

Carbon Dioxide Exchange of *Alnus rubra* A Mathematical Model

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Received July 15, 1974

Summary. The CO₂ exchange response of plants to multiple environmental variables is often difficult to frame for purposes of comparison. In this paper, a nonlinear model relating CO₂ exchange to light and temperature is derived from experimental curves determined in other investigations. Parameter values, determined from a least-squares fit of the model to CO₂ exchange data, are useful for comparing responses to light and temperature in terms of seasonal phenology, population heterogeneity, or species variation.

The model was fitted to CO₂ exchange data of a group of 40 *Alnus rubra* Bong. (red alder) seedlings for steady-state combinations of light and temperature. The average deviation of the data from the model was $\pm 6.7\%$. This steady-state expression satisfactorily predicted CO₂ exchange for dynamic conditions of light and temperature occurring in a diurnal cycle.

CO₂ exchange measurements are now made at diverse ecological sites (Mooney *et al.*, 1971; Schulze and Lange, 1972; Koch *et al.*, 1971). Automated instrument systems, which collect CO₂ data, are also used to monitor the environmental variables that influence a CO₂ exchange response. Without a proper framework, however, it is often difficult to simplify these response data to interpret species response to environmental variables. One framework suitable for comparative purposes is that of parameter estimation from nonlinear models. In this paper, a mathematical formulation relating CO₂ exchange to light and temperature is presented and its derivation discussed with regard to its general applicability to C-3 species that do not experience a limiting water stress. Parameter values, which result from a fit of the model to CO₂ exchange data, are useful for comparing responses to both light and temperature. Data on CO₂ exchange of red alder, *Alnus rubra* Bong., taken at steady-state conditions, have been collected for model validation. In addition, the ability of the model to predict CO₂ exchange for a daily dynamic pattern of light and temperature is examined.

The Model

The net CO₂ exchange, $\pm \Delta[\text{CO}_2]_{\text{app}}$ (Larcher, 1968), responses to light and temperature have been repeatedly established for single leaves or small seedlings for many of the C-3 plants. These responses are generalized in Fig. 1. Investigators recently reporting these responses include Kriedemann and Smart (1971) and Lange and Schulze (1971). Most studies have reported on net CO₂ exchange

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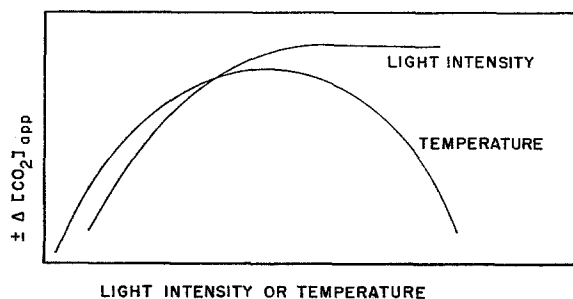


Fig. 1. Generalized $\pm \Delta[\text{CO}_2]_{\text{app}}$ response to light and to temperature

response to light at a constant temperature or net CO_2 exchange response to temperature at a fixed light intensity. In general, the response depends on both temperature and light intensity. For example, both the light compensation point and the saturation value are controlled by temperature (Rabinowitch, 1969). This complexity has been included in the following model.

The light curve can be constructed with the expression:

$$\pm \Delta[\text{CO}_2]_{\text{app}} = -A(T) + B(T)[1 - \exp(-CI)]. \quad (1)$$

Parameters $A(T)$ and $B(T)$ are functions of temperature and determine the abscissa intercept and the asymptotic value of light-saturated CO_2 influx. The exponential parameter, C , is independent of temperature.

The response of $\pm \Delta[\text{CO}_2]_{\text{app}}$ to temperature has been studied extensively. $\pm \Delta[\text{CO}_2]_{\text{app}}$ increases with temperature until a maximum is reached. Higher temperatures result in a decrease in net CO_2 influx. This relationship is essentially symmetric about the temperature of maximum net CO_2 influx and can be represented with the following expression:

$$\pm \Delta[\text{CO}_2]_{\text{app}} = a - b(T - c)^2. \quad (2)$$

$\pm \Delta[\text{CO}_2]_{\text{app}}$ has a maximum, a , at a temperature of c . Parameter b determines the "flatness" of the response, and will be referred to as the curvature coefficient.

