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Agricultural and Forest Meteorology 90 (1998) 1–25

AGRICULTURAL
AND
FOREST
METEOROLOGY

On using eco-physiological, micrometeorological and biogeochemical theory to evaluate carbon dioxide, water vapor and trace gas fluxes over vegetation: a perspective

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Received 22 April 1997; accepted 18 September 1997

Abstract

How eco-physiological, biogeochemical and micrometeorological theory can be used to compute biosphere–atmosphere, trace gas exchange rates is discussed within the framework of a process model. The accuracy of the theory is tested by comparing computations of mass and energy flux densities (water vapor, sensible heat, CO_2 and ozone) against eddy covariance measurements over five distinct canopies (wheat, potato and soybean crops and a temperate broad-leaved and a boreal conifer forest). Once tested, the theory is used to evaluate how interactions between climate and vegetation might influence leaf area and photosynthetic capacity and, in turn, alter energy balance partitioning and the transfer rates of CO_2 and other trace gases over vegetation canopies. Model parameters, derived from biogeochemical and eco-physiological principles, enabled the model to estimate rates of mass and energy exchange with reasonable fidelity. In particular, the theory reproduced the magnitudes and distinct diurnal patterns associated with mass and energy fluxes over a spectrum of vegetation types. Model sensitivity tests revealed that variations in leaf area index and photosynthetic capacity interacted to increase rates of evaporation and carbon dioxide and pollutant uptake, greatly, and in a curvilinear manner. Finally, we conclude that the assignment of many model parameters according to plant functional type has much potential for use in global and regional scale ecosystem, climate and biogeochemistry models. Published by Elsevier Science B.V.

Keywords: Biosphere–atmosphere interactions; Trace gas fluxes; Eddy covariance measurements; Evaporation; Carbon dioxide; Biogeochemistry

1. Introduction

Diagnosing and predicting how concentrations of trace gases may vary with time in the atmosphere depends, in part, on the rates that materials flow into and out of the atmospheric reservoir. Consequently, the study of the physical, biological and chemical processes controlling these fluxes and how trace gas fluxes may respond to environmental perturbations are subjects of much environmental research (e.g., Aber, 1992; Ojima, 1992). Central to this research is the design, construction, testing and application of mathematical models that compute rates of biosphere–atmosphere trace gas exchange. In particular, trace gas flux models are needed to specify rates of mass and energy fluxes in and out of the atmosphere

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0168-1923/98/$19.00 Published by Elsevier Science B.V.
PII S0168-1923(97)00072-5

and for extrapolating information about trace gas fluxes in time and space. Models can also identify weaknesses in our understanding of controlling processes and can be used to design field experiments.

Philosophically, a biosphere–atmosphere gas exchange model should meet several design criteria. Foremost, it should consider the exchanges of *energy and mass* in concert. Flows of energy need to be calculated because the biosphere requires energy to perform work. With regard trace gas exchange, activities requiring energy and work include biosynthesis, evaporation, transport of nutrients and carbon dioxide fixation. Concurrently, these activities require flows of substrate material. Water and carbon and nitrogen based compounds are the most important forms of matter for the sustenance of life.

If we expect to apply the philosophical concepts, just forwarded, towards calculating mass and energy transfer, we must know something about the properties of the underlying surface. One school of ecophysiologists defines components of the biosphere by functional properties (e.g., Running and Hunt, 1993; Potter et al., 1993; Field et al., 1995; DeFries et al., 1995; Bonan, 1995; Neilson, 1995). Vegetative properties having a strong influence on the control the fluxes of water, carbon and energy include: (1) growth form (herbaceous or woody); (2) seasonality (evergreen or deciduous); (3) leaf type (broadleaf or conifer, dicot or monocot); (4) photosynthetic pathway (C_3 or C_4); (5) longevity (annual or perennial) and (6) type or intensity of disturbance (fire, cultivation) (DeFries et al., 1995).

Parameterizing land-surface properties of an atmosphere–biosphere, trace gas exchange model by functional type has several attractions. First, this scheme minimizes the necessity to consider the attributes of every genus and species, in a model domain, when simulating modeling mass and energy fluxes. Consequently, the assignment of many model parameters becomes more systematic. On the other hand, this framework tells us nothing about how to evaluate model parameters or their range of values. In this regard, we propose that properties of trace gas flux models should be linked to biogeochemical and eco-physiological principles. We make this assertion because pools and flows of water, carbon and nitrogen move in concert (see Schimel et al., 1991a; McMurtrie et al., 1992; Aber, 1992; Running and Hunt, 1993; Bonan, 1995; Field et al., 1995). This linked approach also constrains many model parameters by each other (Schulze et al., 1994; Korner, 1994).

An example of linkages between carbon and water cycles and trace gas fluxes involves the conservative interdependence between net primary productivity and evaporation. One body of literature shows that the ratio between canopy photosynthesis (or dry matter production) and evaporation is a modest function of the atmospheric humidity deficit (Cowan, 1982; Tanner and Sinclair, 1983). Another body of data shows a positive correlation between leaf area index and the water balance of a canopy (precipitation minus evaporation) (Gholz, 1982; Waring and Schlesinger, 1985; Woodward, 1987; Bonan, 1993). A conclusion drawn from these two sets of data is that the attainment of high rates of net primary productivity (or the growth of a dense canopy) comes at the expense of high evaporation rates.

A linkage between carbon and nitrogen budgets and trace gas fluxes is manifested through the dependency of photosynthetic capacity on a leaf's nitrogen content (Wong et al., 1985; Field and Mooney, 1986; Field, 1991) or the rate a leaf takes up nitrogen (Woodward and Smith, 1994). Photosynthesis is linked to nitrogen because the enzyme Rubisco, a nitrogen rich compound, catalyses carboxylation. An outcome of the link between photosynthesis and leaf nitrogen content is a dependency of several photosynthetic model parameters on one another (e.g., Amthor, 1994). Wullschleger (1993), for example, reports that maximum rates of carboxylation are a strong function of the maximum rate of electron transport. In a parallel vein, Ceulemans and Saugier (1991), Gifford (1994) and Ryan et al. (1994) present evidence showing that rates of dark respiration are constrained by rates of photosynthesis.

The link between the water and nitrogen cycles is mediated by the stomata. Diffusion through the stomata is the major route by which water vapor, CO_2 and many gaseous pollutants (ozone, SO_2, NO_2, and NH_3) are transferred between the biosphere and atmosphere. Since stomatal conductance is linked to photosynthesis (Wong et al., 1985; Collatz et al., 1991; Korner, 1994), it is also correlated with leaf nitrogen content (Schulze et al., 1994; Kelliher et al., 1994).

At present, several research teams are applying eco-physiological, biophysical and biogeochemical principles to calculate trace gas fluxes at the paddock, landscape, regional and global scales. Examples include model studies on carbon dioxide fluxes (Warnant et al., 1994; Woodward et al., 1995; Leuning et al., 1995; Denning et al., 1996; Williams et al., 1996), ozone deposition (Amthor et al., 1994), and energy exchange (Bonan, 1995; Sellers et al., 1996). Since the use of these concepts is relatively new, they have not been tested widely against field measurements of mass and energy exchange. Nor have these concepts been tested over an assortment of vegetation types (a task that can readily be performed by members of the agricultural and forest meteorology community).

In this paper, we describe a biosphere–atmosphere, trace gas exchange model that combines eco-physiological, biogeochemical and micrometeorological theory (denoted CANVEG). Then, we test the theory's ability to compute mass and energy fluxes (water vapor, sensible heat, CO_2 and ozone) over five distinctly different canopies (wheat, potato and soybean crops and a temperate broad-leaved and a boreal conifer forest) using eddy covariance measurements. Finally, we apply the theory to evaluate how interactions between climate and vegetation may influence leaf area and photosynthetic capacity and, in turn, alter energy balance partitioning and CO_2 and pollutant transfer over vegetation canopies.

2. Theory

2.1. Concepts

Fluxes of mass and energy occur through a balance between demand and supply functions. When the leaf is a sink, physiological processes (e.g., photosynthesis) control rates of demand, while the supply of material from the atmosphere is limited by diffusion through the leaf boundary layer and stomatal pores. Conversely, when a leaf is a trace gas source, physiology controls production (e.g., respiration, transpiration, isoprene synthesis) and molecular diffusion through the stomata and leaf boundary layers limits the transfer of material to the atmosphere.

Two classes of models dominate the field of air-surface exchange. One class of models treats the canopy as a layer of vegetation overlying the soil (e.g., Monteith, 1965; Sinclair et al., 1976; Amthor, 1994). This model class is commonly denoted as the 'big-leaf' approach. It is the simplest model class and uses the fewest number of parameters. Despite the appeal of this approach, it has several limitations. One perceived weakness revolves around the fact that many model parameters of 'big leaf' models do not relate to measurable physiological or physical quantities (Finnigan and Raupach, 1987; Amthor, 1994; Sellers et al., 1996). In practice, these properties are often defined by tuning model parameters with field scale flux measurements (Monteith, 1965; Sellers et al., 1989; Lloyd et al., 1995). Another potential weakness of the 'big-leaf' model approach concerns the impact of neglecting microclimatic gradients and intermittent turbulence on the determination of fluxes (Norman, 1980; De Pury and Farguhar, 1997). Many physiological and physical processes, related to biosphere–atmosphere trace gas exchange, are regulated in a non-linear manner by a host of abiotic variables (solar and terrestrial radiation, temperature, humidity, wind speed and soil moisture). Since many of these driving variables possess non-Gaussian probability distributions, the expected value of a non-linear function may not equal the functional evaluation at the mean of the independent variable (Norman, 1980; Smolander, 1984; Rastetter et al., 1992).

An antidote to the limitations of the 'big-leaf' scaling framework is to employ a multi-layer, integration model. By dividing a canopy into multiple layers, one can simulate how abiotic variables vary with depth through the canopy and how they differ on the sunlit and shaded leaves (Norman, 1979; Meyers and Paw U., 1987; Baldocchi, 1992; De Pury and Farguhar, 1997). Subsequently, one can use this information to evaluate how non-linear biological processes respond to imposed environmental forcings.

