INFLUENCES OF STRUCTURE, PHYSIOLOGICAL-FUNCTION, AND ENVIRONMENT ON CARBON, WATER AND ENERGY FLUXES OF A TEMPERATE BROADLEAVED DECIDUOUS FOREST—AN ASSESSMENT WITH THE BIOPHYSICAL MODEL, CANOAK

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ABSTRACT


How canopy structure, its physiological functioning and environment interact to control and drive the exchange of carbon dioxide and water vapor between a temperate forest stand and the atmosphere is the subject of this essay. First, we present an overview on 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 carbon dioxide and water vapor fluxes. Then, using 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 carbon dioxide, water vapor and sensible heat exchange. Finally, we discuss issues relating to how much detail is needed in a model to predict fluxes of carbon dioxide and water vapor with acceptable fidelity.

*Key Words:*

*biosphere-atmosphere interactions; biocomplexity, canopy photosynthesis, evaporation, ecophysiology*
1. Introduction

On walking through a temperate hardwood forest, one of the first impressions one draws is that a forest is a structurally complex. Immediately, one observes trees of multiple stature, age and species (Whittaker, 1975; Smith and Huston, 1989; Parker, 1995). Stopping and looking upward into the canopy crown, one sees that many leaves are sunlit leaves, their inclination angles are rather erect, they are rather thick and they tend to be arranged in clumps (Hutchison et al., 1983; Kruijt, 1986; Ellsworth and Reich, 1993; Parker, 1995). At eye-level, tree trunks, understorey vines, saplings and shrubs immediately come to view. Understorey leaves are relatively thin and they tend to be oriented horizontally, to absorb as much light as possible, in the sun-dappled shade. Looking downward one sees fresh and decomposing litter, soil, rocks, fallen logs, seedlings, herbs and shrubs.

Unseen by the naked eye are the physiological activities of the forest. As stomata open to allow CO₂ to diffuse into the mesophyll for photosynthesis, water is lost (Makela et al., 1996). And under the forest floor, respiration by roots and microbes is releasing CO₂ to the atmosphere.

Structural and functional aspects of a forest are not static. On visiting a forest many times over a year, one will observe both gradual and dramatic transitions in structure and function. During the winter, the hardwood forest is leafless and dormant, but respiring. With the occurrence of spring comes a flush of growth. Rapid changes in biological activity and structure occur as leaves expand, nodes elongate, roots grow and reproductive organs emerge (Larcher, 1975; Hutchison and Matt, 1977; Parker, 1995). Coincidently, photosynthetic capacity of leaves changes rapidly during this period.
(Wilson et al., 2000, 2001a), as chloroplast with nitrogen-rich RUBP are constructed. During the summer, gradual changes in canopy structure, maximum stomatal conductance and physiological capacity occur as leaves age, they experience water deficits, acclimate, are eaten or drop due to prolonged drought (Falge et al., 1996; Niinemets et al., 1999; Wilson et al., 2000, 2001a). With the approach of autumn, the face of the landscape changes yet again. Leaves re-translocate nitrogen back to stems, their photosynthetic capacity diminishes, they senesce, change color and drop from the trees (Larcher, 1975; Hutchison and Matt, 1977; Wilson et al., 2000).

Spatial and temporal variations in canopy structure and function, cited above, affect the canopy microclimate and, consequently, influence carbon dioxide and water vapor exchange in numerous ways. For example, interactions between structural and functional properties of forests alter: 1) wind and turbulence within and above the canopy; 2) the interception and scattering of photons throughout the canopy; 3) the heat load on leaves and the soil; 4) the 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 discuss and quantify how variations of canopy structure, physiological function and environment affect carbon dioxide and water vapor exchange of a temperate broadleaved forest. We accomplish this goal by using a biophysical model, CANOAK. This work builds upon earlier analyses, which have 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; Williams et al., 1998; Raupach, 1998;
Baldocchi and Meyers, 1998; Wu et al., 2000; Albertson et al., 2001), by focusing on annual sums of carbon, water and energy exchange.

2. Concepts and Principles

To quantify fluxes of carbon dioxide, water and energy between a forest and the atmosphere several subjects must be considered. First, one must first identify the biophysical and ecophysiological processes that influence trace gas exchange significantly. Then one needs to represent these processes mathematically and integrate them throughout the domain of the canopy on the basis of local environmental drivers. This second task depends upon how we define, geometrically, the forest canopy and the distribution of leaves throughout. In this section we discuss the biophysical and mathematical principles used in contemporary biophysical models such as \textit{CANOAK}.

A. Biophysical Principles

The exchange of carbon dioxide 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) the 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) a coupling of stomatal conductance to carbon and water fluxes, nutrient content of leaves and soil moisture in the root zone (Norman, 1979; Meyers and Paw U, 1986; Leuning et al., 1995; Sellers et al., 1997; Baldocchi and Meyers, 1998; Wohlfahrt et al., 2001; Williams et al., 2001; Albertson et al. 2001).
The conservation of mass and energy forms the fundamental foundation of any biophysical model that predicts carbon dioxide, 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 not varying—states that the vertical flux divergence ($\frac{\partial F}{\partial z}$) equals the vegetative source-sink strength ($S$). For CO$_2$, the daytime sink strength in a layer of canopy is determined by the balance between a biochemical and physiologically-limited demand of leaves and the diffusional-limited supply from the atmosphere and through the leaf boundary layer (Farquhar et al., 1980). Mathematically, the source-sink strength of vegetation is proportional to leaf area density ($a(z)$) and the differences between the scalar concentration in the atmosphere ($C_a$) adjacent to leaves and that inside the leaves ($C_i$) (Meyers and Paw U, 1986). In addition, it is inversely proportional to the sum of the aerodynamic ($r_a$) and stomatal resistances ($r_s$):

