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Source: *Ecology*, Vol. 63, No. 1 (Feb., 1982), pp. 84-93

Published by: Ecological Society of America

Stable URL: <http://www.jstor.org/stable/1937034>

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PHOTOSYNTHETIC DYNAMICS IN VARYING LIGHT ENVIRONMENTS: A MODEL AND ITS APPLICATION TO WHOLE LEAF CARBON GAIN¹

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Abstract. The light environment of a plant microsite can be highly dynamic with sunflecks lasting from seconds to minutes in length. Whole leaf photosynthetic response to such variations is complex and species-specific. A mathematical model based on a single enzyme pool is derived to mimic leaf response in varying light. The model is used to analyze carbon gain in *Fragaria virginiana*. I find that sunflecks can be responsible for an appreciable proportion of leaf carbon gain throughout a day, especially under light-limited conditions. Model results also indicate that the standard methods of estimating carbon gain in varying light using steady-state photosynthetic rates often give overestimates.

Key words: carbon uptake; *Fragaria virginiana*; leaf; mathematical model; photosynthesis; sunflecks; variable environments.

INTRODUCTION

The light environment of terrestrial plants, especially for those below canopy, is highly dynamic on a number of time scales. Variations in cloudiness, changes in the sun's angle during a day, and wind movement of upper canopy leaves produce sunflecks of durations from 0.01 s to several minutes (Pollard 1970, Desjardins et al. 1973, Kriedemann et al. 1973, Hutchison and Matt 1977, Young and Smith 1979). These short-term sunflecks can supply the majority of the quantum flux of photosynthetically active radiation (PAR) which hits a particular point below canopy (Björkman and Ludlow 1972).

Despite these great variations in irradiance, the vast majority of photosynthetic studies in an ecological context to date have investigated only constant light level conditions. A large number of studies (reviewed in Rabinowitch 1956) have investigated the chemical kinetics of photosynthesis at light variation frequencies much higher than those observed in the field. However, these contribute little to our understanding of the ecological importance of light variation. The relatively few studies of the effect of light variation on whole leaf photosynthesis (McCree and Loomis 1969, Pollard 1970, Komov and Mokronosov 1971, Kriedemann et al. 1973, Marks and Taylor 1978, Wilson et al. 1978, Gross and Chabot 1979) indicate that a complex response to light variation exists.

In this paper I summarize the available information on whole leaf photosynthetic response to light variation and derive a mathematical model which mimics leaf response. The model is used to investigate the effect of sunflecks on whole leaf carbon gain. Due to the great number of sensors necessary to quantify light

environments accurately (Reifsnnyder et al. 1971, Hutchison and Matt 1977), this model should also prove useful in deriving efficient sampling procedures to use as inputs to productivity and crop yield models in order to maintain a given accuracy in the photosynthesis submodels.

PHOTOSYNTHESIS IN VARYING LIGHT

Photosynthetic dynamics due to light variation has been investigated experimentally using both step changes in irradiance and alternations between two light levels, usually light and dark. An early study (Garner and Allard 1931) on the growth of whole plants in intermittent light with periods ranging from 10 s to 24 h indicated that only plants in the shortest and longest periods showed near-normal growth. A study of alternations between irradiances using combinations of four different irradiance levels with periods of alternation varying from 0.4 to 600 s (Pollard 1970) found that photosynthetic rates in aspen leaves varied with the alternation period. The photosynthetic rates computed were means over time periods long in comparison to the period of the light fluctuations. The data in this study are consistent with the hypothesis that at short periods of alternation the leaf acts to integrate irradiance, while at long periods of alternation it averages the steady-state photosynthetic rates obtained at the two light levels used in the alternation (Fig. 1).

In contrast to this, in a study on the whole plant carbon uptake of cucumber in alternating light with periods from 2 s to 30 min, McCree and Loomis (1969) claim that the plants were perfect integrators of photosynthate, not light. Thus they state that "the photosynthetic rate was always within a few percent of that calculated from the steady-state values." However, these conclusions are not supported by their data, which indicate a clear trend toward higher pho-

¹ Manuscript received 31 July 1980; revised 15 January 1981; accepted 4 February 1981.

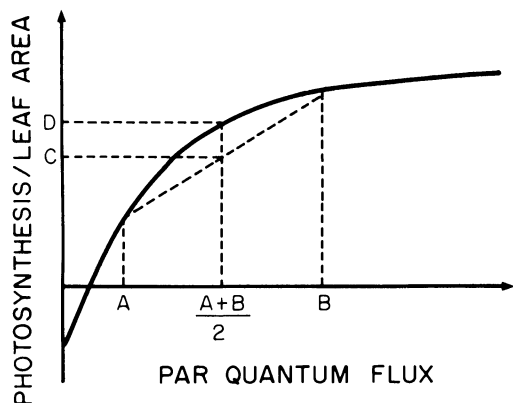


FIG. 1. The effect of alternation of irradiance between levels A and B with equal times at each of A and B. The solid line gives the photosynthetic rate obtained under constant light conditions. Alternations with short periods effectively cause a leaf to integrate irradiance, thus producing a mean uptake rate of D. Long period alternations cause an integration of the steady-state photosynthesis rates, producing a mean rate of C. As A and B move closer together, the difference between C and D is reduced. In experimental tests, the rates obtained in short and long period alternations should only be discernible when A is far from B and the nonlinear form of the curve becomes important.

photosynthetic rates at the short period light alternations. This trend is predicted by the hypothesis illustrated in Fig. 1. Also McCree and Loomis' own data give cases in which the carbon uptake rate in fluctuating light was as much as 30% higher than the rate calculated by integrating steady-state rates. Pollard's data include cases with rates >60% higher than the steady-state rates. Data on light/dark alternations of lengths 0.05 and 0.2 s, respectively, in grapevine leaves (Kriedemann et al. 1973) are also consistent with the hypothesis illustrated in Fig. 1. Thus it appears that McCree and Loomis' conclusion that valid community photosynthetic rates in varying environments can be computed simply from steady-state leaf uptake rates is not correct for some types of variation.

