Green-light Supplementation for Enhanced Lettuce Growth under Red- and Blue-light-emitting Diodes

Hyeon-Hye Kim1
NASA Biological Sciences Office, Mail Code YA-E4-B, Kennedy Space Center, FL 32899

Gregory D. Goins
North Carolina A&T State University, Biology Department, Barnes Hall, 1601 East Market Street, Greensboro, NC 27411

Raymond M. Wheeler and John C. Sager
NASA Biological Sciences Office, Mail Code YA-E4-B, Kennedy Space Center, FL 32899

Additional index words. dry-weight accumulation, photosynthesis, spectral quality, yield photon flux

Abstract. Plants will be an important component of future long-term space missions. Lighting systems for growing plants will need to be lightweight, reliable, and durable, and light-emitting diodes (LEDs) have these characteristics. Previous studies demonstrated that the combination of red and blue light was an effective light source for several crops. Yet the appearance of plants under red and blue lighting is purplish gray making visual assessment of any problems difficult. The addition of green light would make the plant leave appear green and normal similar to a natural setting under white light and may also offer a psychological benefit to the crew. Green supplemental lighting could also offer benefits, since green light can better penetrate the plant canopy and potentially increase plant growth by increasing photosynthesis from the leaves in the lower canopy. In this study, four light sources were tested: 1) red and blue LEDs (RB), 2) red and blue LEDs with green fluorescent lamps (RGB), 3) green fluorescent lamps (GF), and 4) cool-white fluorescent lamps (CWF), that provided 0%, 24%, 86%, and 51% of the total PPF in the green region of the spectrum, respectively. The addition of 24% green light (500 to 600 nm) to red and blue LEDs (RGB treatment) enhanced plant growth. The RGB treatment plants produced more biomass than the plants grown under the cool-white fluorescent lamps (CWF treatment), a commonly tested light source used as a broad-spectrum control.

Plants will be an integral part of any long-term future space mission. A major challenge to growing plants in space will be controlling and supplying a sufficient quantity and quality of light (Bugbee and Salisbury, 1988; Langhans and Dressen, 1988; Sager and Wheeler, 1992; Salisbury and Bugbee, 1988). Light-emitting diodes (LEDs) are a promising electric light source for space-based plant growth chambers and bioregenerative life support because of their small mass and volume, solid-state construction, superior safety, and longevity (Barta et al., 1992; Bulau et al., 1991). Light-emitting diode lighting systems are currently under evaluation by NASA. The combination of red (600 to 700 nm) and blue (400 to 500 nm) light has proven to be an effective lighting source for producing spinach, radish, pepper, Swiss chard, wheat, and lettuce biomass in controlled environments (Brown et al., 1995; Goins, 2002; Goins et al., 1997, 2001; Goins and Yorio, 2000; Yorio et al., 1998, 2001). Plant leaves readily absorb red and blue light, so absorbance is high and reflectance is relatively low in these ranges of the spectrum (Klein, 1992; Smith, 1993). Therefore, even healthy plants grown under red and blue LEDs alone appear purplish gray to humans. However, green light has a relatively higher reflectance than red and blue light (Klein, 1992; Smith, 1993). Hence, the addition of green light to red and blue LED arrays would enable plants to appear green to the crew. The familiar appearance of the plants would be aesthetically pleasing and would allow the crew to visually assess plant health status.

The addition of green light in combination with red and blue LEDs may promote increased plant growth, since green light can penetrate into the plant canopy better than red or blue light (Klein, 1992; Smith, 1993). Leaves in the lower canopy would be able to use the transmitted green light in photosynthesis. Results from previous studies have been inconclusive as to the physiological benefits of green light. Dougher and Bugbee (2001b) reported that many previous controlled environment studies have been plagued with lighting problems. For example, Klein et al. (1965) reported that the supplemental green radiation (530 to 585 nm) caused repressed growth of Tagetes erecta and Sordaria fimicola, but the study reported light measurements in footcandles. Huh et al. (1997) reported that high green band output (500 to 600 nm) increased plant height in Hibiscus syriacus. Song et al. (1997) reported that green light appeared to be the least effective in promoting plant growth and development in H. syriacus. These green light studies did not provide lighting sources with clean cut-offs. There was also incomplete information on the spectral outputs of the lighting and/or filter sources. Light-emitting diodes are well suited to test the use of supplemental green light on the growth of plants, since the lighting in the growing area can be well controlled. For the current study, small fluorescent lamps that emit green light were installed with an array of red and blue LEDs. This is due to the lack of available high output green LEDs that could provide the required photon flux.

