4 Figures, 1 Table, 0 Appendices, 2 Highlighted Boxes (with 1 figure), 3 Footnotes

Chapter 1. The General Nature of Biosphere-Atmosphere Fluxes

The atmosphere and its manifold changes have held fascination for men and women ever since human beings have trod this Earth. Its study played an integral role in the evolution of natural philosophy from which all of our present sciences have sprung.

F. Sherwood Rowland
Nobel Prize Banquet Speech, 1995

It is widely believed that the abundance of the principal gases N_2 and O_2 is determined by equilibrium chemistry. One of the larger problems in the atmospheric sciences is that of reconciling that belief with the uncomfortable fact that these same gases are cycled by the Biosphere with a geometric mean residence time in thousands of years.

James Lovelock and Lynn Margulis (1974)

Sherwood Rowland's comment at the banquet held to honor his receipt, along with Paul Crutzen and Mario Molina, of the 1995 Nobel Prize in Chemistry, places the atmosphere at the center of some of the most influential scientific discoveries to have been made during human history. Within Rowland's comment we can recognize Thales of Miletus who in the 6th Century B.C. struggled to understand the different states of water and the phenomenon of evaporation, Lavoisier in the late 18th Century discerning the exchange of oxygen between organisms and the atmosphere, and Arrhenius in the early part of the 20th Century calculating the relation between changes in the atmospheric carbon dioxide content and Earth's surface temperature. The importance of the atmosphere in the history of natural philosophy is clearly underscored by these seminal studies. Within all of these studies, however, is the undeniable influence of the earth's surface and in particular the earth's biosphere, on the composition and chemical dynamics of the atmosphere. The two are linked in a type of 'co-dependency' in which processes and change can only be understood through studies that include both biotic and abiotic systems. The requisite nature of the nexus between the biotic and abiotic domains of the earth system is recognizable, albeit in an extreme form, in the controversial concept of 'Gaian homeostasis' laid out by James

Lovelock and Lynn Margulis in their 1974 paper in the journal Tellus. While we (the authors) do not in its entirety endorse the tenets of a Gaian earth, we do recognize the value of this concept in defining the biosphere and atmosphere as coupled and interdependent systems. It is this interdependency, and the processes that maintain it, that will be the focus of this book.

In this opening chapter, we will present the concept of biosphere-atmosphere interactions through some relatively general aspects of biogeochemical fluxes. We begin by establishing the biosphere and atmosphere as components of the earth system connected through the coupled biogeochemical cycling of energy and mass. We will then establish the concept of flux, as a unifying principal in the transport of mass and energy, and we will explore the fundamental driving forces and constraints that govern the directions and magnitudes of fluxes. Finally, we will consider some of the general cybernetic features of biosphere-atmosphere exchange, noting in particular the tendencies for non-linear relations and feedbacks, and we will present a hierarchical framework within which we can understand biosphere-atmosphere interactions. It is important at the outset to make the point that in this book mass and energy will be discussed with regard to *changes in state and exchanges among components of the earth system*. We will not focus on pool sizes or biogeochemical budgeting. This is a challenge because we are much more confident in our ability to observe states of the biosphere and atmosphere, compared to changes in them. It's the interactions among biogeochemical pools and earth system components, however, that drives dynamics in the state variables and thus forces time-dependent changes in those variables. It’s the role of biosphere-atmosphere exchange as an agent of change in the earth system that we want to keep as a principal point of focus as we launch into our initial discussions.

1.A. Biosphere-atmosphere exchange as a biogeochemical process

Biogeochemistry is the study of changes in the earth system due to the combined activities of chemical, geological and biological processes and reactions. Many of the trace gases that are exchanged between the biosphere and atmosphere are produced from the reduction-oxidation (redox) reactions that drive the biogeochemical cycling of elements, principally C, O, N and S. Biogeochemical cycling is powered by the flow of solar photons through the atmosphere and biosphere, where a part of it is absorbed and used to energize electrons, which in turn drive redox reactions. This coupling between the solar energy flux and redox chemistry is exemplified in the biological processes of photosynthesis and nitrogen fixation. In both processes the energy state of electrons is increased at the expense of solar energy, and those energized electrons are used in the construction of organic compounds from inorganic compounds. The energy from the electrons is captured within the molecular structure of organic compounds, providing them with a higher potential energy state than their inorganic precursors. This is biogeochemical cycling in its most basic form, and it's the basis by which energy is used to construct and maintain the biotic component of the earth system.

The fundamental biogeochemical unit within the biotic component of the earth system is the *ecosystem*. Formally, an ecosystem is the sum of the organisms and their environment within a three-dimensional space. However, it's the *synergistic interactions* among biotic and abiotic processes that create interdependencies between organisms and their environment, and which determines the dynamic nature of the ecosystem. Thus, we will treat the ecosystem as ***both*** the 'theater' and the 'play' within which organisms transform energy into the redox reactions that drive biogeochemical cycling. Although we will spend most of our time on biogeochemical exchanges within ecosystems – it's important to recognize that ecosystems aren't truly discrete; they have porous, diffuse boundaries through which exchange also occurs with the surroundings. Interactions at those boundaries tie ecosystems into broader regional and global processes.