Despite the attractiveness of the 'multi-layer' approach, it has been criticized for requiring a large number of parameters (Raupach and Finnigan, 1988) and for being difficult to apply in ecosystem and global change models (Amthor, 1994). We attempt to assuage this criticism, by demonstrating that eco-physiological and biogeochemical concepts can be used to parameterize a multi-layer, biosphere–atmosphere gas exchange model.

A schematic representation of how trace gas fluxes are linked to the carbon, nutrient and water cycles is shown in Fig. 1. Central to this figure is the plant stand and its leaf area index. Information on leaf area index is paramount since it determines the population of biologically active material that is exchanging gas and energy with the atmosphere. Quantitatively, a canopy's integrated source or sink strength is proportional to the product of its leaf area and its surface conductance (Finnigan, 1985; Meyers and Paw U., 1987). The amount of leaf area also affects how much solar radiation and momentum is intercepted and absorbed by the plant and soil surfaces, respectively (Norman, 1979; Myneni et al., 1989).

A qualitative understanding on how leaf area index directly and indirectly controls the partitioning of mass and energy exchange among the vegetation and the soil can be acquired by following some of the arrows on Fig. 1. For one example, consider the case of an ecosystem which maintains a low leaf area index (less than two). First, a sparse canopy will intercept less sunlight than a dense stand. Hence, it will experience relatively low rates of photosynthesis

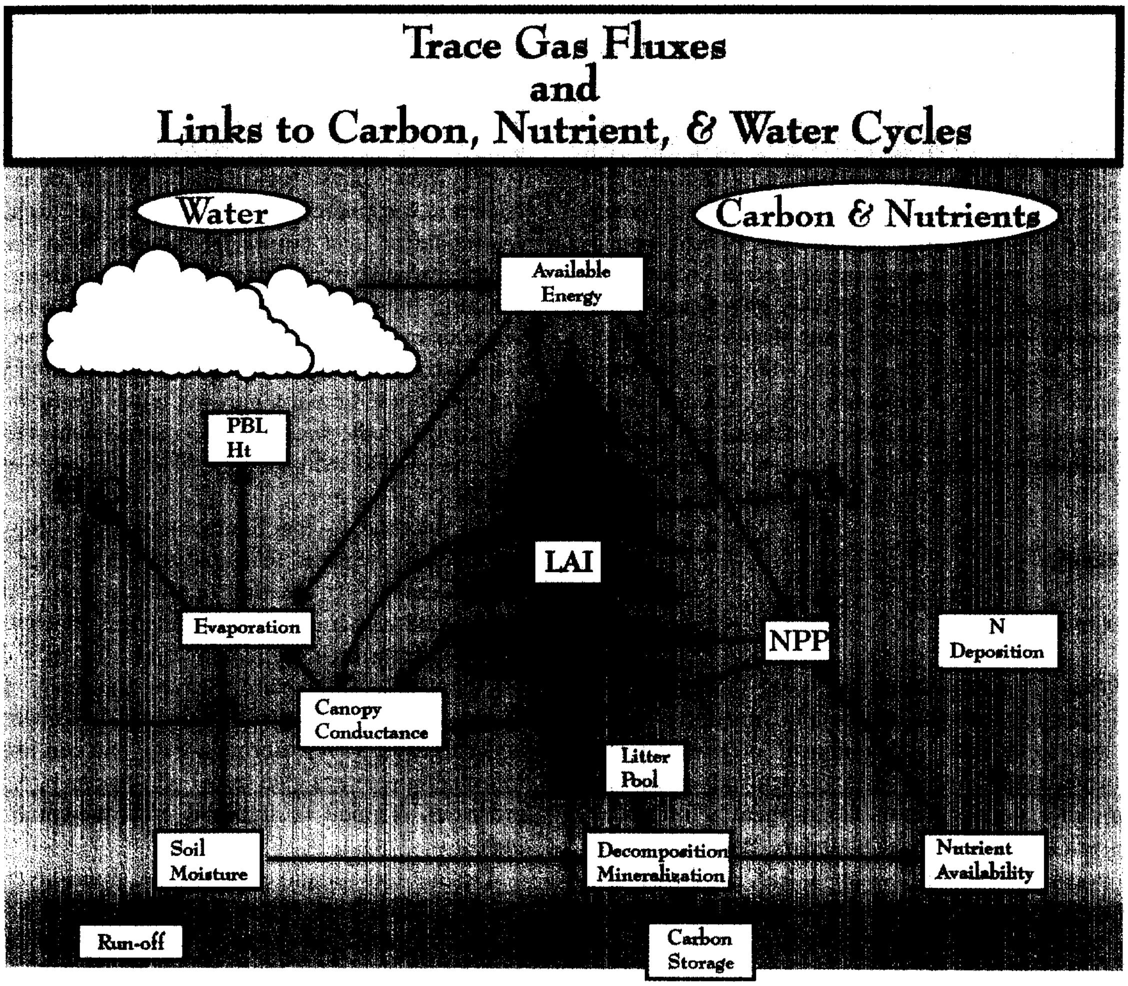

Fig. 1. A schematic representation of the flows of energy, carbon and nutrients between a plant canopy and the atmosphere and how they contribute to the fluxes of water vapor, sensible heat and CO_2 between land and the atmosphere.

per unit ground area. These two occurrences will translate into relatively low canopy conductances, low rates of evaporation and relatively higher rates of sensible heat transfer. One short-term consequence of these linkages and feedbacks will be on the height to which the planetary boundary layer develops over the course of a day (McNaughton and Spriggs, 1986). A deeper and drier planetary boundary layer will develop over a sparse, unproductive region than would otherwise occur over a moister and more productive region (Betts et al., 1996; Nobre et al., 1996). A long-term consequence of these plant–atmosphere interactions involves lower inputs of biomass and nutrients into the soil system. This effect will set limits on decomposition, net primary productivity, leaf area and evaporation (e.g., Schimel et al., 1991a; McMurtrie et al., 1992; Aber, 1992).

2.2. Integrating mass and energy fluxes from leaf to canopy scales

In this exercise, we use a one-dimensional, multilayer biosphere–atmosphere gas exchange model to compute water vapor, CO_2 and ozone flux densities. The model consists of coupled micrometeorological and eco-physiological modules. The micrometeorological modules compute leaf and soil energy exchange, turbulent diffusion, scalar concentration profiles and radiative transfer through the canopy. Environmental variables, computed with the micrometeorological module, in turn, drive the physiological modules that compute leaf photosynthesis, stomatal conductance, transpiration and leaf, bole and soil/root respiration. We discuss the salient aspects of the model system, we name CANVEG, below.

2.3. Modeling stomatal conductance, leaf photosynthesis and respiration: a linked approach for examining environmental control and feedbacks on mass and energy exchange

For the past decade, a majority of climate and weather models (e.g., Dickinson, 1983; Sellers et al., 1986; Noilhan and Planton, 1989; Avissar and Pielke, 1991; Mascart et al., 1991; Dickinson, 1991) and gaseous deposition models (e.g., Baldocchi et al., 1987; Hicks et al., 1987; Meyers and Baldocchi, 1988; Wesely, 1989; Gao and Wesely, 1995) have used the multiplicative and empirical model of Jarvis (1976) to calculate stomatal conductance of leaves, g_s. This stomatal conductance model has much appeal, for it considers the impact of a light, temperature, humidity and soil moisture conditions on stomatal conductance and gaseous deposition. On the other hand, a multiplicative, stomatal conductance algorithm requires a considerable amount of tuning and calibration to yield reasonable mass and energy flux densities (Baldocchi et al., 1987; Sellers et al., 1989; Mascart et al., 1991; Baldocchi, 1992). For example, information on maximum conductances and curvature coefficients for the light, temperature, humidity deficit and soil moisture response functions are needed. Furthermore, this model does not account for interactive effects between environmental variables. Nor is this model readily amenable for quantifying the impacts of CO_2 concentration and leaf nitrogen on stomatal conductance, transpiration and photosynthesis.

Advances in eco-physiological theory have lead to an alternative approach for calculating stomatal conductance. In the late 1970s, Wong et al. (1979) reported that stomatal conductance was tightly coupled to leaf photosynthesis. They argued that stomata opened and closed to keep the ratio between intercellular and atmospheric CO_2 nearly constant (near 0.7 for C_3 plants). Ball et al. (1988), Leuning (1990) and Collatz et al. (1991) drew upon those observations and their own laboratory experiments to publish a model that linked stomatal conductance to leaf photosynthesis, humidity deficits and CO_2 concentration at the leaf's surface (C_s).

$$g_s = \frac{m A \,\mathrm{rh}}{C_s} + g_0 \qquad (1)$$

The coefficient m is a dimensionless slope, rh is relative humidity, g_0 is the zero intercept, and A (μmol m^{-2} s^{-1}) is leaf photosynthesis. Eq. (1) has several appealing attributes. First, this scheme provides us with an algorithm that is able to calculate how stomatal conductance correlates with eco-physiological and biogeochemical factors, such as leaf photosynthetic capacity and nutrition (Schulze et al., 1994; Kelliher et al., 1994; Korner, 1994; Leuning et al., 1995) and ambient CO_2 concentration. Second, this stomatal conductance model requires fewer tuning parameters. In particular, there is an accumulating body of evidence is showing that m is a constrained parameter; it centers around 10, ±20% (Collatz et al., 1991; Leuning, 1990; Harley and Tenhunen, 1991; De Pury, 1995). Only under conditions of moderate to severe soil moisture deficits (Sala and Tenhunen, 1994; Baldocchi, 1997) or cases involving old trees with decreased hydraulic conductivity (Falge et al., 1996) does m seem to deviate significantly from a cardinal value.

Though we choose to use Eq. (1) as our stomatal conductance model, we note that it has not escaped criticism. Some investigators argue that stomatal conductance is dependent on water vapor saturation deficit (Aphalo and Jarvis, 1991; Leuning, 1995) and transpiration (Mott and Parkhurst, 1991; Monteith, 1995), rather than relative humidity. This limitation, however, seems to be consequential only under dry soil and atmospheric conditions (De Pury, 1995).

The evaluation of Eq. (1) depends upon a photosynthesis and respiration model. The biochemical equations for the carbon exchange processes are taken from Farquhar et al. (1980), Farquhar and von Caemmerer (1982) and Harley et al. (1992). These equations are mechanistic and have been tested widely (Collatz et al., 1991; Harley et al., 1992; Leuning et al., 1995).

