

Introduction

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WHAT IS BIOGEOCHEMISTRY?

Today life is found from the deepest ocean trenches to the heights of the atmosphere above Mt. Everest; from the hottest and driest deserts in Chile to the coldest snows of Antarctica; from acid mine drainage in California, with pH < 1.0, to alkaline groundwaters in South Africa. More than 3.5 billion years of life on Earth has allowed the evolutionary process to fill nearly all habitats with species, large and small. And collectively these species have left their mark on the environment in the form of waste products, byproducts, and their own dead remains. Look into any shovel of soil and you will see organic materials that are evidence of life—a sharp contrast to what we see on the barren surface of Mars. Any laboratory sample of the atmosphere will contain nearly 21% oxygen, an unusually high concentration given that the Earth harbors lots of organic materials, such as wood, that are readily consumed by fire. All evidence suggests that the oxygen in Earth's atmosphere is derived and maintained from the photosynthesis of green plants. In a very real sense, O₂ is the signature of life on Earth (Sagan et al. 1993).

The century-old science of biogeochemistry recognizes that the influence of life is so pervasive that there is no pure science of geochemistry at the surface of Earth (Vernadsky 1998). Indeed, many of the Earth's characteristics are only hospitable to life today because of the current and historic abundance of life on this planet (Reiners 1986). Granted some Earthly characteristics, such as its gravity, the seasons, and the radiation received from the Sun,

are determined by the size and position of our planet in the solar system. But most other features, including liquid water, climate, and a nitrogen-rich atmosphere, are at least partially due to the presence of life. Life is the *bio* in biogeochemistry.

At present, there is ample evidence that our species, *Homo sapiens*, is leaving unusual imprints on Earth's chemistry. The human combustion of fossil fuels is raising the concentration of carbon dioxide in our atmosphere to levels not seen in the past 20 million years (Pearson and Palmer 2000). Our release of an unusual class of industrial compounds known as chlorofluorocarbons has depleted the concentration of ozone in the upper atmosphere, where it protects the Earth's surface from harmful levels of ultraviolet light (Rowland 1989). In our effort to feed 7 billion people, we produce vast quantities of nitrogen and phosphorus fertilizers, resulting in the runoff of nutrients that pollute surface and coastal waters (Chapter 12). As a result of coal combustion and other human activities, the concentrations of mercury in freshly caught fish are much higher than a century ago (Monteiro and Furness 1997), rendering many species unfit for regular human consumption. Certainly we are not the first species that has altered the chemical environment of planet Earth, but if our current behavior remains unchecked, it is well worth asking if we may jeopardize our own persistence.

UNDERSTANDING THE EARTH AS A CHEMICAL SYSTEM

Just as a laboratory chemist attempts to observe and understand the reactions in a closed test tube, biogeochemists try to understand the chemistry of nature, where the reactants are found in a complex mix of materials in solid, liquid, and gaseous phases. In most cases, biogeochemistry is a nightmare to a traditional laboratory chemist: the reactants are impure, their concentrations are low, and the temperature is variable. About all you can say about the Earth as a chemical system is that it is closed with respect to mass, save for a few meteors arriving and a few satellites leaving our planet. This closed chemical system is powered by the receipt of energy from the Sun, which has allowed the elaboration of life in many habitats (Falkowski et al. 2008).

Biogeochemists often build models for what controls Earth's surface chemistry and how Earth's chemistry may have changed through the ages. Unlike laboratory chemists, we have no replicate planets for experimentation, so our models must be tested and validated by inference. If our models suggest that the accumulation of organic materials in ocean sediments is associated with the deposition of gypsum ($\text{CaSO}_4 \cdot 2\text{H}_2\text{O}$), we must dig down through the sedimentary layers to see if this correlation occurs in the geologic record (Garrels and Lerman 1981). Finding the correlation does not prove the model, but it adds a degree of validity to our understanding of how Earth works—its biogeochemistry. Models must be revised when observations are inconsistent with their predictions.

