Photochemistry and Photobiology, 2001, 73(2): 208–212

Evidence for Yellow Light Suppression of Lettuce Growth¶

Tracy A. O. Dougher* and Bruce Bugbee

Crop Physiology Laboratory, Department of Plants, Soils and Biometeorology, Utah State University, Logan, UT

Received 24 July 2000; accepted 30 October 2000

ABSTRACT

Researchers studying plant growth under different lamp types often attribute differences in growth to a blue light response. Lettuce plants were grown in six blue light treatments comprising five blue light fractions (0, 2, 6% from high-pressure sodium [HPS] lamps and 6, 12, 26% from metal halide [MH] lamps). Lettuce chlorophyll concentration, dry mass, leaf area and specific leaf area under the HPS and MH 6% blue were significantly different, suggesting wavelengths other than blue and red affected plant growth. Results were reproducible in two replicate studies at each of two photosynthetic photon fluxes, 200 and 500 μmol m^{-2} s^{-1}. We graphed the data against absolute blue light, phytochrome photoequilibrium, phototropic blue, UV, red:far red, blue:red, blue: far red and 'yellow' light fraction. Only the 'yellow' wavelength range (580–600 nm) explained the differences between the two lamp types.

INTRODUCTION

The use of different lamps in controlled environments has led to the discovery of gross changes in plant morphology caused by altered spectral quality. The photomorphogenic changes caused by altered phytochrome photoequilibrium (PPE)† are well documented (1). However, lamp types with similar PPE can significantly alter leaf and stem morphology. These studies suggest that morphological differences are caused by differences in the blue portion of the spectrum (2–7). Unfortunately, nonblue wavelengths also varied with lamp types in these studies, so definitive conclusions have to be questioned. In a companion paper (8), we compared lettuce growth under high-pressure sodium (HPS) lamps with metal halide (MH) lamps that were filtered to 6% blue. Chlorophyll concentration, dry mass, leaf area and specific leaf area (SLA) were sensitive to the remaining spectral output. Here we examine other known spectral responses to explain the morphological and growth differences we observed with this plant species.

MATERIALS AND METHODS

Lettuce (*Lactuca sativa*, cv. Grand Rapids) was grown in six blue light treatments (0, 2, 6% from HPS lamps and 6, 12, 26% from MH lamps) comprising five blue light fractions (Table 1, cols. 1–3) at a photosynthetic photon flux (PPF) of 200 and 500 μmol m^{-2} s^{-1} and a 16 h photoperiod. There were two replicate studies at each PPF level. A comparison of HPS (Sylvania Lumalux) and MH (Sylvania Metalarc) at 6% blue was used to determine if any parameter differences were caused by other wavelengths. Plants were grown hydroponically at 26/22°C day/night temperature, 70% relative humidity and elevated carbon dioxide (1000 μmol mol^{-1}). Other growing procedures, environmental conditions and measurement techniques are described in the companion paper (8).

RESULTS AND DISCUSSION

As reported in the companion paper (8), the two 6% blue treatments produced significantly different chlorophyll concentrations, dry masses, leaf areas and SLA in lettuce. This phenomenon was visually apparent in each replicate trial of this experiment and in preliminary trials before this experiment (9). It is unlikely that these differences were caused by other environmental differences between compartments because (1) treatments were randomized each time; and (2) atmospheric differences (carbon dioxide, humidity and temperature) between compartments were minimized by the use of a common air conditioning system. Apparently in lettuce, some wavelength(s) acts in conjunction with blue to affect plant growth. The data for chlorophyll concentration and total dry mass (Figs. 1a and 2a) are representative of the results for the other parameters. Here we analyze the effects of the other wavelengths we have considered.

Thermal radiation

Although the thermal radiation (700–10 000 nm) emitted by unfiltered HPS and MH lamps is considerable and different for the two lamp types, the thermal radiation in these experiments was equalized by recirculating, chilled water barriers.

Amount of blue photons

As discussed in the companion paper (8), some plant responses are determined by the quantity of blue photons rather than the fraction of blue photons. However, both of the 6% blue treatments had the same amount of blue photons at each PPF: 12 μmol m^{-2} s^{-1} blue at 200 μmol m^{-2} s^{-1} or 30

¶Posted on the website on 30 November 2000.