Parameters a , b , and c in expression (2) are influenced by many factors. Pisek *et al.* (1969) studied the net CO_2 exchange rates of several species in both summer and winter. His data show that the maximum net photosynthesis and the temperature of the maximum depend upon species and season. Mooney and Shropshire (1967) found that different preconditioning environments shift both maximum net photosynthesis and the corresponding temperature of the maximum. Data from other studies indicate that, for steady-state conditions, the symmetric relationship given in Eq. (2) is an excellent representation of the $\pm \Delta[\text{CO}_2]_{\text{app}}$ response to temperature.

Returning to Eq. (1), the functions for $A(T)$ and $B(T)$ adopted for this work are:

$$A(T) = a' \exp[b'(T - c') - \exp b'(T - c')], \quad (3)$$

$$B(T) = d - e(T - f)^2. \quad (4)$$

$A(T)$, which is the CO_2 efflux when light intensity is zero, has a maximum, $a'/\exp(1)$, when temperature is equal to c' . At low temperature, the function is asymptotic to 0, becomes maximum at $T=c'$, and then decreases rapidly and becomes asymptotic to 0 at high temperature. $B(T)$ is a quadratic similar to Eq. (2).

Methods and Materials

Red alder was used as the test species to develop the model for steady-state conditions. Red alder is probably the most important hardwood in the Pacific Northwest. It grows rapidly and is found near the coast at low elevations, commonly on bottomlands. It does not perform well on droughty sites.

Alder seedlings, from 15 to 30 cm tall and 1 year old, were removed from an area near the Pacific Coast before propagation in the greenhouse. Plants were grown in an aerated nutrient solution (Russell and Evans, 1967), which was changed weekly. Light was supplied for 14 hrs daily with a bank of fluorescent lights augmented with incandescent bulbs. Total short-wave radiation from the artificial lights was $0.021 \text{ cal cm}^{-2} \text{ min}^{-1}$ at the plant level. Light energy in the greenhouse during daylight hours was from $0.042 \text{ cal cm}^{-2} \text{ min}^{-1}$ for cloudy conditions to $0.14 \text{ cal cm}^{-2} \text{ min}^{-1}$ at full sunlight. Day temperature was $21^\circ\text{C} \pm 3^\circ\text{C}$ and night temperature was $10^\circ\text{C} \pm 3^\circ\text{C}$. After the seedlings were in full leaf, 40 were placed in five polyvinyl chloride tubes, which were 5 cm in diameter. Nutrient solution was supplied with a system described by Webb (1971). Plants were maintained in these tubes for 4 weeks, at which time the tops of the plants were sealed from the roots at the root collar.

Net CO_2 exchange was measured in an 1780-l, gas-tight, controlled-environment chamber described by Webb (1973). The seedlings were grown in this system for one week under a light and temperature regime corresponding to the greenhouse conditions. The light source was a 6000-watt xenon arc. CO_2 exchange was measured for 5 light levels between 0.068 and $0.68 \text{ cal cm}^{-2} \text{ min}^{-1}$ at temperatures between 5 and 30°C with an infrared gas analyzer in a closed-flow system (Webb, 1973). For each light level, air temperature was changed at the rate of 1° per 5 min beginning at 15°C and proceeding to 30°C . Measurements were then made by decreasing temperature at the same rate until near 5°C , at which time temperature was increased to 15°C . Measurements made during an increasing temperature were not different from those made while the temperature decreased. Root temperature was held at $12^\circ\text{C} \pm 1^\circ\text{C}$, and relative humidity varied from 65 to 75%. All measurements were made during three successive days.

Light intensity, air temperature, and humidity were monitored at the plant level in the chamber at 1-min intervals throughout the experiment. Radiation was measured with a Kipp solarimeter located in the center of the chamber at the top of the plants. Wet-bulb depression and dry-bulb temperature were monitored with a psychrometer (Lourence and Pruitt, 1969) from air sampled near the center of the seedlings. Root temperature was measured with a thermocouple located in the nutrient solution. Net CO_2 exchange was measured between ambient chamber concentrations of 320 and 335 ppm.

