

Lecture 8

Integrating and Scaling Information from Leaves to Canopy Scales: Concepts, Principles and Big Leaf Models, part 1

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Outline

- a. Introduction
- b. Soil-Vegetation-Atmosphere Transfer (SVAT) models: history and hierarchy
- c. Non-linearities, scaling and integrating information
 1. concepts
- d. History

1. Conceptual , Mathematical and Computation Framework of SVAT Models

'Homage to gas exchange'

I stand upon a hill so green
And spy upon a leaf.
Its occupied with chlorophyll,
Beyond the mind's belief.

Microchasms everywhere!!
Stomatal holes of Hell.
Cascades of carbon swallowed,
For vapor they expel.

It's this molecular ballet,
That makes chestnuts grow so tall.
Breathing air so silently,
'Til expiring in Fall.

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The rates at which trace gases are transferred between the biosphere and the atmosphere depend upon a complex and non-linear interplay among physiological, ecological, biochemical, chemical and edaphic factors and meteorological conditions. Information on fluxes of trace gases between the biosphere and atmosphere is needed at a variety of time and space scales by models that predict ecosystem carbon water and nutrient balances, weather and climate and tropospheric chemistry. Time scales of processes that are associated with the transfer of trace gases between vegetation and the atmosphere span seconds, hours, days, seasons, years and decades. The range of spatial information that is needed by an ecosystem-scale trace gas exchange model bridges the dimension of cells, leaves, tree crowns, and their placement across a landscape, region and continent (Jarvis, 1995; Osmond, 1989). How to model and parameterize the processes that govern trace gas fluxes throughout the spectrum of biologically relevant time and space scales and to test such schemes remains a challenge to contemporary ecologists, biometeorologists and biogeochemists (Hurt et al., 1998; Moorcroft, 2003; Moorcroft, 2006; Rastetter, 1996).

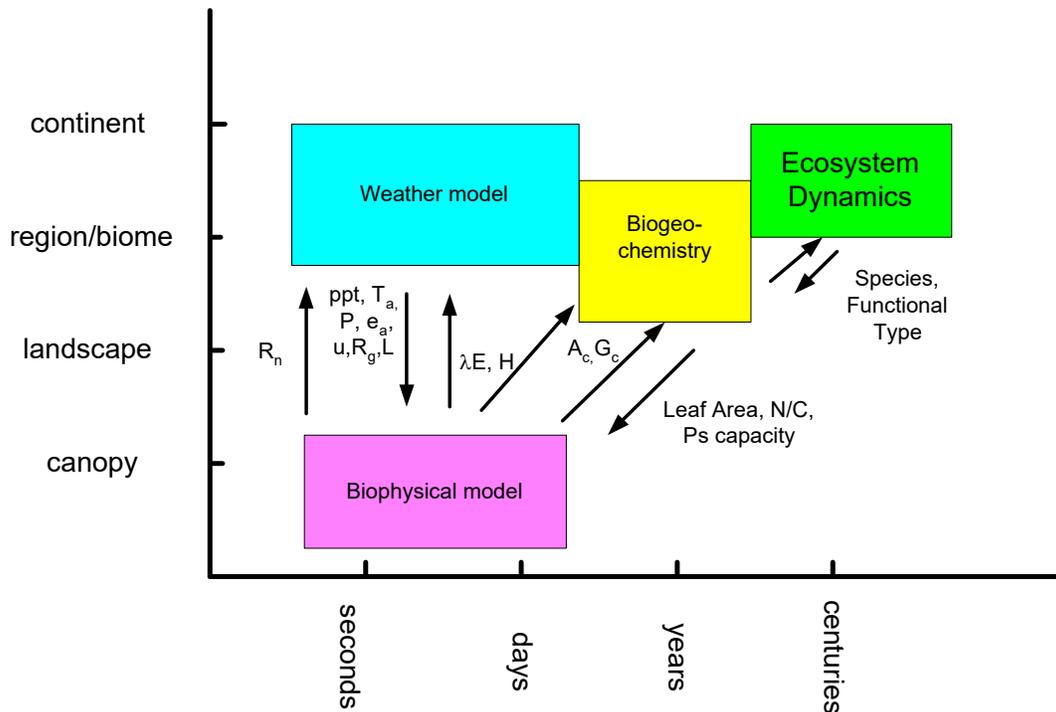


Figure 1 Space and time scales and Processes affecting Trace gas fluxes

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. 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. Consequently, contemporary SVAT models have several common attributes, no matter what their level of sophistication. They all consider: 1) the radiation balance and 2) turbulent transfer of heat, moisture and momentum, in one form or another, to and from plants and the soil. And as models evolve into the modern era, where we consider biogeochemical problems, we want models with multiple constraints, e.g. tying stomatal conductance to carbon and water fluxes and nutrient content.

Ecosystems are inherently complex, a term we distinguish complex from complicated. Complex systems are: 1) non-linear, 2) they possess scale emergent properties, 3) the solutions to their governing equations are sensitive to initial conditions, 4) these solutions are path dependent, and they can exhibit properties of self-organization.

For modeling ecosystem trace gas fluxes, two classes of *complexity* are associated with the model hierarchy problem. One class of complexity relates to how driving variables are defined and used as inputs to non-linear model algorithms. In other words, how do we translate information from some distant weather station to the micro-environment sensed by leaves, possessing different orientations or positions relative to the top of the canopy. Another level of complexity involves the breadth and linkage of functional components that describe the biophysics of trace gas exchange. We also must face a level of *complication*, which involves the geometric abstraction of the canopy.

Class One complexity involves evaluating non-linear functions that are forced by variables that possess non-Gaussian probability distributions. Classic examples, as will be discussed below, involve assessing photosynthesis on sunlit and shaded leaves (Norman, 1981; Sinclair et al., 1976). Another difficulty arises because the relative role of controlling biophysical processes changes as one transcends time and space scales. For instance, new processes may emerge at one space or time scale and become inconsequential at another. For example, if we are studying evaporation, we need only to consider leaf transpiration at the leaf scale, but must assess soil evaporation and soil heat flux at the canopy scale, in addition to the sum of transpiration from leaves and evaporation of water on the leaf surface.

Class Two Complexity involves the consideration of how biophysical processes link with one another and the feedbacks they produce. One conceptual vision of how trace gases are exchanged between the biosphere and atmosphere involve linkages between biometeorological, biogeochemical and eco-physiological principles (Figure 2). 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 (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 (Goudriaan, 1977; Norman, 1979).

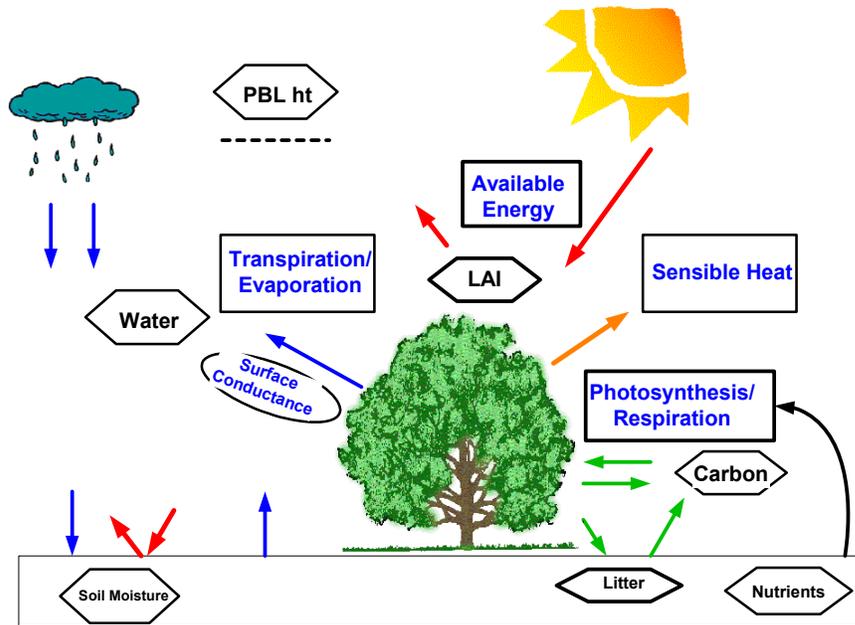


Figure 2

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 in the Figure. We emphasize that a different suite of processes will dominate the feedbacks on short and long time scales and whether a canopy is sparse or forms a closed canopy.

In the short-term, leaf area affects many biophysical processes such as light interception and the net radiation balance, canopy photosynthesis, surface conductance, evaporation and transpiration, soil moisture and dynamics of the planetary boundary layer. A sparse canopy, for example, will intercept less sunlight than a dense stand. Hence, it will experience relatively low rates of photosynthesis 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 (Denmead et al., 1996; McNaughton and Spriggs, 1986; Raupach et al., 1992). 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 (Barr and Betts, 1997).

Long-term, ecological, climate and biogeochemical factors control the amount of leaf area and plant structure and functionality. For instance, a landscape cannot support an amount of vegetation that can potential transpire more than the available water budget or one that will respire more than the amount of potential gross primary productivity. Another long-term consequence of these plant-atmosphere interactions involves lower inputs of biomass and nutrients into the soil system and temporal variations in canopy structure and functioning. These effects will set limits on decomposition, net primary productivity, leaf area and evaporation (Schimel et al., 1991; Woodward and Lomas, 2004). And on the time scales

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of centuries, one may even need to consider ecosystem dynamics, how species, plant structure and function change with time, if one wants to assess the impact of climate change on trace gas fluxes (Foley et al., 2000; Friedlingstein et al., 2006; Friend et al., 2007).

The dynamic response of ecosystem CO₂, water vapor and trace gas exchange to any environmental perturbation is the summation of individual responses of component compartments. Ecosystem CO₂ exchange, for example, is comprised of carbon fluxes associated with four compartments, leaves, boles, roots and soil organic matter. Canopy evaporation consists of water vapor that is lost through plant transpiration and soil evaporation.

The temporal dynamics of gas exchange between an ecosystem and the atmosphere is complicated because an ensemble of physiological, ecological, biochemical, chemical and edaphic factors and meteorological conditions that interact in a non-linear manner (Rastetter et al., 1992). The resulting interplay of these gas exchange processes and their environmental drivers can introduce phase lags, filtering, amplifications and chaos on signals being assessed (Braswell et al., 1997; Zeng et al., 1990).

Class One Complication involves the detail by which one wants to use to design a model. A conceptual hierarchy of biophysical model (in terms of structure and function) exist integrate leaf-scale fluxes to the canopy scale (Leuning et al., 1995; Raupach and Finnigan, 1988; Sellers et al., 1997).