*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:* B:FR, blue to far-red ratio; B:R, blue to red ratio; HPS, high pressure sodium; MH, metal halide; PPE, phytochrome photoequilibrium; R:FR, red to far-red ratio; SLA, specific leaf area.

Table 1. Ratios and amounts of radiation for the blue light fractions used in these studies. Two lamp types were used, HPS and MH

PPF	Lamp type	Blue light			UV		Ratios				Yellow light
		Fraction (% of 320–700 nm)	Photons (320–496 nm) (μmol m^{-2} s^{-1})	Phototropic* (300–520 nm) (μmol m^{-2} s^{-1})	Fraction (% of 320–496 nm)	Photons (320–400 nm) (μmol m^{-2} s^{-1})	PPE (P_{fr}/P_{total})	R:FR 600–700 nm/ 700–800 nm	B:R 320–496 nm/ 600–700 nm	B:FR 320–496 nm/ 700–800 nm	(580–600 nm) (% of 320–700 nm)
200	HPS	0.1	0.2	0.1	0.5	0.001	0.86	2.80	0.003	0.012	32
	HPS	1.5	3	1.8	3.3	0.1	0.85	2.71	0.033	0.155	26
	HPS	6†	12	6.8	3.7	0.44	0.86	2.86	0.133	0.661	25
	MH	6	12	6.3	12.0	1.44	0.84	4.39	0.220	1.306	27
	MH	12	24	13	16.6	3.98	0.83	4.13	0.453	2.593	25
	MH	26†	52	29	14.9	7.76	0.82	5.11	1.209	7.818	19
500	HPS	0.1	0.5	0.3	0.5	0.0025	0.86	2.80	0.003	0.012	32
	HPS	1.5	7.5	4.1	3.3	0.25	0.85	2.71	0.033	0.155	26
	HPS	6†	30	17	3.7	1.10	0.85	2.86	0.133	0.661	25
	MH	6	30	16	12.0	3.60	0.85	4.39	0.220	1.306	27
	MH	12	60	31	16.6	9.95	0.84	4.13	0.453	2.593	25
	MH	26†	130	71	14.9	19.40	0.82	5.11	1.209	7.818	19

*Weighting factors from Baskin and Iino (10). PPF = photosynthetic photon flux; PPE = phytochrome photoequilibrium.
†Blue fraction from the lamp filtered only with tempered glass and water, others filtered with tempered glass, water, and yellow cellulose triacetate.

μmol m^{-2} s^{-1} blue at 500 μmol m^{-2} s^{-1} (Table 1, col. 4). Graphically, data points for 6% blue between PPF levels are separated, but the two data points within PPF levels are not separated (Figs. 1b and 2b). The quantity of blue photons could not have caused the differences in growth between the two 6% blue treatments.

Phototropic blue

Considering that the range of wavelengths that we used to define 'blue light' may not be the most appropriate for lettuce, we reanalyzed the data using the blue response curve for phototropism developed by Baskin and Iino (10). This phototropic response curve unequally weights the different wavelengths from 300 to 520 nm based on curvature response of alfalfa seedlings. Weighting our data with this curve yielded blue levels that were similar to our 6% blue treatments (Table 1, col. 5), so the response curves look very similar to the absolute blue light curves (Figs. 1c and 2c). Therefore, differences in growth between 6% blue HPS and 6% blue MH were not related to phototropic blue levels.

Absolute UV

MH emits more UV (300–400 nm) than HPS lamps, but our system had a water and tempered glass barrier that greatly reduced the UV from both sources. However, not all UV was filtered out and the MH treatments still had three to four times more UV (Table 1, col. 7). The UV difference between the two 6% blue treatments further separates the data (Figs. 1d and 2d). The differences between the two 6% blue treatments were not related to differences in the amount of UV.

UV as a percent of blue

We included UV-A (320–400 nm) as part of the blue range, but MH attains more of its 'blue light' from the UV range. Indeed at 6% blue, UV as a percent of blue is higher for MH than for HPS (Table 1, col. 6). However, graphing the data this way also further separates the data in the wrong direction (Figs. 1e and 2e).

Phytochrome photoequilibrium

The PPE for all treatments ranged from 0.82 to 0.86 (Table 1, col. 8). This range is likely too small to elicit varied phytochrome effects. At the low light level, the data tends to become separated, while at the higher light level the PPE are similar for the 6% blue treatments (Figs. 1f and 2f).

