

How the environment, canopy structure and canopy physiological functioning influence carbon, water and energy fluxes of a temperate broad-leaved deciduous forest—an assessment with the biophysical model CANOAK

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Summary This paper focuses on how canopy structure, its physiological functioning and the environment interact to control and drive the exchange of carbon dioxide (CO₂) and water vapor between a temperate forest stand and the atmosphere. First, we present an overview of how temporal and spatial variations in canopy structure (e.g., leaf area index, species, leaf inclination angles, leaf clumping) and physiological functioning (e.g., maximal stomatal conductance, photosynthetic capacity) modulate CO₂ and water vapor fluxes. Then, with the biophysical model CANOAK, we quantify the effects of leaf dimension and thickness, vertical variations in leaf area and photosynthetic capacity, leaf clumping, leaf inclination angles, photosynthetic capacity, stomatal conductance and weather on the annual sums of CO₂, water vapor and sensible heat exchange. Finally, we discuss how much detail is needed in a model to predict fluxes of CO₂ and water vapor with acceptable fidelity.

Keywords: *biocomplexity, biosphere–atmosphere interactions, canopy photosynthesis, ecophysiology, evaporation.*

Introduction

Temperate hardwood forests are structurally complex, comprising trees of multiple stature, age and species (Whittaker 1975, Smith and Huston 1989, Parker 1995). Even in pure stands of even-aged trees there is much variation in structure. For example, sunlit leaves in the upper canopy tend to be relatively thick, oriented close to the vertical and arranged in clumps (Hutchison et al. 1986, Kruijt 1989, Ellsworth and Reich 1993, Parker 1995), whereas understory leaves are relatively thin and tend to be oriented horizontally.

The structural and functional aspects of a forest are not static. During winter, hardwood forests are leafless and dor-

mant, but respiring. In spring, rapid changes in biological activity and structure occur as leaves expand, nodes elongate, roots grow and reproductive organs develop (Larcher 1975, Hutchison and Matt 1977, Parker 1995). Leaf photosynthetic capacity also changes rapidly during this period (Wilson et al. 2000, 2001a). During the summer, gradual changes in canopy structure, maximum stomatal conductance and physiological capacity occur as leaves age, experience water deficits, acclimate, are eaten or drop as a result of prolonged drought (Falge et al. 1996, Niinemets et al. 1999, Wilson et al. 2000, 2001). With the approach of autumn, leaves export nitrogen to stems, reduce photosynthetic capacity, senesce and abscise (Larcher 1975, Hutchison and Matt 1977, Wilson et al. 2000).

Spatial and temporal variations in canopy structure and function affect the canopy microclimate and, consequently, influence carbon dioxide (CO₂) and water vapor exchange in numerous ways. For example, interactions between structural and functional properties of forests alter turbulence within and above the canopy, photon interception and scattering, heat load on leaves and soil, and physiological resistances to water and CO₂ transfer (Meyers and Paw U 1986, Baldocchi and Meyers 1998, Albertson et al. 2001).

The objective of this paper is to use the biophysical model CANOAK to illustrate and quantify how variations in the environment, canopy structure and canopy physiological functioning affect CO₂ and water vapor exchange of a temperate broad-leaved forest on an annual time scale. The work builds on earlier analyses that focused on how short-term fluxes of carbon dioxide and water respond to environmental drivers when canopy structural and functional features are altered (e.g., de Wit 1965, Duncan et al. 1967, Norman 1979, 1993, Meyers and Paw U 1986, Long 1991, Baldocchi and Harley 1995, Leuning et al. 1995, Baldocchi and Meyers 1998, Raupach 1998, Williams et al. 1998, Wu et al. 2000, Albertson et al. 2001).

Concepts and principles

To quantify fluxes of CO₂, water and energy between a forest and the atmosphere, several subjects must be considered. First, the biophysical and ecophysiological processes that significantly influence trace gas exchange must be identified. Second, these processes must be represented mathematically and integrated throughout the domain of the canopy on the basis of local environmental drivers. The second task depends on how we define, geometrically, the forest canopy and the distribution of leaves. In this section we discuss the biophysical and mathematical principles used in contemporary biophysical models such as CANOAK.

Biophysical principles

The exchange of CO₂ and water vapor between a forest and the atmosphere is the consequence of a suite of biological, physical and chemical processes acting in concert. Key features in contemporary soil–vegetation–atmosphere–transfer (SVAT) models include subroutines that evaluate: (1) conservation of mass and energy; (2) the radiation balance of leaves and the soil; (3) turbulent transfer of heat, moisture and momentum; (4) radiative transfer through the foliage; and (5) coupling of stomatal conductance to carbon and water fluxes, nutrient content of leaves and soil water in the root zone (Norman 1979, Meyers and Paw U 1986, Leuning et al. 1995, Sellers et al. 1997, Baldocchi and Meyers 1998, Albertson et al. 2001, Williams et al. 2001, Wohlfahrt et al. 2001).

The conservation of mass and energy forms the foundation of any biophysical model that predicts CO₂, water and energy exchange of a vegetated canopy. A simplified version of the conservation of mass—which is valid when a forest is horizontally homogeneous and the environmental conditions are constant—states that the vertical flux divergence ($\partial F/\partial z$) equals the vegetative source–sink strength (S). For CO₂, the daytime sink strength in a canopy layer is determined by the balance between the biochemically and physiologically limited demand of leaves and the diffusion-limited supply from the atmosphere and through the leaf boundary layer (Farquhar et al. 1980). The source–sink strength of vegetation is proportional to leaf area density ($a(z)$) and the differences between the CO₂ concentration in the atmosphere (C_a) adjacent to leaves and that inside the leaves (C_i) (Meyers and Paw U 1986). In addition, S is inversely proportional to the sum of the aerodynamic (r_a) and stomatal resistances (r_s):

$$\frac{\partial F}{\partial z} = S(z) = -a(z) \frac{(C_a(z) - C_i)}{r_a + r_s} \quad (1)$$

Because photosynthesis, transpiration, stomatal conductance and respiration depend on temperature and light, it is necessary to assess the leaf energy balance in tandem with the assessment of the conservation of mass. The energy balance of a leaf is defined by the shortwave and longwave radiation it absorbs (Campbell 1981). This energy is used to evaporate water, generate sensible heat and assimilate carbon dioxide.