For a space mission, highly optimized lighting systems are necessary to conserve power and maximize plant growth, so there is a need to investigate advanced lighting technologies. Among them, supplemental green light needs to be evaluated. Growing salad crops with LEDs would also fulfill NASA’s near-term goal of supplementing the crew’s diet with fresh salad-type (perishable) crops (Goins et al., 1998; Kliss and MacElroy, 1990; Salisbury and Clark, 1996). We are not aware of reports on the response of lettuce to supplemental green light. The objective of this study was to investigate the effects of green light supplementation for growing lettuce under red and blue LEDs.

Materials and Methods

Cultural conditions. Lettuce seeds (Lactuca sativa ‘Waldmann’s Green’) were planted in plastic pots (7 cm tall, 164-mL capacity, two seeds per pot) containing horticultural vermiculite and Canadian sphagnum peatmoss (Terra-Lite Agricultural Mix; The Scotts Co., Marysville, Ohio). Within the growth chamber (PGW-36; Conviron, Pembina, N.D.; 7.8-m3 interior plant growth volume), 16 pots were arranged inside of a 0.3-m2 tray under each light treatment. The lighting treatments were systematically rotated for each replication to minimize edge or position effects within the growth chamber. To further minimize any edge or position effects within each treatment the pots were rearranged every other day. At 7 d after planting (DAP), the lettuce seedlings were thinned to a density of one plant per pot. The air temperature, relative humidity, and CO2 levels for all treatments were maintained at 21 ± 0.3 °C, 70% ± 4.1%, and 1200 ± 48.9 μmol·mol−1 (0.12 kPa), respectively. Fresh half-strength Hoagland’s nutrient solution (Hoagland and Arnon, 1950; Mackowiak et al., 1989) was added as needed to the bottom of each tray to supply nutrients and replenish.
Table 1. Spectral data for red and blue light-emitting diodes (LEDs) (RB), red and blue LEDs with green fluorescent lamps (RGB), green fluorescent lamps (GF), and cool-white fluorescent lamps (CWF). Spectral scans were recorded at the top of the plant canopy with a spectroradiometer.

<table>
<thead>
<tr>
<th>Parameter</th>
<th>RB</th>
<th>RGB</th>
<th>GF</th>
<th>CWF</th>
</tr>
</thead>
<tbody>
<tr>
<td>Photon flux (µmol·m⁻²·s⁻¹)</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>PPF (400–700 nm)</td>
<td>150</td>
<td>150</td>
<td>150</td>
<td>150</td>
</tr>
<tr>
<td>Blue (400–500 nm)</td>
<td>24</td>
<td>23</td>
<td>15</td>
<td>29</td>
</tr>
<tr>
<td>Green (500–600 nm)</td>
<td>0</td>
<td>36</td>
<td>129</td>
<td>76</td>
</tr>
<tr>
<td>Red (600–700 nm)</td>
<td>126</td>
<td>92</td>
<td>6</td>
<td>45</td>
</tr>
<tr>
<td>Far-red (700–800 nm)</td>
<td>2</td>
<td>2</td>
<td>2</td>
<td>7</td>
</tr>
<tr>
<td>Yield photon flux *</td>
<td>130</td>
<td>127</td>
<td>122</td>
<td>134</td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>Fraction (%)</th>
<th></th>
<th></th>
<th></th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td>PPF</td>
<td>100</td>
<td>100</td>
<td>100</td>
<td>100</td>
</tr>
<tr>
<td>Blue</td>
<td>16</td>
<td>15</td>
<td>10</td>
<td>19</td>
</tr>
<tr>
<td>Green</td>
<td>0</td>
<td>24</td>
<td>86</td>
<td>51</td>
</tr>
<tr>
<td>Red</td>
<td>84</td>
<td>61</td>
<td>5</td>
<td>30</td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>Irradiance (W·m⁻²)</th>
<th></th>
<th></th>
<th></th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td>280–2,800 nm</td>
<td>28</td>
<td>33</td>
<td>39</td>
<td>41</td>
</tr>
<tr>
<td>2,800–50,000 nm</td>
<td>2</td>
<td>13</td>
<td>134</td>
<td>16</td>
</tr>
</tbody>
</table>

*Calculated according to Sager et al. (1988).