Leaf photosynthesis (A) is a function of the carboxylation (V_c), oxygenation (V_O, photorespiration) and dark respiration (R_d) rates of CO_2 exchange between the leaf and the atmosphere.

$$A = V_c - 0.5V_O - R_d \tag{2}$$

The term: $V_c - 0.5\ V_o$ is expressed by Farquhar et al. (1980) as:

$$V_c - 0.5V_O = \min[W_c, W_j]\left(1 - \frac{\Gamma}{C_i}\right). \tag{3}$$

Equation 3 is assessed by adopting the minimum value between W_c, the rate of carboxylation when ribulose bisphosphate (RuBP) is saturated, and W_j, the carboxylation rate when RuBP regeneration is limited by electron transport. The variable, Γ, is the CO_2 compensation point in the absence of dark respiration and C_i is the intercellular CO_2 concentration. Evaluating Eq. (3), in terms of C_i, implicitly assumes that the mesophyll conductance is infinite. There are conditions when this assumption may be flawed (Loreto et al., 1992; Harley et al., 1992), but most determinations of kinetic coefficients in the literature are based on this assumption.

If W_c is minimal, then:

$$V_c - 0.5V_O = W_c = \frac{V_{cmax}(C_i - \Gamma)}{C_i + K_c\left(1 + \frac{[O_2]}{K_O}\right)}. \tag{4}$$

In this case V_{cmax} is the maximum carboxylation rate when RuBP is saturated and K_O and K_c are the Michaelis–Menten coefficients for O_2 and CO_2. If W_j is minimal, then:

$$V_c - 0.5V_O = W_j = \frac{J(C_i - \Gamma)}{4C_i - 8\Gamma} \tag{5}$$

where J is the potential rate of electron transport. J is evaluated as a function of incident photosynthetic photon flux density (I):

$$J = \frac{\alpha I}{\sqrt{1 + \frac{\alpha^2 I^2}{J_{max}^2}}}. \tag{6}$$

The variable, α, is the quantum yield and J_{max} is the maximum rate of electron transport.

A simple conductance relation is employed to express C_i:

$$C_i = C_s - \frac{A}{g_s} \tag{7}$$

where C_s is the surface CO_2 concentration and g_s is stomatal conductance. Finally, the system of equations and unknowns for computing leaf photosynthesis is closed by expressing the CO_2 concentration at the leaf's surface (C_s) in terms of the atmosphere's CO_2 concentration (C_a) and the conductance across the laminar boundary layer of a leaf (g_b):

$$C_s = C_a - \frac{A}{g_b}. \tag{8}$$

The variables, C_a and g_b, are external inputs to the leaf biochemistry model and are determined from the micrometeorology of the canopy. Either numerical or analytical solutions for the coupled leaf photosynthesis-stomatal conductance model can be used to compute these fluxes (e.g., Collatz et al., 1991; Baldocchi, 1994, Leuning et al., 1995; Nikolov et al., 1995; Su et al., 1996).

The evaluation of some photosynthetic model parameters merits further comment. The coefficients for $J_{\max}$, V_{cmax} and Γ, K_{O_2}, K_{C} and R_{d} are strong, non-linear functions of temperature (Johnson and Thornley, 1985; Harley and Tenhunen, 1991). One temperature function used for $J_{\max}$ and V_{cmax} is:

$$f(T)=\frac{\exp\left(E_{\mathrm{a}}\cdot(T_{\mathrm{l}}-T_{\mathrm{opt}})/(R\cdot T_{\mathrm{l}}\cdot T_{\mathrm{opt}})\right)}{1+\exp\left(\dfrac{\Delta S\cdot T_{\mathrm{l}}-\Delta H)}{R\cdot T_{\mathrm{l}}}\right)}. \qquad (9)$$

E_{a} is the activation energy, R is the universal gas constant, T_{l} is leaf temperature and T_{opt} is the optimum temperature. The terms ΔH and ΔS represent changes in enthalpy and entropy (Johnson and Thornley, 1985). The Arrenhius temperature function is used to describe temperature dependencies for Γ, K_{O_2}, K_{C} and R_{d}, with respect to a reference temperature (T_{ref}):

$$f(T)=\exp(E_{\mathrm{a}}\cdot(T_{\mathrm{l}}-T_{\mathrm{ref}})/(R\cdot T_{\mathrm{l}}\cdot T_{\mathrm{ref}})). \qquad (10)$$

2.4. Dark respiration

Respiration provides energy for metabolism and synthesis. Many researchers report that variations in respiration rates deviate from a base rate according to an exponential function of leaf temperature (Amthor, 1994; Ryan et al., 1994). Several approaches are available for determining the base rate of respiration. McCree (1974) uses an additive equation that splits respiration into components associated with growth and maintenance. Another option is to scale dark respiration according to photosynthetic capacity (Ceulemans and Saugier, 1991; Gifford, 1994; Ryan et al., 1994). Gifford (1994), for example, reports that the ratio between respiration and photosynthesis is about 0.4 for a wide range of vegetation. He also reports that this ratio is independent of temperature. In a similar vein, Ryan et al. (1994) reported that the ratio between respiration and photosynthesis for conifers is less conservative. Their data ranges between 30 and 70%, but higher respiratory costs were associated with older trees. At the leaf level, Collatz et al. (1991) and Amthor (1994) model dark respiration as a function of V_{cmax}—a typical value being R_{d} equals 0.015 times V_{cmax}. Their assumption implies that R_{d} is a function of leaf nitrogen.

2.5. Micrometeorology

The conservation budget for a passive scalar provides the foundation for computing scalar fluxes and their local ambient concentrations. If a canopy is horizontally homogeneous and environmental conditions are steady, the scalar conservation equation can be expressed as an equality between the change, with height, of the vertical turbulent flux and the diffusive source/sink strength, $S(c,z)$:

$$\frac{\partial F(c,z)}{\partial z}=S(c,z). \qquad (11)$$

The diffusive source/sink strength of a scalar in a unit volume of leaves is proportional to the concentration gradient normal to individual leaves, the surface area of individual leaves and the number leaves in the volume. The diffusive source strength can be expressed in the form of a resistance–analog relationship (Finnigan, 1985; Meyers and Paw U., 1987):

$$S(c,z)=-\rho_{\mathrm{a}}a(z)\frac{(C(z)-C_{\mathrm{i}})}{r_{\mathrm{b}}(z)+r_{\mathrm{s}}(z)} \qquad (12)$$

where $a(z)$ is the leaf area density, $(C(z)-C_{\mathrm{i}})$ is the concentration difference between air outside the laminar boundary layer of leaves and the air within the stomatal cavity, r_{b} is the boundary layer resistance to molecular diffusion, r_{s} is the stomatal resistance and ρ_{a} is air density.

2.6. Turbulence and diffusion

The interdependence between sources and sinks ($S(c,z)$) and scalar concentrations ($C(z)$) requires the use of a turbulent diffusion model. We used a Lagrangian random walk model to evaluate diffusion. Although, an Eulerian model, which adopts higher order closure principles, can be used instead

(Finnigan, 1985; Meyers and Paw U., 1987; Raupach, 1988).

With regard to the Lagrangian model, concentration differences between an arbitrary level (C_z) and a reference level (C_r) (located above a plant canopy) were computed by summing the contributions of material diffusing to or from different layers in the canopy (Raupach, 1988). Numerically, this relation is expressed as:

$$C_z - C_r = \sum_{j=1}^{N} S_j(C_j) D_{z,j} \Delta z_j \tag{13}$$

The dispersion matrix ($D_{z,j}$) was calculated using the random walk algorithm of Thomson (1987). A discussion on how this random walk model is implemented in our canopy micrometeorology model is presented elsewhere (Baldocchi, 1992; Baldocchi and Harley, 1995).

Leaf boundary layer resistances for molecular compounds were computed using flat plate theory (Schuepp, 1993). In principle such resistances, under forced convection, are a function of a leaf's length scale (l), molecular diffusivity (d) and the Sherwood number, Sh.

$$r_b = \frac{l}{d \cdot \mathrm{Sh}} \tag{14}$$

To acquire wind speed, which are required to assess Sh, we applied the logarithmic wind law above the canopy and the exponential wind profile within it. Under free convection, we applied an alternative algorithm, which is a function of the Grasshof number and the leaf to air temperature difference.

2.7. Radiative transfer

The transfer of photons through the canopy must be simulated to evaluate photosynthesis, stomatal conductance and leaf and soil energy balances. A radiative transfer model is also needed to evaluate the area of sunlit and shaded leaves. For a random canopy, the sunlit leaf area equals the integration of the probability of beam penetration, with respect to leaf area.

The radiative transfer model was derived from probabilistic theory (Norman, 1979; Myneni et al., 1989). The radiative transfer model assumes that foliage is randomly distributed in space, that leaves have a spherical inclination angle distribution and the sun is a point source. In this case, the probability of beam penetration is calculated using a Poisson distribution:

$$P_O = \exp\left(-\frac{LG}{\sin\beta}\right) \tag{15}$$

where L is leaf area index, β is the solar elevation angle and G is the foliage orientation function. G represents the direction cosine between the sun and the mean leaf normal. For the ideal case, in which leaves have a spherical angle distribution, G is constant and equals one-half.

Native vegetation has clumped foliage. In such circumstances, the Poisson probability density function is inadequate for computing probabilities of photon transmission through vegetation. Instead, a Markov model can be employed (Myneni et al., 1989; Chen, 1996), where the probability of beam penetration is:

$$P_O = \exp\left(-\frac{LG\Omega}{\sin\beta}\right) \tag{16}$$

Ω is a clumping factor and ranges between zero and one.

The probability of diffuse radiation penetration is computed by integrating Eq. (15) or Eq. (16) over a sky's hemisphere. The scattering of light is computed using this slab approach of Norman (1979).

2.8. Leaf energy balance

Leaf temperature was calculated to determine enzymatic rates associated with carboxylation, electron transport, and respiration and to evaluate transpiration, sensible heat fluxes and infrared emission. Leaf temperature was computed by evaluating its energy balance. An analytical solution to a quadratic form of the leaf energy balance was used (Paw U., 1987; Su et al., 1996).

