CHAPTER 3

Biogeochemistry

The Physiology of Ecosystems

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Topography, species composition, and land use are characteristics that can be directly viewed. Patterns of change across the regional landscape are accessible to an interested observer. In contrast, important processes that determine ecosystem function, and the role of ecosystems in regional environmental quality, are invisible. Leaves exchange water for carbon through small pores, but both water vapor and CO_2 are invisible gases. Pollutants such as ozone can alter the rates of exchange, but both the pollutant and the process are inaccessible to our vision and can be "seen" only with various instruments. Because of this, important ecosystem processes are less intuitive than structural elements and may require some introduction.

Biogeochemistry is one term that has come to be associated with the measurement of those functions of ecosystems that we study at the Harvard Forest. As the name implies, it is an interdisciplinary endeavor, combining elements of biology, geology, and chemistry. Several other disciplines could be added as well (hydrology, microbiology, and physics), making the name completely intractable! Biogeochemistry can be thought of as the metabolism or physiology of the landscape. It is the study of the movements of energy and materials through ecosystems, which are the units of study within the landscape.

Many of the important ecosystem services through which environmental quality is maintained rely upon exchanges between ecosystems and the atmosphere, or ecosystems and streams or groundwater. Forest stands at the Harvard Forest now take up more CO_2 through photosynthesis than they give off through respiration, thereby reducing atmospheric concentrations of this greenhouse gas. Excess nitrogen in rainfall derived from air pollution is strongly retained within these same forests, providing protection against acidification of soils and streams. Because of the historical resurgence of forests over the past century, the physiology of the New England landscape is determined largely by the biogeochemistry of ecosystems like those we study at the Harvard Forest. Will those functions change over time? One part of predicting our regional environmental future requires that we understand ecosystem function (or biogeochemistry) and its dynamics over time.

Energy, Carbon, Nitrogen, and Water: Interactions among Resources

Plants require energy (sunlight), carbon (CO_2), nitrogen (mostly in simple inorganic forms), and water as well as a number of other elements and compounds to produce new organic matter (also called *biomass*). A central concept in biogeochemistry is that we should not think of these resources individually, but should focus on interactions among them. As an example, we can present the interacting cycles of water, carbon, and nitrogen that form the basis of most of the biogeochemical research at the Harvard Forest.

The energy for all processes occurring in the forest comes ultimately from solar radiation. Two key processes driven by sunlight are *photosynthesis* and *transpiration* (Figure 3.1). Photosynthesis converts CO_2 in the atmosphere to simple sugars, which are then used in the plant for both energy and as the first building blocks in producing plant tissues. Photosynthesis requires that the leaves be open to the atmosphere so that CO_2 can diffuse into the intercellular spaces in the leaves where the actual fixation of carbon occurs. Carbon dioxide enters the leaf through pores called *stomates,* and the rate of this exchange is a function of how many of these pores are present and how open they are (summarized in a term called *conductance,* or the opposite of resistance to gas exchange between the atmosphere and internal leaf air spaces).

Cell surfaces within the leaf are always moist, so water evaporates into the air spaces within the leaf. This water vapor will diffuse out through the stomates at a rate related to both the conductance of the leaf and the relative humidity of the atmosphere. This process of evaporation from within leaves is called transpiration. Water lost in this way must be replaced by uptake from the soil if the plant is to avoid wilting. This creates a large demand for water, which is ultimately provided by precipitation. If this demand is not met, and water stress develops within the plants, then the stomates will close to reduce water loss. This also reduces the exchange of CO_2 with the atmosphere, shutting off photosynthesis.