Mathematically, the energy balance on one side of a leaf (R_n) is expressed as:

$$\begin{aligned} R_n &= (1 - \rho - \tau)R^\downarrow + (1 - \epsilon)L^\downarrow - \epsilon\sigma T_l^4 \\ &= H + \lambda E = \rho_a C_p \frac{(T_a - T_l)}{r_{a,h}} + \frac{\rho_a m_v (e_s(T_l) - e_a)}{P m_a (r_{a,v} + r_s)} \end{aligned} \quad (2)$$

i.e., the energy balance of a leaf is a function of its reflectance (ρ), transmittance (τ) and infrared emissivity (ϵ) and the flux densities of incoming global solar (R^\downarrow) and terrestrial (L^\downarrow) radiation. The Stefan-Boltzmann constant is represented by σ . The radiation balance is partitioned into sensible (H) and latent heat (λE) flux densities. In turn, these energy flux densities are evaluated using Ohm's Law resistance analog equations, which are dependent on air density (ρ_a), the specific heat of dry air (C_p), air temperature (T_a), leaf temperature (T_l), boundary layer resistances for heat and vapor transfer ($r_{a,h}$ and $r_{a,v}$), stomatal resistance (r_s), pressure (P), the molecular masses of water vapor (m_v) and air (m_a), the saturation vapor pressure at leaf temperature ($e_s(T_l)$) and atmospheric vapor pressure (e_a). At the stand level, energy exchange with the soil and boles must also be considered.

With Equations 1 and 2 providing the biophysical framework, we can associate the physical and functional attributes of single leaves, individual plants and plant stands with factors that affect CO₂, water vapor and energy exchange. Such information is tabulated in Table 1. In principle, the maximum rates of photosynthesis and transpiration that a leaf can achieve are constrained by leaf morphology, photosynthetic capacity, root–shoot allocation and resource acquisition (e.g., nutrients and soil water) (Field 1991, Korner 1994, Schulze 1994, Schulze et al. 1994, Reich et al. 1997). At the stand scale, structural factors affecting light absorption and the aerodynamics of the canopy govern maximum rates of carbon dioxide, water vapor and energy exchange.

Mathematical principles

The challenge in building a biophysical model is to represent the information produced in Table 1 adequately and on appropriate time and space scales. In this section we discuss ways of accomplishing this task.

Integrating nonlinear functions

Many biophysical processes (photosynthesis, respiration, stomatal conductance, infrared energy emission, saturation vapor pressure, transpiration) are nonlinear functions of independent environmental variables, such as R^\downarrow , wind velocity (u), air temperature (T), humidity deficits (D) and CO₂ concentration, or themselves. Proper assessment of nonlinear biophysical functions requires translation of the state external driving variables to the point of action—a task performed with the coupling of a micrometeorology model. For example, it is incorrect to compute photosynthetic rates of a leaf buried deep in the canopy based on the flux density of light energy incident at the top of the canopy.

Table 1. Structural and functional attributes of leaves, plants and plant stands and their impact on carbon, water and energy fluxes. Impacted factors include: aerodynamic conductance, G_a ; surface conductance, G_s ; light transmission through a leaf or canopy, $P(0)$; absorptance, α ; and leaf internal CO₂ concentration, C_i .

Characteristic	Structural or functional attribute	Factors
<i>Leaves</i>		
Photosynthetic pathway	C ₃ , C ₄ , CAM, maximal stomatal conductance	C_i , G_s
Leaf size/shape	Needle/planar/shoot; projected/surface area, penumbra/umbra	G_a , $P(0)$
Leaf inclination angle distribution	Spherical, erectophile, planophile	$P(0)$
Leaf azimuthal angle distribution	Symmetric/asymmetric	$P(0)$
Exposure	Sunlit/shaded; acclimation	C_i , G_s , α
Optical properties	Leaf and soil reflectance, transmittance, emittance	α
Leaf thickness	Photosynthetic capacity, supply of CO ₂ to chloroplast, leaf optical properties, stomatal conductance capacity	C_i , G_s , α
Stomatal distribution	Amphistomatous/hypostomatous	G_s
<i>Plants/trees</i>		
Crown volume shape	Cone, ellipse, cylinder	$P(0)$, G_a
Plant species	Monoculture, mixed stand, functional type	$P(0)$, G_a , G_s , C_i
Spatial distribution of leaves	Random, clumped, regular	$P(0)$
Plant habit	Evergreen/deciduous; woody/herbaceous; annual/perennial	G_a , G_s , α
Plant height	Roughness, darkness, water transport	G_a , G_s , α
Rooting depth	Accessible water and nutrients, plant water relations	G_s
Leaf area/sapwood ratio	Hydraulic conductivity	G_s , C_i
<i>Forest stand</i>		
Leaf area index (LAI)	Openness, degree of canopy closure	$P(0)$, G_s , G_a
Vertical distribution of LAI	Uniform, skewed, multi-storied	G_a , $P(0)$
Seasonal variation of LAI	Evergreen/deciduous; winter or drought deciduous	G_a , G_s
Age structure	Disturbed/undisturbed; plantation; agriculture; regrowth	G_a , G_s , $P(0)$
Stem density	Spatial distribution of plants	G_a , α
Woody biomass index	Amount of woody biomass	G_a , $P(0)$
Topography	Exposure, water balance, insolation	G_a , G_s
Site history	Fires, logging, plowing, regrowth	G_a , G_s , C_i

There are two complications in assessing nonlinear functions. First, many of the environmental variables vary throughout the canopy, and second, they possess probability density functions ($p(x)$) that are often non-Gaussian (Rastetter et al. 1992, Norman 1993, Jarvis 1995, Rastetter 1996). This combination of events requires that we evaluate the expected value ($E[f(x)]$) of the nonlinear functions of biophysical processes:

$$E[f(x)] = \int_{-\infty}^{\infty} f(x)p(x)dx. \quad (3)$$

Note that evaluating these nonlinear functions on the basis of the mean value of the independent variable $E[f(x)] \approx f(\bar{x})$, instead, produces a significant bias error, because of the phenomenon known as Jensen's Inequality (Rastetter et al. 1992, Norman 1993, Ruel and Ayers 1999).

The dual source technique is a discrete but powerful means of assessing Equation 3. It involves computing the fractions of sunlit and shaded leaves and evaluating the nonlinear biophysical functions according to the environment of these two leaf classes (Sinclair et al. 1976, Norman 1979, Norman et al. 1993, DePury and Farquhar 1997).

To assess nonlinear biophysical functions over a growing season or a year, it is necessary to evaluate how model scaling and curvature parameters vary with time and space (Wilson et al. 2001), species (Wullschleger 1993, Wohlfahrt et al. 2000) and plant functional type (Wullschleger 1993, Körner 1994, Schulze et al. 1994).

Finally, there is a group of biophysical processes that are quasi-discontinuous. For example, the transitions between free and forced convection, laminar and turbulent flow and Rubisco limit and saturated rates of photosynthesis are rather abrupt (Farquhar et al. 1980, Collatz et al. 1991, Schuepp 1993). Mathematical equations describing these processes can only be solved numerically, rather than analytically.

