

# Canopy Photosynthesis: History, Measurements, and Models

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## I. Introduction

A plant canopy consists of an assemblage of plants with leaves that possess a particular spatial distribution and assortment of angle orientations (de Wit, 1965; Monsi *et al.*, 1973). How a collection of leaves intercepts sunlight and uses light energy to assimilate CO<sub>2</sub> is the basis of canopy photosynthesis. The major factors affecting canopy photosynthesis, through light interception, include the angular relationship between leaves and Earth–sun geometry and the leaves' vertical and horizontal positions. Other factors affecting canopy photosynthesis include environmental conditions (temperature, wind speed, humidity, and CO<sub>2</sub> concentration), the life history of leaves, the availability of soil moisture and nutrients, stomatal conductance, and specific photosynthetic pathways (Schulze, 1986; Gutschick, 1991; Stenberg *et al.*, 1995).

The complexity of canopy photosynthesis can be illustrated with a closed canopy on a fair day during the growing season. Inside the canopy some leaves are fully sunlit, others are exposed to frequent sunflecks, and the remainder exist in deep, but occasionally punctuated, shade (Chazdon, 1988; Oker-Blom *et al.*, 1991). Many sunlit leaves of C<sub>3</sub> species will experience saturated rates of carboxylation if CO<sub>2</sub> supply is limited (Farquhar and von Caemmerer, 1982). Furthermore, sunlit leaves are often warmer than shaded leaves. This situation promotes dark respiration (Amthor, 1994), decreases the solubility of CO<sub>2</sub> relative to O<sub>2</sub> (Farquhar *et al.*, 1980), and decreases the CO<sub>2</sub> specificity factor of ribulose, biphosphate, and carboxylase/oxygenase (rubisco) (Harley and Tenhunen, 1991).

The photosynthetic response of leaves to sunflecks does not have the same relationship observed during steady light conditions. As the light exposure

of a leaf transcends from a dark to bright condition, a dynamic response, known as induction, occurs if the previous dark exposure period was prolonged and it deactivated rubisco. The consequence of this enzymatic deactivation is a delay in the attainment of the next steady-state level of photosynthesis and a reduction of its magnitude. The duration of this delayed response can exceed 20 min, but this time response diminishes if the leaf is exposed to repeated light flecks (Chazdon, 1988; Pearcy, 1990). Postillumination carbon fixation is another important dynamic response experienced by leaves in fluctuating light. When a leaf's exposure to the sun is eclipsed, rates of carbon fixation can be sustained for a spell, as accumulated pools of photosynthetic metabolites are consumed. In fluctuating light environments, the occurrence of postillumination photosynthesis enhances assimilation rates in comparison to rates that would otherwise occur under steady conditions with the same mean level of light exposure (Pearcy, 1990).

The photosynthetic capacity of leaves deep in a canopy adapts to shade (Stenberg *et al.*, 1995). In the case of  $C_3$  plants, less rubisco is allocated to shaded leaves than to sunlit ones (Field, 1991; Hollinger, 1996). This effect causes their photosynthetic rates to saturate at lower light levels (Bjorkman, 1981). It also causes their photosynthetic capacity to be lower than that of leaves at the top of the canopy.

The light climate of needles in conifer stands is even more complex, because the geometric structure of shoots causes needles to cast penumbral and umbral shade on other needles (Oker-Blom *et al.*, 1991). This shoot structure causes their photosynthetic rate, under direct light, to be less than would occur if the needles were displayed in a planar pattern (Oker-Blom *et al.*, 1991; Stenberg *et al.*, 1995). On the other hand, the structure of shoots enhances their ability to harvest diffuse radiation and it allows conifer stands to maintain more leaves compared to angiosperms.

The goal of this chapter is to discuss several aspects of canopy photosynthesis. To accomplish this goal, we will extract information from the disciplines of plant biochemistry, ecophysiology, radiative transfer theory, micrometeorology, and biogeochemistry. First, we give a general history of measuring and modeling canopy photosynthesis. Next, we discuss micrometeorological and ecophysiological concepts that are being adopted to evaluate canopy photosynthesis. Third, we describe some general attributes of canopy photosynthesis that have been derived from field studies. Finally, we close this chapter with a few comments on some avenues of research that we think are worth exploring.

## II. History

### A. Measurements

The earliest measurements of whole-plant  $CO_2$  exchange occurred during the first half of the twentieth century (Boysen-Jensen, 1918; Henrici, 1921;

Lundegardh, 1922). Pioneering investigators evaluated canopy  $\text{CO}_2$  exchange by encasing plants in translucent chambers. Dr. Eckardt, whom the symposium honors, also made early contributions toward chamber design and the measurement of canopy photosynthesis (Eckardt, 1968).

Over the years, closed, semiclosed, and open chamber systems have been used (Jarvis and Catsky, 1971; Field *et al.*, 1989). Closed chamber systems measure photosynthesis as a function of the time rate of change of  $[\text{CO}_2]$ . This method is subject to bias error if  $\text{CO}_2$  in the chamber deviates from the background concentration, because photosynthesis is a function of  $[\text{CO}_2]$ . One way to circumvent this artifact is to use a semiclosed chamber. This method operates on the null-balance principle.  $\text{CO}_2$  in the chamber is kept relatively constant by delivering regulated amounts of  $\text{CO}_2$  to compensate for its drawdown as a leaf photosynthesizes, or buildup as it respire. Open systems evaluate carbon assimilation fluxes by measuring concentration differences between air flowing into and exiting the chamber and the volumetric flow rate through the chamber. This method enables a plant in a chamber to be relatively coupled to its external environment.

Overheating, humidification, disturbance of turbulent mixing, and imperfect light transmission are bias errors introduced by chamber methods (Musgrave and Moss, 1961; Tranquillini, 1964; Billings *et al.*, 1966; Denmead *et al.* 1993). When electrical power is ample, air conditioning and dehumidification systems can be employed to minimize these problems (Tibbitts and Langhans, 1993).

