Tree Physiology 5, 357–377
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Turbulent transfer in a deciduous forest

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Received January 31, 1989

Summary

Carbon dioxide, water vapor and other passive scalars are physically transferred between a plant canopy and the atmosphere by turbulence. Intense and intermittent sweep and ejection events transfer most of the mass. Although the capacity for turbulence to transfer material is high, mass transfer is coupled to the diffusive source or sink strength of the foliage and soil and is ultimately limited to a minimum level set by the supply of material, or the demand for it. The diffusive source/sink strength of material leaving or entering leaves and the soil is a function of many physical, biological and chemical attributes and processes. These attributes and processes include the amount and distribution of foliage, the leaf boundary layer and surface resistances, the turbulence and radiative regimes in the canopy, biochemical and photochemical reactions and the scalar concentration field within and above the canopy and inside leaves and the soil. Here we discuss how these factors contribute to turbulent transfer in a deciduous forest.

Introduction

The transfer of gases, energy and momentum between a plant canopy and the overlying atmosphere is critical for the sustenance of life. Without turbulent transfer, plants cannot effectively exchange CO_2 and O_2, which are essential substrates for assimilation and respiration, and they cannot effectively transpire water vapor and convect sensible heat to maintain a viable heat balance.

The rate of turbulent transfer of scalars is dependent on biological, chemical and physical processes. Biological and biochemical processes synthesize and break down materials and regulate their transfer between the vegetation and the atmosphere. Physical processes govern turbulence and diffusion, which transport material between the atmosphere and the plant and soil surfaces. Chemical reactions in the canopy airspace affect turbulent transfer if reactive chemical constituents are present and if the time scales of the chemical reactions are shorter than those associated with turbulent transfer (Fitzjarrald and Lenschow 1983, Brost et al. 1988).

A strong link exists among the physical, biological and chemical processes that control the rate of turbulent transfer. Ambient conditions affect the biological and chemical sources and sinks, and the presence and nature of vegetation affect turbulence and the ambient conditions.

We can illustrate this link by considering CO_2 exchange. Photosynthesis and respiration are biochemical processes that consume and produce CO_2, respectively. These processes are dependent on many environmental variables including light, temperature and CO_2 concentration. Photosynthesis and respiration are also dependent on many biological variables. The stomata, for example, regulate the transfer of

CO_2 in and out of a leaf. Carbon dioxide is transferred through the atmosphere by turbulent fluctuations. Turbulence is generated by interactions between the wind and the biologically determined physical features of the canopy. These interactions produce turbulent shear and wakes because the foliage, stems and trunks exert drag forces and perform work against the wind. Canopy elements also intercept and absorb solar and terrestrial radiation. Absorbed solar radiation is the source of energy for photochemical reactions that are responsible for carbon reduction and stomatal action. Absorbed radiation that is partitioned into sensible heat will contribute to the buoyant production or suppression of turbulence.

This paper describes the physical, biological and chemical processes that affect turbulent transfer in a deciduous forest canopy. The discussion is supported with data and examples pertaining to ecophysiological processes that are of interest to tree physiologists. The microclimate of a deciduous forest is not discussed because detailed reviews are presented elsewhere (Rauner 1976, 1977, Hutchison and Matt 1977, Galoux et al. 1981, Hutchison and Baldocchi 1989). Information on the form, function and physiological ecology of deciduous forests has been discussed by Hinckley et al. (1981), Jarvis and Leverenz (1983), Hicks and Chabot (1985), Johnson and van Hook (1989).

Theoretical framework for turbulent transfer

Turbulence, radiation, thermal, physiological and structural properties of a deciduous forest canopy vary most in the vertical dimension (Rauner 1977, Galoux et al. 1981, Hutchison and Baldocchi 1989). Dividing the canopy into multiple layers is a preferred theoretical approach to examining the processes that contribute to turbulent transfer in a deciduous forest.

The conservation equation for a scalar provides the basic framework for describing turbulent transfer in a plant canopy. The conservation equations are discussed here on the premise that the canopy is horizontally uniform, the mixing ratio of the scalar does not vary with time and no chemical reactions are occurring. The vertical turbulent flux divergence ($\partial F/\partial z > 0$) or convergence ($\partial F/\partial z < 0$) of a scalar in an averaging volume will thereby equal the diffusive source or sink strength of the vegetation in that volume (Finnigan 1985):

$$\frac{\partial F}{\partial z} = \text{source/sink} = D_c/V \sum_{1}^{m} \iint_{S_i} \partial c/\partial n \, ds\,. \tag{1a}$$

The vertical turbulent flux divergence or convergence is represented by the vertical gradient in the turbulent flux of a scalar (F). The integral is evaluated over the surface (S_i) of m leaves in a unit volume, V. The term D_c is the molecular diffusivity of the scalar c and n is a unit vector normal to the leaf surface. Equation 1a can be parameterized using a resistance-analog relationship:

$$\frac{\partial F(z)}{\partial z} = \frac{-\rho_a\, a(z)\,(c(z) - c(i))}{r_b(z) + r_s(z)}\,, \tag{1b}$$

where ρ_a is air density, $a(z)$ is the leaf area density at height z and is equal to the leaf area per unit volume, $c(i)$ is the scalar mixing ratio inside a leaf and r_b and r_s are the leaf boundary layer and surface resistances to material transfer, respectively. Differences in $c(i)$ and r_s on sunlit and shaded leaves must be considered when applying Equation 1b (Meyers and Paw U 1987).

It is not possible to integrate Equation 1, with respect to z, to compute a turbulent flux to or from the canopy. This framework is intractable because it provides a system with only one equation but two unknowns, F and c. Solutions for F and c are found only by obtaining an equal set of equations and unknowns. Additional equations must be introduced and parameterized to close the system.

Early models on turbulent exchange in plant canopies adopted a first-order closure approach, commonly called "K-theory" (see Waggoner et al. 1969, Thom 1975). "K-theory" models assume that turbulent transfer and molecular diffusion are analogs—a turbulent flux is assumed to be proportional to the vertical scalar gradient and a "turbulent diffusivity" (K):

$$F = -\rho_a K \, \partial c / \partial z \, . \tag{2}$$

Corrsin (1974) states that several conditions must hold to apply "K-theory." The length scales of turbulence must be less than those associated with the curvature of the mean vertical scalar gradient and the length scales of turbulence must be constant over the distance that the gradient of the scalar changes appreciably.