Geometric abstraction

The structural and functional complexity of leaves and forest stands varies with climate, soil, stand age, species composition and functional type (Whittaker 1975, Aber and Melillo 1991, Parker 1995). In this section we discuss how best to represent the geometric attributes of a leaf or canopy in a mathematical model to compute flux densities of CO₂ and water vapor with acceptable fidelity.

Leaves

The cross section of an angiosperm leaf consists of the external cuticle, an upper and lower epidermis, palisade mesophyll, spongy mesophyll, stomata and intercellular space. Leaves are usually between 50 and 200 μm thick (Parkhurst 1986, Vogelmann et al. 1989). In general, sun leaves in broad-leaved forests are thicker than shade leaves, have greater specific mass and possess more stomata per unit area (Terashima and Saeki 1985, Ellsworth and Reich 1993, Reich et al. 1997, Terashima et al. 2001). Information on leaf thickness provides an excellent surrogate for estimating a number of model parameters. In principle, compared with thin leaves, thicker leaves have higher leaf nitrogen content, photosynthetic capacity, respiration rates and stomatal conductances (Evans 1989, Field 1991, Schulze et al. 1994, Reich et al. 1997, Wilson et al. 2000).

With respect to water vapor and CO_2 diffusion through the stomata, it is necessary to consider that leaves may be hypostomatous (having stomata on one side) or amphistomatous (having stomata on both sides of the leaf). Amphistomatous leaves tend to be thicker, have higher photosynthetic capacity and occur in habitats with full sun and adequate soil water (Terashima et al. 2001). With respect to mass and energy exchange, it is necessary to consider that water vapor originates from the inner side of the guard cells and from the subsidiary cells. Carbon dioxide diffuses across the intercellular air spaces of the mesophyll.

Mathematically, one can treat a leaf in three-dimensional geometric detail (Parkhurst 1986, Farquhar 1989, Roth-Nebelsick 2001), as a one-dimensional system (Terashima et al. 2001) or as a holistic, integrated entity (Gaastra 1959, Norman 1979). If one treats the leaf as an integrated unit, it is assumed that diffusion through the stomata on the top and bottom sides of amphistomatous leaves occurs in parallel.

The rate of photosynthesis is a function of the chloroplast CO_2 concentration (Farquhar et al. 1980, Farquhar 1989). In practice, parameters required for the Farquhar photosynthesis model are obtained from leaf gas exchange measurements, but are expressed in terms of the intercellular CO_2 concentration (C_i). Intercellular CO_2 concentration is a function of both leaf photosynthesis (A) and leaf conductance (g) (Farquhar 1989):

$$C_i = C_a - \frac{A}{g} \quad (4)$$

By treating a leaf as a single entity, one ignores spatial gradients in CO_2 diffusion (Parkhurst et al. 1988, Terashima et al. 2001), photosynthetic capacity (Terashima and Saeki 1985) and radiation (Terashima and Saeki 1985, Vogelmann et al. 1989) that occur within the mesophyll and across the leaf (Roth-Nebelsick 2001). Generally, it is assumed either that the CO_2 concentrations in the substomatal cavity, in the intercellular spaces and in the chloroplast stroma are equal, or that boundary layer and mesophyll conductances are infinite compared with stomatal conductance.

Patchy stomatal responses complicate estimation of C_i . Values of C_i calculated from gas exchange can be erroneous,

particularly when leaves experience low leaf water potentials and stomatal closure occurs in patches (Laisk 1983, Mott and Buckley 2000). Exact estimates of bulk mean C_i values thus requires weighting C_i values of the patches by their respective stomatal conductances (Farquhar 1989).

The forest stand

At the canopy scale, biophysical models vary in the way they represent canopy structure and function (Raupach and Finnigan 1988, Norman 1993, Sellers et al. 1997). Plant canopies can be abstracted as a "big-leaf" (Monteith 1965, Sellers et al. 1997), but this assumption is an extreme simplification of how forests exist and function (Pyles et al. 2000). Increased fidelity is achieved by means of dual source abstraction, a concept that accounts for the different environments of sunlit and shaded leaves (Sinclair et al. 1976, Norman 1993, DePury and Farquhar 1997). For open-forest stands, a two-layer model, with distinct soil and plant compartments, is a reasonable representation (Norman et al. 1995, Van den Hurk and McNaughton 1995). For multi-storied canopies, one-dimensional, multi-layer models incorporate sufficient pertinent detail on canopy structure (Norman 1979, Meyers and Paw U 1986, Leuning et al. 1995, Baldocchi and Meyers 1998, Pyles et al. 2000, Wu et al. 2000, Williams et al. 2001, Wohlfahrt et al. 2001). Multi-layer models tend to produce more accurate simulations of mass and energy exchange than "big-leaf" models (Sinclair et al. 1976, Norman 1980, Pyles et al. 2000).

Detailed multi-layer models can guide development of simpler and mechanistically based "big-leaf" and dual-source algorithms. For example, Leuning et al. (1995) used a detailed biophysical model to deduce that the canopy-scale light response curve for photosynthesis is nonlinear on an hour-by-hour basis, but linear on a daily-integrated time scale. Baldocchi and Meyers (1998) have used CANOAK to develop scaling relations for normalized evaporation that are a function of leaf area index (LAI) and photosynthetic capacity.

Open canopies are better represented using three-dimensional models that consider individual trees (Wang and Jarvis 1990, Sinoquet et al. 2001), but three-dimensional models are extremely difficult to parameterize and implement. Open canopies require accurate representations of mass and energy exchange at the soil surface, where substantial energy exchange occurs (Baldocchi et al. 2000).

Features such as honami (waving plants in wind), leaf flutter and horizontal scale variations in canopy and structure are beyond the scope of this paper, but can also alter mass and energy exchange (Raupach and Finnigan 1997, Albertson et al. 2001, Ikeda et al. 2001).

Model overview

Because the biophysical model CANOAK is used here to quantify the impacts of varying canopy structure and physiological function on canopy-scale CO_2 and water vapor exchange, a brief overview of the model is presented. The CANOAK model consists of coupled micrometeorological and physiological modules. The micrometeorological model com-

putes leaf and soil energy exchange, turbulent diffusion, scalar concentration profiles and radiative transfer through the canopy at hourly time steps. Environmental variables, computed with the micrometeorological module, in turn drive the physiological models that compute leaf photosynthesis, stomatal conductance, transpiration, and leaf, bole and soil + root respiration. The model is driven by a minimal number of environmental variables. These include incident photosynthetic photon flux density (Q_p), air and soil temperature, wind speed, relative humidity and CO₂ concentration. The subcomponents and the entire model have been tested and validated with eddy covariance measurements during the summer growing season (Baldocchi and Harley 1995, Baldocchi and Meyers 1998) and over the course of several years (Baldocchi and Wilson 2001, Wilson and Baldocchi 2001).