1.B Flux – a unifying concept in biosphere-atmosphere interactions

Reciprocity is obvious in biosphere-atmosphere interactions. Reciprocity underlies the interdependencies that tie together components of the earth system, and it is reflected in the flows of mass and energy among those components. Within the earth system, changes in the size of biogeochemical pools are forced by unequal reciprocities. Reciprocity in biogeochemical flows is formally described through an analysis of *fluxes*.[1] Flux forms the basis of the biosphere-atmosphere interactions we will consider in this book; whether it be the exchange of shortwave radiant energy between the sun and earth (a flux of photons), or the movement of water between leaves and the atmosphere (a flux of mass). We will be most concerned with the fluxes of mass, momentum and heat. These entities are described by scalars, in the case of mass and heat, or vectors in the case of momentum. A *scalar* is any quantity that can be described by a quantitative scale, but has no specified direction (e.g., mass or time). A *vector* can be described with a quantitative scale and has an associated direction (e.g., wind velocity). Fluxes, themselves, are vector quantities (they have direction); in accordance with vector mathematics, gross fluxes that occur in opposite directions can be added to provide net fluxes. Gradients in scalar or vector density are also vector quantities, as they have direction. Formally, flux is a velocity multiplied by scalar or vector density.[2]

Following fundamental thermodynamic tendencies net fluxes of mass and energy will occur in the direction that opposes their associated gradients in scalar or vector density; i.e., *net flux* will occur from higher density toward lower density. The net flux works to diminish the gradient. The magnitude of fluxes, like the direction, is dependent on the density gradient. The velocity component of a flux scales in direct proportion to the magnitude of the associated density gradient. In most biogeochemical systems, density gradients are determined by the location and magnitude of *sources* and *sinks*.[3] The sources and sinks that drive biogeochemical fluxes of mass are those chemical or biochemical processes that consume or produce chemical compounds. The sources and sinks that determine the direction and magnitude of atmospheric momentum are inertia and viscosity, respectively.

One prominent example of the relations among fluxes, density gradients, and the location of sources and sinks occurs at the hemispheric scale in the record of CO_2 concentration that has been deduced for the past two millennia. In pre-industrial times (prior to the late 1800's), the global carbon budget was roughly in balance; on average, the net CO_2 *source from the biosphere to the atmosphere* almost exactly compensated for the net CO_2 *sink from the atmosphere to the biosphere* (i.e., global respiration was, on average, equal to global gross primary productivity). This balance is deduced from observations of the CO_2 content in ancient ice recovered from deep inside polar ice sheets; air samples taken from the cores reflect a nearly constant atmospheric CO_2 concentration over at least the millennium prior to the late 19th Century (Fig. 1.1A). Since the Industrial Revolution in the late 1800's, human activities have emitted progressively more CO_2 to the atmosphere each year; thus, representing an additional CO_2 source and unbalancing the natural carbon cycle. The anthropogenic CO_2 that is added to the atmosphere is partly absorbed by photosynthesis in ocean and terrestrial ecosystems. However, not all the additional CO_2 can be absorbed, leading to an imbalance in global CO_2 sources and sinks. This imbalance has caused an increase in the atmospheric CO_2 concentration. The pre-industrial balance in the global carbon budget, and subsequent imbalance, provide a convenient lesson in the concept of *continuity*, which we will take up in more detail in a later chapter. Continuity requires that in the presence of equal exchanges of conserved quantities, such as those for mass and energy, to and from a controlled volume, the concentration of the quantity must remain constant. If an imbalance appears in the sources and sinks, and thus in the associated fluxes, it must be reflected as a change in mean concentration. We can observe the principle of continuity in action in the near-continuous record of atmospheric CO_2 concentration that has been collected since the 1950's from an observatory at Mauna Loa, Hawaii and since the 1970's from the South Pole, and is familiar to most students of the earth system sciences (Fig. 1.1B). Oscillations in the atmospheric CO_2 mole fraction reflect seasonal changes in the shifting dominance between net photosynthesis and net respiration. Thus, with the onset of the growing season, the photosynthetic flux of CO_2 from the atmosphere to terrestrial ecosystems (hemispheric sink) is greater than the respiratory flux from ecosystems to the atmosphere (hemispheric source), and the CO_2 mole fraction of the atmosphere decreases as the growing season progresses. This pattern is reversed during the winter. Here, in an example of global proportions, we can fully appreciate the coupling between CO_2 fluxes to density gradients, and the determination of density gradients by the location and magnitude of sources and sinks.

It's important to recognize that a gradient in the density of a scalar or vector is only one determinant of the magnitude of a flux. State variables that characterize the flux system, such as temperature and pressure, also have the potential to influence a flux. Temperature, pressure and density are related through the equation of state, which will be discussed in a future chapter. Furthermore, the flux of one scalar or vector can be coupled to the flux of a different scalar or vector. For example, the flux of solar photons into a leaf is coupled to the flux of CO_2, through the processes of photosynthesis. In general, we will refer to the principal influences on flux magnitude as *driving variables*.

1.C Non-linear tendencies in biosphere-atmosphere exchange

One of the challenges that we face in describing biosphere-atmosphere interactions is the non-linear form of mathematical relations between fluxes and their associated driving variables (Table 1.1). Non-linear relations can be traced to processes at the smallest spatial and temporal scales in ecosystems, and are amplified as those processes are transferred to progressively larger and longer scales. As examples of non-linear tendencies, we will briefly consider three processes; two at the sub-cellular scale and one at the leaf-to-landscape scale. In the case of enzymes, the nature of the enzyme-substrate interaction that controls reaction velocity changes as the availability of substrate changes; thus forcing the relation between velocity and substrate concentration toward non-linearity. We can represent this non-linearity with the Michaelis-Menten model presented in the uppermost equation of Figure 1.2. At low substrate concentration the velocity of the reaction is determined by the affinity of the protein catalyst (enzyme) for the substrate (reflected in the K_m term of the Michaelis-Menten model), the velocity by which the enzyme can convert the substrate into product (the substrate turnover rate, reflected in the V_{max} term of the Michaelis-Menten model), and the frequency by which enzyme molecules interact with substrate molecules (which in the case of the Michaelis-Menten model is solely dependent on substrate concentration, [S]). As substrate concentration increases in the presence of rate-saturating enzyme concentration, the velocity of the reaction is determined less by K_m, and more by V_{max}. Mathematically, the dependence of reaction velocity on substrate concentration is resolved as a rectangular hyperbola, reflecting a shift from approximately first-order dependence at low substrate concentrations toward approximately zero-order dependence at high substrate concentrations.