Very few studies have investigated the response of leaf photosynthesis to step changes of irradiance in an ecological context. A study of the time course of response in *Rubus chamaemorus* to light changes indicated that the time to equilibrate to a new level varied from 1 min for decreases in irradiance to as long as an hour for light increases (Marks and Taylor 1978). Potato leaves show similar fast time responses to light decreases with slower response to light increases (Kosmov and Mokronosov 1971). A study of *Arnica cordifolia* in the field shows photosynthetic equilibration times of 10–15 min when a leaf enters a sunfleck (D. R. Young, *personal communication*).

The above-mentioned studies did not calibrate their instrumental response systems accurately enough to separate the instrumental factors from the plant's response to light change. In a study of *Fragaria virgin-*

iana (Gross and Chabot 1979), such a calibration was performed and produced estimates of whole leaf response to step changes of irradiance of varying amounts. Two components of leaf response were obtained: a time lag between the time of the light change and the time the photosynthetic rate just began to change, and a time constant measuring the time necessary to cover approximately 63% of the distance to the new steady-state photosynthesis rate. The measured time lag remained a constant of approximately 10 s, except for a significantly longer lag at the lowest light level change, believed to be caused by stomatal effects (Gross 1981). The time constants exhibited large leaf-to-leaf variances, but the responses to light decreases were always very fast. The time constant for light level increases appeared to increase with the magnitude of the high level, with values ranging from 5 s at low light to 80 s at high light. These differences are not caused by diffusional limitations within the leaf, but rather appear to be due to photochemical and/or biochemical subprocesses (Gross 1981). One possible mechanism for the observed time course of photosynthesis is that certain amounts of enzymes may be activated very quickly following a light increase, but mobilization of more than these amounts takes progressively longer (Gross and Chabot 1979). Some evidence of this type of response has been found for ribulose 1,5-bisphosphate carboxylase (Lorimer et al. 1978).

The available information on the time course of photosynthesis in varying light are summarized in the following observations:

- I. Light variations with short periods of fluctuation, a few seconds or less, are averaged by the leaf. The photosynthetic rate achieved is at the mean light level.
- II. Light variations with long periods of fluctuation, a few minutes or longer, cause an averaging of photosynthetic rates, not irradiance. The mean photosynthetic rate over a time scale longer than the period of the fluctuations is the average of the photosynthetic rates achieved at the light levels of the fluctuations.
- III. The time lag before photosynthetic rate begins to respond to a sudden light change is relatively constant over most increases and decreases in irradiance. Increases in irradiance from very low light levels produce somewhat longer time lags.
- IV. Photosynthetic response to a sudden decrease in irradiance is always very rapid.
- V. Photosynthetic response to an increase in irradiance is always much slower than for a decrease in light. The response is faster at low light levels than at high ones.

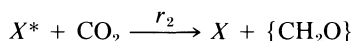
DERIVATION OF THE MODEL

My aim is to produce a model for carbon uptake in a varying light environment which is consistent with

the above observations. As my interest is mainly in processes on the ecological level, I do not deal with the specifics of the photochemical and biochemical subprocesses. Although some attempts have been made to model these subprocesses (Hall and Björkman 1975, Crill 1977, Milstein and Bremermann 1979), the system involved is very complicated and is still not well understood in areas such as photorespiration (Hesketh and Jones 1976). Many modelling efforts aimed toward ecological applications have taken a more empirical approach (Lommen et al. 1971, Tenhunen et al. 1976, Lange et al. 1977), and despite much work on mechanistic models for input to ecosystem simulations (Hesketh and Jones 1980), the system dynamics has generally been ignored.

In a theoretical investigation of whole leaf photosynthetic dynamics, Thornley (1974) proposes a model for the response to a step change in irradiance. Based upon a simple biochemical model with a single enzyme pool, the model predicts a first-order, exponential-type response to a light change. Using this, it is possible to show that fast light variations produce a photosynthetic rate which is the mean of the rates at the light levels of the fluctuation. Thus the model fits well with observations I and II above. However, the time constant for the photosynthetic response derived in this model decreases as the light level is increased. Thus the model gives a larger time constant for a light decrease than for a light increase, and predicts that a leaf would attain a high value of photosynthesis at a faster rate than it would attain a low value. This contradicts observations IV and V above. Also, Thornley's model does not exhibit any time lag behavior corresponding to observation III. I therefore proceed to derive an alternative model which is not only consistent with the known data, but is also not limited to the case of step changes in light.

As I do not wish to model explicitly the intricate photochemical and biochemical subprocesses involved in photosynthesis, I take as the point of departure a simple, single-enzyme-pool situation similar to that used by Thornley (1974). I make no claim that this underlying biochemical system is a realistic simplification of the actual complex of interactions in the process, but rather use it as an intuitive base upon which to structure a holistic model at a level above the biochemical. The underlying system is



where X is an unactivated enzyme which is activated to X^* under light, L , at a rate r_1 which is a function of light level. The activated enzyme then catalyzes the reaction which transforms CO_2 into a hydrocarbon $\{\text{CH}_2\text{O}\}$ at a rate r_2 with the assumption that H and O are available and not limiting the reaction.