A summary of the results from a test of the model's ability to compute net ecosystem-atmosphere CO₂ exchange (NEE), latent heat (λE) and sensible heat (H) flux densities is presented in Table 2. Intercepts were close to zero and regression slopes for CO₂ and water vapor exchange were within 15% of the one-to-one line. The model calculations of NEE, λE and H reproduce temporal variations of field measurements on diurnal, weekly, seasonal and annual time scales with generally high fidelity ($r^2 < 0.80$) (Baldocchi and Wilson 2001).

The model computations are for a 60-year-old, temperate broad-leaved forest growing near Oak Ridge, TN. The forest consists of a mix of two oak species (*Quercus alba* L. and *Quercus prinus* L.), maple (*Acer rubrum* L.) and tulip poplar (*Liriodendron tulipifera* L.). Model parameters and canopy properties for baseline computations are listed in Table 3. The meteorological drivers come from hourly data measured in 1997, a year with ample soil water. Hence, the discussion that follows does not consider the effects of soil water deficits on CO₂ and water vapor exchange.

Reference values of LAI and photosynthetic capacity were adjusted during the growing season, based on field measurements (Baldocchi and Wilson 2001, Wilson et al. 2001). Photosynthetic model parameters (V_{cmax} , J_{max} , R_d) were adjusted for temperature using kinetic-based Arrhenius functions (Farquhar et al. 1980).

Table 2. Regression coefficients of the comparison between measured and computed flux densities of carbon dioxide (NEE), latent (λE) and sensible heat (H) (adapted from Baldocchi and Wilson 2001). Computations and measurements are for 1997. Data were binned by hour for 2-week periods and averaged to reduce sampling error, producing a database with 624 degrees of freedom.

	NEE ($\mu\text{mol m}^{-2} \text{s}^{-1}$)	λE (W m^{-2})	H (W m^{-2})
Intercept	0.908	4.96	-0.71
Slope	1.085	1.14	1.24
r^2	0.815	0.83	0.67
Annual sum	***	1500 MJ m^{-2} year^{-1}	1080 MJ m^{-2} year^{-1}

Table 3. Parameter values used by the CANOAK model in the simulations of canopy CO₂, water vapor and energy exchange. Abbreviations: V_{cmax} is the maximum carboxylation velocity when ribulose-1,5-bisphosphate is limited; J_{max} is the maximum rate of electron transport; and R_d is dark respiration.

Parameter	Value	Units
V_{cmax} (311 °K)	73	$\mu\text{mol m}^{-2} \text{s}^{-1}$
J_{max} (311 °K)	$2.32V_{\text{cmax}}$ (311 °K)	$\mu\text{mol m}^{-2} \text{s}^{-1}$
R_d	$0.0046V_{\text{cmax}}$	$\mu\text{mol m}^{-2} \text{s}^{-1}$
Maximum LAI	6	–
Canopy height	26	m
Leaf dimension width	0.10	m
Stomatal conductance factor, k	9.5	–
Quantum yield, α	0.22	mol electron (mol photons) ⁻¹
Clumping factor, Ω	0.84	–
Latitude	35.9	degrees
Longitude	84.3	degrees

Results and discussion

In this section we use the CANOAK model to quantify the impacts of varying structural and functional attributes of a hardwood, broad-leaved forest on CO₂ and water vapor fluxes, at leaf and canopy scales.

Leaf scale

Leaf size in a temperate forest can vary by a factor of ten. Changes in leaf size and shape alter the boundary layer conductance for water and CO₂ diffusion (g_x), which is quantitatively a function of molecular diffusivity (D_x), a characteristic length scale (l) and the dimensionless Sherwood number (Sh), which is a function of wind speed (u):

$$g_x = \frac{1}{r_x} = \frac{D_x \text{Sh}}{l} \approx \left(\frac{u}{l}\right)^{1/2} \quad (5)$$

The diffusive boundary layer is much thinner over small leaves and needles than around big leaves or complex shoots (Schuepp 1993). Smaller leaves, therefore, experience larger boundary layer conductances. Hence, small leaves and needles are more efficient at transferring heat, moisture and CO₂ between their surface and the atmosphere, and are better coupled to their local environment than big leaves (Jarvis and McNaughton 1986, Schuepp 1993, Roth-Nebelsick 2001).

Reducing the mean leaf dimension (length scale) of an oak leaf from 0.10 m (the size of *Quercus alba*) to 0.01 m (the size of *Q. douglasii*) increases the modeled estimate of net annual

CO₂ exchange by less than 2% (Table 4). With respect to latent and sensible heat exchange, evaporation decreases by 2%, whereas sensible heat increases by about 6%. Small differences in the sums of CO₂, water vapor and heat exchange reflect, in part, the impact of the prolonged dormant period when the canopy is leafless. If we examine summer days in detail, we find that there are instances when a modeled canopy with small leaves should take up 0.25 g C m⁻² day⁻¹ more than the reference case (a 10% increase).

There are several limitations associated with the computations in Table 4. We have ignored gradients of temperature across leaves (Roth-Nebelsick 2001), dynamic responses of photosynthesis and stomatal conductance to sunflecks (Kirschbaum et al. 1988, Pearcy 1990), dynamic response of the leaf energy balance to wind (Su et al. 1996) and the impact of leaf size on penumbra and light distribution through the canopy (Denholm 1981). Models with greater detail will be needed to evaluate the impact of these features.

In many temperate deciduous forests, leaf mass per unit area, maximum carboxylation capacity (V_{cmax}) and nitrogen per unit area are closely correlated. All these leaf properties vary with height in a similar manner (Ellsworth and Reich 1993, Kull and Niinemets 1998, Wilson et al. 2000a). In some cases, their variation within a canopy can be as great as their variability across a range of species or functional types (see Schulze et al. 1994, Reich et al. 1997). We quantified the influence of leaf thickness on net CO₂ exchange by examining how sensitive these fluxes are to leaf photosynthetic capacity. Reducing V_{cmax} from the reference value of 73 $\mu\text{mol m}^{-2} \text{s}^{-1}$ to 50 $\mu\text{mol m}^{-2} \text{s}^{-1}$ produced a decrease in NEE of 1–2 g C m⁻² day⁻¹ during the growing season, which occurred as a result of the subsequent reduction of leaf photosynthesis and stomatal conductance. On an annual basis, a 21% reduction in NEE is predicted (Table 5).

Calculations presented in Table 5 did not consider the impact of leaf nutrition on litter composition and soil respiration, which are functions of the ratio between nitrogen and lignin content (Melillo et al. 1982). A decrease in the ratio causes litter decomposition to slow. Had this effect been incorporated into the model calculations, it would have offset the reduction in canopy photosynthesis that results from lower V_{cmax} and countered the inferred reduction in NEE.