Earth's conditions, such as the composition of the atmosphere, change only slowly from year to year, so biogeochemists often build steady-state models. As an example, in a steady-state model of the atmosphere, the inputs and losses of gases are balanced each year; the individual molecules in the atmosphere change, but the total content of each stays relatively constant. The assumption of a steady-state brings a degree of tidiness to our models of Earth's chemistry, but we should always be cognizant of the potential for nonlinear and cyclic behavior in Earth's characteristics. Indeed, some cycles, such as the daily rotation of

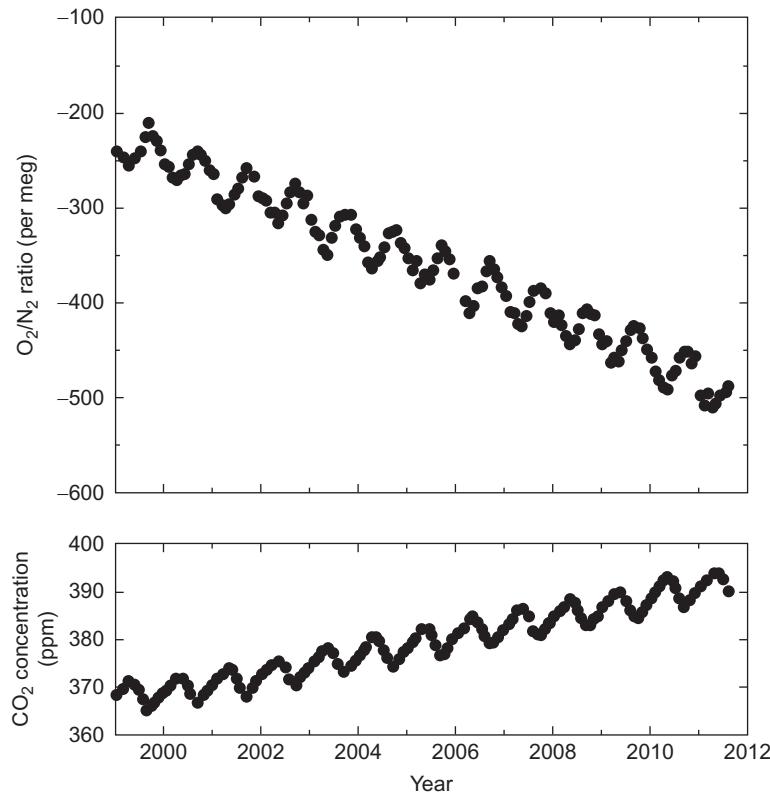


FIGURE 1.1 Annual cycles of CO₂ and O₂ in the atmosphere. Changes in the concentration of O₂ are expressed relative to concentrations of nitrogen (N₂) in the same samples. Note that the peak of O₂ in the atmosphere corresponds to the minimum CO₂ in late summer, presumably due to the seasonal course of photosynthesis in the Northern Hemisphere. *Source: From Ralph Keeling, unpublished data used by permission.*

the Earth around its axis and its annual rotation about the Sun, are now so obvious that it seems surprising that they were mysterious to philosophers and scientists throughout much of human history.

Steady-state models often are unable to incorporate the cyclic activities of the biosphere, which we define as the sum of all the live and dead materials on Earth.¹ During the summer, total plant photosynthesis in the Northern Hemisphere exceeds respiration by decomposers. This results in a temporary storage of carbon in plant tissues and a seasonal decrease in atmospheric CO₂, which is lowest during August of each year in the Northern Hemisphere (Figure 1.1). The annual cycle is completed during the winter months, when atmospheric CO₂ returns to higher levels, as decomposition continues when many plants are dormant or leafless.

¹ Some workers use the term biosphere to refer to the regions or volume of Earth that harbor life. We prefer the definition used here, so that the oceans, atmosphere, and surface crust can be recognized separately. Our definition of the biosphere recognizes that it has mass, but also functional properties derived from the species that are present.

Certainly, it would be a mistake to model the activity of the biosphere by considering only the summertime conditions, but a steady-state model can ignore the annual cycle if it uses a particular time each year as a baseline condition to examine changes over decades.

Over a longer time frame, the size of the biosphere has decreased during glacial periods and increased during post-glacial recovery. Similarly, the storage of organic carbon increased strongly during the Carboniferous Period—about 300 million years ago, when most of the major deposits of coal were laid down. The unique conditions of the Carboniferous Period are poorly understood, but it is certainly possible that such conditions are part of a long-term cycle that might return again. Significantly, unless we recognize the existence and periodicity of cycles and nonlinear behavior and adjust our models accordingly we may err in our assumption of a steady state in Earth's biogeochemistry.

