

BETTER LIVING THROUGH BIOGEOCHEMISTRY

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Abstract. During the past 50 years, biogeochemistry has emerged as the premier scientific discipline to examine human impacts on the global environment. Important advances have derived from the synthesis of biogeochemical cycles at the global level, from the recognition that biochemical stoichiometry constrains the composition of living tissue, and from large-scale experiments that address the response of whole ecosystems to human impact. Future work will further pursue these avenues, with frequent use of modern, molecular methods to ascertain the role of individual species and species diversity in ecosystem function. Biogeochemists will increasingly need to translate the important results of their work to help formulate effective environmental policy.

Key words: biodiversity; biogeochemistry; global cycles; human impacts; large-scale experiments; stoichiometry.

INTRODUCTION

By all accounts, biogeochemistry is a maturing science. It has its own journals (*Biogeochemistry* and *Global Biogeochemical Cycles*); its own textbooks (Schlesinger 1997); and sections for its practitioners in major scientific societies, such as the American Geophysical Union and the Ecological Society of America. At least one paper reviews the history of biogeochemistry (Gorham 1991), and its future is captured in the report *Grand Challenges in Environmental Sciences*, which recognizes studies of biogeochemical cycles as the nation's highest priority in global change research (National Research Council 2001). The new Biogeosciences Program in the Geosciences Directorate of the National Science Foundation formalizes a source of funding for biogeochemical research, supporting studies ranging from astrobiology to the future of life on Earth.

The launch of the Biogeosciences Section of the Ecological Society of America demands some attention to the scientific challenges before us. Here, I attempt to see some clear paths for future research and suggest some critical areas in biogeochemistry that need our exploration.

Foremost, we must learn more about the chemical environment in which we live and about how our planet works as an integrated chemical system in which life, especially microbial life, is a major player—hence *biogeochemistry*. The chemical arena at the surface of the Earth has determined the milieu for life for the past 3.5 billion years or so, and biology has had a major impact on its characteristics. Many paleoecologists speculate how the first oxygen-producing photoauto-

trophs must have changed the chemical environment of the anoxic Precambrian seas. The introduction of oxygen may have been the first time that the action of a few species made life miserable for most of the other inhabitants on the planet. Now, at least since the Industrial Revolution, we find ourselves in another era in which a single species, in this case *Homo sapiens*, is casting an enormous pall on the Earth's chemical composition. Many humans now enjoy the “good life” and many others strive to do so, but as the Earth's chemistry changes, its effects on the Earth's biota and climate may well determine the future for all life on this planet.

GLOBAL CYCLES

Humans have enormous impact on the global movement of chemical materials. To date, most biogeochemical research has focused on the carbon cycle, in which, by extraction of carbon-based fossil fuels from the Earth's crust, humans add >22 billion tons of carbon dioxide (nearly 7×10^{15} g C) to the atmosphere annually. The average U.S. citizen contributes more than 6 Mg of carbon to the atmosphere each year, roughly one-third of it from private, personal transport. The global anthropogenic flux of carbon is equivalent to only 7% of the total annual exchange of CO₂ to and from the atmospheric reservoir by photosynthesis (Table 1), yet this comparatively modest human impact to the carbon cycle is the basis for worldwide concern about climate change and global warming.

Our impact on the global cycles of other materials is even greater. We use roughly half of the available fresh water on Earth (Postel et al. 1996), and future shortages of good quality fresh water will be critical to much of the human population globally (Vörösmarty et al. 2000, Jackson et al. 2001). Largely in an attempt to feed the world's growing population, we mobilize large amounts of N and P into their global biogeochemical cycles, altering the natural availability of

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TABLE 1. Contributions of abiotic and biotic processes, including humans, to global biogeochemical cycles.