Nonsteady-state CO_2 exchange data were taken on the same plants for a 14-hr day. The purpose was to compare this response with the CO_2 exchange predicted by the model developed from steady-state data. Root temperature and wet-bulb depression were constant as above. Temperature and light energy were varied according to Fig. 7. At the end of the experiment, the leaves were harvested, dried for 24 hrs at 70°C , and the data expressed as milligrams CO_2 per hr per gram leaf dry weight.

Results and Discussion

Fig. 2 illustrates the $\pm \Delta[\text{CO}_2]_{\text{app}}$ data as a function of temperature for each of the five light levels. The maximum CO_2 uptake rate was $12.1 \text{ mg CO}_2 \text{ gm}^{-1} \text{ d.w. leaf hr}^{-1}$ and occurred at $0.68 \text{ cal cm}^{-2} \text{ min}^{-1}$ at 23.8°C . This uptake rate is lower than that reported for *Alnus rubra* by Krueger and Ruth (1969), who found

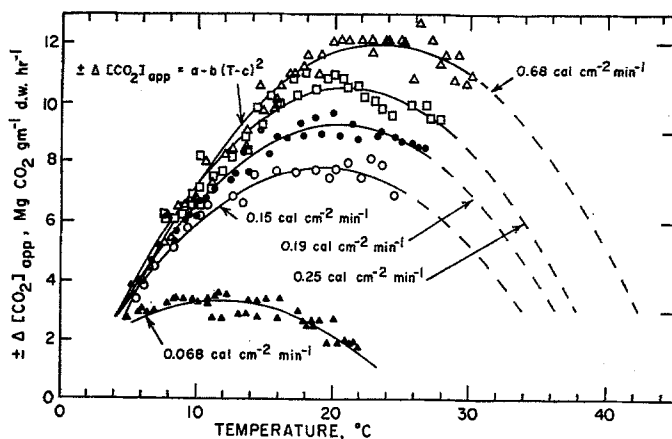


Fig. 2. CO_2 exchange of *Alnus rubra* for temperatures between 5 and 30°C at five light levels. Data fit to quadratic expression, $\pm \Delta[\text{CO}_2]_{\text{app}} = a - b(T - c)^2$

Table 1. Maximum $\pm \Delta[\text{CO}_2]_{\text{app}}$, temperature of maximum, and curvature coefficient for *Alnus rubra* at five light intensities

	Radiation ($\text{cal cm}^{-2} \text{min}^{-1}$)				
	0.068	0.15	0.19	0.25	0.68
Maximum $\pm \Delta[\text{CO}_2]_{\text{app}}$ ($\text{mg gm}^{-1} \text{d.w. hr}^{-1}$)	3.36 ± 0.077	7.934 ± 0.085	9.318 ± 0.074	10.621 ± 0.103	12.109 ± 0.088
Temperature of maximum ($^{\circ}\text{C}$)	11.8 ± 0.34	19.3 ± 0.45	20.5 ± 0.30	21.1 ± 0.38	23.8 ± 0.34
Curvature coefficient	0.017 ± 0.002	0.023 ± 0.002	0.025 ± 0.001	0.027 ± 0.002	0.026 ± 0.002

^a ± 1 standard error.

values as high as $40 \text{ mg gm}^{-1} \text{d.w. hr}^{-1}$. Their measurements, however, were made on a single, fully illuminated leaf normal to the incident radiation. The average value reported here reflects the integration of such factors as stem respiration and self-shading of leaves. This reduces net CO_2 influx per unit of photosynthesizing tissue below the maximum for a single leaf.

The quadratic function of Eq. (2) was fitted to the data in Fig. 2 for each light level. Extrapolation of the function to higher temperatures, indicated by dashed lines, predicts reduced CO_2 influx. Although no data of $\pm \Delta[\text{CO}_2]_{\text{app}}$ response of red alder at high temperatures have been reported, investigations with other species have consistently shown $\pm \Delta[\text{CO}_2]_{\text{app}}$ to decrease when the temperature exceeds some "optimum". Mooney and Shropshire (1967) found rates of *Encelia californica* to decline to zero flux at 30°C from a maximum at 18°C. In a field study, Kriedemann and Smart (1971) found rates decreased to 60% of maximum when afternoon temperatures reached 41°C.