"K-Theory" models were initially adopted because scientists assumed that turbulence was produced in the wakes of the foliage—the length scales of this turbulence would resemble those of the foliage elements and would be smaller than the length scale of the curvature of the mean vertical scalar gradient (see Legg and Monteith 1975, Thom 1975, Finnigan 1985). An accumulating body of evidence shows that these early assumptions are wrong. Turbulent transfer in plant canopies is dominated by large-scale, intermittent and coherent events (Allen 1968, Shaw et al. 1974, Finnigan 1979*b*, Wilson et al. 1982, Baldocchi and Meyers 1988*a*, Amiro and Davis 1988, Gao et al. 1989). Consequently, the length scales of turbulence are often much larger than those of the foliage, tree crowns and the curvature of mean vertical scalar gradient. Counter-gradient transport can occur as a result (Denmead and Bradley 1985, 1987).

Higher order closure models are based on budget equations for first-, second-, and sometimes third-order moments associated with turbulent transfer (see Wilson and Shaw 1977, Raupach and Shaw 1982, Meyers and Paw U 1986, 1987, Wilson 1988). First-order moments include horizontal wind velocity (u) and the scalar mixing ratio (c). Second-order moments include the mean covariances between vertical velocity and scalar concentration fluctuations (these covariances represent turbulent fluxes) and the velocity variances (velocity variances are components of turbulent kinetic energy). The budget equation of a particular moment includes terms of the next higher moment. Consequently, parameterization schemes must be introduced to close the set of budget equations. The formulation of the closure schemes remains controversial and is a limitation of the technique. On the other hand, the advantage of higher order closure models is their ability to simulate counter-gradient transfer when it occurs inside plant canopies (Wilson and Shaw 1977, Meyers and Paw U 1986, 1987).

Lagrangian models follow the trajectory of an ensemble of fluid parcels as they are advected and diffused by the mean wind and turbulence. These models realistically mimic the transport process in plant canopies (Raupach 1987, Wilson 1988). They can also be easily adapted to simulate turbulent exchange in two or three dimensions. Utility of these models, however, is limited by the need to know the characteristics of canopy turbulence and the source/sink distribution of material *a priori*.

Mechanisms of turbulent transfer in a deciduous forest

In the following sections we will dissect Equation 1 to examine the mechanisms that govern the rates of material exchange in a deciduous forest canopy.

Canopy structure

Deciduous forest canopies are tall and are closed during the growing season, except for gaps created by tree falls (Hicks and Chabot 1985). The heights of dominant trees typically exceed 20 m and can reach 30 m (Hicks and Chabot 1985). Below crown closure is a relatively empty trunk space. Near the ground is a vegetated understory of suppressed saplings, shrubs and herbaceous plants (Hicks and Chabot 1985). The species composition of deciduous forest canopies varies with climate and soil. The composition of major deciduous forest communities in North America include associations among oak, hickory and chestnut and among maple, beech and basswood (see Hicks and Chabot 1985, Hutchison et al. 1986, Johnson and van Hook 1989).

The leaf area index of deciduous broadleaf forest canopies ranges between four and seven (Hutchison et al. 1986, Jarvis and Leverenz 1983). Deciduous forest canopies generally grow enough leaf area to intercept over 95% of incoming radiation (Jarvis and Leverenz 1983, Hicks and Chabot 1985, Hutchison and Baldocchi 1989).

The flux divergence of a scalar (Equation 1b) is directly proportional to leaf area density. The vertical distribution of leaf area in a North American deciduous forest is highly skewed. Over 75% of the leaf area is in the upper 25% of the canopy (Figure 1). The clumped spatial distribution of leaves in the crown contributes to this large concentration. Leaf area densities in the lower third of the canopy are nearly zero. It follows from Equation 1b that the trunk space contributes little to the canopy turbulent flux of scalars.

The canopy radiation field, which provides energy for photosynthesis, evaporation and convective and conductive heat transfer, is a function of the angle between incoming light rays and the mean leaf normal (Ross 1981, Myneni et al. 1989). The radiation environment in a deciduous forest is unique because the mean leaf inclination angle varies with depth (Miller 1967, Hutchison et al. 1986), the mean leaf

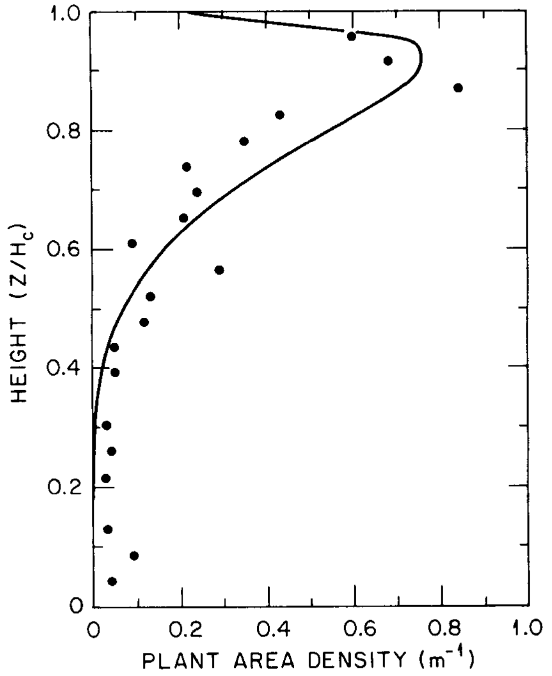

Figure 1. Vertical profile of plant area density of a fully leafed deciduous forest in the southeast United States (after Baldocchi and Meyers 1988*a*).

inclination angle is about 40° near the top of the canopy and about 10° near the forest floor (Hutchison et al. 1986).

The canopy structure of a deciduous forest differs from that of conifer stands (Jarvis et al. 1976, Jarvis and Leverenz 1983) and most agricultural crops (see Ross 1981, Shaw and Pereira 1982). Its structure resembles that of broadleaf evergreen forests (Nagano and Kira 1978, Hollinger 1989). Shuttleworth (1989), in an independent analysis, comments on the structural similarities between tropical and temperate forests. He notes that both ecosystems consist of tall, extensive, dense and perennial vegetation.