2.9. Soil

Soil constitutes the lowest boundary of a canopy-scale, water vapor, CO_2 and trace gas exchange model. Flux densities of convective and conductive heat transfer and evaporation at the soil/litter boundary and soil temperature profiles were computed using a ten-layer numerical soil heat transfer model (Campbell, 1985). Surface energy fluxes were computed using an analytical solution to a surface's energy balance. Soil evaporation was computed using an algorithm reported in Mahfouf and Noilhan (1991):

$$E_s = \frac{\rho}{R\mathrm{soil}}(\varphi \cdot q_{\mathrm{sat}}(T) - q_a) \qquad (17)$$

where R_{soil} is the resistance of the soil to evaporation, ρ is air density, φ is the relative humidity of the soil matrix, q_a is the mixing ratio of the air and q_{sat} is the saturated mixing ratio. For these calculations we assumed R_{soil} was 1500 s m^{-1} and that the vapor pressure at the evaporating site was 80% of the saturation vapor pressure (φ q_{sat} (T)). For future reference, relations between volumetric water content, R_{soil} and φ are given in Mahfouf and Noilhan (1991).

Soil respiration was computed with the Arrhenius equation (Eq. (10)) (Lloyd and Taylor, 1994). For this paper, base respiration rates where taken from studies reported in the literature (Table 1). However, it is possible to scale soil respiration rates to external climatic and plant variables. At the ecosystem scale, annual rates of soil respiration correlate with annual temperature, annual precipitation and net primary productivity (Raich and Schlesinger, 1992).

2.10. Model parameterization

An objective of this work is to examine how well a leaf to canopy integration model can simulate water vapor, sensible heat and CO_2 exchange rates over a range of environmental conditions using simple input variables and constrained parameters. Variable model inputs include photosynthetic photon flux density, air temperature, humidity, wind speed and soil temperature at a deep reference point. CO_2 concentration is required for the photosynthesis model. For cases when CO_2 data was not available we assumed it equalled 350 ppm. The key extrinsic plant input parameters are leaf area index and V_{cmax}. Other model parameters are scaled to these two parameters, or they are representative of the vegetation's functional type (e.g., roughness length, zero plane displacement, canopy height).

Table 1 lists the parameter values used for the model calculations presented in this paper. Most parameter values for V_{cmax} were taken from the review of Wullschleger (1993); photosynthetic parameter values for the temperate forest are taken from Baldocchi and Harley (1995). Values of J_{max} and R_d were calculated with scaling relations described by Wullschleger (1993), Leuning (1997) and Collatz et al. (1991). For leaf temperatures equalling 20°C, J_{max} equals 2.68 times V_{cmax} (Leuning, 1997). Kinetic coefficients for biochemical reactions were taken from Farquhar et al. (1980) and Harley and Tenhunen (1991). All model runs were performed assuming that the quantum yield equalled 0.055 mol CO_2 (mol quanta)$^{-1}$, an intermediate between the values recommended by Farquhar et al. (1980) and Harley and Tenhunen (1991).

For most cases, the slope coefficient (m) was assumed to equal 10 and the zero intercept was 0.01 mol m^{-2} s^{-1}. These coefficients agree with data derived from a wide range of C_3 species (Leuning, 1990; Collatz et al., 1991). Only for the conifer case was a different m value employed, based on recent empirical evidence by Joe Berry and Sullivan et al. (1997).

Evaluation of the Lagrangian dispersion matrix requires information on the vertical variation in the standard deviation of vertical velocity (σ_w). Algorithms and parameters presented by Raupach (1988) were used to calculate the dispersion matrix for a given friction velocity. Dispersion matrices for other conditions were scaled to friction velocity.

For aerodynamic calculations, the roughness parameter was set at 10% of canopy height. We assumed that the zero plane displacement (d) was 60% of canopy height for the crops and conifer stand. For the deciduous forest, d was set at 85% of canopy height. An exponential relation was employed to calculate wind speeds within the canopy. The attenuation coefficient was set at 2.5, a reasonable assumptions for canopies with leaf area indices ranging between two and six and having a zero plane dis-

Table 1
Key properties of the vegetation canopies used in the in the model computations of trace gas flux densities

Variable	Potato	Wheat	Soybean	Temperate broad-leaved forest	Boreal conifer forest
Latitude	45.7	45.7	40.4	35.9	53.9
Longitude	119.7	119.7	88.3	84.3	104.4
Study: year	1992	1991	1996	1995	1994
Study: days	159–160	158–169	240–249	168–182	202–207
Leaf area index	2.2	2.85	4.75	4.7	2.04
Canopy height (m)	0.4	0.8	1.0	24	14
V_{cmax} at 25°C (μmol m^{-2} s^{-1})	72	83	75	39.7	45.7
Stomatal factor, m	10	10	10	9.5	7.5
Ω^{a}	1.0	1.0	1.0	0.84	0.735
R_b (μmol m^{-2} s^{-1})	11	11	0.18; 0.59	0.71	2.5
T_b (K)	300	300	273; 293	273	288
E_a^{b}	53,000	53,000	40,372; 62,468	51,609	49,458
Leaf dimension (m)	0.77	0.16	0.1	0.1	0.05
Functional properties	Herb, dicot, C_3, annual	herb, monocot, C_3, annual	herb, dicot, C_3, annual	woody, dicot, C_3, perennial, deciduous	Woody, conifer, C_3, perennial, evergreen

[a] Markov clumping factors for the forest canopies were derived from our field measurements (temperate forest) or taken from Chen (1996). We assumed the clumping factor equaled one for crops.

[b] Soil respiration values were gleaned from the literature. Wheat: Rochette et al. (1991); Soybeans Rochette et al. (1995) or da Costa et al. (1986); Deciduous forest: Hanson et al. (1993); jack pine forest: Lavigne et al. (1997). We assumed that soil respiration rates from the potato and wheat were equal since the study was on nearby sandy soils.

placement equal to 60% of canopy height (Pereira and Shaw, 1980).

For computations of radiative transfer, leaf reflectance and transmittance values were taken from Norman (1979). Values of the Markov clumping parameter are listed in Table 1.

2.11. Model testing

2.11.1. Site and crop characteristics

Model calculations were tested against fluxes of mass and energy measured over a wheat, potato, and soybean crop and a temperate broad-leaved and a boreal conifer forest canopy. Attributes of the sites and vegetation are reported in Table 1.

2.11.2. Eddy flux density measurements

The eddy covariance method was used to measure flux densities of water vapor, CO_2, sensible heat and ozone over the crops and forests. Negative flux densities symbolize uptake by the surface and positive values denote the loss of mass and energy by the crop. The eddy flux measurement system captured most flux-containing eddies by sampling the sensors rapidly (10 Hz) and by averaging velocity-scalar fluctuation products for 30 min.

2.11.3. Instrumentation and data acquisition

Orthogonal wind velocities and virtual temperature were measured with a sonic anemometer. An Applied Technology anemometer (model SWS-211/3K, Boulder, CO) was employed over wheat, potatoes and the forest experiments. A Gill ultrasonic anemometer (Lymington, England) was employed during the soybean experiment. Water vapor and CO_2 concentrations were measured with an open-path infrared absorption spectrometer (Auble and Meyers, 1992). Mean CO_2 concentrations were measured with a closed path infrared spectrometer (LICOR, model LI-6252, Lincoln, NE).

During the 1996 soybean field campaign, mean background ozone concentrations were measured with an ozone monitor (Dasibi Environmental, model 100B-AH). Ozone fluctuations were measured with a system that detects photons emitted from the chemiluminescent reaction between ozone and a target impregnated with Coumarin (Gusten et al., 1992). The system sampled air through a 3-m teflon tube, whose opening was placed near the sonic anemometer.

Voltages from the sonic anemometer and the chemical sensors were sampled and digitized at 10 Hz by an analog to digital converter. Digital signals were then transmitted from the field to a personal computer. The computer software transformed the data and computed fluxes. Turbulent fluctuations were computed as the difference between instantaneous and mean quantities. Mean values were determined, in real-time, using a digital recursive filter with a 400 s time constant. The coordinate system of the three orthogonal wind vectors was rotated to obtain a mean vertical velocity of zero and to orient the longitudinal component (u) along the mean wind. Data were rejected when winds were not coming from the field, when it was raining or when the irrigation system passed through the upwind fetch. The infrared spectrometer measures fluctuations in scalar density, not mixing ratio. Consequently, CO_2 and water vapor flux densities were corrected for density fluctuations imposed by temperature and humidity fluctuations.

2.11.4. Ancillary meteorological and plant measurements

Soil temperature was measured with a thermocouple probe down to 0.32 m below the surface. Photosynthetic photon flux density (I) and the net radiation balance (R_n) were measured above each crop a quantum sensor (LICOR, model LI-190S) and a net radiometer (REBS Model Q7, Seattle, WA), respectively. Air temperature and relative humidity were measured with appropriate sensors (Vaisala, model HMP 35A). Wind speed and direction were measured with a wind monitor (RM Young, model 05701, Traverse City, MI). Ancillary meteorological variables were sampled at 1 Hz with a Campbell Scientific (model CR-21x, Logan, UT) data logger and the data were averaged over one-half periods. Solar panels and batteries powered the soybean flux measurement system.

3. Results

3.1. Verifying the model scheme

The ability of the integrated biosphere–atmosphere model (CANVEG) to calculate latent heat fluxes over three crops (potato, wheat, and soybeans), whose leaf area indices differ widely, is shown in Fig. 2. A second, and tougher test of the CANVEG model system, involves its ability to predict evaporation over non-uniform, temperate hardwood and boreal conifer forests (Fig. 3). To obtain a representative ensemble of data with robust statistics (e.g., Moncrieff et al., 1996), diurnal patterns of model calculations were tested against field measurements that were obtained over a duration of 2 to 14 days during the growing season, when the soil was well supplied with moisture.