The accuracy of canopy photosynthesis measurements is also a function of the physicochemical techniques used to measure  $[\text{CO}_2]$  (see Sestak *et al.* 1971; Jarvis and Catsky, 1971). The simplest analytical method involves colorimetric detection of  $\text{CO}_2$  by a dry absorbent (typical sensitivity is  $50 \mu\text{l liter}^{-1}$ ). Wet analytical methods are more sensitive ( $0.5$  to  $1 \mu\text{l liter}^{-1}$ ) and accurate ( $\pm 2$ – $7\%$ ). Typically, air samples are bubbled through a dilute solution of alkali hydroxide (KOH, NaOH). The amount of  $\text{CO}_2$  absorbed by the solution is detected by electrical conductivity or titration measurements. Errors associated with chemical titration and conductivity analytical methods include sensitivity to temperature and difficulty maintaining the dilution of the alkali solution low enough to absorb all of the  $\text{CO}_2$  (Sestak *et al.*, 1971). Wet analytical methods are also labor and time intensive, taking 5–10 min to make each measurement.

The invention of the nondispersive infrared absorption spectrometer (or IRGA), in the 1950s, led to a renaissance of photosynthesis measurements. Infrared absorption spectrometers are sensitive ( $0.5 \mu\text{l liter}^{-1}$ ), accurate, and can be operated continuously and automatically. Musgrave and Moss (1961), Tranquillini (1964), and Billings *et al.* (1966) were among the first workers to employ IRGAs to measure whole-plant photosynthesis with chambers. At the same time, micrometeorologists started using IRGAs to measure  $\text{CO}_2$  fluxes across the canopy–atmosphere interface. Inoue (1957), Lemon

(1960), and Monteith and Szeicz (1960) conducted some of the earliest micrometeorological studies on canopy  $\text{CO}_2$  exchange.

In comparison to chambers, micrometeorological methods have several appealing features. They are *in situ*, they do not disturb the vegetation, and they sample a relatively large area. They can also be applied over forests, which are cumbersome to enshroud. Nevertheless, micrometeorological methods have drawbacks, especially the application of flux-gradient theory over forests. Besides the need to erect tall towers, eddy exchange coefficients do not conform to similarity theory in the roughness sublayer (Raupach and Legg, 1984). It is also difficult to measure vertical concentration gradients that resolve physiologically meaningful fluxes over well-mixed forests.

Advances in the development of fast-responding IRGAs, sonic anemometers, and digital software are making some criticisms of micrometeorological methods *passé*. Today, the eddy covariance method is being employed to measure canopy-scale  $\text{CO}_2$  fluxes directly and for extended periods (Wofsy *et al.*, 1993; Greco and Baldocchi, 1996). A major unresolved problem with this technology involves evaluating  $\text{CO}_2$  fluxes at night, when the atmosphere is stable and turbulent transfer is intermittent.

At this writing, only a handful of comparison studies between chambers and micrometeorological methods exist (Held *et al.*, 1990; Denmead *et al.*, 1993; Dugas *et al.*, 1997). On one hand, the imperfect transmission and diffusion of light through chamber walls can cause assimilation rates of enclosed trees to outperform trees outside a chamber (Denmead *et al.*, 1993). On the other hand, warmer soil within a chamber system can cause it to measure smaller rates of  $\text{CO}_2$  uptake compared to a micrometeorological method (Dugas *et al.*, 1997).

In practice, chambers or micrometeorological methods rarely measure canopy photosynthesis, specifically. Rather, leaf-scale measures of  $\text{CO}_2$  exchange ( $F_l$ ) include both photosynthesis and dark respiration ( $R_d$ ). Similarly, measurements of  $\text{CO}_2$  exchange ( $F_c$ ) made at the biosphere-atmosphere interface include contributions from photosynthesis, plant respiration, and heterotrophic respiration. Although gross canopy photosynthesis is difficult to attain, an estimate of net canopy photosynthesis ( $P_n$ ) can be acquired. This involves simultaneous measurements of  $\text{CO}_2$  exchange at the plant-atmosphere interface and over the soil, plus a measure of the storage of  $\text{CO}_2$  in the air between the soil and flux measurement height (Baldocchi *et al.*, 1987; Ruimy *et al.*, 1995). Groups led by Monteith (Monteith *et al.*, 1964; Biscoe *et al.*, 1975), Baumgartner (1969), Denmead (1976), and Rosenberg (Brown and Rosenberg, 1971; Verma and Rosenberg, 1976) pioneered the approach of measuring  $P_n$  by this difference approach.

## B. Models

Saeki (1960), de Wit (1965), and Duncan *et al.* (1967) are credited with some of the earliest models of canopy photosynthesis. Their pioneering efforts

stemmed from the development of algorithms to compute leaf photosynthesis and the transfer of solar radiation through plant canopies (Monsi and Saeki, 1953; de Wit, 1965).

The earliest canopy photosynthesis models assumed solar radiation was the only independent variable and that the canopy was a turbid medium. Later models considered the distinct geometric configuration of the canopy, as radiative transfer models became more sophisticated, or focused on microenvironmental variables that controlled mass and heat transfer and stomatal conductance (Cowan, 1968; Waggoner *et al.*, 1969). Over the years, canopy photosynthesis models have been adapted that consider the distinct geometry of row crops (Fukai and Loomis, 1976), orchards (Cohen and Fuchs, 1987), and conifer trees (Wang and Jarvis, 1990) and the clumping of foliage within the volume of a canopy (Gutschick, 1991; Baldocchi and Harley, 1995).

