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**The Development of a Generic Model for Assessing the
Effects of Elevated CO₂ on Ecosystems**

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I. Photosynthesis Model

Peter Harley

The terminology used here is analogous to that used in the model code and is consistent with that of Farquhar. There is general agreement that the rate of net photosynthesis (A) may be represented by,

$$A = V_C - 0.5 \cdot V_O - R_d$$

where V_C and V_O are the rates of RuBP carboxylation and oxygenation, respectively, and R_d is "day respiration", i.e., the rate of CO_2 evolution from processes other than photorespiration (i.e., mitochondrial respiration which continues in the light or mitochondrial respiration from non-autotrophic tissue). The stoichiometry of this expression reflects the fact that 0.5 mols CO_2 are released in photorespiration for each oxygenation of RuBP. This expression may be rewritten as,

$$A = V_C \cdot (1 - \Gamma^*/CO_2) - R_d$$

where Γ^* is the CO_2 compensation point in the absence of R_d . Γ^* is a function of enzyme kinetic parameters, as discussed below.

At any given temperature and internal CO_2 concentration (C_i), the model calculates the potential rate of carboxylation by Rubisco (RuBP carboxylase/oxygenase), which is dependent only on those two variables (plus $[O_2]$, assumed to be constant at 21%). This potential rate, which assumes saturating amounts of the CO_2 acceptor, RuBP, is termed W_C . The only parameters which affect W_C are the kinetic parameters associated with Rubisco, i.e., the Michaelis constants and the V_{max} values for carboxylation and oxygenation, K_C , K_O , V_{Cmax} and V_{Omax} , respectively. K_C and K_O represent intrinsic kinetic properties of Rubisco, and although there is some indication of differences in the values of K_C and K_O between C_3 species, these differences are fairly small. Until compelling evidence to the contrary arises, K_C and K_O may reasonably be treated as constants. The only good estimates of the temperature dependencies of K_C and K_O are from Badger and Collatz (1977) and we've chosen to use those values in the model. Unlike the Michaelis constants, the V_{max} values are variable, changing as a function of total Rubisco concentration in the leaves, and these changing levels are one of the primary means by which leaves adjust their photosynthetic apparatus. Since both carboxylation and oxygenation are catalyzed by Rubisco, it is reasonable to assume that the maximum rates of the two processes change in parallel, i.e., V_{Omax} is proportional to V_{Cmax} . Farquhar has assumed a proportionality constant of 0.21, and we have adopted that value (although both he and we recognize that it is based on minimal experimental data). Thus, with K_C and K_O treated as constants, and $V_{Omax} = 0.21 \cdot V_{Cmax}$, we are left with the single parameter V_{Cmax} affecting W_C . We should note here that Γ^* , referred to above, is defined as,

$$\Gamma^* = 0.5 \cdot V_{o\max} \cdot K_C \cdot O_2 / V_{c\max} \cdot K_O = 0.105 \cdot K_C / K_O \cdot O_2$$

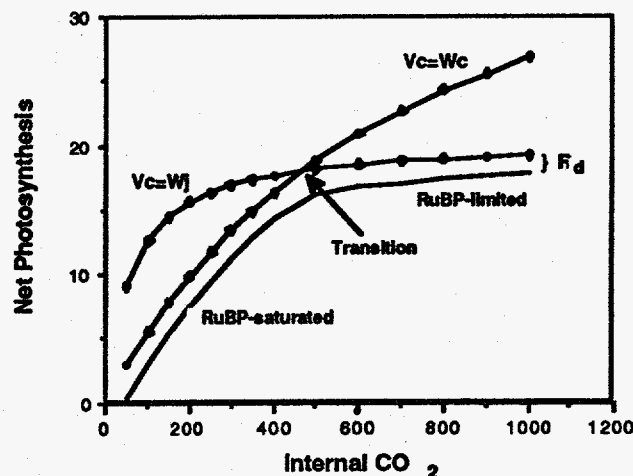
W_C assumes saturating amounts of the substrate, RuBP, but this is often not the case. RuBP concentration is affected by several factors. A single RuBP molecule is broken down for each carboxylation or oxygenation reaction at Rubisco, and RuBP is simultaneously being regenerated via the Calvin cycle and, indirectly, via the photorespiratory cycle. At a given combination of light, temperature and C_i , the integrated Calvin and photorespiratory cycles, driven by energy (ATP) and reducing power (NADPH) from the "light reactions" regenerate RuBP at a certain rate, setting an upper limit on the actual rate of carboxylation by the enzyme, i.e., carboxylation plus oxygenation cannot proceed at a rate greater than that at which RuBP is regenerated. Under certain conditions, the rate of resupply is sufficient to saturate the enzyme allowing it to operate at maximum (i.e., at W_C); under other conditions, such as low light or high CO_2 , the rate of resupply is insufficient and carboxylation is limited by [RuBP]. Farquhar introduces the variable W_J , the rate of carboxylation that would result if this rate of RuBP resupply were the only limitation. Thus, depending on prevailing irradiance, temperature and C_i , the actual rate of carboxylation, V_C , is limited either by the kinetic properties of Rubisco (W_C) or by the rate at which RuBP is regenerated (W_J); i.e.,

$$V_C = \min \{ W_C, W_J \}$$

and,

$$A = (1 - \Gamma^* / CO_2) \cdot \min \{ W_C, W_J \} - R_d$$

The relationship between the RuBP-limited and RuBP-saturated portions of the response is seen in the simulated CO_2 curve below.



Based on the assumption that [ATP] is limiting RuBP regeneration, Farquhar has developed a semi-empirical formulation which relates W_J to (1) the ratio of electrons passing through the electron transport chain to the number of ATP molecules produced, and (2) the ATP requirements of the Calvin cycle. We could switch over to

this slightly more mechanistic formulation, but at present we use a more empirical formulation, the historical roots of which lie in the way we parameterize this portion of the model. Our parameter, P_m , the CO_2 -saturated photosynthetic rate (an easily measurable value) is related to W_J according to the following relationship,

$$W_J = W_C \cdot P_m / (W_C + W_0)$$

A number of model parameters contribute to the determination of P_m . The temperature dependency of the light-saturated rate of P_m , designated P_{mI} , is described by an equation containing four parameters, ΔH_a (activation energy), ΔH_d (energy of deactivation), an entropy term (ΔS) and a constant (c). The constant (c) and ΔH_a serve to move the maximum rate of RuBP regeneration up and down, while the other parameters affect both maximum rates and the temperature optimum. The light dependency of P_m is described using P_{mI} and a parameter, α , which is analogous to quantum use efficiency (on an incident light basis) and is determined from the initial slope of the light response curve obtained under CO_2 -saturating conditions.

R_d is dependent only on temperature in the model, and is described by an exponential function.

The newly incorporated Farquhar/Wong empirical conductance model assumes a direct link between mesophyll photosynthetic processes and conductance. Such a link might be NADPH or RuBP pools, but the model assumes that the interaction is mediated via [ATP]. Farquhar and Wong derive a series of equations which result in a variable, T , which is "loosely related" to [ATP] in the mesophyll chloroplasts, and is assumed to be proportional to stomatal conductance. The proportionality constant is, in effect, a scaling factor. The model iterates for a value of internal CO_2 which is compatible with both the photosynthetic rate and conductance predicted by the model. The value of this constant affects final predicted values of conductance, photosynthesis and C_i and must therefore be treated as an additional parameter, GFAC, requiring estimation.

***Quercus cocclifera* simulations at ambient and elevated CO_2**

We have attempted to simulate measured diurnal photosynthesis and conductance data obtained for *Quercus cocclifera* on three dates in 1983, characterized by increasingly severe water stress. Although certain model parameter values were obtained experimentally for *Q. cocclifera* in 1983, it is unreasonable to assume that they will necessarily be valid for all three measurement dates. Data for assigning values to other parameters are simply missing. We are therefore reduced to assigning what appear to be reasonable values, then modifying them incrementally until we obtain a good overall fit to the data. Of course a good fit to the measured data alone is not sufficient basis on which to conclude parameterization is correct; simulations carried out beyond the range of measured data may be quite different depending on model parameterization. This is particularly true with respect to simulations at elevated CO_2 as we shall see.

Figures 1-6 represent pairs of model fits to each of the three diurnal courses of

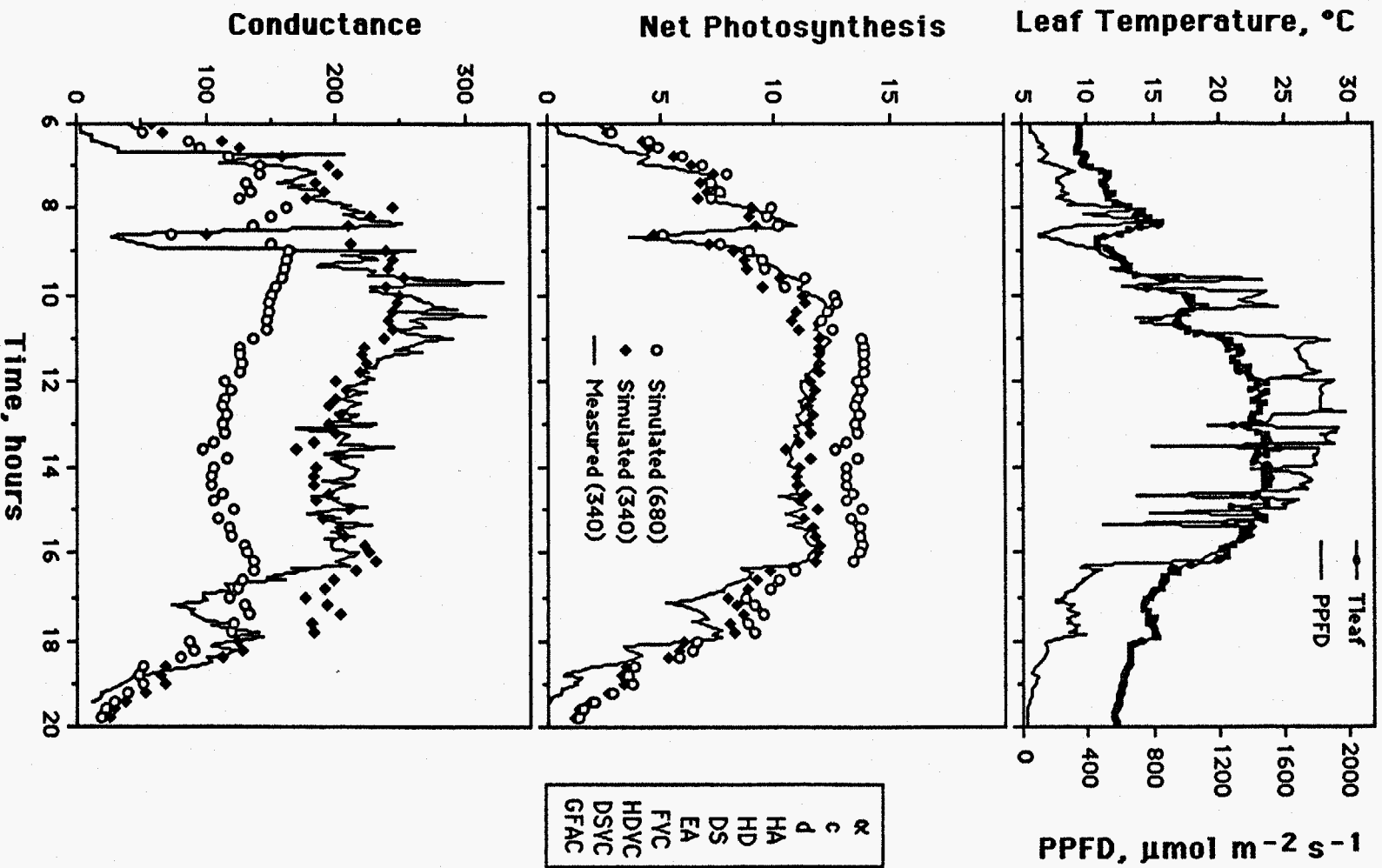


Fig. 1. Rates of net photosynthesis and leaf conductance, measured in the field on May 16, 1983 at 340 ppm, compared with model simulations at 340 and 680 ppm, using parameter values shown.