Evapotranspiration water losses.

**Light treatments.** The four light sources were 1) red and blue LEDs (RB), 2) red and blue LEDs with green fluorescent lamps (RGB), 3) green fluorescent lamps (GF), and 4) cool-white fluorescent lamps (CWF). Figure 1 shows the spectral distribution scans taken (at approximately equal total photosynthetic photon flux, PPF, 400 to 700 nm) from 300 to 1100 nm at 2 nm steps with a spectroradiometer (LI-1800; LI-COR, Lincoln, Neb.). Contributions of blue (400 to 500 nm), green (500 to 600 nm), red (600 to 700 nm), far-red (700 to 800 nm) and total PPF were determined from bandwidth integration. From the spectroradiometric data for each light treatment the yield photon flux (YPF; Sager et al., 1988), the quantum ratios of red, far-red, blue, and the calculated amount of phytochrome in Pₜₜ form relative to total phytochrome at photoequilibrium (P/PPF; Sager et al., 1988) were determined. Short-wave (280 to 2,800 nm) and thermal long-wave (2,800 to 50,000 nm) radiation were measured with Eppeley PSP and PIR radiometers (Eppeley Laboratories, Newport, R.I.)(Table 1).

For RB treatments, plants were grown under nine LED arrays (Snap-Lite: Quantum Devices, Inc., Barneveld, Wis.) equipped with red gallium-aluminum-arsenide (GaAlAs) and blue gallium-nitride (GaN) LEDs. Each array contained 150 red and 75 blue individual diodes. For RGB treatments, four green fluorescent lamps (F15T8/G; Interlectric Corp., Warren, Pa.) were mounted around another set of nine red and blue LED arrays (Snap-Lite) and supplied 24% green light of the total PPF. For GF treatments, plants were grown under six green fluorescent lamps (F15T8/G; Interlectric Corp., Warren, Pa.) that provided 86% green light of the total PPF. For CWF treatments, plants were grown under 12 cool-white fluorescent lamps (F15T12-CW; General Electric Co., Cleveland, Ohio) with a 3.5-mm-thick Plexiglas heat barrier that provided 51% of the total PPF in the green region of the spectrum. A vestibule made of black, opaque plastic precluded light noise from entering growth area that contained LED arrays and fluorescent lamps.

Lighting for all treatments was 18-h photoperiod (18-h light/6-h dark) with approximately equal PPF at 150 µmol·m⁻²·s⁻¹ (9.7 mol·m⁻²·d⁻¹). Photosynthetic photon flux levels were measured at the top of the plant canopy with a quantum sensor (LI-190SA; LI-COR) calibrated with a spectroradiometer (LI-1800). As the plant canopies grew closer to the light banks, PPF levels were maintained by adjusting the height of the pots.

**Plant measurements.** Beginning at 7 DAP, four plants were harvested from each light treatment. Harvesting continued on a weekly interval with final harvest at 28 DAP prior to canopy closure to minimize spectral quality changes caused by canopy closure. Measurements included leaf area, specific leaf area (SLA), shoot fresh weight (shoot FW), and shoot dry weight (shoot DW). Due to the strong bond between the plant roots and the potting media, measurements did not include root fresh and dry weights. Only the edible biomass was measured. Plant tissue samples were dried in a drying oven for 48 h at 70 °C before weighing. Standard growth analysis was used to calculate leaf area index (LAI, m² leaf·m⁻² · crop) and crop growth rate (CGR) for the 7-d interval based on average values. Chlorophyll (Chl) measurements were made using several representative samples from leaves and analyzed by the method of Moran (1982). Canopy leaf temperature data were logged under each lighting source with infrared transducers (model IRTS-P; Apoage Instruments Logan, Utah).

