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Steady-state and dynamic photosynthetic response of *Adenocaulon bicolor* (Asteraceae) in its redwood forest habitat

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Summary. The gas exchange characteristics under steady-state and transient light conditions were determined for a redwood forest understory herb *Adenocaulon bicolor*, that depends on use of sunflecks for a large fraction of its daily carbon gain. Measurements under steady-state conditions indicated that this species has photosynthetic characteristics that are typical for understory plants. The mean light-saturated assimilation rate was 5.26 μmol CO_2 m^{-2} s^{-1}; the light saturation and compensation occurred at 243 and 2 μmol photons m^{-2} s^{-1}, respectively. This light compensation point was much less than the photon flux density under diffuse light in the understory so that positive assimilation could be maintained throughout the day. When leaves that had been in diffuse light for at least 2 h were exposed to a sudden increase in PFD to saturating levels, 10–30 min were required for both assimilation and stomatal conductance to reach maximum values. Calculation of intercellular CO_2 pressures, however, suggest that for the first 10 min after the light increase, biochemical factors were responsible for most of the increase in assimilation. Thereafter stomatal opening caused a further increase in assimilation that was no more than 25% of the total. When fully induced leaves were returned to low light, induction was rapidly lost even though stomatal conductance decreased only slowly. This rapid loss of induction limited the capacity of *A. bicolor* to use sunflecks after low light periods that lasted longer than 1–2 min. However, during periods when sunflecks are more frequent there is probably little loss of induction. Under these conditions, sunflecks are used with high efficiency for assimilation.

Key words: Puantum yield – Photosynthetic induction – Shade adaptation – Sunflecks – Transient photosynthesis

The majority of our understanding of plant photosynthetic response to environmental conditions has been derived from experiments done under conditions of steady-state illumination. The dynamics of light in forest understories is such that plants infrequently experience periods of high light that are long enough for steady-state rates of assimilation to be obtained. Knowledge of the dynamics of photosynthetic responses to changing light is necessary in order to understand and ultimately predict patterns of carbon gain by understory plants.

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Recent advances in gas exchange technology have enabled a characterization of transient photosynthetic responses to changing light (Pearcy et al. 1985; Chazdon and Pearcy 1986a, b; Kirschbaum and Pearcy 1988a, b). These laboratory studied have shown that the ability of a plant to exploit the energy available in sunflecks depends on two general factors: the photosynthetic induction state of the leaf, and its capacity for post-illumination carbon fixation. Photosynthetic induction state is a complex function of light-dependent stomatal opening and closing responses and the time courses of light-regulated enzyme activation and deactivation. All of these factors combine to determine the potential light-saturated photosynthetic rate at any given moment and therefore the potential photosynthetic rate that can be achieved during a sunfleck. Post-illumination carbon fixation occurs when photosynthetic intermediates synthesized during a sunfleck are used for continued assimilation after the sunfleck has passed.

Our goal in this study has been to characterize the steady-state and dynamic photosynthetic response to light of a plant growing in its natural understory habitat. This is the first detailed investigation of photosynthetic induction and lightfleck response of an understory plant in situ. It is part of a larger study with a redwood forest understory herb, *Adenocaulon bicolor*, that addresses the question of the ecological significance of sunflecks for understory plants. In a companion paper we report the results of measurements of daily carbon gain under natural light conditions (Pfitsch and Pearcy 1989).

Materials and methods

This study was conducted during 1987 and 1988 in the understory of a second-growth coastal redwood forest at Samuel P. Taylor State Park near Fairfax, Calif. This forest has an overstory composed primarily of *Sequoia sempervirens* and *Pseudotsuga menziesii*, with a locally abundant subcanopy tree, *Lithocarpus densiflora*. *Adenocaulon bicolor* Hook. (Asteraceae) is a common herb in the understory vegetation of this and other moist forests in western North America (Munz and Keck 1959). It is a deciduous rosette with 8–15 leaves at maturity. In coastal redwood forests the growing season of *A. bicolor* lasts from February through August. Large (40–100 mm long) deltoid leaves on equally long petioles make this an ideal species for gas exchange studies. An earlier study indicated that *A. bicolor* had typical shade-plant photosynthetic response and biochemistry (Björkman 1968).