Assuming the reactions go on at a rate proportional to the concentrations of the reactants and letting $X(t)$, $X^*(t)$, and $C(t)$ be the concentrations of unactivated and activated enzyme and CO_2 at time t , one derives

$$\frac{dX}{dt} = -r_1(L)X + r_2CX^* \quad (2)$$

$$\frac{dX^*}{dt} = r_1(L)X - r_2CX^*.$$

Since $\frac{dX}{dt} + \frac{dX^*}{dt} = 0$, the model assumes $X(t) + X^*(t) = X_0$, i.e., there is a fixed amount of enzyme available, and although the proportion in the activated vs. unactivated state may vary with time, the total amount does not.

The photosynthetic rate, $P(t)$, is the rate of production of $\{\text{CH}_2\text{O}\}$ given by

$$P(t) = hr_2CX^* \quad (3)$$

where I multiply by leaf thickness h in order transform unit volume to unit leaf area measurements. Assuming that the CO_2 concentration at the carboxylation site is fixed, Eqs. 2 and 3 give

$$\frac{dP}{dt} = hr_2CX_0r_1(L) - (r_1(L) + r_2C)P(t). \quad (4)$$

By defining

$$\begin{cases} K_1(L) \equiv hX_0r_1(L) \\ K_2 \equiv hX_0Cr_2 \\ \gamma \equiv hX_0 \end{cases} \quad (5)$$

Eq. 4 becomes

$$\frac{dP}{dt} = \frac{1}{\gamma}[K_2K_1(L) - (K_1(L) + K_2)P(t)]. \quad (6)$$

To complete the model, the manner in which light controls the effective enzyme activation rate $K_1(L)$ must be described. I first assume that at steady state, after the system has had time to equilibrate under a constant light regime, the activation rate $K_1(L)$ is proportional to the quantum flux of PAR hitting the leaf. Following any light change, this equilibrium activation rate is assumed to be approached at a rate proportional to the difference of the current and equilibrium activation rates. The time constant for this approach to equilibrium depends upon the light regime over the past. This assumption follows from the remarks on enzyme mobilization made earlier that, following a light increase, the rate at which enzyme is activated decreases. With these assumptions, the model becomes

$$\begin{cases} \frac{dP}{dt} = \frac{1}{\gamma}[K_2K_1(t) - (K_1(t) + K_2)P(t)] \\ \frac{dK_1}{dt} = \frac{1}{R(\ell)}[\tilde{K}_1L(t) - K_1(t)]. \end{cases} \quad (7)$$

Here K_1 has been changed to be a function of time, since light level varies with time. $L(t)$ is a measure of the current irradiance "sensed" by the leaf, \bar{K}_1 is a proportionality constant, and $R(\ell_i)$ is the time constant for the activation rate response and is a function of ℓ_i , the light level over part of the past, i.e., $\ell_i(\theta) = \ell(t + \theta)$, $-A \leq \theta \leq 0$ where $\ell(t)$ is the PAR quantum flux at time t .

Under constant light conditions, the activation rate $K_1(t)$ approaches $\bar{K}_1 L$ and the steady-state photosynthetic rate is

$$P = \frac{\bar{K}_1 K_2 L}{\bar{K}_1 L + K_2} \quad (8)$$

This is the standard Michaelis-Menten type expression which is often fit to photosynthetic response data (Thornley 1976). \bar{K}_1 is the slope of the response curve at zero light level and K_2 is the maximum photosynthetic rate. These parameters may be estimated from data on leaf response curves obtained under steady-state light conditions. Note that at zero light the rate is zero, so the model does not include the effects of dark respiration. Although light respiration is not included explicitly, its effect may be viewed as decreasing r_2 . Thus fitting a response of the form Eq. 8 to an experimentally obtained net photosynthesis response curve, with the dark respiration rate added to it, is justified.

Next I specify the form for $L(t)$, the irradiance sensed by the leaf. I view observation III as indicating that a leaf integrates the radiant flux hitting it over a short time period, with the observed time lag being related to this integration time. Physiologically this may be viewed as a reaction time for the light change throughout the three-dimensional leaf structure. A very general form for $L(t)$, the time average of PAR, would be

$$L(t) = \frac{1}{\tau_2} \int_{t-\tau_1-\tau_2}^{t-\tau_1} \int_{\nu_1}^{\nu_2} \ell(s, \nu) k(\nu) d\nu ds \quad (9)$$

where $\ell(s, \nu)$ is the quantum flux at frequency ν at time s , the function $k(\nu)$ represents the utilization of frequency ν in the photochemical processes of photosynthesis, and τ_1 and τ_2 define the interval over which the leaf physiologically integrates PAR. Since I have no data relating the effect of the spectral quality of light to photosynthetic dynamics in this work, I take $k(\nu) = 1$ over the PAR frequency range (ν_1, ν_2). This is an area for future research, however, since the spectral quality of direct beam solar radiation reaching below canopy in a sunfleck may be quite different from that transmitted through upper leaves (Sinclair and Lemon 1973).