### III. Current Theoretical Concepts

#### A. Leaf Photosynthesis and Stomatal Conductance

Most terrestrial plants accomplish photosynthesis using the  $C_3$  biochemical pathway. Alternative means for performing photosynthesis involve the  $C_4$  and CAM pathways. The  $C_4$  photosynthesis pathway is more efficient than the  $C_3$  pathway because leaf anatomy and metabolism concentrate  $CO_2$  within chloroplasts, a mechanism that inhibits photorespiration (Ehleringer and Monson, 1993). Ecologically,  $C_4$  photosynthesis tends to be associated with tropical and subtropical grassland ecosystems. Spatially, the  $C_4$  pathway may account for 10–25% of global photosynthesis (Lloyd and Farquhar, 1996).

Modern physiological  $CO_2$  exchange models link calculations of photosynthesis, respiration, stomatal conductance, and transpiration to one another. At present, Farquhar's photosynthesis model (Farquhar *et al.*, 1980) is used in many models for  $C_3$  leaves (Collatz *et al.*, 1991; Nikolov *et al.*, 1995; Su *et al.*, 1996). For  $C_4$  leaves, the physiological model of Collatz *et al.* (1992) is a reliable candidate.

Farquhar's photosynthesis model is gaining wide acceptance because it is based on sound biochemical principles. This feature allows it to predict effects of light, temperature,  $CO_2$ , and rubisco amount on photosynthesis. Moreover, a huge database of model parameters is available (Wullschleger, 1993), allowing the Farquhar model to be used widely.

Farquhar *et al.* (1980) evaluate leaf  $CO_2$  assimilation  $A_1$  as the balance of photosynthesis, photorespiration, and respiration:

$$A_1 = V_c - 0.5V_o - R_d, \quad (1)$$

where  $V_c$  is the rate of carboxylation,  $V_o$  is the rate of oxygenation, and  $R_d$  is the rate of dark respiration. The coefficient, 0.5, implies that two oxy-

generations lead to one photorespiratory decarboxylation. The term,  $V_c - 0.5V_o$ , is evaluated as

$$V_c - 0.5V_o = \min[W_c, W_j](1 - \Gamma^*/C_i), \quad (2)$$

where  $W_c$  is the rate of carboxylation when ribulose biphosphate (RuBP) is saturated,  $W_j$  is the carboxylation rate when RuBP regeneration is limited by electron transport,  $\Gamma^*$  is the  $\text{CO}_2$  compensation point in the absence of dark respiration, and  $C_i$  is the intercellular  $\text{CO}_2$  concentration (Farquhar and von Caemmerer, 1982).

The value of  $W_c$  is calculated from

$$W_c = \frac{V_{c \max}(C_i - \Gamma)}{C_i + K_C(1 + [O_2]/K_O)}, \quad (3)$$

where  $V_{c \max}$  is the maximum carboxylation rate when RuBP is saturated and  $K_O$  and  $K_C$  are the Michaelis–Menten coefficients for  $\text{O}_2$  and  $\text{CO}_2$ . Here  $W_j$  is defined as

$$W_j = \frac{J(C_i - \Gamma)}{4C_i + 8\Gamma}, \quad (4)$$

where  $J$  is the potential rate of electron transport;  $J$  is evaluated as a function of incident photosynthetic photon flux density ( $I$ ), the quantum yield ( $\alpha$ ), and the maximum rate of electron transport ( $J_{\max}$ ):

$$J = \frac{\alpha I}{\sqrt{1 + \alpha^2 I^2 / J_{\max}}}. \quad (5)$$

The evaluation of some photosynthetic model parameters merits further comment. Several photosynthetic model parameters (e.g.,  $V_{c \max}$ ) depend on leaf nitrogen because rubisco is a nitrogen-rich compound (Field, 1991; Wullschleger, 1993). Furthermore, maximum rates of carboxylation ( $V_{c \max}$ ) are strongly correlated with the maximum rate of electron transport ( $J_{\max}$ ) (Wullschleger, 1993) and rates of dark respiration are constrained by rates of photosynthesis (Gifford, 1994). Model coefficients describing kinetic reactions and photosynthetic capacity have strong nonlinear dependencies on temperature (Thornley and Johnson, 1990; Harley and Tenhunen, 1991). Therefore, the application of photosynthesis models, in the field, requires an evaluation of the leaf energy balance.

The supply of  $\text{CO}_2$  to the intercellular spaces is regulated by diffusion through the leaf boundary layer and stomata. Contemporary models evaluate stomatal conductance ( $g_s$ ), for well-watered plants, as an empirical func-

tion of leaf photosynthesis, humidity, and [CO<sub>2</sub>] (Collatz *et al.*, 1991). Typically, the proportionality constant between stomatal conductance and photosynthesis is a constrained parameter. Limited soil moisture availability and limited hydraulic conductivity are among the factors causing the stomatal conductance factor to deviate below its cardinal value (Sala and Tenhunen, 1996; Falge *et al.*, 1996; Ryan and Yoder, 1997).

### B. Scaling or Integrating Carbon Dioxide Fluxes from Leaf to Canopy Dimensions

By definition, canopy photosynthesis ( $A_c$ ) is equal to the integrated sum of photosynthesis by leaves throughout the canopy volume. Three classes of models dominate the field of canopy photosynthesis (see Jarvis, 1993). Two of them treat the canopy as a layer of vegetation overlying the soil, and are denoted as “big-leaf” models. The third model class divides a canopy into multiple layers, shells, or cubes and simulates the impact of spatial gradients of microclimatic variables on the system of equations defining leaf photosynthesis.

The simplest big-leaf photosynthesis model is a scaling model. One version stems from Monteith (1972), and evaluates canopy photosynthesis as a function of the canopy’s photosynthetic efficiency ( $\epsilon$ ), the canopy’s light absorption efficiency ( $f$ ), and the amount of incident solar radiation ( $S_0$ ):

$$A_c = \epsilon f S_0. \quad (6)$$

Another version of the big-leaf scaling model considers a dependence on physiological quantities, such as rubisco kinetic parameters (Amthor *et al.* 1994; Lloyd *et al.*, 1995; Aber *et al.*, 1996). The appeal of big-leaf scaling models is their dependence on a limited number of variables that have a linear dependence on one another. They can also be evaluated using data observed from satellites to yield estimates of global net primary productivity (Ruimy *et al.*, 1994). In practice the parameters of big-leaf scaling models do not relate to measurable physiological or physical quantities, so they must be tuned (Lloyd *et al.*, 1995).