With respect to energy exchange, a concurrent reduction in stomatal conductance occurs with a reduction in V_{cmax} (Schulze et al. 1994, Wilson et al. 2000a) that alters the partitioning of net radiation (Table 5). On an annual basis, latent

Table 4. Annual sums of net CO₂ exchange (NEE) and latent (λE) and sensible heat (H) exchange as a function of leaf dimension.

Flux	Leaf dimension (m)		
	0.1	0.01	0.001
NEE (g C m ⁻² year ⁻¹)	-577	-588	-586
λE (MJ m ⁻² year ⁻¹)	1690	1652	1615
H (MJ m ⁻² year ⁻¹)	1096	1164	1202

Table 5. Annual sums of net CO₂ exchange (NEE) and latent (λE) and sensible heat (H) exchange as a function of photosynthetic capacity.

Flux	V_{cmax} ($\mu\text{mol m}^{-2} \text{s}^{-1}$)		% Difference
	73	50	
NEE (g C m ⁻² year ⁻¹)	-577	-454	-21.3
λE (MJ m ⁻² year ⁻¹)	1690	1584	-6.3
H (MJ m ⁻² year ⁻¹)	1096	1199	9.3

heat exchange is reduced 6% and sensible heat exchange is increased by 9%.

Knowledge of C_i is required to simulate photosynthesis accurately (Farquhar et al. 1989, Katul et al. 2000). Evolutionary pressures on leaf thickness and morphology have produced a conservative ratio of internal to external CO₂ concentration near 0.7 for C₃ leaves and 0.4 for C₄ leaves (Wong et al. 1979). On the other hand, with the CANOAK model we produce theoretical evidence that spatial variations in C_i/C_a occur as a result of gradients in light and photosynthetic capacity. Figure 1 shows that values of C_i/C_a for sunlit leaves range between 0.7 and 0.8 and the lowest values occur in the canopy crown. Values of C_i/C_a for shade leaves decrease from 0.75 to 0.95 from the top of the canopy to the stem space. In the lower reaches of the canopy, C_i/C_a is relatively constant, near 0.96. These computed values are consistent with values inferred from independent carbon isotope measurements near our field site (Garten and Taylor 1992) and other published data (Kull and Niinemets 1998). The marked vertical variation in C_i/C_a and its impact on computing leaf photosynthesis is one reason to prefer a multi-layer or dual-source model as opposed to a "big-leaf" model for computing canopy photosynthesis.

Factors and feedbacks ignored in the calculations involving variations in leaf size include how changes in leaf thickness alter the diffusion of CO₂ and the absorption and transmission of

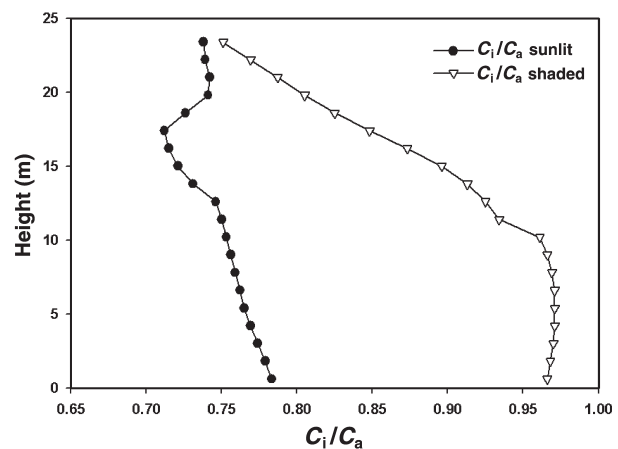


Figure 1. Computed vertical profiles of the ratio of the intercellular and ambient CO₂ concentrations (C_i/C_a) on the sunlit and shaded leaf fractions for a midday period on Day 180. These vertical profiles in C_i/C_a reflect the impact of vertical variations in sunlight, temperature, CO₂, humidity and leaf nitrogen.

photons through the mesophyll (e.g., Terashima et al. 2001). However, we may not need a detailed one- or three-dimensional leaf diffusion model for calculating photosynthesis, because the computed range of C_i/C_a values is in general agreement with data inferred from carbon isotope measurements (Baldocchi and Bowling 2002).

Plant and stand scale

The amount of leaves and their spatial distribution are among the structural features identified in Table 1 that affect mass and energy exchange at the plant and stand scales. For forest stands, LAI shows substantial spatial variability across both relatively uniform (Chason et al. 1991) and heterogeneous forest landscapes (Law et al. 2001). At our Oak Ridge field site, LAI can range between 5 and 7 across ridges, slopes and valleys (Chason et al. 1991).

The sensitivities of annual fluxes of CO₂, water vapor and sensible heat to small differences in LAI are shown in Table 6. In this case, reducing LAI from 6 to 5, a 16% change, reduced NEE by less than 2%. This discrete change in leaf area also had minor impacts on computations of λE and H , causing λE to decrease by 4% and H to increase by about 4%.

Theoretically, the sensitivity of mass and energy exchange to changes in LAI is hyperbolic. Trace gas fluxes approach a saturating value once the canopy closes (e.g., deWit 1965, Baldocchi and Meyers 1998, Williams et al. 1998). It is only after LAI drops below 3 that changes in LAI start to force proportional changes in NEE, λE and H and canopy conductance (Kelliher et al. 1995, Law et al. 2001).

Though the sensitivity of λE to changes in LAI is small, for a closed forest canopy, differences accumulate so that computations of annual latent heat exchange at LAI = 5 (662 mm) produce a value closer to our measurement of 611 mm (Wilson et al. 2000) than to the computations derived using LAI = 6 (692 mm). The alternative computation is plausible considering the range of vegetation viewed by the 200 to 1000 m flux footprint of our eddy covariance measurement system.

Interactions not accounted for in the calculations presented in Table 6 include how turbulence statistics, diffusion and gradients of CO₂, humidity and temperature within the canopy respond to changes in LAI. To study these interactions, one can use an Eulerian, higher-order closure model (e.g., Meyers and Paw U 1986, Su et al. 1996, Pyles et al. 2000) or large-eddy simulation model (Albertson et al. 2001) to improve the Lagrangian-based turbulence model that we used (e.g., Massman and Weil 1999, Lai et al. 2000). Ignoring alterations to

canopy turbulence caused by changes in leaf area will have an inconsequential impact on predicting annual budgets of NEE and small effects on λE (Baldocchi and Wilson 2001). Sensible heat exchange, however, is sensitive to small changes in the temperature profile within a canopy (Baldocchi and Wilson 2001) and deserves additional study using turbulence statistics with a higher-order closure model.