Measurements of carbon dioxide and water vapor exchange of individual, attached leaves were made using a transportable gas exchange system modified from that described previously (Pearcy and Calkin 1983; Pearcy 1987). Air of desired CO_2 concentration was mixed with mass flow controllers (Tylan Inc.) from CO_2-free air and 5% CO_2 in air supplied from compressed air cylinders. The dewpoint of the air mixture was set by first saturating it with water vapor and then passing it through a peltier-cooled condenser. An open system configuration of the gas exchange apparatus was employed with a Binos infra-red gas analyser and Vaisala Humicap thin-film capacitance-type sensors for differential analysis of CO_2 and water vapor respectively. The humidity sensors were mounted in a heated aluminum block that was thermostatted at 34° C to maintain a linear humidity response over the range of vapor pressures encountered in the chamber. The gas analyser signal was corrected for dilution effects of water vapor and its interaction with the CO_2 signal. Over-pressure in the system was measured by a Validyne Inc. electronic pressure transducer and was generally in the range of 20 mbar.

Calculations of gas exchange rates, stomatal conductances (g_s), and intercellular CO_2 partial pressures (p_i) were based on equations given by von Caemmerer and Farquhar (1981). All measurements were made with leaf temperatures approximately equal to the ambient air temperature at the time (12°–25° C) and a low leaf to air vapor pressure difference (<10 mbar bar^{-1}). The reference partial pressure of CO_2 was maintained at 350–355 μbar unless otherwise noted.

Light was provided with a 150-W quartz iodide projection lamp and photon flux densities (PFD) were measured with a cuvette-mounted galium arsenide phosphide (GaAsP) photodiode (Model G1118, Hamamatsu Corp). The sensor was calibrated against a Quantum Sensor (LI-COR Model 190s). During calibrations the Quantum Sensor was mounted under the lid of the chamber in the position of the leaf. The dependence of photosynthetic rate on PFD was determined by first increasing PFD to values well above saturation and waiting for a steady-state rate of CO_2 uptake to be obtained. Neutral-density glass filters were then used to decrease the PFD in steps to darkness. Measurements of gas exchange rates were made after steady-state conditions were obtained at each step. The CO_2 dependence of photosynthesis was determined by adjusting the flows of the CO_2-free air and the 5% CO_2 mixture to produce the desired CO_2 partial pressure. After measurement of steady-state rates at approximately ambient CO_2 levels (350 μbar), the CO_2 pressure of the ingoing air (p_a) was then decreased to near the compensation point ($\simeq 60$ μbar) and then increased in steps up to 1000 μbar. Gas exchange measurements were made at each step after steady-state signals were obtained. The CO_2 response data were fitted by least-squares regression to a seven-parameter biochemical model described in Kirschbaum and Farquahar (1984).

In order to assess the ability of *A. bicolor* to respond to sudden increases in PFD, the time course of assimilation and stomatal conductance following a step-increase in PFD from diffuse levels (5–15 μmol m^{-2} s^{-1}) to above light saturation levels (300–500 μmol m^{-2} s^{-1}) was determined. In most cases the measurements were done on leaves that had not been exposed to sunflecks for at least the previous 2 h. The photosynthetic induction state of the leaf is defined as

$$\text{Induction State} = A - A_{dif}/A_{max} - A_{dif}$$

where A is the measured assimilation 1 min after illumination with saturating PFD, A_{dif} is the rate of assimilation under diffuse light and A_{max} is the steady-state light-saturated assimilation rate (Chazdon and Pearcy 1986a).

The rate of loss of photosynthetic induction was determined by first bringing the leaf to full induction at saturating PFD and then exposing it to various periods of diffuse PFD. The time-course of assimilation was determined following re-illumination with saturating PFD.

Experimental lightflecks were produced by either manually removing and inserting a neutral density filter between the light source and the leaf chamber or by an electronic shutter between the lamp and the chamber. The efficiency of lightfleck use was examined by exposing fully-induced leaves to 3 different random series of saturating lightflecks of different length (2, 4, 8, 16, 32 and 64 s). All lightflecks were preceeded and followed by 120 s of diffuse light. This time in low light was required to allow a full reequilibration to the steady-state assimilation rate in diffuse light before the next lightfleck was given. Equilibration was delayed in particular after long lightflecks because of a significant post-illumination CO_2 burst lasting for as long as 60 to 90 s. Data were logged at 0.6-s intervals. The total assimilation due to a lightfleck was determined by integration of the assimilation rate during the lightfleck plus the following 120 s of diffuse light and then subtracting the amount that would have been due to diffuse light alone. The latter was determined from the average of the photosynthetic rates just before the lightfleck and at the end of the 120-s diffuse light period multiplied by the integration period. The lightfleck use efficiency was calculated as the measured assimilation due to the lightfleck relative to the assimilation that would occur given an instantaneous response to changes in PFD (Chazdon and Pearcy 1986b).