Quercus coccifera May 16, 1983

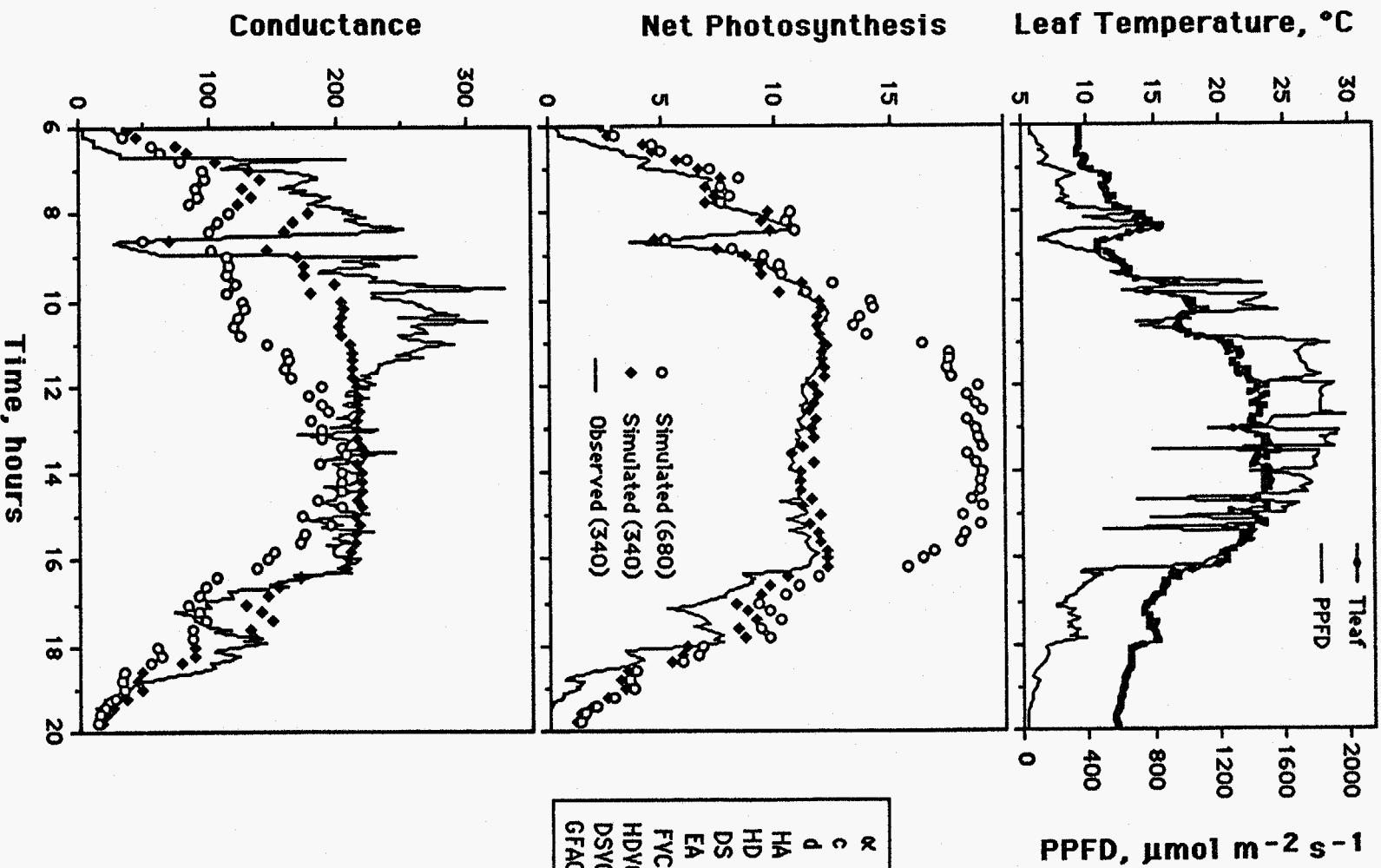


Fig. 2. Rates of net photosynthesis and leaf conductance, measured in the field on May 16, 1983 at 340 ppm, compared with model simulations at 340 and 680 ppm, using parameter values shown.

Quercus coccifera June 21, 1983

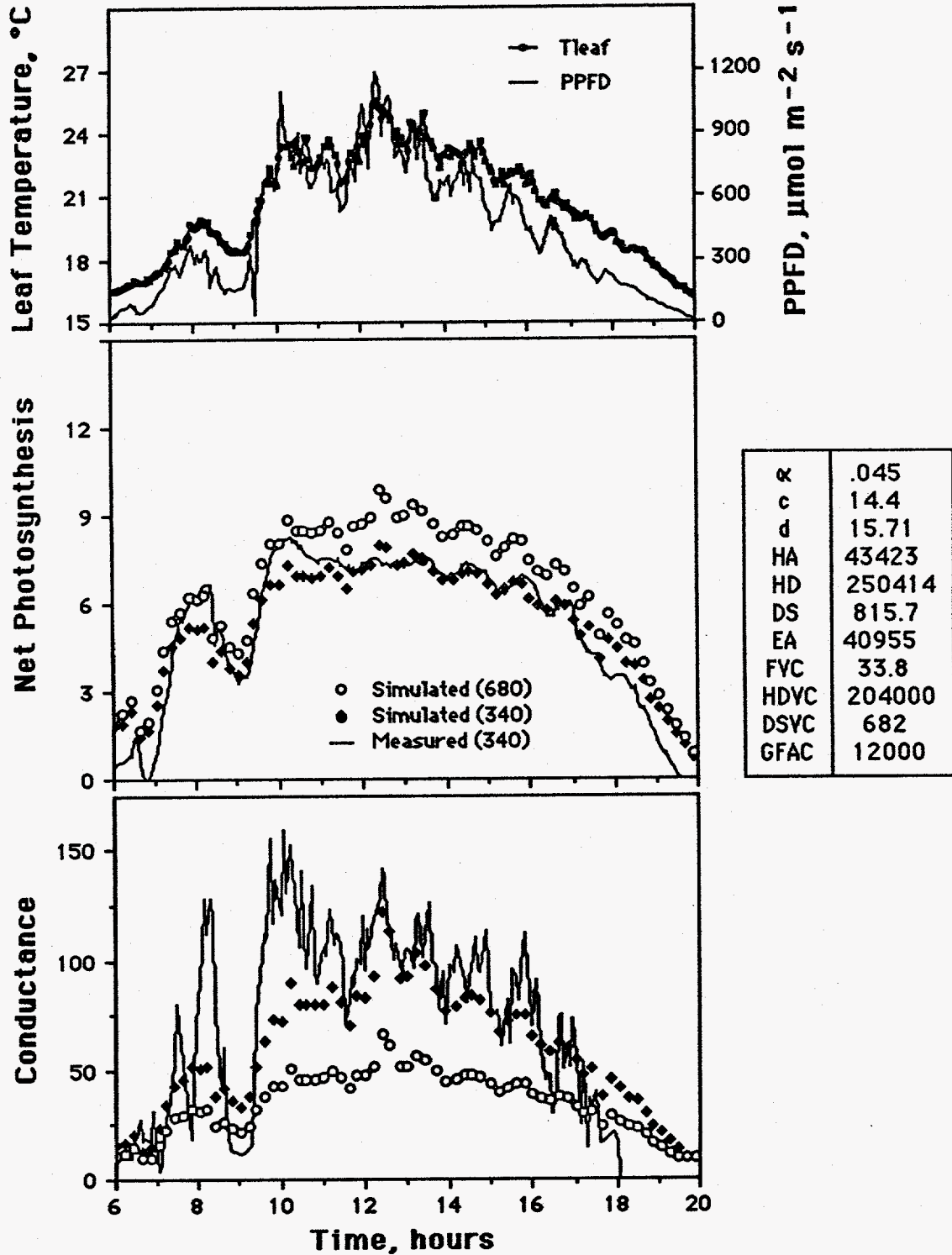


Fig. 3. Rates of net photosynthesis and leaf conductance, measured in the field on June 21, 1983 at 340 ppm, compared with model simulations at 340 and 680 ppm, using parameter values shown.