Finally, the form of the time constant $R(\ell_i)$ must be determined. It is here that I include the inherently different effects of light increases vs. decreases, a decrease causing an energy limitation to the leaf due to

external conditions, with the response to an increase being limited by processes within the leaf. Due to these differences in response, $R(\ell_i)$ cannot be a function of only a single time-integrated light level, but must have a dependence on at least two light levels over different intervals in the past. I therefore assume that $R(\ell_i)$ is a function not only of the current "sensed" light level from Eq. 9

$$L(t) = \frac{1}{\tau_2} \int_{t-\tau_1-\tau_2}^{t-\tau_1} \ell(t) dt, \quad (10)$$

but also an earlier integrated light level

$$L_0(t) = \frac{1}{T(L(t))} \int_{t-\tau_1-\tau_2-T(L(t))}^{t-\tau_1-\tau_2} \ell(t) dt. \quad (11)$$

These could of course be generalized by including weighting functions inside the integrals in order to weight certain times more than others, but it will be clear later that this is not necessary to obtain the desired behavior. In what follows, I write $R(\ell_i)$ as $R(L_0, L)$.

Note that the time interval of integration for the earlier light level L_0 depends upon the current level L . The form used for $T(L)$ is

$$T(L) = \eta (1 - \exp\{-(aL + c)\}) \quad (12)$$

$a > 0, c > 0$

where a and c are obtained from the leaf time constant data (e.g., Table III of Gross and Chabot 1979) and η is three times the maximum observed time constant. This choice of η gives a time during which the photosynthetic rate converges to 95% of its value if a step change in light occurred. Increasing the current light level L gives feedback in the system from times further in the past.

I now must define $R(L_0, L)$ as a function of two light levels. Since responses to light decreases are very fast with no discernible dependence on light level, I take R to be small and constant for $L_0 \geq L$. Call this value R_{\min} . For $L_0 < L$, I assume that R depends only on $L - L_0$ and L . This assumption is somewhat justified by the data in Gross and Chabot (1979), though due to the large standard errors observed, considerably more experimental work would be necessary fully to justify it. Under these assumptions, I take

$$R(L_0, L) = \begin{cases} R_{\min} & \text{if } L_0 \geq L \\ R_{\min} + (R_{\max} - R_{\min})(1 - \exp\{-Ly\}) \\ & (1 - \exp\{-(L - L_0)x\}) & \text{if } L_0 < L. \end{cases} \quad (13)$$

This assures that R is continuous as L changes with time. Here R_{\max} is the maximum observed time constant (so $R_{\max} = \eta/3$), while x and y are constants estimated from the leaf photosynthetic response data. By choosing x very large and choosing y consistent with the time constant data, this form for R has the desired property of giving small time constants for

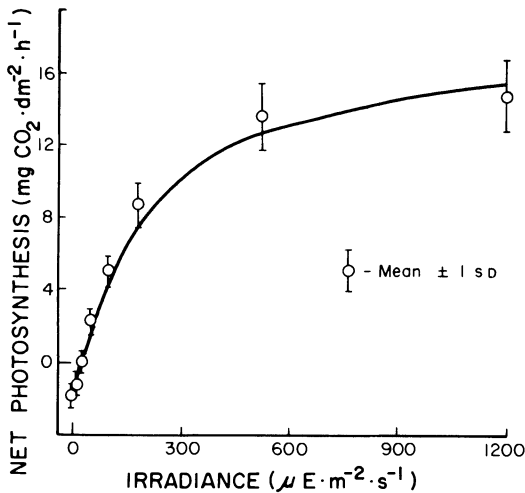


FIG. 2. Fitted response curve for high-light-grown leaves of *Fragaria virginiana*. Least squares fit of Eq. 8 to the data means from Table 1 of Gross and Chabot (1979).

light decreases and progressively larger ones for higher and higher light increases.

The model has thus been constructed to include almost all the available knowledge on time constants. I have ignored the observation that the time lag or integration time is somewhat longer for very low light levels. This could be included by allowing τ_1 and τ_2 to depend on $L(t)$. However, the light levels involved are much lower than those observed in the field and so I avoid that complication in this work. I have not explicitly used observations I and II in the model construction and if the model is any good it should exhibit the behavior indicated by these facts.

MODEL BEHAVIOR

The mathematical analysis of the model and a numerical solution technique are discussed in the Appendix. To test and apply the model, the parameters were all estimated from data on *F. virginiana* (Gross and Chabot 1979). An equation of the form of Eq. 8 was fit, using nonlinear least-squares, to the net photosynthetic rate data after adding the dark respiration rate (Fig. 2). So the parameters \bar{K}_1 and K_2 were obtained from steady-state data, the parameters τ_1 and τ_2 from time lag data, and γ , η , a , c , R_{\min} , R_{\max} , x and y were all estimated from the time course data. The values used were:

$$\text{in Eq. 7, } \gamma = 2.0 \times 10^{-3} \text{ mg/dm}^2$$

$$\begin{aligned} \text{in Eq. 8, } \bar{K}_1 &= 2.78 \times 10^{-3} \text{ mg/}\mu\text{E} \\ K_2 &= 20.52 \text{ mg} \cdot \text{dm}^{-2} \cdot \text{h}^{-1} \\ \bar{K}_1 &= 3.24 \times 10^{-3} \text{ mg/}\mu\text{E} \\ K_2 &= 15.68 \text{ mg} \cdot \text{dm}^{-2} \cdot \text{h}^{-1} \end{aligned} \left. \begin{array}{l} \text{for high-} \\ \text{light-grown} \\ \text{leaves} \\ \text{for low-} \\ \text{light-grown} \\ \text{leaves} \end{array} \right\}$$