Results and discussion

Steady-state response

The light response characteristics of *Adenocaulon bicolor* growing under natural forest understory conditions were typical of a shade-adapted species (Fig. 1, Table 1). Both dark respiration rates and light compensation points were very low. Carbon assimilation (A) was light-saturated generally at about 10% of full sun with maximum rates of

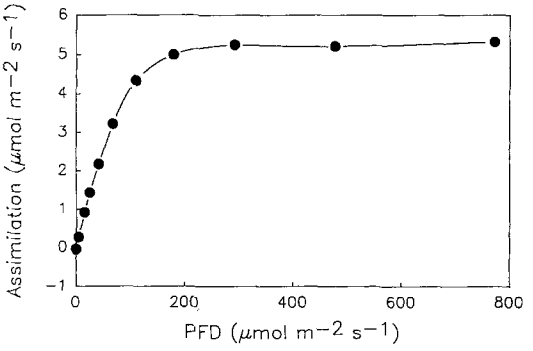

Fig. 1. A representative light response curve of photosynthesis of *Adenocaulon bicolor*. Measurements were made at a leaf temperature of 20° C and leaf-air vapor pressure deficit 6 mbar

Table 1. Summary of steady-state photosynthetic light response characteristics for *Adenocaulon bicolor*[a]

	n	Mean	SD	Range
Apparent quantum yield mol CO_2 mol^{-1} photons	13	0.054	0.007	0.040–0.065
PFD (μmol m^{-2} s^{-1})				
at compensation	9	2	1	1– 3
at 95% A_{max}	13	243	91	137–394
CO_2 exchange (μmol m^{-2} s^{-1})				
Maximum	13	5.26	1.55	2.67 –9.06
Dark respiration	9	0.15	0.09	0.05 –0.37
Stomatal conductance (mmol m^{-2} s^{-1})				
Diffuse light	34	58	30	8 –124
Maximum	15	163	43	97 –234
Intercellular CO_2 pressure (μbar)				
Diffuse light	34	331	22	240 –355
At maximum *A*	15	278	10	258 –299

[a] Measurements were made at ambient leaf temperatures (13°–25° C, ambient CO_2 pressures 345–355 μbar, and leaf-air water vapor pressure deficits <10 mbar)

about 5 μmol m^{-2} s^{-1} (Table 1). There was variation among leaves in light-saturated assimilation rate that apparently was related to variation in canopy openness with individuals in more open sites having higher maximum rates. There was also evidence of seasonal or leaf age effects, with higher rates observed early in the year.

Photosynthetic induction state

An induction period of 10 to 30 min was required before steady-state *A* and g_s were achieved when leaves that had been in low light for at least 2 h were exposed to saturating light (Fig. 2). Assimilation increased rapidly following the light increase and reached 50% of the maximum values within an average of 2.7 min (range 1 to 7.5 min, $n=10$). The rate of increase in *A* then gradually slowed as the maximum was approached (Fig. 2A), reaching 95% of maximum after an average of 15 min (range 8–22, $n=10$). In contrast, g_s exhibited a nearly constant rate of increase up to the maximum value (Fig. 2B). Induction occurred at a similar rate when alternating periods of saturating and diffuse light (1 min high, 2 min low) were given rather than continuous light (data not shown). Thus, as observed in other species (Pearcy et al. 1985; Chazdon and Pearcy 1986a), *A. bicolor* does not require continuous high PFD for induction.

