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Photomorphogenesis, photosynthesis, and seed yield of wheat plants grown under red light-emitting diodes (LEDs) with and without supplemental blue lighting

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Abstract

Red light-emitting diodes (LEDs) are a potential light source for growing plants in spaceflight systems because of their safety, small mass and volume, wavelength specificity, and longevity. Despite these attractive features, red LEDs must satisfy requirements for plant photosynthesis and photomorphogenesis for successful growth and seed yield. To determine the influence of gallium aluminium arsenide (GaAlAs) red LEDs on wheat photomorphogenesis, photosynthesis, and seed yield, wheat (*Triticum aestivum* L., cv. 'USU-Super Dwarf') plants were grown under red LEDs and compared to plants grown under daylight fluorescent (white) lamps and red LEDs supplemented with either 1% or 10% blue light from blue fluorescent (BF) lamps. Compared to white light-grown plants, wheat grown under red LEDs alone demonstrated less main culm development during vegetative growth through pre-anthesis, while showing a longer flag leaf at 40 DAP and greater main culm length at final harvest (70 DAP). As supplemental BF light was increased with red LEDs, shoot dry matter and net leaf photosynthesis rate increased. At final harvest, wheat grown under red LEDs alone displayed fewer subtillers and a lower seed yield compared to plants grown under white light. Wheat grown under red LEDs + 10% BF light had comparable shoot dry matter accumulation and seed yield relative to wheat grown under white light. These results indicate that wheat can complete its life cycle under red LEDs alone, but larger plants and greater amounts of seed are produced in the presence of red LEDs supplemented with a quantity of blue light.

Key words: *Triticum aestivum* L., red light, blue light, subtillering, bioregenerative advanced life support.

Introduction

Light is the energy source for photosynthesis, and it regulates many aspects of plant development. A major challenge to growing plants in space will be controlling and supplying sufficient quantity and quality of light (Salisbury and Bugbee, 1988; Langhans and Dreesen, 1988; Sager and Wheeler, 1992). Light-emitting diodes (LEDs) are a promising electric light source for space-based plant growth chambers and bioregenerative advanced life support because of their small mass and volume, solid state construction, safety, and longevity (Barta *et al.*, 1992; Bula *et al.*, 1991). In the photosynthetically active radiation range, the electrical efficiency (μmol J^{-1})of gallium aluminium arsenide (GaAlAs) red LEDs has been reported to be greater than that of fluorescent lamps and comparable to high-pressure sodium lamps (Barta *et al.*, 1992). Red LEDs emit a narrow spectrum of light (660 nm with 25 nm bandwidth at half peak height) that is close to the maximum absorbance for both chlorophyll and phytochromes. Although red LEDs have great potential for use as a light source to drive photosynthesis, plants are adapted to utilize a wide-spectrum of light to control photomorphogenic responses (Kendrick and Kronenberg, 1994). Both red light, via phytochrome, and blue light, via blue/UV photoreceptor(s), are effective in inducing photomorphogenic responses (Barnes and Bugbee, 1991; Cosgrove, 1981; Mohr, 1987). Therefore, the growth,

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development, and seed production of different species of plants grown under specific wavelengths and narrow bandwidth must be characterized and understood before red LEDs can be accepted as an alternative light source for growing plants in space and in controlled environments.