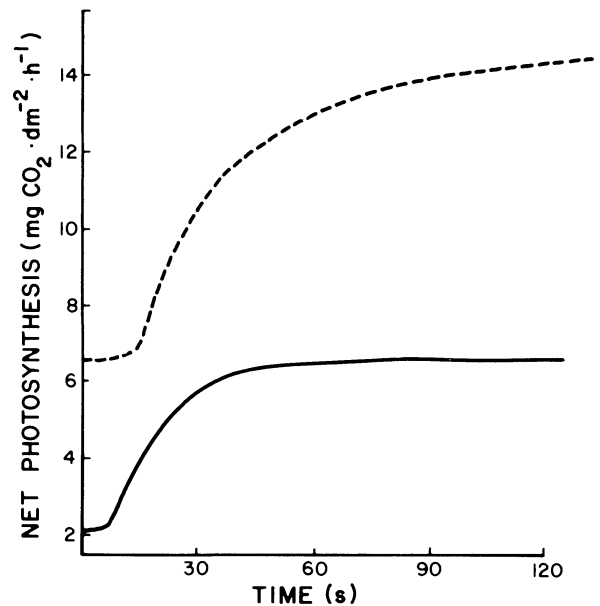


FIG. 3. Model prediction for time course of photosynthetic response following a step change of light. Light change occurs at time 0. Solid line is change from 24 to 97 $\mu\text{E} \cdot \text{m}^{-2} \cdot \text{s}^{-1}$, dashed line is a change from 97 to 525 $\mu\text{E} \cdot \text{m}^{-2} \cdot \text{s}^{-1}$. Parameters used are for high-light-grown leaves.

$$\begin{aligned} \text{in Eq. 10, } \tau_1 &= 7.0 \text{ s} \\ \tau_2 &= 5.0 \text{ s} \end{aligned}$$

$$\begin{aligned} \text{in Eq. 12, } \eta &= 195 \\ a &= 5.31 \times 10^{-5} \text{ dm}^2 \cdot \text{h} \cdot \mu\text{E}^{-1} \\ c &= 0.167 \end{aligned}$$

$$\begin{aligned} \text{in Eq. 13, } R_{\min} &= 0.1 \text{ s} \\ R_{\max} &= 65.0 \text{ s} \\ y &= 7.72 \times 10^{-5} \text{ dm}^2 \cdot \text{h} \cdot \mu\text{E}^{-1} \\ x &= 3.09 \times 10^{-3} \text{ dm}^2 \cdot \text{h} \cdot \mu\text{E}^{-1} \end{aligned}$$

As this model was specifically constructed to mimic the response indicated by observations III–V, and the parameters were chosen to coincide with the observations of Gross and Chabot (1979), it is expected that the model response to step changes of light should be very similar to those observed. For this case the model is descriptive rather than mechanistic. Despite the large number of parameters and somewhat arbitrary choice of the functions T and R , the model does present a powerful method to extend laboratory results on light step-changes to any varying light environment. In this sense the model is predictive and any real test of the model must await the availability of a wide range of data on photosynthetic uptake in varying light.

Fig. 3 shows the model results for two sample step-change increases in irradiance. The time course of the model response gives equilibrium times similar to those observed in the laboratory for all step-change

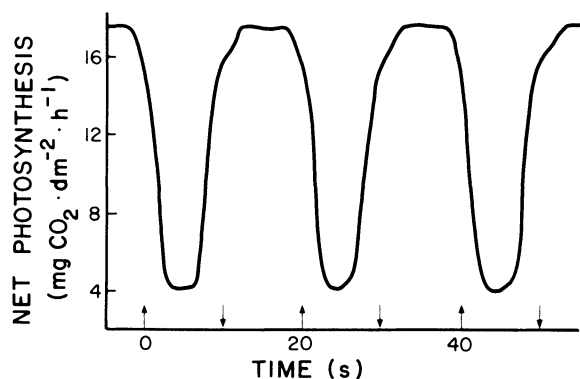


FIG. 4. Model response to alternating light with period 20 s. Light was switched between 48 and $1200 \mu\text{E} \cdot \text{m}^{-2} \cdot \text{s}^{-1}$. Upward arrows indicate times of increases of light, downward arrows times of decreases. Parameters used were for high-light-grown leaves.

increases. However, the model response, especially at high light level, was often faster than exponential. This is illustrated by the dashed line in Fig. 3. For this case the time to equilibrium was approximately 140 s, indicating a time constant of around 40 s. Thus after 40 s the rate observed should have covered about 63% of the distance to equilibrium. Instead the model response indicates 72% of the distance was covered. Although this effect was not expected from the model construction, it is a useful aspect of the model. When the time constants were derived (Gross and Chabot 1979) the response appeared to be somewhat faster than exponential, although the form of this response could not be estimated due to inadequacies in the experimental system. This faster-than-exponential effect was especially marked for high light level increases. Thus the model results are quite consistent with the observations. Also, the model response to step-change decreases in irradiance was very fast, with the new equilibrium level being reached in 7–10 s.