The parameters of the quadratic function, derived by a least-squares fit of the data in Fig. 2, refer to maximum net photosynthesis, the temperature of this maximum, and the curvature coefficient. These values, and the standard errors,

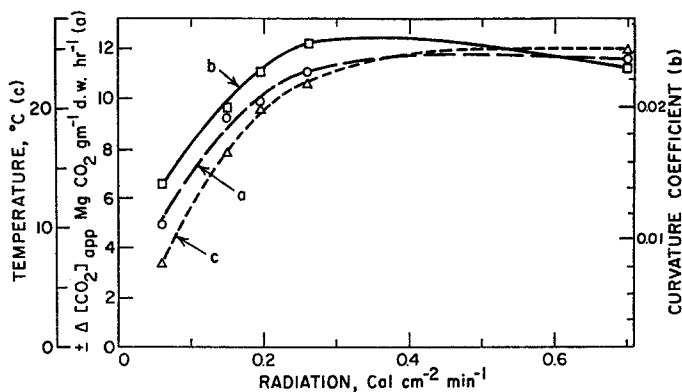


Fig. 3. Effect of light intensity on maximum CO_2 exchange (a), temperature of maximum (c), and curvature coefficient (b)

are listed in Table 1 for each light level. Increased radiation resulted in an increase in all three parameters, with a single exception. The curvature coefficient decreased slightly, from 0.027 to 0.026, when light intensity was increased from 0.25 to $0.68 \text{ cal cm}^{-2} \text{ min}^{-1}$. The small standard errors in Table 1 indicate the differences in parameters are significant and the increase in maximum net photosynthesis and corresponding temperature of this maximum are real. Schulze (1971) also reported a decrease in the temperature of maximum relative CO_2 influx as light was decreased from 12 klux to 1 klux. It seems clear from these data that a statement of "optimum" temperature for a species must, at the very least, include a measure of light energy.

The reduction in the temperature of maximum $\pm \Delta[\text{CO}_2]_{\text{app}}$ may be an adaptive feature. As low light levels and low temperatures occur together in nature, it is perhaps not surprising that CO_2 uptake is more efficient at lower temperatures when light energy becomes lower.

The mathematical coupling of the $\pm \Delta[\text{CO}_2]_{\text{app}}$ response to light to the $\pm \Delta[\text{CO}_2]_{\text{app}}$ response to temperature is assumed to be multiplicative, that is, $\pm \Delta[\text{CO}_2]_{\text{app}}$ is proportional to $f(T) \cdot g(I)$ where $f(T)$ and $g(I)$ are the symmetric quadratic (2) and light curve (1), respectively. Fig. 3 illustrates the relationship between light intensity and each of the three parameters from Table 1 (namely, maximum net photosynthesis, temperature of the maximum, and the curvature coefficient). In all three instances, the relationship is similar to the light curve. This strongly suggests that the hypothesized multiplicative coupling is valid for these two functions.

The following is the reparameterized model of CO_2 exchange from expression (1), where $A(T)$ and $B(T)$ are explicit.

$$\pm \Delta[\text{CO}_2]_{\text{app}} = a \cdot \exp [b(T - c) - \exp b(T - c)] + [d - e(T - f)^2] [1 - \exp(-gI)] \quad (5)$$

The seven parameters in this model were evaluated from the data in Fig. 2 using an algorithm developed by Marquardt (1963).

$$\pm \Delta[\text{CO}_2]_{\text{app}} = -78.4 \exp [0.096(T - 46.9) - \exp(0.096(T - 46.9))] + [31.3 - 0.0078(T - 62.3)^2] [1 - \exp(-10.2I)] \quad (6)$$