Past studies have examined photomorphogenic responses of plants to red and blue light from broad-spectrum sources (Barnes and Bugbee, 1992; Britz and Sager, 1990; Wheeler *et al.*, 1991; Yorio *et al.*, 1995) and LEDs (Brown *et al.*, 1995; Bula *et al.*, 1991; Hoenecke *et al.*, 1992; Tennessen *et al.*, 1994). Pepper [*Capsicum annuum* L.] (Brown *et al.*, 1995), lettuce [*Lactuca sativa* L.] (Hoenecke *et al.*, 1992), and kudzu [*Pueraria lobata* (Willd) Ohwi.)] (Tennessen *et al.*, 1994), have been successfully grown under red LEDs for limited time periods. However, little published information is available on the use of LEDs to support plants through a complete life cycle (Barta *et al.*, 1990). The effect of red and blue light on wheat morphology has been studied using broad-spectrum lighting sources and selective filters (Barnes and Bugbee, 1991, 1992). Prior research using filters with broad-spectrum light sources did not allow investigation into the effects of an environment deficient in both blue and far-red, which may explain the absence of observed differences in the morphology of plants that were grown in a blue-deficient environment versus broad-spectrum light (McMahon *et al.*, 1991). With broad-spectrum light sources, longer wavelengths may overcome deficiencies in blue light (McMahon *et al.*, 1991). LEDs are useful for photobiological research due to their wavelength specificity (Brown *et al.*, 1995; Tennessen *et al.*, 1994). There was a specific interest in wheat because it is particularly useful for bioregenerative advanced life support applications and early spaceflight testing (Salisbury and Bugbee, 1988). The wheat cultivar 'USU-Super Dwarf' is a hard red spring wheat that was specifically developed (Utah Agricultural Experiment Station in co-operation with the National Aeronautics and Space Administration – NASA) for spaceflight and controlled environment applications where volume for growth is limited, but seed yield is at a premium (Salisbury and Bugbee, 1988). The objectives of this study were (1) to determine the usefulness of red LEDs in growing wheat through one full generation to produce seeds, and (2) to determine if supplemental blue radiation is required with red LEDs to achieve normal wheat photomorphogenesis, photosynthesis, and seed yield.

Materials and methods

Cultural conditions

Wheat seed (*Triticum aestivum* L., cv. 'USU-Super Dwarf') were imbibed in the dark on moistened germination paper for 72 h at 4 C followed by incubation at room temperature for 24 h. The newly germinated seedlings were transplanted into plastic pots (10 cm tall, 450 ml capacity, 12 seedlings pot^{-1}) containing peat-vermiculite media (Metro-Mix 220, Grace Sierra Co., Milpitas, CA). Within each of three growth chambers (Conviron PGW-36, Pembina, ND; 7.8 m^3 interior plant growth volume), nine pots were arranged in a 3×3 configuration inside of a 0.2 m^2 tray under each light treatment. To minimize edge and positional effects within each 3×3 configuration, pots were systematically rotated every other day. At 7 d after planting (DAP), the wheat seedlings were thinned to a density of 10 plants pot^{-1}. Growth chamber air temperature and relative humidity for all treatments were maintained at 22–24 °C and 65–75%, respectively. Fresh $0.25 \times$-strength modified Hoagland's nutrient solution (Hoagland and Arnon, 1950; Mackowiak *et al.*, 1989) was added daily to the bottom of each tray to supply nutrients and replenish evapo-transpirative water loss.

Light treatments

The four light sources were red LEDs alone, red LEDs + 1% blue fluorescent (BF), red LEDs + 10% blue fluorescent (BF), and daylight fluorescent (white). Spectral distribution scans were taken (at approximately equal total photosynthetic photon flux, *PPF*, 400–700 nm) from 300–1100 nm in 2 nm steps with a spectroradiometer (Model LI-1800; Li-Cor, Lincoln, NE). Contributions of blue (400–500 nm), red (600–700 nm), far-red (700–800 nm) and total *PPF* were determined from bandwidth integration. For the red LED treatments, plants were grown under arrays equipped with red gallium-aluminium-arsenide (GaAlAs) LEDs. The arrays were mounted in a 0.17 m^2 ventilated enclosure and contained 2624 individual diodes. For the red LEDs + blue light supplemented treatments, BF lamps (Philips 20-W F20T12/BB) were mounted around the LED arrays to supply approximately 1% or 10% of the total *PPF* (350 $\mu mol\ m^{-2}\ s^{-1}$) as determined by quantum sensor (Model LI-189; Li-Cor, Lincoln, NE) measurements at the top of the plant canopy. A vestibule made of black, opaque plastic precluded outside light from entering growth chambers which contained LED arrays. Control plants were grown under broad-spectrum daylight fluorescent lamps (Sylvania 115 W F48T12/D/VHO with a 3.5 mm-thick Plexiglas heat barrier) that provided approximately 30% of the total *PPF* in the blue region of the spectrum (400–500 nm).