Blue to red and blue to far red ratios

Goins *et al.* (11) suggested that the blue response could be altered by an interaction between blue and red (B:R) or blue and far-red (B:FR). Once again, there is a difference between 6% blue HPS and MH values for B:R and B:FR (Table 1, cols. 9 and 10), but these ratios also tend to separate the data (Figs. 1g,h and 2g,h).

Red to far-red ratio

Although PPE should predict more accurately the phytochrome responses than the red to far-red ratio (R:FR), most phytochrome response research utilizes R:FR ratio rather

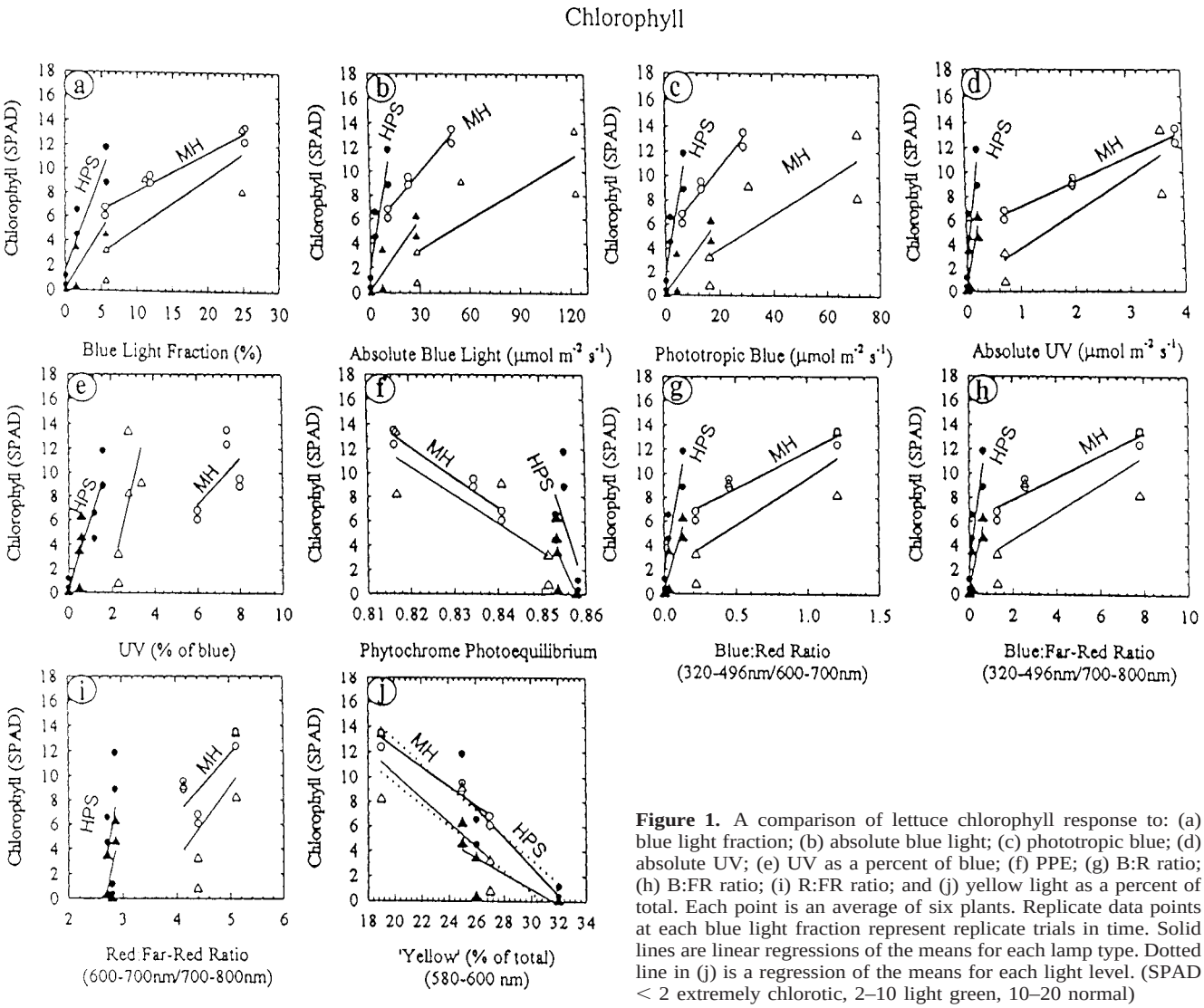

Figure 1. A comparison of lettuce chlorophyll response to: (a) blue light fraction; (b) absolute blue light; (c) phototropic blue; (d) absolute UV; (e) UV as a percent of blue; (f) PPE; (g) B:R ratio; (h) B:FR ratio; (i) R:FR ratio; and (j) yellow light as a percent of total. Each point is an average of six plants. Replicate data points at each blue light fraction represent replicate trials in time. Solid lines are linear regressions of the means for each lamp type. Dotted line in (j) is a regression of the means for each light level. (SPAD $<$ 2 extremely chlorotic, 2–10 light green, 10–20 normal)

than PPE (1). The R:FR ratios from the MH lamps are almost double those from the HPS lamps (Table 1, col. 11), but again graphing on an R:FR axis further separates the data (Figs. 1i and 2i).

'Yellow' wavelengths

We analyzed the lamp outputs in 20 nm increments to find a wavelength range that would make the data fit a continuous curve. The light fraction output of the two lamp types varies considerably at certain wavelengths (Fig. 3), for example between 500 and 550 nm. Because the plant responses under 2% HPS and 6% MH are not