Quercus coccifera June 21, 1983

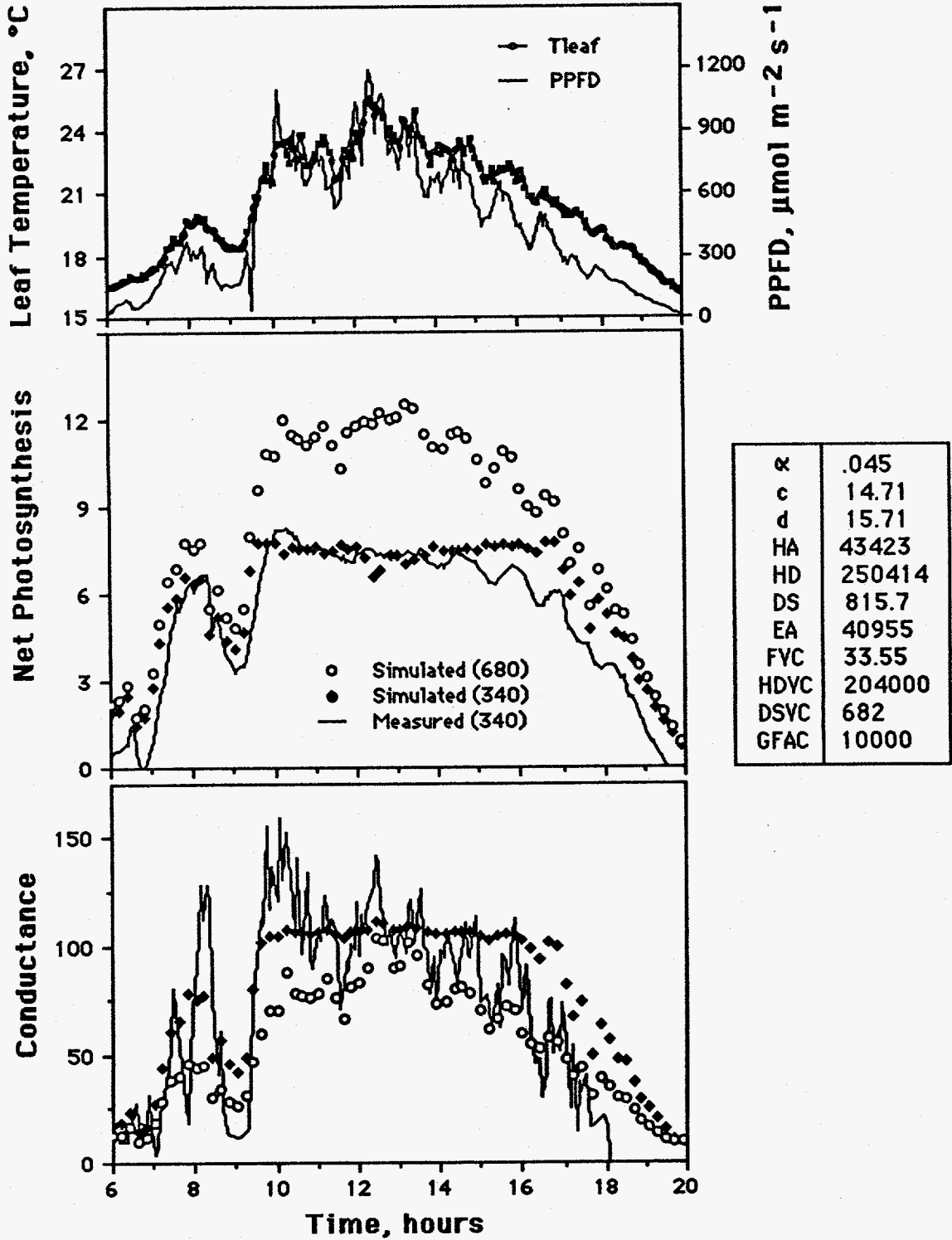


Fig. 4. Rates of net photosynthesis and leaf conductance, measured in the field on June 21, 1983 at 340 ppm, compared with model simulations at 340 and 680 ppm, using parameter values shown.

Quercus coccifera July 21, 1983

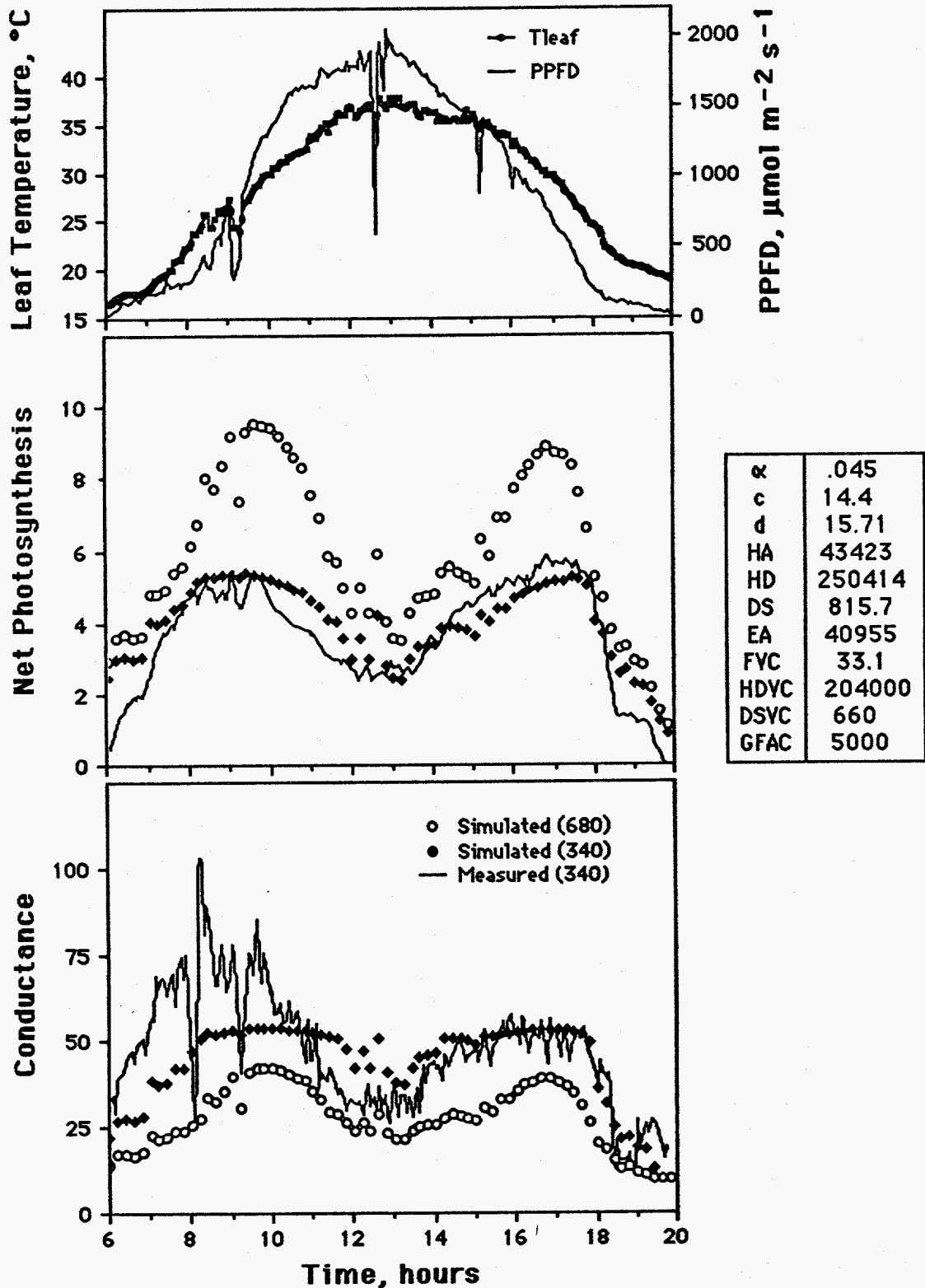


Fig. 5. Rates of net photosynthesis and leaf conductance, measured in the field on July 21, 1983 at 340 ppm, compared with model simulations at 340 and 680 ppm, using parameter values shown.

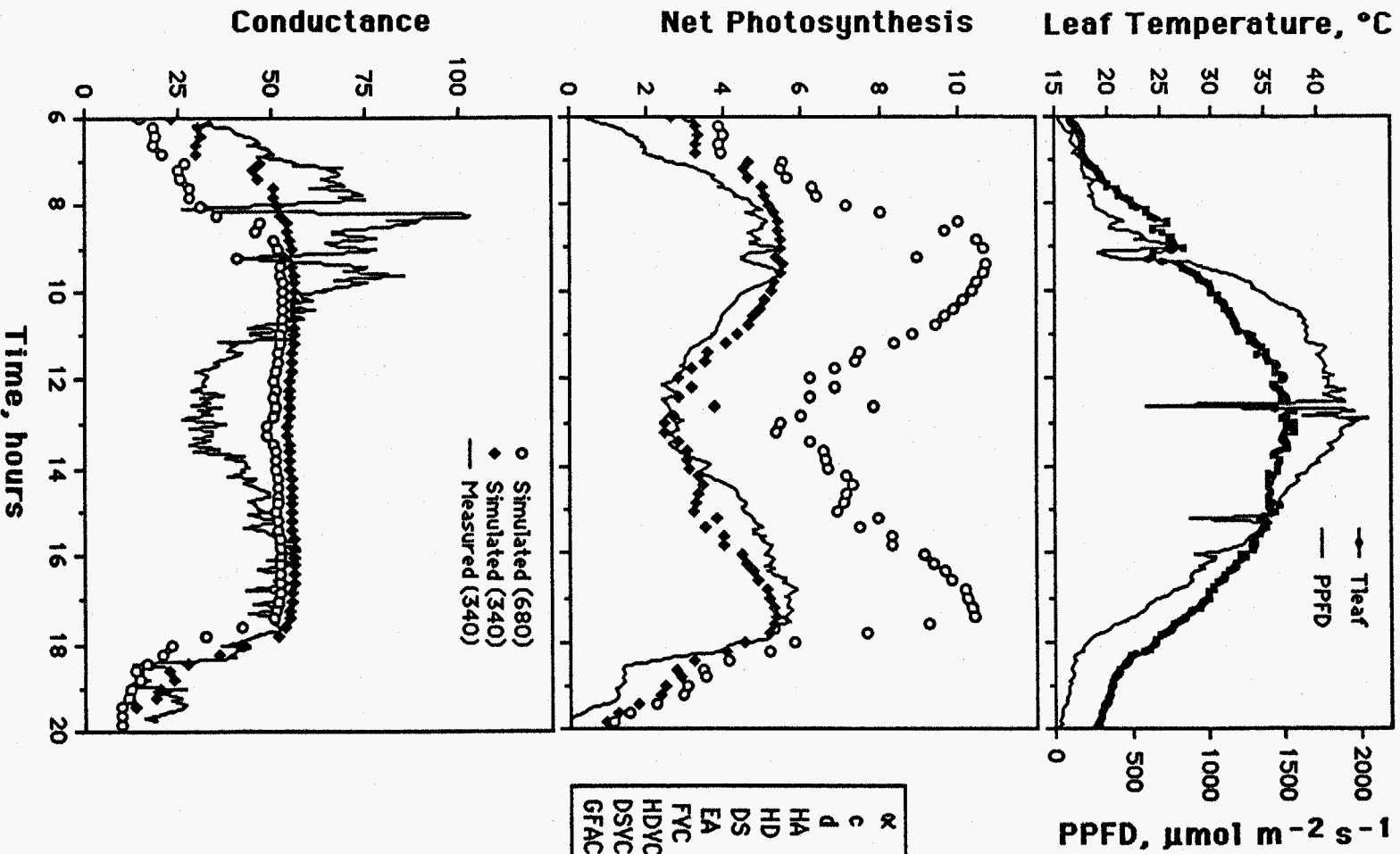


Fig. 6. Rates of net photosynthesis and leaf conductance, measured in the field on July 21, 1983 at 340 ppm, compared with model simulations at 340 and 680 ppm, using parameter values shown.

measured photosynthesis and conductance. Note that for each date, the model fit of simulated to measured photosynthesis at 340 is quite good and similar in both model parameterizations. However, the simulated photosynthesis rates at 680 ppm are quite different. In addition the fits to measured conductance data are quite different depending on parameter values used. [It should be mentioned that these data, in which mid-day depression of photosynthesis and conductance is pronounced, represent a significant challenge to modelling efforts, inasmuch as the physiological basis for the phenomenon is only beginning to be elucidated.]