A second set of interactions missing in this analysis is the influence of leaf area on litterfall and soil and bole respiration. For sparse canopies, one needs to down-scale bole respiration and use a biogeochemical cycling model to scale how changes in litter input will alter heterotrophic soil respiration (Raich and Tufekcioglu 2000). Hence, we do not recommend pushing the NEE sensitivity computations, based on CANOAK, to low leaf area indices without the inclusion of algorithms that consider the longer-term cycling of carbon. New allometric scaling principles, however, may serve as a means for extending our calculations to other ranges of LAI (Enquist and Niklas 2001). There is also the potential for scaling root respiration on the basis of canopy photosynthesis (Högberg et al. 2001).

As canopies become more open, a larger fraction of heat and vapor exchange will occur at the soil surface. The partitioning of solar energy into sensible, latent and soil heat flux will be sensitive to how well the soil physics submodel evaluates atmospheric thermal stratification, surface wetness and the thickness of the litter layer (Baldocchi et al. 2000).

One restriction of using multi-layer models is their dependence on "hard-to-attain" information about the vertical profile of LAI (Raupach and Finnigan 1988). However, information on how LAI in forests varies with height has accumulated over the last decade and is reducing this restriction. We can now generalize that an unmanaged temperate forest usually contains six distinct zones: an emergent layer, the outer canopy, the overstory, the middle story, the understory and the ground layer (Aber and Melillo 1991, Parker 1995). Broad-leaved forests of intermediate age tend to have their leaf area distribution skewed with height and concentrated in the overstory (Smith and Huston 1989, Parker 1995). At the Oak Ridge site, about 75% of leaf area is in the upper 25% of the forest (Hutchison et al. 1986). Leaf area profiles in older stands tend to be more uniform and old-age stands tend to be inverted canopies with more leaf area distributed close to the ground (Aber and Melillo 1991, Parker 1995).

In Table 7, we compare computations of annual mass and energy fluxes based on leaf area being evenly distributed or skewed toward the top of the canopy. These computations show that this difference in vertical leaf area distribution had a negligible influence on annual fluxes of CO₂, water vapor and energy. Our calculations are in agreement with the independent simulations made by Wu et al. (2000).

More important in the modeling analysis than the vertical profile of LAI is the number of layers used in the simulation. Wu et al. (2000) and Pyles et al. (2000) recommend at least 20 layers. Norman (1979) recommends that the leaf area of a layer should be less than 0.5, to apply statistically based radiative transfer models correctly.

Table 6. Annual sums of net CO₂ exchange (NEE) and latent (λE) and sensible heat (H) exchange as a function of leaf area index (LAI).

Flux	LAI		
	6	5	4
NEE (g C m ⁻² year ⁻¹)	-577	-569	-540
λE (MJ m ⁻² year ⁻¹)	1690	1617	1548
H (MJ m ⁻² year ⁻¹)	1096	1142	1203

Within a forest stand, the inclination angle of leaves will have a major impact on light interception. Modeled distributions of leaves include spherical, erectophile and planophile classes (deWit 1965, Campbell 1981). We examined the sensitivity of the annual course of daily NEE to leaf inclination angle (θ) for three cases, an erect ($\theta = 80^\circ$) and planar ($\theta = 10^\circ$) leaf angle distribution and the measured leaf angle distribution with clumped leaves. For the reference case with clumped leaves, the mean leaf angle was 40° at the top and 10° near the bottom of the canopy. Variations in leaf inclination angle ranging from planar to erect caused NEE to vary widely between 200 and $1100 \text{ g C m}^{-2} \text{ year}^{-1}$. The impact of leaf inclination angle on H and λE , on the other hand, was modest by comparison, less than 25% (Table 8). Also shown in Table 8 are computations for a spherical leaf angle distribution ($\theta = 60^\circ$) and one with randomly distributed leaves, but with the measured leaf angle distribution. These additional cases produced values of NEE that fell between the reference case and the case with the most erect leaves. Higher sums of net primary productivity, predicted for canopies with erect leaves growing at mid-latitudes, are consistent with the short-term calculations pioneered by de Wit (1965) and Duncan et al. (1967). We also note that canopies with erect leaves had a lower albedo, which produced more net radiation and higher values of H and λE than in other cases.

From an evolutionary standpoint, maximizing carbon gain or minimizing water loss are not the only pressures acting on these trees, otherwise more forest canopies would exist with erect leaves. Shading understory plants and optimizing the content and distribution of nitrogen (N) in leaves are other important factors, beside optimal leaf angle for light absorption, that merit consideration. On the other hand, these calculations lend support for the selection of fast-growing poplar clones with erect leaves.

Many investigators have hypothesized that plant canopies maintain a vertical gradient in leaf nitrogen to optimize daily photosynthesis (Field 1991). Alternatively, Chen et al. (1993) conclude that plants coordinate the vertical distribution of leaf nitrogen to keep the carboxylation rate when ribulose-1,5-bisphosphate (RuBP) regeneration is limited by electron transport (W_j) in balance with the carboxylation rate when RuBP is saturated with respect to CO_2 (W_c). Biophysical models with vertical resolution can provide us with a tool to examine how canopy structure and physiological capacity interact with the microclimate (light and CO_2) to limit W_j and W_c with respect to

one another.

Data in Figure 2 show vertical profiles of W_j and W_c on sunlit and shaded leaves for noon on a typical summer day. There is close theoretical agreement between W_c and W_j on the sunlit leaves, suggesting that the canopy has coordinated the distribution of N, as hypothesized by Chen et al. (1993). An exception occurs in the upper 10% of the canopy, where the diffusion of CO_2 to the leaves is the limiting factor, indicated by W_c being less than W_j . Photosynthesis by shaded leaves, on the other hand, should be light-limited, because W_j is less than W_c throughout the canopy.

To determine the sensitivity of mass and energy fluxes of a deciduous forest to vertical variations in photosynthetic capacity, calculations for the two cases were performed. One case assumes that photosynthetic capacity is constant and scales with the value of the upper sunlit leaves. The other case scales photosynthetic capacity with height. This analysis differs from previous studies that started with a given amount of nitrogen in the canopy and determined the effect of distributing it uniformly or with a gradient. Under these conditions, V_{cmax} at the top of a uniform canopy would be much less than V_{cmax} at the top of a canopy in which nitrogen content varied vertically.

Data shown in Figure 2 and Table 9 indicate that the vertical distribution of leaf photosynthetic capacity has little impact on the amount of CO_2 , water vapor and heat exchange that is computed on a daily or annual time scale. Consequently, what does matter, from an ecological and biogeochemical perspective, is the nitrogen economy of the forest stand. In other words, a forest can maintain the same level of productivity without investing expensive nitrogen in leaves deep in the canopy, which rarely have the opportunity to attain high rates of photosynthesis.