The amount of leaf area and its spatial distribution affects the aerodynamics of a canopy (Shaw and Pereira 1982). We expect the aerodynamic properties of a broadleaf deciduous forest to resemble those of broadleaf, temperate and tropical evergreen forests. A deciduous forest stand is aerodynamically rougher than short agricultural canopies and smoother than coniferous forest stands (Jarvis et al. 1976, Verma et al. 1986).

Leaf boundary layer resistance and concentration field

Material must pass through a diffusive laminar boundary layer of some thickness as it either leaves a source or enters a sink. From engineering theory (see Grace 1980), the laminar boundary layer resistance is defined as:

$$r_b = l/(D_x\, S_h)\,, \tag{3}$$

where l is a characteristic length scale, D_x is the molecular diffusivity of the scalar and S_h is the Sherwood number. Using relationships derived for flow over flat plates as an analog for leaves, the boundary layer resistance is an inverse function of scalar wind speed (U) to the one-half power:

$$r_b = \text{constant}\ (l/U)^{1/2}\,. \tag{4}$$

An expression for the vertical gradient in c can be derived from a budget equation for a scalar (c) (Finnigan 1985):

$$\partial\bar{c}/\partial z = (\underset{\text{Ia}}{-\overline{w'c'}/t_l} - \underset{\text{Ib}}{\partial\overline{w'w'c'}/\partial z})/\underset{\text{Ic}}{\overline{w'^2}}\,, \tag{5}$$

where t_l is a time constant and w is the vertical wind velocity. Primes denote fluctuations from the mean and overbars represent time averages. The concentration profile inside a plant canopy depends on the vertical distribution and magnitude of the local turbulent flux ($\overline{w'c'}$) (Ia), the vertical transport of material (Ib) and vertical turbulent mixing (Ic).

Wind speed and turbulence within a plant canopy must be evaluated to estimate r_b and the concentration field. Wind and turbulence are described by the budget equations for mean horizontal wind velocity ($\bar{u}$), tangential momentum stress ($\overline{w'u'}$) and turbulent kinetic energy (TKE). In the following subsections we briefly describe the turbulence and budget equations, report on observations of turbulence measured inside a deciduous forest, and discuss how the characteristic turbulence regime in a forest canopy affects the estimate of the leaf boundary layer resistance and concentration gradient.

Theory

The budget equations for $\bar{u}$, $\overline{w'u'}$ and TKE are presented for steady-state conditions and a horizontally homogeneous canopy. For simplicity we do not include the dispersive terms that arise from volume averaging (see Raupach and Shaw 1982); the dispersive terms typically make only a small contribution to turbulent exchange (Raupach et al. 1986).

The horizontal mean wind velocity budget is:

$$\frac{\partial\bar{u}}{\partial t} = 0 = \underset{\text{IIa}}{\frac{\partial\overline{w'u'}}{\partial z}} + \underset{\text{IIb}}{C_d\, a\, \overline{uU}}\,, \tag{6}$$

where C_d is the effective drag coefficient. This equation represents the balance between the flux divergence of tangential Reynolds stress (IIa) and bluff-body, drag forces imposed by the vegetation on the mean wind (IIb).

The tangential momentum stress budget is expressed as:

$$\frac{\partial \overline{w'u'}}{\partial t} = 0 = \underset{\text{IIIa}}{-\overline{w'^2}\frac{\partial \bar{u}}{\partial z}} - \underset{\text{IIIb}}{\frac{\partial \overline{w'w'u'}}{\partial z}} + \underset{\text{IIIc}}{g\,\overline{u'\theta'}/\bar{\theta}} + \underset{\text{IIId}}{[\overline{u'\partial p'/\partial z} + \overline{w'\partial p'/\partial x}]}\,, \tag{7}$$

where p is kinematic pressure, g is the acceleration due to gravity and $\bar{\theta}$ is absolute potential temperature. Term IIIa represents the gradient production of $\overline{w'u'}$. Term IIIb is a transport term that describes the import or export of stress from adjacent layers. Term IIIc describes the contribution of buoyancy to either enhance or suppress the production of $\overline{w'u'}$. Term IIId describes the pressure–velocity interactions, which act to destroy the $\overline{w'u'}$ correlation and return the fluid motions to a state of isotropy.

The turbulent kinetic energy (TKE) budget describes the processes that contribute to the production, transport and removal of turbulent fluctuations:

$$\frac{1}{2}\frac{\partial \overline{q'^2}}{\partial t} = 0 = \underset{\text{IVa}}{-\overline{w'u'}\frac{\partial \bar{u}}{\partial z}} - \underset{\text{IVb}}{\partial\left[\frac{1}{2}\overline{w'q'q'} + \overline{p'w'}\right]/\partial z} + \underset{\text{IVc}}{C_d\, a(z)\,(\overline{U^3} - \bar{u}\,\overline{uU})} - \underset{\text{IVd}}{g\,\overline{w'\theta'}/\bar{\theta}} - \underset{\text{IVe}}{\varepsilon}\,, \tag{8}$$

where $\overline{q'^2} = (\overline{u'^2} + \overline{v'^2} + \overline{w'^2})$. Term IVa represents shear production. Term IVb represents the import or export of turbulent kinetic energy from adjacent levels. Work by velocity fluctuations against form drag, which produces wake turbulence, is described by term IVc. The buoyant production or destruction of turbulent fluctuations is described by term IVd and the rate that turbulent kinetic energy is eventually dissipated into heat is denoted by term IVe.

For a detailed discussion of the derivation of Equations 5 through 8 the reader is referred to Raupach and Thom (1981), Businger (1982), Raupach and Shaw (1982), Meyers and Paw U (1986) and Wilson (1989).

Canopy structure affects the turbulence regime directly through bluff-body drag forces (term IIb, Equation 6) and work by velocity fluctuations against form drag (term IVc, Equation 8).

The canopy turbulence regime is linked to the canopy radiation field and water status through term IVd in Equation 8. The amount of net radiation partitioned into sensible heat flux ($\rho_a C_p \overline{w'\theta'}$) contributes to atmospheric stability and the production or suppression of turbulent fluctuations.

Turbulence within the canopy

The theory discussed above identified the mean wind vectors and turbulence moments that describe turbulence in a plant canopy. Below we discuss the mean characteristic properties of turbulence in a deciduous forest.