Overall, the CANVEG model system was able to mimic the magnitude and diurnal course of evaporation over the five canopies, whose leaf area indices ranged between 2 and 5 and whose photosynthetic

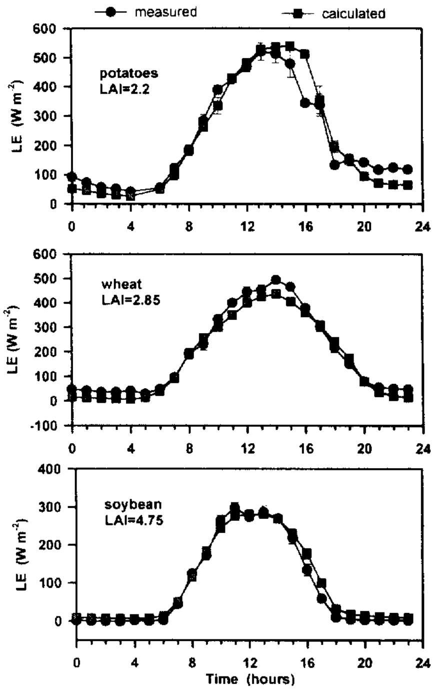

Fig. 2. Mean diurnal patterns of latent heat flux densities measured and calculated over a potato, wheat and soybean canopy.

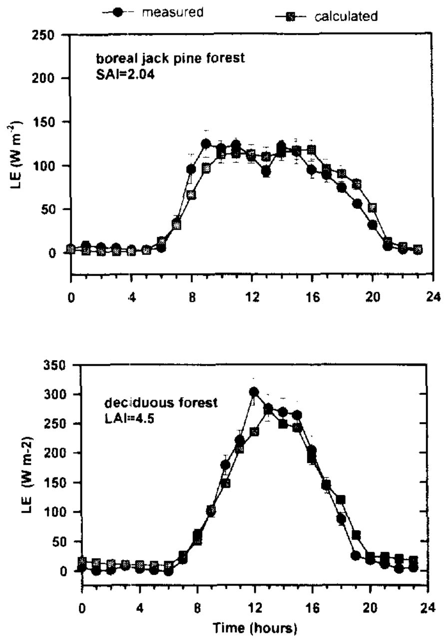

Fig. 3. Mean diurnal patterns of latent heat flux densities measured and calculated over a temperate broad-leaved and a boreal jack pine forest.

capacities ranged between 35 and 80 μmol m^{-2} s^{-1}. Furthermore, the model was able to calculate reasonable values of LE over canopies growing in a range of climate regimes and experiencing evaporation rates from near zero to 600 W m^{-2}. With respect to the crop canopies, the CANVEG model was able to simulate relatively greater evaporation rates measured over the wheat and potato crops, despite their leaf area indices being almost two units less than the soybean and temperate forest canopies. The existence of these irrigated crops in a dry, windy climate can account for much of this difference.

To obtain favorable model results over forests, two attributes of the model system had to be modified. Because vegetation of forests is clumped, we found it necessary to calculate radiative transfer with a model that employs the Markov probability function (Eq. (16)), instead of the Poisson equation (Eq. (15)) (see Baldocchi and Harley, 1995; Baldocchi, 1997). Second, the boreal jack pine forest was an old stand, growing on well-drained and nutrient poor sand. Physiological observations on old conifers (Falge et al., 1996; Ryan and Yoder, 1997; Dang et al., 1997) show that photosynthesis and stomatal conductance is reduced by a hydraulic limitation derived from slow growth and smaller tracheids and vessels. Using physiological gas exchange measurements on jack pine needles (Sullivan et al., 1997; Joe Berry, Carnegie Institute of Washington, Stanford, CA, personal communication) we applied as lower value of the m coefficient of the stomatal conductance model (Eq. (1)) to account for this effect (see Table 1).

The ability of the model to reproduce markedly lower rates of LE lends theoretical support to the empirical hypothesis that we (Baldocchi et al., 1997) and Ryan and Yoder (1997) have forwarded in earlier papers. We argue that short-term, biophysical factors and long-term biogeochemical processes interact to reduce rates of evaporation of a boreal jack pine forest. On the short term, humidity deficits and a hydraulic response to the relatively low soil moisture content restricts stomatal opening. On the long term, growth, hydraulic conductance and photosynthetic capacity are restricted in the boreal region due to climate and low rates of decomposition and nutrient cycling. In turn, these factors limit the stand's maximal canopy conductance and its leaf area.

The favorable results reported here for LE are valid only for well watered conditions and dry canopies. When a forest experiences soil moisture deficits, afternoon estimates of LE, based on CANVEG, differs greatly from measurements (Baldocchi, 1997). A tree is an organ with leaves and has a capacity to store water in its boles. The transport of water through these two compartments causes hysteresis between rates of soil water uptake and transpiration (Jones, 1982, Williams et al., 1996). So the diurnal variability of the transport resistance exerted by the conducting xylem of tree boles must be considered when modeling evaporation over water-stressed forests. At the other extreme, the presence of moisture on the surface of leaves causes evaporation rates to exceed rates predicted by the Priestly–Taylor equation, which is a function of available energy (Shuttleworth and Calder, 1979). We did not consider dew fall and its evaporation.

An ability to model sensible heat flux well is required to model the rate of growth of the planetary boundary layer, cloud development and convective precipitation (e.g., McNaughton and Spriggs, 1986;

Betts et al., 1996). Fig. 4 presents comparisons between sensible heat flux measurements and model calculations over the three crops that are being examined. On average, measurements and model calculations experienced similar diurnal trends. And absolute values generally agreed within 20 W m^{-2} of one another. Better agreement between measurements and model calculations of sensible heat flux density were observed for the forest cases (Fig. 5). The model system was able to predict daytime sensible heat fluxes that approached 300 W m^{-2} over the jack pine stand, as well rates that were half as large over the deciduous forest. Only at night was there a tendency for the model to underestimate sensible heat fluxes markedly.

Fig. 6 presents measured and modeled CO_2 flux densities for the potato, wheat, and soybeans crops, while Fig. 7 presents a similar comparison for temperate deciduous and boreal conifer forest canopies, respectively. In general, the CANVEG model was able to mimic the wide range of maximum CO_2 exchange that was encountered by the diverse canopy types, where the lowest values occurred over the boreal forest and greatest values were associated with the fertilized and highly productive wheat crop. For example, it was able to predict the maximum rates of net ecosystem–atmosphere exchange (N_E), during the day, that ranged between -8 and -40 μmol m^{-2} s^{-1}. Also noteworthy, was the ability of the CANVEG model to mimic the distinct mono-modal and bi-modal diurnal patterns that were experienced by the crops and forests.

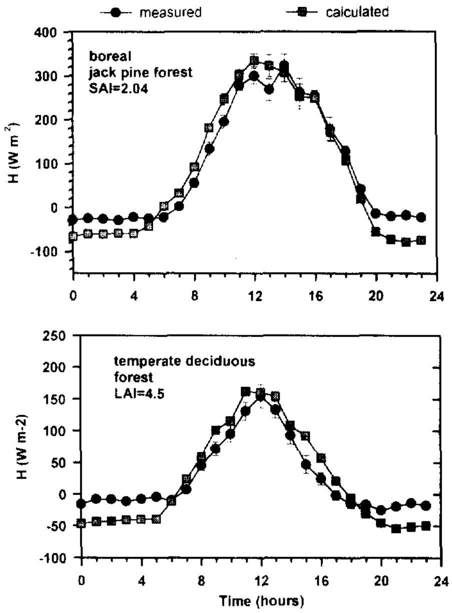

Fig. 5. Mean diurnal patterns of sensible heat flux densities measured and calculated over a temperate broad-leaved and a boreal jack pine forest.

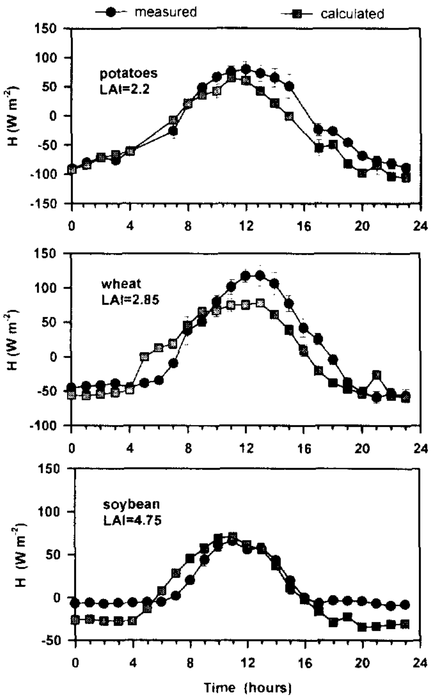

Fig. 4. Mean diurnal patterns of sensible heat flux densities measured and calculated over a potato, wheat and soybean canopy.

To obtain these favorable results for calculating CO_2 exchange rates, we had to account for several functional attributes delineated by DeFries et al. (1995). With respect to the soybean simulations, we adjusted the literature value of leaf photosynthetic capacity for a seasonal effect. The soybean data were acquired late in the growing season, after pods had set. During this phase, empirical data shows that photosynthetic capacity is diminished from its peak value by a factor of 1.11 (Rochette et al., 1995), so we reduced V_{cmax}, that was obtained in the review of

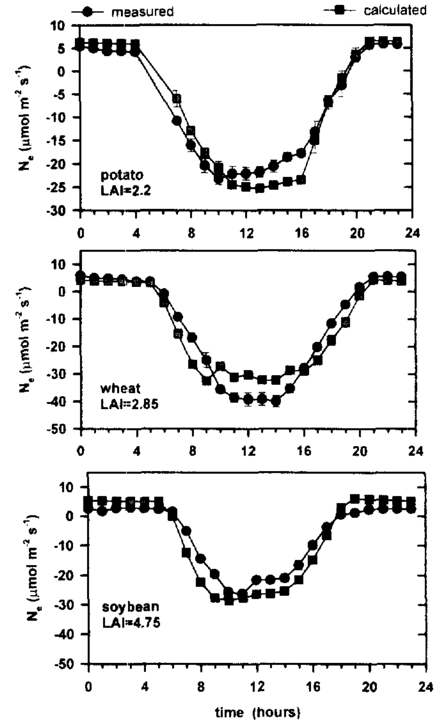

Fig. 6. Mean diurnal patterns of carbon dioxide flux densities measured and calculated over a potato, wheat and soybean canopy.