Integrating leaf photosynthetic rates with respect to leaf area index ( $L$ ) derives the second type of a big-leaf model. Examples of this approach have been used by Saeki (1960), Thornley and Johnson (1990), and Sellers *et al.* (1996). Derivation of  $A_c$  depend on the adoption of a functional form for  $A_1$  that can be integrated. A common approach is to model  $A_1$  as a function of sunlight, using the rectangular hyperbola formula, and assume that maximum photosynthesis,  $A_m$ , is constant with depth (Thornley and Johnson, 1990). This approach yields

$$A_c = \frac{A_m}{k} \ln \left[ \frac{\alpha k I_0 + A_m(1 - m)}{\alpha k I_0 \exp(-kL) + A_m(1 - m)} \right], \quad (7)$$

where  $I_0$  is the incident photon flux density,  $\alpha$  is the photosynthetic efficiency,  $m$  is the leaf transmission coefficient, and  $k$  is the radiation extinction coefficient.

When one assumes that  $A_m$  varies with depth in the canopy at the same rate that the mean light environment is attenuated, Eq. (7) simplifies to

$$A_c = A_l(I_0) \frac{(1 - \exp(-kL))}{k}. \quad (8)$$

The advantage of an integrated, big-leaf photosynthesis model is its ability to be parameterized in terms of leaf-level photosynthetic measurements (Sellers *et al.*, 1996). On the other hand, compromising assumptions must be made sometimes to allow a system of equations to be integrated analytically. For example, a 5–10% overestimate of canopy photosynthesis can occur when leaf nitrogen is not distributed optimally throughout the canopy (Hollinger, 1996; de Pury and Farquhar, 1997). Big-leaf integration models also rely on flux-gradient, K-theory, which is violated within plant canopies because countergradient transfer occurs within the volume of vegetation (Raupach, 1988).

Multilayer or shell models can deal with the geometric properties of open vegetation (Wang and Jarvis, 1990; Myneni, 1991) and are able to consider the impacts of nonlinear physiological and physical processes on canopy photosynthesis (Jarvis, 1993; Stenberg *et al.*, 1995). Multilayer models can also be coupled with micrometeorological theories, such as higher order closure (Su *et al.*, 1996) and Lagrangian (Baldocchi and Harley, 1995) models, that evaluate turbulent diffusion and accommodate countergradient transfer. The current state-of-the-art computing of canopy photosynthesis couples modules associated with (1) turbulent diffusion, (2) radiative transfer, (3)  $C_3$  (or  $C_4$ ) leaf photosynthesis, (4) stomatal conductance, (5) leaf energy balance, and (6) soil and stem respiration. A canopy micrometeorology model is needed to assess the light, temperature, humidity,  $CO_2$ , and wind environment within and above vegetation, which drive physiological functions. Examples of coupled, multilayer canopy photosynthesis models include those of Norman (1979), Norman and Polley (1989), Wang and Jarvis (1990), Gutschick (1991), Baldocchi and Harley (1995), Leuning *et al.* (1995), Su *et al.* (1996), and Williams *et al.* (1996).

Special considerations are needed to integrate photosynthesis rates of conifer needles to the canopy scale. These issues involve the effects of shoot structure, penumbra, and age stratification. Because these topics are beyond the scope of this chapter, we refer the reader to Jarvis (1993) and Stenberg *et al.* (1995).

### C. Model Validation

Although numerous models on canopy photosynthesis exist, relatively few have been tested with field data. One constraint has been the lack of field

data. Consequently, the earliest tests of canopy photosynthesis models were performed against fewer than 30 data points (Sinclair *et al.*, 1976; Norman and Polley, 1989; Baldocchi, 1993). In retrospect, these tests yielded inconclusive results because atmospheric variability caused fluxes to possess rather large sampling errors for statistical confidence tests. Nor did small data sets encompass a wide enough range of conditions to put a model through its paces. Within the past 5 years, data sets with over 200 data points have become available (Kim and Verma, 1991; Amthor *et al.*, 1994; Baldocchi and Harley, 1995), and now, with seasonal and annual scale studies underway (Goulden *et al.*, 1996; Greco and Baldocchi, 1996; Valentini *et al.*, 1996), data sets one to two orders of magnitude larger are available for model testing.

Independent tests show that big-leaf models can yield accurate (within  $\pm 20\%$ ) assessments of canopy  $\text{CO}_2$  exchange rates (Sinclair *et al.*, 1976; Amthor *et al.*, 1994; Lloyd *et al.*, 1995; Aber *et al.*, 1996; Frolking *et al.*, 1996; dePury and Farquhar, 1997). Favorable model results stem from several facts. First, many accurate big-leaf models are an artifact of tuning (e.g., Lloyd *et al.*, 1995). Second, canopy photosynthesis is relatively insensitive to gradients in  $\text{CO}_2$  concentration and turbulent mixing (Baldocchi, 1993). Third, marked improvements in the performance of big-leaf models are obtained by simply partitioning the canopy into two light classes, the sunlit and the shaded fractions (Sinclair *et al.*, 1976; dePury and Farquhar, 1997).