At 28 DAP and 2 h after onset of the photoperiod, photosynthetic rates (Pn) were measured from four of the youngest fully expanded leaves per treatment using a portable photosynthesis system (LI-6400; LI-COR). The red (630 ± 10 nm peak wavelength) and blue (470 ± 10 nm peak wavelength) LED light source built into the leaf cuvette was calibrated against an internal photodiode. The measurements were alternated among the treatments. During all measurements, PPF, leaf temperature, relative humidity, and CO₂ levels within the cuvette were held at 150 µmol·m⁻²·s⁻¹, 21 °C, 65%, and 1200 µmol·mol⁻¹, respectively.

Measurements of leaf reflectance and transmittance were made using an external integrating sphere (1800-12S; LI-COR) internally coated with a highly reflective, diffusive material, barium sulfate and coupled to a spectroradiometer (LI-1800; LI-COR) with a fiber optic cable. Collimated light was provided by a 10-W glass-halogen lamp (Sylvania, Danvers, Mass.) stabilized by a regulated power supply (1800-12B; LI-COR). Measurements of reflectance and transmittance were made from leaves by scanning from 400 to 700 nm at 29 DAP. Absorptance was calculated as absorptance = 1 (reflectance + transmittance).

**Statistical analysis.** The experiment was repeated three times with means calculated from 16 plants per repetition. Using 5% as the level of significance, statistical analysis was subjected to analysis of variance followed by Duncan’s multiple range tests (SPSS Inc., Chicago, Ill.).

**Results and Discussion.**

The LEDs used in this study had narrow spectral outputs (25 nm band width at half peak height) in each red and blue region of the spectrum. The narrowly distributed spectral outputs of the LEDs were in contrast to the broad spectrum of green and cool-white fluorescent lamps (Fig. 1). The lower relative weighting of the blue (400 to 500 nm) and red (600 to 700 nm), and the higher weighting of the green (500 to 600 nm) reduced the YPF for the green fluorescent lamps. The red to far-red ratio of the GF and CWF were 3 and 6, respectively, whereas that of RB and RGB were 63 and 46, respectively. The calculated P/PPF values for all the treatments were ± 0.80. More long-wave radiation was measured from the GF lamps than from the other lighting treatments (Table 1), but this did not significantly impact the average canopy leaf temperatures among the different treatments (Table 2).

Table 2 shows the results of the physiological measurements from all treatments. The plants with the greatest leaf area were grown under RGB, followed by RB and CWF, and then GF. The specific leaf area of the GF treatment plants was the highest among the treatments, followed by RB and CWF, and then RGB. The RGB plants also had the greatest shoot fresh and dry weights with the RB and CWF, and then GF treatments following in descending order. The photosynthetic rates were lower in plants grown under GF and there was no significant difference in chlorophyll content among treatments (Table 2). Leaf area index and CGR were decreasing in the order of plants grown under RGB, CWF, RB, and GF (Fig. 2).

Yield photon flux (YPF) has been used as a tool for explaining biomass accumulation...
because it weighs photons according to their relative quantum efficiency for photosynthesis (McCree, 1972a; Sager et al., 1988). The use of YPF to accurately describe dry-weight accumulation has been demonstrated in wheat (*Triticum aestivum*) and soybean (*Glycine max*), but not in lettuce (Dougher and Bugbee, 1999, 2001a; Yorio et al., 2001). In this research, the average PPF was 150 μmol·m⁻²·s⁻¹ and the YPF for RB, RGB, GF, and CWF were 130, 127, 122, and 134 μmol·m⁻²·s⁻¹, respectively (Table 1). The YPF was higher in the RB and CWF than RGB and GF, yet the DW accumulation was higher under RGB than under RB and CWF (Table 2). This suggests that using YPF to compare plant growth between spectrally biased and broad-spectrum sources may not be valid.

