Efficiency of photosynthesis in continuous and pulsed light emitting diode irradiation

Daniel J. Tennessen 1,2*, Raymond J. Bula 2 & Thomas D. Sharkey 1

1 University of Wisconsin Madison, Department of Botany, 430 Lincoln Drive, Madison, WI 53706, USA;
2 Wisconsin Center for Space Automation and Robotics, College of Engineering, University of Wisconsin Madison,
1500 Johnson Drive, Madison, WI 53706, USA; *Present address of corresponding author: Department of
Floriculture and Ornamental Horticulture, Cornell University, 20 Plant Sciences Bldg, Ithaca, NY 14853-5908,
USA

Received 23 September 1994; accepted in revised form 10 April 1995

Key words: light emitting diode, LED, pulse, capacitance, light utilization efficiency, photon requirement, photosynthetic efficiency

Abstract

The light utilization efficiency and relative photon requirement of photosynthesis in pulsed and continuous light from light emitting diodes (LEDs) has been measured. First, we characterized the photon requirement of photosynthesis from light of LEDs that differ in spectral quality. A photon requirement of 10.3 ± 0.4 was measured using light from a 658 nm peak wavelength (22 nm half band width) LED over the range of 0–50 μmol photons m⁻² s⁻¹ in 2 kPa O₂ in leaves of tomato (Lycopersicon esculentum Mill., cv. VF36). Because the conversion of electrical power to photons increased with wavelength, LED lamps with peak photon output of 668 nm were most efficient for converting electricity to photosynthetically fixed carbon. The effect of pulsed irradiation on photosynthesis was then measured. When all of the light to make the equivalent of 50 μmol photons m⁻² s⁻¹ was provided during 1.5 μs pulses of 5000 μmol photons m⁻² s⁻¹ followed by 148.5 μs dark periods, photosynthesis was the same as in continuous 50 μmol photons m⁻² s⁻¹. When the pulse light and dark periods were lengthened to 200 μs and 19.8 ms, respectively, photosynthesis was reduced, although the averaged photon flux density was unchanged. Under these conditions, the light pulses delivered 10¹⁷ photons m⁻², which we calculate to be equivalent to the capacitance of PSI or PS II. Data support the theory that photons in pulses of 100 μs or shorter are absorbed and stored in the reaction centers to be used in electron transport during the dark period. When light/dark pulses were lengthened to 2 ms light and 198 ms dark, net photosynthesis was reduced to half of that measured in continuous light. Pigments of the xanthophyll cycle were not affected by any of these pulsed light treatments even though zeaxanthin formation occurred when leaves were forced to dissipate an equal amount of continuous light.

Abbreviations: CWF – cool white fluorescent; EPS – xanthophyll epoxidation state; LED – light emitting diode; LUE – light utilization efficiency; PFD – photon flux density; PR – photon requirement (for CO₂ fixation); PSI, PSII – primary donor in Photosystem I, II; RPR – relative photon requirement

Introduction

Advances in light emitting diode (LED) technology have made them an excellent light source for photosynthesis research (Tennessen et al. 1994) and plant growth (Barta et al. 1992; Ignatius et al. 1992; Bula et al. 1994). The LED can make photon fluxes well in excess of 2000 μmol m⁻² s⁻¹ yet can be turned fully on and fully off extremely rapidly (200 ns).

Pulsed lighting has been used to study details of photosynthetic electron transport (Emerson and Arnold 1932; Kok 1956; Jursinic and Pearcy 1988; Chow et al. 1989) and carbon metabolism (Sharkey et al. 1986; Stitt 1986; Kirschbaum and Pearcy 1988; Sassenrath-
Cole et al. 1994). Time constants for photosynthetic processes can be divided into three ranges: (1) primary photochemistry, (2) electron shuttling and (3) carbon metabolism. Primary photochemistry, from light harvesting through charge separation in the reaction centers, occurs in picosecond to nanosecond speeds (Diner 1986). Slightly slower reactions involving microseconds (μs) to milliseconds (ms) occur in electron shuttling between the photosystems (Whitmarsh and Cramer 1979; Harbinson and Hedley 1988; Whitmarsh 1992). Finally, carbon metabolism within the chloroplast occurs in seconds, while sucrose metabolism and enzyme activation takes minutes (Kirschbaum and Pearcy 1988; Sassenrath-Cole and Pearcy 1992). These three photosynthetic processes can be uncoupled by providing pulses of light within the appropriate range for each process. At high frequencies, pulsing light treatments can be used to separate the light reactions (light harvesting and charge separation) of photosynthetic electron transport from the dark reactions (electron shuttling) of photosynthetic electron transport.