Thus, we find that the present version of the model is quite capable of producing adequate fits to measured data; in fact, there is sufficient flexibility that similar fits can be obtained using quite different parameterizations. Without having measured data at elevated CO₂ however, it is impossible to choose which of the large number of potential parameterization sets is most correct. We agree that a mechanistic model is necessary to predict responses outside the range of experimental data. However, these simulations point out the fact that even a mechanistic physiological model is only as good as its parameterization. These fits were obtained by making reasonable *guesses* about parameter values, then essentially conducting a curve fitting exercise. If we're to have confidence in our predictions beyond the range of measured data, we must begin to take the experimental steps necessary to accurately parameterize the model for those species and growth conditions (including elevated CO₂) of interest.

Parameterizing the Photosynthesis Model

As indicated above, model utilization requires the estimation of a number of parameter values; as we've shown elsewhere (Harley *et al.* 1985, 1986) these may be estimated from gas exchange data alone, obtainable under either laboratory or field conditions. The following experimental data are *ideally* required to obtain parameter values for leaves of a given species grown under a given environmental regime (including [CO₂]):

(1) To obtain the temperature dependency of V_{Cmax} requires a family of CO₂ response curves of net photosynthesis obtained at light saturation over the relevant temperature range. Although complete curves (compensation to saturation) are desirable, only the initial slope (compensation to ≈500 ppm) is essential.

(2) To obtain the temperature dependencies of α and the light and temperature dependencies of P_m requires a family of light response curves of net photosynthesis obtained at CO₂ saturation over the relevant temperature range.

(3) To obtain the temperature dependency of R_d, one needs to measure a temperature curve of dark respiration, which can be done in conjunction with (2) above. [A promising new technique which provides an independent estimate of Γ^* as well as improved estimates of R_d involves measurement of the initial slope of A vs. C_i curves at several low light intensities (Brooks and Farquhar 1985)].

(4) Assigning a value to GFAC, the proportionality constant relating stomatal conductance to mesophyll [ATP], is somewhat problematic at this point. After other parameter values are assigned, GFAC must be assigned a value which provides

reasonable values of C_i .

The data sets outlined above allow the direct estimation of all model parameters, but require considerable experimental effort (2-3 days). Such elaborate procedures will not be possible in many cases, and such data sets are rare in the literature. Below is a list of parameters, values of which must be incorporated into the model.

Param.	Definition	Comments
K_o	Michaelis constant for CO_2	Assumed same for all C_3 spp.; $f(T)$
K_c	Michaelis constant for CO_2	Assumed same for all C_3 spp.; $f(T)$
$V_{o_{max}}$	Max. rate of oxygenation	Assumed equal to $0.21 \cdot V_{c_{max}}$; $f(T)$
$V_{c_{max}}$	Max. rate of carboxylation	Proportional to CE; proportional to leaf [N]; $f(T)$
ΔH_a	Activation energy of P_{ml}	Could be same for all C_3 spp. (?)
ΔH_d	Deactivation energy of P_{ml}	Shifts T_{opt} of P_{ml}
c	Scaling factor for P_{ml}	May be \pm proportional to $V_{c_{max}}$
ΔS	Entropy factor	Shifts T_{opt} of P_{ml}
α	Incident quantum yield	Proportional to [Ch]; \pm constant, except under stress
R_d	Day respiration	May be \pm proportional to $V_{c_{max}}$
GFAC	Conductance=GFAC \cdot [ATP]	May be \pm proportional to $V_{c_{max}}$

As indicated in the table, several parameters (K_c , K_o , α) are assumed to remain constant. Others ($V_{c_{max}}$, R_d , GFAC and the constant, c ,) are expected to vary but always in the same direction and more or less proportionally. Our initial assumption, in agreement with Farquhar, is that the three factors which tend to control leaf to leaf and plant to plant variation are $V_{c_{max}}$, the constant, c , and R_d , all of which (1) are known to vary widely among plants and for different growth conditions, and (2) lead to large changes in model behavior. Although we expect these three parameters to be the critical drivers of the model, more subtle changes such as shifts in temperature optimum may involve other parameters.

Initial development of sets of parameters for different species and variable growth environment will be fairly demanding in terms of both time and effort. It is expected, however, that as additional data sets are generated, certain generalities and trends will emerge which will simplify the procedure. Ranges of variation for each parameter and the relationship between parameters will be established, for example, as will those parameters which are critical drivers of the model. We expect model parameterization to eventually become fairly routine, involving one or two days of measurement for each leaf type, canopy layer, growth condition, etc., to be parameterized.

Finally, in addition to parameterization data sets, validation data sets will be required, particularly in the early stages of model development. In the context of the CO_2 project, it will be necessary to validate at both ambient and elevated CO_2 levels. Ideally, these validation data sets should be similar to those simulated above, in which field grown plants respond to naturally occurring environmental conditions. Alternatively, or additionally, validation data sets could consist of measured functional dependencies (i.e., photosynthetic responses to light, CO_2 or temperature) measured under conditions beyond the range of the parameterization data set.

II. Implementation of the Photosynthesis Model in a Canopy Context

Robert L. Dougherty

The photosynthesis model described in Part I is also being implemented in the CANDO canopy model (see PRECO Greenbook, Part III). The current work has four goals:

1. To parameterize the model for a plant canopy.
2. To investigate the direct effects of CO₂ enrichment on whole-plant photosynthesis, transpiration and water-use efficiency.
3. To analyze the importance of potential indirect effects of CO₂ enrichment (i.e., changes in canopy architecture) on the direct influences on photosynthesis, transpiration and water-use efficiency.
4. To test strategies for developing simplified models of whole-plant photosynthesis and transpiration that respond to atmospheric CO₂.

Progress towards meeting these four goals will be briefly discussed and illustrated with examples.

Parameterization of model at the canopy level

The parameterization of the photosynthesis model is currently aimed at determining parameter values for sun leaves. Once the behavior of the model for single leaves is well-documented and validated, the behavior of shade-adapted leaves of lower canopy levels can be represented by appropriate parameter values. Tentatively, we have identified four model parameters that have been adjusted with depth in a simulated *Quercus coccifera* canopy to provide decreased photosynthesis and conductance, similar to results observed in the field (Caldwell *et al.* 1986.). These parameters, and their values for top and bottom canopy layers, are listed below.

Parameter	Top	Bottom	Comments
FVC	33.27	32.8	decreases max. carboxylation
C	14.71	14.3	decreases CO ₂ -saturated PS
GFAC	10000	6000	decreases stomatal response
D	15.71	15.5	increases respiration

The effects of these parameter adjustments on simulated photosynthesis and conductance are shown in Figure 7.

Simulated whole-plant photosynthesis is illustrated in Figure 8.

Further parameterizations will be made as the leaf model is improved, and as

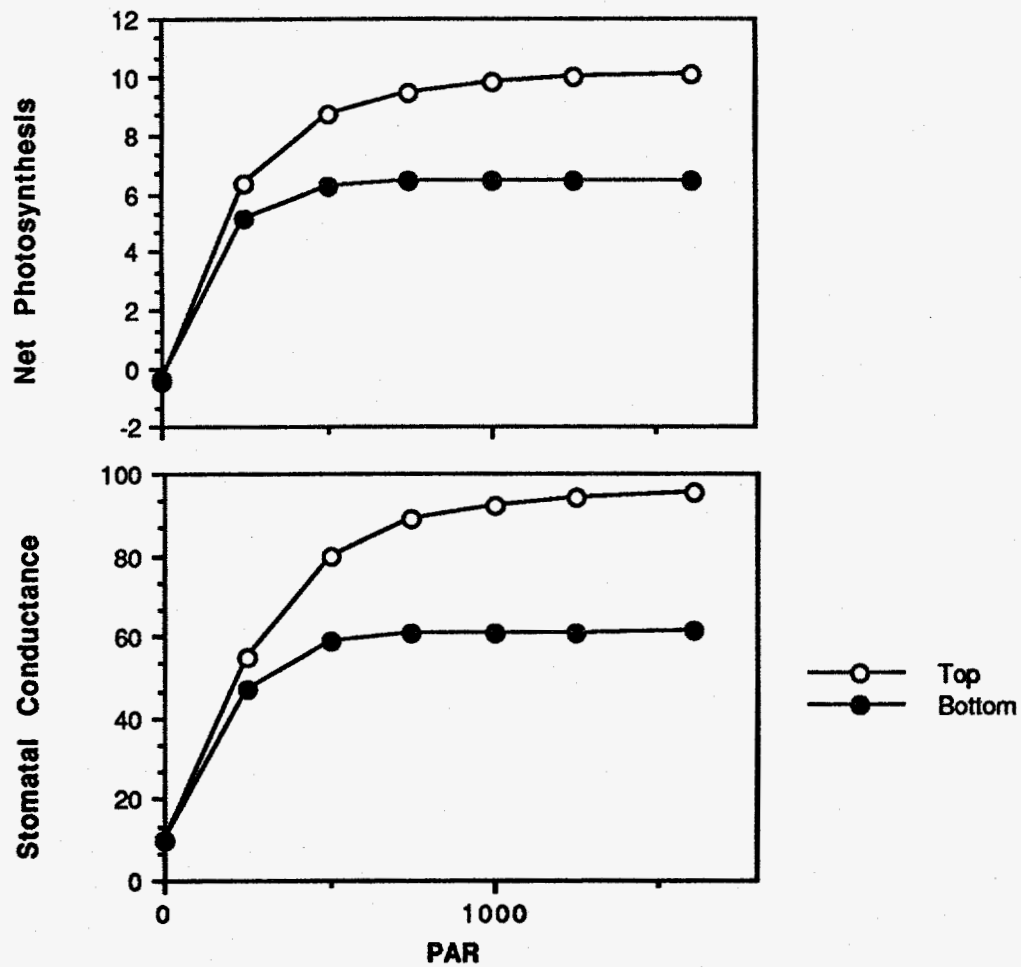


Figure 7. Simulated light response of photosynthesis and conductance for leaves in top and bottom layers of a *Quercus coccifera* canopy.