Lighting for all treatments was continuous (24/0 h light/dark photoperiod) with approximately equal *PPF* at 350 $\mu mol\ m^{-2}\ s^{-1}$. *PPF* levels were measured daily at the top of the plant canopy with a quantum sensor. As the plant canopies grew closer to the light banks, *PPF* levels were maintained by adjusting the height of the pots and/or adjusting input wattage on separate power supplies for the LEDs (PD35–20D; Kenwood Corp., Tokyo) and BF lights (Model No. FX0696–4, Mercron, Richardson, TX). The daylight fluorescent (white) light bank and the array with red LEDs alone were in separate growth chambers. The red LED arrays supplemented with 1% or 10% BF light were located in the same growth chamber. The red LEDs + 1% BF light bank was positioned on the upper tier of the same rack immediately above the red LEDs + 10% BF light bank to eliminate enrichment of the 1% BF light treatment from the 10% BF light treatment. From the spectroradiometric data for each light treatment, red:far-red ratio (R:FR) and phytochrome photostationary state (PSS) were determined using the methods of Rajapakse *et al.* (1992) and Sager *et al.* (1988), respectively.

Plant measurements

Plant measurements were recorded to coincide with vegetative growth (15 d after planting; DAP), at pre-anthesis (25 DAP), and with grain fill (40 DAP). Main culm development at 15 and 25 DAP was measured as Haun stage (Haun, 1973). Flag leaf length was measured at 40 DAP. Shoot tissue after each harvest was immediately freeze-dried and then weighed for dry matter at 15, 25, and 40 DAP. Using the youngest fully expanded leaf (15 and 25 DAP) or the flag leaf (40 DAP), net leaf photosynthesis concentration was measured with a Li-Cor portable photosynthesis meter (Li-Cor Model LI-6200). Leaf stomatal conductance was measured in the youngest fully expanded leaf at 21 and 28 DAP using a steady state porometer (Li-Cor Model LI-1600).

For each treatment, final harvest occurred at 70 DAP, when the flag leaves were senescing and the main culm spikes were desiccating. Plant tissues were dried in an oven for 48 h at 70 °C before weighing. Final harvest measurements included: shoot dry matter, main culm length, main culm spike dry matter, subtiller number, subtiller spike number, and subtiller spike dry matter. In addition, seed dry matter, number, and yield were measured after final harvest. All shoots originating from the base of the plant (main culm) were scored as subtillers (Klepper *et al.*, 1983). Main culm length was the distance between the plant stem base at the soil line to the base of the main culm spike.

The experiment was repeated three times with means derived from 10 plants per repetition. Using 5% as the levels of significance, all data were subjected to analysis of variance (ANOVA, SAS Institute, Cary, NC). Mean separation was by Duncan's multiple range test.

Results

Lighting source characteristics

Spectroradiometric scans of the light sources demonstrated the contrasting spectral distribution between the narrow-spectrum 660 nm red LEDs (25 nm band width at half peak height) versus the broad spectral output of the daylight fluorescent (white) lamps (Fig. 1). Approximately 30.0–31.4% of the photosynthetic photon flux (*PPF*) from daylight fluorescent lamps was in the blue (400–500 nm) region of the spectrum (Table 1). Blue fluorescent lamps provided approximately 0.9–1.0% or 8.6–10% of the *PPF* in the blue region for red LEDs + 1% BF light and red LEDs + 10% BF light, respectively. For the red LED array without supplemental blue fluorescent lamps (red LEDs alone), there was no blue spectral component detected. The red:far-red (R:FR) ratio was 4.9 for the daylight fluorescent lamps (white light), while the red LED arrays had R:FR ratios ≥ 110. The phytochrome photostationary state (PSS) was 0.88 for the treatments involving red LED arrays, whereas the PSS for daylight fluorescent lamps was slightly lower at 0.80.