The different time courses for *A* and *g* caused the p_i to initially decline from 325–210 μbar, but then gradually increase to the steady-state value in high light of 270 μbar (Fig. 2c). If changes in *A* during induction were due only to increases in g_s then values of *A* versus p_i should all fall along the steady-state *A* versus p_i curve. Following the light increase, values of *A* versus p_i were initially well below the steady-state curve and required 5–7 min to reach it (Fig. 3). The initial increase in assimilation during induction was therefore primarily due to an increase in the biochemical carboxylation capacity. After 5–7 min the increase in *A* fell along the *A* versus p_i curve. Nearly 60% of the total increase

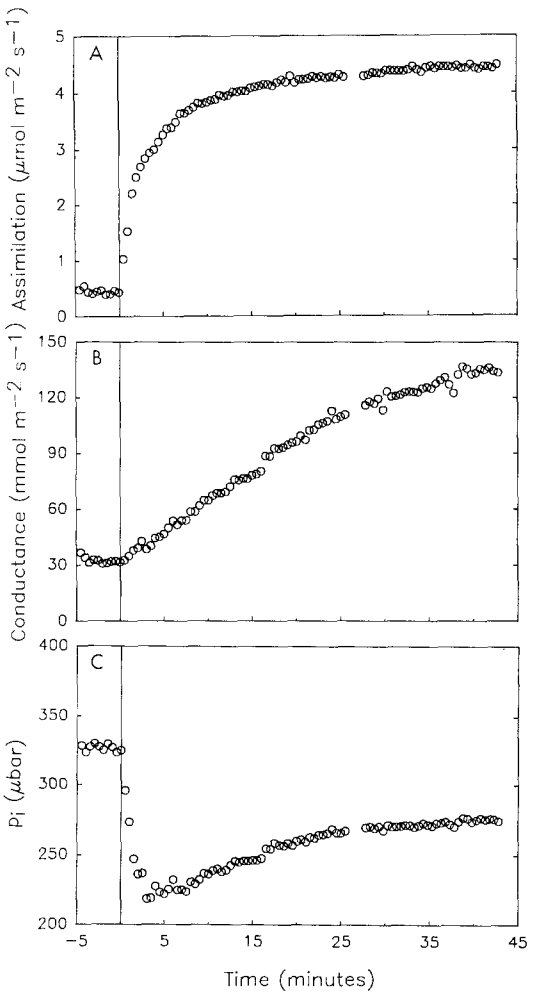

Fig. 2. A representative time course of (**A**) photosynthetic induction, (**B**) stomatal conductance, and (**C**) intercellular CO_2 pressure of *Adenocaulon bicolor* following an increase in PFD from 10–300 μmol m^{-2} s^{-1}. Leaf temperature was 18° C, and leaf-air vapor pressure deficit was 8.5 mbar

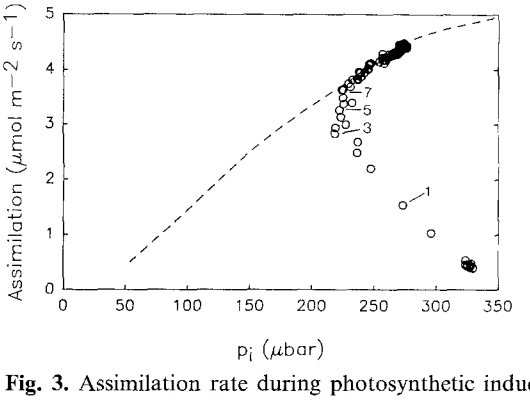

Fig. 3. Assimilation rate during photosynthetic induction plotted against the calculated intercellular CO_2 pressure. Data are the same as were plotted in Fig. 2. Numbers indicate the time (min) after the increase in PFD. The dashed line is the steady-state relationship between assimilation and intercellular CO_2 pressure measured for the same leaf

in g_s during induction occurred after 7 min, but only 25% of the total increase in assimilation occurred after this time. Thus biochemical limitations to *A* predominate during induction in *A. bicolor*.