Plants grown under RB and CWF had similar DW accumulation. This indicated that normal growth for lettuce could be achieved with only red and blue photons. Yorio et al. (2001) reported similar results for lettuce (‘Waldmann’s Green’) when plants were grown with red LEDs with blue fluorescent lamps. Hoenecke et al. (1992) suggested that a blue-photon flux level between 15 and 30 μmol·m⁻²·s⁻¹ for 12 h each day would be an acceptable level for lettuce growth. In the present study, the blue photon flux level was 15 to 29 μmol·m⁻²·s⁻¹, which suggested that the difference in blue photon flux level among treatments was negligible.

In this research, the major spectral waveband difference in the PPF region was the relative ratio of green (500 to 600 nm) or red (600 to 700 nm) light rather than that of blue (400 to 500 nm) light to the PPF. The P/P_{total} values were ≥0.80 for all treatments, which was near the maximum of 0.89 (Sager et al., 1988). This indicated that the phytochrome photostationary state difference between treatments was negligible. There was very little far-red radiation present among spectral environments. The highest amount of far-red originated from the CWF (7 μmol·m⁻²·s⁻¹). Hence, the differences in plant growth appeared to originate from the difference in the amount of green light rather than a change in red light.

Dougher and Bugbee (2001a, 2001b) grew lettuce (‘Grand Rapids’) plants under six blue light treatments comprising five blue light fractions: 0%, 2%, and 6% from high-pressure sodium (HPS) lamps and 6%, 12%, and 26% from metal halide (MH) lamps. Lettuce chlorophyll concentration, dry weight, leaf area and specific leaf area under the HPS and MH 6% blue were significantly different, which suggested that yellow light from 580 to 600 nm suppressed plant growth. In the present study, the yellow light (580 to 600 nm) fractions for RB, RGB, GF, and CWF were 0%, 1%, 4%, and 17% of total PPF, respectively. The data from this study do not suggest yellow light suppression of lettuce growth, since the DW of RB (0% yellow light) and CWF (17% yellow light) plants were similar (Table 2). Apparently the response of different plant species or cultivars under various light environments is too complicated to interpret using one quantitative light quality parameter (Kim et al., 2002; Rajapakse et al., 1992).

The red and blue LEDs with 24% green light treatment (RGB) gave the highest plant growth. The contribution made by green light transmission into the lower canopy could not be determined, since the lettuce plants were harvested prior to canopy closure to minimize the changes in spectral quality. In a dense canopy, the addition of green light may further increase plant growth, since green light can better penetrate into the plant canopy than red or blue light (Klein, 1992; Smith, 1993). Leaves in the lower canopy would be able to use the transmitted green light in photosynthesis and perhaps reduce levels of leaf senescence and/or shedding within the canopy (Preece and Read, 1993).

The addition of 5% green light had negligible impact on plant growth and photosynthesis in our preliminary study (unpublished data). This was somewhat expected, since green light is only slightly less effective at photosynthesis than red or blue lights (McCree, 1972b) and drives carbon fixation deep within leaves (Sun et al., 1998). However, the addition of supplemental green light at higher input levels resulted in decreased plant growth. Among RGB, CWF, and GF plants, increasing the green light fraction to 24%, 51%, and 86%, respectively, decreased lettuce growth in terms of leaf area and dry weight. This suggested that light sources with a high fraction of green photons (>50%), such as CWF and GF, are not only energetically wasteful compared to reduced green light sources, but they can also reduce plant growth.

Light, to be effective, must be intercepted and absorbed by photosynthetic tissue. The fraction of absorbed light for GF and CWF were relatively low, 63% and 73%, respectively (Fig. 3). This was mainly due to the low absorption in green waveband (500 to 600 nm) that was the main portion of the total PPF in these treatments. However, the fraction of absorbed to incident light does not explain plant growth, since for RB the ratio was 89%, compared to 82% for RGB (Fig. 3). The main difference between the RB and RGB treatments was RB had 0% green light while RGB had 24% green light.

Green light is often assumed to be unimportant in driving photosynthesis mainly

### Table 2: Influence of light quality on leaf area, specific leaf area (SLA), shoot fresh weight (shoot FW), shoot dry weight (shoot DW), single leaf net photosynthesis (Pn), total chlorophyll (Chl) content, and canopy leaf temperature at 28 d after planting.

