

Stem length. For radish and soybean, absolute blue light was a better indicator of stem length than relative blue light (Fig. 3). Stem length decreased with increasing absolute blue light up to 50 $\mu mol \cdot m^{-2} \cdot s^{-1}$ and then remained constant. Interestingly, this response was observed although PPE was nearly constant across all three treatments (Table 1; Fig. 4). Wheat was minimally responsive to blue light (Fig. 3), confirming the results of Dougher and Bugbee (2001a). Tamulaitis et al. (2005) saw similar results for blue light effects on radish stem length and Dougher and Bugbee (2001a) and Wheeler et al. (1991) saw similar results for soybean. However, Wheeler et al. (1991) reported that the absolute amount of blue light was a better indicator of soybean stem length, whereas Dougher and Bugbee (2001a) found that the relative amount was a better indicator. The underlying cause for the differences among studies is unclear, but it may be associated with differences in the degree of canopy closure at harvest. Wheeler et al. (1991) reported plant number but not growing area, whereas Dougher and Bugbee (2001a) reported both plant number and growing area. Both of these studies likely provided greater spacing between plants than in this study. The plants in this study formed a closed canopy immediately before harvest.

Branching/tillering and Haun stage. In soybean, only branches 1 cm or greater in length were counted. It appeared that branching was dependent on *PPF*. The number of branches per plant was uniform across all three high light treatments; however, branching was infrequent in the low light treatments (data not shown). In wheat, tillering was also dependent on *PPF* (tiller number was greater in the high light treatment). As blue light levels increased, the number of tillers produced by each plant increased slightly (data
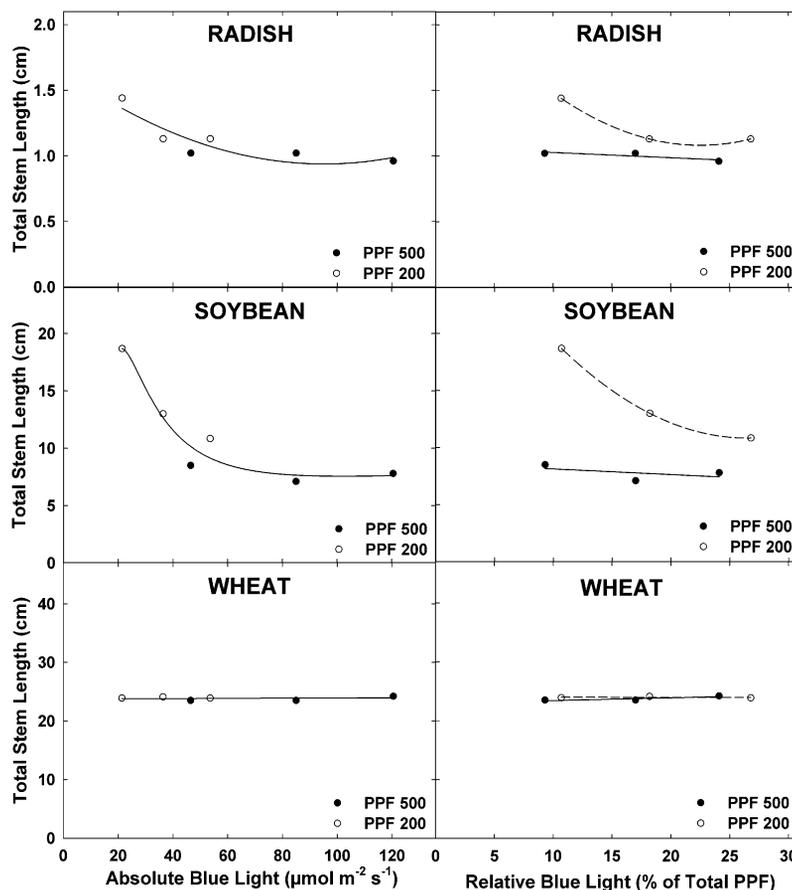

Fig. 3. The effect of absolute and relative blue light on stem length in radish, soybean, and wheat. For radish and soybean, each data point represents the average of five plants with measurements taken 14 and 17 DAE, respectively; for wheat, each data point represents the average of 12 plants grown for 22 DAE. Stem length was better predicted by absolute blue light than relative blue light. Wheat was unaffected by blue light. DAE = days after emergence.

not shown). Tillers were only counted if 1 cm or greater in length with the average number of tillers per plant calculated for each light treatment at high and low light. Haun stage followed the same trend as tiller number although not as dramatic (data not shown). It was impossible to determine whether these responses were the result of the absolute or relative amount of blue light, but these results are comparable to Barnes and Bugbee (1992) and Dougher and Bugbee (2001a).