Modeling frameworks treat the canopy as a:

- 1) big-leaf (Monteith, 1981)
- 2) two-layer systems (plant/soil) (Shuttleworth and Wallace, 1985)
- 3) dual-source system (sun/shade) (dePury and Farquhar, 1997; Wang and Leuning, 1998)
- 4) two-layer/dual source (plant/soil, sun/shade) (Norman, 1981; Sinclair et al., 1976)
- 5) one-dimensional multi-layer system (Baldocchi and Harley, 1995; Goudriaan, 1977; Norman, 1979)
- 6) two-dimensional array (Chen et al., 2008)
- 7) three-dimensional array (Kobayashi et al., 2012; Medlyn, 2003; Wang and Jarvis, 1990)

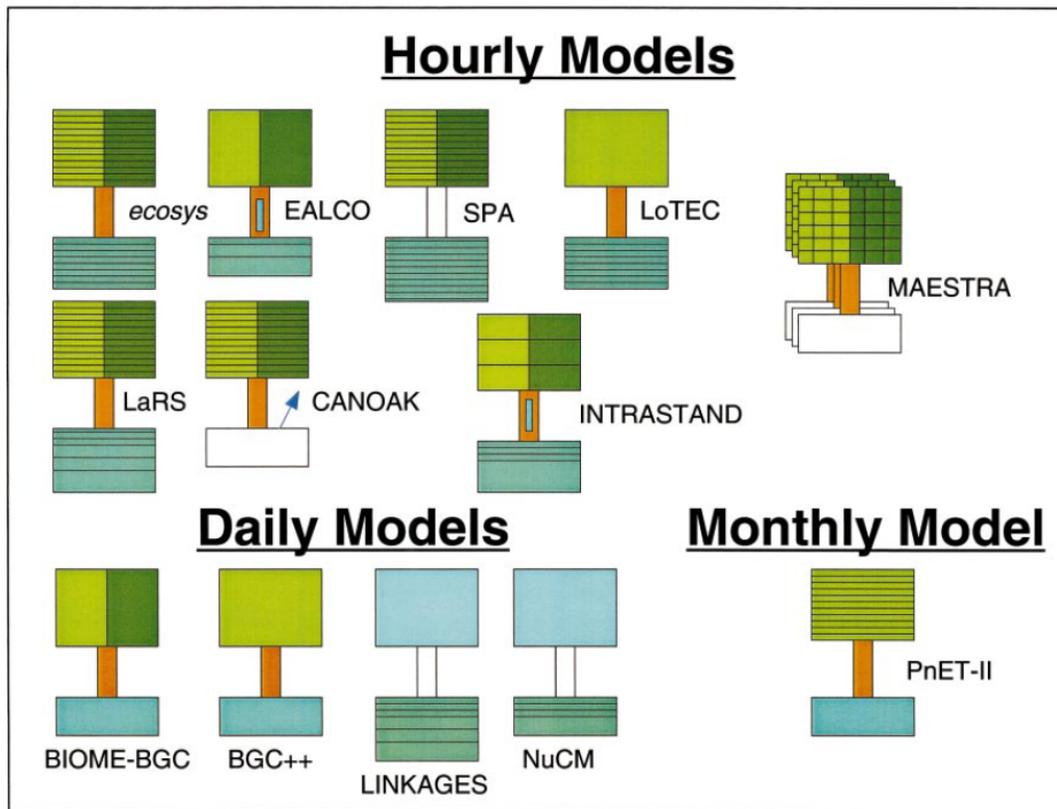


Figure 3 From Hanson et al., 2004

To address these topics on modeling trace gas exchange between a plant canopy and the atmosphere, we divide this lecture according to three themes. These include: 1) coupled, non-linear biophysical processes; 2) how model processes and their drivers vary in space, both vertically and horizontally and 3) how model processes and their drivers vary with time.

a. Issues of Scaling and Integration: Coupling Biophysical Processes

In ecological sciences, the philosophy of Occam’s Razor is often invoked as a guiding principle for designing a model of a complex system. Under this principle, the simplest of competing theories is preferred to explain a phenomenon. To capture the dynamics of a complex biophysical system in the simplest way (i.e. the Principle of Occam’s Razor), we need to recognize when and where model simplifications are appropriate or inappropriate.

Practical means of synthesizing this information involves ‘scaling’ or integration models (Jarvis, 1995). Scaling models are well-known in engineering and ecology. Attributes about a system tend to vary as an exponential function of size.

$$f(x) \sim ax^n$$

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Using a contemporary example, the biodiversity of a landscape scales with the area or the length of a coastline increases with the reduction of the scale at which it is viewed. With regards to mass and energy exchange, a common, but imperfect, scaling factor is leaf area index. For example, Kelliher et al. (Kelliher et al., 1995) scale stomatal conductance of a leaf as a function of leaf area to estimate the surface conductance of a landscape.

$$G_c \sim g_s \cdot L$$

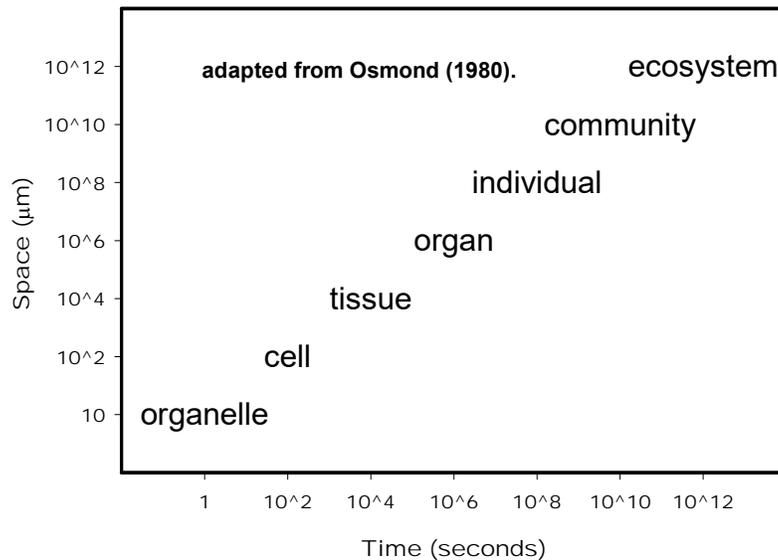
Integration is distinct from scaling, though the terms are often interchanged (see (Jarvis, 1995)). Integration involves summing. A classic example of integration involves the summing of leaf-based information to the canopy dimension.

$$G_c = \int_0^L g_s(l) dl$$

Two key challenges arise when transferring information for one scale to the next. One challenge involves determining what processes are controlling the system at the scale of interest and the other entails evaluating key regulating processes at the scale being probed. The first challenge is relevant because processes that are important at one scale may not be at another, or vice versa; for example, the energy balance of a canopy is affected by soil and vegetation heat storage and soil evaporation, while a leaf's energy balance is not affected by these processes.

The second challenge is noteworthy because interactions between plant canopies and their microenvironment often cause governing variables to vary in time and space. They can also cause the coupling to be imperfect. Hence, the status of a governing variable above a plant canopy can be distinct from its state at the leaf surface. Consequently, it is best to assess leaf gas exchange rates by evaluating key governing variables at the surface of leaves (Collatz et al., 1991; Grantz and Meinzer, 1990) rather some remote and potentially decoupled variable such as the atmospheric humidity deficit. This factor is one motivation for using multiplayer models that couple micrometeorology and physiology. Our goal is to provide information on drivers at the location they are needed.

Evaluating ecological information is very complicated as one can transcend up to 14 orders of magnitude in time and 14 orders of magnitude in space (Jarvis, 1995; Katul et al., 2001; Osmond, 1989).



Hierarchy theory is often used to guide how information can be transferred across time and space scales (O'Neill, 1989). Typically, the mechanics and the dynamics of the operational-scale is described at the smallest and fastest scales. For an ecosystem, this corresponds to the scale of leaves and how they respond to second by second variations in light and wind. Information at the operational-scale is obtained by integrating reductionist-scale information in both time and space. The state variables that drive the operational-scale are imposed from the higher or macro-scale. In this case, a canopy-scale trace gas flux model would use weather and leaf area information as external inputs.

We typically do not concern ourselves with supra-fine scale information because its influence typically does not transfer linearly across larger time and space scales. Albeit, this scaling recommendation is conservative. However, it has been used successfully as a modeling framework for many years by C.T de Wit (deWit, 1970), who stated:

'Seven-stage simulation models by means of which ecosystems may be explained on basis of the molecular sciences are impossible large and detailed and it is naïve to pursue their construction'

But many of us feel (Baldocchi and Wilson, 2001; Moorcroft, 2003; Sellers et al., 1997) that modern scientists risk 'getting it wrong' by constraining contemporary ecological studies to only +/- one scale (a breadth of 2 scales). Too many important processes transcend several scales. Which is why many of us are starting to examine ecosystem mass and energy fluxes over the courses years and decades (Katul et al., 2001; Stoy et al., 2007) or from leaves, canopies and the globe (Ryu et al., 2011; Sellers et al., 1997). As we endeavor to address ecological processes across more than 3 time scales, information that was provided as in input by the macro-scale will need to be predicted by coupling mass and

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energy exchange models with climate and ecosystem models that predict future weather, vegetation and how the two interact. In fact the emerging state of art of coupled climate modeling involves a merging of biophysical, ecophysiological and ecosystem dynamic models (Cox et al., 2000; Foley et al., 1996; Friend et al., 2007). The coupling of carbon, water and energy fluxes also seems to better constrain the system of equations.

An illustrative example why it is important to study processes across more than 2 time scales, for example, include loss of carbon from boreal forests due to warming. With a parochial, short-term view one may conclude that warming lengthens the growing season, speeds the kinetic rates of photosynthesis and leads to more carbon uptake. Taking a longer view, we see that warming may lower the water table, exposing peat and organic matter than had been laid down since the last glaciation. Its exposure allows it to respire and causes the system to lose carbon.

Today, with our wealth of data and new understanding how many important model parameters may scale, and our need and desire to conduct global ecology, we hope this view is dated. For example, there is many efforts using data assimilation methods to set priors and define parameter uncertainty, to produce the best yet model computations. Yet there remain concerns that the parameters may not be biologically or physically realistic, and represent fancy tuning. Plus there remain reservations about how well these models can predict in the future. On the other hand, these models use all the information available and seem to be the best option towards assessing and diagnosing fluxes across small to large scales

a. Issues of Scaling and Integration: Quantifying Non-Linear Processes

Many biophysical processes that contribute to trace gas exchange are non-linear functions and are forced by environmental variables that possess non-Gaussian probability distributions (Baldocchi and Meyers, 1998; Gu et al., 1999b; Leuning et al., 1995). For example, the leaf energy balance equation has one term that is an exponential function of leaf temperature and another term that raises leaf temperature to the fourth power! State-of-art models solve the energy balance equation with solutions to quadratic or quartic equations (Paw U and Gao, 1988). In turn, these equations need physiological information on stomatal conductance. Contemporary stomatal conductance models are coupled to models that predict photosynthesis. Iterative methods (Collatz et al., 1991)) or a solution to a cubic equation (Baldocchi, 1994; Nikolov et al., 1995; Su et al., 1996)) can be used to solve set resulting set highly non-linear and coupled equations.