The reciprocal exchange of CO_2 and water in Figure 3.1 is summarized in the term *water-use efficiency* (the amount of carbon fixed per unit of water transpired) and is one example of a term that captures the interaction between the cycles of two resources, in this case water and carbon. Because of the low concentration of CO_2 in the atmosphere and the high humidity inside leaves, forests can lose much more water than they gain carbon. Depending on the humidity of the atmosphere, water loss can range from 20 to 500 grams per gram of carbon fixed (water-use

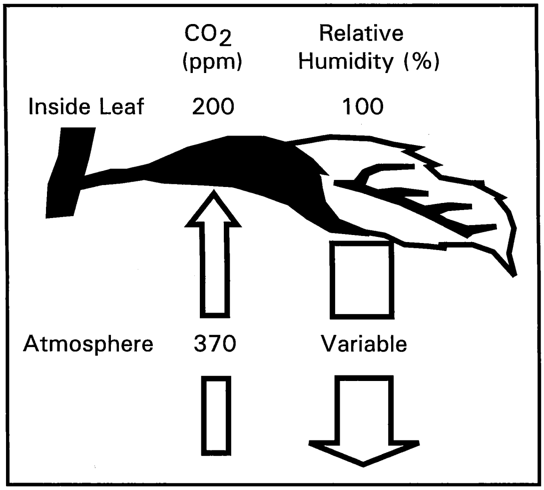


Figure 3.1. Leaves gain carbon dioxide (CO_2) from the atmosphere at the expense of water lost through transpiration. The concentration of CO_2 in the atmosphere is relatively constant day to day (although is it rising rapidly year to year), as is CO_2 inside the leaf. The lower concentrations in the leaf derive from fixation of CO_2 by photosynthesis and drive the diffusion of CO_2 into the leaf through stomatal pores. Similarly, plant cell surfaces are saturated with water, which evaporates into the internal leaf spaces and then out through the leaf pores. The rate of diffusion through the stomates into the atmosphere (transpiration) is controlled by the degree to which the stomates are open and the relative humidity of the atmosphere outside the leaf.

efficiency values of 0.002 to 0.05). This value will be lower still if it is calculated using the amount of biomass produced (photosynthesis minus plant respiration) rather than carbon fixed in photosynthesis.

Dark green leaves tend to fix carbon through photosynthesis more rapidly than lighter leaves. Darker leaves have more chlorophyll and also tend to have more of the proteins and enzymes required to carry out photosynthesis. As nitrogen is a major component of chlorophyll and proteins, the rate at which both photosynthesis and transpiration occur in leaves is partially a function of their nitrogen content, resulting in a strong three-way linkage among water, carbon, and nitrogen in ecosystems (Figure 3.2).

Very little of the nitrogen in this year's leaves came from the atmosphere this year. Although 78 percent of the atmosphere is nitrogen gas, the symbiotic relationship between plants and soil microbes that results in the direct fixation of nitrogen gas from the atmosphere into organic materials is relatively unimportant in the forests of New England. Atmospheric pollution may have increased the nitrogen content of precipitation by a factor of four or more. Even so, nitrogen deposition in rain