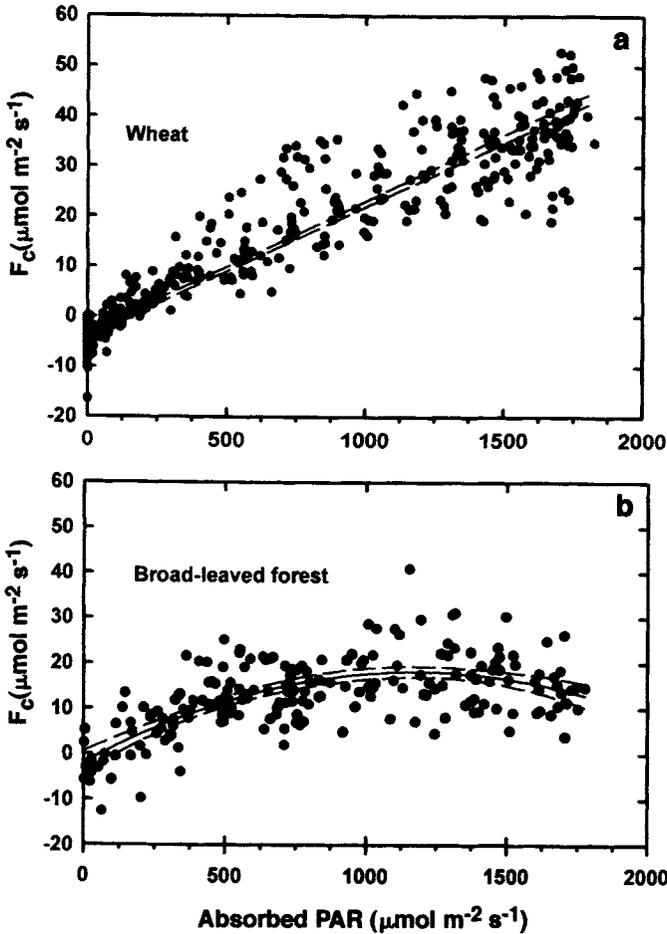
Tests of multilayer canopy photosynthesis models have yielded favorable results, too (Baldocchi and Harley, 1995; Williams *et al.*, 1996; Baldocchi and Meyers, 1998; dePury and Farquhar, 1997). They are able to mimic the mean diurnal patterns and magnitudes of  $\text{CO}_2$  exchange over a diverse range of vegetation classes (crops and broadleaved and conifer forests) during the growing season, when soil moisture is ample. To get the favorable results over forests, however, the models must consider the effect of clumped foliage on radiative transfer through forest stands and the effects of age and nutrition on reducing the ability of trees to conduct water (see Ryan and Yoder, 1997).

A present challenge is to apply canopy photosynthesis models to the task of computing seasonal patterns of canopy  $\text{CO}_2$  exchange. Provided enough information on soil moisture and phenology is available, initial studies are yielding encouraging results (Aber *et al.*, 1996; Frolking *et al.*, 1996).

## IV. Processes: Response of Canopy Photosynthesis to External Forcings

### A. Sunlight

Although leaf photosynthesis is a hyperbolic function of sunlight, many micrometeorological studies shows that canopy  $\text{CO}_2$  exchange rates ( $F_c$ ) are



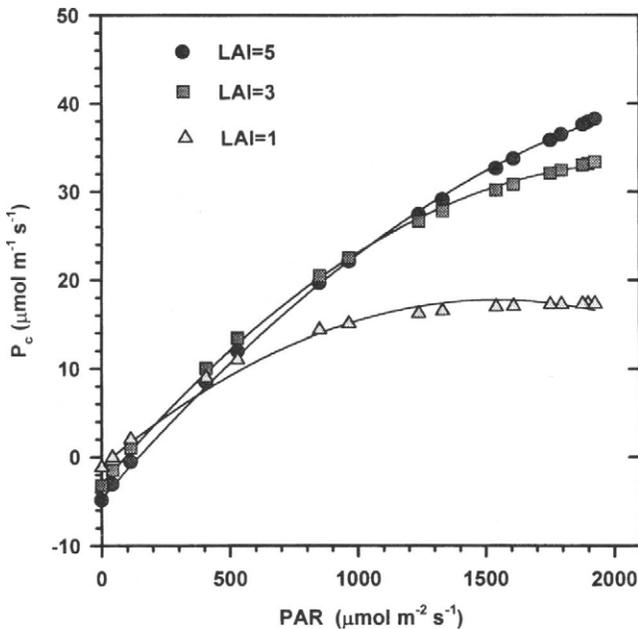
**Figure 2-1** The relationship between canopy scale measurements of CO<sub>2</sub> flux density and available photosynthetic photon flux ( $Q_a$ ). Carbon fluxes were measured with the eddy covariance method. (a) Wheat: variations in  $Q_a$  accounted for 91% of the variance in  $F_c$  (after Baldocchi, 1994). (b) Temperate broadleaved forest: variations in  $Q_a$  accounted for 42% of the variance in  $F_c$  (after Baldocchi, 1997).

a quasilinear function of absorbed sunlight (Baldocchi, 1994; Ruimy *et al.*, 1995; Rochette *et al.*, 1996). This quasilinear response tends to be associated with closed, well-watered crop canopies (Fig. 2-1a) or with data averaged over the course of a day (Leuning *et al.*, 1995). Forests and sparse vegetation, on the other hand, experience a markedly nonlinear response between  $F_c$  and absorbed sunlight (Fig. 2-1b) (Hollinger *et al.*, 1994; Fan *et al.*, 1995; Valentini *et al.*, 1996).