As a different example, we see that the response of respiration (a flux of CO_2) to temperature is also non-linear, but in a manner that reflects increased capacity for metabolism as temperature increases. In this case, increased temperature forces enzyme and substrate molecules to interact (collide) more frequently and thus drives higher reaction rates. Additionally, due to flexibility in protein molecules, changes in temperature can cause changes in the shape and charge characteristics of the active sites of enzymes, which in turn can change the nature of their catalytic interactions with substrates. The net result of these temperature-dependent effects is an amplification, or acceleration, of respiratory reactions as temperature increases. We can describe this acceleration with an increasing power-law function (as shown in the second example equation in Figure 1.2).

In a third example, the exchange of latent heat (the product between the latent heat of vaporization and the rate of evaporation) between a leaf or canopy surface and the atmosphere can be described by the Penman-Monteith model (as shown in the third example equation in Figure 1.2). The flux of water from the wet, cellular surfaces inside a leaf to the well-mixed atmosphere above a leaf is dependent on the atmospheric water vapor concentration. The air in the intercellular spaces of a leaf is typically saturated with water vapor; so it's the air in the ambient atmosphere that determines the overall gradient in water vapor density that drives the evaporative flux. However, the diffusive flux of water from leaves is mitigated by a *flux resistance*, because the evaporation stream is channeled through narrow pores, known as stomata, as it exits the leaf. The diameters of those pores, and thus their diffusive resistances, are sensitive to changes in atmospheric humidity. Furthermore, changes in the loss of latent heat from the leaf or canopy surface, as atmospheric humidity changes, can cause the leaf surface temperature to change, which in turn causes the water vapor concentration difference between the air next to the surface and the bulk atmosphere to change. These multiple effects interact in complex ways as atmospheric humidity changes, forcing the relation between leaf or canopy latent heat loss and atmospheric humidity to reflect the non-linear form represented in the Penman-Monteith model.

Non-linear relations provide challenges to the modeling of ecosystem-atmosphere exchanges. In the case of fluxes, non-linear responses mean that the exchange rates can exhibit large changes (either increase or decrease) as a function of small changes in a driving variable. Thus, small errors in designation of a driving variable can produce large errors in predicted flux. Additionally, non-linear relations do not lend themselves easily to linear averaging; failure to recognize non-linear relations between an averaged dependent variable estimated from an averaged independent variable can also cause significant error. We will consider these errors further when we discuss the details of non-linear flux relations in leaf-scale CO_2 and H_2O exchange.

1.C.1 Feedback – a frequent source of flux non-linearities

The redistribution of mass, momentum, or heat caused by a flux can cause feedback that modifies the flux (see Box 1.1). *Feedback* is defined as a mitigation (negative feedback) or amplification (positive feedback) of flux caused by the flux itself. Feedback is one of the principal causes of non-linearities in the mathematical relations that describe the earth system. The difficulties in understanding feedback arise because we not only have to understand the quantitative nature of primary interactions between driving variables and fluxes, but also the secondary interactions that modify the primary interactions. This creates non-linearities that evolve over time. To illustrate the concept of feedback, let's return to the process of latent heat transport, in this case from a forest landscape to the atmosphere. As solar energy is absorbed by the forest, water evaporates from leaves and the soil. Turbulent wind eddies transport the evaporated water vertically through the atmosphere to a critical height where a fraction of the water condenses on suspended atmospheric particles and forms clouds. Clouds reflect solar radiation, causing a reduction in the energy flux received by the forest, and reducing the rate of evapotranspiration (Fig. 1.3). If there is adequate moisture in the forest soil and a strong thermal difference between the surface and higher levels in the atmosphere, the vertical wind eddies can take on high velocities, creating convective updrafts that form dark, cumulus clouds at the critical condensation height, and triggering precipitation. When taken together, these processes exemplify negative feedback in two ways. First, the flux of solar energy to the forest has caused the formation of clouds, a condition that reduces the further flux of solar energy to the forest and thus reduces further surface warming. Second, in the condition of adequate soil moisture, the flux of water vapor from the forest has caused a condition that triggers rain and increased atmospheric humidity, both of which tend to reduce the further flux of water vapor from the forest.

Recently, feedbacks have come to the forefront of discussions on interactions between the biosphere and the climate system (Field et al. 2007). In this case, many of the feedbacks occur at the regional-to-global scale. Fundamental questions that have emerged from this analysis include: (1) whether biospheric carbon fluxes will change sign, from net uptake to net loss, switching from a negative to positive feedback on climate change, respectively, (2) whether changes in the earth's albedo due to melting ice at high latitudes will trigger a positive feedback by enhancing solar energy absorption, and (3) whether human-caused land-use change will trigger positive or negative feedbacks by altering the distribution of carbon-sequestering ecosystems from the landscape or altering surface albedo. Beyond questions as to the mathematical sign of potential feedbacks, future models of ecosystem-atmosphere interactions will have to be capable of resolving the magnitude of regional and global feedbacks, and the relation among feedbacks with different time constants. Understanding the rate at which feedbacks operate is crucial to predicting the rates by which fluxes can cause acceleration or deceleration of compound turnover in important biogeochemical pools and cause imbalance in the global energy budget in the face of future climate change.

