Photosynthetic Dynamics in Chrysanthemum in Response to Single Step Increases and Decreases in Photon Flux Density

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ABSTRACT

The time-course of CO₂ assimilation rate and stomatal conductance to step changes in photosynthetic photon flux density (PPFD) was observed in Chrysanthemum × morifolium Ramat. ‘Fiesta’. When PPFD was increased from 200 to 600 micromoles per square meter per second, the rate of photosynthetic CO₂ assimilation showed an initial rapid increase over the first minute followed by a slower increase over the next 12 to 38 minutes, with a faster response in low-light-grown plants. Leaves exposed to small step increases (100 micromoles per square meter per second) reached the new steady-state assimilation rate within a minute. Both stomatal and biochemical limitations played a role during photosynthetic induction, but carboxylation limitations seemed to predominate during the first 5 to 10 minutes. Stomatal control during the slow phase of induction was less important in low-light compared to high-light-grown plants. In response to step decreases in PPFD, photosynthetic rate decreased rapidly and a depression in CO₂ assimilation prior to steady-state was observed. This CO₂ assimilation ‘dip’ was considerably larger for the large step (400 micromoles per square meter per second) than for the small step. The rapid photosynthetic response seems to be controlled by biochemical processes. High- and low-light-grown plants did not differ in their photosynthetic response to PPFD step decreases.

Standard methods of estimating crop photosynthetic production are based on CO₂ exchange rate measurements at steady-state conditions following equilibration to a constant light, humidity, and temperature. Most plant growth models estimate carbon gain based on periodic, often hourly, measurements of irradiance. Even if recorded more frequently, irradiance measured over shorter intervals (1-min periods) is often averaged over an hour interval to simplify analysis. Under conditions of varying light, however, these methods can be inadequate and may result in an overestimation of photosynthetic production (8). Pearcy and Calkin (15) observed that in some environments up to 50% of the daily carbon gain was made under conditions of rapidly fluctuating light. Knapp and Smith (11) concluded that most plants experience frequent fluctuation in irradiance rather than continuous sunlight, but most conclusions about ecophysiological adaptation have been derived from measurements taken under constant irradiance. Only recently have the responses of plants to natural, short-term variation in sunlight been explored (11).

Plant response to light fluctuations is complex. Gross (7) indicated that responses to increased and decreased light were two separate processes and concluded that the response to an increase in light was always slower than for a decrease. When leaves are exposed to a light increase following a long period of low light or darkness, an induction period exists before steady-state photosynthesis at the new light level is reached (4, 9). The time-course and duration of the photosynthetic induction can vary within species and with environmental factors, PPFD being the most important. Studies on the understory plant Alacasia macrorhiza indicated that during induction both stomatal and biochemical factors can be important (4). The relative importance of these biochemical and stomatal control mechanisms during induction was dependent on the stomatal conductance at the time of PPFD increase. If conductances were low, increases in assimilation rate were predominantly controlled by increases in stomatal conductance, whereas when conductances were high, biochemical induction was more important (9). Studies of the biochemical changes occurring during photosynthetic induction have suggested that both a low concentration of photosynthetic metabolites (6, 13) and a light activation requirement for Calvin cycle enzymes (12, 23) limit the rate of CO₂ assimilation during induction. Following a sudden decrease in irradiance, illuminated leaves can show a lag in the rate of photosynthetic carbon assimilation prior to the new steady-state photosynthesis rate (18).

Most work concerning photosynthetic response to light variations has been done on species in deeply shaded understory environments exposed to very short lightflecks (for review, see Pearcy [17]). Knapp and Smith (11) separate plants into ‘trackers,’ with stomata responding rapidly to short-term changes in sunlight and photosynthesis, while other species are relatively unresponsive to short-term changes in sunlight (‘non-trackers’). There is some indication that rainforest species have nonresponsive stomata (11). Knapp and Smith (11) found that a given species can alternate between tracking and nontracking patterns depending on seasonal water status. Almost no data exist, however, on how the initial PPFD level affects the photosynthetic response to step changes of varying magnitude and most data do not clearly distinguish between

1 The research reported in this publication was funded (in part) by the North Carolina Agricultural Research Service.
PHOTOSYNTHETIC RESPONSE TO PPFD STEP CHANGES

the effects of the different components of a step change (i.e., initial PPFD level and PPFD step size). Knapp and Smith (11) concluded that more research is needed to address the adaptive significance of nonsteady-state response patterns in plants to environmental variability.

