Light Response Curves of Selected Plants under Different Light Conditions

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Abstract

Photosynthesis rates under HPS light were measured on various plant species. *Euphorbia pulcherrima*, *Plectranthus scutellarioides* and *Lactuca sativa* were selected for more detailed experiments under natural light and artificial light provided by HPS lamps or LEDs under controlled environment conditions. Comparisons have been made between gas exchange characteristics like the light compensation point and the slope of light response curves under practice-relevant light intensities. Light compensation points under light qualities with input of red LEDs were between 13-15 µmol m⁻² s⁻¹ in all three model plants. Average photosynthetic rates at 100 and 200 µmol m⁻² s⁻¹ PPF red and blue/red LED light were above other calculated values for the other light qualities.

INTRODUCTION

Different wavelengths are used in diverse response systems by plants. The relationship between light and photosynthesis is one of the best described mechanisms. Although light controls, or at least influences a number of other growth processes, photosynthesis still is the most important target variable for producers. When considering the applicability of new and expensive narrow-band light sources like LEDs, maximizing productivity an important issue. Here, the grower is always challenged to prevail economically within the limits of plant growth and cost reduction. Because of that new recommendations regarding the intensity and quality are needed. To have a profound base for these benchmarks light response curves for different species are needed. Therefore tests were carried out on photosynthesis rates of different plant species under in practice-relevant light intensities and various light qualities by CO₂ leaf gas exchange.

MATERIALS AND METHODS

Experimental plants were cultivated in a greenhouse under natural light with additional light supplied by high pressure sodium lamps. Acclimatisation took place at least 12 hours before measuring the photosynthesis rates.

CO₂/H₂O gas exchange measurements were carried out with the portable photosynthesis system Circas1® (PP-Systems) and the leaf cuvette PLC B at 300 ml min⁻¹ flow rate. Leaf cuvette reference CO₂ concentration was between 363 and 399 ppm depending on the ambient CO₂ concentration and temperature was 19 °C ± 1 K. Values
were taken from the three youngest unfolded leaves per experimental plant at each run. Leaves were allowed to come to steady-state at each level of PPF. All measurements were made in the course of the day till 11 a.m. at the latest. Photosynthesis rates [µmol m⁻² s⁻¹] were estimated by the device using the following calculations:

\[
E = \frac{[W \times (e_{\text{out}} - e_{\text{in}})]}{(P - e_{\text{out}})}
\]

\[
A = C_{\text{in}} \times W - C_{\text{out}} \times (W + E) = - [W \times (C_{\text{out}} - C_{\text{in}}) + C_{\text{out}} \times E]
\]

\[A = \text{photosynthesis rate; } C_{\text{in}} = \text{CO}_2 \text{ concentration entering the cuvette; } C_{\text{out}} = \text{CO}_2 \text{ concentration leaving the cuvette; } E = \text{calculated transpiration rate; } e_{\text{in}} = \text{water vapour pressure of the air entering the cuvette; } e_{\text{out}} = \text{water vapour pressure of the air entering the cuvette; } P = \text{atmospheric pressure; } W = \text{mass flow of air per unit leaf area entering the cuvette}\]

The trials taken place in a research greenhouse and accordingly in a phytotron. Ambient air temperature was 19 °C ± 1 K. Humidity was kept between 55 and 65 RH% at ambient CO₂.

Sources of radiation were high pressure sodium lamps (HPS) Osram Plantastar® 400 W and a customised LED lamp. The LED lamp contains 20 blue (Osram LD W5AM deep blue), 20 green (Osram LT W5AM true green) and 64 red diodes (Osram LH W5AM hyper red) and is infinitely dimmable and switchable. The relative spectral distributions of the used light sources are shown in figure 1. LEDs have been controlled in equal relative intensity (e.g. 50% LED blue/red: 50% power input Osram LD W5AM deep blue and 50% power input Osram LH W5AM hyper red). PPF in mixed light qualities is given as sum of the single flux densities. Light measurements were made with the Basic Quantum Meter (400-700 nm; BQM-Sun, Apogee Instruments), the Field Scout UV Meter (250-400 nm; 3414 F, Spectrum Technologies) and the internal light sensor of the portable photosynthesis system (400-700 nm; filtered silicon cell). To get data from different natural light intensities data plots were taken at different weather conditions and at different times of the day. Artificial light intensities were regulated by adjusting the distance between light sources and plant or by dimming the LEDs. Intensities have been adjusted ascending.