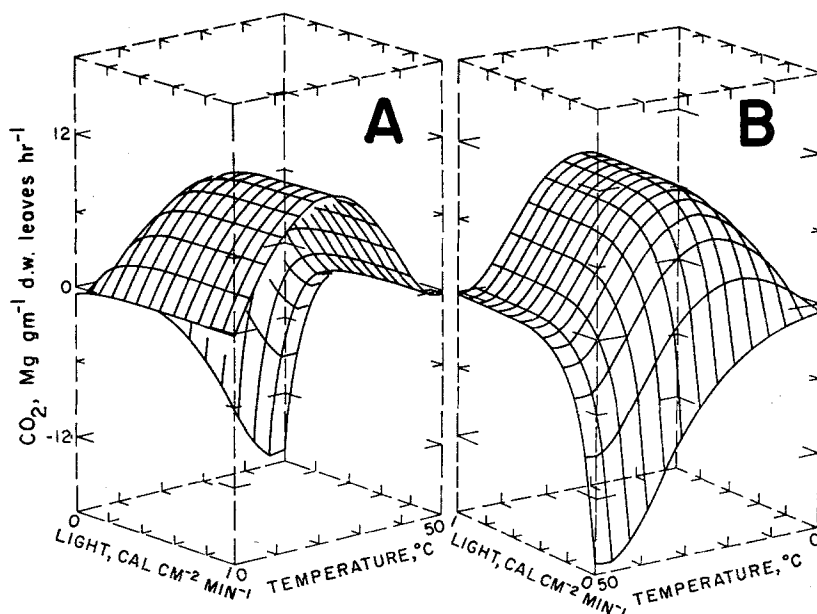


Fig. 4. Two views of model surface generated by $\pm \Delta [\text{CO}_2]_{\text{app}} = -78.4 \exp(0.096 T - 46.4) - \exp(0.096 (T - 46.4)) + [31.3 - 0.0078 (T - 62.2)^2] [1 - \exp - (10.21)]$

Two views of the surface generated by this function are illustrated in Fig. 4 for temperatures between 0 and 50°C, and for radiation between 0.0 and 1.0 cal cm⁻² min⁻¹. The responses to light and temperature, generalized in Fig. 1, are apparent in the surfaces. View A illustrates the symmetrical response to temperature as well as light saturation of net photosynthesis. The light curve is illustrated in view B. Also, in view B, at zero radiation, $\pm \Delta [\text{CO}_2]_{\text{app}}$ becomes negative, and decreases with temperature until a minimum is reached at 46.4°C. This represents CO₂ losses that are accelerated by temperature increases in darkness. A numerical analysis of expression (6) indicates that the maximum CO₂ influx is 12.1 mg CO₂ gm⁻¹ d.w. hr⁻¹ and occurs at 24°C and at 0.68 cal cm⁻² min⁻¹.

The fit of the model to the data is evaluated in Fig. 5, which is a plot of predicted minus observed $\pm \Delta [\text{CO}_2]_{\text{app}}$ for temperatures of 5–30°C at five light levels. These residuals appear random for three light levels, 0.15, 0.19, 0.25 cal cm⁻² min⁻¹. There is a bias at high and low light. The model will slightly underpredict those combinations of low temperature and low light, as well as high temperature and high light. An overprediction will occur at high light and low temperatures as well as combinations of low light and high temperatures. Overall, however, the model represents the data quite well. The average positive relative residual is 6.67% and the average negative residual is 7.04%.

As the model is continuous over a wide range of light intensities and temperatures, it can be rearranged easily to predict special cases of CO₂ fluxes that have physiological significance. For example, Eq. (1) can be solved analytically for conditions of light and temperature that result in zero CO₂ flux or the light compensation point.