The objectives of the present work were (a) to characterize the time course and factors controlling CO₂ assimilation in response to single step increases and decreases in PPFD and (b) to investigate the effect of growth light environment on this response.

MATERIALS AND METHODS

Plant Material and Growth Conditions

Cuttings of Chrysanthemum × morifolium Ramat. ‘ Fiesta’ were rooted in 0.7 L plastic pots containing soilless media (Metromix 360, W. R. Grace, Inc.) and were placed on heated mist beds for 2 weeks. At the end of the second week, rooted plants were transferred from the greenhouse to the NCSU unit of the Southeastern Plant Environment Laboratory (phytotron). Two controlled environment rooms were set at different irradiance levels. The PPFD level in the ‘low-light’ chamber was kept at 200 μmol m⁻² s⁻¹, while the ‘high-light’ chamber was held at 600 μmol m⁻² s⁻¹. Adjustments were made to the mixture of incandescent and fluorescent lights so that the light spectrum, and in particular the infrared/red ratio (measured with an ISCO spectroradiometer), was approximately the same in both chambers. During the first week, the photoperiod treatment consisted of long days (0800–1800 h) with a dark interruption of 3 h (0100–0400 h). Thereafter, plants were grown under long night conditions (1800–0800 h) to induce flowering. Day/night temperatures were set at 22°C/18°C. Plants were grown in high and low irradiance treatments for at least 2 weeks before responses to step changes were measured. Plants were watered and fertilized every day with a modified half-strength Hoagland solution (5).

Treatment Chamber Specifications

A controlled environment chamber was modified so that the PPFD level could be increased from 100 to 600 μmol m⁻² s⁻¹, in steps of 100 μmol m⁻² s⁻¹, using a combination of incandescent light (100 W lamps controlled by two light dimmers, type 126U Powerstat Inc., Bristol, CT) and fluorescent light (T-12,15,000-mA, cool-white fluorescent lamps connected to different switches). The proper adjustment of the incandescent lights to minimize spectral changes during PPFD variations was determined so that the infrared/red ratio remained essentially constant throughout the steps and approximately the same in the treatment chamber as in the high- and low-light chambers. The chamber temperature during the PPFD treatments was set at the day temperature for the growth chambers of 22°C.

Gas Exchange Measurements

Gas exchange measurements were made on young, fully expanded leaves in an open gas exchange system. Measurements of the photosynthetic response to step changes in PPFD were made with a portable CO₂ exchange apparatus (1). The gas stream entering the cuvette consisted of humidified air from gas cylinders containing 370 ppm CO₂ and 21% O₂ balanced with nitrogen. Humidity was controlled by passing the dry gas mixture, from the gas bottle, through an Erlenmeyer flask partly filled with water. The RH of the gas stream leaving the flask and entering the leaf cuvette averaged around 50% during the tests. Temperature and humidity of the gas stream entering the cuvette were recorded before and after each test by closing the empty cuvette. These measurements indicated little change over time; therefore, the incoming temperature and RH were interpolated from initial and final measurements for each test. The flow rate of the gas stream was kept at a constant level of 5 mL s⁻¹ by a flow meter (KD8 flow controller, ASU-8349; ADC Co., Ltd. England).

Treatment Description

The effects of step increases and decreases in PPFD on the time course of photosynthesis were studied separately. Each step change can be characterized by an initial level and a step size. Both of these factors can vary independently from each other and their individual effect on photosynthetic parameters can be determined by selecting specific levels for each.

The PPFD step increase treatments used in this study included two step sizes (100 and 400 μmol m⁻² s⁻¹) and two initial levels (200 and 500 μmol m⁻² s⁻¹) resulting in the following treatments: (a) 200 to 300; (b) 500 to 600, and (c) 200 to 600 μmol m⁻² s⁻¹. The step decrease treatments were exactly the reverse. The minimum initial PPFD level of 200 μmol m⁻¹ s⁻¹ was chosen because it was assumed that normal plant development could be disrupted if a lower PPFD level was installed. Because of growth chamber limitations, the highest PPFD level was set at 600 μmol m⁻² s⁻¹.