RESULTS AND DISCUSSION

Figure 2 shows the light response curves (LRC) of five ornamental plants (× Begonia coralline, Euphorbia pulcherrima, Plectranthus scutellarioides, × Gerbera jamesonii, Pelargonium grandiflorum ‘pac Aristo Candy Regcan’) and Lettuce (Lactuca sativa ‘Archimedes RZ’) as a representative of vegetable crops under HPS light. This data were collected to verify the correct application of Ciras® and values captured under LED light. The following figures 3-5 describe the more detailed light response curves (LRC) for the three selected plant species Euphorbia pulcherrima, Plectranthus scutellarioides and Lactuca sativa. Table 1 summarises the characteristic points which were identified during the analysis of the LRSs.

Chalker (1980) recommended exponential functions to describe the light response curves. In this study logarithmic functions as inverse function of exponential curves were used because of our special interest on light compensation points (LCP). The corresponding coefficients of determination are satisfying (average R²=0.873). Scatters
are unavoidable in face of careful plant selection and care on the basis of the individual plant vitality.

Obtained data are conclusive against the background of some other studies. The records describe well that plants under the same light and climate conditions can react in different ways. It is clearly shown that shade plants like Begonia achieve the LCP at lower light intensities than plants with higher light requirements. Calculated LCPs ranged between 13 and 29 \( \mu \text{mol m}^{-2} \text{s}^{-1} \) PPF. Normally LCPs are higher under HPS light. This can be explained by the composition of light and the integral light measurement. The used measuring devices are only able to specify the PPF integrated between 400 and 700 nm. Measured values from LEDs with the narrowband, monochromatic radiation characteristics can be distinguished easily. HPS lamps, however, emit polychromatic light. When radiation areas of the three used LEDs are placed across the spectrum of the Plantastar®, the areas of these spectral regions are integrated and then stacked into the overall ratio. Then it becomes clear that only about 20% of the total radiation power of the HPS lamp between 400 and 700 nm are congruent with LED spectral regions.

The calculated LRCs are also in a consistent area. Tang et al. (2010) found photosynthetic rates around 5.8 \( \mu \text{mol m}^{-2} \text{s}^{-1} \) for lettuce plants 33 days after planting with light intensities about 320 \( \mu \text{mol m}^{-2} \text{s}^{-1} \) PPF at plant level supplied by fluorescent lamps. LRCs on LED light should be judged carefully from light intensities above 200 \( \mu \text{mol m}^{-2} \text{s}^{-1} \) PPF. Because of technical limitations Ciras® measurements above this level could not be taken.

LCPs under pure blue LED influence were above those of the other LED combinations except for lettuce. As expected LRCs progression was shallower (Yanagi et al., 1996). The slopes were slightest between 50 and 100 \( \mu \text{mol m}^{-2} \text{s}^{-1} \) PPF compared to the other light qualities with an average of 0.015-0.020 \( \mu \text{mol m}^{-2} \text{s}^{-1} \) increase of photosynthetic activity per additional unit PPF.

Blue light is used as a source of energy in the photosynthetic systems, but the effect is less than one might expect due to the absorption (Schopfer and Brennicke, 2010). Here the main values are information that is generated by plants through the perception of corresponding photons. Phototropins, cryptochromes, ZTL (Zeitlupe), FKF1 (Flavin-binding Kelch repeat F-box1) and LKP2 (LOV Kelch Protein 2) as well as BLUF-proteins are involved in this sensing processes (Ahmad et al., 1998; Ballaré et al., 1997; Lin, 2002; Gomelsky and Klug, 2002; Yanovsky and Kay, 2003).