Leaf area. In radish and soybean, relative blue light was a better indicator for leaf area (LA) than absolute blue light, but the species responded differently (Fig. 5). In radish, LA decreased up to 15% blue light and then remained constant; in soybean, LA appeared to linearly decrease as relative blue light increased, and the effect was dependent on *PPF*. The unusually low point in the high light (500 $\mu mol \cdot m^{-2} \cdot s^{-1}$) treatment in both soybean graphs is attributed to experimental error rather than a blue light effect caused by neutral white LEDs.

Unlike the effect of blue light on leaf area, radish cotyledon area was better predicted by absolute blue light and decreased as blue light increased up to 50 $\mu mol \cdot m^{-2} \cdot s^{-1}$ (the same pattern as seen with stem elongation). LA was not measured in wheat. Although the

Fig. 4. The effect of absolute blue light ($\mu mol \cdot m^{-2} \cdot s^{-1}$ of blue photons) on soybean stem length at 9 DAE in the low light treatment (200 $\mu mol \cdot m^{-2} \cdot s^{-1}$). Stem elongation decreased with increasing blue light although phytochrome photoequilibria (PPE) was nearly constant across treatments. DAE = days after emergence.

shape of the curve for soybean in our study differs slightly from Dougher and Bugbee (2001a), these results confirm theirs in that relative blue light is a better indicator of LA than absolute blue light. We were unable to find any previous studies on the effects of blue light on radish development.

Carbon partitioning to leaves/tillers. Percent leaf DW was better predicted by absolute
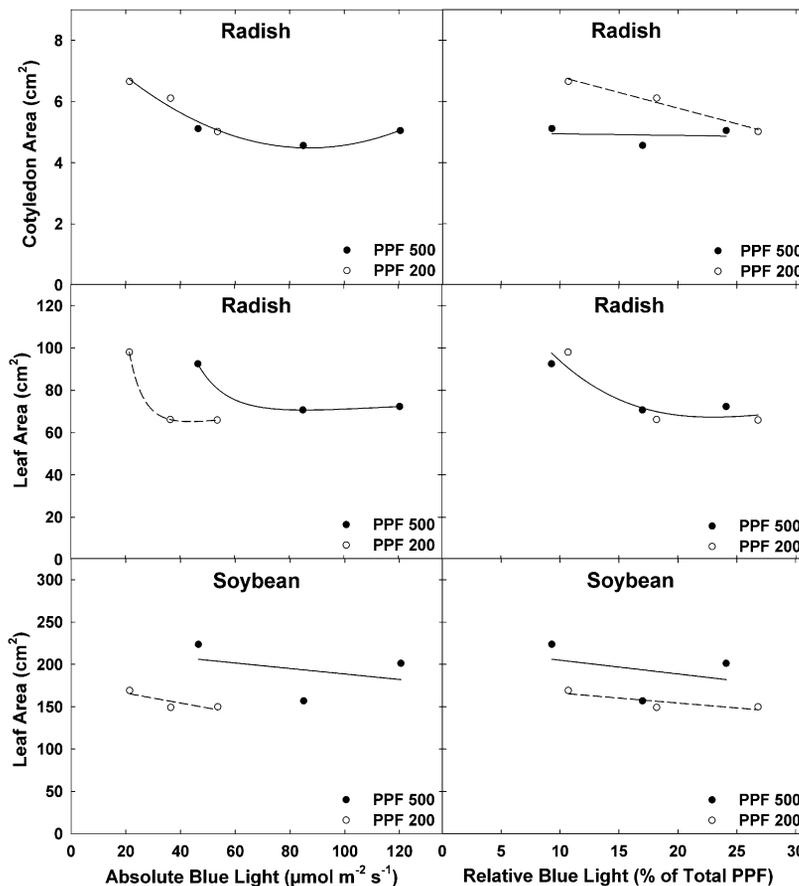
Fig. 5. Effect of absolute and relative blue light on cotyledon and leaf expansion. For radish and soybean, each data point represents the average of five plants with all measurements taken 14 and 17 DAE, respectively. Leaf area was not measured for wheat. The unusually low point in the high light (500 μmol·m^{-2}·s^{-1}) treatment in both soybean graphs is attributed to experimental error rather than a blue light effect caused by neutral white LEDs. DAE = days after emergence; LEDs = light-emitting diodes.