The following procedure was applied for each treatment. First, the PPFD level in the treatment chamber was set at the initial level (200 or 500 μmol m⁻² s⁻¹ for a step increase and 600 or 300 μmol m⁻² s⁻¹ for a step decrease). Second, a single plant was transferred from a growth chamber (high-light or low-light) to the treatment chamber, and a young fully expanded leaf was clamped in the leaf cuvette until steady-state assimilation rate was reached (minimum time of 1 h) before any light change was made. Third, once the initial steady-state assimilation was reached, a PPFD step change was induced and photosynthetic response recorded during a minimum time of 50 min for a step increase or 20 min for a step decrease. Preliminary experiments indicated that these time periods were long enough to allow the leaf to adapt to its new light environment. Thereafter, the plants were removed from the treatment chamber and excluded from further experiments. Finally, the empty treatment chamber was kept undisturbed for a period of 20 min (after removal of the plants and prior to the beginning of a new treatment cycle) to allow air temperature and humidity to stabilize. The treatments were randomly assigned to the time of day. The variability due to the time of day was therefore included into the error term. All treatments were replicated at least three times.
Data Analysis

Gas Exchange Parameters

The signals from the CO₂ analyzer were logged at 5 s intervals by an ADC datalogger, type DL-2, connected to a second datalogger (21 X, Campbell Scientific, Inc.). Calculations of gas exchange parameters were based on equations by Parkinson (14) and von Caemmerer and Farquhar (27) as described by Ball (2). Gas exchange measurements were corrected for two instrumental time lags, an exponential one due to the leaf chamber and gas analyzer volume and a linear one due to the tubing volume. The lengths of the gas tubes to the analyzer were minimized as much as possible to decrease the time lag between instrument and changes in CO₂ assimilation. A tubing lag of 2.81 s was calculated based on length of the butyl tube and velocity of the air moving through it (24), and subtracted from the gross response time before the exponential correction was made. A technique described by Bartholomew et al. (3) and modified by Pearcy et al. (16) was used to calculate instantaneous CO₂ exchange rates (24). This method is based on the fact that after a change in CO₂ in the leaf cuvette of an open flow system, the CO₂ concentration measured by the analyzer exponentially approaches a new equilibrium concentration, assuming the gas in the chamber is uniformly mixed. This projected equilibrium is defined as the CO₂ concentration if the system response was instantaneous and the chamber volume negligible. This method effectively removed the lags due to the chamber and gas analyzer volume. In our calculations, the equations described in the ADC-datalogger instruction manual (1) were modified by replacing the CO₂ partial pressure in the air leaving the cuvette with the calculated instantaneous CO₂ exchange rate. The ADC equations were also corrected for the humidification of the gas stream as described by Stoop (24).

Time-Course Parameters

Step Increase. The steady-state CO₂ assimilation rate at each initial (A₀)² and final (Aₙ) PPFD level was calculated by taking the mean assimilation rate over the last 10 min (Fig. 1). The standard deviation of these observations were used to construct a confidence limit on each steady-state assimilation rate (Aᵢ ± 1 SD and Aₙ ± 1 SD). The time to reach the new steady-state assimilation rate, Tiso, was defined as the time when the CO₂ assimilation rate intercepted the lower limit of the Aᵢ confidence interval (Fig. 1).

Step Decrease. Leaves exposed to a PPFD step decrease can show a dip in the CO₂ assimilation prior to achieving the new steady-state rate (8, 18). This is characterized by an initial drop to a minimum CO₂ assimilation rate followed by a slow increase up to the new steady-state assimilation (Fig. 2). This phenomenon will be referred to as the CO₂ assimilation 'dip.' Three time constants were defined to characterize the 'dip' in CO₂ assimilation rate. T₁ represented the time from PPFD decrease up to the time where the CO₂ assimilation crossed the mean assimilation level (Aᵢ). T₂ measured the required time to reach the minimum CO₂ assimilation rate, and T₃ indicated the time to reach the final steady-state assimilation rate (Fig. 2). All of these times were measured from the point of PPFD decrease.

Statistical Analyses

Steady-state CO₂ assimilation rates and time constants associated with the photosynthetic response to PPFD changes were statistically evaluated with analyses of variance and Duncan multiple range tests (SAS Inst., Cary, NC). All statistical calculations were based on data points measured every 5 s whereas graphs were made from 20-s interval data points. The figures show results for single leaves that were representative for all experiments.