All current observations of global change must be evaluated in the context of underlying cycles and potentially non-steady-state conditions in the Earth's system. The current changes in atmospheric CO₂ are best viewed in the context of cyclic changes seen during the last 800,000 years in a record obtained from the bubbles of air trapped in the Antarctic ice pack. These bubbles have been analyzed in a core taken near Vostok, Antarctica (Figure 1.2). During the entire 800,000-year period, the concentration of atmospheric CO₂ appears to have oscillated between high values during warm periods and lower values during glacial intervals. Glacial cycles are linked to small variations in Earth's orbit that alter the receipt of radiation from the Sun (Berger 1978; Harrington 1987). During the peak of the last glacial epoch (20,000 years ago), CO₂ ranged from 180 to 200 ppm in the atmosphere. CO₂ rose dramatically at the end of the last glacial (10,000 years ago) and was relatively stable at

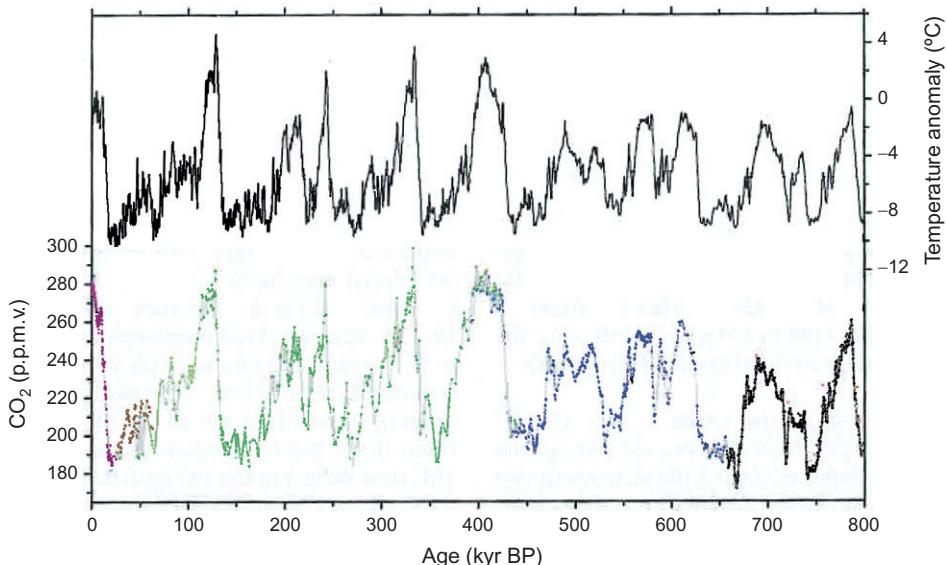


FIGURE 1.2 An 800,000-year record of CO₂ and temperature, showing the minimum temperatures correspond to minimum CO₂ concentrations seen in cycles of ~120,000 periodicity, associated with Pleistocene glacial epochs. Source: From Lüthi et al. (2008)

280 ppm until the Industrial Revolution. The rapid increase in CO₂ at the end of the last glacial epoch may have amplified the global warming that melted the continental ice sheets (Sowers and Bender 1995, Shakun et al. 2012).

When viewed in the context of this cycle, we can see that the recent increase in atmospheric CO₂ to today's value of about 400 ppm has occurred at an exceedingly rapid rate, which carries the planet into a range of concentrations never before experienced during the evolution of modern human social and economic systems, starting about 8000 years ago (Flückiger et al. 2002). If the past is an accurate predictor of the future, higher atmospheric CO₂ will lead to global warming, but any observed changes in global climate must also be evaluated in the context of long-term cycles in climate with many possible causes (Crowley 2000; Stott et al. 2000).

The Earth has many feedbacks that buffer perturbations of its chemistry, so that steady-state models work well under many circumstances. For instance, Robert Berner and his coworkers at Yale University have elucidated the components of a carbonate–silicate cycle that stabilizes Earth's climate and its atmospheric chemistry over geologic time (Berner and Lasaga 1989). The model is based on the interaction of carbon dioxide with Earth's crust. Since CO₂ in the atmosphere dissolves in rainwater to form carbonic acid (H₂CO₃), it reacts with the minerals exposed on land in the process known as rock weathering (Chapter 4). The products of rock weathering are carried by rivers to the sea (Figure 1.3).