1.D Modeling – a tool for prognosis in ecosystem-atmosphere interactions

If there is one dominant theme that emerges from this book we hope it is the utility of organizing observations within a framework of quantitative models. Mathematical models provide the means to convert observations into predictions. Models are the tools for prognosis, allowing us to ask 'what if' questions about how processes operate in conditions that transcend those associated with our observations. Models also provide a means of organizing observations into explicit mathematical expressions from which mechanistic insight can be extracted. We must keep in mind, however, that both models and observations are imperfect representations of the true state of the earth system. Because of these imperfections, we are forced to accommodate errors and uncertainty in both observations and models.

Models are generated in one of two ways: (1) observations are organized into statistical correlations, with the correlation function used as the means to generate values of dependent (unknown) variables from values of independent (known) variables, and (2) knowledge of process theory is used to develop mathematical expressions that relate a dependent (unknown) variable to an independent (known) variable. Models developed by the first approach are often referred to as *empirically-based models*, and those of the second type are referred to as *mechanistic*, or *first-principle models*. Empirically-based models contain the implicit assumption that correlations among variables are conserved in conditions different than those of the original observations. First-principle models are often limited in their development by available theory; in the absence of adequate theory, assumptions are often made to fill gaps in knowledge. Conventional wisdom states that mechanistic models are more accurate at predicting unobserved states of the earth system because empirically-based models are based on inadequate observations that don't necessarily overlap future states of the system. It's important to realize, however, that gaps in the theory can introduce just as much, or more, error into model predictions as inadequate observations.

Models are developed and used with either a 'bottom-up' or 'top-down' approach. In bottom-up modeling, processes and parameters are defined at the smallest scales of space or time and used as dependent variables in functions that permit prediction for larger scales. The mechanistic forms of these models are often designed to include transport mechanisms and concentration gradients. Bottom-up modeling is often referred to as *forward modeling*, because it reflects the traditional ‘forward’ logic of defining effects (at higher scales) from causes (at lower scales). In top-down modeling, parameters are measured at the highest scale in order to constrain the upper bound (or output) of a nested mathematical scheme. Working backwards through the nested scheme of equations, the highest layer is forced to define the output for the next layer down, and so on until an output is derived for the lowest scale of consideration. Top-down modeling is often referred to as *inverse modeling*. In inverse modeling we aim to estimate causes from effects (Box 1.2).

Inverse modeling has become increasingly favored in the earth systems sciences since the early 1990's. This trend has been driven by the increased availability of broadly distributed, large sets of observational data, from which model outputs can be well-constrained. At the scale of eddy flux towers, inverse modeling is increasingly used to infer the physiological and biochemical process rates at the leaf and plot scales, working backwards from observations of fluxes at the landscape scale. Inverse modeling at the global scale has become especially useful for identifying the spatial distribution of sources and sinks given known scalar gradients (Dewar 1992). At the global scale, researchers use a global transport model to 'work backward' from a global network of observed scalar concentrations to resolve the spatial distribution of sources and sinks that most likely caused the observed distribution. Global inverse models have limitations caused by inadequate coverage of the observed concentration distribution, errors and uncertainties in the transport model, and high sensitivity of the inversion process to these limitations.

1.E A hierarchy of processes in surface-atmosphere exchange

"Knowledge of processes in plants and vegetation is largely at small scales. The transfer of this knowledge up to larger spatial and longer temporal scales is an open-ended process with potential errors arising from heterogeneity and patchiness in the distribution of processes and non-linearities in the functional relationships between processes and environmental variables."

P.G. Jarvis (1995)

Scaling processes according to space, time and biomass has become a fundamental focus in the earth systems sciences, principally as a means for nesting the perspectives of reductionism into higher levels of biogeochemical and ecological organization, and for identifying universal scaling functions that simplify the organization of reductionist principles into simple quantitative relations at larger scales (Brown and West 2000). The biosphere interacts with the atmosphere through fluxes that occur across a broad range of spatial and temporal scales. At the smallest scales, organisms interact with the atmosphere through diffusive fluxes. The diffusion of molecules across a leaf surface, for example, can be described at the scale of millimeters or less. These small scale processes, however, can accumulate to produce global ramifications – an amplification that crosses spatial scales of 10^{18} or greater. The mechanisms that drive fluxes at larger scales are fundamentally different from those that drive fluxes at the smallest scales. As scale increases, mass transport takes over as a dominant flux mechanism, and diffusion becomes less important. As a general rule, as scale increases, flux mechanisms become more efficient at moving scalars and vectors across space (Fig. 1.4). For example, at the global scale, geographic gradients in atmospheric pressure drive material around the circumference of the earth (on the order of 10^6 m) within a couple of weeks (on the order of 10^6 seconds). This translates to transport efficiency on the order of 10 m s^{-1}. At the sub-cellular scale, molecular concentration gradients drive diffusion across organelle membranes (on the order of 10^{-6} m) within fractions of a second (on the order of 10^0 seconds). This translates to transport efficiency on the order of 10^{-6} m s^{-1}. The process of diffusion, which is effective as a transport mechanism at the smallest scales, is negligible at the largest scales.