Wullschleger (1993), by this factor. With regard to the forests, it was necessary to apply the Markov model instead of the Poisson model for computing the probability of beam transfer (Chen, 1996; Baldocchi and Harley, 1995).

With respect to respiration of the crops and forests, the magnitude of nocturnal CO_2 effluxes, measured and calculated, was relatively constrained. Typical values ranged between 3 and 7 μmol m^{-2} s^{-1} over all stands. Nocturnal respiration rates (positive CO_2 flux densities) over the crops agreed within the bounds of experimental error of the typically quoted for flux covariance measurements (±20%) (Moncrieff et al., 1996). In this instance, potential errors attributed to the assessment of the storage of CO_2 in the air were small. The crops were short, they were on flat terrain, they were far from anthropogenic combustion sources and they were exposed to adequate nocturnal ventilation. In contrast, biases between measured and modeled respiration rates over the forests were significant. The data from the Oak Ridge, TN, temperate forest, for example, was obtained over undulating terrain and during relatively calm, but intermittent, nocturnal conditions. Under this circumstance, it is harder to satisfy the assumption of horizontally homogeneity and steady-state conditions (Moncrieff et al., 1996; Lee et al., 1996). Hence, there is a potential for CO_2 to drain out the bottom of the volume of air under study and not be sensed by the eddy covariance or storage profile measurement systems.

Next we apply the model principles, that have been expounded upon, towards calculating ozone deposition over a soybean field. Computations of ozone deposition velocities agreed well with most field measurements, and followed the same diurnal course (Fig. 8). The model, however, failed to simulate the extreme measurements, that approached 1

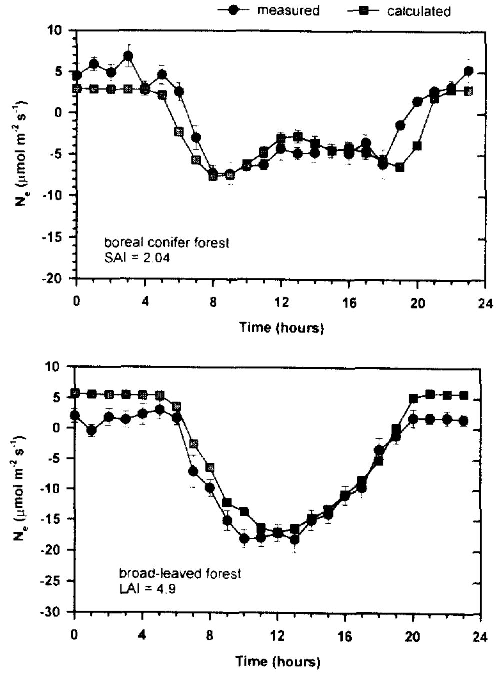

Fig. 7. Mean diurnal patterns of carbon dioxide flux densities measured and calculated over a temperate broad-leaved and a boreal jack pine forest.

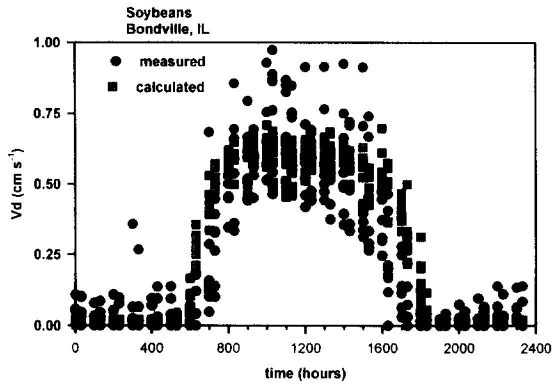

Fig. 8. Mean diurnal pattern of ozone deposition velocities measured and calculated over a soybean crop.

cm s^{-1}, and it did not mimic the band of observations recorded at night.

4. Discussion

With a working theory at hand, we evaluate how interactions between climate and vegetation may influence leaf area and photosynthetic capacity, and in turn govern energy balance partitioning and CO_2 and trace gas transfer.

For diagnostic purposes and model application, leaf area index needs to be measured or assigned. Latitudinal, longitudinal and altitudinal variations in the availability of soil moisture and temperature will affect decomposition, nutrient availability, plant growth and ultimately a canopy's leaf area index (McMurtrie et al., 1992; Running and Hunt, 1993; Bonan, 1995; Neilson, 1995).

To illustrate and quantify the impact of climatic and ecological factors on leaf area index (L), we derived a simple, empirical, scaling index. The index is non-dimensional and is a function of annual evaporation, precipitation and leaf nitrogen content. The rationale for adopting this index stems from empirical studies reporting a relation between leaf area index and ecological variables. For example, leaf area index has been correlated directly with net primary productivity (Gholz et al., 1979; Waring and Schlesinger, 1985), a site's water balance and its annual temperature (Gholz et al., 1979; Waring and Schlesinger, 1985; Tanner and Sinclair, 1983; Neilson, 1995). An indirect link between leaf area and the nutrient cycle can be inferred through the correlation between photosynthetic capacity and leaf nitrogen content (Field and Mooney, 1986; Woodward and Smith, 1994).

Fig. 9 shows a positive relation between L and this simple scaling index among plant stands ranging from grass to forests and across tropical to boreal climate zones. The correlation between the independent and dependent variables accounts for 67% of the variation in leaf area index observed. From this figure, it can be surmised that humid, temperate and tropical regions tend to maintain canopies with relatively high leaf areas (greater than four), while arid

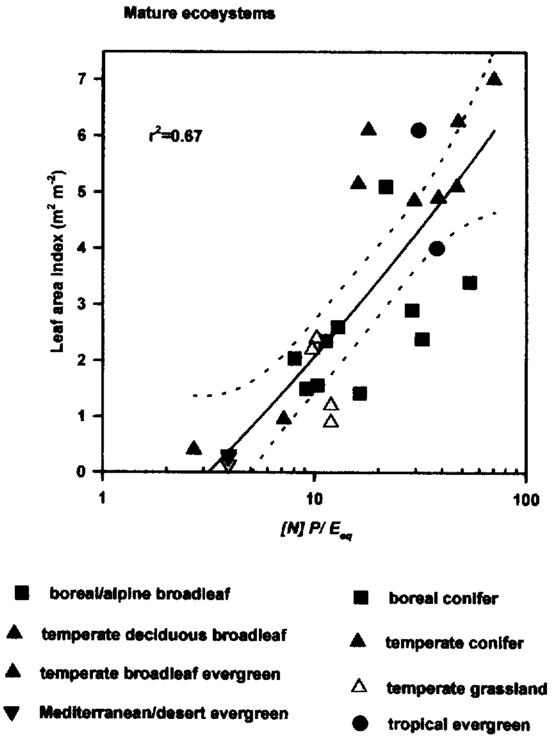

Fig. 9. An empirical relationship between potential leaf area index and an index derived from the product of leaf nitrogen ([N]), annual precipitation (P) and annual equilibrium evaporation (E_{eq}). Annual E_{eq} was computed as $s/(s+\gamma)\ R_n$. Literature sources include: Schulze et al., 1995; Chen, 1996; Hutchison et al., 1982; Galloux et al., 1981; Neumann et al., 1989; Hollinger et al., 1994; Valentini et al., 1996; Jornada LTER database; Runyon et al., 1993; Schimel et al., 1991b; Roberts et al., 1996; and the EUROFLUX database.

and cold regions are only be able to sustain canopies with low leaf areas (less than two). The dependency of leaf area index on a few climatic and biological variables concurs with analyses by Woodward (1987) and Neilson (1995). On the other hand, this leaf area scaling index does a poor job of predicting variations of L within plant types at a given locale (e.g., the grassland and boreal forest data). Hence, this relation should be applied with caution at the intra-biome scale.

In addition to spatial differences in leaf area, many deciduous forests and crops experience a wide range of leaf area indices over the course of a growing season. Between bud break and full leaf expansion, for example, leaf area index of a broad-leaved forest can range between zero and six (Breda and Granier, 1996). And the leaf area index of many crops may range between zero and five over the course of the growing season. The seasonal greening of the biosphere has been shown to affect the surface energy (Schwartz, 1992) and carbon (Myneni et al., 1997) balances. How variations in leaf area index and leaf photosynthetic capacity interact to influence the partitioning of available energy into latent heat and CO_2 exchange are explored theoretically next.

Model sensitivity calculations were run for a representative crop and deciduous forest, to account for their different aerodynamic properties. Diurnal courses of mass and energy exchange were calculated for a permutated range of leaf area indices (1 to 6) and maximum carboxylation capacities (25 to 100 μmol m^{-2} s^{-1}). For the sake of astronomical calculations, the crop was assumed to reside at Bondville, IL, and the forest was at Oak Ridge, TN. We also assumed environmental conditions representative of the middle of the growing season (day 180). Incoming solar radiation skies was calculated with the algorithms of Weiss and Norman (1985), on the assumption that the sky was relatively clear (diffuse radiation was about 10% of total). A sinusoidal pattern was applied to air temperature and friction velocity to mimic their daily march and time lags, with respect to solar radiation. Air temperature ranged between 25 and 28°C and was maximal at 1500 h. Friction velocity ($u*$) ranged between 0.1 and 0.5 m s^{-1}. Relative humidity varied between 85% at night and 65% during the afternoon. For the purpose of the following analysis we express energy partitioning as the ratio between LE and equilibrium LE, which is defined as:

$$\mathrm{LE}_{\mathrm{eq}} = \frac{s}{s+\gamma}(R_n - G) \qquad (18)$$

where s is the slope of the saturation vapor pressure–temperature curve and γ is the psychometric constant.

Theoretically, evaporation over crop and deciduous forest has a curvilinear dependence on the product of maximum carboxylation velocity (V_{cmax}) and leaf area index (Fig. 10). Normalized rates of evaporation increased with any combination of photosynthetic capacity or canopy cover until the dependent variable ($L \times V_{\mathrm{cmax}}$) approached a value equal to 300. For crops, which are fertilized and attain V_{cmax} values approaching 100 μmol m^{-2} s^{-1} (Wullschleger, 1993; Table 2), this critical value would correspond with a leaf area index near three. The critical point, where LE approaches saturation with respect to L, is close to the one shown experimentally by Brun et al. (1972).