Process	Non-linearity
Long wave energy emission	T^4
Saturation vapor pressure	$\exp(T)$

Leaf/soil respiration	$\exp(T)$
Leaf temperature	$aT_l^2 + bT_l + c$
Evaporation	$aE^2 + bE + c$
Leaf photosynthesis	$aA^2 + bA + c$
Leaf photosynthesis	$\frac{Q_p P_{\max}}{K + Q_p}$

Non-convergence and chaotic behavior commonly occurs when applying iterative solutions to this problem. When solving higher order algebraic equations, multiple roots are possible and there are no *a priori* arguments on which root is correct. We have found that physically and biologically meaningful solutions can switch roots under certain conditions. These instabilities indicate that the non-linearities and feedbacks of coupled biophysical processes must be examined over a broad range of biotic and abiotic conditions.

Integrating leaf-scale information to the canopy-scale requires estimating the expected value of a dependent function ($E[f(x)]$) in terms of independent variables that vary in time and space. This scaling is complicated by the non-linearity of many key dependent processes and by the non-Gaussian temporal and spatial distributions of many driving independent variables, such as light, wind, temperature, humidity and CO₂ within a canopy (Jarvis, 1995; Norman, 1981; Norman, 1993; Rastetter et al., 1992). For example, many physiological and physical processes, related to canopy photosynthesis, stomatal conductance and transpiration are regulated in a non-linear manner by a host of abiotic variables (solar and terrestrial radiation, temperature, humidity, wind speed and soil moisture). Another example of non-linear relationships can be demonstrated by examining the leaf energy balance equation. It has one term that is an exponential function of leaf temperature and another term that raises leaf temperature to the fourth power! State of art models solve the energy balance equation for evaporation and leaf temperature with iterative solutions (Bristow, 1987) and quadratic or quartic equations (Paw U and Gao, 1988):

$$E = f(R_n, T_l, D, g_s, g_b) \therefore$$

$$aE^2 + bE + c = 0$$

$$T_l = f(R_n, T_a, D, g_s, g_b) \therefore$$

$$aT_l^2 + bT_l + c = 0$$

Remember the quadratic equation is used to solve second order equation and yields solutions with 2 roots:

$$y = \frac{-b \pm \sqrt{b^2 - 4ac}}{2a}$$

In turn, these equations need information on stomatal conductance and provide information on surface temperature for kinetics computations. Modern models couple photosynthesis and stomatal conductance with Fick's Law diffusion models using iteration (Collatz et al., 1991) or a solution to a cubic equation (Baldocchi, 1994; Su et al., 1996):

$$A = f(Q_p, T_l, g_s, C_i) \therefore$$

$$aA^3 + bA^2 + cA + d = 0$$

Mathematically, the expected value of a non-linear function may not equal the function evaluated according to the mean value of the independent variable. This relation is also referred to as Jensen's (1859-1925) inequality (Ruel and Ayres, 1999).

We can see how this effect occurs by manipulating either Reynold's averaging rules or by examining Taylor's expansion series. On the basis of Reynolds' averaging we readily observe that the expected value of a non-linear function is not related to the function evaluated solely as a function of the means.

$$E[x \cdot y] = \overline{x \cdot y} \neq \overline{x} \cdot \overline{y}$$

$$E[x^2] = E[(\overline{x} + x')(x + \overline{x})] = \overline{x^2} + \overline{x'x'}$$

Error will occur in relation to the variance or covariance. I also note that the magnitude of the covariance is a function of the correlation between x and y and their respective standard deviations.

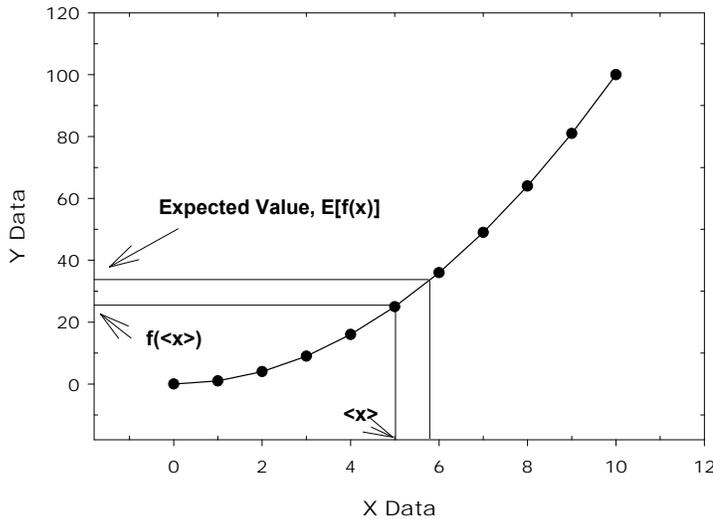
$$\overline{x'y'} = r_{xy} \sigma_x \sigma_y$$

We can examine this problem more formally by evaluating the expected value of non-linear functions with the mean value of an independent variable, x, using Taylor series expansion. The expected value of a function P is:

$$E[f(x)] = f(\overline{x}) + \frac{1}{2} f''(\overline{x}) \sigma^2$$

where the error is equivalent to the second term on the RHS of equation and is proportional to the *second derivative* of the function and the variance of the independent variable x.

The simplest case is to examine a quadratic equation



Assuming a set of numbers from one to ten has a mean of 5. The standard deviation of this span is 3.3. If we evaluate 5 squared we arrive at a functional value of 25. If we square each integer and average, we arrive at the expected value of x^2 , which yields 35. The ‘error’ term is on the order of 10 units, or a 40% different, by evaluating the function at the mean variable rather than the expected value. This simple math exercise also shows the power of using Taylor’s expansion as:

$$E[f(x)] = f(\bar{x}) + \frac{1}{2} f''(\bar{x}) \sigma^2$$

$$25 + \frac{1}{2} 2 \cdot 3.3^2 = 35$$

We can quantify the normalized error as a function of the coefficient of variation

$$\left(\frac{E[f(x)] - f(\bar{x})}{E[f(x)]} \right) = \frac{1}{2} \frac{f''(\bar{x}) \sigma^2}{E[f(x)]} = \frac{1}{2} f''(\bar{x}) cv^2 E[f(x)]$$

In reality many of independent variables possess non-Gaussian probability distributions, so the concepts described above may fail. Another way of expressing the expected value of any function (f), as when simulating canopy photosynthesis, transpiration or stomatal conductance, is to evaluate it in terms of the probability distribution:

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

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where p is the probability density function. Technically, the integration of leaf fluxes to the canopy scale requires a parallel assessment of controlling abiotic variables.

The evaluation of non-linear, light-dependent functions merits careful attention because the probability distribution for radiation can be bimodal. In many portions of the canopy few leaves experience the mean flux density of sunlight. They experience the full intensity of light in sunflecks, or the low intensity of light in the shade.

In practice, a simple, discretized version of the previous equation can be used to assess photosynthesis or stomatal conductance (Norman, 1981; Norman, 1993):

$$E[f(I, L)] = f(I_s)P_s(L) + f(I_u)P_u(L) + f(I_p)P_p(L)$$

Equation weights the functional dependence on solar radiation (I) at a given cumulative leaf area (L) according to the fractions of leaf area that are associated with the sunlit (P_s), umbral (P_u) and penumbral (P_p) classes; P_s , P_u and P_p sum to one and can be estimated with a canopy radiative transfer model that computes the probability of light transmission and interception. This concept will be discussed in greater detail when we discuss multi-layer models.

b. Quantifying Spatial Variation:

Plant canopies experience spatial heterogeneity in the vertical and horizontal dimensions at the scale of leaves and the canopy itself. Many studies show that CO_2 , light and photosynthetic capacity gradients exist through the cross-section of a leaf (Parkhurst et al., 1988; Terashima et al., 2001; Ustin et al., 2001). The attenuation of light is greater through the palisade layer than through the spongy parenchyma. Leaf thickness and nitrogen distribution, hence photosynthetic capacity will vary with leaf exposure (Givnish, 1988; Niinemets et al., 2004). In low light harvesting organelles capture a preferential amount of nitrogen. In high light nitrogen is invested in structures that increase photosynthetic capacity. There is some controversy whether or not gradients of P_s capacity exist in a cell, but data is clear that gradients occur across a leaf. Acclimation of a leaf will alter properties of the chloroplast. Changes in leaf thickness, photosynthetic capacity also affect CO_2 diffusion through the leaf. To maximize diffusion and minimize CO_2 drawdown, leaves should be narrow. To capture light, leaves should be thick.

Stomatal aperture varies widely across the surface of a leaf (Farquhar and Sharkey, 1982). Studies by Mott and colleagues show that stomata exhibit patchy behavior.

How much model complexity is needed?

This question was addressed in 1988, by Mike Raupach and John Finnigan in a provocative paper entitled: 'Single layer models of evaporation from plant communities are incorrect, but useful, whereas multi-layer models are correct but useless'. (Raupach and Finnigan, 1988).

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One camp criticizes ‘big-leaf’ models as being too simple, as they ignore canopy gradients and they do not account for counter gradient transfer and the separate partitioning of flux, as is associated with the soil and plant compartments. The other camp criticizes multi-layer models as being too complex. Opponents claim their performance is artificial, as these models need many tuning coefficients. Proponents claim that they are based on physics and mechanisms and they consider the impact of inter-canopy gradients on material flux. In the end, they conclude that both single layer and multi-layer models are useful. And their correctness depends upon the use. Big leaf models are often appropriate for specifying the lower boundary flux for large-scale models. Unfortunately, the constituent resistances are difficult to assess from first principles, as fluxes may scale linearly but resistances do not.

I also argue that the criticism of tuning is diminishing as we learn to constrain and parameterize the models with increased ecophysiological information and ecological scaling rules (Reich et al., 1997; Wullschleger, 1993); though circa 2012 there is a new revolution using data assimilation methods to fit models with data (Braswell et al., 2005; Fox et al., 2009; Williams et al., 2009; Zobitz et al., 2011).

It is important to evaluate non-linear functions on the basis of the local environmental drivers, not some variable measured high above the canopy. For this reason it is often common practice to use a micrometeorological model to translate the light, wind, temperature and humidity environment to that of a leaf buried deep in the canopy. Not doing so is analogous to using general California weather, from Sacramento or Bakerfield, to drive a climate model of San Francisco. We know that huge climate gradients exist, as Sacramento may be 40 C on a summer day, while San Francisco may be buried in fog and 10 C.