<table>
<thead>
<tr>
<th>Parameter</th>
<th>RB</th>
<th>RGB</th>
<th>GF</th>
<th>CWF</th>
</tr>
</thead>
<tbody>
<tr>
<td>Leaf area (cm²)</td>
<td>524.8</td>
<td>689.9</td>
<td>419.2</td>
<td>595.3</td>
</tr>
<tr>
<td>SLA (m²·kg⁻¹)</td>
<td>34.1</td>
<td>30.1</td>
<td>49.4</td>
<td>33.9</td>
</tr>
<tr>
<td>Shoot FW (g)</td>
<td>24.6</td>
<td>35.7</td>
<td>15.3</td>
<td>26.9</td>
</tr>
<tr>
<td>Shoot DW (g)</td>
<td>1.54</td>
<td>2.26</td>
<td>0.83</td>
<td>1.76</td>
</tr>
<tr>
<td>PN (µmol CO₂/m²/s)</td>
<td>9.3</td>
<td>8.6</td>
<td>7.4</td>
<td>8.8</td>
</tr>
<tr>
<td>Chl (g·m⁻²)</td>
<td>0.21</td>
<td>0.21</td>
<td>0.18</td>
<td>0.20</td>
</tr>
<tr>
<td>Canopy leaf temperature (ºC)</td>
<td>20.5</td>
<td>20.4</td>
<td>20.7</td>
<td>20.3</td>
</tr>
</tbody>
</table>

*See Fig. 1 and Table 1 for spectral characteristics.

*Mean comparison within a row by Duncan’s multiple range test, P = 0.05. Means with same letter are not significantly different.

---

**Fig. 1:** Spectral distribution of light from red and blue LEDs (RB), red and blue LEDs with green fluorescent lamps (RGB), green fluorescent lamps (GF), and cool-white fluorescent lamps (CWF). Spectral scans were recorded at the top of the plant canopy with a spectroradiometer.
lengths not absorbed are repeatedly reflected photosynthetic apparatus is small, the wave-
green wavelengths being absorbed into the (Sun et al., 1998). Although the chances of
may include absorption by ancillary pigments thesis in higher plants (McCree, 1972a). This
effective spectral region to power photosyn-
photosynthesis shows that green light is in an
refl ection does not occur, so the absorptance
containing dissolved chlorophyll, the internal
from chloroplast to chloroplast in the complex
network of photosynthetic cells. With each
reflection, a small percentage of those wave-
lengths not absorbed are repeatedly refl ected
from chloroplast to chloroplast in the complex
network of photosynthetic cells. Each with
reflection, a small percentage of those wave
lengths is absorbed, until fi nally half or more
are absorbed by most leaves and are used in
photosynthesis. In a spectrophotometer cuvette
containing dissolved chlorophyll, the internal
refl ection does not occur, so the absorptance
of green wavelengths is very low (Salisbury
and Ross, 1992). The response spectra for
photosynthesis shows that green light is in an
effective spectral region to power photosyn
thesis in higher plants (McCree, 1972a). This
may include absorption by ancillary pigments
and transference of the energy to the reaction
centers. In living leaves, light absorption by
the carotenoids shifts from the blue portion of the spectrum into the green and some
photosynthesis is conducted (Klein, 1992;
Nobel, 1999; Salisbury and Ross, 1992; Taiz
and Zeiger, 1991). Most of the carotenoids
(both β-carotene and the xanthophylls) in the
thylakoids efficiently transfer their excitation
energy to the same reaction centers as do chlo
rophylls, also contributing to photosynthesis
(Salisbury and Ross, 1992; Siefermann-Harms,

Single-leaf photosynthetic rates were lower
in plants grown under GF than RB, RGB, and
CWF (Table 2). Lower Pn under GF may be
associated with lower leaf mass per unit leaf
area, i.e., higher specifi c leaf area (Table 2).
The higher projected leaf area per unit leaf
dry mass (equivalent to SLA) under GF is a
good indicator of higher photosynthetic surface
area per unit investment in leaf tissue and is
often positively associated with shade-type
physiology (Hanba et al., 2002; Lambers et
al., 1998; Pearcy, 1998; Salisbury and Ross,
1992). This suggested that under the GF treat-
ment with green-biased light more resources
were allocated toward greater leaf area produc-
tion, while carbon-assimilation capacity per
unit leaf area was reduced compared to other
treatments. The changes in leaf ultrastructure
among the spectral environments also could
have signifi cantly impacted the density of
chloroplasts within the leaves or the propor-
tion of incident light that is captured by the
photosynthetic apparatus.