statistically different, we sought wavelengths where the spectral output for 2% HPS and 6% MH were equivalent. At 580–600 nm, lamp plus filter spectral output is equivalent for the 2% HPS and 6% MH treatments. At 580–600 nm the 6% HPS and 12% MH treatments also have similar spectral outputs (Table 1, col. 12). The response curve quickly becomes less continuous when the 'yellow' wavelength range is altered by adding, subtracting or shifting wavelengths. From this analysis, 'yellow' light (580–600 nm) appears to inhibit lettuce growth.

Although there is no known relationship between human perception of color and plant physiological response, 580–600 nm is generally considered to be 'yellow' light (12). There is sparse literature on 'yellow' light (580–600 nm) effects on plant growth because researchers tend to classify wavelengths from 500 to 600 nm as 'green' light. However, there are two major reasons we are making comparisons to the 'green' light literature: (1) 'Green' light research often includes 500–600 nm wavelengths and therefore includes 'yellow' light; and (2) because 'yellow' (580–600 nm) and 'green' (500–580 nm) wavelengths are both equally and more readily transmitted through the canopy, both 'yellow' and 'green' wavelengths may be signals to inhibit growth below the canopy. In our analysis, we have included citations from several 'green' light studies, which include wavelengths outside the 580–600 nm range, but which we feel may be related to our results. Where the data was available, the actual wavelengths studied are included in parentheses so that readers may draw their own conclusions.

Our analysis suggests that 'yellow' light from 580 to 600 nm suppresses chlorophyll or chloroplast formation (Fig. 1j).