Mean, normalized horizontal wind velocity profiles inside a deciduous forest vary strongly with depth into the canopy (Figure 2a). A region of strong shear occurs in the upper 25% of the canopy, which is coincident with the region of densest foliage (Figure 1). A reversal in the wind velocity gradient occurs below crown closure. This reversal is a common feature inside a forest canopy. It is attributed to term IIIb exceeding the pressure-velocity interactions (term IIId) in the $\overline{w'u'}$ budget (Equation 7) (Wilson and Shaw 1977).

There is a marked difference between daytime and nighttime normalized wind velocity profiles. The nocturnal wind profile is shifted toward greater values in u/u_*. This shift is attributed to the stability of the nocturnal boundary layer, which acts to dampen turbulence and reduce tangential momentum stress above and within the canopy (Shaw et al. 1988); u_* equals $\overline{w'u'}^{1/2}$.

Turbulence intensities inside the canopy vary with depth (Figure 2b). The largest values occur near the level where canopy density is maximal (see Figure 1). Maximum turbulence intensities inside the canopy approach one. Turbulence intensities are greater during the day because buoyant effects contribute to the production and suppression of turbulent fluctuations during the day and night, respectively (Equation 8). Shaw et al. (1988) reported that turbulence intensities in a deciduous forest decrease as atmospheric stability varies from unstable to stable conditions. The values in Figure 2b agree with those measured in a deciduous forest (Shaw et al. 1988) and are greater than values observed in shorter and smoother vegetation (see Cionco 1972).

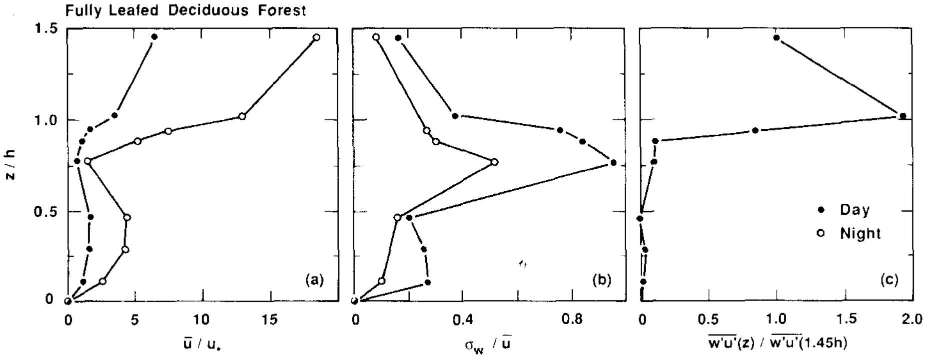

Figure 2. Vertical profiles of turbulence statistics measured in a fully leafed deciduous forest (adapted from Baldocchi and Meyers 1988*b*).

(a) Horizontal wind velocity (u), normalized by friction velocity (u_*).

(b) Vertical velocity turbulence intensities. These are defined as the ratio between the standard deviation in vertical velocity (σ_w) and horizontal wind velocity ($\bar{u}$).

(c) Tangential momentum stress ($\overline{w'u'}$) normalized by the value measured at a reference value above the canopy.

The dense leaf area in the upper canopy imposes appreciable drag on the wind, causing a strong gradient in the vertical profile of tangential momentum stress ($\overline{w'u'}$) (Figure 2c). Below crown closure, where foliage is sparse, the vertical gradient of tangential momentum stress is weak or negligible. Tangential momentum stress is also influenced by atmospheric stability. Stress values inside a forest canopy decrease markedly as stability proceeds from unstable to stable conditions (Shaw et al. 1988).

Examination of the mean wind velocity and tangential momentum stress profiles (Figure 2a and 2c) reveals the occurrence of counter-gradient momentum transport inside a deciduous forest. These results add to the body of data, initiated by Denmead and Bradley (1985, 1987), that document counter-gradient transfer inside forest canopies.

Turbulent fluctuations exist on many scales, ranging in size from kilometers to millimeters (Panofsky and Dutton 1984). Figure 3 shows a typical power spectrum for vertical velocity variance measured in the crown. Wave numbers for peak turbulent fluctuations range between 0.1 to 0.2 m^{-1}, corresponding to turbulence length scales of the order of 5 to 10 m. These length scales are less than those measured above the canopy and in the trunk space (Baldocchi and Meyers 1988*a*).

Wave numbers greater than the spectral peak are associated with the inertial cascade of energy (see Panofsky and Dutton 1984). According to Kolmogorov's

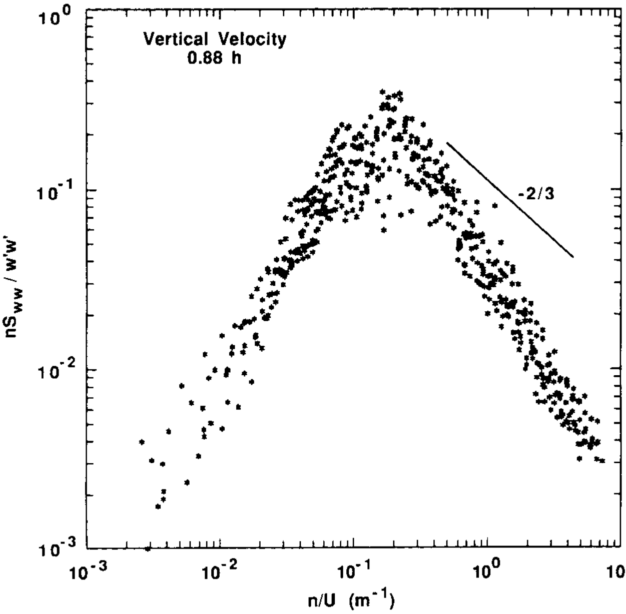

Figure 3. Vertical velocity power spectra measured in the crown space of a fully leafed, deciduous forest (after Baldocchi and Meyers 1988*a*). The velocity power spectrum describes how the variance of velocity is distributed with respect to frequency. The spectral density, plotted on the ordinate axis, is multiplied by natural frequency and is normalized by the mean variance. Natural frequency (*n*) is plotted on the abscissa and is normalized by local horizontal wind velocity, to estimate wave number (*k*).