Red spectral regions of light have the strongest impact on the rates of photosynthesis in plants. Photosystem (PS) I and II absorb wavelengths around 650 nm (PS II) and 700 nm (PS I) (Schopfer and Brennicke, 2010). The basis for the perception of corresponding photons is provided by phytochromes named phyA–phyE (Frankhauser, 2001). Light compensation points under light qualities with input of red LEDs were between 13-15 \( \mu \text{mol m}^{-2} \text{s}^{-1} \) in all three model plants. Average photosynthetic rates at 100 and 200 \( \mu \text{mol m}^{-2} \text{s}^{-1} \) PPF red LED light were above other calculated values for the other light qualities (Tab. 1). The same holds true for slopes of LRCs between 50 and 100 \( \mu \text{mol m}^{-2} \text{s}^{-1} \) PPF. Only the measurement series for E. pulcherrima provides an exception. In this case, the slope under HPS light was with 0.041 \( \mu \text{mol m}^{-2} \text{s}^{-1} \) increase of photosynthetic activity per additional unit PPF higher than under light qualities with involvement of red LEDs (red: 0.034 \( \mu \text{mol m}^{-2} \text{s}^{-1} \); blue/red: 0.037 \( \mu \text{mol m}^{-2} \text{s}^{-1} \)).

Investigations on the influence of red LEDs on photosynthetic rates under are insofar incompletes that no measurements under dark red LEDs could be made. That would have been interesting because of the close link (e.g. photosynthesis, shade-
avoidance syndrome, root, leaf, flower and fruit development) of this spectral ranges (Ballaré et al., 1997; Moe et al., 2002; Smith, 1982).

In order to produce marketable qualities that have no variety untypical deformation, a proportion of blue light is necessary (Moe, 1997). Furthermore blue light has influences stomata movement, phototropism, synthesis of anthocyanin and chlorophyll, lengths of internodes, sprout and leaves as well as dry mater production (Goins et al., 1997; Moe et al., 2002; Sager and Wheeler, 1992; Smith, 1982). In addition Franklin and Whitelam (2005) assembled the interaction between blue, red and far red light with regard to shade-avoidance syndrome. So, it is beneficial to use red and blue spectral regions despite the lower yield of photosynthesis under blue monochromatic light. Combinations of red and blue LEDs for plant illumination are available on the market for quite some time. There are many references to the “right” proportion of blue light. However they can not necessarily overall transferred on all plant species. This may be one reason why commercial LED providers have some difficulties with matching light compositions for different plant species and stages of development. Brazaitytė et al. (2006) recommended 0% blue light for lettuce production at least for the initial production phase for a more rapid lettuce development, but for the prize of senescence effects four weeks after germination. Goins et al. (1997) conclude in their analysis, that wheat can complete its life cycle under red LEDs alone. But by adding ca. 10% blue light greater amounts of seed and larger plants could be achieved.

Data to the combination of light sources OSRAM LD W5AM deep blue and OSRAM LH W5AM hyper red show hardly changes in terms of LCP and photosynthetic rate compared to monochromatic red light. The combination of both light sources and the qualitative shift in favour of higher energetic blue light did not lead to significant shifts in terms of the photosynthetic activity.

Completion of blue/red light by green light has interesting aspects besides plant physiological questions. Green light penetrates plant canopy better than other wavelengths. Transmitted green light could be used for photosynthesis from plant organs in the lower canopy (Kim et al., 2006). In addition colour perception under blue/red light is considerably worse. Thus working conditions could be improved significantly by the addition of green light.

There were no differences between LCPs in the series of measurements under blue/red and blue/green/red exposure. Differences on the photosynthetic rates were found. These were lower at 100 and 200 µmol m⁻² s⁻¹ PPF under blue/green/red light compared to blue/red light (Plectranthus: -12-13% and Lactuca -6%-4%). The consideration of slopes between 50 and 100 µmol m⁻² s⁻¹ PPF supports these observations. The increase of photosynthetic performance per unit PPF of Plectranthus was 0.037 µmol m⁻² s⁻¹ under blue /red light, whereas the slope was 0.031 µmol m⁻² s⁻¹ under blue/green/red light conditions.