We have structured the book to reflect the hierarchy of processes presented in Figure 1.4. Processes that drive fluxes at the biochemical scale are considered first, progressing to processes at the leaf, canopy and planetary boundary layer scales. We have tried to construct the discussions such that smaller scales are nested within larger scales through the progression of chapters. There is logic to this design in that higher scale processes reflect lower scale drivers, at least to some degree; with appropriate allowance for novel relationships that emerge.

Table 1.1. Causes and effects of non-linearities in biosphere-atmosphere exchanges

Causes
1. Processes tend to be highly dependent on initial conditions
2. Processes are controlled simultaneously by multiple rate-limiting, forcing variables
3. Processes are influenced by interacting scales of space and time
4. Processes are subject to positive and negative feedbacks
Effects
1. Emergent (synergistic) interactions among processes
2. Power-law scaling between process rates and driving variables
3. Time- and space-dependent patterns of abrupt (amplified or muted) change

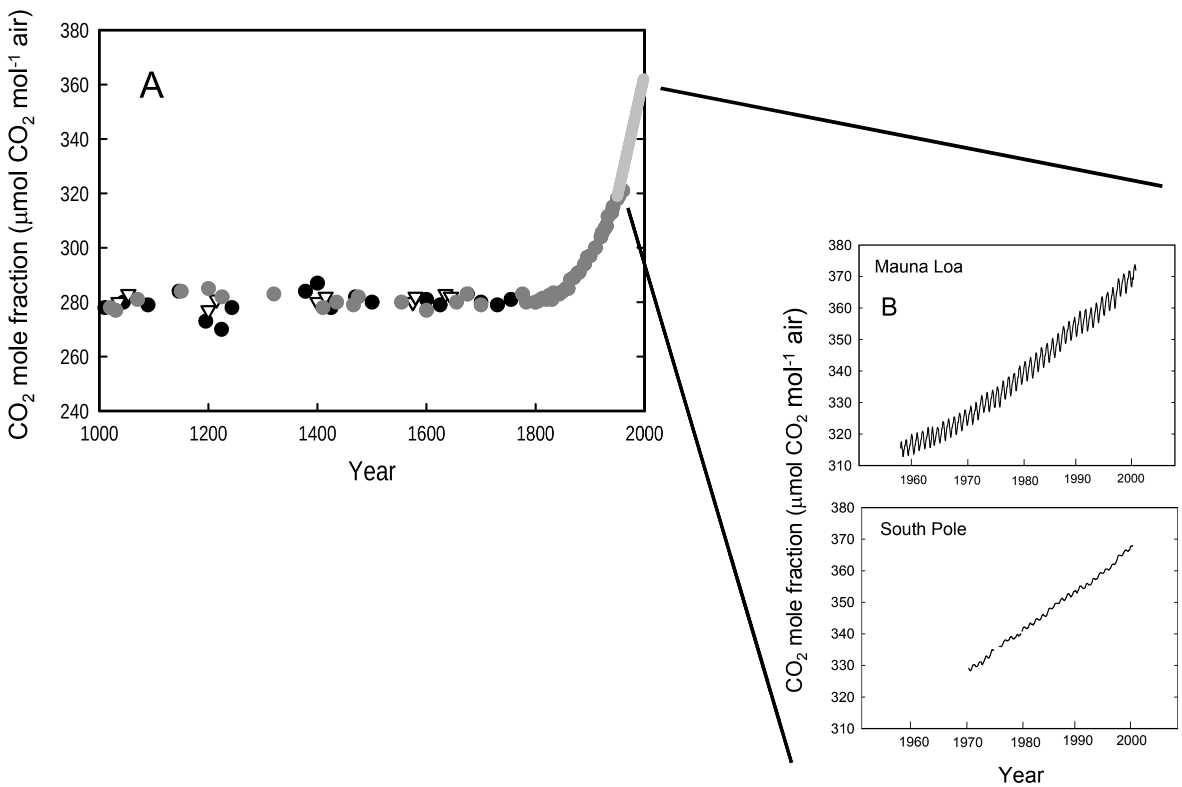
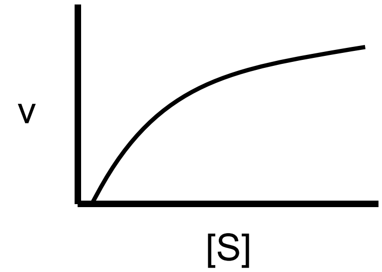
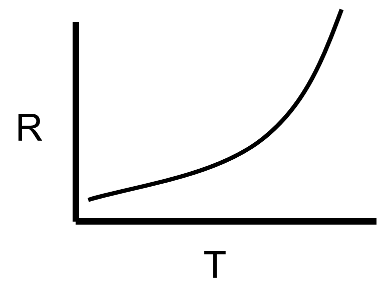


Figure 1.1. A. Atmospheric CO_2 mole fraction obtained from measurements on ice cores (prior to the 20th Century) and direct measurements of the atmosphere (since the late 20th Century). The stable CO_2 mole fraction through most of the past millennium is indicative of balanced CO_2 fluxes into and out of the atmosphere, on average, including those associated with the biosphere. The increase in CO_2 mole fraction over the past century is due higher fluxes of CO_2 from the earth's biosphere to the atmosphere, compared to those from the atmosphere to the biosphere. The different symbols are indicative of different data sets. Redrawn from the Intergovernmental Panel on Climate Change Summary for Policy Makers Report (IPCC 2001). **B.** Details of the seasonal variations in CO_2 mole fraction measured at Mauna Loa, Hawaii or the South Pole. Data from the U.S. National Oceanic and Atmospheric Administration.