RESULTS AND DISCUSSION

Photosynthetic Response to a Step Increase

To compare the effect of different treatments, the steady-state CO₂ assimilation rate at initial (Aᵢ) and final (Aₙ) PPFD level, as well as the time to reach the new steady-state assimilation rate, Tiso, were determined as described in “Materials and Methods.” Analyses of variance and Duncan multiple range tests (SAS Inst., Cary, NC) were used to determine which treatments differed significantly in the parameters produced. Data from high- and low-light-grown plants were analyzed separately for effect of step changes (Table I).
Steady-State Assimilation Rates

As expected, steady-state assimilation rates were significantly higher at the higher final irradiances. Whether irradiances were increased in steps of 100 or 400 μmol m⁻² s⁻¹ did not affect the steady-state values (A₀) at 600 μmol m⁻² s⁻¹ (Table I) in either the high- or low-light-grown leaves. Similar results were seen when data were analyzed separately for effect of light history within each step increase treatment (data not shown).

Time-Course of CO₂ Assimilation (A) and Stomatal Conductance (g)

Effect of the PPFD Step Size on the Photosynthetic Response. When a high-light-grown leaf was exposed to a large increase in PPFD (i.e. from 200–600 μmol m⁻² s⁻¹), the assimilation curve was characterized by two distinct phases. An initial rapid increase over the first minute was followed by a slower increase over the next 38 min until steady-state assimilation was reached (Fig. 3A). The stomatal conductance of a high-light-grown leaf showed a large increase after a large PPFD increase (400 μmol m⁻² s⁻¹) occurred (Fig. 3B), but during the first 5 to 10 min the increase in g lagged behind the increase in assimilation rate. Thereafter, g increased slowly until a steady-state level was reached. This sigmoidal shape for g was found in all high-light plants exposed to a large step increase. Cᵢ was characterized by an initial drop, followed by a 5 to 25 min interval of constant Cᵢ and a slow increase after that to the steady-state level (Fig. 3C).

Figure 3 clearly illustrates that during the first 5 to 10 min after the irradiance increase no change in stomatal conductance was observed, whereas Cᵢ decreased rapidly to a minimum, indicating that the rapid increase in CO₂ assimilation was probably limited by biochemical mechanisms. During the next 50 min, CO₂ assimilation increased by 25%, g increased by a factor of 1.7, and Cᵢ increased by only 25 μbar, suggesting that the slow phase of induction was under partial stomatal control. However, because the increase in Cᵢ (25 μbar) was too small to explain the 25% increase in assimilation rate, it might be concluded that under these experimental conditions the slow phase of photosynthetic induction was controlled by both biochemical and stomatal processes.

Similar biphasic CO₂ assimilation responses have been reported for shade-adapted plants (16) and for the C₄ plant Zea mays (21). The relative importance of biochemical and stomatal control mechanisms during photosynthetic induction has been subject to considerable debate (17) and can change because of variations in stomatal conductance in low PPFD and irradiance conditions prior to the light increase (9).

Kirschbaum and Pearcy (9) observed a biphasic response in Alocasia macrorrhiza exposed to a large PPFD increase (490 μmol m⁻² s⁻¹) and showed that the slow phase of induction was due to light activation of Rubisco and stomatal opening.

The fast initial response during the induction period has been studied in A. macrorrhiza (10) where it was thought to represent an increase in the capacity to regenerate RuBP and to be an important determinant of a leaf’s potential for photosynthetic carbon gain in environments with fluctuating light. Seeman et al. (20) report that in A. macrorrhiza, the rate of increase of whole leaf photosynthetic CO₂ assimilation in response to a step increase in PPFD is often limited both by the rate at which Rubisco catalytic sites are activated and the rate at which the tight-binding Rubisco inhibitor, CA1P is degraded. When PPFD decreases, the rate of activity loss by Rubisco is much slower than the rate of decline of photosynthesis. This slower rate of loss by Rubisco may give rainforest species such as A. macrorrhiza a greater capacity to take advantage of successive lightflecks.