To evaluate the presented results the technical design of the used LED lamp should receive attention. Through specific energy levels of the photons and the different number of LEDs diverse energy levels where generated to influence the plants. For future work on the subject, it seems useful to differentiate light spectra and the associated intensities more clearly. PPF designates the density of photons over the wave band of radiation between 400-700 nm as an integral. It is not possible to indicative of the actual performance in the responded wavelength regions. Indirect conclusions on that can be found through detailed consideration of the available lamp spectra and additional measurements of PPF in different intensities. In trails on blue/red light the proportion of
blue light was 31% in low power settings and 41% at full power. In the presented experiments on blue/green/red light the proportion of green light was between 12% and 14% of total PPF. Kim et al. (2004) observed no impact on lettuce growth with 5% additional green from LEDs in combination with red and blue LEDs at 136 $\mu$mol m$^{-2}$ s$^{-1}$ total PPF. In a later publication (Kim et al., 2006) they summarised that the addition of 24% green light to red and blue LEDs enhanced the growth of lettuce whereas more than 50% green light had negative effects on plant growth. Presented results to the LRCs are, despite the specified repeatability, snapshots from the selected model plants at a specific stage of development. It is therefore quite conceivable that at least the growth of lettuce is promoted by light qualities with additional green in the used proportion.

Acknowledgements
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Literature Cited


Tables

Tab. 1: Calculated characteristic points of the light response curves

<table>
<thead>
<tr>
<th>Light compensation point \ ([µmol m(^{-2}) s(^{-1})]</th>
<th>Natural light</th>
<th>HPS</th>
<th>LED blue</th>
<th>LED red</th>
<th>LED blue/red</th>
<th>LED blue/green/red</th>
</tr>
</thead>
<tbody>
<tr>
<td>Euphorbia pul.</td>
<td>15</td>
<td>22</td>
<td>21</td>
<td>14</td>
<td>15</td>
<td>―</td>
</tr>
<tr>
<td>Plectranthus scut.</td>
<td>–</td>
<td>29</td>
<td>23</td>
<td>13</td>
<td>15</td>
<td>14</td>
</tr>
<tr>
<td>Lactuca sativa</td>
<td>–</td>
<td>17</td>
<td>15</td>
<td>15</td>
<td>13</td>
<td>14</td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>Net photosynthesis \ ([µmol m(^{-2}) s(^{-1})] at 100 µmol m(^{-2}) s(^{-1}) irradiation)</th>
<th>Natural light</th>
<th>HPS</th>
<th>LED blue</th>
<th>LED red</th>
<th>LED blue/red</th>
<th>LED blue/green/red</th>
</tr>
</thead>
<tbody>
<tr>
<td>Euphorbia pul.</td>
<td>2.6</td>
<td>4.4</td>
<td>2.2</td>
<td>4.9</td>
<td>5.0</td>
<td>―</td>
</tr>
<tr>
<td>Plectranthus scut.</td>
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<td>2.4</td>
<td>1.6</td>
<td>5.5</td>
<td>5.1</td>
<td>4.5</td>
</tr>
<tr>
<td>Lactuca sativa</td>
<td>–</td>
<td>4.2</td>
<td>2.3</td>
<td>5.1</td>
<td>5.2</td>
<td>4.9</td>
</tr>
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<tr>
<th>Net photosynthesis \ ([µmol m(^{-2}) s(^{-1})] at 200 µmol m(^{-2}) s(^{-1}) irradiation)</th>
<th>Natural light</th>
<th>HPS</th>
<th>LED blue</th>
<th>LED red</th>
<th>LED blue/red</th>
<th>LED blue/green/red</th>
</tr>
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<tbody>
<tr>
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<td>3.6</td>
<td>6.4</td>
<td>3.2</td>
<td>6.6</td>
<td>6.9</td>
<td>―</td>
</tr>
<tr>
<td>Plectranthus scut.</td>
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<td>7.5</td>
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<td>6.1</td>
</tr>
<tr>
<td>Lactuca sativa</td>
<td>–</td>
<td>5.8</td>
<td>3.1</td>
<td>7.0</td>
<td>6.9</td>
<td>6.6</td>
</tr>
</tbody>
</table>
Fig. 1. Relative spectral distribution of radiation of the used light sources (edited; Nilsen, 1971; Osram, 2009; Osram, 2010; Osram, 2011)

Fig. 2. Light response of net photosynthesis in leaves of selected plant species under HPS.