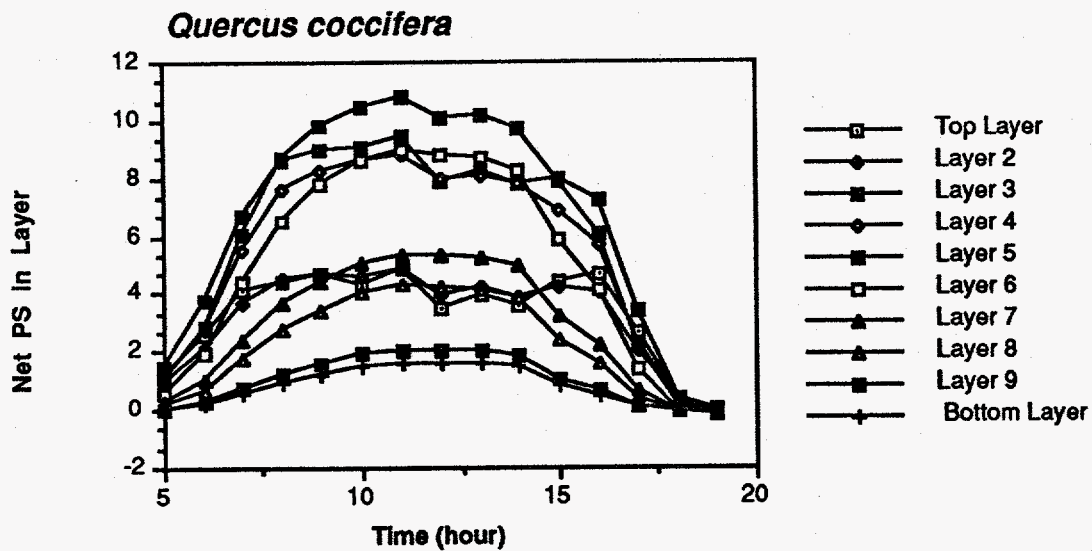


Figure 8. Simulated diurnal time course of photosynthesis in 10 canopy layers of *Quercus coccifera*.

more data become available. Currently, there is a need for data to parameterize this model for soybean so validation can be done with the large database on whole-plant soybean photosynthetic response to CO₂.

Effects of Increased CO₂

The model is being used for simulation of direct effects of increased CO₂ concentration on photosynthesis (and ultimately, growth) at the whole-plant level. These efforts are somewhat limited by the lack of a good database on *Quercus* leaf responses to elevated CO₂. Consequently, the results shown here are quite preliminary.

The canopy-level simulations of diurnal time courses of photosynthesis and transpiration (Figure 9) show moderate responses to elevated CO₂. While the degree of the response is due to the current parameterization of the model, the ability to represent changes in conductivity and transpiration at a mechanistic level represents a significant advance over the model originally in the canopy model (PRECO Greenbook, Part III).

Analysis of Influences of Modified Plant Architecture on Primary Effects of CO₂

Changes in plant morphology are known to occur as indirect effects of CO₂ enhancement (Strain 1985). Observed responses include increased leaf area (Cure and Acock 1986), thicker leaves and greater light absorption (Leadley *et al.* 1987), larger individual leaves and petioles (Overdieck 1986), and increased ratios of nonphotosynthetic-to-photosynthetic tissues (Oberbauer *et al.* 1985). All of these responses, by influencing light interception, light utilization efficiency and thermal balances of the whole plant, would be expected to influence photosynthesis (Sionit *et al.* 1982). Moreover, differences between species in their morphological responses to increased CO₂ may influence community composition (Sionit *et al.* 1985).

The importance of plant architecture on the harvesting of light for photosynthesis provides the rationale for analyzing CO₂ effects at the canopy level. Canopy models that include mechanistic leaf simulators allow us to separate the effects of CO₂ on leaf photosynthesis from those due to changes in the arrangement of leaves in the plant canopy. As more is learned about the individual processes controlling these effects, our canopy-based models can more realistically simulate whole-plant response.

As an initial effort to characterize the degree to which modified plant architecture may feed back on primary plant processes, we are conducting a set of model simulations that portray the interactions between CO₂ concentration and canopy architecture as they mutually influence photosynthesis and transpiration. The results of one such analysis for leaf area index are shown in Figure 10. These results indicate that small increases in leaf area index may accentuate the CO₂-enhancement of photosynthesis, while decreasing the effect on transpiration. The results of these opposing interactions is that the

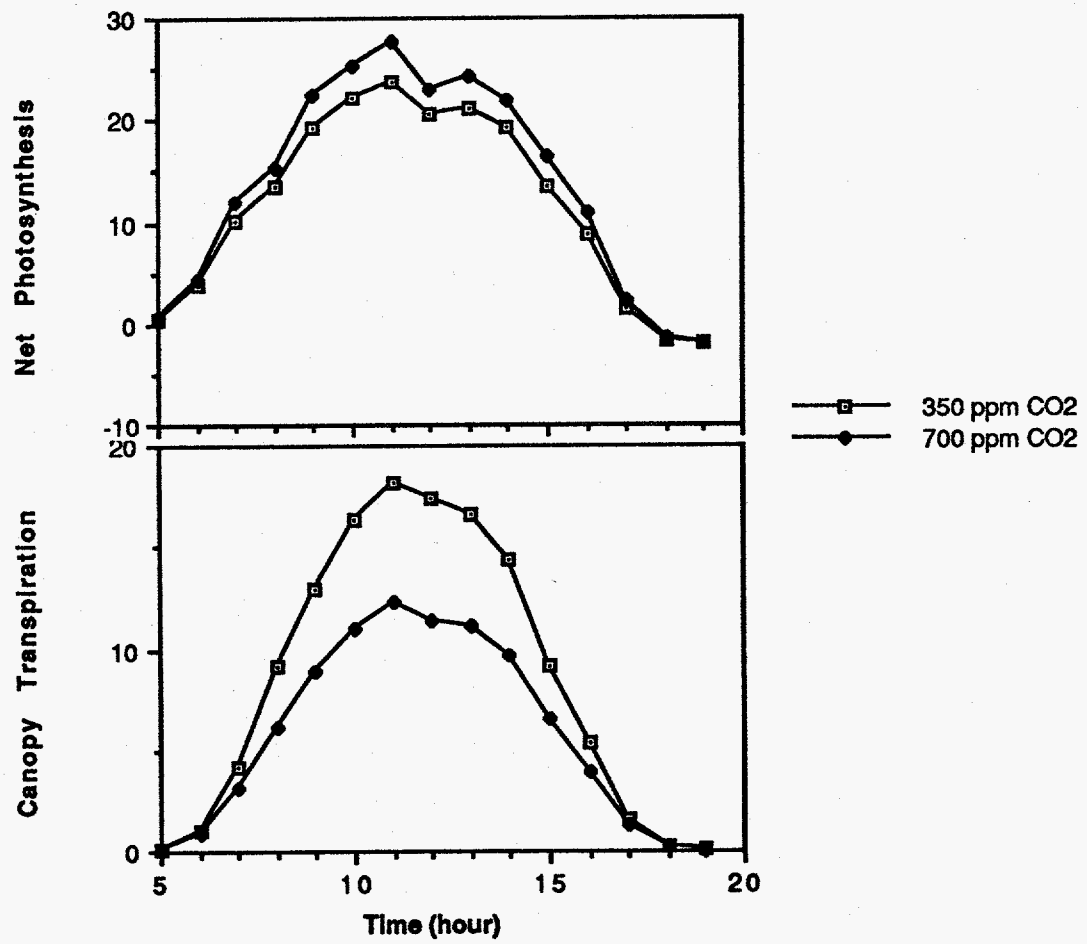


Figure 9. Diurnal time courses of photosynthesis and transpiration at two levels of atmospheric carbon dioxide.

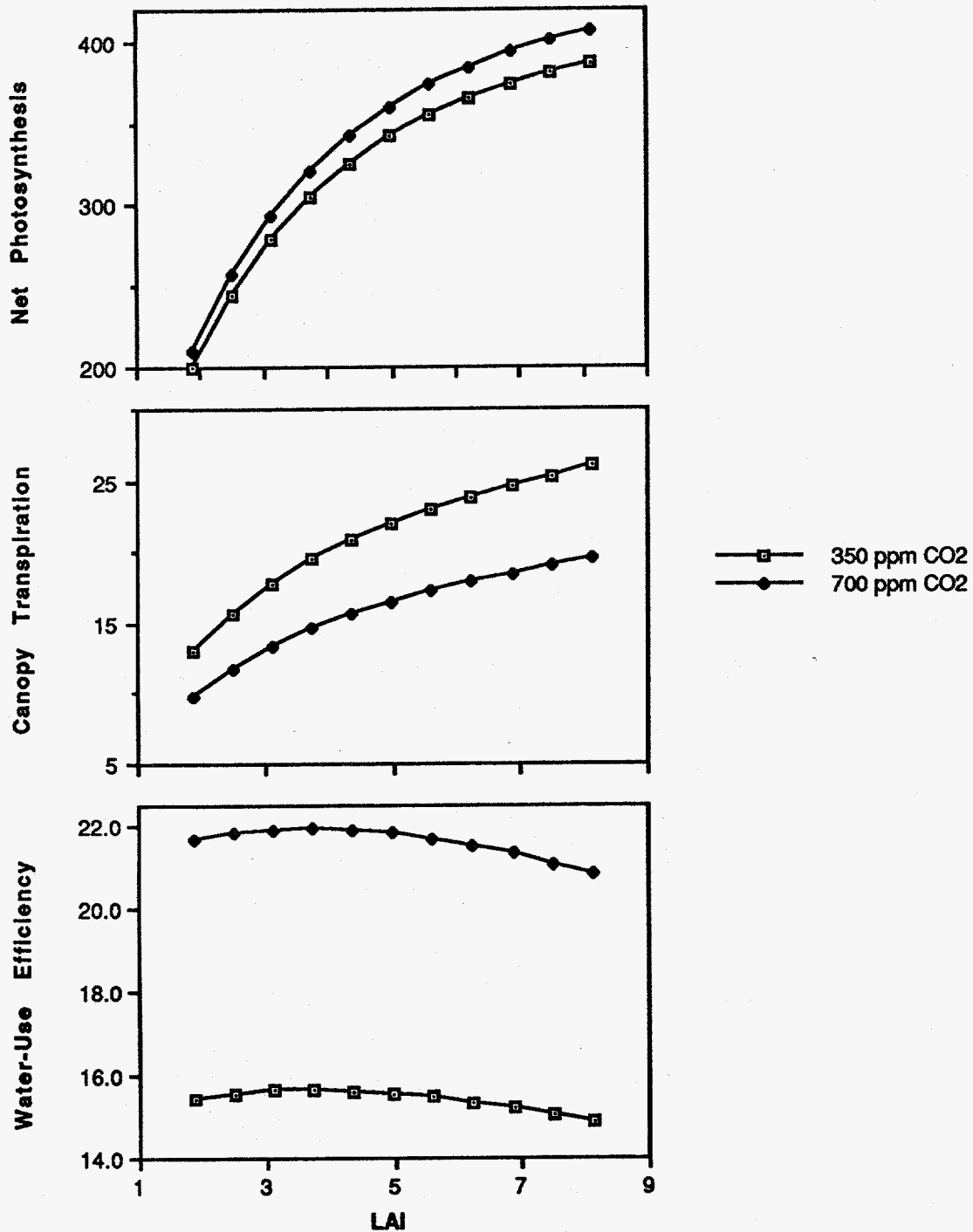


Figure 10. Results of simulations of canopy photosynthesis, transpiration, and water use efficiencies at a range of canopy Leaf Area Indices. Simulations represent *Quercus coccifera* canopies during 3 hours in morning (8AM-11AM).

direct effect of increased CO₂ concentration on water-use efficiency is not strongly influenced by leaf area index. Of course, these conclusions may change substantially when changes are made in parameter values, such as those controlling respiration. Nonetheless, this exercise represents an important use of the canopy simulation model for analyzing some of the myriad interactions likely in plants' response to increased CO₂ concentration.