blue light in radish and soybean, but the effects were in opposite directions (Fig. 6). As absolute blue light increased, percent leaf DW decreased in radish and increased in soybean. As absolute blue light increased, percent tiller DW (an indication of branching) increased dramatically up to 100 μmol·m^{-2}·s^{-1}. This dramatic increase was the result of an increased number of tillers, not necessarily larger tillers. Yorio et al. (2001) saw the same trend in radish, although they were not able to determine whether relative or absolute blue light was a better indicator for the response. For soybean, Dougher and Bugbee (2001a) found a larger effect of blue light on carbon partitioning to leaves and associated it with relative blue light. Differences between studies could be the result of spectral differences between the lamps used in their study (HPS and MH) and the white LEDs used in ours. Spectral differences can cause complex interactions that are difficult to explain (Dougher and Bugbee, 2001b). No studies report absolute blue light increasing percent tiller DW directly, but they do report increased tillering with increased blue light levels (Barnes and Bugbee, 1992).

Effect of PPF on dry weight. Surprisingly, there was no significant effect of blue light on total dry weight gain in any of the three

species. Nevertheless, as expected, total DW increased with increasing PPF for all three species. For radish and soybean, the relationship was nonlinear; for wheat, the relationship was linear (Fig. 7). Considering the significant effect of blue light on morphology, we were surprised to find that there was no significant effect of blue light on total DW. Although Dougher and Bugbee (2001a) saw significant effects of blue light on growth at extremely low blue light levels in soybeans and wheat, they also found no effect of blue light between 10% and 26%. These results warrant further investigation because the increase in leaf expansion in low blue light should result in increased radiation capture and thus increased DW gain.

Specific leaf area. Neither blue light parameter was a better indicator of specific leaf area (SLA). In general, as blue light increased, SLA decreased linearly in both radish and soybean. This response appeared to be dependent on PPF (data not shown). For the ranges of blue light levels used in this study, these results are comparable to Dougher and Bugbee (2001a) for soybean. No comparable literature was found that reported SLA for radish grown under varying amounts of blue light. SLA was not calculated for wheat.

Chlorophyll concentration. Increased blue light decreased leaf area and slightly increased leaf DW (thus resulting in denser leaves). As a result, the concentration of chlorophyll per unit LA increased. Interestingly, this did not increase the amount of chlorophyll per unit leaf mass. Specific chlorophyll concentration (relative amount of chlorophyll per gram), which was determined by taking the product of CCI (relative amount of chlorophyll per meter^2) and SLA (m^2·g^{-1}), was unaffected by blue light (data not shown). Like with SLA, CCI was equally predicted by both absolute and relative blue light. In general, for both radish and soybean at high and low light, CCI linearly increased as blue light increased (data not shown). CCI was not measured in wheat because differences were not visually apparent. For soybean, these results differ from Dougher and Bugbee (2001a) who reported no difference in chlorophyll concentration as blue light increased. No literature was found on CCI for radish grown under varying amounts of blue light. Because CCI was not measured for wheat, it could not be compared with the literature.

Phytochrome photoequilibrium. It is unlikely that the variation in the amount of far red radiation (700 to 800 nm) among the three types of white LEDs contributed to photomorphogenic responses by affecting phytochrome. Differences were less than 0.02 (Table 1), indicating that any phytochrome involvement in the spectral responses observed in these studies would likely be negligible.