In our study, when a high-light leaf was exposed to a step increase from 200 to 300 μmol m⁻² s⁻¹ (Fig. 4A) or 500 to 600 μmol m⁻² s⁻¹ (Table I), only a fast increase up to A₀ was observed with steady-state being reached quickly (Tᵢ₀ less than 1 min). The stomatal conductance did not change sig-

Table I. Comparison of Means of Assimilation Rate (μmol CO₂ m⁻² s⁻¹) at Initial (A₀) and Final (Aₙ) PPFD Level and Induction Period (Tᵢ₀ minutes), using Duncan Multiple Range Tests for PPFD Step Increases

<table>
<thead>
<tr>
<th>PPFD Increase (μmol m⁻² s⁻¹)</th>
<th>High-light leaf</th>
<th>Low-light leaf</th>
</tr>
</thead>
<tbody>
<tr>
<td>200–300</td>
<td></td>
<td></td>
</tr>
<tr>
<td>A₀</td>
<td>3.71 b</td>
<td>7.86 a</td>
</tr>
<tr>
<td>Aₙ</td>
<td>5.29 b</td>
<td>10.79 a</td>
</tr>
<tr>
<td>Aₙ - A₀</td>
<td>1.58 b</td>
<td>2.93 a</td>
</tr>
<tr>
<td>Tᵢ₀</td>
<td>0.96 b</td>
<td>38.51 a</td>
</tr>
</tbody>
</table>

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<thead>
<tr>
<th>PPFD Increase (μmol m⁻² s⁻¹)</th>
<th>High-light leaf</th>
<th>Low-light leaf</th>
</tr>
</thead>
<tbody>
<tr>
<td>200–600</td>
<td></td>
<td></td>
</tr>
<tr>
<td>A₀</td>
<td>3.99 b</td>
<td>8.76 a</td>
</tr>
<tr>
<td>Aₙ</td>
<td>10.79 a</td>
<td>19.95 a</td>
</tr>
<tr>
<td>Aₙ - A₀</td>
<td>6.80 a</td>
<td>11.19 a</td>
</tr>
<tr>
<td>Tᵢ₀</td>
<td>1.55 b</td>
<td>5.65 a</td>
</tr>
<tr>
<td>500–600</td>
<td></td>
<td></td>
</tr>
<tr>
<td>A₀</td>
<td>6.80 a</td>
<td>11.19 a</td>
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</tr>
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<td>Aₙ - A₀</td>
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<td>28.76 a</td>
</tr>
<tr>
<td>Tᵢ₀</td>
<td>5.65 a</td>
<td>11.40 a</td>
</tr>
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* Alpha = 0.05; means with the same letter are not significantly different.
nificantly after a 100 μmol m\(^{-2}\) s\(^{-1}\) increase in PPFD (Fig. 4B). After the initial drop, \(C\) stayed relatively constant (Fig. 4C). Because no apparent change in stomatal conductance was observed, the rapid increase in \(C\) assimilation during induction was apparently attributable solely to biochemical changes. The induction period of both treatments lasted less than 1 min and was significantly smaller than the 38 and 12 min \(T_{\text{ind}}\) of the large step treatment (200–600 μmol m\(^{-2}\) s\(^{-1}\)) in both high and low light treatments, respectively (Table I).

**Effect of Light History on the Photosynthetic Response.** Leaves grown under low-light conditions and exposed to large step increases (400 μmol m\(^{-2}\) s\(^{-1}\)) showed rapid increases in photosynthesis over the first minute followed by a small increase until \(A\) was reached (Fig. 5A). This time course was similar to that of high-light-grown leaves (Fig. 3) with the exception that \(T_{\text{ind}}\) was significantly smaller for low-light leaves (12 min) as compared to high-light leaves (38 min). Low-light leaves exposed to a large increase (400 μmol m\(^{-2}\) s\(^{-1}\)) had generally similar curves for stomatal conductances (Fig. 5B) and internal \(C\) pressures (Fig. 5C) as high-light-grown leaves. The conductance increase, however, was less sigmoidal and the time lag (20 min) before the slow increase in \(g\) was much longer than in high-light leaves, and the increase in \(C\) did not occur for 30 min and was very slight.

Because the stomatal conductance and \(C\) of low-light-grown leaves remained relatively constant during photosynthetic induction following a large increase, both the rapid and slow phases of the \(C\) assimilation increase were probably caused by biochemical changes only. This is in contrast to high-light-grown leaves, where stomatal conductance increased significantly during the slow phase of induction. Low-light-adapted leaves responded to small step increases (i.e., 200–300 and 500–600 μmol m\(^{-2}\) s\(^{-1}\)) in a way similar to high-light leaves for values of \(A_i\) and \(A_f\) - \(A_i\), but \(A_f\) was higher in low-light-grown plants in the 200 to 300 μmol m\(^{-2}\) s\(^{-1}\) treatment, and \(T_{\text{ind}}\) was less in low-light-grown plants with both the 200 to 300 step treatments (0.52 versus 0.96 min) and the 500 to 600 treatment (0.30 versus 0.58 min).