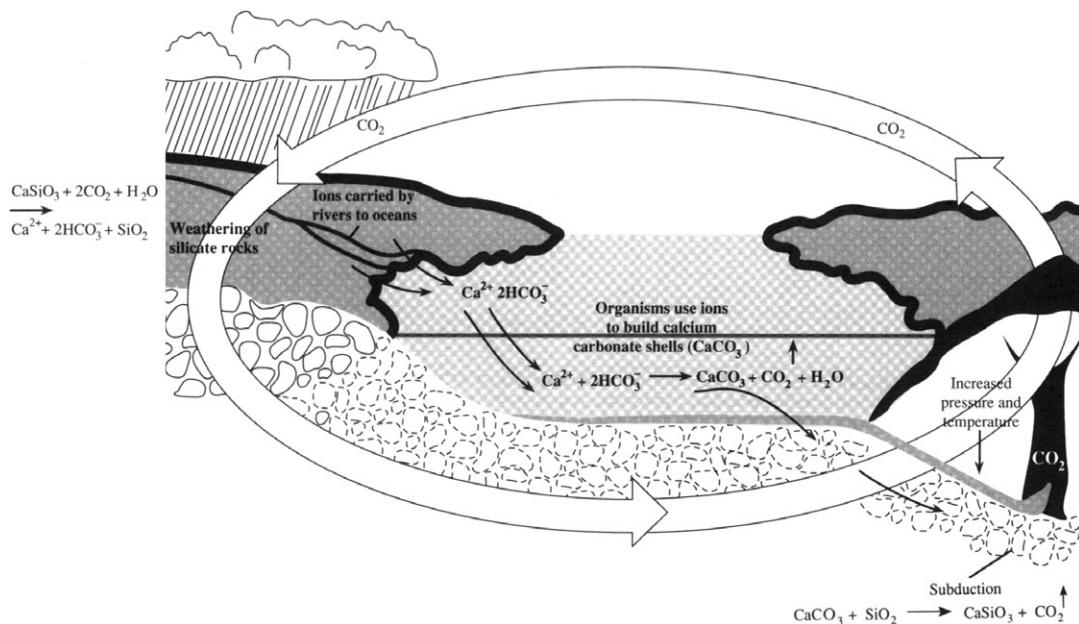


FIGURE 1.3 The interaction between the carbonate and the silicate cycles at the surface of Earth. Long-term control of atmospheric CO₂ is achieved by dissolution of CO₂ in surface waters and its participation in the weathering of rocks. This carbon is carried to the sea as bicarbonate (HCO₃⁻), and it is eventually buried as part of carbonate sediments in the oceanic crust. CO₂ is released back to the atmosphere when these rocks undergo metamorphism at high temperature and pressures deep in Earth. *Source:* Modified from Kasting et al. (1988).

In the oceans, limestone (calcium carbonate) and organic matter are deposited in marine sediments, which in time are carried by subduction into Earth's upper mantle. Here the sediments are metamorphosed; calcium and silicon are converted back into the minerals of silicate rock, and the carbon is returned to the atmosphere as CO₂ in volcanic emissions. On Earth, the entire oceanic crust appears to circulate through this pathway in <200 million years (Muller et al. 2008). The presence of life on Earth does not speed the turning of this cycle, but it may increase the amount of material moving in the various pathways by increasing the rate of rock weathering on land and the rate of carbonate precipitation in the sea.

The carbonate–silicate model is a steady-state model, in the sense that it shows equal transfers of material along the flow-paths and no change in the mass of various compartments over time. In fact, such a model suggests a degree of self-regulation of the system, because any period of high CO₂ emissions from volcanoes should lead to greater rates of rock weathering, removing CO₂ from the atmosphere and restoring balance to the system. However, the assumption of a steady state may not be valid during transient periods of rapid change. For example, high rates of volcanic activity may have resulted in a temporary increase in atmospheric CO₂ and a period of global warming during the Eocene, 40 million years ago (Owen and Rea 1985). And clearly, since the Industrial Revolution, humans have added more carbon dioxide to the atmosphere than the carbonate–silicate cycle or the ocean can absorb each year ([Chapter 11](#)).