The model response to alternating light was calculated next. The input light environment was switched back and forth between two light levels with equal times at each of the two levels. Various periods of fluctuation were used and in all cases the response settled down to a stable pattern within a few periods. Fig. 4 shows the model response to one of these alternating light environments after stabilizing. As the figure illustrates, the photosynthetic response may be out of phase with the light environment. This is caused by the assumed integration time of the leaf and the choice of τ_1 and τ_2 . Data of Komov and Mokronosov (1971) indicate that in some cases photosynthetic response can indeed be out of phase with the light environment. Fig. 4 also shows that for this case the photosynthetic rate remains at the upper rate for considerably longer than at the lower rate, even though the times under low and high light are equal. This is

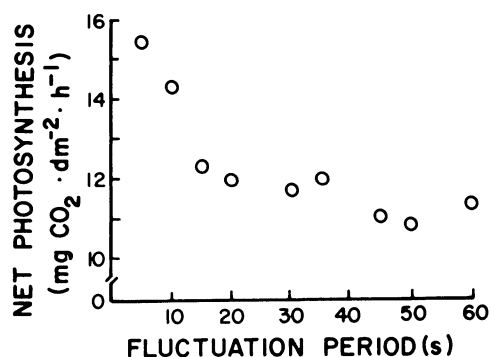


FIG. 5. Mean photosynthetic rate in alternating light as predicted by the model for various periods of fluctuation. Light was switched between 48 and $1200 \mu\text{E} \cdot \text{m}^{-2} \cdot \text{s}^{-1}$, the time of each level being one-half of the period. Means were calculated over times of several periods in length. The parameters used were for high-light-grown leaves. The photosynthetic rate at the mean light level is $15.4 \text{ mg CO}_2 \cdot \text{dm}^{-2} \cdot \text{h}^{-1}$. The mean photosynthetic rate, assuming instantaneous adaptation to changes in light, is $10.7 \text{ mg CO}_2 \cdot \text{dm}^{-2} \cdot \text{h}^{-1}$.

somewhat counterintuitive since the data and model both give much faster responses to decreases than to increases. It may be caused by both the assumed integration times of the leaf and the assumed form for R in Eq. 13. Unfortunately no adequate data exist to test this prediction of the model.

Fig. 5 shows the model's prediction for mean photosynthetic rate in alternating light at a number of different periods of fluctuation. As indicated, for fast fluctuations the mean rate was near the photosynthetic rate at the mean light level, while slower fluctuations gave rates close to the average of the steady-state rates at the two light levels in the fluctuation. Thus the model conforms to observations I and II. The data of Pollard (1970) on aspen leaves are very similar to the model predictions shown in Fig. 5, though the increase in uptake rate with decreasing period of fluctuation is more gradual in his data than that obtained from the model.

CARBON GAIN DUE TO SUNFLECKS

Having established that the model gives results which agree with the available data, I next consider questions regarding the utilization of sunflecks by understory leaves. My aim is to determine the significance of these short-term pulses of light to the carbon economy of the leaf. This is done by measuring the amount of photosynthate accumulated by the leaf (usable for reproduction, maintenance, and growth) that would not have been available if the pulse had not occurred. To estimate the fraction of photosynthate due to a sunfleck, the model was applied to pulses of light of varying lengths from a lower steady-state level. The percent of photosynthate due to a single pulse in 1 h at the low light level was then calculated from

TABLE 1. Percent of photosynthetic uptake due to a single sunfleck of irradiance $1200 \mu\text{E} \cdot \text{m}^{-2} \cdot \text{s}^{-1}$ and length T in 60 min at the indicated low light level. Growth light level L indicates that plants were grown at $80 \mu\text{E} \cdot \text{m}^{-2} \cdot \text{s}^{-1}$; level H was $290 \mu\text{E} \cdot \text{m}^{-2} \cdot \text{s}^{-1}$. Calculations based on simulations of the model in Eqs. 7 and 10–13.

T (min)	Growth light level	Low light level ($\mu\text{E} \cdot \text{m}^{-2} \cdot \text{s}^{-1}$)			
		24	48	97	182
Percent of uptake					
0.5	L	2.9	1.4	0.6	0.2
	H	3.7	2.0	0.8	0.3
1.0	L	6.2	3.1	1.5	0.6
	H	8.3	4.3	2.0	0.8
2.0	L	12.7	6.6	3.1	1.4
	H	16.8	9.0	4.4	2.0

$$\frac{B}{A + B} \quad (14)$$

where A is the photosynthate assimilated over the hour due to the low light level and B is the total accumulated during the pulse minus that which would have been accumulated at the low light level if there were no pulse. The calculations were made using the fitted response curves for high- and low-light-grown leaves (Gross and Chabot 1979). These curves are the sum of the net photosynthetic rates and the dark respiration rate and thus include the effects of light respiration. Table 1 gives the calculated values.

Note that this method gives a rather conservative estimate of the importance of sunflecks. By including the photosynthate used for maintenance, i.e., dark respiration, it does not take into account the disproportionate effect this has on photosynthetic gains at low vs. high light levels. Dark respiration constitutes a higher percentage of net photosynthesis plus dark respiration at low light than at high light. The above method has been used in order to allow the calculation of gains attributable to sunflecks even when the ambient low light level is below the leaf's light compensation point. Subtracting dark respiration does change the relative importance of sunflecks, especially as the low light level approaches the light compensation point. For example, in Table 1 the percent photosynthate due to a 60-s sunfleck for a low growth level leaf would change from 6.2 to 10.5%, and from 3.1% to 3.7% at 24 and $48 \mu\text{E} \cdot \text{m}^{-2} \cdot \text{s}^{-1}$, respectively. These values are the fraction of photosynthate accumulated by the leaf usable for growth and reproduction, but not maintenance, which would not have been available if the sunfleck had not occurred. In what follows, Eq. 14 is used to estimate the importance of sunflecks.