Many studies show a close coupling between stomatal conductance and leaf photosynthesis (Collatz et al. 1991, Mäkelä et al. 1995). In this paper, stomatal conductance is computed as a function of leaf photosynthesis (A), relative humidity (RH) and CO_2 at the leaf surface (C_s) (Collatz et al. 1991):

$$g_s = \frac{kARH}{C_s} \quad (5)$$

A survey of the literature indicates that the proportionality constant, k , tends to center near 10, but ranges between 8 and 12 for temperate broad-leaved forest species (Harley and Baldocchi 1995, Medlyn et al. 2001) and crops (Collatz et al. 1991). This proportionality constant decreases as soil water content decreases (Sala and Tenhunen 1996) or for trees growing in drought-prone Mediterranean climates (Medlyn et al. 2001). Table 10 shows how sensitive calculations of annual NEE, λE and H are to moderate changes in k (20%). Model computations indicate that the prescribed changes in k translate into differences in NEE of only 10%, but that they alter energy partitioning significantly. Increasing k to 12 produces a change in the Bowen ratio from 0.64 to 0.47. Reducing k to 8 increases the Bowen ratio to near 0.8. In comparison, the mea-

Table 7. Annual sums of net CO_2 exchange (NEE) and latent (λE) and sensible heat (H) exchange as a function of leaf area profile.

Flux	Leaf area profile		% Difference
	Skewed distribution	Uniform distribution	
NEE ($\text{g C m}^{-2} \text{ year}^{-1}$)	-577	-568	-1.5
λE ($\text{MJ m}^{-2} \text{ year}^{-1}$)	1690	1688	-0.1
H ($\text{MJ m}^{-2} \text{ year}^{-1}$)	1096	1097	+0.1

Table 8. Annual sums of net CO₂ exchange (NEE) and latent (λE) and sensible heat (H) exchange as a function of leaf inclination angles and clumping. We assumed the mean angle for the erect and plane canopies was 80° and 10°, respectively. The mean direction cosine between the sun and the leaf normal is 0.5 for the spherical case. For the random and varying leaf angle cases, we assumed the Markov clumping factor (Ω) was 1.00.

Flux	Clumped	Random	Spherical	Erectophile	Planophile
NEE (g C m ⁻² year ⁻¹)	-577	-354	-720	-1126	-224
λE (MJ m ⁻² year ⁻¹)	1690	1551	1774	2023	1473
H (MJ m ⁻² year ⁻¹)	1096	1032	1095	1171	1008

sured Bowen ratio at this site during 1997 was 0.72 (Wilson and Baldocchi 2000).

The environment

Radiation, temperature, vapor pressure deficit, CO₂ concentration and wind speed are important drivers of biophysical algorithms for photosynthesis, stomatal conductance and the leaf energy balance of leaves. Yet, the meteorological conditions measured at a reference station above a forest do not represent the microenvironment adjacent to leaves, as the environment inside the canopy is often decoupled from that above. Micrometeorological submodels are, therefore, necessary tools for translating the conditions measured above the canopy to those adjacent to leaves deep within the canopy.

During the day, sensible heat is generated at all levels of the canopy by the heat load of the sun and is directed upward. The air temperature profile that responds to this forcing is shown in Figure 3. Starting from the ground, air temperature increases with height, up to the densest portion of the canopy crown. Thereafter, air temperature decreases with height. The range of temperature, in the canopy, is about 1 °C. Temperature gradients will be stronger or weaker depending on the heat load on the vegetation and degree of turbulent mixing.

The temperature profile in Figure 3 represents a distinct case when counter-gradient transfer is occurring. Simple

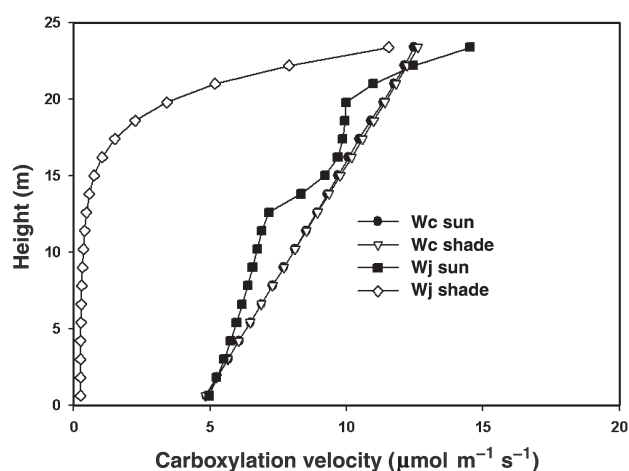


Figure 2. Vertical profiles of carboxylation for the conditions of W_j , limited by electron transport, or W_c , limited by RUBP regeneration, for sunlit and shaded leaf fractions.

K-theory models are unable to capture this physical phenomenon because large-scale eddies dominate the transfer of material and energy in a canopy (Raupach and Finnigan 1988). K-Theory models also do not accurately reflect the feedbacks between local air temperature and the source-sink strength of sensible heat. Compared with K-theory models, stochastic Lagrangian (as used here), higher-order closure and large-eddy simulation models (Meyers and Paw U 1986, Su et al. 1996, Pyles et al. 2000, Albertson et al. 2001) are able to reproduce counter-gradient transfer of mass and energy and the source-sink distribution of sensible heat more accurately.

New empirical evidence shows that the statistical prediction of canopy photosynthesis is improved by using direct and diffuse streams of PAR as independent variables, rather than air temperature and humidity deficits (Gu et al. 2002). Furthermore, numerous field and theoretical studies demonstrate that changes in the fraction of diffuse radiation will modulate canopy photosynthesis (deWit 1965, Gu et al. 1999). What has not been quantified is how changes in direct and diffuse solar radiation, as may occur in response to volcanic eruptions, dust or aerosols (Olmo et al. 1999), affect CO₂, water vapor and energy exchange over the course of a year.

To answer this question, we recomputed the annual course of mass and energy exchange by assuming that the flux density of direct radiation was reduced by 20%, but that total available energy was unchanged. Data in Table 11 show that reducing direct radiation flux density by 20% can cause a temperate deciduous forest to assimilate an extra 78 g C m⁻² year⁻¹, a 14% increase (Table 11). Changes in evaporation and sensible heat exchange due to the directionality of light, on the other hand, were negligible.

At face value, these calculations imply that the Mt. Pinatubo eruption may have led to an increase in regional photosyn-

Table 9. Annual sums of net CO₂ exchange (NEE) and latent (λE) and sensible heat (H) exchange as a function of varying the maximum carboxylation velocity with height in the canopy or keeping it constant.