Vegetative, pre-anthesis, and grain fill

Compared to white light-grown plants, wheat grown under red LEDs, regardless of supplemental BF light, generally showed less main culm development at 15 and 25 DAP (Table 2). At 15, 25, and 40 DAP, shoot dry matter (Table 2) and rate of net leaf photosynthesis (Table 3) were both significantly lower in wheat grown under red LEDs alone relative to white light-grown wheat. In the presence of red LEDs supplemented with BF light, wheat had greater amounts of shoot matter and higher leaf net photosynthesis rates at 15, 25, and 40 DAP than wheat grown under red LEDs alone. Moreover, shoot dry matter and leaf net photosynthesis increased in wheat grown under red LEDs as BF light increased from 1% to 10%. Wheat grown under red LEDs + 10% BF showed similar amounts of shoot dry matter and leaf net photosynthesis rates to white light-grown wheat during most observations up until grain fill. The flag leaf at 40 DAP was significantly longer for plants grown under red LEDs alone relative to plants grown under white light or red LEDs supplemented with 1% or 10% BF light (Table 2).

Final harvest

In comparison to white light-grown wheat at final harvest (70 DAP), plants under red LEDs alone had significantly lower amounts of dry matter in terms of the shoot, main culm, and subtiller spikes, as well as showing fewer subtillers and subtiller spikes (Table 4). Seed number and yield were significantly greater in white light-grown wheat relative to wheat grown under red LEDs alone (Table 5). Supplementing LEDs with 10% BF light produced wheat similar to white light-grown wheat relative to shoot and main culm dry matter, subtiller number, seed yield, and seed number, while wheat grown under red LEDs + 1% BF light produced final harvest data more like observations for wheat under red LEDs alone. Wheat main culm length was significantly greater under red LEDs alone than plants under all other light regimes (Table 4).

Discussion

At the vegetative and pre-anthesis growth stages (15 and 25 DAP), the data (Table 2) agreed with previous studies that have shown that red-biased, blue-deficient light sources induce increased plant internode length, stem length and leaf elongation (Barnes and Bugbee, 1992; Britz and Sager, 1990; Brown *et al.*, 1995; Warrington *et al.*, 1976; Wheeler *et al.*, 1991) and decreased plant dry mass (Brown *et al.*, 1995; Smith, 1982). Because growth volume will most likely be limited in space-based bioregenerative life-support systems and controlled environments (Salisbury and Bugbee, 1988; Olsen *et al.*, 1988), overall plant growth area and stem length is of critical importance to future considerations of lighting technology. The flag leaf (Table 2) and main culm (Table 4) displayed significantly greater lengths when plants were grown under red LEDs alone as opposed to red LEDs supplemented with BF light. Thus, growth chamber space-saving advantages gained through utilizing red LEDs