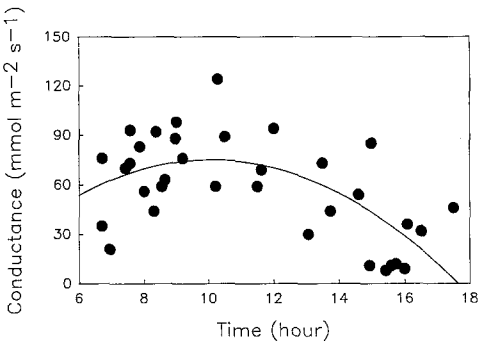

Fig. 4. The stomatal conductance of leaves in diffuse light in the understory. All values are for leaves that had received only diffuse light for at least 1 h prior to the measurement and are from measurements throughout the growing season. Ambient CO_2 pressures were 350±10 μbar, leaf temperatures of 13°to 25° C, and a leaf-air vapor pressure deficit <10 mbar

The conclusion that the limitations to induction are biochemical in origin must be tempered because the role of stomata can be underestimated when g_s is low if the cuticular conductance to water vapor (g_c) is not taken into account in the calculation of p_i (Kirschbaum and Pearcy 1988a). The g_c of *A. bicolor* leaves was not measured but in nearly all cases g was so high that it would have caused by most only a small change in p_i. An upper limit for g_c is set by the minimum g_s of 8 mmol m^{-2} s^{-1} measured for *A. bicolor*. The true g_c is almost certainly less than this value. By comparison, the minimum g_s for *Alocasia macrorrhiza* was 7 mmol m^{-2} s^{-1} and the estimated g_c was 3.2 mmol m^{-2} s^{-1} (Kirschbaum and Pearcy 1988a). Since g_s for *A. bicolor* was generally between 30 and 90 mmol m^{-2} s^{-1} (Fig. 4), there would be almost no effect of ignoring the cuticular path for water vapor loss on the calculated p_i.

Why should the stomata be so open in diffuse light? Curves of assimilation versus p_i (Fig. 5A) show that assimilation is nearly CO_2 saturated at PFD of 19 or 45 μmol m^{-2} s^{-1} and p_i that result from the minimum g measured for this leaf (48 mmol m^{-2} s^{-1}). Thus, stomata could close to much lower values of g_s, effecting a savings in water with only a slight decrease in assimilation. However, when the dependence of the quantum yield of CO_2 uptake on p_i is determined, the advantage of a high g_s in diffuse light is apparent. In agreement with the calculations of Pearcy (1987) and observations of Ehleringer and Björkman (1977), the incident quantum yield was strongly dependent on p_i (Fig. 5B). Thus, if stomata closed to maintain p_i at 270 μbar, the same value observed at light saturation, the quantum yield would have been 5% lower than at the diffuse light p_i of 330 μbar. In a light-limited environment such as the redwood forest understory the small additional carbon gain probably outweighs the disadvantages associated with the resulting higher water loss. Relatively high values of g_s and consequently p_i in diffuse light have been observed in several understory species (Björkman et al. 1972; Pearcy and Calkin 1983). However, Weber et al. (1985) found low conductances that appeared to regulate p_i at values around 240 μbar in sugar maple seedlings in a Michigan forest understory. Thus, there may be variation in the priority placed on increasing carbon gain via enhanced quantum yields and the minimization of water loss in plants found in forest understories.