$$v = \frac{V_{max}\,[S]}{K_m + [S]}$$



$$R = R_0\, e^{\left(\ln Q_{10}/10\right)\Delta T}$$



$$\lambda_w E = \frac{s\left(R_n - G\right) + \rho_a\, c_p \left(c_{wa}^{*} - c_{wa}\right)/\,r_H}{s + \gamma \dfrac{r_v}{r_H}}$$

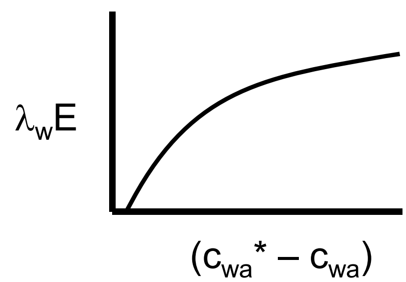


Figure 1.2. General non-linear forms of relations between some of the important processes involved in plant-atmosphere exchanges. **Top:** Relation between the enzyme-catalyzed reaction velocity (v) and substrate concentration [S], as determined by biochemical parameters of the protein enzyme (represented in this particular model as V_{max} and K_m). **Middle:** Relation between respiration rate (R) and temperature (T) in plant mitochondria. **Bottom:** Relation between leaf or canopy latent heat exchange (the product of the latent heat of water vaporization, λ_w, and evaporation from leaf or ground surfaces, E) and the difference between the saturation concentration of water vapor in air (c_{wa}^{*}) and the actual concentration of water vapor in air (c_{wa}) at a constant temperature. At this time, we only wish to present these relations as examples of non-linear equations, without further and more explicit definition of parameters and coefficients. We will consider these relations in more detail in future chapters.

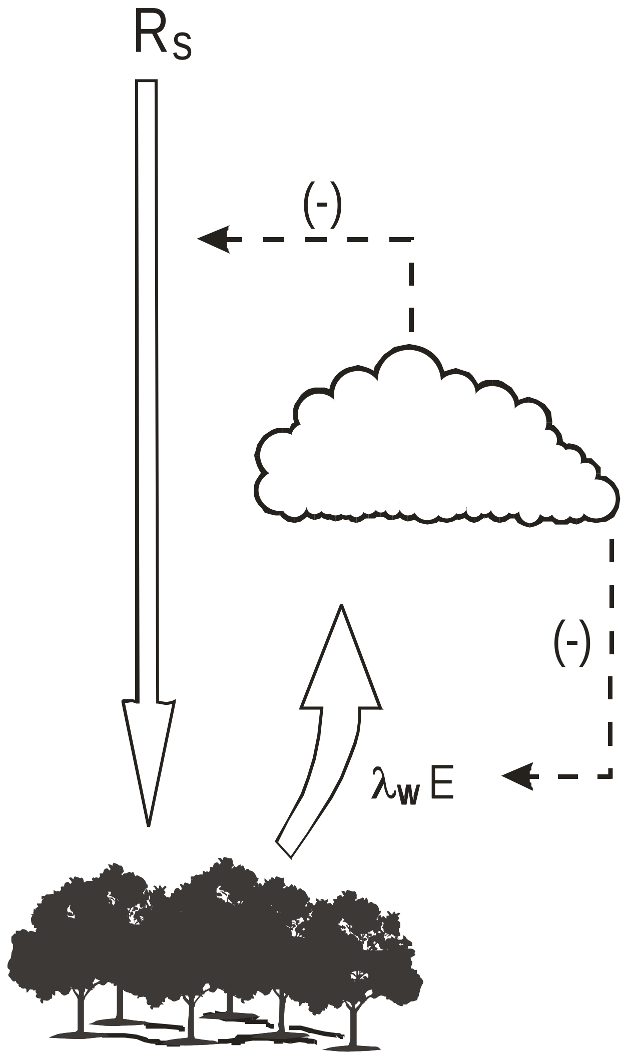


Figure 1.3. Diagrammatic representation of negative feedback with respect to latent heat flux ($\lambda_w E$); i.e., the evapotranspiration flux expressed in terms of latent heat energy. The absorption of shortwave radiant (solar) energy (R_s) and consequent evaporation of water results in cloud formation which decreases the further flux of solar energy (a negative feedback), and decreases the rate of further latent heat flux from the forest (also a negative feedback).