Because the atmosphere is well mixed, changes in its composition are perhaps our best evidence of human alteration of Earth's surface chemistry. Concern about global change is greatest when we see increases in atmospheric content of constituents such as carbon dioxide, methane (CH₄), and nitrous oxide (N₂O), for which we see little or no precedent in the geologic record. These gases are produced by organisms, so changes in their global abundance must reflect massive changes in the composition or activity of the biosphere.

Humans have also changed other aspects of Earth's natural biogeochemistry. For example, when human activities increase the erosion of soil, we alter the natural rate of sediment delivery to the oceans and the deposition of sediments on the seafloor (Wilkinson and McElroy 2007, Syvitski et al. 2005). As in the case of atmospheric CO₂, evidence for global changes in erosion induced by humans must be considered in the context of long-term oscillations in the rate of crustal exposure, weathering, and sedimentation due to changes in climate and sea level (Worsley and Davies 1979, Zhang et al. 2001).

Human extraction of fossil fuels and the mining of metal ores substantially enhance the rate at which these materials are available to the biosphere, relative to background rates dependent on geologic uplift and surface weathering (Bertine and Goldberg 1971). For example, the mining and industrial use of lead (Pb) has increased the transport of Pb in world rivers by about a factor of 10 (Martin and Meybeck 1979). Recent changes in the content of lead in coastal sediments appear directly related to fluctuations in the use of Pb by humans, especially in leaded gasoline (Trefry et al. 1985)—trends superimposed on underlying natural variations in the movements of Pb at Earth's surface (Marteel et al. 2008, Pearson et al. 2010).

Recent estimates suggest that the global cycles of many metals have been significantly increased by human activities ([Table 1.1](#)). Some of these metals are released to the atmosphere and deposited in remote locations (Boutron et al. 1994). For example, the combustion of

TABLE 1.1 Movement of Selected Elements through the Atmosphere

Element	Natural		Volcanic		Anthropogenic		Ratio anthropogenic: natural
	Continental dust ^a		Dust	Gas	Industrial particles	Fossil fuel	
	Al	Fe	Cu	Zn	Pb		
Al	356,500	132,750	8.4	40,000	32,000		0.15
Fe	190,000	87,750	3.7	75,000	32,000		0.38
Cu	100	93	0.012	2,200	430		13.63
Zn	250	108	0.14	7,000	1,400		23.46
Pb	50	8.7	0.012	16,000	4,300		345.83

^a All data are expressed in 10^8 g/yr.

Source: From Lantzy and MacKenzie (1979). Used with permission.

coal has raised the concentration of mercury (Hg) deposited in Greenland ice layers in the past 100 years (Weiss et al. 1971). Recognizing that the deposition of Hg in the Antarctic ice cap shows large variations over the past 34,000 years (Vandal et al. 1993), we must evaluate any recent increase in Hg deposition in the context of past cyclic changes in Hg transport through the atmosphere. Again, human-induced changes in the movement of materials through the atmosphere must be placed in the context of natural cycles in Earth system function (Nriagu 1989).

SCALES OF ENDEAVOR

The science of biogeochemistry spans a huge range of space and time, spanning most of the geologic epochs of Earth's history (see inside back cover). Molecular biologists contribute their understanding of the chemical structure and spatial configuration of biochemical molecules, explaining why some biochemical reactions occur more readily than others (Newman and Banfield 2002). Increasingly, genomic sequencing allows biogeochemists to identify the microbes that are active in soils and sediments and what regulates their gene expression (Fierer et al. 2007). Physiologists measure variations in the activities of organisms, while ecosystem scientists measure the movement of materials and energy through well-defined units of the landscape.

Geologists study the chemical weathering of minerals in rocks and soils and document Earth's past from sedimentary cores taken from lakes, oceans, and continental ice packs. Atmospheric scientists provide details of reactions between gases and the radiative properties of the planet. Meanwhile, remote sensing from aircraft and satellites allows biogeochemists to see the Earth at the largest scale, measuring global photosynthesis (Running et al. 2004) and following the movement of desert dusts around the planet (Uno et al. 2009). Indeed the skills needed by the modern biogeochemist are so broad that many students find their entrance to

this new field bewildering. But the fun of being a biogeochemist stems from the challenge of integrating new science from diverse disciplines. And luckily, there are a few basic rules that guide the journey, as described in the next few subsections.