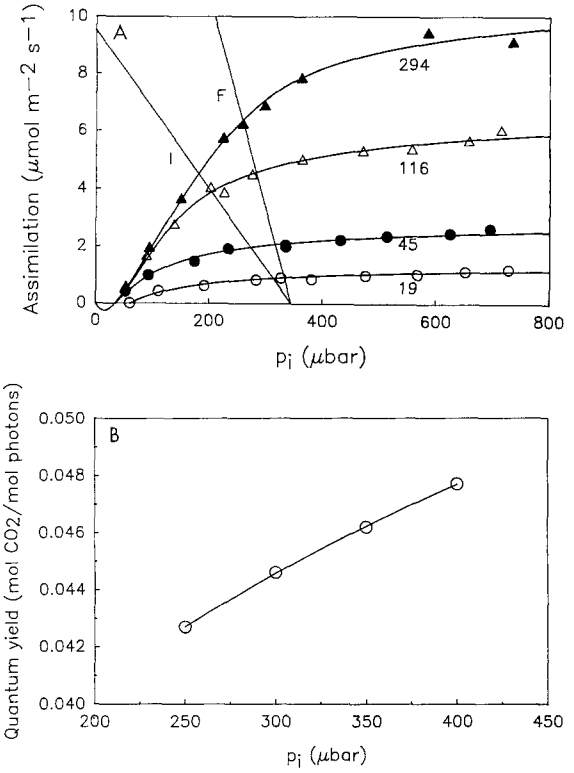

Fig. 5. (**A**) Assimilation as a function of intercellular CO_2 pressure at 4 different PFDs. The curves were fit using a biochemical model for C_3 assimilation (Kirschbaum and Farquhar 1984). *I* and *F* are the CO_2 "supply functions" (Farquhar and Sharkey 1982) for an initial g_s prior to induction and a final g_s of 48 and 135 mmol m^{-2} s^{-1}, respectively. Leaf temperatures were 20° C and leaf-air vapor pressure deficit of 9.5 μbar/bar. (**B**) Relationship between quantum yield and internal CO_2 pressure derived from the A/P_i curves done at PFDs of 19 and 45 μmol m^{-2} s^{-1}

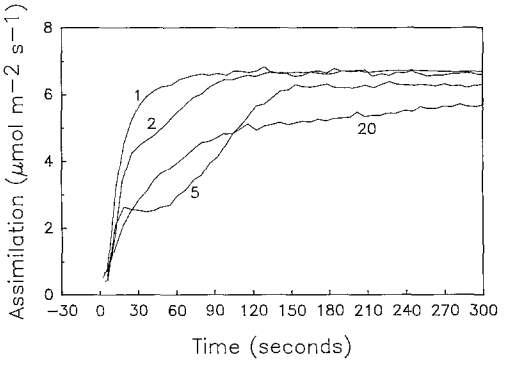

Fig. 6. The initial time course of photosynthetic induction following diffuse light intervals of 1, 2, 5, and 20 min. The leaf was fully-induced prior to each diffuse light period. Leaf temperatures were 20° C, and leaf-air vapor pressure deficits were 9±1 mbar

Of equal importance as the rate of induction gain for sunfleck use is the rate of induction loss. If significant induction loss occurs between sunflecks then carbon gain would be reduced. We examined the time-course of the loss of photosynthetic induction by exposing fully-induced leaves to diffuse light for various lengths of time. After 1 min in diffuse light the increase in assimilation appeared to be monophasic and rapidly approached the steady state values measured at full induction (Fig. 6). By contrast, after 2 min and especially after 5 min of diffuse light the increase

Table 2. Photosynthetic induction state and stomatal conductance as a percent of maximum 1 min after reillumination with saturating PFD after various intervals of diffuse light. Mean and standard deviation (SD)

Diffuse light (min)	*n*	Induction state		Conductance	
		(%)	SD	(%)	SD
1	4	96	2.3	94	4.9
5	5	56	14.8	82	26.5
20	4	68	14.4	83	11.4
40	2	55	20.4	61	23.9

Table 3. Lightfleck use efficiency (%) relative to prediction based on instantaneous response for lightflecks of different lengths for fully-induced leaves of *Adenocaulon bicolor*. Lightflecks were approximately 300 μmol photons m^{-2} s^{-1} and were preceeded and followed by 2 min of diffuse light (7–15 μmol m^{-2} s^{-1}). Means and Standard Deviations for 3 leaves, each leaf value was the average of determinations in 2 or 3 random sequences

Lightfleck length (s)	Mean	SD
2	105.5	8.5
4	93.5	12.9
8	76.8	3.2
16	62.6	10.7
32	71.6	2.4
64	64.4	8.9

in assimilation was distinctly biphasic. After 5 min there was a distinct peak followed by a slight decline before assimilation rates increased again. About 150 s elapsed from the first peak to the time that assimilation rates approached values only slightly less than the final steady state. The biphasic recovery was evident after at least 10 min of diffuse light exposure (data not shown). By 20 min of diffuse light, however, the increase in assimilation was again monophasic but only gradually approached the steady-state values. The rapid induction loss and biphasic recovery was not due to a rapid stomatal response since *g* decreased only about 20% from the maximum values by 5 min (Table 2), and changed slowly relative to the biphasic increase in assimilation.

The mechanisms underlying this rapid induction loss and the biphasic response are unclear. Light-regulation of ribulose bisphosphate carboxylase (Rubisco) is generally much slower than the rapid induction loss seen here (Seemann et al. 1988). However, some fast regulatory response of Rubisco in this species cannot be ruled out. More likely is regulation of another enzymes in the RuBP regeneration part of carbon metabolism. Kirschbaum and Pearcy (1988b) have identified a fast component in the induction response of *Alocasia macrorrhiza* that appears to be related to a limitation in RuBP regeneration.