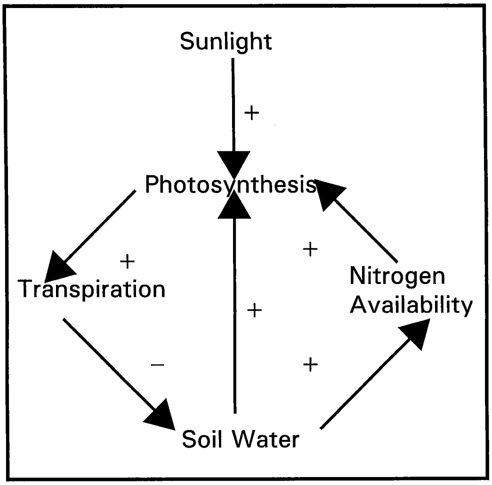
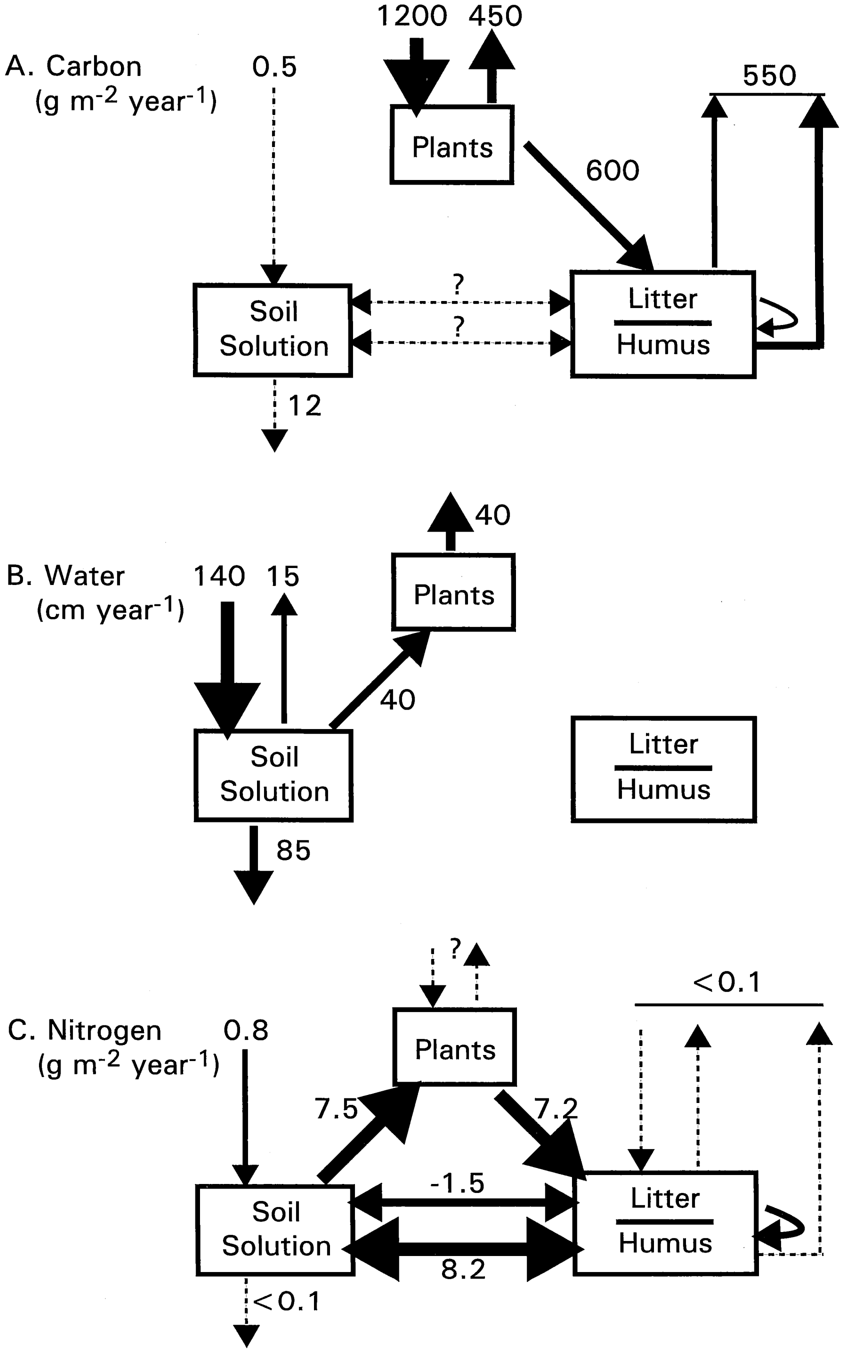


Figure 3.2. Schematic diagram of the interactions among energy, water, carbon, and nitrogen cycles (+ indicates a positive effect on the rate of a process, − a negative effect). Sunlight drives photosynthesis and transpiration. Transpiration reduces soil water content. Since high soil water content increases photosynthesis (and the lack of soil water decreases photosynthesis), continued photosynthesis in the absence of precipitation will eventually reduce both photosynthesis and transpiration. Reduced soil water content can also reduce nitrogen mineralization, and hence nitrogen availability, reducing nitrogen content in foliage the next year and the maximum rate at which photosynthesis can occur.

and snow is still only 5 to 15 percent of the annual requirement of nitrogen for forest growth.

