Carbon Dioxide Exchange of *Alnus rubra*

A Mathematical Model

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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 ±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, ±Δ[CO₂]_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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response to light at a constant temperature or net CO₂ 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:

$$\pm \Delta [\text{CO}_2\text{app}] = -A(T) + B(T)\left[1-\exp\left(-C T\right)\right].$$  (1)

Parameters $A(T)$ and $B(T)$ are functions of temperature and determine the abscissa intercept and the asymptotic value of light-saturated CO₂ 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 CO₂ influx. This relationship is essentially symmetric about the temperature of maximum net CO₂ influx and can be represented with the following expression:

$$\pm \Delta [\text{CO}_2\text{app}] = a - b(T - c)^2.$$  (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 CO₂ 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:

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

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