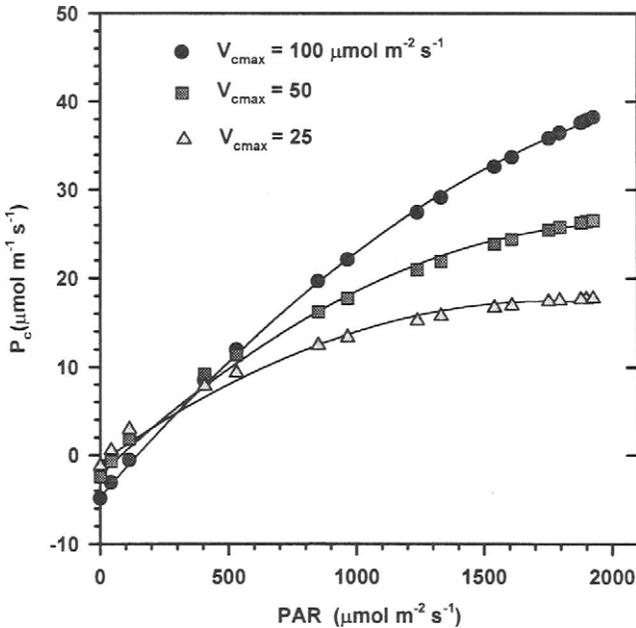
The linear and nonlinear dependencies of canopy photosynthesis on ab-

sorbed sunlight can be explained, in part, by an interaction between leaf area index ( $L$ ) and carboxylation capacity,  $V_{c \max}$ . Theoretically, canopy photosynthesis ( $P_c$ ) of vegetation with a high carboxylation capacity ( $V_{c \max} = 100 \mu\text{mol m}^{-2} \text{s}^{-1}$ ) becomes saturated at moderate photon flux densities, when a canopy is sparse ( $L = 1$ ). In contrast, the theoretical response of  $P_c$  to light is quasilinear when the canopy is closed ( $L = 5$ ) (Fig. 2-2). Model calculations also reveal that the photosynthesis–light response of a closed crop canopy ( $L = 5$ ) changes from a saturated response to a more linear one as  $V_{c \max}$  increases from 25 to  $100 \mu\text{mol m}^{-2} \text{s}^{-1}$  (Fig. 2-3).

The slope of the relationship between canopy  $\text{CO}_2$  exchange rates and available sunlight ( $Q_a$ ) is affected by whether the sky is clear or cloudy. Often,  $F_c$  can double when sky conditions change from clear to cloudy and  $Q_p$  remains the same (Hollinger *et al.*, 1994; Fan *et al.*, 1995; Rochette *et al.*, 1996). Photosynthetic rates can be lower on clear days at a given  $Q_p$  because sunlit leaves can be light saturated. They also experience a higher heat load, compared to leaves exposed to diffuse radiation, which enhances respiration of the former (Baldocchi and Harley, 1995; Rochette *et al.*, 1996).



**Figure 2-2** Model calculations on the impact of leaf area index (LAI) on canopy photosynthesis of a highly productive canopy ( $V_{c \max} = 100 \mu\text{mol m}^{-2} \text{s}^{-1}$ ). Calculations were generated by a coupled canopy photosynthesis/micrometeorology model (CANVEG) (Baldocchi and Meyers, 1998).



**Figure 2-3** Model calculations on the impact of maximum carboxylation velocity on canopy photosynthesis of a closed canopy ( $\text{LAI} = 5$ ). Calculations were generated by a coupled canopy photosynthesis/micrometeorology model (CANVEG) (Baldocchi and Meyers, 1998).

## B. Leaf Architecture

Theoretical calculations predict that photosynthetic rates of canopies with erect leaves, and high leaf area indices, are less inclined to light-saturate. Consequently, canopies with erect leaves can achieve photosynthetic rates that are 70–100% greater than those whose leaves are arrayed horizontally (de Wit, 1965; Duncan *et al.*, 1967; Monsi *et al.*, 1973; Wang *et al.*, 1992). Conversely, field data from subalpine communities show that canopy photosynthesis was greatest over tall herb and dwarf shrubs that concentrated flat leaves in the upper layers (Tappeiner and Cernusca, 1996).

The spatial pattern of plant stands and leaves also affects canopy photosynthesis. Crowns that shade 100% of the ground attain canopy photosynthetic rates that are almost double those that shade only 25% of the ground (Wang *et al.*, 1992). Clumping of leaves within a crown enhances the probability of beam penetration through canopies and increases rates of canopy photosynthesis as compared to a canopy with leaves that have a random spatial distribution and spherical angle distribution (Gutschick, 1991; Baldocchi and Harley, 1995).

### C. Wind

Some studies report a positive correlation between CO<sub>2</sub> fluxes and wind speed, whereas others indicate no significant relationship between these two variables. Lemon (1960) and Uchijima (1976), for example, conclude that photosynthesis is limited on sunny days when wind speeds are low because a lack of turbulence limits the CO<sub>2</sub> supply to the crop. Yet, this concept is suspect because those fluxes were derived from the aerodynamic method. Data from a method independent of wind speed (Brown and Rosenberg, 1971) and theoretical calculations (Baldocchi, 1993) suggest that turbulent mixing supplies adequate amounts of CO<sub>2</sub> to a crop during the day. If wind does affect canopy photosynthesis, it may stem from the impact that movement of the canopy (*honami*) has on the distribution of light through the canopy (Baldocchi *et al.*, 1981) or its leaf energy balance and respiration.

### D. Temperature

The response of canopy CO<sub>2</sub> exchange rates to temperature is parabolic. The temperature optimum of canopy CO<sub>2</sub> exchange rates of many crops and forests growing in temperate continental climates, under full sunlight, is on the order of 20–30°C (Jeffers and Shibles, 1969; Baldocchi, 1997; Price and Black, 1990). The temperature optimum, however, is very plastic and can vary with species, ecotype, site, and time of year (Stenberg *et al.*, 1995). Hollinger *et al.* (1994), for example, reported a 5°C shift in the temperature optimum of a *Nothofagus* (beech) forest between spring and summer.

In general, leaf photosynthesis decreases markedly at leaf temperatures exceeding 37°C. This diminution occurs from a decrease in membrane stability, a decrease in the relative solubility of CO<sub>2</sub> as compared to O<sub>2</sub>, a decrease in the specificity factor of rubisco, an exponential increase in dark respiration rates, and an accumulation of carbohydrates (Harley and Tenhunen, 1991). Only temperatures exceeding 40–50°C cause damage to photosynthetic machinery (Bjorkman, 1981).