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

Since photosynthesis, transpiration, stomatal conductance and respiration depend upon temperature and light, it is incumbent that we assess the leaf energy balance in tandem with assessing the conservation of mass. The energy balance of a leaf is defined by 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:

$$R_n = (1 - \rho - \tau) R^B + (1 - e) L^B - e\sigma T^4_l = H + \lambda E = \rho C_p \frac{(T_a - T_i)}{r_{a,k}} + \frac{\rho_a \cdot m_a}{P \cdot m_a} \frac{(e_a(T_i) - e_s)}{r_{a,v} + r_s} \quad (2)$$
The energy balance of a leaf is a function of the reflectance ($\rho$), transmittance ($\tau$) and infrared emissivity ($\varepsilon$) of a leaf and the flux densities of incoming global solar ($R_{\downarrow}$) and terrestrial ($L_{\downarrow}$) radiation. The radiation balance is partitioned into sensible ($H$) and latent heat ($\lambda E$) flux densities. In turn, these energy flux densities are evaluated using Ohm’s Law resistance analog equations, which are dependent upon air density ($\rho_a$), 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 ($P$), $m_v$ and $m_a$ are the molecular masses of vapor and air, the saturation vapor pressure at leaf temperature ($e_s(T_l)$) and the atmospheric vapor pressure ($e_a$). At the stand level, energy exchange with the soil and boles must also be considered, too.

With a biophysical framework in hand (Eqs. 1 and 2), one can associate the physical and functional attributes of single leaves, individual plants and plant stands with factors that impact carbon dioxide, water vapor and energy exchange. Such information is tabulated in Table 1. In principle, the ultimate 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 moisture) (Field, 1991; Schulze, 1994; Schulze et al. 1994; Korner, 1994; Reich et al., 1997). At the stand scale, structural factors affecting light absorption and the aerodynamics of the canopy govern ultimate rates of carbon dioxide, water vapor and energy exchange.

<table>
<thead>
<tr>
<th>Characteristic</th>
<th>Structural or Functional Attribute</th>
<th>Factors</th>
</tr>
</thead>
<tbody>
<tr>
<td>Leaves</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

Table 1. Structural and functional attributes of leaves, plants and plant stands and their impact on carbon, water and energy fluxes. Impacted factors include: $G_a$: aerodynamic conductance; $G_s$: surface conductance; $P(0)$: light transmission through a leaf or canopy; $\alpha$: albedo or reflectivity; $C_i$: biochemical capacity
<table>
<thead>
<tr>
<th>Photosynthetic pathway</th>
<th>C₃, C₄, CAM, maximal stomatal conductance</th>
<th>( C_i, G_s )</th>
</tr>
</thead>
<tbody>
<tr>
<td>Leaf size/shape</td>
<td>Needle/planar/ shoot; projected/surface area, penumbra/umbra</td>
<td>( G_{a}, P(0) )</td>
</tr>
<tr>
<td>Leaf inclination angle distribution</td>
<td>Spherical, erectophile, planophile</td>
<td>( P(0) )</td>
</tr>
<tr>
<td>Leaf azimuthal angle distribution</td>
<td>Symmetric/asymmetric</td>
<td>( P(0) )</td>
</tr>
<tr>
<td>Exposure</td>
<td>Sunlit/shaded; acclimation</td>
<td>( G_s, \alpha )</td>
</tr>
<tr>
<td>Optical properties</td>
<td>Reflectance, transmittance, emittance</td>
<td>( \alpha )</td>
</tr>
<tr>
<td>Leaf thickness</td>
<td>Photosynthetic capacity, supply of CO₂ to chloroplast, optical properties, Stomatal conductance capacity</td>
<td>( C_i, G_s, \alpha )</td>
</tr>
<tr>
<td>Stomatal distribution</td>
<td>Amphistomatous/hypostomatous</td>
<td>( G_s )</td>
</tr>
</tbody>
</table>

**Plants/Trees**

<table>
<thead>
<tr>
<th>Crown volume shape</th>
<th>Cone, ellipse, cylinder</th>
<th>( P(0), G_a )</th>
</tr>
</thead>
<tbody>
<tr>
<td>Plant species</td>
<td>monoclure, mixed stand, functional type</td>
<td>( P(0), G_{a}, G_s, C_i )</td>
</tr>
<tr>
<td>Spatial distribution of leaves</td>
<td>Random, clumped, regular</td>
<td>( P(0) )</td>
</tr>
<tr>
<td>Plant habit</td>
<td>Evergreen/deciduous; woody herbaceous; annual/perennial</td>
<td>( G_{a}, G_s, \alpha )</td>
</tr>
<tr>
<td>Plant height</td>
<td>Short (&lt; 0.10 m)</td>
<td>( G_{a}, \alpha )</td>
</tr>
<tr>
<td>Rooting depth</td>
<td>Tall (&gt; 10 m)</td>
<td>( G_s )</td>
</tr>
<tr>
<td>Leaf area/sapwood ratio</td>
<td>Hydraulic Conductivity</td>
<td>( G_{s}, C_i )</td>
</tr>
</tbody>
</table>