Element	Flux						Ratios, human mobilization 2000 to:	
	Juvenile abiotic flux [†]	Atmospheric exchange		Biotic cycle	Human mobilization		Juvenile flux	Total atmospheric exchange
		Abiotic [‡]	Biotic [§]		2000 [¶]	2050 [#]		
B	0.3	1.5	0.35	8.8	0.6	unknown	2.0	0.32
C	200	90 000	67 000	105 000	7000	15 000	35	0.05
N	5	13	228	9200	156	267	31.2	0.65
P	9	1	0.04	1260	12–15	37	1.3–1.6	11.5–14.4
S	82	152	20	500	150	42–127	1.83	0.87
Cl	2	6000	5	0	141.5		71	0.02

Note: Flux data are Tg/yr; ratios are unitless.

[†] Mobilization into chemical cycles at the surface of the Earth by processes such as rock weathering and emissions from volcanoes and hydrothermal vents. For N, this is N fixation by lightning (5 TgN/yr) and volcanic flux (0.04 TgN/yr).

[‡] Annual flux of element to or from the atmosphere that can be attributed to abiotic processes, including production of sea-salt aerosols, wind erosion, and gaseous exchange with seawater (e.g., for N, ammonia volatilization [Schlesinger and Hartley 1992]).

[§] Annual flux of element to or from the atmosphere that can be attributed to biotic processes, e.g., net primary production; N fixation (Galloway et al. 2003); biogenic gases including phosphine and methyl chloride, and gases from the burning of organic materials. For carbon, this is calculated as net primary production on land (Field et al. 1998) plus the carbon in the organic and inorganic components of “new production” in the oceans, following Lee (2001).

^{||} Annual uptake and loss of elements from living tissues: C is derived from NPP (Field et al. 1998); other elements calculated from ratio to C in NPP in terrestrial and marine habitats; Cl is assumed to be zero.

[¶] Human mobilization from industrial activities, mining, and fossil fuel combustion in year 2000.

[#] Estimates for year 2050: C is from IPCC projections (IPCC 2001); N and P are from Tilman et al. (2001). The projected flux of S will largely depend on policies that are adopted to mitigate SO₂ emissions (Austin et al. 2003).

these elements to the biosphere (Table 1). The resulting impacts are well known, ranging from the eutrophication of lakes with excessive phosphorus loading, to the enrichment of entire watersheds and their coastal waters by excessive loads of nitrogen fertilizer. Humans have nearly doubled the annual mobilization of S in its global cycle, and our effect is manifest in the acid deposition that scrubs SO₂ from the atmosphere in regions downwind of industrial activity. Indeed, looking broadly at the periodic table, we see that humans have significant impact on the global cycle of nearly every chemical element with economic value, dominating the mobilization of metallic elements from the Earth's crust (Bertine and Goldberg 1971), their movement through the atmosphere (Lantzy and MacKenzie 1979), and their content in river flow (Martin and Meybeck 1979).

Among the first tasks facing today's biogeochemists is to understand fully the natural, global biogeochemical cycles of water and the various chemical elements, and the human impacts on each of them. A look to the past shows a compelling motivation for doing so. For example, when we were able to articulate clear and complete budgets for the natural and perturbed global cycles of lead (Pb), the need to remove lead from gasoline appeared starkly before policy makers who knew the effects of excessive lead on human health. The global budget for Cl allows us to see how the small amounts of chlorofluorocarbons released by humans are the source of nearly all the Cl that mixes into the stratosphere (Graedel and Keene 1995), where it destroys ozone (Molina and Rowland 1974). We need to be able

to provide the same level of insight for the global carbon cycle, and the nagging persistence of the “missing sink” for atmospheric CO₂ weakens our case for immediate policy actions to stem global warming. Policy makers will also delay action on global problems concerning N, P, Hg, and S, until their global cycles are better known.

The global budgets for each element should show the exchange of materials between the atmosphere, the oceans, and the land surface (e.g., Park and Schlesinger 2002). Regional analyses would be most welcome as a means of focusing attention on the cause of regional ecosystem problems, such as the nitrogen pollution of estuaries (Howarth et al. 1996). Applications of remote sensing, with the data captured in Geographic Information Systems (GIS) and global grid models, will allow a formal aggregation of local data to apply to larger scales. Further studies of paleochemistry—derived from ice cores, sediments, and novel data sources (e.g., Pb in French wine [Lobinski et al. 1994] and N in herbarium specimens [Peñuelas and Filella 2001])—will inform us about biogeochemical cycles in the past and human impacts on them.