The zero crossing for canopy CO<sub>2</sub> exchange occurs in the range between 30 and 35°C (Jeffers and Shibles, 1969; Baldocchi, 1997). This threshold is too low to be the sole artifact of photosynthetic kinetics and solubility (Bjorkman, 1981). Elevated soil respiration, which increases exponentially with soil temperature, normally explains the premature decrease of canopy photosynthesis with temperature.

Freezing is another temperature-related phenomenon that affects canopy photosynthesis. Several field studies on evergreen conifers (Tranquillini, 1964; Jarvis *et al.*, 1976; Stenberg *et al.*, 1995) and corn (McGuinn and King, 1990) report that freezing reduces subsequent photosynthetic capacity appreciably. Low soil temperatures can also reduce photosynthesis through effects on water balance and stomatal conductance (Stenberg *et al.*, 1995).

### E. Vapor Pressure Deficits

High vapor pressure deficits ( $D$ ) can limit  $\text{CO}_2$  uptake rates over a variety of forests (Jarvis *et al.*, 1976; Price and Black, 1990; Fan *et al.*, 1995), crops (Petigrew *et al.*, 1990), and savanna shrublands (Verhoef *et al.*, 1996). On the other hand, the influence of  $D$  and temperature on  $\text{CO}_2$  exchange of temperate broadleaved forests is difficult to distinguish because the two variables are correlated (Verma *et al.*, 1986; Hollinger *et al.*, 1994). Within aerodynamically smooth vegetation, the air remains humid near actively transpiring leaves. Consequently, the atmosphere's vapor pressure deficit (vpd) will have a limited effect on canopy conductance and photosynthesis (Grantz and Meinzer, 1991).

### F. Leaf Nitrogen

In the past decade, many investigators have reported that photosynthetic capacity varies with depth in a canopy (Field, 1991; Hollinger, 1996). Theoreticians suggest that plants either distribute leaf nitrogen optimally through the canopy (Leuning *et al.*, 1995; Sands, 1995; Hollinger, 1996; dePury and Farquhar, 1997) or they coordinate the vertical distribution of N to maintain a balance between  $W_c$  and  $W_j$  (Chen *et al.*, 1993). In either case, the photosynthetic rates of plant stands that distribute leaf nitrogen with depth exceed those of canopies that distribute N uniformly.

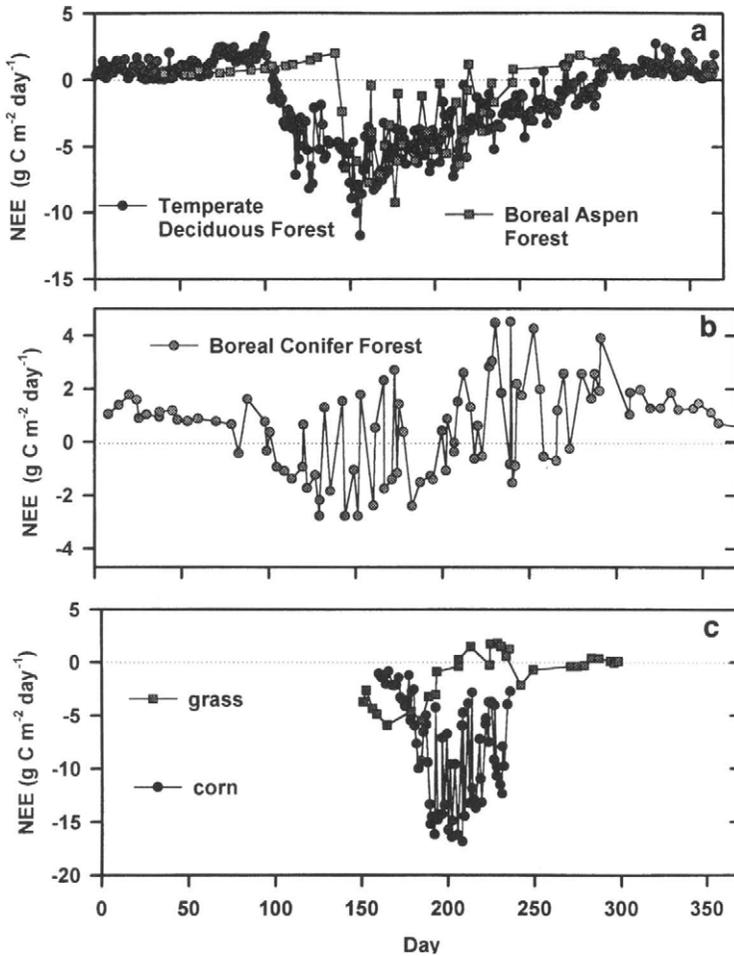
### G. Water Relations

Soil moisture deficits impact the magnitude and the diurnal course of canopy-scale  $\text{CO}_2$  exchange rates (Biscoe *et al.*, 1975; Kim and Verma, 1991; Olioso *et al.*, 1996; Verhoef *et al.*, 1996; Baldocchi, 1997). When plants are exposed to cool and humid air and adequate soil moisture, the diurnal pattern of canopy  $\text{CO}_2$  exchange rates is single peaked and the maximum occurs near midday. For plants suffering from modest soil moisture deficits, peak rates of  $\text{CO}_2$  uptake occur in the morning. Double-peaked patterns of daily photosynthesis tend to occur when the air is hot ( $T_{\text{air}} > 30^\circ\text{C}$ ) and dry (vpd  $> 3$  kPa) or when leaf temperature exceeds the optimum for photosynthesis (Olioso *et al.*, 1996; Verhoef *et al.*, 1996). These conditions cause midday stomatal closure, promote dark and photorespiration, and suppress photosynthesis (Schulze, 1986).

