6. J. Kochi, *ibid.*, p. 1958.
7. C. Walling and A. A. Zavitsas, *ibid.*, p. 2084.
8. J. Kochi and R. Subramanian, *ibid.*, **87**, 4855 (1965).
9. J. Kerr and A. Trotman-Dickenson, *Progr. Reaction Kinetics* **1**, 107 (1961).
10. E. Collinson, F. Dainton, B. Mile, S. Tazuke, D. Smith, *Nature* **198**, 26 (1963); *Discussions Faraday Soc.* **29**, 188 (1960).
11. G. Olah, *Chem. Soc. London Spec. Pub.* **19**, 21 (1965).
12. F. Lossing, J. deSousa, R. Pottie, R. Taubert, *J. Amer. Chem. Soc.* **81**, 281 (1959); *ibid.* **83**, 4737 (1961); *ibid.* **84**, 1521 (1962). The values for oxidation-reduction potentials can be influenced greatly by solvent. Unfortunately, these values are known well only in aqueous solutions. Estimates in nonaqueous solvents are qualitatively correct.
13. J. Halpern, R. Legare, R. Lumry, *ibid.* **85**, 680 (1964); P. Hurwitz and K. Kustin, *Inorg. Chem.* **3**, 823 (1964).
14. R. Marcus, *Trans. Faraday Soc.* **56**, 21 (1960), and earlier papers.
15. H. McConnell and H. Weaver, *J. Chem. Phys.* **25**, 307 (1956).
16. J. Bjerrum, *Kem. Maanelsblad* **26**, 24 (1945).
17. S. Manahan and R. Iwamoto, *Inorg. Chem.* **4**, 1409 (1965).
18. J. Kochi and R. Subramanian, *ibid.*, p. 1527.
19. J. Kochi, *J. Amer. Chem. Soc.* **84**, 2795 (1962); C. Walling and W. Thaler, *ibid.* **83**, 3871 (1961).
20. J. Kochi and D. Mog, *ibid.* **87**, 522 (1965).
21. J. Kochi, *ibid.* **84**, 774 (1962); *ibid.*, p. 3271.
22. H. Taube, *Chem. Rev.* **50**, 69 (1952).
23. J. Kochi and D. Davis, *J. Amer. Chem. Soc.* **86**, 5264 (1964).
24. M. Szwarc, C. Leigh, A. Sehon, *Proc. Roy. Soc. London Ser. A* **209**, 97 (1951).
25. A. Streitwieser and C. Perrin, *J. Amer. Chem. Soc.* **86**, 4938 (1964).
26. R. Gilliom and B. Ward, *ibid.* **87**, 3944 (1965).
27. J. Kochi and D. Davis, *Nature* **202**, 690 (1964).
28. H. Taube and A. Ogard, *J. Amer. Chem. Soc.* **80**, 1084 (1958); "Mechanism of Inorganic Reactions," *Amer. Chem. Soc. Pub. No. 49* (1965).
29. W. Kray and C. Castro, *J. Amer. Chem. Soc.* **86**, 4603 (1964).
30. C. Castro, private communication.
31. L. Menapace and H. Kuivila, *J. Amer. Chem. Soc.* **86**, 3047 (1964); *ibid.* **88**, 571 (1966).
32. D. Benson, P. Proll, L. Sutcliffe, J. Walkley, *Discussions Faraday Soc.* **29**, 60 (1960); *Trans. Faraday Soc.* **56**, 246 (1960).
33. J. Kochi, *J. Amer. Chem. Soc.* **87**, 3609 (1965).
34. ———, *J. Org. Chem.* **30**, 3265 (1965).
35. W. Lundberg, *Autoxidation and Antioxidants* (Interscience, New York, 1962); Y. Kamiya and K. Ingold, *Can. J. Chem.* **41**, 2020 (1963), and later papers.
36. L. Boguslavskaya, *Russ. Chem. Rev. (English Transl.)* **34**, 503 (1965).
37. F. Minisci and R. Galli, *Tetrahedron Letters* **1963**, 357 (1963).
38. J. Kochi and H. Mains, *J. Org. Chem.* **30**, 1862 (1965).
39. M. Asscher and D. Vofsi, *J. Chem. Soc.* **1963**, 1887 (1963); *ibid.*, p. 3921.
40. S. Dickerman, K. Weiss, A. Ingberman, *J. Amer. Chem. Soc.* **80**, 1904 (1959); J. Kochi, *ibid.* **79**, 2942 (1958).
41. W. Brackman and E. Havinga, *Rec. Trav. Chim.* **74**, 937 (1955); *ibid.* **84**, 579 (1965); and later papers.
42. Support from the National Science Foundation is gratefully acknowledged.

Nutrient Cycling

Small watersheds can provide invaluable information about terrestrial ecosystems.

F. H. Bormann and G. E. Likens

Life on our planet is dependent upon the cycle of elements in the biosphere. Atmospheric carbon dioxide would be exhausted in a year or so by green plants were not the atmosphere continually recharged by CO_2 generated by respiration and fire (*1*). Also, it is well known that life requires a constant cycling of nitrogen, oxygen, and water. These cycles include a gaseous phase and have self-regulating feedback mechanisms that make them relatively perfect (*2*). Any increase in movement along one path is quickly compensated for by adjustments along other paths. Recently, however, concern has been expressed over the possible disruption of the carbon cycle by the burning of fossil fuel (*3*) and of the nitrogen cycle by the thoughtless introduction of pesticides and other substances into the biosphere (*4*).