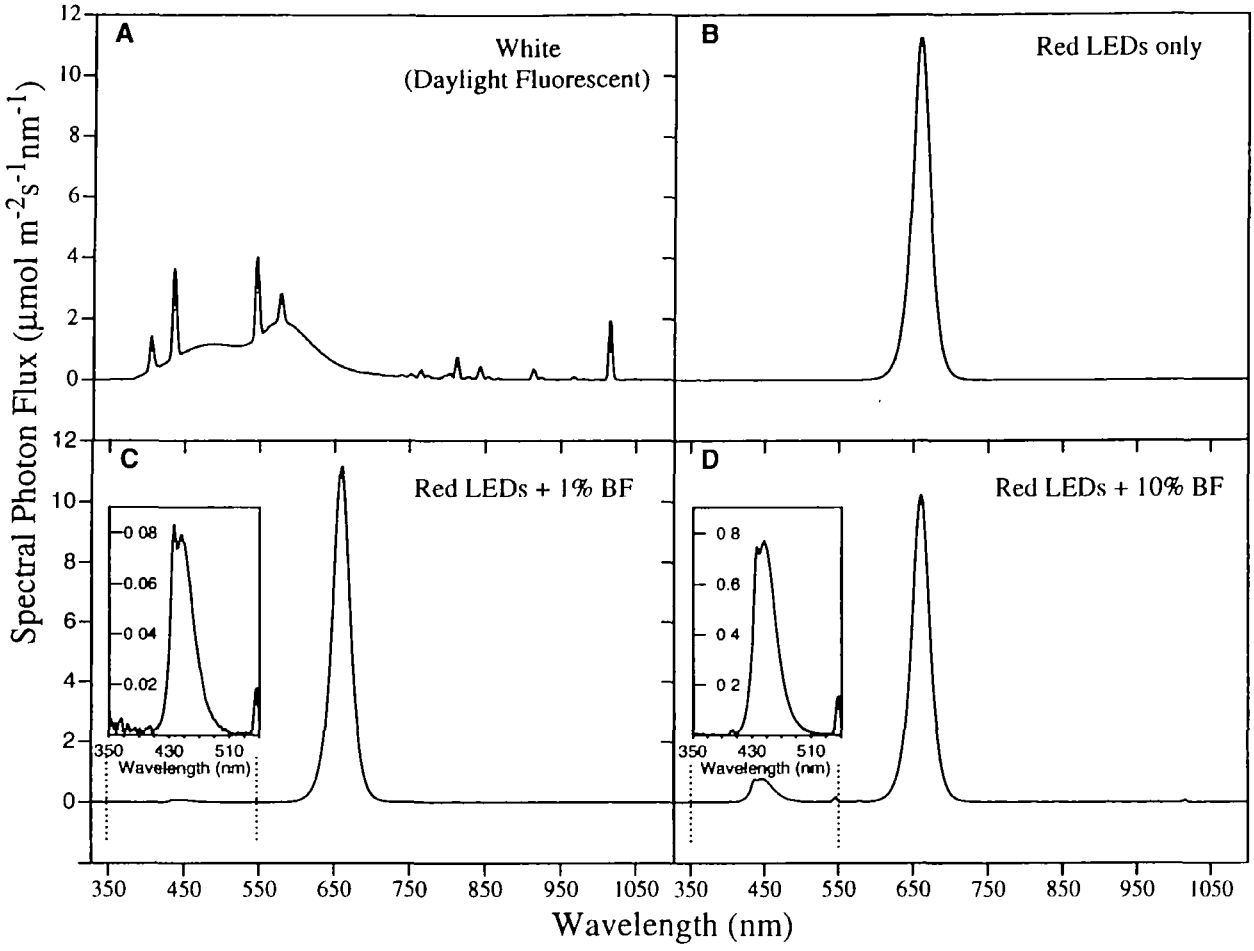

Fig. 1. Spectral distribution (300–1100 nm) of light from (A) daylight fluorescent lamps, (B) red light-emitting diodes (LEDs), (C) red LEDs + 1% blue fluorescent (BF) lamps, and (D) red LEDs + 10% BF lamps. Spectral scans were recorded at the top of the plant canopy with a spectroradiometer. Total *PPF* was approximately 350 μmol m^{-2} s^{-1} for all treatments.

Table 1. *Spectral data for daylight fluorescent lamps (white), red LEDs + 10% BF*[a] *lamps, red LEDs + 1% BF lamps, or red LEDs alone*

Measurements were taken at the top of the plant canopy with a spectroradiometer.

Characteristic	Lamp			
	White	Red + 10% BF	Red + 1% BF	Red
		(μmol m^{-2} s^{-1})		
300–400	3	0	0	0
400–500	110	30	3	0
500–600	171	2	1	0
600–700	69	319	345	349
700–800	14	3	3	2
800–1100	29	1	0	0
PPF[b] (400–700)	350	351	349	349
Total photon flux (300–1100)	396	354	352	351
R · FR[c]	4.9	110.4	127.3	150.6
PSS[d]	0 80	0.88	0.88	0.88

[a] BF = Blue fluorescent.
[b] *PPF* = Photosynthetic photon flux.
[c] R = 600–700 nm: FR = 700–800 nm (Rajapakse *et al.*, 1992).
[d] Phytochrome photostationary state calculated according to Sager *et al.* (1988).