**Forest Stand**

<table>
<thead>
<tr>
<th>Leaf area index</th>
<th>Open, sparse, closed</th>
<th>( P(0), G_{s}, G_a )</th>
</tr>
</thead>
<tbody>
<tr>
<td>Vertical distribution of LAI</td>
<td>Uniform, skewed</td>
<td>( G_{a}, P(0) )</td>
</tr>
<tr>
<td>Seasonal variation of LAI</td>
<td>Evergreen/deciduous; winter or drought deciduous</td>
<td>( G_{a}, G_s )</td>
</tr>
<tr>
<td>Age structure</td>
<td>Disturbed/undisturbed; plantation; agriculture; regrowth</td>
<td>( G_{a}, G_s, P(0) )</td>
</tr>
<tr>
<td>Stem density</td>
<td>Spatial distribution of plants</td>
<td>( G_{a}, \alpha )</td>
</tr>
<tr>
<td>Woody biomass index</td>
<td>Amount of woody biomass</td>
<td>( G_{a}, P(0) )</td>
</tr>
<tr>
<td>Topography</td>
<td>Exposure, site history, water balance</td>
<td>( G_{a}, G_s )</td>
</tr>
<tr>
<td>Site history</td>
<td>Fires, logging, plowing, re-growth</td>
<td>( G_{a}, G_{s}, C_i, \alpha )</td>
</tr>
</tbody>
</table>
B. Mathematical Principles

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

i. Integrating Non-Linear Functions

Many biophysical processes (photosynthesis, respiration, stomatal conductance, infrared energy emission, saturation vapor pressure, transpiration) are non-linear functions of independent environmental variables, such as light ($R_\downarrow$), wind velocity ($u$), air temperature ($T$), humidity deficits ($D$) and $CO_2$, or themselves. Proper assessment of non-linear biophysical functions requires translating 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 photosynthesis rates of a leaf buried deep in the canopy with the flux density of light energy incident at the top of the canopy.

One complication in assessing non-linear functions is introduced by the fact that the state of many of the environmental variables varies throughout the canopy and that 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 non-linear functions of biophysical processes:

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

Evaluating these non-linear functions on the basis of the mean value of the independent variable ($E[f(x)] = f(\bar{x})$), instead, produces a significant bias error, due to a
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 non-linear biophysical functions according to the environment on those two leaf classes (Sinclair et al., 1976; Norman et al., 1979, 1993; dePury and Farquhar, 1997).

When assessing non-linear biophysical functions over the course of a season or year one needs to evaluate how model scaling and curvature parameters vary with time and space (Wilson et al., 2001a), by species (Wohlfarht et al., 2000; Wullschleger, 1993), or by plant functional type (Schulze et al., 1994; Korner, 1994; Wullschleger, 1993).

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.

C. Geometric Abstraction

The structural and functional complexity of leaves and forest stands vary with climate, soils, stand age, species composition and functional type (Whittaker, 1975; Aber and Melillo, 1991; Parker, 1995). The question we address in this section is: how should the geometric attributes of a leaf or canopy be represented in a mathematical model that computes flux densities of carbon dioxide and water vapor with acceptable fidelity?

i. Leaves
The cross section of a 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 are thicker than shade leaves, have greater specific mass and they possess more stomata per unit area (Terashima and Saeki, 1983; 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, thicker leaves have more leaf nitrogen content and greater photosynthetic capacity, respiration rates and stomatal conductances (Evans, 1989; Field, 1991; Schulze et al., 1994; Reich et al., 1997; Wilson et al., 2000).

With regards to water vapor and CO₂ diffusion through the stomata, leaves may be hypostomatous (having stomata on one side) or amphistomatous (having stomata on both sides of the leaf). Amphistomatous leaves tend to be associated with thicker leaves, and ones with higher photosynthetic capacity and inhabiting habitats with full sun and adequate soil moisture (Terashima et al., 2001). With regards to mass and energy exchange, water vapor originates from the inner side of the guard cells and from the subsidiary cells. CO₂ 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, diffusion through the stomata on top and bottom sides of amphistomatous leaves is assumed to occur in parallel.
Technically, photosynthesis is a function of the CO$_2$ concentration of the chloroplast (Farquhar et al., 1980; Farquhar, 1989). In practice, parameters of the Farquhar photosynthesis model are evaluated from gas exchange measurements and are evaluated in terms of the intercellular CO$_2$ concentration ($C_i$). Conceptually, intercellular CO$_2$ concentration ($C_i$) is a function of leaf photosynthesis ($A$) and a leaf conductance ($g$) (Farquhar, 1989):

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

By treating a leaf as a lumped entity, one ignores spatial gradients in diffusion (Parkhurst et al., 1988; Terashima et al., 2001), photosynthetic capacity (Terashima and Saeki, 1983) and radiation (Terashima and Saeki, 1983; Vogelmann et al., 1989), which occur within the mesophyll, and across the leaf (Roth-Nebelsick, 2001). Therefore, one either assumes that the CO$_2$ concentration in the substomatal cavity, in the intercellular spaces and in the chloroplast stroma are equal or that the boundary layer and mesophyll conductances are infinite, as compared with the stomatal conductance.

Patchy stomatal closure complicates the assessment of the intercellular CO$_2$ concentration. Calculated values of intercellular CO$_2$ ($C_i$) from gas exchange can be erroneous if there is ‘patchy’ stomatal closure, as when leaves experience low leaf water potentials (Laisk 1983; Mott and Buckley, 2000). Proper estimates of a bulk average $C_i$ values requires weighting $C_i$ values of the patches by their respective stomatal conductances (Farquhar, 1989).