Development of simplified models

While process-oriented models such as PRECO and its canopy component are valuable for addressing questions concerning responses of leaves, leaf assemblages and whole plants, the CO₂ modeling effort is also seeking to extrapolate the behavior of these models to higher level processes such as plant competition and system-level production. To address this need, we are developing procedures to scale up the predictions of the canopy model to larger spatial scales. The following example illustrates one strategy for building a phenomenological simulator of plant production that uses information contained in the leaf and canopy simulators.

A simulator of population, community or ecosystem primary production can be constructed by developing response surfaces from models representing individual canopies. The light use efficiency of a stand of plants can be calculated from the response of a mechanistic photosynthesis model to varying amounts of absorbed light (Norman and Arkebauer 1988). Similarly, we are predicting canopy light use efficiency for a *Quercus* stand as a function of incident light intensities (Figure 11). The canopy light use efficiency can then be used as a parameter in a phenomenological model that predicts primary production at larger scales than would be feasible from the canopy model alone. Such a model would achieve the tractability of an empirical model of stand production, while retaining much of the flexibility and theoretical soundness of the process model used to parameterize it.

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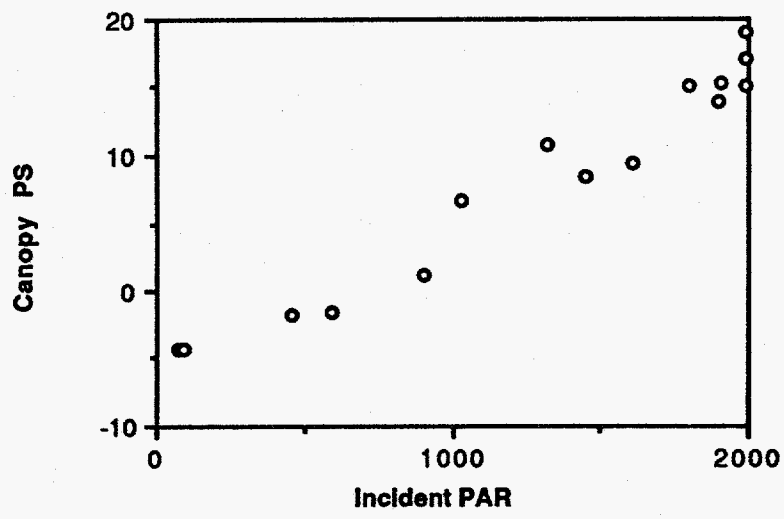


Figure 11. Simulated photosynthesis of *Quercus coccifera* canopy, shown in relation to incident Photosynthetically Active radiation (PAR).

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III. Optimal leaf nitrogen concentrations related to carbon dioxide, nutrition, and light

David W. Hilbert

ABSTRACT

Nitrogen concentrations in leaves vary in response to resource availability, generally increasing with increasing light or soil nitrogen and decreasing when plants are grown at higher than ambient carbon dioxide concentrations. This decrease in leaf nitrogen which commonly occurs at elevated levels of carbon dioxide is intriguing and important for a number of reasons. Since leaf nitrogen and photosynthetic capacity are correlated, plants grown at high levels of carbon dioxide often do not display remarkable increases in growth and productivity. This study asks: 1) Is decreased leaf nitrogen in plants grown at elevated carbon dioxide levels an adaptive response of plants? and 2) Is this response predictable and consistent with responses to light and nutrition?

Here, the optimal leaf nitrogen concentration which maximizes relative growth rate is found quantitatively as a function of root specific activity, light, and carbon dioxide. The optimal leaf nitrogen concentration occurs when the change in net photosynthesis due to increased leaf nitrogen equals the consequent increase in root respiration plus the photosynthesis lost due to decreased allocation to leaf area. Predictions of the analysis are consistent with general observations under a wide range of conditions and suggest that the response of plants to all these factors, including high carbon dioxide concentrations, is adaptive. The difference between light and carbon dioxide responses are due to differences in the way that these two factors affect the photosynthesis versus leaf nitrogen curve.

INTRODUCTION

Leaf nitrogen concentrations are known to vary with nitrogen availability, light level, and carbon dioxide concentrations experienced during growth. While there has been some work on optimal leaf nitrogen concentrations related to light and nutrition, there has been no analysis of the effect of elevated atmospheric carbon dioxide and no attempt to predict the simultaneous response to all of these factors. This paper presents an analysis which qualitatively predicts the generally observed responses of leaf nitrogen to all three of these factors.

The primary motivation for the study of leaf nitrogen concentration is the strong correlation between it and photosynthetic capacity (Björkman, 1968; Evans, 1983; Field and Mooney, 1986; Gauhl, 1968; Gulmon and Chu, 1981; Medina, 1971; Mooney *et al.*, 1987) and ultimately plant growth rates. The reason for this relationship is that a large proportion of leaf nitrogen is contained in photosynthetic enzymes, including both RuBPCarboxylase (Evans, 1983; Huffaker, 1982; Yashimata and Fujino, 1987) and enzymes involved in electron transport and the regeneration of RuBP (Field and Mooney, 1986; Kirk and Tilney-Bassett, 1978).

The effect of light level on leaf nitrogen has been well established in a number of studies. Leaf nitrogen is generally lower for species occurring in shaded versus open habitats (Björkman, 1968; Goodchild *et al.*, 1972) and most species respond by increasing leaf nitrogen concentration when grown in full versus low light (Langenheim *et al.*, 1984; Björkman, 1968; Björkman *et al.* 1972).

The optimal leaf nitrogen content (N_{opt}) of plants has been most discussed with regard to light. Mooney and Gulmon (1979) present a qualitative, graphical argument for the increase in leaf nitrogen which is generally observed in plants growing in high

light conditions. Field (1983), Hirose and Werger (1987), and Charles-Edwards et al. (1987) discuss the optimal spatial allocation of a fixed amount of nitrogen in a canopy with respect to varying light levels and observations generally support their analyses of optimal nitrogen distribution.

The effect of nitrogen availability on leaf nitrogen concentration and photosynthetic capacity is also well known. Generally leaf nitrogen concentration and nitrogen availability are positively correlated (Medina, 1971; Huffaker, 1982; Makino et al., 1983). Perhaps because this response appears obvious, there has been less discussion of N_{opt} in relation to nutrition than for light, although Mooney and Gulmon (1979) suggest that the cost of acquiring nitrogen should increase when nitrogen is relatively unavailable and that N_{opt} should consequently be lowered.

The response of leaf nitrogen concentration when plants are grown at elevated levels of carbon dioxide is surprising and as yet unexplained. Many studies of plants grown at high levels of carbon dioxide show decreased leaf nitrogen concentrations compared with plants grown at ambient levels (Hocking and Meyer, 1985; Larigauderie, Hilbert, and Oechel, in press; Madsen, 1975; Norby et al., 1986; Peet and Willits, 1984; Williams et al., 1986; Wong, 1979). This decrease in leaf nitrogen concentration can lead to a decrease in photosynthetic capacity which then limits the growth response of plants exposed to high carbon dioxide concentrations (Mortensen, 1987; Porter and Grodzinski, 1984; Peet et al., 1986). At first glance this response appears to be maladaptive, especially since it is the opposite to that observed for light. Since both light and carbon dioxide have the same immediate effect of increasing photosynthetic rates one would expect similar responses of leaf nitrogen.

The following is a general quantitative analysis of optimal leaf nitrogen concentration as affected by the levels of resource availability to the root and shoot (light, carbon dioxide, and nitrogen uptake rates which are a function of nitrogen availability). It is a more rigorous analysis of the factors which determine this optimum than has previously been described and demonstrates that decreased leaf nitrogen concentrations in plants grown at high levels of carbon dioxide is adaptive.

Derivation of the optimization criterion

This approach to finding optimal leaf nitrogen concentrations is relatively simple, using a simple model for the relative growth rate of a plant which is a function of leaf nitrogen concentration. The optimal leaf nitrogen concentration which maximizes relative growth rate is found by setting the derivative of the relative growth rate function with respect to leaf nitrogen concentration to zero.

I begin with the common assumption that growth rate is proportional to net carbon gain and use a simple model first described by Monsi (1968)

$$dW/dt = k(h\sigma_s W_s - rW_r) \quad (1)$$

where W is the total plant dry weight (g), W_s and W_r are the dry weight of shoots and roots respectively (g), k is the growth efficiency (g biomass $\cdot \mu\text{mol CO}_2^{-1}$ fixed), h is the leaf area ratio ($\text{m}^2 \cdot \text{g}^{-1}$), r is the root respiration rate ($\mu\text{mol CO}_2 \cdot \text{g}^{-1} \cdot \text{s}^{-1}$), and σ_s is the shoot specific activity or net photosynthetic rate ($\mu\text{mol CO}_2 \cdot \text{m}^{-2} \cdot \text{s}^{-1}$). Dividing both sides of Equation (1) by total plant weight (W) gives the expression for relative growth rate

$$(1/W) dW/dt = k(h\sigma_s f_s - r f_r) \quad (2)$$

where f_s and f_r are the fraction of biomass in the shoot and root respectively (note that $f_s + f_r = 1$.) To find the leaf nitrogen concentration which maximizes relative growth rate we find the partial derivative of Eqn. (2) with respect to leaf nitrogen concentration (N) in units of g nitrogen $\cdot \text{m}^{-2}$ and set the derivative equal to zero.