I suspect that model complexity and the impact of non-linear feedbacks will vary with leaf area. Simple one-dimensional models may be *apropos* for very sparse (leaf area index less than one) and closed canopies (leaf area index greater than four). Complex models may be needed for canopies with intermediate coverage, as light, wind, temperature and humidity gradients in and out of the canopy will be most severe.

As a model is applied for longer time-periods, information on future climate and weather, the structural and nutrient status of the plant canopy and the soil water balance is needed. Many trace gas model parameters, for example, vary significantly over the course of the year, as leaves age, resources change and plants experience periodic drought.

The advection of material across patches over a heterogeneous landscape is another topic that merits attention. In an open row crop or desert, the soil temperature in the open may be 50C, yet under the plant, 30 cm away it may be 25 C, a huge gradient.

A common assumption is that the size of the patch is large enough that it is independent of its neighbors. This claim is not true under circumstances that lead to the horizontal advection of heat, moisture and momentum. Examples include the placement of an irrigated field adjacent to desert, forests on steep hills, vegetated landscapes next to lakes, and forests next to crops or grasslands. On the other hand, if the scale of the

heterogeneity is smaller than the scale of turbulent mixing, the atmosphere may average such heterogeneities, as in the case of temperature gradients across row crops.

Complexity also depends on how coupled fluxes are to turbulent or radiative transfer. The issues of K theory not treating counter gradient transfer are true, but our model tests show that models that treat turbulent transfer in great detail do not yield greatly improved fluxes of CO₂ and water vapor (Leuning et al., 1995). On the other hand using an inappropriate radiative transfer submodel can produce huge errors (Baldocchi and Wilson, 2001).

For a counter example, heat and nitric acid vapor transfer are very dependent on surface boundary layer conductances. Using an oversimplified turbulence model will produce great errors in the estimation of those fluxes. Considering gradients in C and g_b are very important.

Do we need to include supra-fine scale information when scaling CO₂ and water vapor exchange from a leaf to a canopy?

Farquhar (Farquhar, 1989) suggests that the distribution of light across a leaf may not complicate the computation of leaf photosynthesis because a leaf optimizes the distribution of nitrogen (a surrogate for photosynthetic substrate) across a leaf.

The variability in CO₂ throughout a leaf will be small if diffusion is rapid to compensate for demand. The problem of diffusion through a leaf and how it alters CO₂ gradients has been treated by Parkhurst (Parkhurst et al., 1988). Spatial variability in C_i across a leaf causes the internal CO₂, generally estimated in the substomatal cavity, to overestimate the mean CO₂ concentration throughout the mesophyll. A difference of CO₂ across a 0.35 mm leaf could be 35 microbars (3.5 Pa, or 35 ppm). Gradients would be greatest as stomata close and leaves continue to photosynthesis.

Farquhar (Farquhar, 1989) addresses the problem by examining C_i in terms of many patches

$$C_i = C_a - \frac{A}{g_s} = C_a - \frac{A_1 + A_2 + \dots + A_n}{g_1 + g_2 + \dots + g_n}$$

This leads to a conductance-weighted version of C_i, as $A = g_s (C_a - C_i)$

$$C_{i,g} = \frac{g_1 C_1 + g_2 C_2 + \dots + g_n C_n}{g_1 + g_2 + \dots + g_n}$$

which is valid for linking transpiration and assimilation. C_i will be weighted more by the effect of open stomata than closed stomata

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If one is interested in how patches affect isotope discrimination then we need to weight C_i by A_i , instead:

$$C_{i,A} = \frac{A_1 C_1 + A_2 C_2 + \dots + A_n C_n}{A_1 + A_2 + \dots + A_n}$$

In principle $C_{i,A} < C_{i,g}$

If supra-fine scale information is deemed critical to scaling, it may be possible to assess such information by using a nested hierarchy of models. A nested model can be used to lump finer-scaled, biophysical information and provide information that is compatible with the needs of the higher scale. One example is to develop a model that computes photosynthesis according to light and chlorophyll gradients across a leaf (Terashima and Saeki, 1985) and accounts for CO_2 diffusion through the three-dimensional intercellular spaces (Parkhurst et al., 1988). A problem with this approach deals with correctly evaluating forcing variables at such fine scales. The outlined procedure requires information on the spatial distribution of cells and differential scattering properties of light in narrow wavebands due to pigment absorption. To obtain this information for leaves throughout a plant canopy is impractical and will increase the potential for error propagation. Yet, despite these problems, nesting cellular-based models into canopy models can be viewed as means of guiding research to obtain more mechanistic information on canopy-scale exchange rates.

Leaf photosynthesis, transpiration and stomatal conductance of leaves are also known to respond differently to a given stimulus due to differences in age, physiology, species and acclimation to the local environment (Field, 1991). In particular, leaf photosynthetic capacity diminishes with depth into the canopy because less nitrogen needs to be invested to fix carbon in this low light environment. There is also a body of literature showing that leaf inclination angles and clumping differs with depth (Kull and Jarvis, 1995).

Terashima et al (Terashima et al., 2001) developed a one dimensional leaf diffusion model for examining the trade-offs between diffusion and demand limitations.

Do we need to worry about the attributes of every species in a landscape or can we parameterize the system as a functional unit?

With regards to processes, one class of models compute physiological resistances with empirical algorithms (Raupach and Finnigan, 1988) while others couple equations of photosynthesis, stomatal conductance, nutrient status and leaf energy balance (Baldocchi and Meyers, 1998; Katul et al., 2000; Leuning et al., 1995; Sellers et al., 1997). At present there are no general rules when simple or complex biophysical models are warranted, but there are some guidelines based on hierarchy theory.

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In many cases, as with CO₂, energy and water vapor exchange, functional attributes of the forest stand (e.g. leaf area index, canopy conductance) are more important than the unique attributes of each species and tree in a stand. At the regional and global scale, vegetative properties with the strongest 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 (C₃ or C₄), 5) longevity (annual or perennial) and 6) type or intensity of disturbance (fire, cultivation). Power scaling rules for parameterizing models can be derived from work by Reich et al (Reich et al., 1997) and Wright et al. (Wright et al., 2005).

In 2014, the idea of plant functional types is starting to be replaced with the idea of plant functional traits, generated from large databases like TRY and based on scaling laws (Kattge et al., 2011; Wright et al., 2005)

Can Models and Their Parameters be Static in Time?

The dominant periods of time scales affecting canopy-atmosphere gas exchange have durations of hours, days, seasons and years. On a diurnal time scale, variations in CO₂ and water vapor exchange are forced by daily rhythms in solar radiation, air and soil temperature, humidity, CO₂, stomatal aperture, photosynthesis and respiration. In the middle latitude regions, weekly fluctuations in trace gas fluxes are induced from synoptic weather changes that are associated with the passage of high and low-pressure systems and fronts. These events will cause distinct periods of clear skies, overcast, and partly cloudy conditions. The passing of weather fronts also changes air temperature, humidity deficits, and pressure. Weather fronts, therefore, can impose weekly-scale fluctuations on photosynthesis, respiration and stomatal opening, as these physiological processes respond to changes in cited meteorological variables (Baldocchi and Wilson, 2001; Gu et al., 1999a; Katul et al., 2001; SIQUEIRA et al., 2006). Frontal passages may also cause the measurement of ecosystem CO₂ exchange to be biased. Associated changes in wind direction and speed may cause a tower site to view a different flux footprint (Kim et al., 2006; Schmid, 2002). The implication of this effect is to view different patches of underlying vegetation, which may have different functionality and capacity for trace gas exchange.

In recent years, a series of studies have shown that model parameters like photosynthetic capacity vary over the growing season (Wilson et al., 2001; Xu and Baldocchi, 2003) and estimates of canopy photosynthesis are in error if this seasonality is neglected (Wang et al., 2007; Wilson et al., 2001).

On seasonal times scales, an ecosystem experiences the effects of the seasonal change in the sun's position. This effect alters the potential amount of sunlight received, the surface's temperature and water balance. Superimposed upon these meteorological factors is a cord struck by an ecosystem's phenology. Examples include the timing and occurrence of leaf expansion and the timing of plant development and growth, photosynthetic capacity leaf area index, and leaf-fall. The timing of leaf-out, for instance, has a distinct impact on the humidity and temperature of the planetary boundary

layer (Schwartz and Crawford, 2001) and the Bowen ratio at the Earth's surface. Persistent drought and wet spells occur on monthly to seasonal time scales, too (Brubaker and Entekhabi, 1996; D'Odorico and Porporato, 2004). Dry spells can exert a significant reduction on the net ecosystem CO₂ and water vapor exchange, as compared to periods when soil moisture is ample. The movement of nitrogen from leaves to stems before leaf senescence is an example of a phenological event that will alter photosynthetic capacity.

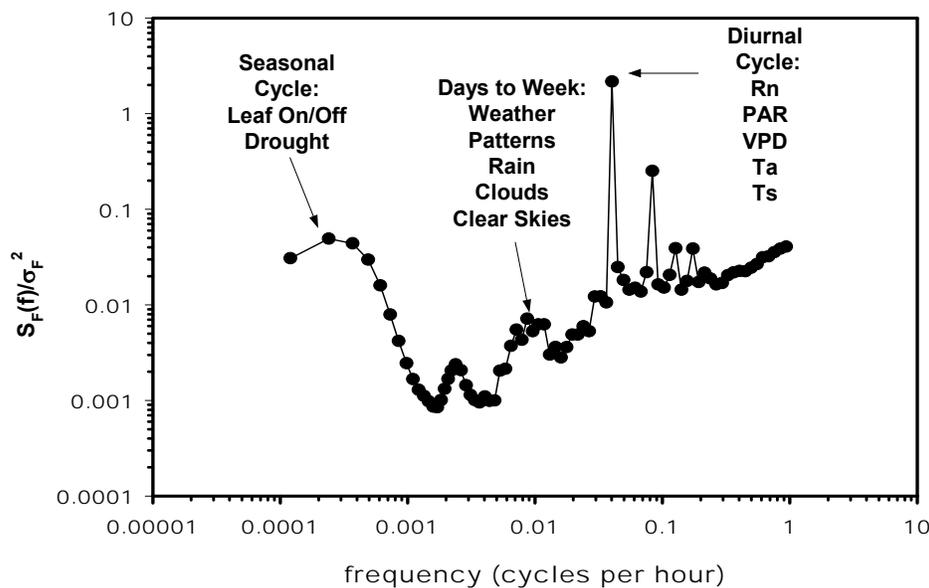
At inter-annual time scales, the timing of phenological switching events, such as leaf-out, may be advanced or delayed by a month due to large-scale climatic features that can be associated with *El Nino-La Nina* cycles (Keeling et al., 1996; Myneni et al., 1997). Growing season duration has a profound influence on net biosphere productivity (Baldocchi et al., 2001; Churkina et al., 2005) and can have a major impact on inter-annual fluxes of carbon dioxide (Randerson et al., 1999).

b. Theoretical Evaluation: Modeling ecological dynamics with biometeorological mechanisms.