Lightfleck experiments

Photosynthetic lightfleck-use efficiency was dependent on lightfleck length (Table 3) but was low in comparison to other shade species studied so far. Efficiencies exceeded 100% only for 2-s lightflecks and averaged only 66% for lightflecks longer than 8 s. By contrast lightfleck use efficiencies for 5-s lightflecks are often 130 to 180% for other shade species (Chazdon and Pearcy 1986b; Pearcy et al. 1985).

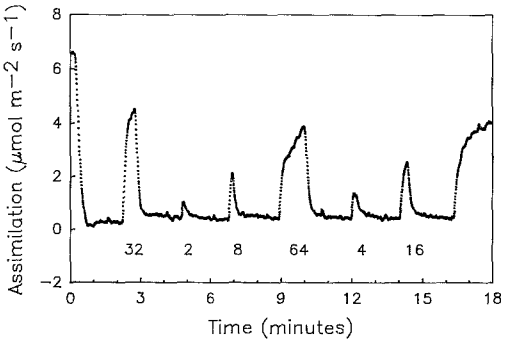

Fig. 7. Response of assimilation to lightflecks (294 μmol m^{-2} s^{-1}) of varying duration. The numbers below each lightfleck give its duration (s). Each lightfleck was separated by 2 min of diffuse light. Leaf temperatures were 20° C, and leaf-air vapor pressure deficits were 9 mbar

The low lightfleck-use efficiencies of *A. bicolor* appear to be related to the rapid induction loss found in this species. This is evident in the lightfleck sequence shown in Fig. 7 where the assimilation rate attained in the first lightfleck, which was 32 s long, was much greater than the rate achieved in a subsequent 64-s lightfleck. Moreover, a biphasic response is clearly evident in the response to the 64-s lightfleck. For any given lightfleck duration, the efficiency of lightfleck use was dependent on its position in the sequence. Thus, the efficiencies in Table 3 reflect a combination of enhancements due to postillumination CO_2 assimilation and limitations imposed by loss of induction during the treatment sequence.

We examined whether or not lightfleck-use efficiencies might be higher under more natural sunfleck frequencies and durations. During periods of sunfleck activity the median sunfleck length was found to be 2 s and the median duration between sunflecks was 2–4 s (Pfitsch and Pearcy 1989). We exposed a leaf to 10 min of a lightfleck regime consisting of 2 s of saturating PFD and 4 s of low light. The response time of the gas exchange system did not allow a resolution of the responses to individual lightflecks. Instead, the apparent assimilation rate approached a steady value of 2.9 μmol m^{-2} s^{-1} after 3–4 min. There was no evidence of a progressive loss of induction during this sequence. Since the assimilation rate in low light was 0.5 μmol m^{-2} s^{-1}, the total assimilation due to a 2 s lightfleck in the sequence had to equal 14.4 μmol m^{-2} in order to yield the observed integrated response. The steady-state, light-saturated assimilation rate for this leaf was 5.9 μmol m^{-2} s^{-1}. If the response to a lightfleck had been an instantaneous increase to the steady-state rate, then an extra 10.8 μmol m^{-2} s^{-1} (5.4 μmol m^{-2} s^{-1} × 2 s) should have been fixed. These values yield an efficiency of 133%.

In the redwood forest understory, as in other forests (Chazdon 1988; Pearcy 1983, 1987), if a leaf is exposed to a sunfleck the probability is great that it will experience another within a several seconds (Pfitsch and Pearcy 1989). Induction will increase rapidly during a period of sunfleck activity, and since the median sunfleck length and time between sunflecks are quite short, post-illumination CO_2 fixation should make a significant contribution to the total, especially when the induction state is high. The rapid de-

cline in induction during exposure to diffuse light (Table 2, Fig. 6) means that the initial photosynthetic response in a cluster of sunflecks preceeded by only 5 min of diffuse light would be relatively independent of the induction state at the end of the preceeding period of sunfleck activity. Incomplete induction may therefore be an important limitation to carbon gain if periods of sunfleck activity are short (<10 min), and separated from each other by similarly short intervals of diffuse light. In a companion paper (Pfitsch and Pearcy 1989) we show that indeed low induction state apparently limits carbon gain under natural sunfleck regimes.

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