inertial subrange theory, normalized velocity power spectra, measured in the surface boundary layer, should have a slope of $-2/3$. The slope of vertical velocity power spectra measured inside a forest canopy is much steeper than this standard value (Figure 3), being of the order of -1. Velocity spectra measured inside a forest canopy do not follow Kolmogorov's scaling for two reasons. First, work by the mean wind and shear-generated, turbulent kinetic energy (TKE) against form drag rapidly reduces the length scales of the turbulence to those of the wake elements. This process acts to short-circuit the inertial cascade of turbulence because these smaller scale fluctuations are rapidly dissipated (Raupach and Thom 1981, Shaw and Seginer 1985, Wilson 1988). Second, strong shear, large turbulence intensities, and anisotropy of turbulence causes the ratio n/u not to represent wave numbers, as is suggested by Taylor's frozen eddy hypothesis (Jensen and Busch 1982, Wyngaard and Clifford 1977). Thus, *a priori* one does not expect the velocity spectra derived from measurements made in a forest canopy to exhibit a 2/3 slope in the inertial subrange. Recent measurements in an almond orchard (Baldocchi and Hutchison 1988) and a spruce forest (Amiro and Davis 1988) support these observations.

The processes that contribute to the production, transport and removal of turbulent fluctuations vary with height in the canopy. Shear-production (Equation 8, term IVa) is maximal at the canopy–atmosphere interface (Figure 4). Work by velocity fluctuations against form drag (term IVc) dominates the TKE budget in the crown and is maximal at the level of densest foliage. The hypothesis that wake turbulence short-circuits the inertial cascade of the velocity spectra is supported by the large magnitude of term IVc. Little shear or wake production occurs in the trunk space as a

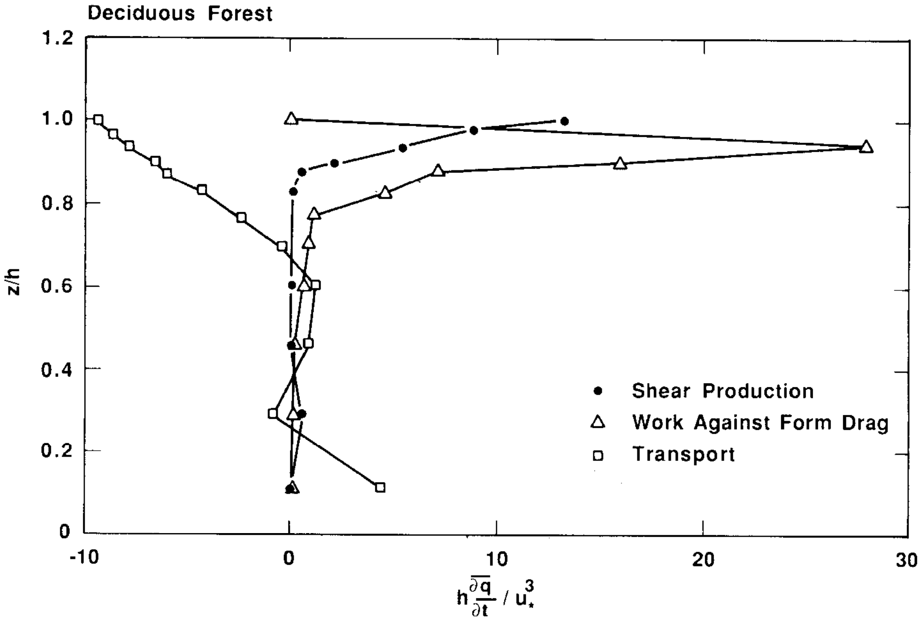

Figure 4. Turbulent kinetic energy budget measured in a fully leafed deciduous forest.

result of the sparse foliage. Turbulent kinetic energy is exported from the crown and is imported to the region below crown closure. The transport of TKE (term IVb) is the major contributor to turbulent fluctuations below crown closure because only large scale turbulence has enough energy to penetrate through the dense crown. Only shear and buoyancy processes produce TKE above the canopy (Maitani 1978, Shi et al. 1987). This production is balanced by the export of TKE and viscous dissipation.

Turbulent fluxes are defined as the mean covariance between fluctuations in vertical velocity and a scalar (c):

$$F_c = -\rho_a \overline{w'c'} \,. \tag{9}$$

Turbulent transfer in a deciduous forest is dominated by the coherent, intense and intermittent events (Finnigan and Raupach 1987, Baldocchi and Meyers 1988*a*, Gao et al. 1989). Material, energy and momentum are physically transferred into and out of a canopy by sweep and ejection events (see Shaw et al. 1983, Finnigan and Raupach 1987)—sweeps represent events of fast, downward moving air and ejections represent slow, upward moving air. In a deciduous forest, sweep events are generally the dominant mechanism for the transfer of tangential momentum stress (Baldocchi and Meyers 1988*b*). Lesser contributions to turbulent transfer are made by ejections. These intense and intermittent turbulent events account for a disproportionate amount of the mass and momentum that is transferred. For example, turbulent events exceeding five times the mean tangential Reynolds stress occur less than one-half of the time, yet they account for 60 to 90% of the mean Reynolds stress measured inside the canopy. Turbulent transfer in shorter canopies is not as intense or intermittent (Shaw et al. 1983, Finnigan 1979*a*), because of its smoother, aerodynamic properties.

We have shown that turbulent transfer in a deciduous forest is associated with large scale turbulence and that counter-gradient transfer occurs. These data suggest that "K-theory" does not represent the processes governing the turbulent transfer of momentum.

Leaf boundary layer resistance

The probability density function of turbulence is non-Gaussian because turbulence is dominated by intermittent and skewed events. Since the leaf boundary layer resistance is a non-linear function of wind speed (Equation 4), the mean value of r_b will not equal the value estimated as a function of the mean wind speed (Figure 5). Evaluations of r_b based on the mean wind speed underestimate expected values of r_b by 5 to 19%. Estimating the expected value of r_b on the basis of probability density functions (PDF) of wind speed that consider skewness and kurtosis improves the estimate of r_b. These results emphasize the need to consider the effects of skewed and intermittent turbulence when evaluating wind speed dependent aerodynamic variables.