The calculations indicate that single sunflecks of durations similar to those observed in the field contribute a rather small percentage of carbon uptake if they occur infrequently and the background light level

TABLE 2. Percent of photosynthate in 1 h due to the indicated number of sunflecks, each of length T . Parameters used are for high-light-grown leaves. Low light level is $48 \mu\text{E} \cdot \text{m}^{-2} \cdot \text{s}^{-1}$, high is $1200 \mu\text{E} \cdot \text{m}^{-2} \cdot \text{s}^{-1}$. Calculations based on Eq. 15 using values in Table 1. Values in parentheses are the percent of quantum flux over the hour that is due to the sunflecks.

T (min)	Sunflecks/h		
	5	10	20
Percent of photosynthate			
0.5	9.3 (50.0)	17.0 (66.7)	29.0 (80.0)
1.0	18.3 (66.7)	31.0 (80.0)	47.3 (88.9)
2.0	33.1 (80.0)	49.7 (88.9)	66.4 (94.1)

is not too low. This occurs even though the quantum flux due to the sunfleck may be quite large. For example, a single sunfleck of length 2 min and irradiance $1200 \mu\text{E} \cdot \text{m}^{-2} \cdot \text{s}^{-1}$ in an hour of low light at $48 \mu\text{E} \cdot \text{m}^{-2} \cdot \text{s}^{-1}$ contributes 44% of the quantum flux over the hour, but produces <10% of the carbon uptake. The calculations also show that a sunfleck from a given low light level contributes a higher percentage of photosynthate to the high-light-grown leaves than to the low-light-grown ones. Since the high light leaves normally are at a higher light level than the low light ones, a given light increase can give a smaller percent increase for them than for low light leaves. This can be seen by comparing the values in Table 1 for low light leaves at $97 \mu\text{E} \cdot \text{m}^{-2} \cdot \text{s}^{-1}$ with those at high light leaves at $182 \mu\text{E} \cdot \text{m}^{-2} \cdot \text{s}^{-1}$.

The estimates above are all for a single sunfleck in the 1-h time period. To calculate the effect of more than one sunfleck, let U_1 be the percent uptake due to a single light burst, given in Eq. 14, and estimated in Table 1. Assume all bursts are nonoverlapping and there is sufficient time at the end of each burst, before the next one, for the photosynthetic rate to equilibrate at the low level again. Then the percent uptake due to n bursts in 60 min is

$$U_n = \frac{nB}{A + nB}$$

where A and B are as in Eq. 14 and n is such that $nT < 60$ where T is the length in minutes of a single burst. Then

$$nB = U_n(A + nB) = (n - 1)U_nB + U_n(A + B)$$

and, rearranged, this gives

$$U_n = \frac{nU_1}{1 + (n - 1)U_1} \quad (15)$$

Thus the percent uptake due to a number of sunflecks can be calculated from that of a single burst without having to redo the model calculations. Some sample results are given in Table 2. As indicated, even

though the vast majority of the quantum flux is due to the sunflecks, they do not account for nearly as much of the photosynthate. This is because the photosynthate accumulated over the hour due to the low mean light level is quite appreciable, and because the photosynthetic response curve is nonlinear. The results do indicate that sunflecks can be responsible for an appreciable percentage of carbon gain, especially if they are frequent and not too short in length. Along one set of diagonals in Table 2, the percent of quantum flux due to sunflecks is constant and the values show that the manner in which the light energy is apportioned does affect carbon gain. Fewer sunflecks of longer duration give higher uptake than an equivalent amount of energy in more sunflecks of shorter length. There is no simple relation between quantity of PAR in sunflecks and increase in carbon uptake due to them.

A standard method used to estimate carbon gains over a day is to integrate light over certain time periods (often hourly, or daily) and then use the steady-state photosynthetic response curve to estimate the uptake rate at this mean light level (Stapleton and Meyers 1971, Fick et al. 1972). To illustrate the error in doing this, consider a single sunfleck of irradiance $1200 \mu\text{E} \cdot \text{m}^{-2} \cdot \text{s}^{-1}$ lasting 1 min during an hour of low light at $48 \mu\text{E} \cdot \text{m}^{-2} \cdot \text{s}^{-1}$. Then the total quantum flux over this hour is $241\,290 \mu\text{E}/\text{m}^2$, giving a mean over the hour of $67.2 \mu\text{E} \cdot \text{m}^{-2} \cdot \text{s}^{-1}$. Using the fitted response curve for high-light-grown leaves (Fig. 2), this gives a CO_2 uptake of $506 \text{ mg}/\text{m}^2$ during the hour. The model results for this situation give a CO_2 uptake of $389 \text{ mg}/\text{m}^2$ due to the low light level and $17 \text{ mg}/\text{m}^2$ due to the sunfleck, or $406 \text{ mg}/\text{m}^2$ for the hour. If instead one integrates photosynthate as McCree and Loomis (1969) suggest, the resulting CO_2 uptake is $412 \text{ mg}/\text{m}^2$, which is only 1% off from the value obtained from the fully dynamic model. Now consider the case of a 1-min sunfleck every 5 min for 1 h. Then integrating light gives a CO_2 uptake of $1180 \text{ mg}/\text{m}^2$, the full model gives 596, and integrating photosynthate gives $661 \text{ mg}/\text{m}^2$ in the hour.