Model parameters that define such characteristics as leaf area index, photosynthetic kinetics, stomatal conductance, and soil respiration vary over the course of a growing season as phenology, soil moisture status and photosynthetic capacity changes (Hanan et al., 1998; Gu et al., 1999). Table 1b catalogues important variables and their time scales of variance.

b) Canopy Structure, Physiology and CO₂ Exchange

A power spectrum of CO₂ fluxes over the course of a year is shown in the next figure. Note the periods of high and low variance. Little variance occurs at monthly time scales. High variance is associated with daily and seasonal time scales, as expected. Moderate variance is associated with sub weekly time scales, as fronts pass, altering light, humidity and temperature.



d. Errors and Validation

SVAT models provide us with a quantitative framework with which to compute rates of trace gas fluxes between the biosphere and atmosphere. By undertaking the challenge to model, we cannot only be interested in developing clever computer code. Any modeling exercise must be cognizant of several sources of error, when constructing and implementing the model. Sources of error will arise from:

- 1) a model's conceptual framework and its complexity;
 - a. Have we considered all the appropriate processes?; bias error will arise if we include one set of processes over another, when both contribute significantly to the fluxes
- 2) How the is model parameterized;
 - a. Are model parameters based on measurable quantities or are they tuned?
 - b. Is the statistical variability in model parameters considered?
- 3) the driving variables that are used to implement it;
 - a. Is the environment in contact with the soil and plant well coupled with that of the external atmosphere?
 - b. Do we need a processing model to transfer above canopy microclimate variables to the site of action?
- 4) the relevance of the time and space scale over which it is applied;
 - a. Can the model be used on an annual basis or is it valid only for the growing season?
 - b. Can the model be applied to a spectrum of plant functional types?
- 5) the validity of the data used to test it; all validation data is not created equal.
 - a. Are the test flux data biased by instrument or theory, are are nocturnal eddy flux measurements?
 - b. Do the data suffer from statistical noise due to variability of the atmosphere?

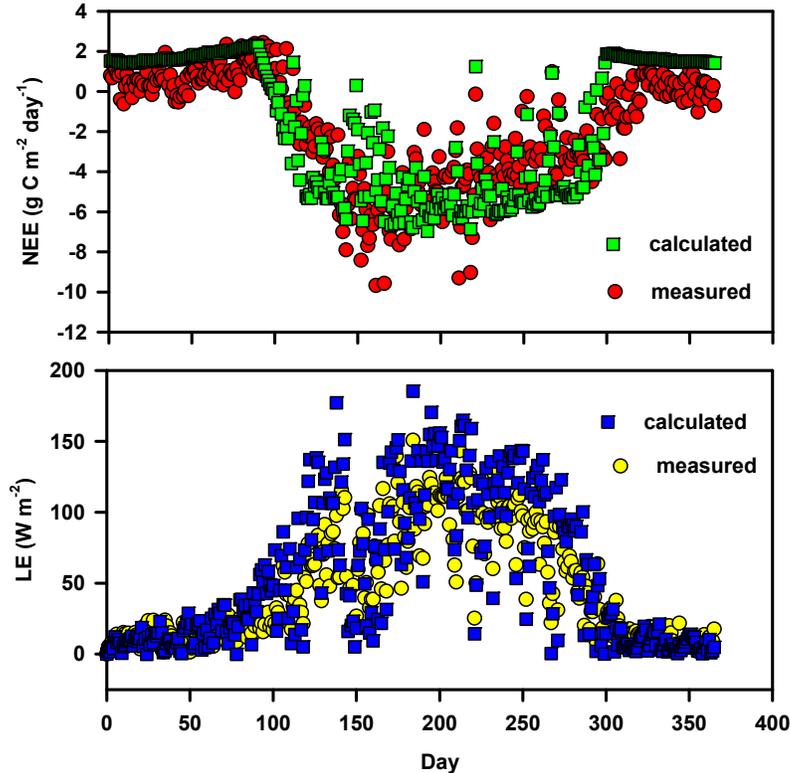
Due to the multiplicity of time and space scales and processes that are associated with modeling trace gas fluxes, model testing is a necessary, but non-trivial, exercise. In practice, no will trace gas exchange model will pass the falsification criteria, which has been advocated by Karl Popper (1959). For example, Rastetter (Rastetter, 1996) shows that the Farquhar photosynthesis model, a key component of a coupled trace gas model, is capable of estimating photosynthesis responses to light and CO₂ correctly on hour to day time-scales. But the model fails to mimic seasonal and multi-year time-scales responses to CO₂, as plants acclimate or down-regulate. To correctly validate a canopy-scale trace gas model, the time and space scale of the model and validation data must match. It is unfair to test a model for conditions it was not intended for using.

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I, and many colleagues, advocate model hierarchy testing and application (Hanson et al., 2004; Juang et al., 2008; Kobayashi et al., 2012; Raupach and Finnigan, 1988; Vogel et al., 1995). There are many circumstances where a detailed process based model can be used to derive model parameters for simpler and more applicable models.

Data from a network of long term eddy flux measurements sites (FLUXNET, <http://www-eosdis.ornl.gov/FLUXNET>) is now available to test a hierarchy of trace gas flux models across a spectrum of forest types, on time scales from hours to years. I stress that the availability of such data is a major advancement in SVAT model development. A decade ago, we were satisfied to have data sets from only few days. These meager data sets, however, tended to yield inconclusive results on model performance. By the mid-1990s, studies started to be conducted for longer intervals. Many contains several weeks of data, and a few started to provide a year or more of data (Black et al., 1996; Greco and Baldocchi, 1996; Wofsy et al., 1993). At present, the Harvard forest team has about a 15 years of data (Urbanski et al., 2007). Data sets at the northern Boreas site, Takayama, Japan and the Walker Branch Watershed, TN and many sites in Europe exceed a decade.

An example of a comparison between model calculations and measurements of carbon dioxide and water vapor exchange over a broad-leaved deciduous forest for the duration of a year is shown in the following figure. Overall, the agreement between measurement and theory is good, as much of the data over lap. How well a model should agree with data is a matter of debate. A $1 \mu\text{mol m}^{-2} \text{s}^{-1}$ difference between calculated and measured carbon flux densities falls within expected measurement and modeling errors. Yet, a bias of this magnitude can cause annual sums of net carbon exchange to differ by 400 g C m^{-2} . There is also the issue relating to the accuracy of the test data, as eddy flux data suffer from bias errors at night and over complex terrain.



A comparison between measured and calculated fluxes of net ecosystem CO₂ exchange (NEE) and latent heat flux densities (LE). The calculations were derived from the CANOAK model. The measurements were derived from the eddy covariance method. The data are from a temperate broad-leaved deciduous forest growing near Oak Ridge, TN.

One also has to consider the impact of the validity of flux data. It will be biased by not measuring fluxes well at night, if energy balance closure is not met, if there is flux divergence or if the flux is not adjusted for different landscapes in the flux footprint, as wind direction and stability varies.

In the modern era our task is not only to reproduce fluxes, but their variance over a time scale of operation. With the CANOAK/CANVEG model, we have been able to reproduce the power spectrum of CO₂ flux using information on meteorology and the seasonal variation in leaf area index and photosynthetic capacity. This is one example, but the key point is that there is now a need to run SVAT models for time durations up to a year and more (Baldocchi and Wilson, 2001; Katul et al., 2007; Richardson et al., 2007; SIQUEIRA et al., 2006).

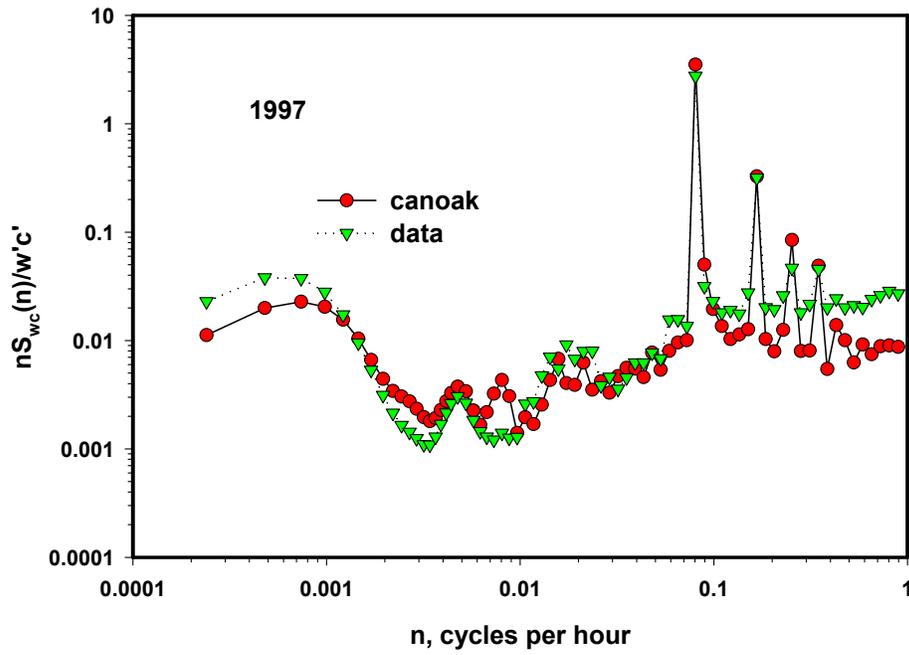


Figure 4

Advancing Modeling beyond meteorological time scales, coupling SVAT and Ecosystem dynamic models.