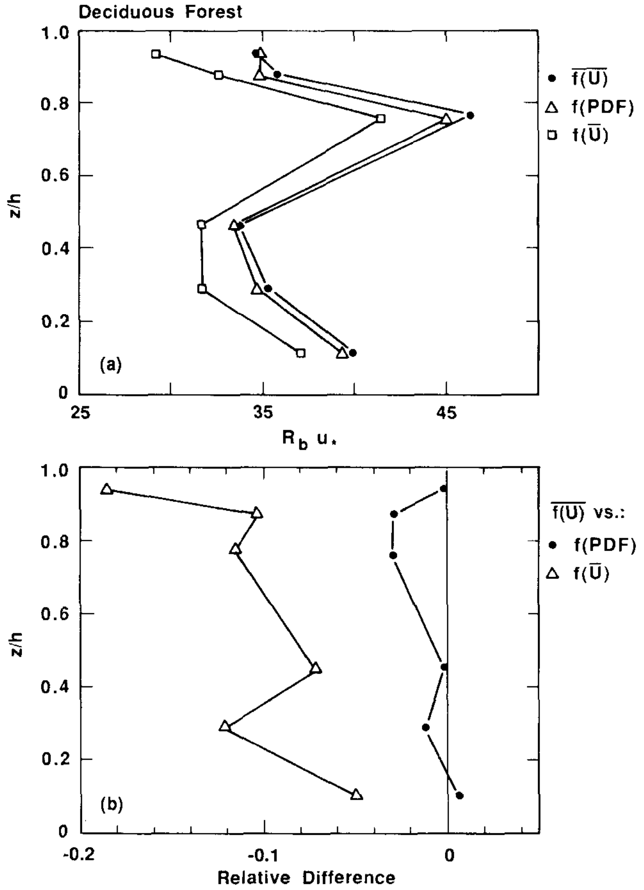

Figure 5.

(a) The vertical variation in the normalized leaf boundary layer resistance for water vapor transfer. Shown are the expected value of $R_b u_*$, evaluated using instantaneous, measured wind speed data, and values computed with the mean wind speed and a probability frequency distribution, derived from mean turbulence statistics (after Baldocchi and Meyers 1989).

(b) The relative difference between the expected value of $R_b u_*$ and values computed as a function of the mean wind speed and a probability frequency distribution.

Concentration gradients

From inspection of Equation 5, we expect that vertical gradients will be relatively weak inside a deciduous forest because vertical turbulent mixing ($\overline{w'^2}$) is generally great. Gao et al. (1989) show that air temperatures inside a deciduous forest differ by less than 0.5 °C over the depth of the canopy. Galoux et al. (1981) also show that gradients of temperature and humidity are weak in a deciduous forest.

Stomatal conductance

A major pathway for the exchange of material between a plant canopy and the atmosphere is through the leaf stomata. The stomatal conductance (g_s)—the inverse of resistance—is a measure of the stomata's ability to retard the transfer of material through its aperture. This conductance is a non-linear function of many environmental and physiological variables, including light, temperature, humidity, water stress and CO_2 (Jarvis 1976, Schulze 1986).

A wide range of stomatal conductances is possible in a plant canopy since the amount of radiation incident on a leaf varies widely; solar radiation incident on a leaf depends on the leaf's vertical position and inclination angle and whether it is exposed to full sun or is situated in either umbral or penumbral shade. The exposure and adaptation of a leaf to either sunlit or shaded regimes influence its response to changes in photon flux densities (Chazdon and Pearcy 1986).

Considering only the influence of solar radiation, the integrated canopy stomatal conductance (g_c) can be computed according to:

$$g_c = \int_0^L g_s(I_s(f))\,P_b(f) + g_s(I_p(f))\,P_p(f) + g_s(I_{sh}(f))\,P_u(f)\,\mathrm{d}f\,, \tag{10}$$

where I_s, I_p and I_{sh} are the flux densities of photosynthetically active radiation (PAR); P_b, P_p and P_u are the probabilities of beam, penumbra, and umbra; L is the cumulative leaf area index; and $\mathrm{d}f$ is an increment of leaf area.

The canopy radiative regime

The radiation regime inside a plant canopy is comprised of direct and diffuse solar radiation that penetrates through gaps in the stand and complementary radiation, which is generated by radiation intercepted and scattered by foliage or the soil (see Ross 1981).

Statistical models are used classically to estimate the probability that a ray of light passes through the foliage (see Ross 1981, Myneni et al. 1989). These models assume that a plant canopy is a plane-parallel, turbid medium, the sun is a point source, the foliage is randomly distributed in space, the azimuth distribution of leaves is symmetrical and the leaf inclination angle distribution is invariant with height. The probability that a ray of light passes through a layer of foliage is a function of the angle between the incoming light ray and the mean leaf normal and the amount of leaf area that the ray must pass through.

In a deciduous forest many of these modeling assumptions are invalid. The sun has a finite radius and casts penumbral shade. Leaf inclination angles vary with height and leaves are spatially distributed in clumps. These factors cause the radiation regime in a deciduous forest to differ from that of simpler canopies (Norman 1979, Baldocchi et al. 1985, Baldocchi and Hutchison 1986).

Penumbra is a region of partial shade that occurs when the solar disk is partially obscured by a leaf or twig, as seen from a given point below. The flux density of radiation incident on a leaf in penumbral shade is less than that if it were exposed to full sun and is greater than that if it were in umbral shade. The flux density of radiation on penumbral-shaded leaves is often below light saturation, so penumbral effects should be considered when calculating biological processes that are nonlinearly dependent on light, such as stomatal conductance and photosynthesis.

Penumbral shade area is a function of the angular radii of the plant elements and sun and the distance between a plant element that partially obscures the solar disk and a reference level situated below. The treatment of penumbra in plant canopies, as used here, is discussed in Denholm (1981*a*, 1981*b*).

The probability of penumbra (P_p) equals:

$$P_p(f) = 1 - P_b(f) - P_u(f), \tag{11}$$

where P_b is dependent on the augmented leaf area due to penumbral shading and P_u is dependent on the diminished leaf area due to penumbral shading and leaf overlap.

The probability of beam penetration depends on the cosine of the angle between the incoming solar beam and the mean leaf normal—commonly called the G-function (Ross 1981). The G-function should be evaluated at all levels in a deciduous forest because the mean leaf inclination angle varies with height. We estimate the G-function from a continuous leaf inclination angle distribution; the Beta distribution is used because it is based on simple inputs (means and variances) and has been shown to provide an acurate estimate of the leaf inclination angle probability distribution (Goel and Strebel 1984).