Most of the nitrogen plants use comes from the large reserves of nitrogen in soil organic matter, which is released very slowly through microbial decay. Therefore, the rates at which carbon is fixed and water is evaporated from forests are both determined in part by the rate at which nitrogen is mineralized (converted from organic to inorganic forms available for plant uptake) in soils. In turn, the relative demand for nitrogen in the production of biomass (the nitrogen concentration in plant tissues) also varies between systems and can be expressed as a ratio of carbon to nitrogen (C:N ratio) in those materials, one measure of nitrogen-use efficiency, which again captures the interaction between two resources.

We can complete the complex set of interactions among these three resources by noting that nitrogen mineralization rates in soils are controlled by the relative content of carbon and nitrogen in soil organic matter (derived from the C:N ratio of plant materials), as well as by the fraction of soil pore space occupied by water.


A. Carbon
(g m-2 year-1)
0.5
1200
450
Plants
600
550
Soil Solution
?
?
Litter
Humus
12
B. Water
(cm year-1)
140
15
40
Plants
40
Soil Solution
Litter
Humus
85
C. Nitrogen
(g m-2 year-1)
0.8
?
Plants
<0.1
7.5
7.2
-1.5
Soil Solution
Litter
Humus
8.2
<0.1

A General Comparison of Budgets

Keeping these interactions in mind, we can discuss the internal processes by which water, carbon, and nitrogen move through ecosystems. The three boxes in Figure 3.3 represent storage of elements in plants and in the soil, with two separate soil compartments shown. The soil solution contains both soil water and all the elements and chemicals, including organics, that are dissolved in that water at any one time. The Litter/Humus box contains elements stored in solid form, which, for carbon and nitrogen, is essentially soil organic matter. Microbial populations are included in this box. Arrows pointing up and down at the top of the diagrams indicate losses to and gains from the atmosphere. The arrow pointing down from the soil solution box indicates leaching of water below the rooting zone and into groundwater or streams. The arrows pointing from the soil solution to plants and from plants to litter capture plant uptake and shedding of senescent leaves and twigs, and the death of whole trees, respectively. The arrow from litter to humus is the production of long-term stable organics from freshly fallen materials. Nutrients are exchanged with the soil solution during this process of litter decay and are ultimately released by the decomposition of humus. In each case, the presence and width of the arrows suggest the relative importance of each process. Typical rates of annual fluxes are also shown in the figure.

The Carbon Cycle

Carbon inputs to forest ecosystems are dominated by a single process, *gross photosynthesis,* which is also called gross primary production (GPP) or gross carbon exchange (GCE). Carbon fixed by photosynthesis is partitioned between the release of carbon back to the atmosphere through plant respiration and the production of new plant biomass, which is called *net primary production* (NPP). After plant materials are shed as litter, microbial decay provides the second major pathway for return of carbon to the atmosphere. Decomposition, however, is generally incomplete and leads to the production of humus, an amorphous, complex organic material that is highly resistant to microbial action and decays only slowly. The total net carbon balance of the system, the difference between gross photosynthesis and the total respi-

Figure 3.3. A more complete diagram of the movement of carbon (A), water (B), and nitrogen (C) through forest ecosystems. See text for a description of pathways. Numbers represent annual fluxes for each pathway for a typical deciduous hardwood forest at the Harvard Forest in the units specified. Note that both carbon and nitrogen contents of these aggrading forests are increasing, and that nitrogen loss below the rooting zone is essentially zero.

ration by plants and soil organisms, is called *net ecosystem production* (NEP) or *net ecosystem exchange* (NEE).

The dashed lines into and out of the soil solution box in Figure 3.3 represent the transfers of carbon as dissolved organics in precipitation, leaching, and exchange with soil organic matter. While these transfers are relatively small in comparison with the processes described above, they are receiving increasing attention for the role they may play in the chemistry of both soils and waters. The composition of these compounds is still poorly known but in soils seems to be similar to that of humus. Rates of production, decomposition, and chemical exchange with soil solids are also poorly know.

Swamped by CO_2 exchanges and so lost in Figure 3.3A are exchanges of other carbon-based trace gases. Among the most important of these are methane (CH_4), carbon monoxide (CO), and a host of reduced carbon compounds produced by plants (for example, hydrocarbons like isoprene). Total fluxes of these compounds are small and rarely affect the total carbon balance of upland forests. However, either by acting as greenhouse gases or by altering critical reaction pathways in the atmosphere, these compounds may play significant roles in atmospheric chemistry and global change.