As these examples illustrate, integrating light to estimate uptake can drastically overestimate carbon gain. These estimates are not too far off if sunflecks are very infrequent, or if there is a regular, high frequency of fluctuations. However, it is the intermediate cases that generally occur under field conditions for below-canopy leaves. Thus my results are in agreement with McCree and Loomis (1969) that light integration is not to be recommended in this case. It should be noted that the method which McCree and Loomis (1969) suggest also overestimates uptake, though not nearly as drastically as using integrated light. The photosynthesis integration method gives its poorest results for the range of fluctuation observed in field data. The above difficulties also indicate that

the use of spectral analysis techniques to describe a varying light environment (Norman and Tanner 1969, Desjardins et al. 1973) are inappropriate for applications concerning carbon uptake (Gross 1979).

In conclusion, the model results indicate that sunflecks can make a significant contribution to leaf carbon gain in *Fragaria virginiana*. The closer the mean low light level is to the light compensation point, the more important sunflecks become. The calculations do not take into account the fact that light below canopy is depleted in the spectral regions that are significant to photosynthesis, and this would enhance the importance of sunflecks. As *F. virginiana* is adapted to a light-limited environment (Jurik et al. 1979), its time response to sunflecks may be expected to be faster than species with photosynthetic rates limited by other factors. Indeed the importance of sunflecks to the distribution of two *Arnica* species is probably tied more to water relations than to photosynthesis (Young and Smith 1979). Nonoptimal growth conditions could cause much slower response times than those reported in Gross and Chabot (1979). The model derived above should still be generally applicable; however, there do not exist adequate data to test it for species with slower response. For such species, estimates of uptake in varying light using either integrated light or the method of McCree and Loomis (1969) would be very inaccurate unless the light levels were all high enough that the photosynthetic rate was near saturation.

ACKNOWLEDGMENTS

I thank Brian Chabot and Simon Levin for numerous discussions and comments on this work. Thomas Givnish gave a very constructive review of the manuscript. Financial assistance was provided by National Science Foundation grants MCS 77-01076 to Simon Levin, DEB 77-08432 to Brian Chabot, and MCS-8002963 to the author. Part of this paper was included in a thesis submitted to Cornell University in partial fulfillment of the requirements for a Ph.D.

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APPENDIX

The model as constructed, consisting of Eqs. 7 and 10–13, is a nonautonomous, nonlinear system. Although there is a dependence on the past, it is only upon the irradiance function $\ell(t)$ which may be viewed as a forcing function. Since there is no dependence on past values of $P(t)$ or $K_1(t)$ in Eq. 7, it is not a functional differential equation system. Thus, for any specified light environment function $\ell(t)$, the standard theory of ordinary differential equations applies. Letting ℓ be continuous, then $L(t)$ and $R(L_0(t), L(t))$ are continuous and because R is bounded away from zero, the system (Eq. 7) satisfies a uniform Lipschitz condition on any bounded region in (t, P, K_1) -space. Standard theorems then apply to give the existence and uniqueness of a solution to the model (Roxin 1972). Due to the nonlinearity and time dependence of the model, proceeding with an analytic approach for even the simplest irradiance functions is not very useful. I thus make use of numerical solution techniques.

The basic model may be viewed as a chemical system with two reactions having different rates. As in many such cases, problems of stiffness arise because the reaction rates can be on quite different time scales (Enright and Hull 1976). The system

$$y' = Ay + \phi(x)$$

where y is an n -vector, A is a constant $n \times n$ matrix, and $\phi(x)$ is a continuous vector-valued function, is called stiff if the eigenvalues λ_i of A are all negative and $\max_i |Re \lambda_i| \gg \min_i |Re \lambda_i|$ (Lambert 1973). In this situation, some of the component equations converge very quickly to an equilibrium while others are much slower and control the transients of the entire system. This causes difficulties in standard numerical solution techniques because extremely small step sizes are required to handle the fast components which then lead to roundoff errors and excessive computation time due to the slow components.

In the model, the Jacobian

$$\begin{pmatrix} -\frac{K_1(t) + K_2}{\gamma} & \frac{K_2 - P(t)}{\gamma} \\ 0 & -\frac{1}{R(\ell_t)} \end{pmatrix}$$

is analogous to the matrix A , and its eigenvalues, the diagonal elements, determine the stiffness of the system. Since the eigenvalues vary with time, so does the degree of stiffness.

This may be measured by the stiffness ratio, defined to be the ratio of the maximum to the minimum eigenvalue (Lambert 1973). When values are chosen for the model parameters, I find that

$$\lambda_1 = -\frac{K_1(t) + K_2}{\gamma}$$

can vary from $-10\,000$ to $-110\,000$ while

$$\lambda_2 = -\frac{1}{R(\ell_t)}$$

can vary from -55 to $-36\,000$, leading to stiffness ratios that may vary from 3 to 2000. As stiffness often causes numerical difficulties when this ratio is above 10, one expects the above

model to call for special techniques. Actually, for low level light increases, standard Runge-Kutta techniques seem to work well since the time constants are not vastly different in this case. However, for moderate or high light level fluctuations, these standard techniques fail.

Enright and Hull (1976) compared a number of techniques for stiff equations in applications to systems arising from chemical kinetics studies. They found that the most suitable and efficient general purpose technique was a revision of the method of Gear (1971). This is a variable-order, variable-step-size technique using a predictor-corrector formula to choose the order in a manner which aims at maximizing the step size. The method is implemented in the International Mathematical and Statistical Library routine DVOGER, and that routine was used to obtain the results reported here.