STOICHIOMETRY: HOW LIFE IS PUT TOGETHER

Dating back to the early studies by Redfield et al. (1963), biogeochemists have often focused on the linkage between chemical elements—in biochemistry and in their global biogeochemical cycles (Reiners 1986, Sterner and Elser 2002). Signal transduction mediated by P activates N fixation in bacteria (Stock et al. 1990). Available Fe determines the rate of pyritization in ma-

rine sediments, hence the O₂ content in Earth's atmosphere (Boudreau and Westrich 1984). And the rate of net primary production by the biosphere is closely regulated by the availability of essential elements that are used to build plant and microbial tissues (Schlesinger 1997). Characteristic ratios between elements determine the basic stoichiometry for the biosphere, allowing us to predict its response to alterations of nutrient availability, such as changing levels of N fixation by cyanobacteria in lakes (Howarth et al. 1988).

Understanding the stoichiometry of life presents a major research challenge to biogeochemists, since we can increasingly expect policymakers to recommend that we engage in ecological engineering of the biosphere to achieve specific human goals. A biogeochemical analysis, based on stoichiometry, can allow us to evaluate the impact of "quick fixes," such as recommendations for greater use of nitrogen fertilizer to increase carbon sequestration in soils (Schlesinger 2000). Our science must provide answers to basic questions, such as "what will be the effects of large-scale fertilization of the oceans with iron to stimulate the uptake of atmospheric carbon dioxide?" Stoichiometry allows us to predict the direction of the response, and perhaps even its magnitude, but we have little understanding of how such a major manipulation of the ocean's biogeochemistry will cascade through other trophic levels, potentially altering the basic function of marine ecosystems.

TEARING DOWN THE BARRIERS

While understanding stoichiometry allows us to see the linkage between the elements of life, we must also recognize and appreciate the linkage between the realms of the biogeochemical arena for life on Earth. Often we use obvious boundaries (e.g., watersheds and lakeshores) to delineate the scope of ecosystem problems we wish to study, as if movements across those boundaries were of no consequence to ecosystem function. Since the world is now bathed in an atmospheric CO₂ concentration unprecedented in the past 20 000 000 years (Pearson and Palmer 2000), I argue that all such boundaries are artificial: there are no "pristine" ecosystems. Everywhere, the Earth functions under the atmospheric chemistry that humans have determined for it.

Boundaries allowed rapid early progress in the study of ecosystems (Bormann and Likens 1967), but adopting a larger, landscape and global approach is now appropriate in our maturing science. The nitrogen applied to a farm field in Iowa is closely tied to the net primary production in the Gulf of Mexico (Alexander et al. 2000, Fisher et al. 2004). The plant productivity on desert hill slopes is directly tied to the disposition of rainfall on mountain ranges several kilometers away. And the nitrogen cycling in remote forests is now affected by the fact that they grow at levels of CO₂ far above those of their evolutionary history. Fluctuations

in global climate affect the production, transport and deposition of arid-land dust, containing P, Si, and Fe and determining the net primary production of the world's oceans and atmospheric CO₂ levels (Falkowski et al. 1998). Dust links terrestrial and marine biogeochemistry and climate through geologic time, and we must focus on the linkages, not the boundaries, if we are to understand how the Earth functions as an integrated biogeochemical system.

Tearing down boundaries also applies to those between our scientific disciplines. We must apply molecular level studies to large-scale field experiments, such as free-air CO₂ enrichment (FACE), which allow us to manipulate one or more variables and quantify the resulting changes in biogeochemistry and ecosystem function (Finzi et al. 2002). We must interpret the results of individual field studies, e.g., eddy-flux measures of forest growth, in the context of changes in regional atmospheric chemistry that are seen in large-scale monitoring networks. And biogeochemists should not forget that the geosciences that have been most cordial in welcoming biologists to their ranks. Studies of rock weathering, soil formation, geomorphology, and erosion are fundamental to understanding terrestrial ecosystems. Studies of sediments provide an invaluable view of how the Earth's ecosystems have functioned in the past—essential perspective for what we forecast for the future.