Thermodynamics

Two basic laws of physical chemistry, the laws of thermodynamics, tell us that energy can be converted from one form to another and that chemical reactions should proceed spontaneously to yield the lowest state of free energy, G , in the environment. The lowest free energy of a chemical reaction represents its equilibrium, and it is found in a mix of chemical species that show maximum bond strength and maximum disorder among the components. In the face of these basic laws, living systems create non-equilibrium conditions; life captures energy to counteract reactions that might happen spontaneously to maximize disorder.

Even the simplest cell is an ordered system; a membrane separates an inside from an outside, and the inside contains a mix of very specialized molecules. Biological molecules are collections of compounds with relatively weak bonds. For instance, to break the covalent bonds between two carbon atoms requires 83 kcal/mole, versus 192 kcal/mole for each of the double bonds between carbon and oxygen in CO_2 (Davies 1972, Morowitz 1968). In living tissue most of the bonds between carbon (C), hydrogen (H), nitrogen (N), oxygen (O), phosphorus (P), and sulfur (S), the major biochemical elements, are reduced or “electron-rich” bonds that are relatively weak ([Chapter 7](#)). It is an apparent violation of the laws of thermodynamics that the weak bonds in the molecules of living organisms exist in the presence of a strong oxidizing agent in the form of O_2 in the atmosphere. Thermodynamics would predict a spontaneous reaction between these components to produce CO_2 , H_2O , and NO_3^- —molecules with much stronger bonds. In fact, after the death of an organism, this is exactly what happens! Living organisms must continuously process energy to counteract the basic laws of thermodynamics that would otherwise produce disordered systems with oxidized molecules and stronger bonds.

During photosynthesis, plants capture the energy in sunlight and convert the strong bonds between carbon and oxygen in CO_2 to the weak, reduced biochemical bonds in organic materials. As heterotrophic organisms, herbivores eat plants to extract this energy by capitalizing on the natural tendency for electrons to flow from reduced bonds back to oxidizing substances, such as O_2 . Heterotrophs oxidize the carbon bonds in organic matter and convert the carbon back to CO_2 . A variety of other metabolic pathways have evolved using transformations among other compounds ([Chapters 2 and 7](#)), but in every case metabolic energy is obtained from the flow of electrons between compounds in oxidized or reduced states. Metabolism is possible because living systems can sequester high concentrations of oxidized and reduced substances from their environment. Without membranes to compartmentalize living cells, thermodynamics would predict a uniform mix, and energy transformations, such as respiration, would be impossible.

Free oxygen appeared in Earth’s surface environments sometime after the appearance of autotrophic, photosynthetic organisms ([Chapter 2](#)). Free O_2 is one of the most oxidizing substances known, and the movement of electrons from reduced substances to O_2 releases large amounts of free energy. Thus, large releases of free energy are found in aerobic metabolism,

including the efficient metabolism of eukaryotic cells. The appearance of eukaryotic cells on Earth was not immediate; the fossil record suggests that they evolved nearly 1.5 billion years after the appearance of the simplest living cells (Knoll 2003). Presumably the evolution of eukaryotic cells was possible only after the accumulation of sufficient O₂ in the environment to sustain aerobic metabolic systems. In turn, aerobic metabolism offered large amounts of energy that could allow the elaborate structure and activity of higher organisms. Here some humility is important: eukaryotic cells may perform biochemistry faster and more efficiently, but the full range of known biochemical transformations is found amongst the members of the prokaryotic kingdom.