In summary, the effect of light history on the photosynthetic response of chrysanthemum to light increases was dependent on the step size. If a large PPFD increase occurred, low-light leaves had a shorter induction period with less stomatal limitations than high-light leaves. When a small increase in PPFD was induced, low-light leaves responded in a way similar to high-light leaves except that \(T_{\text{ind}}\) was slightly smaller.

**Photosynthetic Response to a Step Decrease**

**Steady-State Assimilation Rates**

As with the step increases, \(A_f\) was not affected by the step size or initial PPFD level (Table II). \(A_i\) of low-light leaves was

![Figure 3 (left). A, Time course of \(C\) assimilation; B, stomatal conductance, C, intercellular \(C\) pressure of a 'high light'-grown leaf exposed to a PPFD increase from 200 to 600 μmol m\(^{-2}\) s\(^{-1}\) at the time indicated by (†).

**Figure 4 (right). A, Time-course of \(C\) assimilation; B, stomatal conductance; C, intercellular \(C\) pressure of a 'high light'-grown leaf exposed to a PPFD increase from 200 to 300 μmol m\(^{-2}\) s\(^{-1}\) at the time indicated by (†).**

### Table II. Comparison of Means of Assimilation Rate (μmol CO\(_2\) m\(^{-2}\) s\(^{-1}\)) at Initial (A) and Final (A\(_f\)) PPFD Level, using Duncan Multiple Range Tests for PPFD Step Decreases

<table>
<thead>
<tr>
<th>PPFD Decrease (μmol m(^{-2}) s(^{-1}))</th>
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<th>Low-light leaf</th>
</tr>
</thead>
<tbody>
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<td>300-200</td>
<td>600-200</td>
<td>600-500</td>
</tr>
<tr>
<td>300-200</td>
<td>600-200</td>
<td>600-500</td>
</tr>
<tr>
<td>(A_i)</td>
<td>4.79 b</td>
<td>9.95 a</td>
</tr>
<tr>
<td>(A_f)</td>
<td>9.64 a</td>
<td>6.19 b</td>
</tr>
<tr>
<td>(A_f) - (A_i)</td>
<td>5.85 a</td>
<td>6.96 a</td>
</tr>
<tr>
<td>(A_f)</td>
<td>3.59 b</td>
<td>6.19 b</td>
</tr>
<tr>
<td>(A_f)</td>
<td>7.72 a</td>
<td>4.99 b</td>
</tr>
<tr>
<td>* Alpha = 0.05; means with the same letter are not significantly different.</td>
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indicated by C,, ance; Figure 4. "Materials and Methods" as the CO₂ assimilation dip, was observed prior to establishment of a new steady-state assimilation rate (Fig. 6A). Stomatal conductance decreased slowly after the PPFD decrease and reached a constant level after 10 to 15 min (Fig. 6B). C increased rapidly to a maximum of 320 μbar and then slowly decreased to a steady-state level of 290 μbar (Fig. 6C). The parallel decrease in g and C could indicate stomatal control, but no significant decrease in photosynthesis was observed during that period.

The response of CO₂ assimilation to a small decrease in PPFD (i.e. 100 μmol m⁻² s⁻¹) was always very rapid (Fig. 7A). The CO₂ assimilation dip was smaller than after a large PPFD decrease. Stomatal conductance did not change after a small decrease in irradiance (Fig. 7B) and C after the initial increase, stayed at a constant level (Fig. 7C). As there was no discernible change in stomatal conductance, the decrease in CO₂ assimilation must have been caused by biochemical changes.

Plants grown in low and high light did not differ in the time constants of their photosynthetic response to PPFD step decreases, except that low-light leaves exposed to a decrease from 600 to 500 μmol m⁻² s⁻¹ had a longer T₁ (0.57 min) as compared to high-light leaves (0.42 min). We are unsure of the cause of this difference.