**ii. The Forest Stand**

At the canopy scale, a hierarchy of biophysical models exists that vary in complexity on how canopy structure and function is represented (Raupach and Finnigan,
At the simplest level, 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). Better fidelity is achieved by using a dual source abstraction; a concept that accounts for the different environments on sunlit and shaded leaves, as discussed above (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 (van den Hurk and McNaughton, 1995; Norman et al. 1995). For multi-storied canopies, one-dimensional, multi-layer models are able to incorporate as much pertinent detail on canopy structure that is needed or occurs (Norman, 1979; Meyers and Paw U, 1986; Leuning et al., 1995; Baldocchi and Meyers, 1998; Wu et al., 2000; Wohlfarth et al., 2001; Pyles et al., 2000; Williams et al., 2001). Multi-layer models tend to produce more accurate simulations of mass and energy exchange than do big-leaf models (Sinclair et al., 1976; Norman, 1980; Pyles et al., 2000).

Detailed multi-layer models can also be used as guides to develop 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 non-linear on an hour-by-hour basis, but is 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 and photosynthetic capacity.

Open canopies are better represented using three-dimensional models that treat 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, because a substantial amount of energy exchange occurs there (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 they are features can alter mass and energy exchange (Raupach and Finnigan, 1997; Ikeda et al., 2001; Albertson et al., 2001), too.

3. Model Overview

Since the biophysical model, CANOAK, is used to quantify the impacts of varying canopy structure and physiological function on canopy scale carbon dioxide and water vapor exchange, a brief overview of the model is presented in this section. The CANOAK model consists of coupled micrometeorological and physiological modules. The micrometeorological model computes 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 external variables that were measured above the forest. Environmental inputs include incident photosynthetic photon flux density ($Q_p$), air and soil temperature, wind speed, relative humidity and CO$_2$ concentration. The model and its subcomponents has 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 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. Zero 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 calculation of NEE, λE and H reproduce temporal variations of field measurements on diurnal, weekly, seasonal and annual time scales with high fidelity ($r^2 < 0.80$) (Baldocchi and Wilson, 2001).

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

<table>
<thead>
<tr>
<th></th>
<th>NEE</th>
<th>λE</th>
<th>H</th>
</tr>
</thead>
<tbody>
<tr>
<td>intercept</td>
<td>0.908 μmol m⁻² s⁻¹</td>
<td>4.96 W m⁻²</td>
<td>-0.707 W m⁻²</td>
</tr>
<tr>
<td>slope</td>
<td>1.085</td>
<td>1.14</td>
<td>1.235</td>
</tr>
<tr>
<td>$r^2$</td>
<td>0.815</td>
<td>0.83</td>
<td>0.671</td>
</tr>
<tr>
<td>Annual sum</td>
<td>***</td>
<td>1500 MJ m⁻² a⁻¹</td>
<td>1080 MJ m⁻² a⁻¹</td>
</tr>
</tbody>
</table>

The model computations presented in this paper are based on a case study of a 60 year old, temperate broadleaved forest, growing near Oak Ridge, TN. The species composition of the forest consisted of a mix of oak (Quercus alba, Quercus prinus), maple (Acer rubrum) and tulip poplar (Liriodendron tulipifera). 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 moisture. Hence, the discussion that follows does not consider the effects of soil moisture deficits on carbon dioxide and water vapor exchange.
Reference values of leaf area index and photosynthetic capacity were adjusted during the growing season, based on field measurements (Baldocchi and Wilson, 2001; Wilson et al., 2001a). Photosynthetic model parameters ($V_{cmax}$, $J_{max}$, $R_d$) were adjusted for temperature using kinetic-based, Arrhenius functions (Farquhar et al., 1980).

Table 3. Parameter values used by the CANOAK model in the simulations of canopy CO$_2$, water vapor and energy exchange. $V_{cmax}$ is the maximum carboxylation velocity, when RuBP is limited. $J_{max}$ is the maximum rate of electron transport, and $R_d$ is dark respiration.

<table>
<thead>
<tr>
<th>Parameter</th>
<th>value</th>
<th>units</th>
</tr>
</thead>
<tbody>
<tr>
<td>$V_{cmax} (311 \degree K)$</td>
<td>73</td>
<td>$\mu$mol m$^{-2}$ s$^{-1}$</td>
</tr>
<tr>
<td>$J_{max} (311 \degree K)$</td>
<td>2.32 $V_{cmax}$ (311 \degree K)</td>
<td>$\mu$mol m$^{-2}$ s$^{-1}$</td>
</tr>
<tr>
<td>$R_d$</td>
<td>0.0046 $V_{cmax}$</td>
<td>$\mu$mol m$^{-2}$ s$^{-1}$</td>
</tr>
<tr>
<td>LAI max</td>
<td>6</td>
<td>--</td>
</tr>
<tr>
<td>Canopy Height</td>
<td>26</td>
<td>m</td>
</tr>
<tr>
<td>Leaf dimension</td>
<td>0.10</td>
<td>m</td>
</tr>
<tr>
<td>Stomatal conductance factor, $k$</td>
<td>9.5</td>
<td>--</td>
</tr>
<tr>
<td>Quantum yield, $\alpha$</td>
<td>0.22</td>
<td>mol electron (mol photons)$^{-1}$</td>
</tr>
<tr>
<td>Clumping factor, $\Omega$</td>
<td>0.84</td>
<td>--</td>
</tr>
<tr>
<td>Latitude</td>
<td>35.9</td>
<td>degrees</td>
</tr>
<tr>
<td>Longitude</td>
<td>84.3</td>
<td>degrees</td>
</tr>
</tbody>
</table>

4. Results and Discussion

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

4.1 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 CO$_2$ diffusion ($g_s$), 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 ($u$):

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

Conceptually, the diffusive boundary layer is much thinner over small leaves and needles than 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 CO$_2$ between their surface and the atmosphere and are better coupled to their local environment than are big leaves (Jarvis and McNaughton, 1986; Schuepp, 1993; Roth-Nebelsick, 2001).