YPF/PPF ratio and photosynthetic efficiency. The YPF/PPF ratio of our light sources varied by less than 6% (from 0.86 to 0.91; Table 1). For a given light source, YPF has the potential to provide a better indication of net photosynthesis than PPF because YPF weights the quantum yield (moles of carbon fixed per moles of photons absorbed) for each wavelength of light (McCree, 1972). Thus, YPF should provide a better estimate of the photosynthetic efficiency of a given light source than PPF, and DW gain should increase as YPF increases. We estimated photosynthetic efficiency by calculating DW gain per unit leaf area. Surprisingly, we found that photosynthetic efficiency slightly decreased as YPF increased, especially in high light (Fig. 8). This indicates that YPF was not a better indicator than PPF of the photosynthetic efficiency of the light sources in this study. Furthermore, YPF may undervalue the efficiency of blue and green light in driving photosynthesis in whole plants and plant communities.

Conclusions

Absolute versus relative amounts of blue light. Most, but not all, of our results are similar to Dougher and Bugbee (2001a). Both studies sought to determine the effect of blue light on plant development, but the primary objective of our study was to determine which developmental parameters are best predicted by relative blue light and which by absolute blue light. We found that some developmental responses were a combination of both, but others were better predicted by one or the

other. An increase in absolute blue light, up to 50 $\mu mol \cdot m^{-2} \cdot s^{-1}$, better predicted a decrease in stem elongation in radish and soybean and also predicted a decrease in cotyledon area in radish. Furthermore, as absolute blue light increased, percent leaf DW decreased in radish and increased in soybean. In wheat, as absolute blue light increased, percent tiller DW increased dramatically up to 100 $\mu mol \cdot m^{-2} \cdot s^{-1}$.

However, an increase in relative blue light predicted a decrease in leaf area in radish and soybean. As blue light increased, chlorophyll concentration per unit leaf area (measured as CCI) increased, but chlorophyll concentration per unit leaf mass remained constant. Although an increase in blue light increased branching in soybean and tillering in wheat, and decreased SLA in radish and soybean,

neither the absolute nor relative amount of blue light better predicted any of these responses. As expected, growth increased with increasing *PPF*, but surprisingly, increasing blue light had no effect on total DW. Overall, *PPF* better predicted the photosynthetic efficiency of each light source than YPF. Because many developmental responses are determined by absolute blue light, our results also indicate that high *PPF* can partially substitute for low relative blue light in a given light source.

Manipulating plant growth and development. It is clear that light quantity and quality interact to determine plant morphology. The optimal light spectrum for plant growth and development likely changes with plant age as plant communities balance rapid leaf expansion necessary to maximize radiation capture with prevention of excessive stem elongation. A thorough understanding of this balance is essential to the development of LED light sources for plant growth and development. Overall, the low blue light from warm white LEDs increased stem elongation and leaf expansion, whereas the high blue light from cool white LEDs resulted in more compact plants. Initial growth under cool white LEDs should promote the growth of short, sturdy hypocotyls. Subsequent transition to warm white LEDs should promote leaf expansion. Finally, after canopy closure, cool white LEDs should be used again to prevent excessive stem elongation. These effects could also be obtained by modulating the electrical current to red and blue monochromatic LEDs, thereby achieving different blue ratios without the requirement for two sets of LEDs.