The calculations shown in Fig. 10, allow us to draw the conclusion that normalized rates of evaporation are relatively low (below 1.0) over vegetation canopies that have low leaf area indices or low photosynthetic capacity. The mechanism for this observation is derived from the fact that these factors cause canopy conductance to be low. On the other hand, the model computes a value of LE/LE$_{\mathrm{eq}}$ approaching 1.1 for productive canopies with high

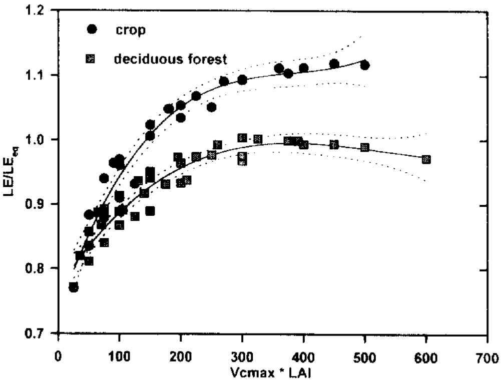

Fig. 10. The theoretical relationship between normalized latent heat flux densities (by their equilibrium value) and the product between maximum carboxylation velocity and leaf area index.

Table 2
A survey of general functional properties of several vegetation classes. Data were gleaned from the surveys published by Schulze et al. (1995) and Wullschleger (1993). Estimates of V_{cmax} were derived by the regression $V_{cmax} = 17.6 + 1.60$ [N], $r^2 = 0.65$. Estimates of potential LE/LE$_{eq}$ were derived from a regression fitted through the data in Fig. 10

Plant category	Leaf N (mg g^{-1})	V_{cmax} μmol (m^{-2} s^{-1})	LAI	Height (m)	Potential LE/LE$_{eq}$
Dicot crops, C_3	38	90	5^{++}	1	1.12
Monocot crops, C_3	33	68	3^{++}	1	1.03
Temperate broad-leaved forests	20	47	5^{++}	25	0.97
Evergreen conifer forests	11	25	7	25	0.93
Boreal conifer	10	25	2	15	0.81
Tropical forests	16	51	6	35	1.00
Schlerophyllous shrubs	11	53	4	10	0.96
Temperate grasslands	26	58^{*}	2	0.75	0.96
Tundra	20.5	50^{*}	1	0.25	0.85

leaf area indices. The asymptote is below observations from a wealth of field studies, which show that LE/LE$_{eq}$ of dry, closed canopies approaches 1.26 (McNaughton and Spriggs, 1986; Baldocchi et al., 1997). Errors in our calculation of net radiation, soil evaporation and soil heat flux densities or a neglect of the feedback between surface evaporation and the vapor pressure deficit of air in the mixed layer (McNaughton and Spriggs, 1986) may account for this slight underestimation.

Despite errors in the absolute value of LE/LE$_{eq}$, the model has the potential to give some insight on the impact of plant functional types on normalized evaporation. Using a regression derived from the calculations in Fig. 10 and characteristic inputs for L and V_{cmax} we produced a list of LE/LE$_{eq}$ values among plant functional types (Table 2). The largest values (> 1.10) are attributed to healthy mature crops, intermediate values (0.90 to 1.1) are associated with temperate and tropical broad-leaved forest and lowest values (< 0.90) are characteristic of boreal conifer and tundra canopies.

At first glance one, may conclude that LE rates of forests experience a diminishing return with respect to L. Such theoretical results would counter recent data published by Breda and Granier (1996); they report that the ratio of transpiration to potential evaporation, computed with the Penman equation, is a linear function of leaf area index, out to values of at least six. Breda and Granier (1996), however, normalized their transpiration measurements with a metric that was independent of soil heat flux density (the Penman equation). If we examine absolute values of LE, instead of normalized values, we also observe that LE increases with LAI (Fig. 11a). The ability of forest LE to increase with L occurs at the

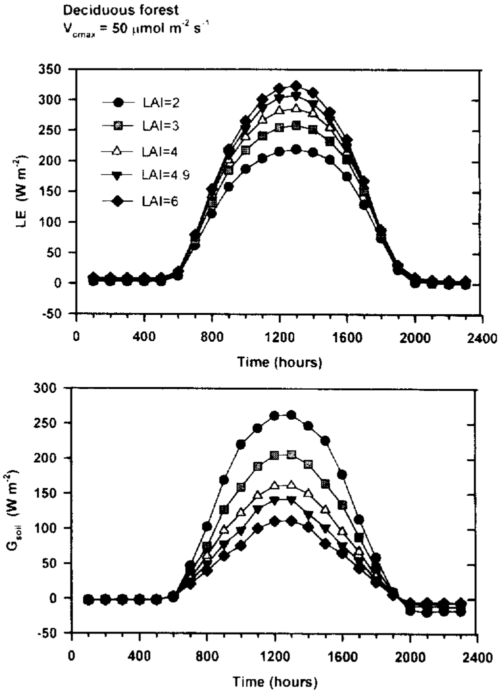

Fig. 11. (a) Mean diurnal pattern of latent heat flux density calculated for an array of leaf area indices. The data are applicable to a temperate broad-leaved forest, whose maximum carboxylation velocity is 50 μmol m^{-2} s^{-1}. The data are representative of the summertime growing season. (b) Mean diurnal pattern of soil heat flux density conducted into the soil under a broad-leaved forest.

expense of diminishing soil heat flux densities (Fig. 11b). Consequently, LE/LE_{eq} remains relatively constant, with respect to a leaf area, because available energy $(R_n - G)$ increases with L and can sustain an increase in LE.

An attribute of a process-based model is its capacity to diagnose the contribution of various components to the net flux of material between the biosphere and atmosphere. One important issue concerns the evaluation of canopy surface conductance, G_c. Lacking independent estimates of G_c for independent assessment of the Penman–Monteith equation, many researchers assume that G_c is equivalent to the integrated canopy stomatal conductance, G_s. The adoption of this assumption has received theoretical (Finnigan and Raupach, 1987; Paw U. and Meyers, 1989; Kelliher et al., 1994; Raupach, 1995; Leuning et al., 1995) and experimental (Baldocchi et al., 1987) criticism over the years. Finnigan and Raupach (1987), for example, showed that the ratio between G_c and G_s is a function of the ratio between surface and aerodynamic conductances.

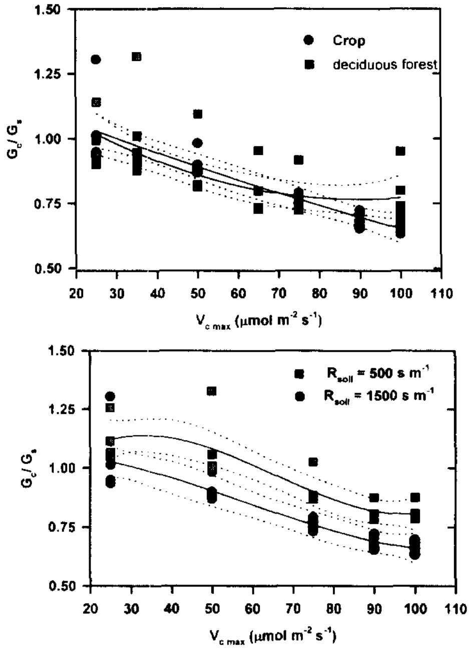

Fig. 12. (a) The theoretical influence of maximum carboxylation velocity on the ratio between the canopy surface conductance (G_c, computed by inverting the Penman–Monteith equation) and the integrated canopy stomatal conductance (G_s) for a crop and forest canopy with a relatively dry soil (R_{soil} equals 1500 s m^{-1}). (b) The theoretical influence of maximum carboxylation velocity on the ratio between the canopy surface conductance (computed by inverting the Penman–Monteith equation) and the integrated canopy stomatal conductance. Calculations are performed for conditions with a relatively dry (R_{soil} equals 1500 s m^{-1}) and wet (R_{soil} equals 500 s m^{-1}) soil.

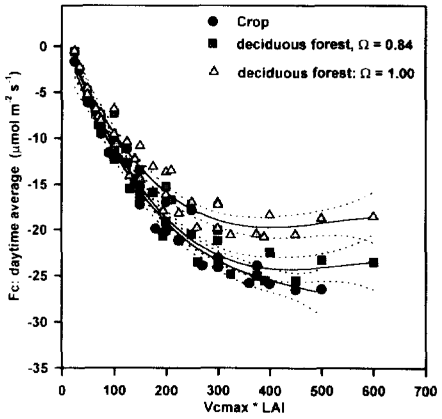

Fig. 13. The theoretical relationship between daytime averaged canopy CO_2 flux densities and the product between maximum carboxylation velocity and leaf area index. The data are applicable to a crop and deciduous broad-leaved forest for conditions of clumped and randomly distributed leaves.

We attempt to update earlier analyzes and examine the interrelationship between G_c and G_s using the CANVEG model. Fig. 12a shows that the ratio G_c/G_s, over canopies with relatively dry soils (R_{soil} equals 1500 s m^{-1}), decreases as the photosynthetic capacity of a canopy increases. The integrated stomatal conductance, G_s, of canopies with high photosynthetic capacity is able to exceed G_c since the canopy stomatal conductance is not diminished by the contribution of evaporation from a dry soil.

We did not find a meaningful correlation between G_c/G_s and L for the range and conditions evaluated. This independence of leaf area is in agreement with data reported by Kelliher et al. (1994) and may arise because both the numerator and denominator of the dependent variable are functions of leaf area. We also observed that results from the crop and forest, which possess different aerodynamic properties, overlap one another.

Another important variable, affecting G_c/G_s is the status of the underlying soil (Paw U. and Meyers, 1989; Raupach, 1995; Leuning et al., 1995), in circumstances with relatively wet and evaporating soils (e.g., R_{soil} equals 500 s m^{-1}), G_c exceeds G_s as V_{cmax} decreases (Fig. 12b). The wet soil provides another evaporating surface, thereby increasing G_c with respect to G_s.

Canopy CO_2 flux densities, averaged over the daylight period, are also a hyperbolic function of the product between photosynthetic capacity and leaf area (Fig. 13). While the dependency of F_c on V_{cmax} is elementary and expected, the influence of L on F_c is furtive. Greater L not only represents a greater population of photosynthesizing leaves, but it alters the relative amount of energy absorbed by the soil and leaves. Hence, sparse canopies have warmer soils and leaves. Consequently, soil respiration is a greater proportion of canopy photosynthesis when leaf area is low (Fig. 14), as soils are warmer and are able to respire at greater rates.