Flux	V_{cmax}		% Difference
	$f(z)$	constant	
NEE (g C m ⁻² year ⁻¹)	-577	-578	0.2
λE (MJ m ⁻² year ⁻¹)	1690	1709	1.1
H (MJ m ⁻² year ⁻¹)	1096	1076	-1.8

Table 10. Influence of the stomatal conductance coefficient (k) on net CO_2 exchange (NEE) and latent (λE) and sensible heat (H) exchange.

Flux	$k = 9.5$	$k = 8$	$k = 12$
NEE ($\text{g C m}^{-2} \text{ year}^{-1}$)	-577	-528	-630
λE ($\text{MJ m}^{-2} \text{ year}^{-1}$)	1690	1544	1897
H ($\text{MJ m}^{-2} \text{ year}^{-1}$)	1096	1233	900

thesis, which would be consistent with the slowed rate of increase of atmospheric CO_2 concentration that was observed at Mauna Loa (Keeling and Whorf 2000). Yet one must be careful when extrapolating our analysis to other conditions. In the calculations presented in Table 11, we assumed that changes in radiation did not affect the annual temperature. Climate records show that the Mt. Pinatubo eruption was followed by a 0.5°C decrease in mean global annual temperature (Hanson et al. 1996), a 33% increase in diffuse radiation and a 3% reduction in global solar radiation (Olmo et al. 1999). Atmospheric cooling can reduce respiration, an occurrence that would also slow the rate of increase in atmospheric CO_2 concentration. Climatic cooling can also shorten the growing season by delaying leaf expansion. This latter effect can reduce the net uptake of CO_2 of temperate deciduous forests by about $6 \text{ g C m}^{-2} \text{ day}^{-1}$ for each day that the growing season is shortened (Baldocchi and Wilson 2001), offsetting the positive impacts of aerosols on canopy photosynthesis during the growing season.

Conclusions

Modeling carbon dioxide and water vapor exchange between forests and the atmosphere is challenging because of the many sources of complexity and uncertainty. These uncertainties stem from structural and functional features of the forest

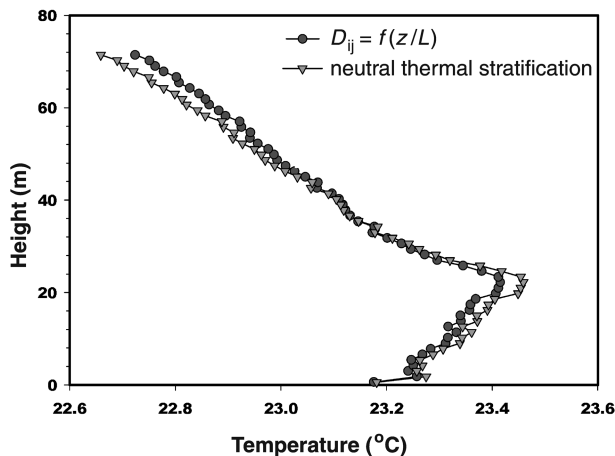


Figure 3. Computed profiles of air temperature within and above a deciduous forest.

Table 11. Influence of diffuse and direct radiation fraction on net CO_2 exchange (NEE) and latent (λE) and sensible heat (H) exchange. In this case, direct radiation was reduced by 20%. Total radiation was held constant.

Flux	Reference	Direct (-20%)	% Difference
NEE ($\text{g C m}^{-2} \text{ year}^{-1}$)	-577	-655	13.5
λE ($\text{MJ C m}^{-2} \text{ year}^{-1}$)	1690	1729	2.3
H ($\text{MJ C m}^{-2} \text{ year}^{-1}$)	1096	1058	-3.5

stand, natural variability of the environment and deficiencies in our knowledge. Based on a modeling point of view, we have partitioned the sources of complexity into several categories. These are associated with: (1) the geometrical representation of leaves and the canopy; (2) the temporal and spatial resolution of the model; (3) the spatial and temporal variability of model parameters; (4) the accuracy of driving environmental variables and how well their information is transferred to the sites of mass and energy exchange; and (5) the accuracy of the test data used to validate the flux measurements.

Any model can approximate a system to a certain degree of accuracy. Two more poignant questions may be: what degree of accuracy do we need to compute CO_2 and water vapor fluxes and how much detail is needed to achieve a specified level of accuracy? Although models will never approach 100% fidelity (see Kuhn 1996), improvements in fidelity have been achieved through use of more complex biophysical models (e.g., Sinclair et al. 1976, dePury and Farquhar 1997, Baldocchi and Meyers 2000, Pyles et al. 2000, Baldocchi and Wilson 2001, Williams et al. 2001). These detailed biophysical models perform well (often accounting for over 80% of the variance and producing flux values within 10% of the mean measured values) because they rely on ecophysiological rules to constrain their model parameters (rather than arbitrary tuning), quantify nonlinear functions more adequately, and consider the distinct environments of sun and shade leaves.

The temporal and spatial resolution of a biophysical model also affects the model's accuracy and performance. Several investigators have reported that computations of mass and energy are sensitive to the number of layers into which the canopy is divided (Norman 1993, Pyles et al. 2000, Wu et al. 2000). In practice, dividing a canopy into 20 to 30 layers or maintaining a layer thickness that contains less than 0.5 m^2 of leaf area per unit land area seems adequate. With respect to temporal resolution, dynamic and prognostic biophysical models like SIB-2 (Sellers et al. 1997) and ACASA (Pyles et al. 2000), which operate on time steps of 15 minutes, and diagnostic models, like CANOAK or CUPID (Norman 1979, 1993), which operate at hourly time steps, can resolve diurnal cycles with high fidelity. Ecosystem models based on coarser time scales (e.g., daily or monthly time steps, such as Biome-BGC or CENTURY (see Cramer et al. 1999)), on the other hand, miss a significant fraction of variance associated with mass and energy exchange at short time scales (Baldocchi and Wilson 2001).

We conclude that better representations of canopy CO₂ and water vapor exchange between forests and the atmosphere will require more and better data. Long-term eddy flux records, provided by projects such as FLUXNET (Baldocchi et al. 2001), will continue to provide a constraint and guide as to the accuracy of such models. However, application of these biophysical models over longer time scales will also require information on how LAI, soil respiration and photosynthetic capacity vary over the course of a season and interannually (e.g., Niinemets et al. 1999, Wohlfahrt et al. 2000, Wilson et al. 2001). Ultimately, we envision a closer coupling between detailed biophysical models, like CANOAK, with modules that compute the dynamics of canopy structure, function and composition (e.g., Foley et al. 1998, Cramer et al. 1999). We also advocate more use of ecophysiological rules and relationships to constrain and quantify model parameters (e.g., Wullschlegel 1993, Schulze et al. 1994) and predict their dynamics (Wirtz 2000).

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