A Poisson probability distribution describes the probability of beam penetration when leaves are randomly distributed in space. Clumped foliage in a deciduous forest, on the other hand, enhances beam penetration. The negative binomial probability distribution describes beam penetration in a canopy with clumped leaves (Nilson 1971, Acock et al. 1970, Baldocchi and Hutchison 1986).

The computation of the penetration of diffuse solar radiation through gaps is made by hemispherically integrating the probability of beam penetration (see Norman 1979). Scattering of PAR depends on the reflection and transmission properties of leaves. Less than 20% of the PAR incident on the topside of leaves of species found in a deciduous forest is reflected and transmitted (Hutchison and Baldocchi 1989). In the computations discussed below, multiple scattering is computed using the approximation technique of Norman (1979).

Computing canopy stomatal conductance

Figure 6 presents computations of the vertical profile of stomatal conductance (Equation 10) made with a canopy radiative transfer model that accounts for penumbra, clumped foliage and vertical variations in leaf inclination angles. Computations of stomatal conductance from light measurements are used as a standard for testing the model. The PAR data are averaged from measurements made on day 272, 1981 between 0800 and 1700 h (see Baldocchi et al. 1985). Computations of stomatal conductance based on the model mimic standard values quite well. Mean daily canopy stomatal conductance values derived from the model and measured values are 0.0216 and 0.0224 m s^{-1}, respectively—a 4% difference.

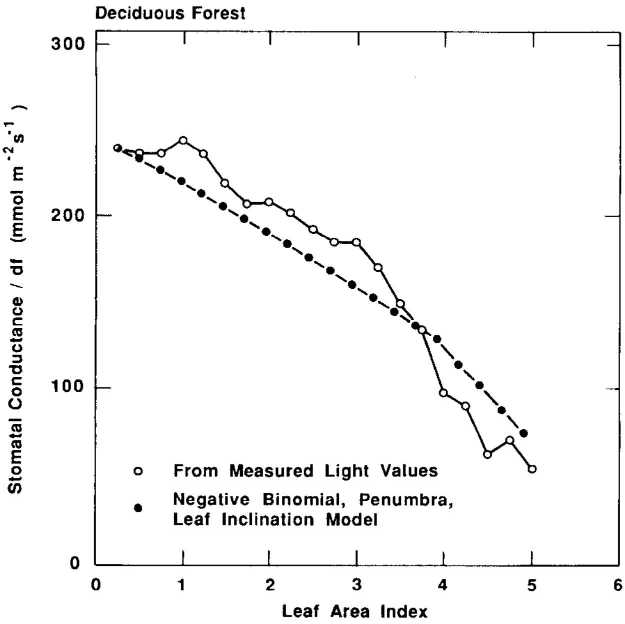

Figure 6. Mean daily vertical profile of stomatal conductance in a deciduous forest. Conductances are a function of photosynthetically active radiation (PAR) and were measured and computed with a canopy radiative transfer model; the radiative transfer model considers clumping, penumbra and vertical variations in leaf inclination angles.

Source–sink strength

A complex interplay occurs between the source or sink strength and the local scalar concentration (Equation 1); the rate that materials are synthesized or broken down affects the local scalar concentration, but the production or destruction of material is also dependent on the local scalar concentration. The magnitude of the source/sink term is, therefore, limited to a value set by the minimum of the demand for, or supply of, the scalar. The role that the demand or the supply of a scalar has in regulating the magnitude of the source/sink term and the net canopy/atmosphere flux is discussed below with an example, CO_2 exchange due to photosynthesis.

The supply of CO_2 to a leaf is dependent on the ambient CO_2 concentration and the ability for turbulence to transfer CO_2 from the free atmosphere to the vicinity of the foliar sink. If turbulence becomes diminished, then the supply of CO_2 to the foliar sink may become limited, because a drawdown in the interstitial CO_2 concentration can occur. The supply of CO_2 to the foliar sink is also limited if the stomata close because of water deficits or some other variable.

The photosynthetic demand for CO_2 depends on the activity of the carboxylating enzyme (ribulose-1,-5-biphosphate (RuP_2), carboxylase-oxygenase) and the capacity of the electron transport system to regenerate RuP_2 (von Caemmerer and Farquhar 1981, Farquhar and von Caemmerer 1982). When adequate amounts of CO_2 are available, photosynthesis is limited by the regeneration of RuP_2 (von

Caemmerer and Farquhar 1981). This regeneration depends on rates of electron transport and photophosphorylation systems, which are dependent on light energy.

Canopy level measurements of gas exchange over a deciduous forest show that the aerodynamic resistance is much smaller than the surface resistance (Verma et al. 1986). Therefore, the carbon dioxide regime in a deciduous forest canopy should be well mixed and canopy photosynthesis should be demand limited. If this is true then physiological estimates of the demand function should be adequate to estimate the flux divergence of CO_2 inside the canopy. We test this hypothesis by comparing measurements of canopy photosynthesis, derived from the eddy correlation technique (Baldocchi et al. 1987), against estimates of canopy photosynthesis that are computed as the integral of the sink function for CO_2 (Equation 1), with respect to canopy height.

The demand for CO_2 and the internal CO_2 concentration (c_i) were computed by coupling the biochemical, leaf photosynthesis model of Farquhar and von Caemmerer (1982) with the canopy radiative transfer and stomatal conductance submodels described above. Computations of leaf photosynthesis were based on data from Jurik et al. (1985) for *Quercus rubra*. Modeling parameters were varied with depth in the canopy to account for differences that are observed in the photosynthesis and respiration rates of sun and shade adapted leaves (see Jurik et al. 1985). The rate of electron transport photophosphorylation was computed with an algorithm that uses parameters that can be obtained from gas exchange experiments (Harley et al. 1985). Leaf boundary layer resistances were computed with Equation 3, using mean wind speeds measured in the canopy (Figure 2a). The CO_2 concentration was assumed to be invariant with height. Measurements of canopy photosynthesis were from periods when the forest was well watered and exposed to near optimal environmental conditions (see Baldocchi et al. 1987).

Model computations of canopy photosynthesis are well correlated with measured values (r = 0.75) (Figure 7). Calculated values underestimate eddy correlation measurements under high light conditions. The differences between measured and calculated values, for much of the data, are within 20%. This difference is well within the range of experimental error associated with flux measurements and prescribed model parameters. Note that maximum model values reach only 17 μmol m^{-2} s^{-1}, whereas maximum measured values reached 25 μmol m^{-2} s^{-1}. Better agreement between modeled and measured values might have been obtained had model parameters been developed from leaves at this more southern and clement site.