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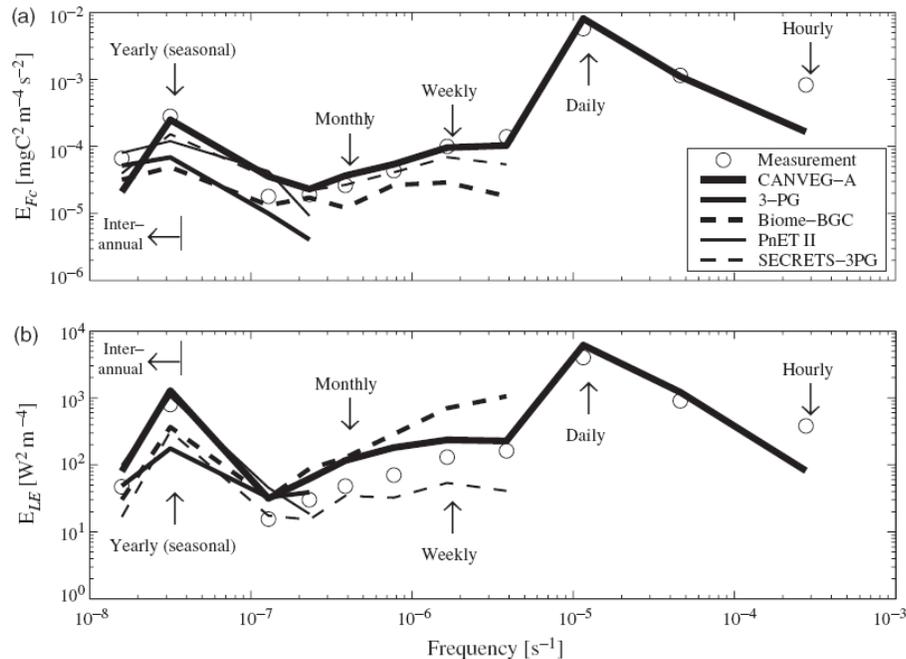


Fig. 4 Measured and modeled power spectra for the CO_2 flux F_c [panel (a)] and latent heat flux LE [panel (b)].

Figure 5

2. Error and Uncertainty Analyses

Due to the multiplicity of time and space scales and processes that are associated with modeling trace gas fluxes, model testing is a necessary, but non-trivial, exercise. In practice, no will trace gas exchange model will pass the falsification criteria, which has been advocated by Popper (1959). To correctly validate a canopy-scale trace gas model, the time and space scale of the model and validation data must match. It is both unfair and wrong to test a model for conditions it was not intended for using (Rastetter, 1996).

Sources of uncertainties

Uncertainties in modeling trace gas exchange of ecosystems stem from structural complexities, natural environmental variability and deficiencies in our knowledge. From a modeling point of view, we partition sources of uncertainties into the following categories:

- Uncertainty of flux measurements.

The eddy covariance method is derived from the conservation equation. Its representation of biosphere-atmosphere fluxes depends on the roles of atmospheric storage and advection (Goulden *et al.*, 1996; Hollinger and Richardson, 2005). One has to be careful when using eddy covariance data to test models, as the flux across the atmosphere-biosphere plane may have not been produced locally, with respect to time. Atmospheric stability can store scalar material in the canopy airspace. Intermittent

eddies can vent this material at some later time. Using an 'enhanced' flux to validate a model will be incorrect. To circumvent these problems we intend to assess important components of the conservation equation in our field-work (e.g. Baldocchi et al., 2000c).

- Uncertainties in basic model parameters.

Mechanistic models of carbon, water and energy exchange of ecosystems integrate basic physiological, biogeochemical and micrometeorological processes. Numerous parameters are required to define these processes, and not all of them are known. For example, in most modeling studies, parameters in defining responses of leaf stomatal conductance and photosynthesis to changes in environmental conditions are borrowed from somewhere else without considering differences in climate, phenology and spatial gradients (Gove and Hollinger, 2006; Medlyn et al., 2005).

Monte Carlo Error analysis of parameters is a useful tool for exploring the ramifications of errors in model parameters, given a known statistical distribution (Verbeeck et al., 2006)

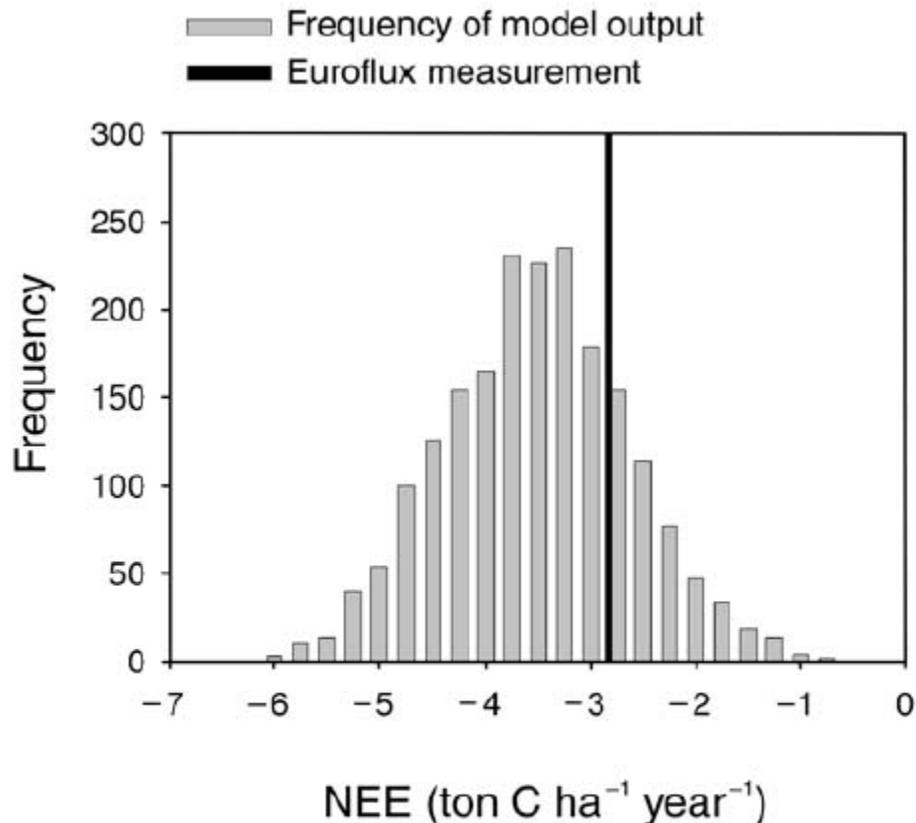


Figure 2. Distribution of the total net ecosystem exchange (NEE; Mg C ha⁻¹ year⁻¹) in 1997 for the Hesse forest in France. The calculation of this distribution is based on 2000 Monte Carlo simulations. Only the uncertainty of ten key parameters was taken into account. The black bar above shows the measured (Euroflux) NEE value and does

- Uncertainties in driving variables.

Biophysical models of mass and energy exchanges are generally driven by common meteorological variables such as radiation, temperature, humidity, precipitation, wind speed, etc. Exposure of the instrument, calibration stability are among the key factors affecting the accuracy of driving variables. Temperature sensors, for example, need to be shielded from the sun and aspirated to produce accurate measurements. Radiometers need to be level and cleaned periodically and not see towers and scaffolding on which they are mounted. Rain gauges need to be positioned so wind does not bias the measurements.

I cannot understate the importance of regularly calibrating meteorological sensors. For instance, it has become well known in the biometeorology community that a standard sensor for measuring PAR may drift by 5 to 10% over the course of a year. Consequently, errors in PAR will cascade into errors in leaf area index, f_{par} and canopy photosynthesis.

In theory, these variables should cover the whole temporal and spatial domains that the models are intended to apply. However, continuous measurements of these variables are rarely available in the temporal domain and even worse in the spatial domain. Some form of gap filling is required to produce continuous data records for model simulations. This activity produces a quantifiable source of error.

- Uncertainties in system complexity representation.

Any model can only approximate a system to a limited degree. Since the truth may never be known, it is only hoped that the more complex the model is, the closer the model is to the 'truth'. However, the degree of complexity that a model can go is constrained not only by the state of knowledge and computing resources but also by the potential model instability usually associated with growing complexity. Our proposal to test a hierarchy of models is a major means for assessing this source of error (Chen et al., 1999; Juang et al., 2008; Vogel et al., 1995).

- Uncertainties in limited temporal and spatial resolutions.

A more challenging issue in uncertainty assessment is limited temporal and spatial resolutions when integration over some temporal and spatial domains are needed. In current practices, biophysical exchanges are often examined on a half hourly basis while horizontal homogeneity is assumed at least for the neighborhood where a flux tower is operated. However, ecologically important meteorological variables normally possess fluctuations in much smaller time scales while horizontal heterogeneity in vital variables such as soil moisture and vegetation structure can be expected to happen in the order of meters. Gu et al. (Gu et al., 1999b) recently argued that spatial heterogeneity created by fair-weather cumulus cloud fields can complicate interpretation of tower-based flux measurements even for horizontally homogeneous ecosystems. Therefore the biophysical exchanges are necessarily irregular functions of time and space. For such functions, numerical approximations of the integration sensitively depend on the steps used. Thus it

is imperative to examine the impacts of temporal and spatial resolutions in the scaling up processes of biophysical exchanges.

3. Soil-Vegetation-Atmosphere Transfer (SVAT) models: history and hierarchy

The history of SVAT modeling can be traced back to the Father of numerical weather forecasting, L.F. Richardson, in 1922. Richardson recognized that he needed to evaluate fluxes at the lower boundary of his conceptual matrix that was being used to predict weather by the equations of motion and continuity. Richardson proposed an algorithm for computing evaporation that was based on a simple Daltonian equation:

$$E = k(f(T_{leaf}) - w_{air})$$

Practical application of such algorithms would lay dormant until the advent of the digital computer, decades later.

b. SVAT modeling in Agriculture, Forestry and Ecology

The history and development of soil-plant-atmosphere transfer models is tied strongly to advances in agricultural meteorology and soil physics. At mid 20th Century, there was considerable interest in developing an equation that predicts evaporation rates from a variety of land surface types. Thornthwaite developed a relation that evaluated monthly evaporation as a function of temperature. The method has many shortcomings due to its long time scale and empirical nature. Firstly, evaporation and temperature are out of phase with one another. Second, it had no physiological feedback. Thirdly, it could not be applied to short-term problems, such as daily crop water use. H.L. Penman at the Rothamsted station in England recognized the weakness of the Thornthwaite approach and developed a relation that had a physical basis. It was formed on the basis of the energy balance equation and a Daltonian equation for mass transfer.

The next generation of models split into two directions, according to model scale and complexity. One direction involved developing 'Big-Leaf' models. The other direction broke the canopy into smaller and smaller and lead to the development of multilayer SVAT models (Cowan, 1968; Waggoner et al. 1969; Shawcroft et al., 1972).