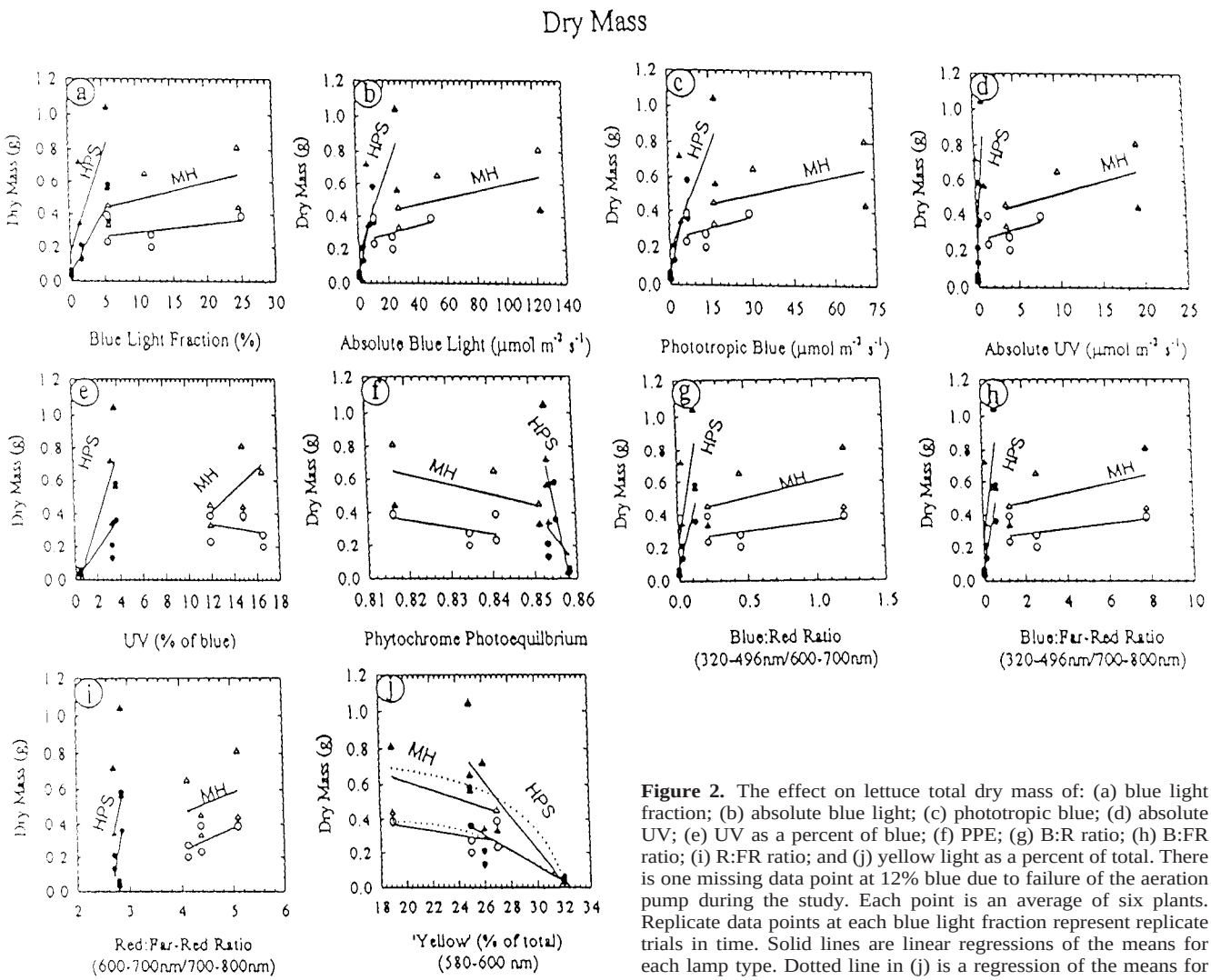

Figure 2. The effect on lettuce total dry mass of: (a) blue light fraction; (b) absolute blue light; (c) phototropic blue; (d) absolute UV; (e) UV as a percent of blue; (f) PPE; (g) B:R ratio; (h) B:FR ratio; (i) R:FR ratio; and (j) yellow light as a percent of total. There is one missing data point at 12% blue due to failure of the aeration pump during the study. Each point is an average of six plants. Replicate data points at each blue light fraction represent replicate trials in time. Solid lines are linear regressions of the means for each lamp type. Dotted line in (j) is a regression of the means for each light level.

In *Euglena,* Schwartzbach (13) determined that 'green' light (peak stimulation at 597 nm) was less effective than blue in the synthesis of chlorophyll when light was saturating. In a review article on green light, Klein (14) cited work finding shrinkage in the chloroplast of *Elodea* and many common species ('green' light ranged 500–550 nm), but failed to cite the work of Possingham *et al.* (15), who found 'green' light (peak output at 525 nm) enlarged chloroplasts compared to high-light controls.

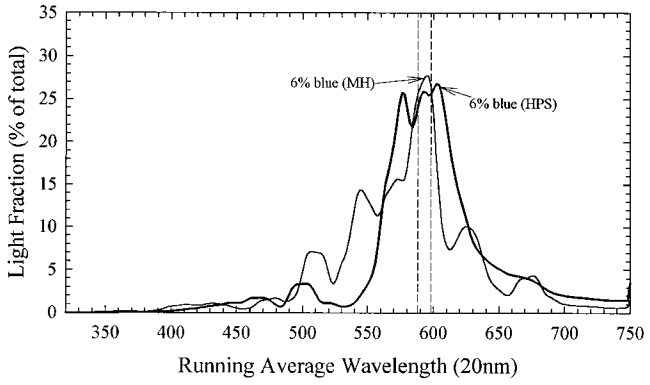

Figure 3. The light fraction as a percent of total for 20 nm running average increments from 320 to 750 nm for the 6% blue light treatments from HPS lamps (thick line) and MH lamps (thin line).