Photosynthetic rate (σ_s) is, in part, a function of leaf nitrogen concentration as are f_s and f_r . Without specifying these functions we take the partial derivative and set the result equal to zero to arrive at the optimization criteria

$$h f_s \delta \sigma_s / \delta N = r \delta f_r / \delta N - h \sigma_s \delta f_s / \delta N .$$

(3)

This equation states that N_{opt} occurs when the increase in net photosynthesis due to increased leaf nitrogen equals the consequent increase in root respiration due to the increased root fraction plus the photosynthesis lost due to a decrease in shoot fraction (as will be seen, $\delta f_s / \delta N$ is negative). The left and right terms of this equation can be interpreted as the marginal revenue and marginal cost of increasing leaf nitrogen concentration, an optimal strategy occurs when marginal cost equals marginal revenue (see Bloom et al. 1985). Our approach differs from previous qualitative analyses of this type in that we do not assume certain components of leaf cost a priori. Rather, we derive the marginal cost of increasing leaf nitrogen directly by finding the conditions which maximize the RGR function. Thus, we have a quantitative measure of leaf cost in relation to increasing nitrogen concentrations rather than having to guess the shape of the cost and marginal cost curves (e.g. Mooney and Gulmon 1979).

Derivation of Equation (3) was possible without specifying the functional relationships between σ_s , f_r , and f_s and leaf nitrogen (N). In order to complete the analysis and determine the effects of CO_2 , light, and nutrition we now specify these functions. To find f_s and f_r as functions of leaf nitrogen concentration we assume balanced exponential growth (e.g. Thornley, 1976) so that the nitrogen concentration in the plant ($g N \cdot g \text{ biomass}^{-1}$) is given by the rate of nitrogen uptake ($g N \cdot s^{-1}$) divided by the growth rate of biomass ($g \text{ biomass} \cdot s^{-1}$) given by Eqn. (1). Multiplying this by the specific leaf weight (h^{-1}) gives the leaf nitrogen concentration ($g N \cdot m^{-2}$)

$$N = \sigma_r W_r / kh(h\sigma_s W_s - rW_r) \quad (4)$$

where σ_r is the specific activity of roots ($gN \cdot g \text{ root}^{-1} \cdot s^{-1}$) which is a function of nitrogen availability. Solving Eqn. (4) for $f_r = W_r/W$ gives

$$f_r = \sigma_s Z / (1 + \sigma_s Z) \quad (5)$$

where

$$Z = kh^2 N / (\sigma_r + rkhN). \quad (6)$$

The partial derivative of f_r with respect to leaf nitrogen is consequently

$$\delta f_r / \delta N = [\sigma_s \delta Z / \delta N + Z \delta \sigma_s / \delta N] (1 + \sigma_s Z)^{-2} \quad (7)$$

where

$$\delta Z / \delta N = kh^2 \sigma_r / (\sigma_r + khrN)^2 \quad (8)$$

The shoot fraction (f_s) is, by definition, $(1 - f_r)$ so

$$\delta f_s / \delta N = - \delta f_r / \delta N . \quad (9)$$

With Equation (5), one can calculate the effect of changes in shoot specific activity, root specific activity, and leaf nitrogen concentration on root:shoot ratio (f_r/f_s). These responses are presented in Figure 12. Root:shoot ratio is an increasing function of both the photosynthetic rate (σ_s) and the nitrogen concentration of the leaves. Thus, any factor which increases shoot specific activity (e.g. increased light or carbon dioxide) requires an increase in root fraction in order to maintain the same leaf nitrogen concentration. Similarly, an increase in (N) requires an increase in f_r and a corresponding decrease in f_s . Increasing root specific activity (σ_r), on the other hand, decreases the root:shoot ratio necessary for any specific leaf nitrogen concentration.

Shape of the photosynthesis vs. leaf nitrogen curve

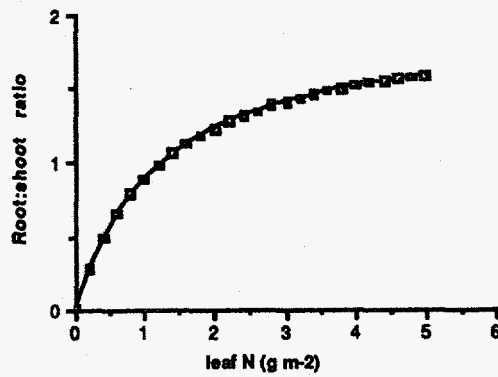


Figure 12a: Root:shoot ratio required as a function of leaf nitrogen concentration, calculated from Eqn.5.

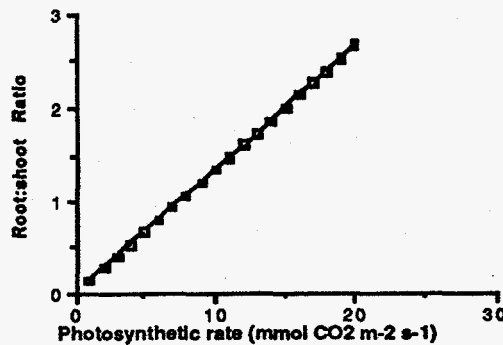


Figure 12b: Variation in root:shoot ratio required to maintain a constant leaf nitrogen concentration (here 2.5 gN.m⁻²). Any factor, such as increased light or CO₂, which increases photosynthetic rate requires an increased root:shoot ratio to maintain a given leaf nitrogen concentration (Eqn.5).

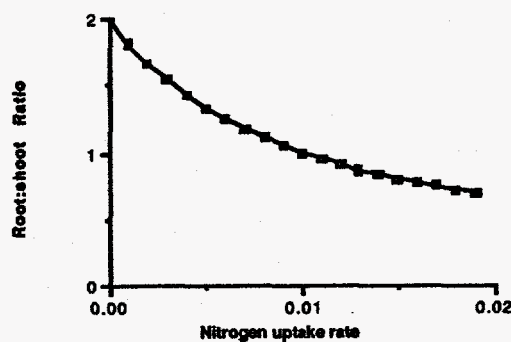


Figure 12c: Effect of root specific activity (a function of nitrogen availability) on the root:shoot ratio necessary for a constant leaf nitrogen concentration. Increasing nitrogen availability decreases root:shoot ratio and consequently decreases the cost of leaf nitrogen.

Equations (1) through (9) are valid irrespective of the form for photosynthesis as a function of leaf nitrogen. To complete the analysis we now specify σ_s as a function of N, carbon dioxide, and light. Here we are particularly interested in the photosynthetic rate as a function of (N) which has not been extensively studied experimentally. Some authors report a linear photosynthesis vs. leaf nitrogen concentration curve (see Field and Mooney, 1986 for a review) while others report a nonlinear function (Evans, 1983; Lugg and Sinclair, 1981; Nevins and Loomis, 1970; Takano and Tsudona, 1971). Since the response of this curve to carbon dioxide and light must also be specified we rely on a theoretically based model of photosynthesis developed by Farquhar, Von Caemmerer, and Berry (1980). Their model was primarily intended to describe the rate of C₃ photosynthesis as a function of light and carbon dioxide (see Appendix I for a complete description of the model and our modifications to it). This model assumes that there is a linear portion of the photosynthesis vs. carbon dioxide curve (A₁) which applies at low carbon dioxide concentrations and a nonlinear portion (A₂) which is dependent on both light and carbon dioxide and applies at higher internal carbon dioxide concentrations. In the linear portion, photosynthesis is limited by the maximum activity of RuBPCarboxylase and the internal carbon dioxide concentration; while, in the nonlinear part, photosynthesis is limited by the light driven regeneration of RuBP. The slope of A₁ depends on the maximum RuBPCarboxylase activity (V_{cmax}) which is equivalent to the carboxylation efficiency. V_{cmax} is known to be a linear function of leaf nitrogen concentration (Field 1983).

The shape of A₂ is a hyperbolic function of the maximum rate of electron transport (J_{max}) which is itself a linear function of leaf nitrogen concentration (Evans, 1983; Field, 1983). A₁ is a hyperbolic function of carbon dioxide while A₂ is a hyperbolic function of both light and carbon dioxide. Finally, leaf dark respiration is also assumed to be a linear function of (N) (citations). By specifying V_{cmax}, J_{max}, and dark respiration (R_d) as linear functions of (N) we can generate the expected shape of the photosynthesis vs. leaf nitrogen curve. Figure (13) examines the effect of both carbon dioxide and light on this function. While both affect the maximum photosynthetic rate, only carbon dioxide influences the initial slope of this curve.

For the optimization analysis we need the partial derivative of this model with respect to (N) which is presented in Appendix II. By substituting Equations (7),(8), and (9) into the optimization criterion (Equation 3), along with the partial derivative of σ_s from Appendix II, we arrive at a complete specification of the requirement for optimal leaf nitrogen concentration. Any combination of carbon dioxide, light, and root specific activity can be chosen and the optimal leaf nitrogen concentration calculated.

Results and Discussion

Ideally, one would solve the optimization criterion (Eqn. 3) directly for the optimal leaf nitrogen concentration. While this is not practical when using the Farquhar *et al.* (1980) photosynthesis model, it is a simple matter to choose values for the parameters and calculate N_{opt} numerically. By varying carbon dioxide, light, and root specific activity the change in N_{opt} due to changes in these factors can be investigated. Figure 14 presents examples of marginal cost and marginal revenue curves found from Eqn. (3). Recall that the left hand term of this equation represents, in economic terminology, the marginal revenue, while the right hand terms represent the marginal cost. Both marginal revenue and marginal cost are affected by the shoot specific activity so changes in light or carbon dioxide concentration will affect the magnitude and shape of these curves, changing the predicted optimal leaf nitrogen concentration.

Figure 15 presents the general response of N_{opt} to increasing light, carbon dioxide, and nitrogen uptake rate:

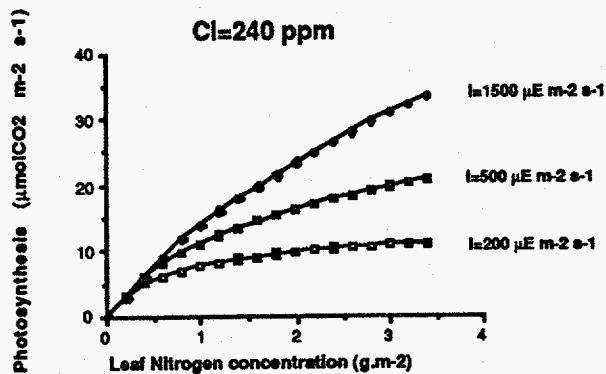


Figure 13a: Photosynthetic rate versus leaf nitrogen concentration calculated from the Farquhar *et al.* model. Note that increasing irradiance changes the maximum photosynthetic rates but does not affect the initial slope.