For both low- and high-light plants, step decreases of 300 to 200 and 600 to 200 μmol m⁻² s⁻¹ did not differ in T₁ and T₂, but T₁ was lower in the 600 to 500 μmol m⁻² s⁻¹ treatment for high-light plants only (0.42 compared to 0.83 and 0.64 min for the 300 to 200 and 600 to 200 μmol m⁻² s⁻¹ treatments, respectively). In the low-light treatment, T₁ was longest with the 400 μmol m⁻² s⁻¹ decrease (2.33 compared to 1.14 and 0.67 min, for the 300 to 200 and 600 to 500 μmol m⁻² s⁻¹ treatments, respectively).

The CO₂ assimilation dip following a decrease in irradiance may be associated with a post-lower-irradiance CO₂ burst (22, 25, 26) which results from the continued turnover of photoreactive intermediates. Prinsley et al. (19) investigated the factors regulating photosynthetic assimilation of a spinach leaf following a large decrease in irradiance. They reported that a decline in assimilatory power (ATP/ADP and NADPH/NADP⁺) resulted in an accumulation of glycerate-3-P together with a decline in RuBP and Rubisco activation. Furthermore, the rate of carbon incorporation into starch adjusted slowly to the decrease in irradiance and eventually the pools of metabolites assumed their correct proportions.

**SUMMARY**

The data presented here show that the CO₂ assimilation response to a sudden increase in irradiance is dependent on

![Figure 5](image_url)  
**Figure 5.** A, Time-course of CO₂ assimilation; B, stomatal conductance; C, intercellular CO₂ pressure of a 'low light'-grown leaf exposed to a PPFD increase from 200 to 600 μmol m⁻² s⁻¹ at the time indicated by (†).

![Figure 6](image_url)  
**Figure 6.** A, Time-course of CO₂ assimilation; B, stomatal conductance; C, intercellular CO₂ pressure of a 'high light'-grown plant exposed to a PPFD decrease from 600 to 200 μmol m⁻² s⁻¹. Arrows indicate the time when irradiance was decreased from 600 to 200 μmol m⁻² s⁻¹.
the PPFD step size and growth light level, whereas the response to a PPFD step decrease is not affected by the light history of the plant. If a large PPFD increase (400 μmol m⁻² s⁻¹) occurred, CO₂ assimilation underwent a biphasic response: a rapid initial increase followed by a more gradual increase to the new steady-state assimilation rate. When a small PPFD increase occurred, only a rapid increase in photosynthetic rate up to the new steady-state level was observed. The induction period was dependent on the PPFD step size but not on the initial level. The larger the step size, the longer it took to reach the new steady-state assimilation rate. Stomatal conductance and intercellular CO₂ pressure calculations suggested that the early phase of the induction period was probably controlled by biochemical processes.

High-light- and low-light-grown leaves had similar time-courses but the photosynthetic induction period was significantly shorter for all low-light-grown leaves. The indication that the early phase of the induction period is probably controlled by biochemical processes can explain the smaller time constants observed for low-light-grown leaves. Plants grown in low-light conditions had a virtually constant stomatal conductance during photosynthetic induction, indicating that the stomatal control was less important for low-light-grown plants than for high-light-grown plants. This suggests that low-light-grown plants behave more like the 'nontrackers' described by Knapp and Smith (11) and high-light plants like the 'trackers.' Presumably this strategy would optimize utilization of irradiance in low-light environments and utilization of water in high-light environments.

In response to step decreases in PPFD, photosynthetic rate decreased rapidly to a point below the new steady-state value and followed by a gradual increase up to the new steady-state level. This CO₂ assimilation dip was considerably longer for the large step decrease (400 μmol m⁻² s⁻¹) than for the small step decrease (100 μmol m⁻² s⁻¹). The rapid photosynthetic response seems to be controlled by biochemical processes. High- and low-light-grown plants did not differ in their photosynthetic response to PPFD step decreases.

PPFD step size appears to be the most important factor affecting photosynthetic response. Under the conditions of this experiment, the plant growth light level affected the photosynthetic response to an increase in irradiance but not to a decrease. Both stomatal and biochemical factors seem to control the photosynthetic response and they are affected by the light history of the leaf.

ACKNOWLEDGMENTS

The authors would like to acknowledge Yoder Brothers Inc. Barberton, OH, for the chrysanthemum cuttings and Dr. Jack Downs, NCSU Phytotron Director, for assistance in chamber modifications for this experiment. We thank D. Walker and R. Pearcy for critical reading of this manuscript.

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