Table 2. *Growth and development measurements for wheat plants grown under white light, red LEDs+10% BF[a] light, red LEDs+1% BF light, or red LEDs alone at 15, 25, and 40 DAP[b]*

DAP	Lamp			
	White	Red+10% BF	Red+1% BF	Red
			Haun stage	
15	3.9 a[c]	3.7 ab	3.6 b	3.6 b
25	6.4 a	6.0 b	6.0 b	5.8 b
			Flag leaf length (cm)	
40	11.3 b	11.3 b	10.5 b	14.7 a
			Shoot DM[d] (g)	
15	0.10 a	0.10 a	0.09 ab	0.07 b
25	0.33 a	0.31 a	0.21 b	0.19 b
40	1.18 a	0.76 b	0.48 c	0.46 c

[a] BF = Blue fluorescent.
[b] DAP = Days after planting.
[c] Within a row, values followed by different letters are significantly different at the 5% probability level.
[d] DM = dry matter.

Table 3. *Net rate of leaf photosynthesis (carbon dioxide uptake) for wheat plants grown under white light, red LEDs+10% BF[a] light, red LEDs+1% BF light, or red LEDs alone at 15, 25, and 40 DAP[b]*

DAP[b]	Lamp			
	White	Red+10% BF	Red+1% BF	Red
			(μmol CO_2 m^{-2} s^{-1})	
15	8.4 a[c]	8.3 a	5.3 b	3.8 c
25	9.3 a	6.7 b	5.1 c	2.9 d
40	7.5 a	6.7 a	5.0 ab	3.2 b

[a] BF = Blue fluorescent.
[b] DAP = Days after planting.
[c] Within a row, values followed by different letters are significantly different at the 5% probability level.

over conventional lighting is greatest when red LEDs are supplemented with blue radiation.

Lower dry matter accumulation (Tables 2, 4) in wheat grown under red LEDs alone may be related to the lower CO_2 assimilation rate, as suggested by the measured lower net leaf photosynthesis rate (Table 3). In another study that compared red LEDs with white light-grown plants, photosynthesis in kudzu was greater under red LEDs at low photon intensities (175 μmol m^{-2} s^{-1}), but was slightly lower at higher photon intensities, and was equal at saturating CO_2 levels (Tennessen *et al.*, 1994). The lower photosynthesis in plants under red LEDs may be associated with lower stomatal conductance (Farquhar and Sharkey, 1982), for stomata have been shown to be controlled more by blue light than red light (Sharkey and Raschke, 1981; Zeiger, 1984). In this study, stomatal conductance increased as the level of blue light increased (data not shown), which suggests that decreased stomatal conductance was a contributing factor to lower photosynthetic rates under red LEDs. It has also been suggested that the narrow peak emission of red LEDs leads to an imbalance of photons available to photosystem I and photosystem II, thus altering the ratio of cyclic to whole chain electron transport, and causing a reduction in net photosynthesis (Tennessen *et al.*, 1994). Moreover, red LEDs produce less non-photosynthetic radiation than conventional lamps (Barta *et al.*, 1992), which implicates differences in photosynthesis utilization efficiency of photons emitted from LEDs relative to broad-spectrum lamps (Sager *et al.*, 1982).

In this study, white light-grown wheat was observed to form subtillers much earlier in their life cycle than wheat grown in the presence of red LEDs, irrespective of supplemental BF (Table 4). Although, earlier forming subtillers are more likely to successfully produce seed bearing spikes (Simmons *et al.*, 1987), subtiller spikes under white light made little contribution to overall seed yield. This was evident by the non-significant difference in seed yield (Table 5) between wheat grown under white light or red LEDs+10% BF, despite white light-grown wheat having significantly more subtiller spikes (Table 4). The main culm spike matures first and has a higher harvest index than subtillers, and thus, less subtiller formation potentially is a desirable characteristic in a controlled environment for maximizing yield per unit time (Barnes and Bugbee, 1992; Bugbee and Salisbury, 1988), while

Table 4. *Shoot, main culm, and subtiller measurements at 70 DAP[a] for wheat plants grown under white light, red LEDs+10% BF[b] light, red LEDs+1% BF light, or red LEDs alone*