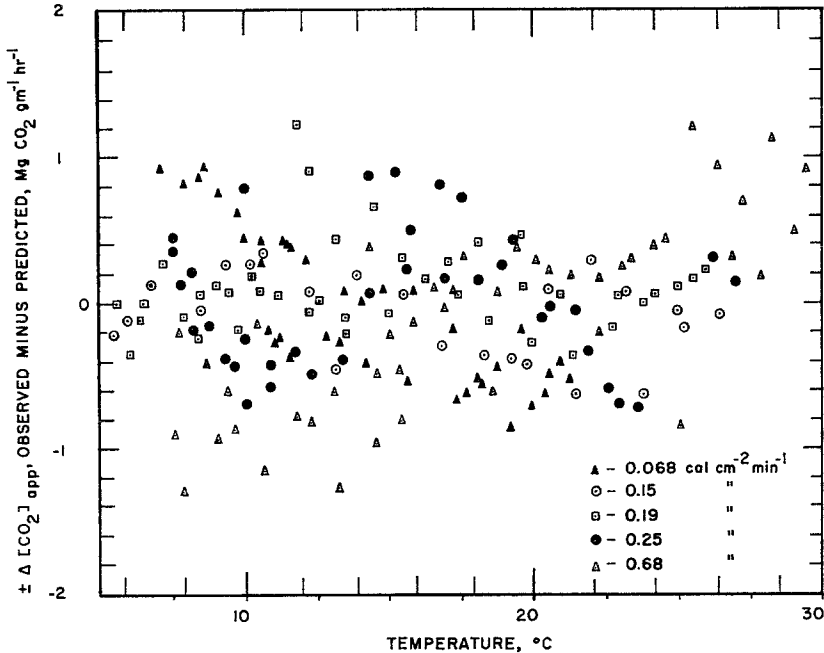


Fig. 5. Observed $\pm \Delta[\text{CO}_2]_{\text{app}}$ minus predicted, from model in Fig. 4, for temperatures from 5–30°C at five light levels

$$\pm \Delta[\text{CO}_2]_{\text{app}} = -A(T) + B(T) [1 - \exp(-CI)] = 0,$$

$$\exp(-CI) = 1 - \frac{A(T)}{B(T)} \quad (7)$$

$$I(T) = -\frac{1}{C} \ln \left[\frac{B(T) - A(T)}{B(T)} \right], \pm \Delta[\text{CO}_2]_{\text{app}} = 0.$$

This expression, which can be termed the light compensation curve, is plotted in Fig. 6, using the parameter values of Eq. (6). Notice that, as temperature increases, higher light energy is required to maintain a zero CO_2 flux. There are no experimental data for red alder to verify this relation. Clarke (1961), however, found that the light-compensation point increased with temperature for both *Abies balsamea* and *Picea glauca*. This indicates that additional light is required for photosynthesis to balance CO_2 losses at higher temperatures. Although photosynthesis has a temperature component, it is not likely to be controlling at low light.

Light energies at the light-compensation point have been reported for species other than red alder. Leith and Ashton (1961) found values between 400 and 1000 lux for *Ranunculus ficaria* and *Allium ursinum*. Geis *et al.* (1967) reported the light compensation for *Acer saccharinum*, *Quercus alba*, *Quercus macrocarpa*, and *Quercus rubra* to be between 50.3 and 102.5 foot candles. The light-compensation values predicted from expression (7) are from 0.025 to 0.04 $\text{cal cm}^{-2} \text{min}^{-1}$ for temperatures between 4 and 20°C. Converting these irradiance values from xenon arc to luminosity values after Gaastri (1959), 0.025 and 0.04 are equivalent

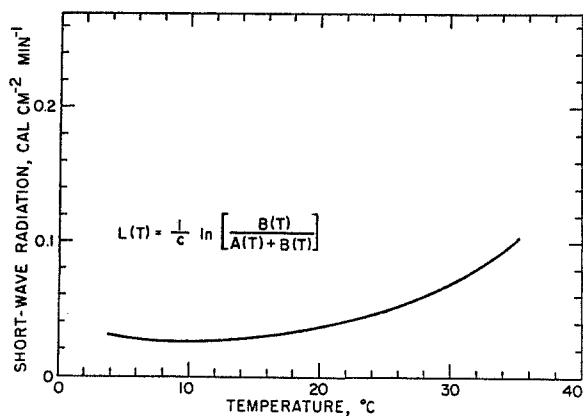


Fig. 6. Predicted relationship between light and temperature at light compensation points. Parameter values from model in Fig. 4