Our data suggest 'yellow' light from 580 to 600 nm also suppresses plant growth (Fig. 2j). This is counterintuitive because we know that 'yellow' light is only slightly less effective at photosynthesis than blue or red lights (16) and important for deep leaf carbon dioxide fixation (17). Klein (14) reviewed the effects of 'green' light on plants, and suggested that 'green' light (studies ranged from 500 to 600 nm) represses plant growth and development. However, the plant studies cited are: (1) a quarter to a half century old, so light measurements (ergs, foot-candles) used to equalize light, we now know, are inaccurate for plants (18,19) or were not equalized (20); (2) did not directly compare 'green' light to other wavelengths (20); (3) varied wavelengths along with 'green' (19); or (4) are misrepresented by Klein—such as Vince *et al.* (21) studied photoperiod and flowering not vegetative growth, and Bjorn *et al.* (22) studied wheat roots not leaves. More recently, Mandoli and Briggs (23) warn against

using green 'safe' lights due to a measured phytochrome response even to low irradiance levels of 'green' (500–550 nm). The effect of 'green' light continues to be controversial. Young *et al.* (24) showed *Hibiscus* increased plant height with increasing 'green' (500–600 nm)/total radiation, but Sup *et al.* (25) showed 'green' light (500–600 nm) to be least effective in promoting *Hibiscus* growth and development. Most relevant to our research, Al-Wakeel and Hamed (26) showed more growth suppression under 'yellow' (peak output at 595 nm) than 'green' (peak output at 520 nm) light in cucumbers. Even recent studies claiming 'green' or 'yellow' light responses use unequal photosynthetic photon fluxes (26,27), do not provide sources with clean cut-off and therefore vary wavelengths other than 'green' (27), or fail to report complete spectral outputs from their lamp and filter sources (26,28–30).

Although whole-plant 'yellow/green' light effects have been reported in many species, few studies have included appropriate controls and the conclusions are contradictory. This may be due to the range of wavelengths included in the studies. More rigorous studies are needed to resolve the conflicting conclusions. Our data also suggest that 'yellow' light repression of growth may be unique to only a few species, including lettuce.

Acknowledgements—This research was supported by the National Aeronautics and Space Administration Advanced Life Support Program administered by the Johnson Space Center, and by the Utah State Agriculture Experiment Station, Utah State University. Approved as journal paper 7319. The authors wish to thank Dr. Ted Tibbitts for his thorough and inciteful review.