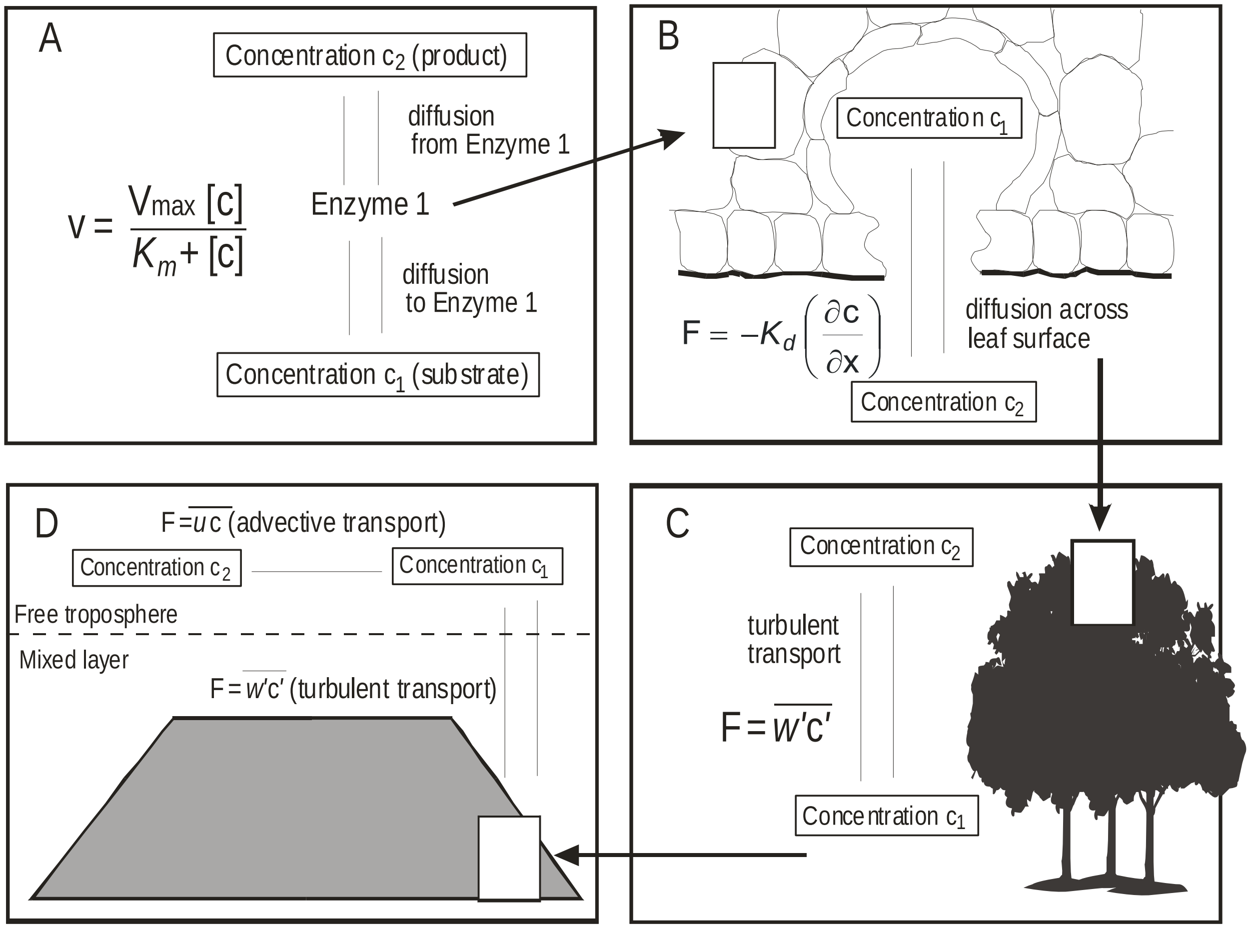


Figure 1.4. Scalar fluxes across spatial scales. **A.** At the scale of biochemistry, the flux of metabolites through metabolic pathways is determined by the kinetic features of protein enzymes. Flux (or in this case, reaction velocity, v) can be determined by the Michaelis-Menten model, which relates the potential for an enzyme to catalyze a specific chemical reaction to substrate concentration. **B.** At the scale of the leaf, fluxes are driven by diffusion through air. Flux can be modeled by an expression of Fick's First Law of diffusion in which the diffusion coefficient (K_d) relates flux to density concentration gradients. **C.** At the scale of a canopy, flux is driven by the turbulent motions of wind eddies. Vertical transport can be calculated as the time averaged statistical covariance in the turbulent wind speed (w') and the turbulent scalar concentration (c'). **D.** At the scale of the landscape, flux is driven by turbulent and advective wind motions. Horizontal advective flux in the free troposphere can be determined as the time averaged product of the mean longitudinal wind speed ($\overline{u}$) and the mean scalar concentration ($\overline{c}$).

Box 1.1 The mathematical concept of feedback

We will discuss several examples of feedback as we progress through this book. Feedback will be an important component of metabolic flux control, the coupled responses of stomata to light and CO_2, and the interactions between surface evapotranspiration and atmospheric humidity. Thus, it's important at the outset to get a sense for the nature of feedback. Here, we present a quantitative treatment of feedback as borrowed from the discipline of electrical engineering.

Feedback describes the tendency for external forcing variables to affect a flux. Feedback can mute or amplify a flux in the case of negative or positive feedback, respectively. A flux that is subjected to negative feedback will be altered in iterative fashion over time until a new, reduced, but stable flux is achieved (i.e., altered flux causes altered feedback which causes altered flux and so on to a stable point). The new stable flux is often called the set-point (or attractor) and in biology the process involving the negative feedback is often called *homeostasis*. A flux subjected to positive feedback is incapable of reaching a set-point unless the feedback itself is susceptible to negative feedback. In the case of positive feedback, a flux will continue to increase away from its original set-point, eventually reaching an explosive state; an example can be appreciated as the outcome of nuclear fission. The influence of feedback on a flux occurs through a f*eedback loop* (Figure B.1.1). Thus, we can describe a flux at an arbitrary initial time point (we will call this the input flux, or F_1), which is altered through sensitivity to an external forcing variable, to produce a new flux at a later point in time (we will call this the output flux, or F_2). Returning to our example of negative feedback on forest evapotranspiration, the forcing variable is the amount of solar radiation incident on the ecosystem (in this case influenced by clouds), and F_1 and F_2 would represent the evapotranspiration flux in the presence of solar radiation without clouds or with clouds, respectively. If we start by assuming no feedback, then we can describe the system in the *open-loop mode*. Sensitivity of the flux to the forcing variable is defined by the open-loop gain (G_o), such that: $F_2 = G_o F_1$ and therefore we can define the open-loop gain as: $G_o = F_2/F_1$. If we now engage a closed feedback loop, such that information (in this case due to increasing clouds) is transferred back to the original flux, modifying it, we can write:

$$F_2 = F_1 G_o + F_2 G_o B \qquad \text{(B.1.1)}$$

where B is the feedback multiplier, being positive in sign for positive feedback and negative in sign for negative feedback. Returning once again to our example of evapotranspiration, B represents the composite of atmospheric processes that convert the evapotranspiration flux into clouds and determine the attenuation of solar radiation by those clouds. We can use algebra to remove F_2 from the right side of Equation B.1.1, resulting in the following equation:

$$F_2 = \frac{F_1\, G_o}{1 - G_o B} \qquad \text{(B.1.2)}$$

Equation B.1.2 defines the resultant flux (F_2) in *closed-loop mode*. We can define the closed-loop gain (G_c) as F_2/F_1, and using Equation B.1.2 to substitute for F_2, we can write:

$$G_c = \frac{G_o}{1 - G_o B} \qquad \text{(B.1.3)}$$

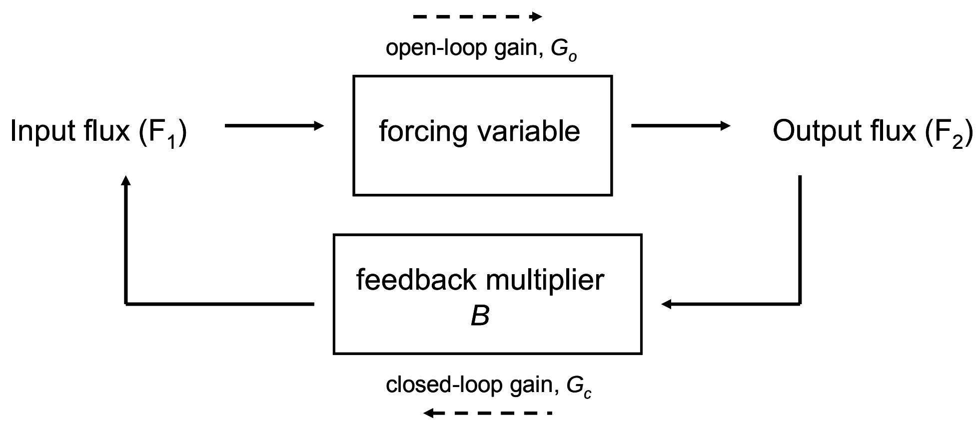


Figure B.1.1 Scheme showing information flow in an open and closed feedback loop. The open-loop gain (G_o) describes sensitivity of a flux to a forcing variable when the feedback loop is not engaged. The closed-loop gain occurs when the output flux 'feeds back' to influence the original flux through a feedback multiplier (B). The closed-loop gain (G_c) describes the sensitivity of the original flux to the feedback multiplier scaled to the output flux.

Box 1.2 The mathematical concept of forward and inverse modeling

Modeling is a core activity in the earth systems sciences. Modeling allows us to organize observations and generate hypotheses about the causes that underlie trends in the observations. Observations are integrated with models in one of two ways: either the model is parameterized by observations and run in *forward mode* to make predictions about the outcome of a process, or observations on the outcome of a process are assimilated into a model and the model is run in *inverse mode* to generate predictions about underlying parameter states. Forward modeling can be thought of as predicting effects from causes. Inverse modeling can be thought of as predicting causes from effects. The relationship between forward and inverse modeling can be expressed mathematically as: $dx/dt = s\ (t, x, \theta)$, where s is a mathematical model (incorporating variables t, x and θ), x_0 at time t_0 is defined, and θ is a causative forcing variable. In the forward projection of the model, θ is defined and the model (represented by s) is used to find $x(t)$ for some $t > t_0$. In the inverse projection of the model, $x(t)$ is defined for $t > t_0$, and the model (s) is used to find θ. To make this logic more relevant to biosphere-atmosphere interactions, imagine that x is the CO_2 concentration in the atmosphere at some specific point in time and space and θ is the surface CO_2 flux that influences x. The model, s, then relates surface CO_2 flux (the cause) to a change in atmospheric CO_2 concentration (the effect). The forward projection of s will allow us to predict the change in CO_2 concentration downwind of the flux. The inverse projection will permit us to work backward to define the surface flux (θ) if the change in CO_2 concentration (x) is observed. (In this simple example, θ would also have to include a component describing the dispersion of CO_2 as it travels downwind.)

Footnotes (Chapter 1)

[1] Proper terminology for flux according to the Système International is *flux density*, which refers to flow (of mass, momentum or heat) per unit of surface area per unit of time. For brevity and convenience, the terms *flux density* and *flux* will be used interchangeably in this book. In some case, we will refer to *total flux* within the context of an integral quantity with respect to finite space and time. For example: "the total flux for global CO_2 uptake is ~122.8 Pg yr^{-1}".

[2] The nature of flux density as the product between velocity and scalar density can be appreciated through an examination of units of expression. Velocity is expressed in units of m s^{-1} and scalar density (at least for the case of scalars with mass) is expressed in units of mol m^{-3} (or mass m^{-3}). In reconciling the product between velocity and molar density, the units emerge as mol m^{-2} s^{-1} or mass m^{-2} s^{-1}, which are both examples of flux density.

[3] The terms 'source' and 'sink' are used in different ways within the biogeochemistry research community; some usages refer to locations (e.g., 'the oceanic sink or terrestrial sink') whereas others refer to processes (e.g., 'photosynthesis as a CO_2 sink or respiration as a CO_2 source'). We will tend to use these terms within the latter context – as processes that drive fluxes.