<table>
<thead>
<tr>
<th>Plant Species</th>
<th>Photosynthetic photon flux density [µmol m⁻² s⁻¹]</th>
<th>Formula Trendline</th>
<th>Coefficient of Determination</th>
</tr>
</thead>
<tbody>
<tr>
<td>× Begonia corallina</td>
<td>13 µmol m⁻² s⁻¹</td>
<td>$y = 2.0544\ln(x) - 5.2603$</td>
<td>$R^2 = 0.8437$ (n = 52)</td>
</tr>
<tr>
<td>Euphorbia pulcherrima</td>
<td>22 µmol m⁻² s⁻¹</td>
<td>$y = 2.93\ln(x) - 9.0839$</td>
<td>$R^2 = 0.8526$ (n = 55)</td>
</tr>
<tr>
<td>Plectranthus scutellarioides</td>
<td>29 µmol m⁻² s⁻¹</td>
<td>$y = 1.9241\ln(x) - 6.4811$</td>
<td>$R^2 = 0.8228$ (n = 54)</td>
</tr>
<tr>
<td>× Gerbera jamesonii</td>
<td>26 µmol m⁻² s⁻¹</td>
<td>$y = 3.0169\ln(x) - 9.8543$</td>
<td>$R^2 = 0.8804$ (n = 55)</td>
</tr>
<tr>
<td>Pelargonium grandiflorum 'pac Aristo Candy Regcan'</td>
<td>27 µmol m⁻² s⁻¹</td>
<td>$y = 2.8738\ln(x) - 9.4396$</td>
<td>$R^2 = 0.9012$ (n = 52)</td>
</tr>
<tr>
<td>Lactuca sativa 'Archimedes RZ'</td>
<td>17 µmol m⁻² s⁻¹</td>
<td>$y = 2.3427\ln(x) - 6.6181$</td>
<td>$R^2 = 0.8891$ (n = 31)</td>
</tr>
</tbody>
</table>
Fig. 3. Light response of net photosynthesis in leaves of *Euphorbia pulcherrima*

Natural light: \( y = 1.3796 \ln(x) - 3.7577 \)
\( R^2 = 0.8881 \) (n = 21)

HPS light: \( y = 2.93 \ln(x) - 9.0839 \)
\( R^2 = 0.8526 \) (n = 55)

LED blue: \( y = 1.4351 \ln(x) - 4.387 \)
\( R^2 = 0.9321 \) (n = 33)

LED red: \( y = 2.4847 \ln(x) - 6.5345 \)
\( R^2 = 0.8517 \) (n = 41)

LED blue/red: \( y = 2.637 \ln(x) - 7.1174 \)
\( R^2 = 0.9336 \) (n = 32)

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Fig. 4. Light response of net photosynthesis in leaves of *Plectranthus scutellarioides*

HPS light: \( y = 1.9241 \ln(x) - 6.4811 \)
\( R^2 = 0.8228 \) (n = 54)

LED blue: \( y = 1.0987 \ln(x) - 3.4239 \)
\( R^2 = 0.8863 \) (n = 33)

LED red: \( y = 2.7648 \ln(x) - 7.1866 \)
\( R^2 = 0.8769 \) (n = 39)

LED blue/red: \( y = 2.7032 \ln(x) - 7.3044 \)
\( R^2 = 0.952 \) (n = 31)

LED blue/green/red: \( y = 2.2633 \ln(x) - 5.9083 \)
\( R^2 = 0.8737 \) (n = 37)

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Fig. 5. Light response of net photosynthesis in leaves of *Lactuca sativa* ‘Archimedes RZ’

HPS light: \( y = 2.3427 \ln(x) - 6.6181 \)
\( R^2 = 0.8914 \) (n = 31)

LED blue: \( y = 1.904 \ln(x) - 3.958 \)
\( R^2 = 0.7555 \) (n = 30)

LED red: \( y = 2.6863 \ln(x) - 7.2444 \)
\( R^2 = 0.8246 \) (n = 40)

LED blue/red: \( y = 2.5418 \ln(x) - 6.525 \)
\( R^2 = 0.913 \) (n = 32)

LED blue/green/red: \( y = 2.478 \ln(x) - 6.4855 \)
\( R^2 = 0.8974 \) (n = 31)