Reducing the mean leaf dimension of an oak leaf from 0.10 m (the size of *Quercus alba*) to 0.01 m (the size of *Q. douglasii*) increases the theoretical estimate of net annual CO$_2$ exchange by less than 2% (Table 4). With regards to latent and sensible heat exchange, evaporation decreases by 2%, while sensible heat increases by about 6%. Small differences in the sums of carbon dioxide, water vapor and heat exchange reflect, in part, the impact of the prolonged dormant period when the canopy was leafless. If we examine summer days in detail, we find that there are potential instances when a theoretical canopy with small leaves can take up 0.25 gC m$^{-2}$ d$^{-1}$ more than the reference case, a 10% difference in this instance.

<table>
<thead>
<tr>
<th></th>
<th>0.1 m</th>
<th>0.01m</th>
<th>0.001 m</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>NEE (gC m$^{-2}$ a$^{-1}$)</strong></td>
<td>-577</td>
<td>-588</td>
<td>-586</td>
</tr>
<tr>
<td><strong>$\lambda E$ (MJ m$^{-2}$ a$^{-1}$)</strong></td>
<td>1690</td>
<td>1652</td>
<td>1615</td>
</tr>
<tr>
<td><strong>$H$ (MJ m$^{-2}$ a$^{-1}$)</strong></td>
<td>1096</td>
<td>1164</td>
<td>1202</td>
</tr>
</tbody>
</table>

*Table 4. Computations of annual sums of net CO$_2$ exchange and latent and sensible heat exchange as a function of leaf dimension.*
There are several limitations associated with the computations in Table 4. Here, 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 mechanistic detail will be needed to address the impact of these features, but their effects are assumed to be rather small compared with the leaf boundary layer effect.

In many temperate deciduous forests leaf mass per unit area, maximum carboxylation capacity ($V_{cmax}$) and nitrogen per unit area are well correlated with one another. These leaf properties vary with height in a concerted manner (Ellsworth and Reich, 1993; Kull and Niinemets, 1998; Wilson et al., 2000a) and their variation within a canopy can be as great as their variability across the range of a species or plant functional types (see Schulze et al., 1994; Reich et al., 1997). We quantify the impact of leaf thickness on net CO$_2$ exchange by examining how sensitive these fluxes are to leaf photosynthetic capacity. Reducing $V_{cmax}$ from the reference value of 73 $\mu$mol m$^{-2}$ s$^{-1}$ to 50 $\mu$mol m$^{-2}$ s$^{-1}$ produced a one to two gC m$^{-2}$ d$^{-1}$ decrease in NEE during the growing season. This reduction occurred through the subsequent reduction 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 a function of the ratio between nitrogen and lignin content (Melillo et al., 1982). Increasing lignin or decreasing nitrogen content
causes the rate of litter decomposition to decrease. Had this effect been worked into the model calculations, it would offset the reduction of canopy photosynthesis that results from lower $V_{\text{cmax}}$ and counter the inferred reduction in $\text{NEE}$.  

With regard to energy exchange, a concurrent reduction in stomatal conductance occurs with a reduction in $V_{\text{cmax}}$ (Schulze et al., 1994; Wilson et al., 2000a), which alters the partitioning of net radiation (Table 5). On an annual basis, latent heat exchange is reduced 6% and sensible heat exchange increases by 9%.

\textbf{Table 5} Annual sums of net CO$_2$ exchange and latent and sensible heat exchange as a function of photosynthetic capacity.

<table>
<thead>
<tr>
<th></th>
<th>$V_{\text{cmax}}(73)$</th>
<th>$V_{\text{cmax}}(50)$</th>
<th>% difference</th>
</tr>
</thead>
<tbody>
<tr>
<td>$\text{NEE (gC m}^{-2} \text{a}^{-1})$</td>
<td>-577</td>
<td>-454</td>
<td>-21.3</td>
</tr>
<tr>
<td>$\lambda E (\text{MJ m}^{-2} \text{a}^{-1})$</td>
<td>1690</td>
<td>1584</td>
<td>-6.3</td>
</tr>
<tr>
<td>$H (\text{MJ m}^{-2} \text{a}^{-1})$</td>
<td>1096</td>
<td>1199</td>
<td>9.3</td>
</tr>
</tbody>
</table>

An accurate quantification of internal CO$_2$ concentration ($C_i$) is required to simulate photosynthesis correctly (Farquhar et al., 1989; Katul et al., 2000). Evolutionary pressures on leaf thickness and morphology have produced a conservative ratio of internal to external CO$_2$ concentration near 0.7, for C$_3$ leaves, and 0.4 for C$_4$ 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 due to 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 $C_i/C_a$ on shade leaves decrease from 0.75 to 0.95 from between the top of the canopy and 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 data in other publications (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 not considered by the calculations involving variations in leaf size include how changes in leaf thickness alter the diffusion of CO$_2$ and the absorption and transmission of 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 ranges of $C_i/C_a$ values are in general agreement with data inferred from carbon isotope measurements.

Figure 1 Computed vertical profiles of the ratio of the intercellular and ambient CO$_2$ concentrations ($C_i/C_a$) on the sunlit and shaded leaf fractions for a midday period on day 180.