DO SPECIES MATTER?

Biogeochemists have a role in the current, heated debate regarding the importance of biodiversity to ecosystem function (Loreau et al. 2001). We know that additions of nutrients lead to a loss of species diversity in natural communities (Huenneke et al. 1990, Wedin and Tilman 1996). Conversely, some recent experiments show an important role of plant diversity in nutrient cycling, as seen in the greater losses of nitrogen in seepage waters beneath depauperate fields in Minnesota (Tilman et al. 1996). Indeed, vascular plants seem to control the vertical distribution of soil nutrients globally (Jobbágy and Jackson 2001, 2004). One can argue that losses of the American chestnut and the passenger pigeon, which probably once dominated some forests of the eastern United States, did not lead to the collapse of those ecosystems. On the other hand, rare and endangered species, such as the loggerhead sea turtle, can play a critical role in nutrient cycling in some ecosystems (Bouchard and Bjorndal 2000). Further field studies of biogeochemistry will help elucidate the role of species in ecosystem function. In the face of dwindling areas that will remain "natural," we must show how to balance the sometimes conflicting goals—the preservation of species richness or the preservation of ecosystem function—as part of our conservation efforts.

Unfortunately, we know very little about biodiversity in the microbial world—where most biogeochem-

ical processes and ecosystem function is determined. New molecular techniques should allow us to recognize the important species more easily, encouraging us not simply to lump together the microbial diversity in soils and sediments (Pace 1997, Newman and Banfield 2002). To understand biogeochemical processes, we need to know “who’s doing it.” My prediction is that molecular approaches will have an impact on our science that is equivalent to what stable isotope analyses have done to elucidate biogeochemical processes during the past few decades.

As the human population rises and the world’s remaining natural land areas shrink, biogeochemists must aid the ensuing debate about agricultural intensification. Will we preserve the greatest levels of species richness by intensifying our agriculture on small areas of land, allowing the greatest area to be saved for nature (Waggoner 1996)? Or will we have lesser impact by returning to less intensive agriculture that is spread across a larger area of landscape? Molecular biology will also bring us genetically modified organisms (GMOs)—including crop plants, as well as designer microbes and parasitodes. How will the availability of GMOs affect this debate?

WHY BIGGER IS BETTER

Large-scale experiments have allowed us to unravel the simultaneous effects of global change on both biodiversity and ecosystem function. For example, soil warming experiments in the alpine tundra of Colorado have shown large changes in ecosystem function (Shaw and Harte 2001) with apparently little change in species richness (Price and Waser 2000). Free-air CO₂ enrichment (FACE) experiments, such as in the Duke Forest, indicate major effects of atmospheric CO₂ on species fecundity and growth rate (DeLucia et al. 1999, LaDeau and Clark 2001), which may determine the future composition of regional forests. Iron fertilization experiments have done the same for our understanding of marine ecosystems in the pelagic ocean (Coale et al. 1996, Boyd et al. 2000).

Biogeochemistry will make its greatest contributions to environmental science if we see greater emphasis on realistic, large-scale, long-term, and multifactor experiments that are integrated with efforts to understand the fundamental processes that govern biogeochemical cycling. Often what is seen during the early years of an ecosystem manipulation differs from the long-term response (Oren et al. 2001, Melillo et al. 2002). Experimental growth of forests at high CO₂ will be most applicable to the management of the Earth’s future environment if we understand the simultaneous effects of greater nitrogen deposition, exposure to high levels of ozone, and warmer temperatures. Soil warming experiments in tundra and boreal forest ecosystems are desperately needed to answer the current debate on future carbon sequestration in those ecosystems. Capturing the important lessons that we have learned from the

design and operation of the ecosystem experiments at Hubbard Brook (Likens 2004), all such experiments should monitor the long-term response of ecosystems using consistent methods and ample, archival storage of samples for future study (e.g., Torn et al. 2002).