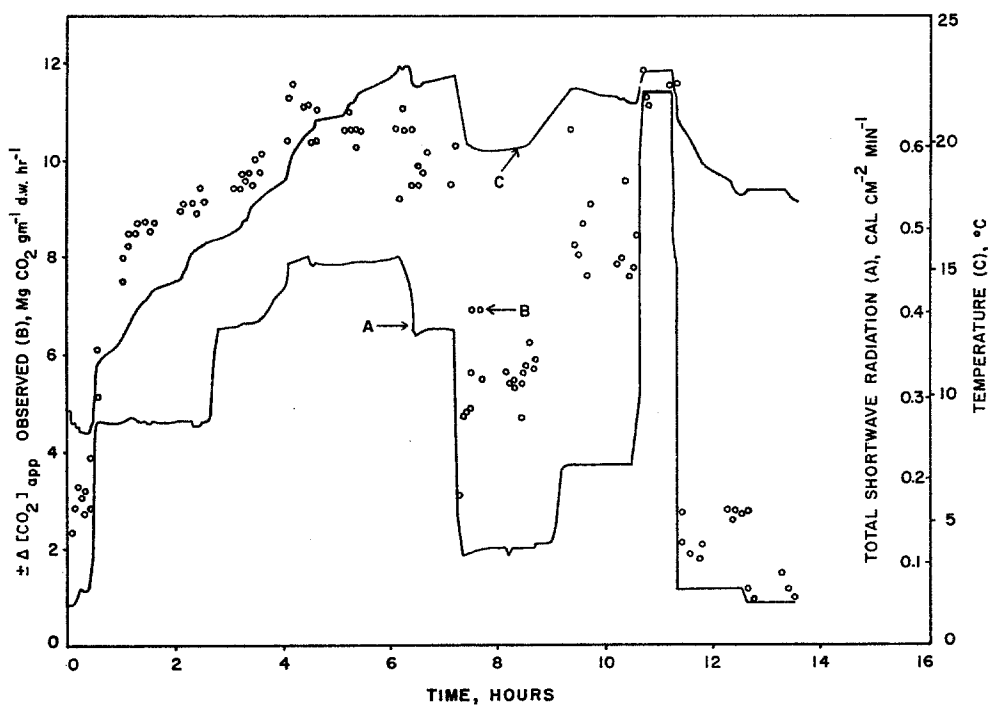


Fig. 7. CO₂ exchange of *Alnus rubra* for 14-hr day, and corresponding temperature and light regime

to 410 and 655 ft-candles. These values are an order of magnitude higher than for most light-compensation values. This illustrates a difference between the response of a whole plant, or group of plants, and the response of single, fully illuminated

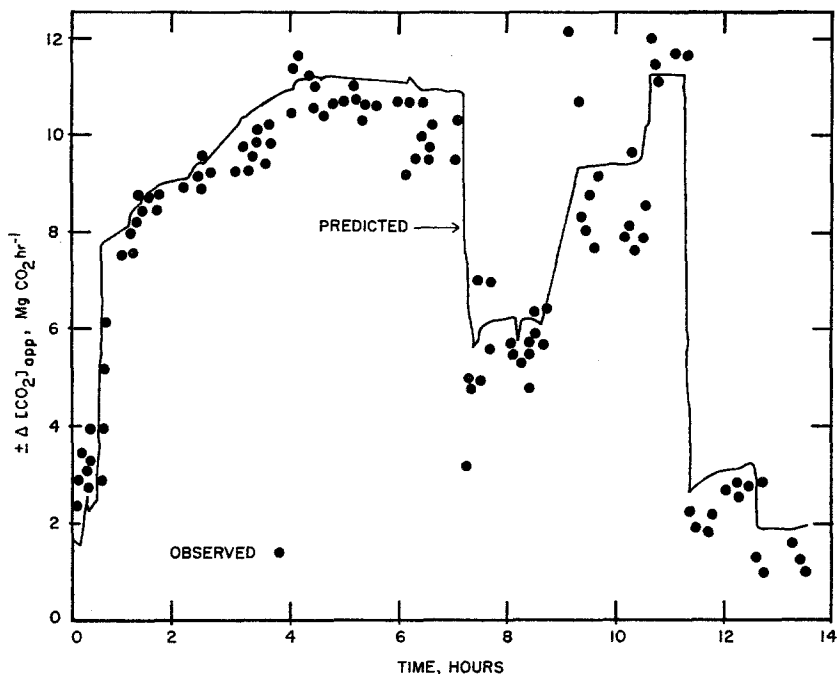


Fig. 8. Observed $\pm \Delta [\text{CO}_2]_{\text{app}}$ of *Alnus rubra* for 14-hr day, and $\pm \Delta [\text{CO}_2]_{\text{app}}$ predicted from model in Fig. 4