The Water Cycle

The water cycle (Figure 3.3B) is also dominated by a single input from the atmosphere, precipitation, which is partitioned into three major outputs: transpiration (from leaves), evaporation (from soil or plant surfaces), and leaching or runoff to streams and groundwater. Internal storage in the soil solution is small relative to the inputs and losses in most forest ecosystems. It is this relatively small storage of water combined with the large and continuing demands for transpiration that can result in intermittent droughts even in areas, such as the Harvard Forest, where annual precipitation is high. Droughts of even two to three weeks in duration can affect soil water content, reducing the water available for transpiration and resulting in stomatal closure, reduced photosynthesis, and eventually reduced NPP. Dry soils also lead to a reduction in microbial activity in soils, reducing CO_2 evolution from soils, so the net effect of drought on NEE can be either positive or negative.

The Nitrogen Cycle

In contrast to water and carbon, inputs to the nitrogen cycle from the atmosphere (Figure 3.3C) come in many forms and are relatively small in comparison with internal cycling rates, at least for stands at the Harvard Forest. Inputs can be as gases, as particles, or in dissolved form or through fixation of nitrogen from the atmosphere. At the Harvard Forest, most nitrogen input is in inorganic form as nitrate (NO_3^-) and ammonium (NH_4^+). Since total nitrogen inputs are much lower than those for carbon or water, small fluxes in novel forms generated by human activity can be an important part of the total nitrogen balance and have received increasing attention. Outputs can also occur as gaseous or dissolved forms, and again the relative importance is a function of site conditions, disturbance, and hydrologic regime, among other factors. All of this means that net input/output balances of nitrogen in forests are difficult to determine accurately. However, these fluxes are small relative to internal recycling. Internal nitrogen pools and rates of cycling tend to change slowly in the absence of disturbance. As we will see in later chapters, the ability of human disturbance to alter nitrogen pools and cycling rates drastically, and the slow nature of recovery from such disturbances, is a major factor affecting current forest ecosystem function at the Harvard Forest.

Note the large arrows in Figure 3.3C pointing in both directions between the soil solution and litter and humus boxes. In general, the flow of nitrogen is into litter and from humus, relative to the plant-available forms in the soil solution, but the two-way arrows capture the processes of gross mineralization and immobilization that make up the net fluxes. Mineralization is the release of nitrogen in inorganic forms (first ammonium, and then possibly nitrate) from organic matter. These are the residual products of microbial activity under conditions of carbon (or energy) limitations. Litter, which is relatively rich in fresh plant products such as sugars and starches and low in nitrogen, is a rich source of energy for microbes. As the microbes grow on these substrates, they require more nitrogen than is present in the decaying material and actually compete effectively against plants for available ammonium and nitrate, taking it out of the soil solution (a process called *immobilization*). Thus, while individual microbes grow and die, taking up and releasing inorganic nitrogen, the net flux in energy-rich litter tends to be toward net immobilization, or removal of inorganic nitrogen from the soil solution (resulting in the negative number in Figure 3.3C). In contrast, humus is a nitrogen-rich material composed of very complex compounds that are difficult to attack and do not yield much of a net energy gain to microbes. Decomposition of humus generates little microbial nitrogen demand and releases nitrogen contained in humus to the soil solution as ammonium (resulting in the positive number in Figure 3.3C).

As with carbon, the study of nitrogen in dissolved organic forms has increased markedly. In relatively unpolluted areas, inputs and losses of nitrate and ammonium are fairly low, and both inputs and losses of dissolved forms can affect the overall balance significantly. In addition, evidence is increasing that plants can take up dissolved organic forms of nitrogen directly from soils, bypassing the need for complete mineralization by microbes. The importance of this form of nitrogen cycling, and the role that the intriguing root/fungal symbiosis known as mycorrhizae plays in this and other forms of nitrogen cycling, is an active area of research and will be discussed again in a later chapter.