White LEDs. Cool white LEDs may be the light source of choice because their high percentage of blue light (25%) means that they can meet the blue light requirements for normal development, even at low *PPFs*. Furthermore, our measurements indicate that cool white LEDs are more electrically efficient than the neutral and warm white LEDs (data not shown). The efficiency of LEDs is rapidly increasing and is approaching the efficiency of HPS lamps (Pimputkar et al., 2009). As the
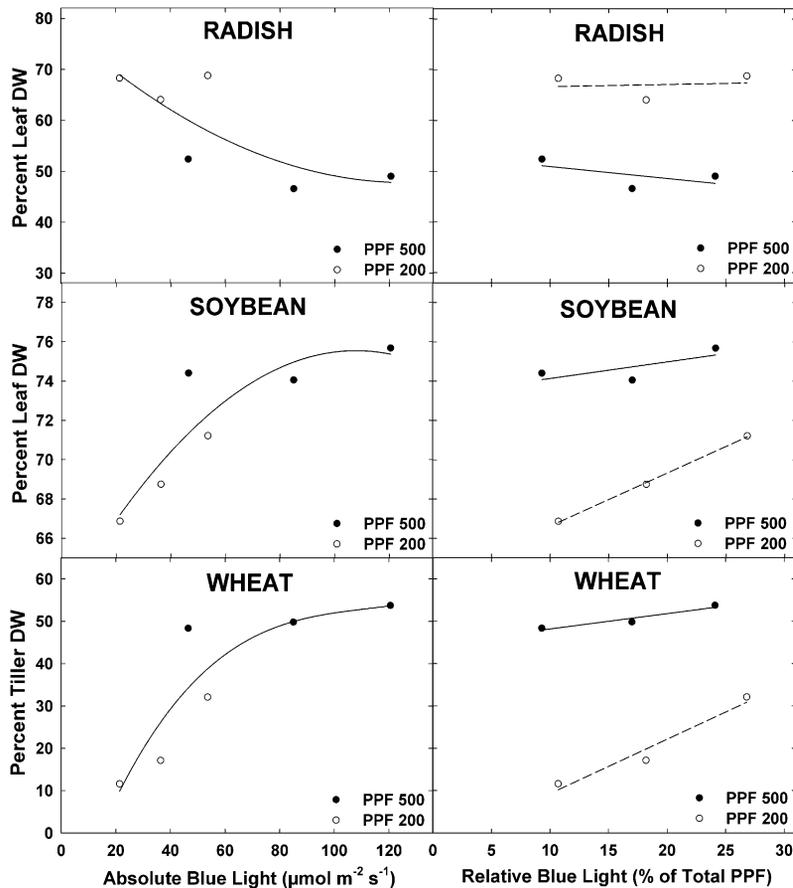

Fig. 6. Effect of absolute and relative blue light on percent leaf dry weight in radish and soybean and percent tiller dry weight in wheat. For soybean and radish, each data point represents the average of five plants with measurements taken 14 and 17 DAE, respectively; for wheat, each data point represents the average of 12 plants with measurements taken 22 DAE. DAE = days after emergence.
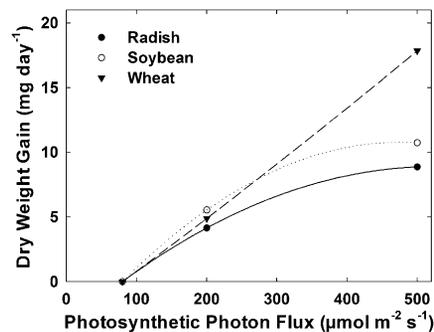

Fig. 7. The effect of photosynthetic photon flux (*PPF*) on dry weight gain. For soybean and radish, each data point represents the average of five plants with measurements taken 14 and 17 DAE, respectively; for wheat, each data point represents the average of 12 plants with measurements taken 22 DAE. The whole plant light compensation point was estimated at 80 $\mu mol \cdot m^{-2} \cdot s^{-1}$ for all three species. DAE = days after emergence.
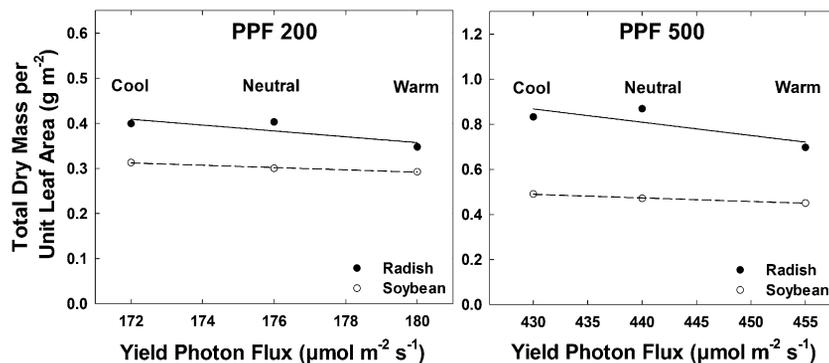

Fig. 8. The effect of yield photon flux (YPF) on total dry mass per unit leaf area. If YPF is an effective predictor of photosynthetic efficiency, the lines should increase with increasing YPF. The downward slope of these lines indicates that other photobiological factors have a larger effect on photosynthesis than YPF. YPF may undervalue the efficiency of blue and green light in whole plants and plant communities.

cost per photon decreases, we expect rapid incorporation into commercial applications.

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