Typically, reductions in canopy photosynthesis during periods of soil moisture deficits are associated with stomatal closure. However, it must be remembered that drought and high-temperature stress often co-occur. Hence, enhanced respiration, during these periods, will also limit canopy  $\text{CO}_2$  uptake rates (Baldocchi, 1997).

### H. Season

Photosynthetic rates of plant systems vary over the course of the growing season as photosynthetic capacity, the availability of solar radiation and soil



**Figure 2-4** Seasonal variations in the daily sum of the net atmosphere/ecosystem  $\text{CO}_2$  exchange (NEE). Negative values denote a net loss of carbon from the atmosphere (but a gain by the biosphere). (a) A temperate (Greco and Baldocchi, 1996) and boreal, broadleaved, deciduous, forest (Black *et al.* 1996). (b) Boreal conifer forest (Grelle, 1997). (c) Temperate grass (Kim and Verma, 1991) and corn crop (Desjardins, 1985).

moisture, and air and soil temperature vary (Thomas and Hill, 1949; Tranquillini, 1964; Monteith *et al.*, 1964). Leaf form (needle, broadleaf), leaf habit (evergreen, deciduous), and latitude also affect the seasonal pattern of  $\text{CO}_2$  exchange. Figure 2-4a shows that broadleaved forest canopies lose carbon when the canopy is dormant. During springtime leaf expansion the direction and magnitude of carbon fluxes switch rapidly as forests change from losing  $1\text{--}3 \text{ g C m}^{-2} \text{ d}^{-1}$  to gaining  $5\text{--}10 \text{ g C m}^{-2} \text{ d}^{-1}$ . A marked in-

fluence in latitude is noted by the observation that the onset of carbon uptake by a boreal aspen forest lags behind a southerly temperate forest by a month. Because of this latitudinal difference, temperate broadleaved forests have the potential to gain 100–200 g C m<sup>-2</sup> more per year compared to boreal forests (Greco and Baldocchi, 1996; Black *et al.*, 1996) and more northern temperate forests (Goulden *et al.*, 1996). Year-to-year variations in the length of the growing season can also affect the net carbon uptake of broadleaved and conifer forests by this magnitude (Goulden *et al.*, 1996; Frohling *et al.*, 1996).

Although conifers also lose carbon during the winter, they can achieve carbon gain in the spring before deciduous forests are able to do so (Fig. 2-4b). On the other hand, net carbon uptake by conifer forests is very sensitive to soil moisture and temperature. Adverse summer heat and dry spells or days with low light levels can cause them to lose carbon during the heart of the growing season (Baldocchi *et al.*, 1997).

The onset of photosynthesis in temperate grasslands and crops is much delayed behind the dates experienced in forests, because annual crops and grasses must germinate from seeds. Native grasslands are more apt to experience soil moisture deficits than are crops (which are either irrigated or grow in more humid regions). Hence, grasslands experience many days with a net transfer of carbon to the atmosphere. Among other observations of agricultural crops, several investigators have observed that canopy photosynthesis by cereal decreases after anthesis (Thomas and Hill, 1949; Biscoe *et al.*, 1975; Baldocchi, 1994) because respiration is stimulated.

## V. Canopy Photosynthesis in the Future

Several key global and regional environmental change factors have the potential to alter photosynthesis significantly by terrestrial ecosystems. Perhaps the most frequently mentioned factor is increasing atmospheric CO<sub>2</sub> concentration. In C<sub>3</sub> leaves, future elevated CO<sub>2</sub> will stimulate photosynthesis and at the same time inhibit photorespiration. The overall effect is likely to be an increase in CO<sub>2</sub> uptake by canopies (Amthor, 1995). In addition, water-use efficiency, light-use efficiency, and leaf N-use efficiency will increase with an increase in ambient CO<sub>2</sub>. In the long run, photosynthesis may acclimate to long-term elevated CO<sub>2</sub>, reducing the positive response to increasing CO<sub>2</sub> (e.g., Amthor, 1995; Lloyd and Farquhar, 1996). We expect relatively small effects of increasing CO<sub>2</sub> on C<sub>4</sub> canopy photosynthesis, although the increase in water-use efficiency resulting from reduced stomatal conductance may enhance canopy development and indirectly increase canopy photosynthesis.

A second important environmental change is the land-surface warming

expected to accompany further increases in atmospheric CO<sub>2</sub>. In the short term, warming can alter several of the component processes of leaf and canopy photosynthesis. We expect, however, that various acclimation and adaptation processes might compensate moderate warming, over many years.

Increasing atmospheric N deposition is a third environmental change that might affect future photosynthesis. In ecosystems that are limited by N availability, increasing N deposition has the potential to enhance N uptake and therefore photosynthesis (through increased leaf N levels). On the other hand, increased N deposition, associated with increased acidity, might be stressful for plants, resulting in reduced photosynthesis and growth.

Changes in tropospheric pollutant levels may also affect future photosynthesis in several ecosystems. For example, an increase in levels of the regional air pollutant O<sub>3</sub> might damage leaves and reduce canopy photosynthesis.

## VI. Research Directions

Many research questions associated with time and space remain unanswered. With regard to time, we do not know how dynamic effects associated with photosynthesis and sunfleck integrate to the canopy scale. At longer time scales, rates of leaf photosynthesis in old trees are lower than in younger trees (Ryan and Yoder, 1997). How this effect sums to the canopy scale and over the course of a growing season remains an unknown.

As we move up in spatial scale and apply canopy photosynthesis to exercises on landscape and global ecology, we will need to confirm our attempts to extrapolate canopy-level concepts to the scale of landscape, regions, and continents. Estimates of canopy photosynthesis on hilly terrain remain untested, too. Networks of long-term eddy covariance measurements are being implemented through the EUROFLUX and AmeriFlux programs to address some of these problems.

With regard to measuring canopy photosynthesis and respiration, there are bias errors associated with the episodic and intermittent nature of nighttime eddy fluxes between the biosphere and atmosphere. More studies are needed on how to measure and evaluate these fluxes.

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