leaves. When radiation on lower leaves is reduced by shading of outer leaves, and when stem respiration is included, the light needed at the vegetation surface to balance CO_2 losses will be considerably higher than that for single leaves.

Application of steady-state models to dynamic conditions is not without problems. Responses to dynamic changes are often characterized by oscillations from lags and corresponding overshoots. Also, hysteresis can invalidate the use of steady-state relationships. To ascertain whether expression (6) could reasonably predict $\pm \Delta [\text{CO}_2]_{\text{app}}$ for a diurnal pattern of light and temperature, measurements of CO_2 exchange were made on the same group of alder seedlings. The only new variable was time. The apparent photosynthesis predicted by the model, for the light and temperature during the diurnal cycle, was compared with measured CO_2 exchange.

Light and temperature patterns and measured CO_2 exchange are presented in Fig. 7. Temperature, which ranged from 8°C to 24°C , was programmed to represent a sequence of morning temperature rise and late afternoon decline. Light intensity was stepped from 0.0 to $0.45 \text{ cal cm}^{-2} \text{ min}^{-1}$, and then changed somewhat randomly to simulate rapid radiation changes that occur on partly cloudy days. In the first 6 hrs, CO_2 influx seemed stable with only minor amounts of experimental noise. During the last 8 hrs, the period of more rapid radiation fluctuation, the CO_2 data had a somewhat more random character. Fig. 8, a comparison of the predicted $\pm \Delta [\text{CO}_2]_{\text{app}}$ and the data, shows good agreement for the first 6 hrs, but the difference between measured and predicted becomes larger in the last 8 hrs.

With a rapid change in radiation, such as at 7, 8.5, 10.5, 11, and 12.5 hrs, the data consistently indicate a response greater than that predicted. For example, at 6.5 hrs, when radiation is decreased from 0.38 to 0.10 cal cm⁻² min⁻¹, CO₂ influx falls to 3.0 mg CO₂ gm⁻¹ d.w. hr⁻¹, but the predicted rate is 6.0 mg CO₂ gm⁻¹ d.w. hr⁻¹. When radiation increases rapidly, such as at 8.5 hrs, CO₂ influx overshoots the predicted. These responses, although consistent, are somewhat masked by experimental noise, and additional testing is needed.

The variation in CO₂ exchange resulting from the diurnal changes in light and temperature are nearly the same as those predicted from the steady-state model. For conditions of rapidly changing light intensity, however, reliability of the steady-state model will decline. Also, for plants that are not well watered, a low water potential will probably reduce a net CO₂ exchange below that predicted by the model. This restriction will not apply to red alder, because it does not usually undergo a limiting water potential.

Conclusions

The model described here is based on measurement of $\pm \Delta [\text{CO}_2]_{\text{app}}$ made by many other investigators in which either the light intensity or the temperature, but not both, were varied. We have constructed a mathematical model that successfully represents $\pm \Delta [\text{CO}_2]_{\text{app}}$ over a wide range of both light intensity and temperature, and have used data from *Alnus rubra* to test the model. If this model is shown to be applicable to other species, it may be possible to include other variables, as, for example, water potential.

The model is to be used primarily as a basis for comparison of CO₂ exchange response to light and temperature. The values of the parameters, which result from a least-squares fit to the data, are directly comparable in terms of temperature optimum and light saturation. Comparisons can be made in both time and space representing population heterogeneity and seasonal phenology.

Acknowledgements. The authors wish to thank the Environmental Health Sciences Center at Oregon State University for their support under the National Institute of Environmental Health Sciences grant ES-0021005. This is paper number F898, Forest Research Laboratory, Oregon State University.

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