Although DW accumulation increased in
plants grown under RGB, the leaf Pn were
similar in plants grown under RB, RGB, and
CWF. Thus, leaf CO2 assimilation rates cannot
fully explain the effect. A possible explana-
tion for the discrepancy between Pn and DW
accumulation could lie in the single point
Pn measurements in this study. Diurnal Pn
and dark respiration measurements of single
leaves or whole canopies would be useful in
determining the fate of carbon in plants grown
under different light quality.

In the Pn measurement device, a red and
blue LED light source was built into the leaf
cuvette, which had a similar light quality only
to the RB treatment. Plant photosynthetic per-
formance may be best presented by measurements
conducted under actinic light quality similar
to that in which the plants were grown, since
there could be important differences in plant
response to measurement spectral quality and
growth spectral quality (Chow et al., 1990).
Therefore, Pn measurements with light qual-
ity similar to growth light quality may avoid
confounding physiological and/or biochemical
responses with alterations in whole-plant ultra
structure and morphology.

The RGB treatment consisted of 61%,
24%, and 15% of red, green, and blue light,
respectively. While RB treatment consists of
84%, 0%, and 16% of red, green, and blue light,
respectively, which is signifi cantly red-biased.
Although YPF and the amount of absorbed
light were higher in the RB treatment, the RGB
treatment resulted in greater biomass produc-
tion. In this case, compensatory adjustments
in the photosynthetic machinery to balance excitation energy between photosystems I and
II (Chow et al., 1990; Murchie and Horton,
1998; Tennessen et al., 1994) could be induced
by over-stimulated PSII, due to the narrow-
spectrum photosynthetic light energy from red
LEDs in red-biased RB treatment. Perhaps, the
RGB treatment achieved a balanced spectral
environment by supplementing a favorable
amount of green light to the plants.

On the other hand, since carbon gain capac-
ity is a function of both total leaf area and Pn,
increases in plant dry weight are not always
associated with an increase in photosynthetic
rate on a unit leaf area basis. Hence, stimulated
leaf area production can completely counteract
a reduction in Pn per unit leaf area, with the
result that Pn by the plant is not reduced or is
even increased (Bugbee and Salisbury, 1988).

Fig. 2. Leaf area index (LAI) and crop growth rate (CGR) of lettuce grown under red and blue LEDs (RB),
red and blue LEDs with green fluorescent lamps (RGB), green fluorescent lamps (GF), and cool-white
fluorescent lamps (CWF). The data points are averages of 12 measurements. See Fig. 1 and Table 1
for spectral characteristics.
A plant canopy with a high LAI can be as productive as a canopy having higher individual unit Pn, but with an overall lower LAI (Goins et al., 2001; Hunt, 1990). Although Pn among plants grown under RB, RGB, and CWF were similar, plants grown under RGB displayed a higher leaf area, which could facilitate greater light interception to improve photosynthesis at low light levels. Figure 2 demonstrates that a high LAI facilitated more incident radiation interception, which in turn enhanced the overall plant growth rate.

This investigation demonstrated that the addition of 24% green light (500 to 600 nm) to red and blue LEDs (RGB treatment) enhanced lettuce growth compared to plants grown under cool-white fluorescent lamps (CWF treatment). Coincidentally, lettuce grown using RGB lighting would have an additional aesthetic appeal of a green appearance.

In this study, small fluorescent lamps that emit green light were installed with an array of red and blue LEDs. Considerable commercial interest has been directed toward improving green LEDs and, therefore, green LEDs that have high output and provide the required photon flux are more available now than before. Further studies are needed to determine required levels of green photons for optimum plant growth and more tests with different green peak wavelengths (using green LEDs) with red and blue LEDs would be useful in determining a green light response spectrum. These findings could then be used to design spectrally balanced LED systems for supporting plant growth, especially for very specialized applications, such as in space.

**Literature Cited**