A notable advancement in the development of 'Big-Leaf' models was produced by John Monteith (Monteith, 1965) then at the Rothamsted research station in England. He was one of the first scientists to incorporate a metric for describing plant physiology, in terms of the surface resistance, into a 'Big-Leaf' model. His contribution, subsequently, became noted as the Penman-Monteith equation, for computing evaporation from a vegetated surface with a closed canopy

Developing row crops and semi-arid vegetation form open canopies. They are examples of two-component systems, as they possess separate vegetation and soil components. These separate compartments exert different control on evaporation, as plants possess active

stomata that act as gates for the control of water vapor. In contrast, evaporation from the soil is relative passive. For these reasons, scientists (in the mid-1980s) recognized an important need to develop two layer models. Among the first schemes to treat the soil and vegetation separately were models by Deardorff (Deardorff, 1978), Shuttleworth and Wallace (Shuttleworth and Wallace, 1985), Sellers et al. (Sellers et al., 1986) and Monteith and Choudhury (1988). Another motivating factor for developing two-layer models was forced by the availability of infrared temperature measurements by satellites or tower-based instruments. Hot dry soils under sparse, transpiring canopies have a disproportionate impact on the radiative temperature, but less on sensible heat transfer. Hence, there was a need to develop models that could weight the radiative temperatures of the soil and vegetation correctly. Kustas (1990) and Norman et al. (1995) were among the first to make advances in this area.

While conceptually sound, the majority of two-layer models rely on K theory, which can be challenged theoretically. They also introduce additional resistances that are hard to characterize (Shuttleworth and Wallace, 1985). By the mid-1990's, advances in Lagrangian diffusion theory by Raupach (Raupach, 1987) began to filter into the new generation of two layer model. van den Hurk and McNaughton (Vandenhurk and Mcnaughton, 1995) used the concepts of near and far field diffusion theory to construct a two-layer 'resistance' model that was based on Lagrangian diffusion. In principle, their model could account of counter-gradient transfer and refute the criticisms that have been levied on other two-layer and 'Big-Leaf' models (Dolman, 1993).

At the turn of the century and millennium, the newest two-layer models began to couple carbon, water and energy (e.g. (Amthor et al., 1994; Sellers et al., 1997) for coupling with global climate models. Yet, recent studies show that this added level of complexity may still be inadequate. The most recent class of models treat each layer as a dual-source, one for the sun and another for shaded fractions of leaves and soil. Wang and Leuning (Wang and Leuning, 1998) and dePury and Farquhar (dePury and Farquhar, 1997)(1998) are among the most recent contributors in this sphere. As a side note, it is interesting how contemporary scientists can re-invent the wheel. The newer dual source, sun/shade models were preceded by ideas advocated nearly thirty years ago by Sinclair et al. (Sinclair et al., 1976) and Norman (Norman, 1979).

Returning to the concept of multi-layer models, the earliest attempts to integrate (rather than scale) water vapor and energy exchange from leaves to canopies focused on horizontally homogeneous crop canopies. This model class needed to resolve two issues. They needed to simulate radiative transfer through the canopy and simulate wind and turbulence in the canopy air space. Initial efforts on radiative transfer through foliage were made possible by contemporary advances in modeling radiative transfer in closed plant canopies (Anderson, 1966; DeWit, 1965; Monsi and Saeki, 2005; Monteith, 1965). These theories had origins in astrophysics (Ross, 1980) and were based on theories that compute radiative transfer through turbid media of inter-galactic space (Chandrasekhar, 1950). Consequently, a plant canopy was abstracted as a multi-layer, turbid medium.

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The earliest micrometeorological scaling models focused on micro-environmental variables that control photosynthesis, transpiration and stomatal conductance. The models were based on K-theory and its sister, the resistance-analog scheme (Cowan, 1968; Waggoner et al., 1969; Miller, 1971; Shawcroft et al., 1974; Allen et al., 1974; Goudriaan, 1977; Norman, 1979, 1982; Jarvis et al., 1985; Caldwell et al. 1986).

The research community soon recognized that ideal plant canopies were more often an exception rather than the rule. Subsequently, more complex geometrical and statistical canopy radiative transfer models were developed. Particular models treated the orientation and spacing of row crops (Jackson and Palmer, 1972; Allen, 1974; Fukai and Loomis, 1976; Mann et al., 1980), the non-random spatial distribution of leaves (Nilson, 1971; Acock et al., 1970; Oker-Blom and Kellomaki, 1983), arrays of plants and leaves (Roberts and Miller, 1977; Norman and Welles, 1983; Myneni and Impens, 1985), the shapes of crowns (Oker-Blom and Kellomaki, 1983; Grace et al., 1987; Wang and Jarvis, 1990), the distribution of needles on stems (Norman and Jarvis, 1975; Oker-Blom et al., 1983) and penumbra (Miller and Norman, 1971; Denholm, 1981a, 1981b; Oker-Blom, 1985; Myneni and Impens, 1985). From these advances in canopy radiative transfer modelling came the next generation of light-dependent photosynthesis, transpiration and stomatal conductance scaling models; these models were adapted for the specific needs of widely spaced rowcrops (Fukai and Loomis, 1976; Gijzen and Goudriaan, 1989), orchards (Cohen and Fuchs, 1987; Cohen et al., 1987), grasslands (Norman and Polley, 1989), desert cactus (Garcia et al., 1985); broadleaf forests (Baldocchi and Harley, 1995)) and conifer forests (Wang and Jarvis, 1990).

In the past two decades, experimental and theoretical advances has also shown that K-theory models are subject to several fundamental weaknesses (Denmead and Bradley, 1987; Wilson, 1988). In plant canopies turbulence does not scale with the size of leaves. Instead it scales with the height of the canopy. The consequence of large-scale turbulence superimposed on a multi-layer source/sink field is the occurrence of counter-gradient transfer. Contemporary scientists are now using higher order (second and third) closure (Katul and Albertson, 1998; Meyers and Paw U, 1987) and Lagrangian (Baldocchi, 1992) to compute carbon dioxide, water vapor and sensible heat exchange within and above plant canopies in order to circumvent the problems associated with K theory. And more recently large eddy simulation (LES) models have been developed for studying canopy turbulence and fluxes (Albertson et al., 2001).

In the past decade mechanistic carbon exchange models, based on biochemical and physiological principles, have been developed (Farquhar et al., 1980; Voncaemmerer and Farquhar, 1981). And other studies are showing close coupling between stomatal conductance and photosynthesis (Collatz et al., 1991; Wong et al., 1979). This information is now being used to model stomatal mechanics and transpiration of leaves (Baldocchi, 1994; Nikolov et al., 1995; Su et al., 1996). In recent years there has been an explosion of activity to incorporate coupled carbon-water-energy algorithms into multi-layer models that compute atmospheric trace gas and energy exchange over crops and broadleaf and coniferous forests. And now these models can be used to simulate fluorescence (van der Tol et al., 2009).

Two factors are partly responsible for this activity. One is a predictive and constrain manner in how to parameterize the models. For instance, Wullschleger (Wullschleger, 1993) and Wohlfahrt et al. (Wohlfahrt et al., 1999) shows a tight coupling between two important parameters for photosynthesis. Schulze et al (Schulze et al., 1994) among others show that these parameters link to leaf nitrogen and stomatal conductance. By coupling ecological theory with micrometeorology, we are learning how leaf area, net primary productivity and evaporation of structurally homogeneous and well-watered ecosystems, such as croplands and temperate and humid forests and grasslands, increase with available water and nitrogen (Baldocchi and Meyers, 1998; Kelliher et al., 1995; Leuning et al., 1995; Schulze et al., 1994). We also understand the relative controls of climate and biology on evaporation from these ideal landscapes. Evaporation by aerodynamically rough forests is governed by surface conductance and humidity deficits and evaporation by aerodynamically smooth vegetation is governed by available energy (Jarvis and McNaughton, 1986).

The next generation of biophysical models for ecosystem-scale carbon, water and energy exchange will need to treat the next level of complexity. Field and modeling studies are needed on: 1) horizontally and vertically heterogeneous landscapes, 2) ecosystems whose structure and function is limited by seasonal soil water deficits and 3) annual and inter-annual variations of mass and energy exchange between the biosphere and atmosphere. The execution of such research requires us to examine the vegetative and soil compartments as individual, but coupled systems, across landscape gradients and over multiple time scales. We also anticipate activities that merge SVAT, Eco-physiology and ecosystem dynamic models (e.g. Foley et al., 1999). SVAT models are needed to compute energy exchange at short time scales, but they will need to rely on ecophysiological models to provide information on stomatal conductance and to link transpiration and photosynthesis. To arrive at information on functionality, leaf area and capacity we will need to predict stand dynamics and their response to climate.

b. SVAT modeling in Climate and Weather Models

While advances were being made in agricultural and forest science, climate researchers were working in relative isolation. In part their needs were different. Due to early constraints on computational power, climate scientists did not want some baroque code to describe the lower boundary of the atmosphere. They also needed algorithms that were compatible with their scale of inquiry, 100 to 500 km on a side, rather than 100 to 500 m. The earliest SVAT schemes used simple models based on energy balance, albedo, emissivity and drag coefficients (e.g Manabe and Wetherald, 1967; Carson, 1980). Part of this simplification was justified by the fact they were conducting calculations for grids that were 100 to 500 km on a side. Turbulent fluxes were evaluated in terms of velocity and bulk transfer coefficients, as concept more typically used by oceanographers:

$$F_x = -C_x u(z) \Delta X(z)$$

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A leaking bucket approach, tied to the hydrological water balance was used to adjust the transfer coefficient for water vapor exchange (Manabe, 1969). It had no physiological feedbacks.

By the late 1970's, it was becoming recognized that the 'leaking bucket' scheme was not satisfactory for treating biosphere-atmosphere interactions. James Deardorff (Deardorff, 1978) developed a new SVAT model for weather prediction models, that circumvented the idea of transfer coefficients. Instead, he altered stomatal resistance to evaluate evaporation rates and the partitioning of available energy.

By the mid-80s, three groups of scientists were interjecting biophysical control on the land-atmosphere system. The lead groups included a team of scientists at NCAR, lead by Bob Dickinson and Ann Henderson-Sellers, who developed the BATS model. Another a group was based at NASA/Goddard. It was responsible for developing the the SIB model (Sellers et al., 1986). A third group was based out of Meteo-France (Noihlan and others). In general, these models were based on the multiplicative stomatal resistance schemes based on the ideas of Paul Jarvis (Jarvis, 1976).

In the last decade, the state-of-art climate models have evolved to consider coupling of carbon, water and energy and are driven by remotely sensed satellite data (Ciais et al., 2005; Sellers et al., 1997).

