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Effects of quantity and daily distribution of irradiance on photosynthetic electron transport and CO₂ fixation in tomato

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Introduction

The reponses of photosynthesis to light intensity in terms of its acclimation or damage produced have been very intensively studied. These investigations, however numerous, have not often attempted to subject plants to controlled daily cycles of irradiance that attempt to reproduce the sinusoidal cycle that is found under natural conditions in the absence of changes in cloud cover. The reasons for this are technical: depending on the lighting technology employed, controlling light-sources to produce a smooth sinusoidal daily cycle of irradiance is difficult or impossible. Using natural light is an option, but has the disadvantage that the daily irradiance regime is unpredictable. Using high-frequency electronic ballasts with an with an intensity control it is possible to construct a light-source that enables light-intensity to be continuously adjusted and controlled in time. Using such a light-source we have investigated the effect of differing daily integrals of irradiance and photoperiods on the photosynthetic properties of leaves of tomato (*Lycopersicon esculentum*).

Materials and Methods

Plants of tomato (cv Moneymaker) were grown from seed in a controlled temperature room (23°C), with an irradiance provided by a bank of high-frequency fluorescent tubes. The ballasts used for these tubes were electronically controllable, and a purpose-built contoller based upon a PIC microcontroller, which was in turn controlled by a desktop computer, was used to modulate the light output of the lamps. The irradiance treatments were a combination of one of two photoperiods (8 or 16h) and and one of two daily integrals of irradiance (19 or 28 mol m^{-2}), giving a total of four treatments. The maximum irradiances reached in each treatment were: 510 $(8h/19mol m^{-2})$, 760 $(16h/28mol m^{-2})$, 1020 $(8h/19mol m^{-2})$ and 1520 $(16h/28mol m^{-2}) \mu molm^{-2}s^{-1}$. Young mature leaves that had developed under the different light regimes were used for measurements of the irradiance dependency of CO₂ fixation (gaseous phase: 360ppm CO₂, 21% O₂ and balance N_2), Φ_{PS2} and Φ_{PS1} . These were measured using equipment described elsewhere (Kingston-Smith et al, 1999), and using an irradiance regime that simulated as closely as possible in both time and intensity the different growth irrdiance regimes, the major difference being that the irradiance used for the measurements, though of a broadly sinusoidal pattern, was increased and



Figure 1: The time course of light intensity, the quantum yield for photosytem II electron transport, and CO_2 fixation for tomato leaves grown under different daily integrals of irradiance and photoperiods. The symbols used for the different treatments are shown in figure 2.

decresed stepwise (fig 1a & d). The absorbance of the leaves for light (reported here as absorption) was measured using an Instaspec spectrophotometer (Oriel) combined with a Li-Cor Taylor-style integrating sphere, and foliar chlorophyll was calculated from the spectra of dimethylformamide extractions of leaf disc pigments.

Results and Discussion

Chlorophyll. The total chlorophyll and chl a/b ratio were both affected by the daylength, and not much by the daily integral of irradiance (fig2a & b); a longer daylength produces more chlorophyll per unit area and a decreased a/b ratio. This in turn has consequences for leaf absorption: this was increased by increasing daylength, but hardly influenced by the daily integral (fig 2c & d).

CO₂ **fixation**. The simulated daily irradiance courses show quite clearly that the maximum rate of CO₂ fixation achieved was related strictly to the daily integral of irrdiance, in stark contrast to foliar chlorophyll properties. For each of the two daily integral treatments (19mol m⁻² & 28mol m⁻²) the maximum rate of CO₂ fixation *achieved* (nb this is not the light-saturated rate of CO₂ fixation) was the same (fig 1c & d), and this rate increased increased from about 15 μ mol m⁻² s⁻¹ at a daily integral of 19 mol m⁻² to about 22 μ mol m⁻² s⁻¹ at a daily integral of 28 mol m⁻². A simple conclusion is that over a given daily irradiance regime the maximum achievable rate of CO₂ fixation is determined by the daily integral of irradiance. The irradiance response of CO₂ fixation (fig 3a) shows that the long daylength leaves both have more efficient



Figure 2: The foliar chlorophyll concentration, the chlorophyll a/b ratios, and leaf absorption for tomato leaves grown under different daily integrals of irradiance and photoperiods. The key to symbols used in all graphs is also included in this figure.

 CO_2 fixation than do the short daylength leaves. This could be due to the higher absorbance of the long daylength leaves, but photochemical light-use efficiency may also play a part.

Photochemical efficiencies of PSII and PSI. The irradiance dependency of Φ_{PS1} (fig 3b) shows that the long daylength leaves maintain a higher quantum efficiency than do the short daylenth leaves, so it seems from this data that the higher light-use efficiency for CO₂ fixation is also due to increased photochemical efficiency. Note that Φ_{PS1} in the short day leaves falls to much lower values than for the long day leaves owing to the higher light intensities employed in the short day irradiance treatments. The results for Φ_{PS2} are not so straightforward (fig 3c). During the irradiance time course the higher light intensities employed for the short day irradiance regimes results in lower Φ_{PS2} values being reached (fig1b & d). When the changes in Φ_{PS2} are plotted against irradiance (fig 3c) then it is clear that though the long daylength leaves maintain a higher efficiency than the short day plants, the difference is considerably less than for Φ_{PS1} (fig 3b). The differences in the responses of Φ_{PS1} and Φ_{PS2} may be due to differences in the photosystem 1 and 2 to irradiance. Photosytem 1 hasd been found to be relatively unresponsive to changes in light intensity, whereas photosystem 2 displays changes in the population of the light-harvesting complexes. The short day leaves have a higher chlorophyll a/b ratio (fig 2b), which implies a decreased LHC (chorophyll b containing) population. However, decreasing the cross-section of photosystem 2 units with out any corresponding increase in the number of photosystem 2 units would result in a imbalance between the two



Figure 3: The irradiance dependency of CO₂ fixation (A), Φ_{PS1} (B), and Φ_{PS2} (C), and the relationship between J_{PS1} and J_{PS2} (these are the products of Φ_{PS1} and Φ_{PS2} and irradiance resp) (D). The symbols etc are as shown in fig. 2.

photosystems, and no such imbalance is apparent. An alternative explanation is that the lower leaf absorption of the short day leaves allows deeper penetration of the red measuring beam using to excite chlorophyll fluorescence. Penetrating more deeply would result in a higher measured average Φ_{PS2} . Support for this comes from the relationship between J_{PS1} and J_{PS2} (fig 3d); this shows that compared to the long day plants, the short day plants appear to have a higher rate of PS2 electron transport relative to PS1 electron transport, this would be consistent with an overestimate of Φ_{PS2} relative to Φ_{PS1} .

Conclusions. Daylength and daily integral of irradiance have different effects on photosynthetic acclimation. Photoperiod has strong effects on chlorophyll content, and on the chlorophyll a/b ratio, whereas daily integral has strong effects on the highest rate of photosynthesis reached during daily irrdiance cycle. Photoperiod has a strong effect on ligh-use efficiency; a long photoperiod implies a decreased maximum irradiance for a given daily integral, and this low-light situation is countered by an increased light-utilisation efficiency, resulting in higher rates of CO_2 fixation at low quantum fluxes, a surprising result which is at odds with the generally encountered responses of decreased capacity for CO_2 fixation following acclimation to low light.

Kingston-Smith, A.H., Harbinson, J. and Foyer, C.H. (1999) *Plant Cell and Environment*, **22**, 1071-1083.