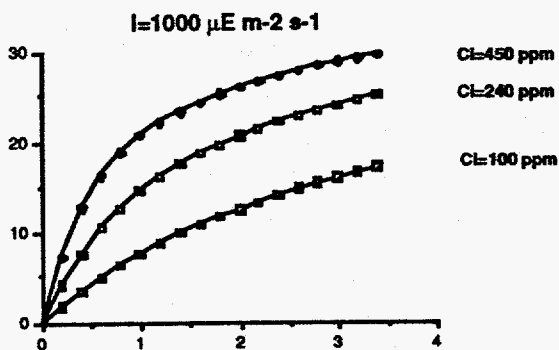


Figure 13b: Photosynthetic rates versus leaf nitrogen concentration, varying internal CO₂ concentration. Increasing CO₂ both increases the initial slope and maximum rates of photosynthesis.

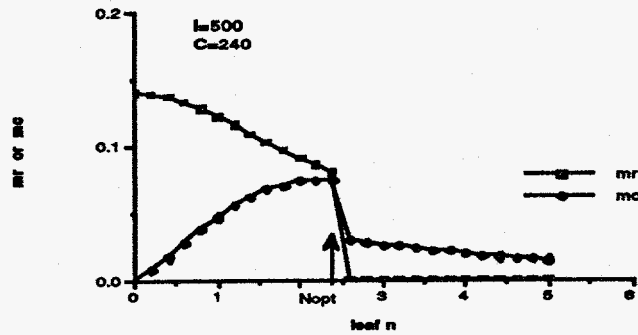


Figure 14a: Marginal revenue and marginal cost from Eqn.3 with ambient CO_2 and irradiance of $500 \mu\text{E}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$. The optimal leaf nitrogen normally occurs where marginal revenue equals marginal cost but, because of the discontinuity in these functions, they may not be equal. In this case, N_{opt} occurs where marginal cost is closest to, but still less than, marginal revenue.

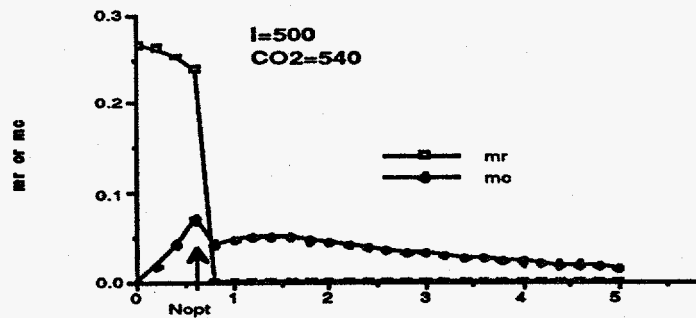


Figure 14 b: Marginal revenue and marginal cost from Eqn.3 for high CO_2 and irradiance of $500 \mu\text{E}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$. High CO_2 decreases the optimal leaf nitrogen concentration.

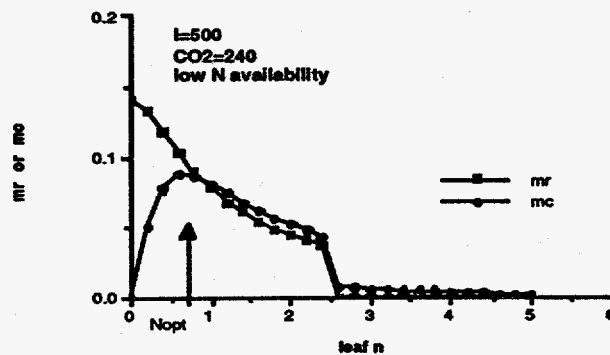


Figure 14 c: Marginal revenue and marginal cost from Eqn.3 with ambient CO_2 , $I=500$, and low root specific activity representing low availability of nitrogen in the soil. Note that, in this case, the marginal revenue and marginal cost curves do intersect.

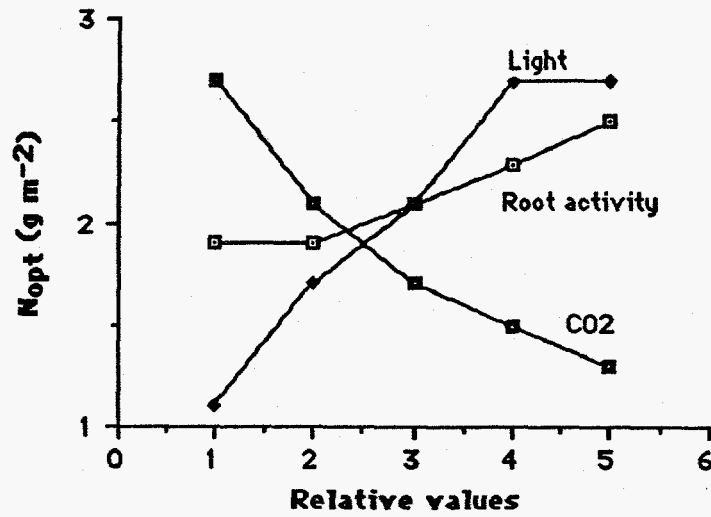


Figure 15: Effects of increasing irradiance, root activity (nitrogen availability), and carbon dioxide on the optimal leaf nitrogen concentration predicted by Eqn.3. The x axis is in arbitrary units since light, root activity, and CO_2 are all in different units. The specific shape of these curves depend on the choice of all parameters in Eqn. 3 but this figure presents the general trend of optimal leaf nitrogen as affected by each factor.

Responses to light

As is generally observed, the predicted leaf nitrogen concentration increases with increasing light. A major reason for this is that light "delays" saturation of the photosynthesis vs. leaf nitrogen curve without affecting the initial slope (see Figure 13).

Responses due to nutrition

Increasing nutrition increases leaf nitrogen, as is generally observed, because the costs associated with leaf nitrogen are decreased. At high levels of nitrogen availability, as in Figure 14 a and b, the optimal leaf nitrogen concentration is solely dependent on photosynthetic characteristics.

Responses due to carbon dioxide

As frequently observed, leaf nitrogen is predicted to decrease at elevated carbon dioxide levels. The primary reason for this is that carbon dioxide increases the initial slope of the photosynthesis vs. leaf nitrogen curve, tending to cause saturation at lower leaf nitrogen concentrations. Thus, the marginal revenue and marginal costs curves cross at lower leaf nitrogen concentrations as in Figure 14b when plants are grown at elevated carbon dioxide levels. **This response does appear to be adaptive since the relative growth rate which the plant maintains under these circumstances is greater than that which would occur if high leaf nitrogen concentrations and high photosynthetic capacity had been maintained.** Photosynthetic capacity is reduced at high carbon dioxide levels but this is preferable to paying the high cost of increased root:shoot ratios necessary for higher leaf nitrogen concentrations.

In summary, the regulation of leaf nitrogen is an important means by which plants adjust their physiological status to prevailing levels of resource availability. Common wisdom suggests that decreased leaf nitrogen concentrations in plants grown at high levels of carbon dioxide is maladaptive since this decreases photosynthetic capacity. This analysis, however, demonstrates that this response is adaptive in that it can optimize relative growth rates. This response, along with similar responses to light and nutrition is predictable using a simple mathematical analysis and this should improve our ability to model the response of species and communities to elevated atmospheric carbon dioxide.

Appendix I : Details of the Farquhar, Von Caemmerer, and Berry (1980) model of photosynthesis

Net photosynthetic rate is given by the minimum of two functions (A_1 and A_2) which correspond to a RuBP saturated (A_1) and a RuBP limited portion of the carbon dioxide response curve.

$$A_1 = V_{cmax} (C-k_1)/(C+k_2) - R_d \quad (1)$$

where V_{cmax} is the maximum RuBPCarboxylase activity, C is the internal carbon dioxide concentration, and R_d is the dark respiration rate.

$$A_2 = J (C-k_1)/(4.5 C + 10.5 k_1) - R_d \quad (2)$$

where

$$J = J_{max} I / (I + 2.1 J_{max}), \quad (3)$$

J_{max} is the maximal rate of whole chain electron transport, and I is irradiance.

Following Field (1983) we make V_{cmax} , J_{max} , and R_d linear functions of (N)

$$V_{cmax} = k_3 N + k_4 \quad (4)$$

$$J_{max} = k_5 N + k_6 \quad (5)$$

$$R_d = k_7 N + k_8 \quad (6)$$

where k_3 through k_8 are empirically derived constants.

Appendix II : Partial derivatives of A_1 and A_2 with respect to N

$$\delta A_1 / \delta N = k_5 N (C-k_1)/(C+k_2) - k_7 \quad (1)$$

$$\delta A_2 / \delta N = \delta J / \delta N [(C-k_1)/(4.5 C + 10.5 k_1)] - k_7 \quad (2)$$

where

$$\delta J / \delta N = k_5 I^2 / (I + 2.1 J_{max})^2 \quad (3)$$

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IV. Ecosystem Level Simulations

J. W. Skiles

The atmospheric concentration of carbon dioxide is expected to double in the next century. Since this increase will directly affect stomatal conductance of plants, it is probable that, at the watershed scale, changes in evaporative demand, transpiration, and runoff will occur. Previous studies modeling the effect of increased CO₂ on the water budgets of watersheds have been "single-factor" exercises wherein a parameter representing stomatal conductance was reduced and the results noted.

We are using a multi-factor ecosystem model to examine the consequences of changes in precipitation and CO₂-induced plant-function characteristics on basin runoff, basin soil evaporation, and plant transpiration. By multi-factor, we mean that components for hydrology, primary producers, and herbivores are explicitly simulated for the watershed.

We have sufficient watershed data from three western locations to establish parameter values and initial conditions for our basin-scale model. The locations are Murphy Creek in the Walnut Gulch watershed near Tucson, Arizona; the Central Plains Experimental Range (CPER) on the Pawnee National Grassland in northeastern Colorado; and Sheep Creek which is part of the Reynolds Creek watershed in southwestern Idaho.

Some of this necessary information is by soil layer and includes porosity, water content at 0.3 and 15 bars, saturated conductivity, and layer depth. We also have hydraulic and channel segment information available for the streams in these watersheds.

While others have predicted a 40 to 90 percent increase in streamflow as a consequence of the doubling of atmospheric CO₂, our preliminary simulations indicate that for arid and semiarid watersheds, there will be little or no response. This is a result of the complex interactions of compensatory mechanisms within ecosystems.

For example, increased CO₂ is expected to increase aboveground plant production with a concomitant increase in leaf area. This vegetation will however, be of lower quality nutritionally since there will be no increase in nitrogen. Herbivores, explicitly simulated as steers with the physiologically based steer component, will consequently have to consume more forage in order to meet their demand for nitrogen. This will offset increase in leaf area and negate the effect of CO₂.

While the simulated steers graze the forage differentially because of user-supplied forage preferences, we can assume that a broad class of foragers, from invertebrates through ungulates utilize the vegetation. They will also increase their consumption to meet dietary requirements. Increased transpiration and changes in runoff amounts at the watershed scale that would be expected due to increased CO₂ are negated because of these compensatory mechanisms.