The assumption of a constant CO_2 concentration profile seems reasonable because under typical field conditions the drawdown of CO_2 in a forest stand is small. For example, Jarvis et al. (1976) show that a typical CO_2 drawdown in a coniferous forest is about 5 to 10 ppm. Carbon dioxide drawdowns of this magnitude should not reduce leaf photosynthesis significantly. Even if we assume an extreme drawdown of 20 ppm, model computations suggest that photosynthesis will only be reduced by 3%.

Some error in the estimate of canopy photosynthesis (Figure 7) can be attributed to errors in modeling the canopy radiation regime. These errors, however, are not

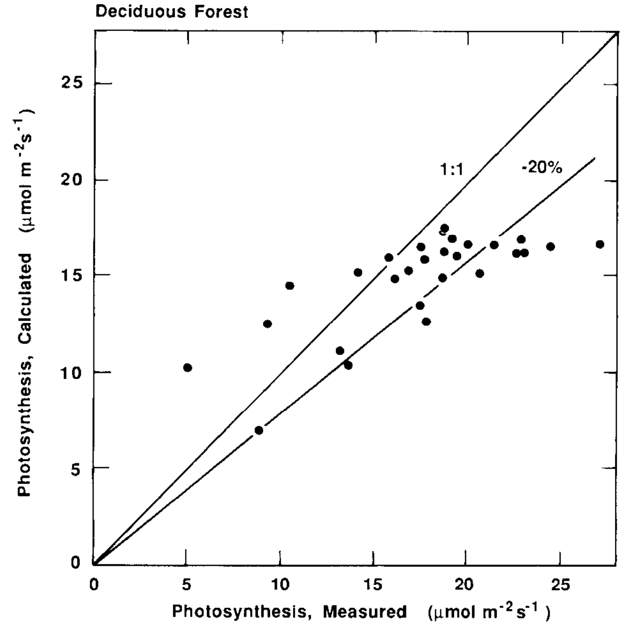

Figure 7. A comparison between canopy photosynthesis, measured with the eddy correlation method (Ps meas), and computed with a numerical model (Ps calc). The measured values are from Baldocchi et al. (1987). The numerical model computes canopy photosynthesis using the leaf photosynthesis model of Farquhar and von Caemmerer (1982) and a canopy radiative transfer model that accounts for the effects of penumbra, clumped foliage and vertical variations in leaf inclination angles.

great. Estimates of mean daily canopy photosynthesis, based on the canopy radiative transfer model, underestimate values derived from light measurements by only 6% (Figure 8).

The model used in this exercise assumes that photosynthesis is operating at steady state. Dynamic effects on stomatal conductance and photosynthesis due to a variable light environment are known to occur in the field, through induction effects (Chazdon and Pearcy 1986). Therefore, it may be worthwhile in future exercises of this type to account for leaf dynamics.

Conclusions

Turbulent transfer in a plant canopy is a complex process, regulated by many physical, physiological and chemical processes and the structural features of the canopy. The processes that contribute to turbulent transfer in a deciduous forest are best described using a multi-layer framework because turbulence, radiation, thermal and structural properties vary appreciably with depth inside the canopy.

The structure of a deciduous forest is unique. Its foliage is concentrated near the top of the canopy and leaves are clumped. Interactions between a deciduous forest and the mean wind and atmospheric turbulence create a wind regime inside the canopy that is more turbulent and intermittent than in shorter crop canopies. The

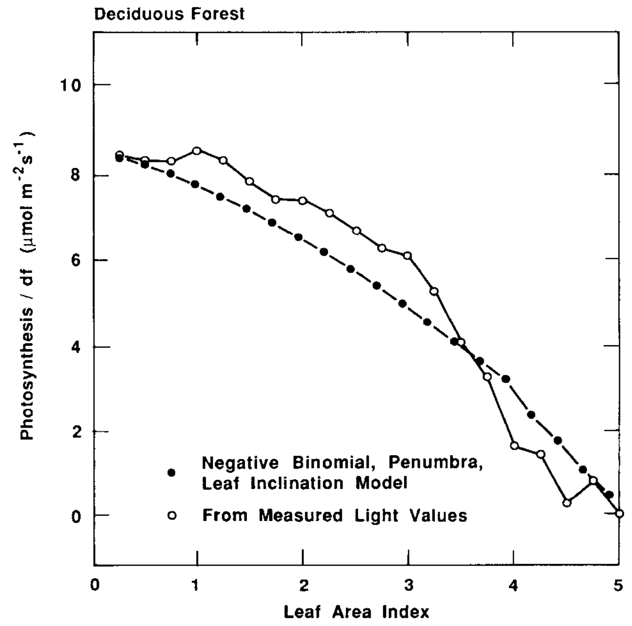

Figure 8. Vertical profile of photosynthesis in a deciduous forest. Photosynthesis is a function of photosynthetically active radiation (PAR) computed with a canopy radiative transfer model and light measurement. These data represent daily means.

structure of a deciduous forest canopy also alters the canopy radiation regime, relative to crops—the penetration of beam radiation is enhanced and penumbral shade is significant.

Conceptually, the turbulent transfer of material is limited by either the supply or demand for material, which are regulated by physical, biological, chemical and structural properties. It is desirable to include a rigorous description of the turbulence regime when modeling turbulent transfer in a plant canopy, for example coupled Lagrangian and higher order closure Eulerian models, when the goal is to simulate flux and scalar concentration profiles in the canopy. However, experience shows that physiologically based, demand models are adequate for estimating canopy-level, turbulent transfer of biologically regulated material in a deciduous forest (such as CO_2, O_3 and SO_2) because the forest is aerodynamically rough and is relatively well mixed (Meyers and Baldocchi 1988).

Characteristics of the properties governing turbulent transfer in a temperate deciduous forest resemble those in the tropics (Shuttleworth 1989). Concepts derived from studying temperate deciduous forests may prove valuable for understanding processes in remote and endangered tropical forest stands.

Acknowledgments

This work was partially supported by the National Oceanic and Atmospheric Administration and the U.S.

Department of Energy. Appreciation is expressed to Dr. Tilden Meyers and Wang Han Jie for their many discussions and reviews of this work.

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