REFERENCES

1. Ballare, C. L., A. L. Scopel and R. A. Sanchez (1995) Plant photomorphogenesis in canopies, crop growth, and yield. *HortScience* **30**, 1172–1181.
2. Britz, S. J. and J. C. Sager (1990) Photomorphogenesis and photoassimilation in soybean and sorghum grown under broad spectrum or blue-deficient light sources. *Plant Physiol.* **94**, 448–454.
3. Warrinton, I. J. and K. J. Mitchell (1976) The influence of blue- and red-biased light spectra on the growth and development of plants. *Agric. Meteorol.* **16**, 247–262.
4. Tibbitts, T. W., D. C. Morgan and I. J. Warrington (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. Hortic. Sci.* **108**, 622–630.
5. Wheeler, R. M., C. L. Mackowiak and J. C. Sager (1991) Soybean stem growth under high-pressure sodium with supplemental blue lighting. *Agric. J.* **83**, 903–906.
6. Yorio, N. C., C. L. Mackowiak, R. M. Wheeler and J. C. Sager (1995) Vegetative growth of potato under high-pressure sodium, high-pressure sodium SON-Agro, and metal halide lamps. *HortScience* **30**, 374–376.
7. Dougher, T. A. O. and B. G. Bugbee (1997) Effect of lamp type and temperature on development, carbon partitioning and yield of soybean. *Adv. Space Res.* **20**, 1895–1899.
8. Dougher, T. A. O. and B. G. Bugbee (2001) Differences in the response of wheat, soybean, and lettuce to reduced blue radiation. *Photochem. Photobiol.* **73**(2), 199–207.
9. Dougher, T. A. O. and B. G. Bugbee (1998) Is blue light good or bad for plants? *Life Support Biosphere Sci.* **5**, 129–136.
10. Baskin, T. I. and M. Iino (1987) An action spectrum in the blue and ultraviolet for phototropism in alfalfa. *Photochem. Photobiol.* **46**, 127–136.
11. Goins, G. D., N. C. Yorio, M. M. Sanwo and C. S. Brown (1997) Photomorphogenesis, photosynthesis, and seed yield of wheat plants grown under red light-emitting diodes (LEDs) with and without supplemental blue lighting. *J. Exp. Bot.* **48**, 1407–1413.
12. Salisbury, F. B. and C. W. Ross (1992) *Plant Physiology*, 4th Ed. Wadsworth Publishing, Belmont.
13. Schwartzbach, S. D. (1990) Photocontrol of organelle biogenesis in *Euglena*. *Photochem. Photobiol.* **51**, 231–254.
14. Klein, R. M. (1992) Effect of green light on biological systems. *Biol. Rev. Camb. Philos. Soc.* **67**, 199–284.
15. Possingham, J. V., D. G. Cran, R. J. Rose and B. R. Loveys (1975) Effects of green light on the chloroplasts of spinach leaf discs. *J. Exp. Bot.* **26**, 33–42.
16. McCree, K. J. (1972) Test of current definitions of photosynthetically active radiation against leaf photosynthesis data. *Agric. Meteorol.* **10**, 443–453.
17. Sun, J., J. N. Nishio and T. C. Vogelmann (1998) Green light drives CO_2 fixation deep within leaves. *Plant Cell Physiol.* **39**, 1020–1026.
18. Vince, D. (1965) Studies on the effects of light quality on the growth and development of plants. II. Formative effects in *Lycopersicon esculentum* and *Pisum sativum*. *J. Hortic. Sci.* **31**, 16–24.
19. Klein, R. M., R. C. Edsall and A. C. Gentile (1965) Effects of near ultraviolet and green radiations on plant growth. *Plant Physiol.* **40**, 903–906.
20. Vlitos, J. and W. Meudt (1975) The effect of light and of the shoot apex on the action of gibberellic acid. *Contrib. Boyce Thompson Inst.* **19**, 55–62.
21. Vince, D., J. Blake and R. Spencer (1964) Some effects of wave-length of the supplementary light on the photoperiodic behaviour of the long-day plants, carnation and lettuce. *Physiol. Plant.* **17**, 119–125.
22. Bjorn, L. O., Y. Suzuki and J. Nilsson (1963) Influence of wavelength on the light response of excised wheat roots. *Physiol. Plant.* **16**, 132–141.
23. Mandoli, D. F. and W. R. Briggs (1981) Phytochrome control of two low-irradiance responses in etiolated oat seedlings. *Plant Physiol.* **67**, 733–739.
24. Young, H. K., C. J. Hwan, K. K. Sun and H. K. Yang (1997) Effects of light quality on growth and flowering of *Hibiscus syriacus* L. *J. Korean Soc. Hortic. Sci.* **38**, 272–277.
25. Sup, S. W., P. H. Soon and L. J. Ho (1997) Effect of light quality on the growth of *Hibiscus syriacus* L. *Res. Rep. Genet. Res. Inst.* 104–111.
26. Al-Wakeel, S. A. M. and A. A. Hamed (1996) Light-quality effect on growth and some biochemical aspects of mild-stressed *Cucurbita pepo* L. *Egyptian J. Bot.* **36**, 217–233.
27. Islam, M. O., S. Matsui and S. Ichihashi (1999) Effects of light quality on seed germination and seedling growth of *Cattleya* orchids *in vitro*. *J. Jpn Soc. Hortic. Sci.* **68**, 1132–1138.
28. Akanda, R. U., J. J. Mullahey and D. G. Shilling (1996) Environmental factors affecting germination of tropical soda apple (*Solanum viarum*). *Weed Sci.* **44**, 570–574.
29. Negretskii, V. A., V. N. Lozhnikova and V. A. Kanevskii (1991) Effect of green light of different spectral length on flowering of the short-day plant red goosefoot (*Chenopodium rubrum* L.). *Dokl. Bot. Sci. Akad. Nauk. SSSR* **313/315**, 73–74.
30. Soni, J. and P. L. Swarnkar (1996) Morphogenetic and biochemical variations under different spectral lights in leaf cultures of *Vigna aconitifolia*. *J. Phytol. Res.* **9**, 89–93.