4.2 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...
scale. With regards to forest stands, leaf area index is a parameter that experiences substantial spatial variability across relatively uniform (Chason et al., 1991) and heterogeneous forest landscapes (Law et al., 2001). At our Oak Ridge field site, leaf area index can range between 5 and 7 across ridges, slopes and valleys (Chason et al. 1991).

The sensitivities of annual fluxes of carbon dioxide, 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 $\lambda E$ and $H$. $\lambda E$ decreased by 4% and $H$ increased by about 4%.

Theoretically, the sensitivity of mass and energy exchange to changes in leaf area index is hyperbolic. Trace gas fluxes approach a ‘saturating’ value once the canopy closes (e.g. deWit, 1965; Williams et al. 1998; Baldocchi and Meyers, 1998). Only as leaf area drops below three do changes in leaf area index start to force proportional changes in $NEE$, $\lambda E$ and $H$ and canopy conductance (Kelliher et al., 1995).

Though the sensitivity of $\lambda E$ to changes in LAI is small, for a closed forest canopy, picking the right leaf area index has an implication on model verification. Model computations of annual evaporation at a leaf area index of five (662 mm) produced a closer value to our measurement of 611 mm (Wilson et al. 2000) than the computations derived using a leaf area index of six (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. Future work needs to combine high-resolution remote sensing images of the site and flux footprint models to assess the spatially integrated and representative leaf area index.
One feedback missing, in the calculations presented in Table 6, is how turbulence statistics, diffusion and gradients of CO₂, humidity and temperature, within the canopy, respond to changes in leaf area index. To address this issue, 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 upon the parameterization of turbulence used by the Lagrangian-based turbulence model used here (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 \( \text{NEE} \) and small effects on \( \lambda E \) (Baldocchi and Wilson, 2001).

We cannot draw a similar conclusion on how \( H \) will respond to feedbacks between leaf area and turbulence fields. Sensible heat exchange is very sensitive to small changes in the temperature profile within a canopy (Baldocchi and Wilson, 2001). Direct calculations of turbulence statistics with a higher order closure model are needed to say more on this matter.

A second feedback 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 one needs a biogeochemical cycling model to scale how changes in litter input will alter heterotrophic soil respiration (Raich and Tufekcioglu, 2000). Hence, it is not recommended to push the \( \text{NEE} \) 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 leaf area index (Enquist and Niklas, 2001). There is also the potential of scaling root respiration on the basis of canopy photosynthesis (Hogberg 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 criticism of using multi-layer models has been their dependency on ‘hard-to-attain’ information on the vertical profile of leaf area index (Raupach and Finnigan, 1988). An accumulating body of ecological data is giving us a better understanding on how leaf area index in forests vary with height, so this criticism may not be as valid as it was a decade ago. For example, a temperate forest contains six distinct zones, an emergent layer, the outer canopy, the overstory, the middle story, the under story and the ground layer (Aber and Melillo, 1991; Parker, 1995). Broadleaved forests of intermediate age tend to have their leaf area distribution skewed with height and concentrated in the overstorey (Smith and Huston, 1989; Parker, 1995). At the Oak Ridge site, about 75% of leaf area was in the upper 25% of the forest (Hutchison et al., 1983). Leaf area profiles in older stands tend to be more uniform and old-age stands tend to be ‘bottom-heavy, having their leaf area distribution weighted close to the ground (Aber and Melillo, 1991; Parker, 1995).
In Table 7, we compare computations of annual mass and energy fluxes based on two cases of vertical leaf area distribution. One case assumes the measured leaf area profile, with the greatest amount of leaf area occurring near the top of the canopy (Hutchison et al., 1983). The other case assumes that the leaf area distribution was uniform with height. Our computations show that these distinct differences in leaf area distribution had a negligible influence on annual fluxes of carbon dioxide, water vapor and energy. These calculations are supported by a recent analysis by Wu et al. (2000).

What proves to be more important 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 7** Annual sums of net CO₂ exchange and latent and sensible heat exchange as a function of leaf area profile.

<table>
<thead>
<tr>
<th></th>
<th>Skewed distribution</th>
<th>uniform</th>
<th>% difference</th>
</tr>
</thead>
<tbody>
<tr>
<td>NEE (gC m⁻² a⁻¹)</td>
<td>-577</td>
<td>-568</td>
<td>-1.5</td>
</tr>
<tr>
<td>λE (MJ m⁻² a⁻¹)</td>
<td>1690</td>
<td>1688</td>
<td>-0.1</td>
</tr>
<tr>
<td>H (MJ m⁻² a⁻¹)</td>
<td>1096</td>
<td>1097</td>
<td>+0.1</td>
</tr>
</tbody>
</table>

Within a forest stand, the inclination angle of leaves will have a major impact upon light interception. Classical distributions of leaves include spherical, erectophile and planophile classes (deWit, 1965; Campbell, 1981). How sensitive the annual course of daily NEE is to leaf inclination angle (θ) is examined for three cases, an erect (θ equal 80 degrees) and planar (θ equal 10 degrees) 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 degrees at the top and 10 degrees near the bottom of the canopy.
Variations in leaf inclination angle ranging from planar to erect caused $NEE$ to range between $-200$ and $-1100 \text{ gC m}^{-2} \text{ a}^{-1}$, a huge range. The impact of leaf inclination angle on $H$ and $\lambda E$, 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 ($\theta$ equals 60 degrees) and one with randomly distributed leaves, but with the measured leaf angle distribution. These additional cases produce values of $NEE$ that fall 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 a more net radiation and higher values of $H$ and $\lambda E$ than for 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 understorey plants and optimizing the content and distribution of nitrogen in leaves are other important factors, beside optimal leaf angle, that merit consideration. On the other hand, these calculations lend support for the development of fast growing poplar clones with erect leaves.