Stoichiometry

A second organizing principle of biogeochemistry stems from the coupling of elements in the chemical structure of the molecules of which life is built—cellulose, protein, and the like. Redfield's (1958) observation of consistent amounts of C, N, and P in phytoplankton biomass is now honored by a ratio that carries his name ([Chapter 9](#)). Reiners (1986) carried the concept of predictable stoichiometric ratios in living matter to much of the biosphere, allowing us to predict the movement of one element in an ecosystem by measurements of another. Sterner and Elser (2002) have presented stoichiometry as a major control on the structure and function of ecosystems. The growth of land plants is often determined from the nitrogen content of their leaves and the nitrogen availability in the soil ([Chapter 6](#)), whereas phosphorus availability explains much of the variation in algal productivity in lakes ([Chapter 8](#)). The population growth of some animals may be determined by sodium—an essential element that is found at a low concentration in potential food materials, relative to its concentration in body tissues.

Although the stoichiometry of biomass allows us to predict the concentration of elements in living matter, the expected ratio of elements in biomass is not absolute, such as the ratio of C to N in a reagent bottle of alanine. For instance, a sample of phytoplankton will contain a mix of species that vary in individual N/P ratios, with the weighted average close to that postulated by Redfield (Klausmeier et al. 2004). And, of course, a large organism will contain a mix of metabolic compounds (largely protein) and structural components (e.g., wood or bone) that differ in elemental composition (Reiners 1986, Arrigo et al. 2005; Elser et al. 2010). In some sense, organisms are what they eat, but decomposers can adjust their metabolism (Manzoni et al. 2008) and enzymatic production (Sinsabaugh et al. 2009) to feed on a wide range of substrates, even as they maintain a constant stoichiometry in their own biomass.

In some cases, trace elements control the cycle of major elements, such as nitrogen, by their role as activators and cofactors of enzymatic synthesis and activity. When nitrogen supplies are low, signal transduction by P activates the genes for N fixation in bacteria (Stock et al. 1990). The enzyme for nitrogen fixation, nitrogenase, contains iron (Fe) and molybdenum (Mo). Over large areas of the oceans, Falkowski et al. (1998) show that iron, delivered to the surface waters by the wind erosion of desert soils, controls marine production, which is often limited by N fixation. Similarly, when phosphorus supply is low, plants and microbes may produce alkaline phosphatase, containing zinc, to release P from dead materials (Shaked

		Oxidized	Reduced		
		H ₂ O/O ₂	C	N	S
Oxidized ↓ Reduced	H ₂ O/O ₂	X	Photosynthesis $\text{CO}_2 \rightarrow \text{C}$ $\text{H}_2\text{O} \rightarrow \text{O}_2$		
	C	Respiration $\text{C} \rightarrow \text{CO}_2$ $\text{O}_2 \rightarrow \text{H}_2\text{O}$	X	Denitrification $\text{C} \rightarrow \text{CO}_2$ $\text{NO}_3 \rightarrow \text{N}_2$	Sulfate-Reduction $\text{C} \rightarrow \text{CO}_2$ $\text{SO}_4 \rightarrow \text{H}_2\text{S}$
	N	Heterotrophic Nitrification $\text{NH}_4 \rightarrow \text{NO}_3$ $\text{O}_2 \rightarrow \text{H}_2\text{O}$	Chemoautotrophy (Nitrification) $\text{NH}_4 \rightarrow \text{NO}_3$ $\text{CO}_2 \rightarrow \text{C}$	Anammox $\text{NH}_4 + \text{NO}_2 \rightarrow \text{N}_2 + 2\text{H}_2\text{O}$?
	S	Sulfur Oxidation $\text{S} \rightarrow \text{SO}_4$ $\text{O}_2 \rightarrow \text{H}_2\text{O}$	Chemoautotrophy (Sulfur-based Photosynthesis) $\text{S} \rightarrow \text{SO}_4$ $\text{CO}_2 \rightarrow \text{C}$	Autotrophic Denitrification $\text{S} \rightarrow \text{SO}_4$ $\text{NO}_3 \rightarrow \text{N}_2/\text{NH}_4$	X

FIGURE 1.4 A matrix showing how cellular metabolisms couple oxidation and reduction reactions. The cells in the matrix are occupied by organisms or a consortium of organisms that reduce the element at the top of the column, while oxidizing an element at the beginning of the row. *Source: From Schlesinger et al. (2011).*

et al. 2006). Thus, the productivity of some ecosystems can be stimulated either by adding the limiting element itself or by adding a trace element that facilitates nutrient acquisition (Arrigo et al. 2005).