SPEAK NOT SOFTLY IN THE DARKNESS

Finally, in a world that feels ever smaller, as telecommunications, rapid air travel, and cultural globalization connect us, we must remember that we live in an integrated chemical system that spans only a thin “peel” about 20 km thick on the surface of planet Earth. How we manage that arena will determine the persistence and quality of life for every one of the species that now inhabit this planet with us. Many species will disappear; others will proliferate globally, bringing huge changes to the ecosystem functions that we have long regarded as “normal.” Like it or not, *Homo sapiens* will be the supervisor of this arena. We can manage it well, manage it poorly, or through purposeful actions of terrorism and war, we can poison Eden. The chemistry of the arena of life—that is Earth’s biogeochemistry—will be at the center of how well we do, and all biogeochemists should strive to articulate that message clearly and forcefully to the public and to leaders of society, who must know our message to do their job well.

LITERATURE CITED

- Alexander, R. B., R. A. Smith, and G. E. Schwarz. 2000. Effect of stream channel size on the delivery of nitrogen to the Gulf of Mexico. *Nature* **403**:758–761.
- Austin, A. T., R. W. Howarth, J. S. Baron, F. S. Chapin, T. R. Christensen, E. A. Holland, M. V. Ivanov, A. Y. Lein, L. A. Martinelli, J. M. Melillo, and C. Shang. 2003. Human disruption of elemental interactions: drivers, consequences, and trends for the twenty-first century. Pages 15–45 in J. M. Melillo, C. B. Field, and B. Moldan, editors. *Interaction of the major biogeochemical cycles*. Island press, Washington, D.C., USA.
- Bertine, K. K., and E. D. Goldberg. 1971. Fossil fuel combustion and the major sedimentary cycle. *Science* **173**:233–235.
- Bormann, F. H., and G. E. Likens. 1967. Nutrient cycling. *Science* **155**:424–429.
- Bouchard, S. S., and K. A. Bjorndal. 2000. Sea turtles as biological transporters of nutrients and energy from marine to terrestrial ecosystems. *Ecology* **81**:2305–2313.
- Boudreau, B. P., and J. T. Westrich. 1984. The dependence of bacterial sulfate reduction on sulfate concentration in marine sediments. *Geochimica Cosmochimica Acta* **48**:2503–2516.
- Boyd, P. W., et al. 2000. A mesoscale phytoplankton bloom in the polar Southern Ocean stimulated by iron fertilization. *Nature* **407**:695–702.
- Coale, K. H., et al. 1996. A massive phytoplankton bloom induced by an ecosystem-scale iron fertilization experiment in the equatorial Pacific Ocean. *Nature* **383**:495–501.
- DeLucia, E. H., J. G. Hamilton, S. L. Naidu, R. B. Thomas, J. A. Andrews, A. Finzi, M. Lavine, R. Matamala, J. E. Mohan, G. R. Hendrey, and W. H. Schlesinger. 1999. Net primary production of a forest ecosystem with experimental CO₂ enrichment. *Science* **284**:1177–1179.