**Table 8.** Annual sums of net CO$_2$ exchange and latent and sensible heat exchange as a function of leaf inclination angles and clumping. We assumed the mean angle for the erect canopy was 80 degrees and it was 10 degrees for the plane canopy. 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 ($\Omega$) was 1.00.
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 RuBP regeneration is limited by electron transport ($W_j$) in balance with the carboxylation 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 shows vertical profiles of $W_j$ and $W_c$ on sunlit and shaded leaves for noon on a typical summer day. Theoretically, we observe that there is close theoretical agreement between $W_c$ and $W_j$ on the sun leaves, suggesting that the canopy has coordinated the distribution of N, as suggested 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, as noted by $W_c$ being less than $W_j$. Photosynthesis by shade leaves, on the other hand, is theoretically light limited, as $W_j$ is less than $W_c$ throughout the canopy.

<table>
<thead>
<tr>
<th>NEE ($gC m^{-2} a^{-1}$)</th>
<th>-577</th>
<th>-354</th>
<th>-720</th>
<th>-1126</th>
<th>-224</th>
</tr>
</thead>
<tbody>
<tr>
<td>$\lambda E$ ($MJ m^{-2} a^{-1}$)</td>
<td>1690</td>
<td>1551</td>
<td>1774</td>
<td>2023</td>
<td>1473</td>
</tr>
<tr>
<td>$H$ ($MJ m^{-2} a^{-1}$)</td>
<td>1096</td>
<td>1032</td>
<td>1095</td>
<td>1171</td>
<td>1008</td>
</tr>
</tbody>
</table>
How sensitive are fluxes of mass and energy of a deciduous forest to vertical variations in photosynthetic capacity? We address this question with calculations for two cases. 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 prior studies that started with a given amount of nitrogen in the canopy and asked whether it was better to distributed it uniformly or with a gradient; in this situation $V_{cmax}$ at the top of the canopy in 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 carbon dioxide, 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 to leaves deep in the canopy, that never experience high rates of photosynthesis.

**Table 9** Annual sums of net CO₂ exchange and latent and sensible heat exchange as a function of varying the maximum carboxylation velocity with height in the canopy.

<table>
<thead>
<tr>
<th></th>
<th>V_{cmax=\text{f(z)}}</th>
<th>V_{cmax=\text{const}}</th>
<th>% difference</th>
</tr>
</thead>
<tbody>
<tr>
<td>NEE (gC m⁻² a⁻¹)</td>
<td>-577</td>
<td>-578</td>
<td>0.2</td>
</tr>
<tr>
<td>λE (MJ m⁻² a⁻¹)</td>
<td>1690</td>
<td>1709</td>
<td>1.1</td>
</tr>
<tr>
<td>H (MJ m⁻² a⁻¹)</td>
<td>1096</td>
<td>1076</td>
<td>-1.8</td>
</tr>
</tbody>
</table>

Many studies show a close coupling between stomatal conductance and leaf photosynthesis (Collatz et al., 1991; Makela et al., 1995). In this paper, stomatal conductance is computed as a function of leaf photosynthesis (A), relative humidity (rh) and CO₂ at the leaf surface (Cₜ) (Collatz et al., 1991):

\[ g_s = \frac{k \cdot A \cdot rh}{C_s} \]  

Surveying the literature one observes that the proportionality constant, k, tends to center near 10, but ranges between 8 and 12 for temperate broadleaved forest species (Harley and Baldocchi, 1995; Medlyn et al. 2001) and crops (Collatz et al., 1991). This proportionality constant decreases from this metric as soil moisture decreases (Sala and Tenhunen, 1996) or for trees growing in xeric Mediterranean climates (Medlyn et al, 2001). Table 10 shows how sensitive calculations of annual NEE,  λE and H are to moderate (20%) changes in k. Model computations indicate that the prescribed changes in k translate into only 10% differences in NEE, but that they alter energy partitioning significantly. Increasing k to 12 produces a change in Bowen ratio from 0.64 to 0.47.
Reducing $k$ to 8 increases Bowen ratio to near 0.8. In comparison, the measured Bowen ratio at this site, during 1997, was 0.72 (Wilson and Baldocchi, 2000).

**Table 10.** Impacts of the stomatal conductance coefficient on CO$_2$, latent and sensible heat exchange.

<table>
<thead>
<tr>
<th></th>
<th>$k=9.5$</th>
<th>$k=8$</th>
<th>$k=12$</th>
</tr>
</thead>
<tbody>
<tr>
<td>$\text{NEE (gC m}^{-2} \text{ a}^{-1})$</td>
<td>-577</td>
<td>-528</td>
<td>-630</td>
</tr>
<tr>
<td>$\lambda E \ (\text{MJ m}^{-2} \text{ a}^{-1})$</td>
<td>1690</td>
<td>1544</td>
<td>1897</td>
</tr>
<tr>
<td>$H \ (\text{MJ m}^{-2} \text{ a}^{-1})$</td>
<td>1096</td>
<td>1233</td>
<td>900</td>
</tr>
</tbody>
</table>

4.3 The Environment

Radiation, temperature, vapor pressure deficit, CO$_2$ 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 state conditions, measured above the canopy, to the local conditions normal to a leaves, buried throughout in 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 upwards. The air temperature profile that responds to this forcing is shown in Figure 3. Starting from the ground, air temperature increase with height, up to the densest portion of the canopy crown. Then 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 K-theory models are unable to capture this physical phenomenon because large scale eddies dominate the transfer of material and energy in a canopy. K-theory models also do not reflect accurately the feedbacks between local air temperature and the source-sink strength of sensible heat. Stochastic Lagrangian (as used here), higher order closure and large eddy simulations models (Meyers and Paw U, 1986; Su et al., 1996; Pyles et al., 2000; Albertson et al., 2001), on the other hand, are capable of reproducing counter-gradient transfer of mass and energy and the source-sink distribution of sensible heat more accurately.