Measurement	Lamp			
	White	Red+10% BF	Red+1% BF	Red
Shoot DM[c] (g)	1.72 a[d]	1.42 ab	0.85 b	0.93 b
Main culm length (cm)	29.9 a	29.5 a	29.3 a	32.5 b
Main culm spike DM (g $plant^{-1}$)	0.77 a	0.71 a	0.38 b	0.38 b
Subtiller number/plant	2.5 a	2.4 a	1.2 b	1.4 b
Subtiller spike number/plant	2.2 a	1.3 b	1.0 b	1.4 b
Subtiller spike DM (g $plant^{-1}$)	0.43 a	0.10 b	0.10 b	0.08 c

[a] DAP = Days after planting.
[b] BF = Blue fluorescent.
[c] DM = Dry matter.
[d] Within a row, values followed by different letters are significantly different at the 5% probability level.

Table 5. *Seed yield measurements at 70 DAP[a] for wheat plants grown under white light, red LEDs + 10% BF[b] light, red LEDs + 1% BF light, or red LEDs alone*

Measurement	Lamp			
	White	Red + 10% BF	Red + 1% BF	Red
DM[c] (mg)/seed	31.5 a[d]	25.6 ab	21.7 b	26.1 ab
Seed yield (g)/plant	0.71 a	0.54 ab	0.27 b	0.29 b
Seed number/plant	23.8 a	22.3 ab	12.8 ab	11.5 b

[a]DAP = Days after planting.
[b]BF = Blue fluorescent.
[c]DM = Dry matter.
[d]Within a row, values followed by different letters are significantly different at the 5% probability level.

conserving growth area. Therefore, given sufficient supplemental BF light, delayed subtiller formation by wheat under red LEDs may be a beneficial photomorphogenic response relative to allocation of plant resources for maximizing final seed yield. Previous studies have shown that wheat produces more subtillers with increasing amounts of blue light, provided that the phytochrome photostationary state (*PSS*) is held constant (Barnes and Bugbee, 1991, 1992).

Optimal yield from other plant species under red LEDs has required supplemental radiation from the blue region of the spectrum (Brown *et al.*, 1995; Bula *et al.*, 1991; Hoenecke *et al.*, 1992). Other wheat studies have reported that reducing *PSS* increases development of the main culm (Barnes and Bugbee, 1992). In this study, the differences in shoot dry matter (Tables 2, 4), net leaf photosynthesis (Table 3), and seed yield (Table 5) among wheat plants under different light treatments appeared to derive from the difference in the amount of blue light rather than a change in *PSS* (Table 1). Red LED arrays had approximately equivalent *PSS* (0.88) and *PPF* (350 μmol m^{-2} s^{-1}), while blue light level varied (Table 1). The *PSS* values ($\geq$0.80 for all treatments) were near the maximum value of about 0.89 (Sager *et al.*, 1988), which might suggest that the *PSS* difference between white light and red LED arrays might be negligible (Smith and Holmes, 1977). In the present study, 1% supplemental BF light appeared to have little effect on final shoot dry matter accumulation (Table 4) and seed yield (Table 5) when compared to red LEDs alone. Whereas, addition of 10% BF light to red LEDs consistently produced shoot dry matter and seed yield close that of white light, despite the fact that white light had a slightly lower *PSS* and higher amounts of blue light. This might suggest that there is an minimum threshold level for blue light (Wheeler *et al.*, 1991) for optimal wheat development under a red-biased light source. Furthermore, this study supported evidence that some differences in light treatments can be explained better by B:R (blue:red) or B:FR (blue:far-red) ratios than R:FR (red:far-red) ratios (Rajapakse *et al.*, 1992; Wheeler *et al.*, 1991). The principle of equivalent action of phytochrome predicts that different light sources with the same *PSS* are perceived by the same, and therefore, should impart the same plant response (Sponga *et al.*, 1986). However, blue light appears to interact with the phytochrome system or through a blue light receptor which elicits plant responses (Gaba and Black, 1987; Rajapakse *et al.*, 1992). This study further demonstrated the important involvement of blue light in regulation of wheat growth, and the complex interactions of these photosystems. However, it is uncertain whether photomorphogenic responses to blue light are interdependent (Mohr, 1987) or independent (Cosgrove, 1981) of the phytochrome response.

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