- Falkowski, P. G., R. T. Barber, and V. Smetacek. 1998. Biogeochemical controls and feedbacks on ocean primary production. *Science* **281**:200–206.
- Field, C. B., M. J. Behrenfeld, J. T. Randerson, and P. Falkowski. 1998. Primary production of the biosphere: integrating terrestrial and oceanic components. *Science* **281**:237–240.
- Finzi, A. C., E. H. DeLucia, J. G. Hamilton, D. D. Richter, and W. H. Schlesinger. 2002. The nitrogen budget of a pine forest under free air CO₂ enrichment. *Oecologia* **132**:567–578.
- Fisher, S. G., R. A. Sponseller, and J. B. Heffernan. 2004. Horizons in stream biogeochemistry: flowpaths to progress. *Ecology* **85**:2369–2379.
- Galloway, J. N. 2003. The global nitrogen cycle. Pages 557–583 in W. H. Schlesinger, editor. *Biogeochemistry*. Volume 8. Treatise of Geochemistry. Elsevier-Pergamon, Oxford, UK.
- Gorham, E. 1991. Biogeochemistry: its origins and development. *Biogeochemistry* **13**:199–239.
- Graedel, T. E., and W. C. Keene. 1995. Tropospheric budget of reactive chlorine. *Global Biogeochemical Cycles* **9**:47–77.
- Howarth, R. W., et al. 1996. Regional nitrogen budgets and riverine N & P fluxes for the drainages to the North Atlantic Ocean: natural and human influences. *Biogeochemistry* **35**:75–139.
- Howarth, R. W., R. Marino, and J. J. Cole. 1988. Nitrogen fixation in freshwater, estuarine, and marine ecosystems. 2. Biogeochemical controls. *Limnology and Oceanography* **33**:688–701.
- Huenneke, L. F., S. P. Hamburg, R. Koide, H. A. Mooney, and P. M. Vitousek. 1990. Effects of soil resources on plant invasion and community structure in Californian serpentine grassland. *Ecology* **71**:478–491.
- IPCC (Intergovernmental Panel on Climate Change). 2001. Working group one, third assessment report. Cambridge University Press, Cambridge, UK.
- Jackson, R. B., S. R. Carpenter, C. N. Dahm, D. M. McKnight, R. J. Naiman, S. L. Postel, and S. W. Running. 2001. Water in a changing world. *Ecological Applications* **11**:1027–1045.
- Jobbágy, E. G., and R. B. Jackson. 2001. The distribution of soil nutrients with depth: global patterns and imprint of plants. *Biogeochemistry* **53**:51–77.
- Jobbágy, E. G., and R. B. Jackson. 2004. The uplift of soil nutrients by plants: biogeochemical consequences across scales. *Ecology* **85**:2380–2389.
- LaDeau, S. L., and J. S. Clark. 2001. Rising CO₂ levels and the fecundity of forest trees. *Science* **292**:95–98.
- Lantzy, R. J., and F. T. MacKenzie. 1979. Atmospheric trace metals: global cycles and assessment of man's impact. *Geochimica Cosmochimica Acta* **43**:511–525.
- Lee, K. 2001. Global net community production estimated from the annual cycle of surface water total dissolved inorganic carbon. *Limnology and Oceanography* **46**:1287–1297.
- Likens, G. E. 2004. Some perspectives on long-term biogeochemical research from the Hubbard Brook ecosystem study. *Ecology* **85**:2355–2362.
- Lobinski, R., C. Witte, F. C. Adams, P. L. Telssedre, J. C. Cabanis, and C. F. Boutron. 1994. Organolead in wine. *Nature* **370**:24.
- Loreau, M., S. Naeem, P. Inchausti, J. Bengtsson, J. P. Grime, A. Hector, D. U. Hooper, M. A. Huston, D. Raffaelli, B. Schmid, D. Tilman, and D. A. Wardle. 2001. Biodiversity and ecosystem functioning: current knowledge and future challenges. *Science* **294**:804–808.
- Martin, J.-M., and M. Meybeck. 1979. Elemental mass-balance of material carried in major world rivers. *Marine Chemistry* **7**:173–206.
- Melillo, J. M., P. A. Steudler, J. D. Aber, K. Newkirk, H. Lux, F. P. Bowles, C. Catricala, A. Magill, T. Ahrens, and S. Morrisseau. 2002. Soil warming and carbon-cycle feedbacks to the climate system. *Science* **298**:2173–2176.