Table 1. An Abbreviated History of Mass and Energy Exchange Models in Biometeorology, Ecology and Climate

Model-Concept	Era	Key Authors
Evaporation algorithm for weather prediction	1920s	L.F. Richardson
Resistance model, coupling Energy Balance and aerodynamics; Penman-Equation	1950	H. Penman
Big-Leaf Model with Canopy Resistance	1960s	Monteith (1965)
Multi-Layer, K-theory; water-energy	1960s	Cowan (1968); Waggoner et al.
Radiative transfer models	1950-60s	Monsi-Saeki; Ross; Anderson; deWit
Multi-Layer, K-Theory; water-energy-carbon	1970s	Shawcroft et al. (1971); Goudriaan (1977); Norman (1979); Jarvis et al (1985)
Bucket models in climate	1970s	Manabe
Dual source Big-Leaf models, sun/shade	1970s	Sinclair et al. (1976); Norman (1980)
2 nd order closure model (turbulence)	1970s	Wilson and Shaw (1977)
Advection, 2 dimensional transfer	1970s	Rider et al (K-theory) ; Rao et al (2 nd order closure)

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Stomatal conductance model driven by environment	1970s	Jarvis (1976)
Early SVAT algorithm in weather models	1970s	Deardorff (1978)
LES concept	1970-80s	Deardorff, Wyngaard and Moeng
2 nd and 3 rd order closure (heat and water)	1980s	Meyers and Paw U (1986)
Bottom-up/Top Down PBL theory	1980s	Wyngaard (1982)
Leaf photosynthesis/stomatal conductance models	1980s	Farquhar et al. (1980); Collatz et al (1989)
Mesoscale models; checker board problem	1980s	Avissar and Pielke
Lagrangian models (concept)	1980s	Raupach (1988)
Big-Leaf, SVAT Models in Climate algorithms (BATS; SiB) (water, heat)	1980s	Dickinson; Sellers
Two-Layer K theory Models	1980s	Wallace and Shuttleworth; Kustas; Norman
Lagrangian model (functional): carbon, water, energy	1990s	Baldocchi (1992; 1997); Baldocchi and Harley (1995); Katul (1998)
Big-Leaf, SVAT Models (water, heat, carbon)	1980s/1990s	Norman (1980, 1983), Sellers (Sib2); Amthor; Leuning; dePury/Farquhar
Ellipsoidal models	1990s	Wang and Jarvis (1990); Norman and Welles
2-layer Lagrangian models (localized near/far field theory)	1990s	Raupach; McNaughton/van den Hurk
Coupled leaf photosynthesis/stomatal conductance models	1990s	Collatz et al. 1991; Baldocchi (1994); Nikolov (1995); Leuning (1995); Su et al. (1997)
model intercomparison studies, eg PILPS project	1990s	Henderson-Sellers; Liang et al; Dolman et al. Stannard, Pittman
Dynamic and coupled energy balance, stomatal conductance, leaf photosynthesis models	1990s	Su et al. (1997); Percy et al.
Coupled meteorology; ecosystem dynamics; ecophysiology models	1990s	Foley et al., (1998); Woodward et al. (1998); Hurtt et al.(1998); Cramer et al (1998); Prentice et al.; Moorcroft et al. (2001)
Satellite Driven SVATS	1990s	Norman, Diak, Anderson; McNider
Long term data sets for	1990s	AmeriFlux; Fluxnet; Euroflux; Law et al.

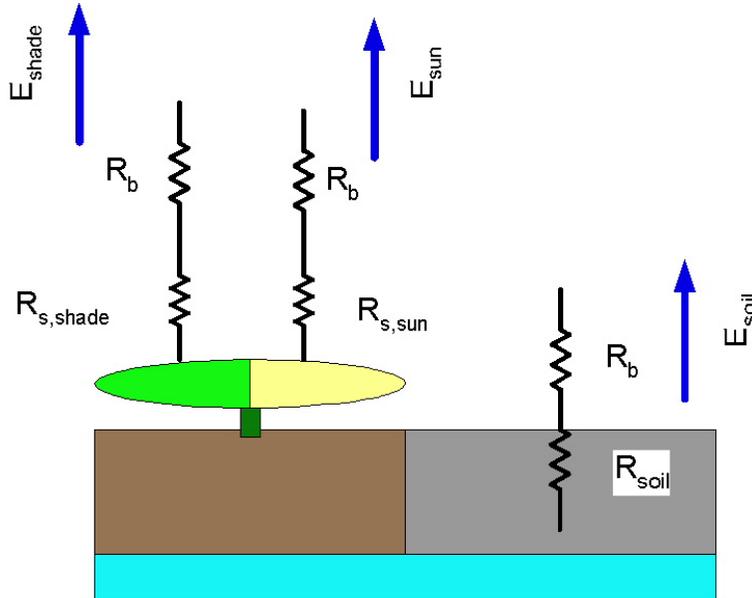
testing and parameterizing models		(2000); Aber et al (2000); Baldocchi and Wilson (2001).
Neural Network models	1990s	Van Wijk and Bouten (1999) Papale and Valentini (2003)
Coupled climate-carbon-water fluxes	2000s	Ciais et al; Friedlingstein et al; Cox et al;
Data assimilation	2010s	Zobitz et al.; Williams et al; Braswell et al

The newest class and most leading coupled land surface- climate models include ORCHIDEE from groups at LSCE/CRNS Gif sur Yvette and the Laplace Institute in Paris France, JULES from the UK Met Office, LPJ of the Lund, Potsdam and Jena/Max Planck Groups, and SIB-2 used by groups in the US (Stanford, Carnegie Institute-Washington, Colorado State) and CLASS and InTec models of Canadian research groups.

Model Hierarchies

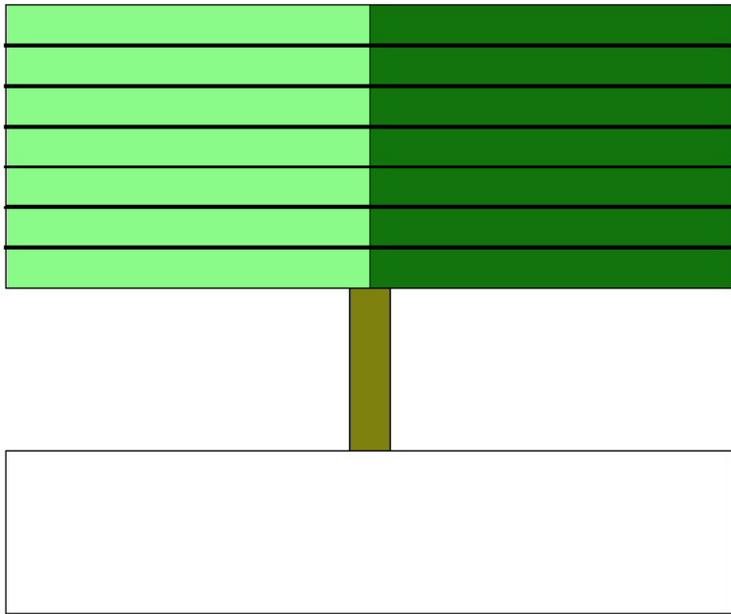
Dual-Source, Two layer model considers vegetation and soil and sun and shade fractions

Dual Source: Two Patch Model



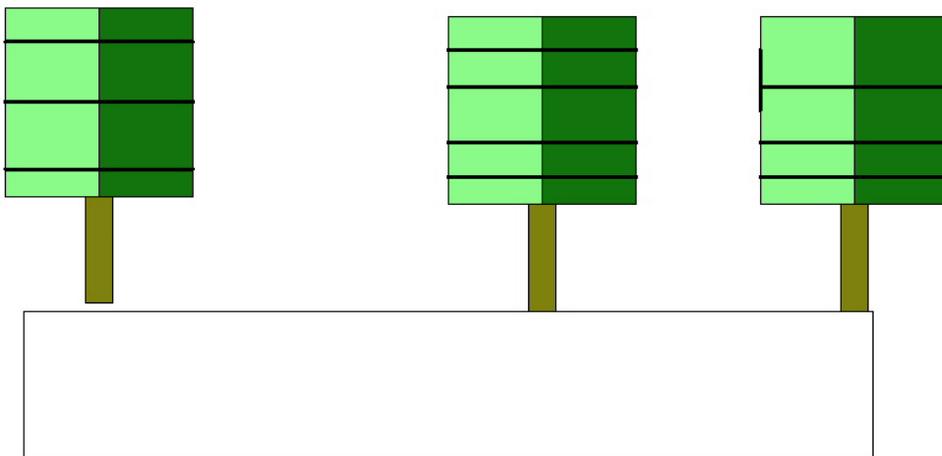
Multilayer, 1-D model, sun/shade, dual source model considers vertical gradients within vegetation, as well as the distinct environment on sun and shade leaves

CANOAK

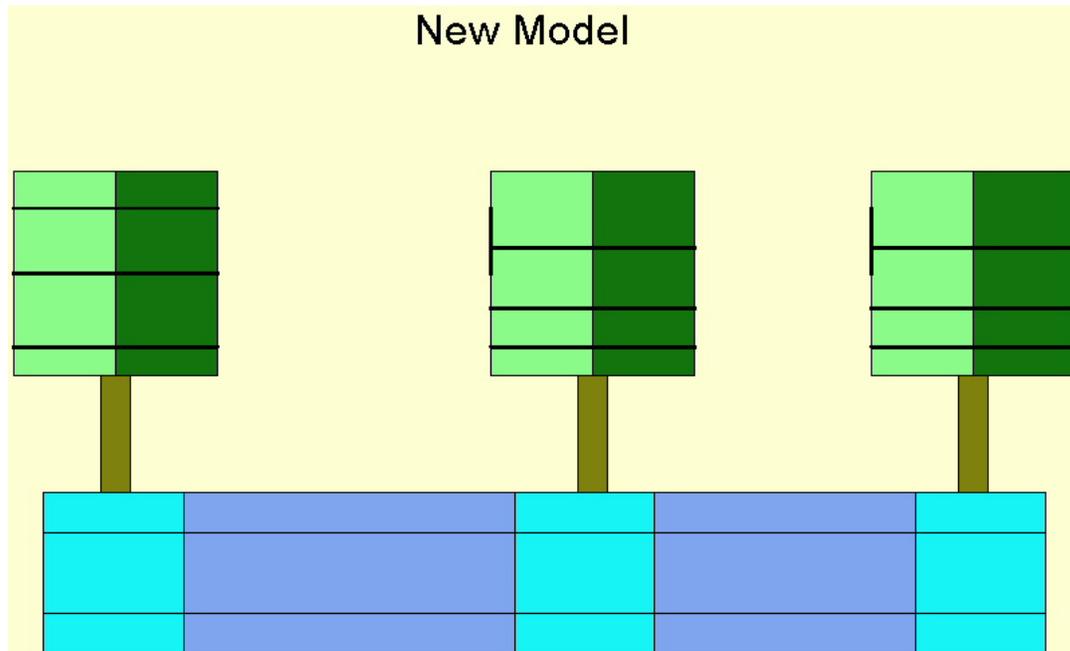


Three-dimensional models, like MAESTRA, can consider the geometry of spatially sparse and horizontally separated foliage volumes. The model also considers sun and shade fractions

MAESTRA



Ideal New Scheme for Heterogeneous landscapes considers spatial heterogeneity in vegetation and the underlying soil, which has different energy balance and root sinks for moisture.



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