The elements of life are also coupled in metabolism, since organisms employ some elements in energy-yielding reactions, without incorporating them into biomass. Coupled biogeochemistry of the elements in metabolism stems from the flow of electrons in the oxidation/reduction reactions that power all of life (Morowitz 1968, Falkowski et al. 2008). Coupled metabolism is illustrated by a matrix, where each element in a column is reduced while the element in an intersecting row is oxidized (Figure 1.4). All of Earth's metabolisms can be placed in the various cells of this matrix and in a few adjacent cells that would incorporate columns and rows for Fe and other trace metals. The matrix incorporates the range of metabolisms possible on Earth, should the right conditions exist (Bartlett 1986).

Large-Scale Experiments

Biogeochemists frequently conduct large-scale experiments to assess the response of natural systems to human perturbation. Schindler (1974) added phosphorus to experimental lakes in Canada to show that it was the primary nutrient limiting algal growth in those ecosystems (Figure 1.5). Bormann et al. (1974) deforested an entire watershed to demonstrate the importance of vegetation in sequestering nutrients in ecosystems. Several experiments have exposed replicated plots of forests, grasslands, and desert ecosystems to



FIGURE 1.5 An ecosystem-level experiment in which a lake was divided and one half (distant) fertilized with phosphorus, while the basin in the foreground acted as a control. The phosphorus-fertilized basin shows a bloom of nitrogen-fixing cyanobacteria. *Source: From Schindler (1974); www.sciencemag.org/content/184/4139/897.short. Used with permission.*

high CO₂ to simulate plant growth in the future environments on Earth ([Chapter 5](#)). And oceanographers have added Fe to large patches of the sea to ascertain whether it normally limits the growth of marine phytoplankton ([Chapter 9](#)). In many cases these large experiments and field campaigns are designed to test the predictions of models and to validate them.

Models

With sufficient empirical observations, biogeochemists can often build mathematical models for how ecosystems function. Equations can express what controls the movement of energy and materials through organisms or individual compartments of an ecosystem, such as the soil. The equations often incorporate the constraints of thermodynamics and stoichiometry. These models allow us to determine which processes control the productivity and biogeochemical cycling in ecosystems, and where our understanding is incomplete. Models that are able to reproduce past dynamics reliably allow us to explore the behavior of ecosystems in response to future perturbations that may lie outside the natural range of environmental variation.

LOVELOCK'S GAIA

In a provocative book, *Gaia*, published in 1979, James Lovelock focused scientific attention on the chemical conditions of the present-day Earth, especially in the atmosphere, that are extremely unusual and in disequilibrium with respect to thermodynamics. The 21% atmospheric content of O₂ is the most obvious result of living organisms, but other gases, including NH₃ and CH₄, are found at higher concentrations than one would expect in an O₂-rich atmosphere (Chapter 3). This level of O₂ in our atmosphere is maintained despite known reactions that should consume O₂ in reaction with crustal minerals and organic carbon. Further, Lovelock suggested that the *albedo* (reflectivity) of Earth must be regulated by the biosphere, because the planet has shown relatively small changes in surface temperature despite large fluctuations in the Sun's radiation during the history of life on Earth (Watson and Lovelock 1983).

Lovelock suggested that the conditions of our planet are so unusual that they could only be expected to result from activities of the biosphere. Indeed, *Gaia* suggests that the biosphere evolved to regulate conditions within a range favorable for the continued persistence of life on Earth. In Lovelock's view, the planet functions as a kind of "superorganism," providing planetary homeostasis. Reflecting the vigor and excitement of a new scientific field, other workers have strongly disagreed—not denying that biotic factors have strongly influenced the conditions on Earth, but not accepting the hypothesis of purposeful self-regulation of the planet (Lenton 1998).

Like all models, *Gaia* remains as a provocative hypothesis, but the rapid pace at which humans are changing the biosphere should alarm us all. Some ecologists see the potential for critical transitions in ecosystem function; points beyond which human impacts would not allow the system to rebound to its prior state, even if the impacts ceased (Scheffer et al. 2009). Others have attempted to quantify these thresholds, so that we may recognize them in time (Rockstrom et al. 2009). In all these endeavors, policy makers are desperate for biogeochemists to deliver a clear articulation of how the world works, the extent and impact of the human perturbation, and what to do about it.

Recommended Readings

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