- Molina, M. J., and F. S. Rowland. 1974. Stratospheric sink for chlorofluoromethanes: chlorine atom-catalyzed destruction of ozone. *Nature* **249**:810–812.
- National Research Council. 2001. Grand challenges in environmental sciences. National Academy Press, Washington, D.C., USA.
- Newman, D. K., and J. F. Banfield. 2002. Geomicrobiology: how molecular-scale interactions underpin biogeochemical systems. *Science* **296**:1071–1077.
- Oren, R., D. S. Ellsworth, K. H. Johnson, N. Phillips, B. E. Ewers, C. Maier, K. V. R. Schäfer, H. McCarthy, G. Hendrey, S. G. McNulty, and G. G. Katul. 2001. Soil fertility limits carbon sequestration by a forest ecosystem in a CO₂-enriched atmosphere. *Nature* **411**:469–472.
- Pace, N. R. 1997. A molecular view of microbial diversity and the biosphere. *Science* **276**:734–739.
- Park, H., and W. H. Schlesinger. 2002. The global biogeochemical cycle of boron. *Global Biogeochemical Cycles* **16**:DOI.10.1029/2001GB001766.
- Pearson, P. N., and M. R. Palmer. 2000. Atmospheric carbon dioxide concentrations over the past 60 million years. *Nature* **406**:695–699.
- Peñuelas, J., and I. Filella. 2001. Herbaria century record of increasing eutrophication in Spanish terrestrial ecosystems. *Global Change Biology* **7**:427–433.
- Postel, S. L., G. C. Daily, and P. R. Ehrlich. 1996. Human appropriation of renewable fresh water. *Science* **271**:785–788.
- Price, M. V., and N. M. Waser. 2000. Responses of subalpine meadow vegetation to four years of experimental warming. *Ecological Applications* **10**:811–823.
- Redfield, A. C., B. H. Ketchum, and F. A. Richards. 1963. The influence of organisms on the composition of seawater. Pages 26–77 in M. N. Hill, editor. *The sea*. Volume 2. Wiley, New York, New York, USA.
- Reiners, W. A. 1986. Complementary models for ecosystems. *American Naturalist* **127**:59–73.
- Schlesinger, W. H. 1997. *Biogeochemistry: an analysis of global change*. Academic Press, San Diego, California, USA.
- Schlesinger, W. H. 2000. Carbon sequestration in soils: some cautions amidst optimism. *Agriculture, Ecosystems and Environment* **82**:121–127.
- Schlesinger, W. H., and A. E. Hartley. 1992. A global budget for atmospheric NH₃. *Biogeochemistry* **15**:191–211.
- Shaw, M. R., and J. Harte. 2001. Response of nitrogen cycling to simulated climate change: differential responses along a subalpine ecotone. *Global Change Biology* **7**:193–210.
- Sterner, R. W., and J. J. Elser. 2002. *Ecological stoichiometry: the biology of elements from molecules to the biosphere*. Princeton University Press, Princeton, New Jersey, USA.
- Stock, J. B., A. M. Stock, and J. M. Mottonen. 1990. Signal transduction in bacteria. *Nature* **344**:395–400.
- Tilman, D., J. Fargione, B. Wolff, C. D'Antonio, A. Dobson, R. Howarth, D. Schindler, W. H. Schlesinger, D. Simberloff, and D. Swackhamer. 2001. Forecasting agriculturally driven global environmental change. *Science* **292**:281–284.
- Tilman, D., D. Wedin, and J. Knops. 1996. Productivity and sustainability influenced by biodiversity in grassland ecosystems. *Nature* **379**:718–720.
- Torn, M. S., A. G. Lapenis, A. Timofeev, M. L. Fischer, B. V. Babikov, and J. W. Harden. 2002. Organic carbon and

- carbon isotopes in modern and 100-year old archives of the Russian steppe. *Global Change Biology* **8**:941–953.
- Vörösmarty, C. J., P. Green, J. Salisbury, and R. B. Lammers. 2000. Global water resources: vulnerability from climate change and population growth. *Science* **289**:284–288.
- Waggoner, P. E. 1996. How much land can ten billion people spare for nature? *Daedalus* **125**:73–93.
- Wedin, D. A., and D. Tilman. 1996. Influence of nitrogen loading and species composition on the carbon balance of grasslands. *Science* **274**:1720–1723.