Photosynthetic responses to pulsed light is ecologically relevant because the light environment experienced by leaves is often highly variable (Norman and Tanner 1969; Desjardins et al. 1973). Much of the light used for photosynthesis by leaves within canopies is from sunflecks (Pätsch and Pearcy 1989; Pearcy 1990). These sunflecks range from milliseconds to minutes in duration and their photon flux densities can be as bright as full sunlight.

We have used LEDs to study the effects of μs to ms light pulses on photosynthesis of intact leaves. We measured the efficiency of the LEDs at converting electrical power to light used in photosynthesis over a range of wavelengths. The light-response of photosynthesis was measured in continuous light and compared to the situation where the same total photon flux was delivered in intense pulses lasting just 1% of the time. We used up to 5000 μmol m⁻² s⁻¹ photons and frequencies from 5000 to 0.5 Hz. The capacitance of Photosystem II was assessed by lengthening the pulse on and off times (maintaining the same integrated light intensity) until photosynthesis became less efficient in the pulsed light than in the continuous light. Under conditions of excess light, leaves can induce dissipation mechanisms that correlate with de-epoxidation of the pigment violaxanthin (Demmig-Adams et al. 1990), or experience a sustained decrease in photosynthetic efficiency, described as photoinhibition (Björkman 1981). Therefore, photoinhibition and de-epoxidation of violaxanthin was tested for in leaves dissipating pulses of light and compared to leaves dissipating the same light energy provided continuously.

**Materials and methods**

**Plant material and growth conditions**

Tomato plants (*Lycopersicon esculentum* Mill., cv. VF36) were grown in reach-in growth chambers (model E15; Conviron, Winnipeg, Manitoba, Canada) under a 16 h photoperiod, 70% relative humidity, and day/night temperatures of 26°/18 °C. Metal halide lamps, supplemented with incandescent lamps, provided 1000 μmol m⁻² s⁻¹ photons at the canopy top. Each plant was grown in a 10 L plastic pot, filled with peatlite (Metro-Mix 360: Grace Sierra Co., Milpitas, CA, USA) and watered to excess 4 times per day with half strength Hoagland's solution B (Hoagland and Amon 1938).

**Gas exchange measurements and calculations**

An aluminum leaf cuvette with a glass window (4.9 cm²) was clamped onto single terminal leaflets of mature leaves. Fully expanded leaves of 30 day old tomato plants were used. Leaf photosynthesis and conductance were calculated by measurement of CO₂ partial pressure and dewpoint of the airstream entering and exiting the leaf cuvette with an infrared gas analyzer operated in differential mode (model 6262; LI-COR, Lincoln, NE, USA). Gas exchange equations used were as described by von Caemmerer and Farquhar (1981). Air entering the cuvette was mixed with mass-flow controllers (Edwards High Vacuum, Wilmington, MA, USA) from cylinders of N₂, O₂ and 5% CO₂ in air. This mixture was passed through warm water for humidification and subsequently through a copper coil in a refrigerated water bath to establish the desired dewpoint in the leaf cuvette. Reference air was cooled to 0 °C in order to obtain a reference dewpoint for differential measurements. Leaf temperature was maintained at 20 ± 0.5 °C using a water bath and was measured by a copper-constantan thermocouple pressed along the adaxial surface of the leaf for 1 cm. After measurements were taken, the PR (Eq. (1)) was calculated (photons absorbed CO₂⁻¹ absorbed) over a range of 0 to 50 μmol photons m⁻² s⁻¹.