While we have identified that it is necessary to consider the effect of clumped leaves on integrating leaf-scale mass and energy fluxes to the canopy scale (Baldocchi and Harley, 1995; Figs. 3, 5 and 7), we have not quantified the magnitude of this impact. Fig. 15 shows that slightly higher values of LE/LE_{eq} (on the order of 5%) are calculated for the clumped forest when the product V_{cmax} and L exceeds about 300. On the other hand, clumping of leaves provides a distinct advantage for a forest to capture energy and to assimilate carbon, as compared with a case where leaves are randomly distributed in space ($\Omega = 1$) (Fig. 13). In fact, the clumping of leaves theoretically enables the CO_2 exchange rates, experienced by a forest, to approach values normally achieved by a crop canopy. An interesting question arising from this information is whether evolutionary selection has preferred canopies that contain plants with clumped leaves, as opposed to random distributions.

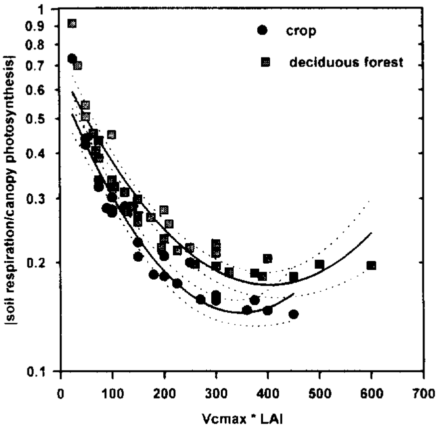

Fig. 14. The theoretical relationship between the ratio of soil respiration and CO_2 flux density and the product between maximum carboxylation velocity and leaf area index. The data are applicable to a crop and deciduous broad-leaved forest that possesses a clumped distribution of leaves.

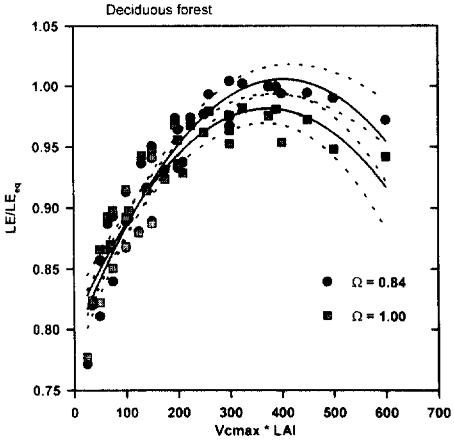

Fig. 15. The theoretical relationship between normalized latent heat flux densities (by their equilibrium value) and the product between maximum carboxylation velocity and leaf area index. The data are applicable to a deciduous broad-leaved forest for conditions of clumped and randomly distributed leaves.

Since stomatal diffusion is the dominant pathway for the exchange of many trace gases between the biosphere and atmosphere (e.g., ozone, SO_2, NO_2, NH_3), we expect rates of atmospheric deposition to depend upon photosynthetic capacity and leaf area index, too. Fig. 16 quantifies how the deposition velocity for ozone, V_d, responds to different values of L and V_{cmax}. Deposition velocities increase hyperbolically with an increase in either photosynthetic capacity or leaf area index. The dependence of V_d on these two variables saturates when their product exceeds about 300. Calculations in Fig. 16 exhibit more variability than what was observed in the analogous figures for LE and F_c. The sensitivity of deposition fluxes to variables defining its surface resistance depends upon the relative difference between the aerodynamic and surface conductance. Computations, not shown here, also suggest a signif-

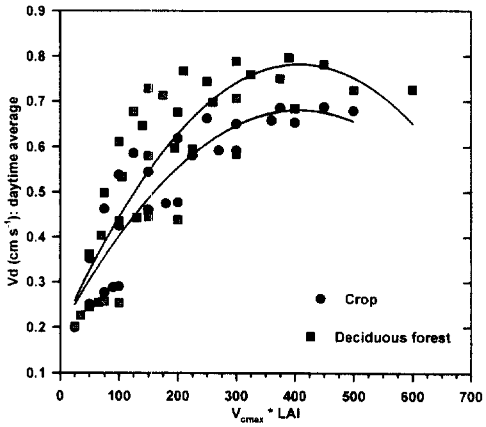

Fig. 16. The theoretical influence of maximum carboxylation velocity on the ozone deposition velocity of over a crop canopy.

icant feedback between deposition fluxes and a drawdown in the ozone concentration field within the canopy.

We have not attempted to investigate the role of nutrient profiles or the impact of cloud cover on the ability of a canopy to assimilate carbon, as interesting and relevant these exercises may be. Leuning et al. (1995), Ruimy et al. (1995) and others have treated these topics well and recently. So we refer the reader to those papers.

5. Conclusions

We showed that model parameters for a multi-layer, biosphere–atmosphere trace gas exchange model are constrained by one another and can be readily attained through the aid of biogeochemical and eco-physiological principles. Support for this contention is derived from the attainment of accurate estimates of canopy scale fluxes of CO_2, water vapor, sensible heat and ozone over a range of canopies, whose leaf area indices range from 2 to 5 and maximum carboxylation velocities range between 40 and 80 μmol m^{-2} s^{-1}. Sensitivity calculations showed a strong interactive effect of V_{cmax} and leaf area index on energy balance partitioning and net ecosystem carbon dioxide exchange. We encourage field studies to be conducted to test these concepts over a wider and more varied range of circumstances.

We emphasize that the schemes discussed here are applicable only to well-watered canopies with dry leaves. A more sophisticated approach for assigning or tuning model parameters will be needed for cases for old forests (Ryan and Yoder, 1997), vegetation suffering from soil moisture deficits (Williams et al., 1996; Baldocchi, 1997) and water-logged ecosystems. Application of the biophysical trace gas flux model on a seasonal basis will require information on how model parameters vary over the course of the growing season and how kinetic adapt with temperature.

We also stress that the model framework is one-dimensional. Therefore, this model system is not valid for open and sparse canopies, or for canopies on hills or mountains, where the interception and utilization of sunlight is three-dimensional (Daudet and Tchamitchian, 1993). Furthermore, the calculations, presented here, did not consider feedbacks surface fluxes and the thermodynamic state of the planetary boundary layer (e.g., McNaughton and Spriggs, 1986). However, this omission is not perceived as a limitation for the model scheme, discussed here, as it is intended to act as a module for the bottom boundary of climate, meteorological or biochemical models, where its incorporation into such higher scale models would allow this feedback to occur.

Finally, we encourage users of gaseous deposition models to update model algorithms derived at NOAA/ATDD and Argonne National Laboratory (e.g., Baldocchi et al., 1987; Hicks et al., 1987; Meyers and Baldocchi, 1988; Wesely, 1989; Gao and Wesely, 1995). We feel that the concepts described in this paper have potential for wide application with minimal tuning.

6. List of symbols

A	Leaf photosynthesis rate (μmol m^{-2} s^{-1})
a	Leaf area density (m^2 m^{-3})
C_a	Atmospheric CO_2 concentration (μmol m^{-1})
C_i	Internal CO_2 concentration (μmol m^{-1})

C_s	Leaf surface CO_2 concentration (μmol m^{-1})
d	Molecular diffusivity of gas of interest(mm^2 s^{-1})
$D_{z,j}$	Dispersion matrix (s m^{-1})
E_a	Activation energy
$F(c,z)$	Vertical flux of constituent c at height z
g_0	Stomatal conductance zero intercept (mol m^{-2} s^{-1})
g_b	Leaf boundary layer conductance (mol m^{-2} s^{-1})
g_s	Stomatal conductance (mol m^{-2} s^{-1})
G_c	Canopy surface conductance (mol m^{-2} s^{-1})
G_s	Canopy stomatal conductance (mol m^{-2} s^{-1})
I	Incident photosynthetic photon flux density (μmol m^{-2} s^{-1})
J	Potential rate of electron transport (μmol m^{-2} s^{-1})
$J_{\max}$	Maximum rate of electron transport (μmol m^{-2} s^{-1})
K_O	Michaelis–Menton constant for O_2
K_c	Michaelis–Menton constant for CO_2
l	Scale length of leaf (m)
L	Leaf area index (dimensionless)
m	Dimensionless slope coefficient
p_{sun}	Probability of sunlit leaf area
p_{shade}	Probability of shaded leaf area
R	Universal gas constant (8.314)
Re	Reynolds' number
R_d	Dark respiration rate (μmol m^{-2} s^{-1})
r_b	Leaf boundary layer resistance
rh	Relative humidity
Sh	Sherwood number
T_l	Leaf temperature (°C)
T_{opt}	Optimum leaf temperature for photosynthesis (°C)
V_c	Carboxylation rate (μmol m^{-2} s^{-1})
V_{cmax}	Maximum carboxylation rate when RuBP is saturated (μmol m^{-2} s^{-1})
V_d	Deposition velocity (cm s^{-1})
V_O	Oxygenation rate
W_c	Carboxylation rate when RuBP is saturated
W_j	Carboxylation rate when RuBP regenerationi is limited by electron transport
α	Quantum yield
ρ_a	Air density (kg m^{-3})
ΔH	Changes in enthalpy
ΔS	Changes in entropy

Acknowledgements

This paper is derived from a talk given at the 1996 AMS conference on Biometeorology and Aerobiology. This research was partially supported by NOAA's Office of Climate Change (projects associated with the GCIP and BOREAS programs), the US Department of Energy's ARM and Terrestrial Carbon Projects and NASA's Mission to Planet Earth project (under a contract from Oregon State University). The first author also acknowledges travel support from the Institut Nationale de la Recherche Agronomique, Statione de Bioclimatologie, Bordeaux, where a draft of this manuscript was written. Appreciation is expressed to Drs. Stan Wullschleger, Jon Lloyd, Bev Law for reading and commenting on an earlier draft of this manuscript. We also thank Dr. Joe Berry for supplying us with physiological data on jack pine and his comments. Thanks are also owed to Riccardo Valentini for his intellectual input on this topic during our many visits.

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