![Graph](image)

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

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., 2001). 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 remains un-quantified is how changes in direct and diffuse solar radiation, as may occur by volcanic eruptions, dust or aerosols (Olmo et al., 1999), may affect carbon dioxide, water vapor and energy exchange over the course of a year?

To address this question, we re-computed 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 gC 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.

On face value, these calculations imply that the Mt. Pinatubo eruption may have led to an increase in regional photosynthesis, which would be consistent with the slowed rate of increase of atmospheric CO$_2$ that was observed at Mauna Loa (Keeling and Whorf, 2000). Yet one has to be careful with extrapolation of our analysis to other conditions. The calculations presented in Table 11 assumed that changes in radiation did not affect the annual temperature. Climate records show that the Mt Pinatubo eruption was followed by a decrease in mean global annual temperature (Hanson et al., 1996), a 33% increase in diffuse radiation and a small reduction (3%) in global solar radiation (Olmo et al., 1999). Atmospheric cooling can reduce respiration, an occurrence that would slow the rate of atmospheric CO$_2$ growth, too. Climatic cooling can also shorten the growing season by delaying the phenological expansion of leaves. This latter effect can reduce the net uptake of CO$_2$ of temperate deciduous forests by about 6 gC m$^{-2}$ day$^{-1}$ for each day that the growing season is shortened (Baldocchi and Wilson, 2001),
offsetting the positive impacts of aerosols that would occur on canopy photosynthesis during the growing season.

Table 11. Impacts of diffuse and direct radiation fraction on CO₂, latent and sensible heat exchange.

<table>
<thead>
<tr>
<th></th>
<th>reference</th>
<th>direct radiation, -20%</th>
<th>% difference</th>
</tr>
</thead>
<tbody>
<tr>
<td>NEE (gC m⁻² a⁻¹)</td>
<td>-577</td>
<td>-655</td>
<td>13.5</td>
</tr>
<tr>
<td>λE (MJ m⁻² a⁻¹)</td>
<td>1690</td>
<td>1729</td>
<td>2.3</td>
</tr>
<tr>
<td>H (MJ m⁻² a⁻¹)</td>
<td>1096</td>
<td>1058</td>
<td>-3.5</td>
</tr>
</tbody>
</table>

5. Conclusions

Modeling carbon dioxide and water vapor exchange between forests and the atmosphere involves overcoming many sources of complexity and uncertainty. These uncertainties stem from structural and functional features of the forest stand, natural variability of the environment and deficiencies in our knowledge. From a modeling point of view, we partition 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: to what accuracy do we need to compute carbon dioxide and water vapor fluxes and how much detail is needed to achieve a specified level of accuracy? Since the truth may never be known with 100% confidence, it is hoped that information produced by more complex biophysical model may be the closer to the
‘truth’ (see Kuhn, 1996). Model tests by our colleagues (e.g. Sinclair et al., 1976; dePury and Farquhar, 1997; Pyles et al., 2000; Williams et al., 2001) and us (Baldocchi and Meyers, 2000; Baldocchi and Wilson, 2001) tend to support this contention. Detailed biophysical models perform well (often accounting for over 80% of the variance and producing flux values within 90% of the mean measured values) because they use ecophysiological rules to constrain their model parameters (rather than tune them arbitrarily) and they quantify non-linear functions correctly, by considering the distinct environments of sun and shade leaves.

The temporal and spatial resolution of a biophysical model has implications on its accuracy and performance, too. 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; Wu et al., 2000; Pyles et al. 2000). In practice, dividing a canopy into 20 to 30 layers or maintaining a layer thickness that contains less then 0.5 m² of leaf area per unit land area seems adequate. With regards to temporal resolution, dynamic and prognostic biophysical models like SIB-2 (Sellers et al., 1997) and ACASA (Pyles et al., 2001), 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 courser 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 that is associated with mass and energy exchange (Baldocchi and Wilson, 2001).

In closing, better representations of canopy carbon dioxide and water vapor exchange between forests and the atmosphere will come at the expense of more and
better data. Long-term eddy flux records, as provided by projects such as FLUXNET (Baldocchi et al., 2001), will continue to provide a constraint and guide post on the accuracy of such models. But, application of these biophysical models over longer time scales will also require information on how leaf area index, soil respiration and photosynthetic capacity vary over the course of a season (e.g., Niinemets et al., 1999; Wohlfahrt et al., 2000; Wilson et al., 2001a). 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., 1997; Cramer et al., 1999). We also advocate more use of ecophysiological rules and relationships to constrain and quantify model parameters (e.g. Schulze et al., 1994; Wullschleger, 1993) and predict their dynamics (Niinemets and Kull, 1999; Wirtz, 2000).

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**References**


Law, B.E., S. van Tuyl, A. Cescatti and D.D. Baldocchi. 2001. Estimation of leaf area index in open canopy ponderosa pine forests at different successional stages and


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