Of no less importance to life are the elements with sedimentary cycles, such as phosphorus, calcium, and magnesium. With these cycles, there is a continual loss from biological systems in response to erosion, with ultimate deposition in the sea. Replacement or return of an element with a sedimentary cycle to terrestrial biological systems is dependent upon such processes as weathering of rocks, additions from volcanic gases, or the biological movement from the sea to the land. Sedimentary cycles are less perfect and more easily disrupted by man than carbon and nitrogen cycles (*2*). Acceleration of losses or, more specifically, the disruption of local cycling patterns by the activities of man could reduce existing "pools" of an element in local ecosystems, restrict productivity, and consequently limit human population. For example, many agriculturalists, food scientists, and ecologists believe that man is accelerating losses of phosphorus and that this element will be a critical limiting resource for the functioning of the biosphere (*1, 5*).

Recognition of the importance of these biogeochemical processes to the welfare of mankind has generated intensive study of such cycles. Among ecologists and foresters working with natural terrestrial ecosystems, this interest has focused on those aspects of biogeochemical cycles that occur *within* particular ecosystems. Thus, information on the distribution of chemical elements and on rates of uptake, retention, and release in various ecosystems has been accumulating (*6*). Little has been done to establish the role that weathering and erosion play in these systems.

Yet, the rate of release of nutrients from minerals by weathering, the addition of nutrients by erosion, and the loss of nutrients by erosion are three primary determinants of structure and function in terrestrial ecosystems. Further, with this information it is possible to develop total chemical budgets for ecosystems and to relate these data to the larger biogeochemical cycles.

It is largely because of the complex natural interaction of the hydrologic cycle and nutrient cycles that it has not been possible to establish these relationships. In many ecosystems this interaction almost hopelessly complicates the measurement of weathering or erosion. Under certain conditions, however, these apparent hindrances can be turned to good advantage in an integrated study of biogeochemical cycling in small watershed ecosystems.

It is the function of this article (i) to develop the idea that small watersheds can be used to measure weathering and erosion, (ii) to describe the parameters of watersheds particularly suited for this type of study, and (iii) to discuss the types of nutrient-cycling problems that this model renders susceptible to attack. Finally (iv), the argument is developed that the watershed ecosystem provides an ideal setting for studies of ecosystem dynamics in general.

Dr. Bormann is professof of forest ecology, Yale School of Forestry, Yale University, New Haven, Connecticut; Dr. Likens is associate professor, department of biological sciences, Dartmouth College, Hanover, New Hampshire.

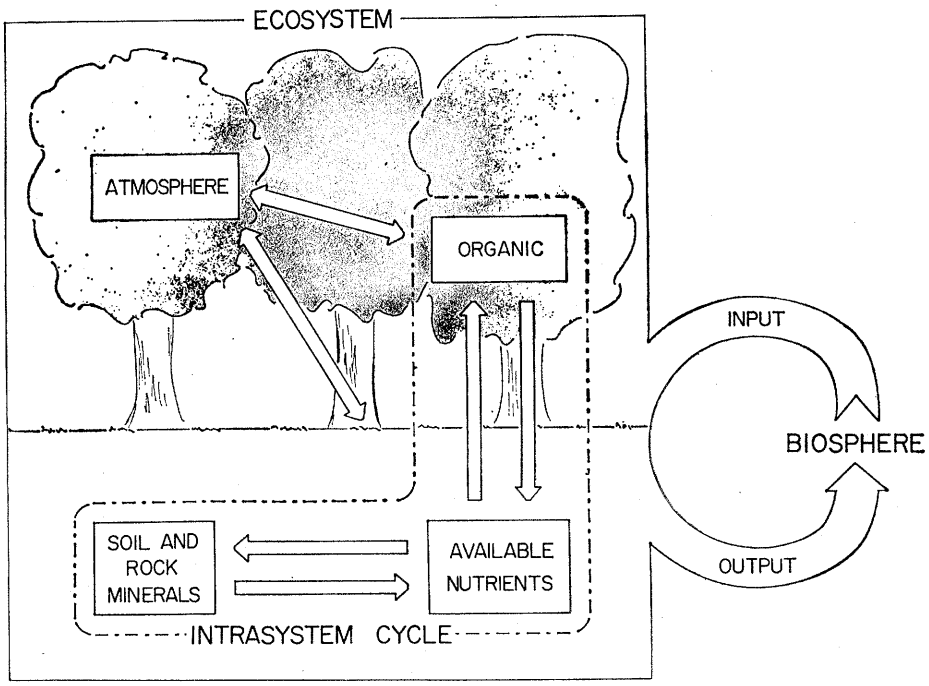

Fig. 1. Nutrient relationships of a terrestrial ecosystem, showing sites of accumulation and major pathways. Input and output may be composed of geologic, meteorologic, and biologic components, as described in the text.

Ecosystem Defined

Communities such as fields and forests may be considered as ecological systems (*7*) in which living organisms and their physical and biological environments constitute a single interacting unit. These ecosystems occupy an arbitrarily defined volume of the biosphere at the earth-atmosphere interface.

Lateral boundaries of an ecosystem may be chosen to coincide with those of a biological community, such as the edges of a forest, or with the boundary of some pronounced characteristic of the physical environment, such as the shoreline of a small island. Most often, however, the continuous nature of vegetation and of the physical environment makes it difficult to establish exact lateral boundaries on the basis of "community" or "environmental discontinuity" (*8*). Often the investigator arbitrarily selects an area that may be conveniently studied.

From a functional point of view it is meaningless to include within the vertical limits of an ecosystem *all* of the column of air above and of soil and rock below the laterally defined ecosystem. For a working model of an ecosystem, it seems reasonable to include *only* that part of the column where atoms and molecules may participate in the chemical cycling that occurs within the system (see the "intrasystem cycle" of Fig. 1). When the biological community is taken as a determinant, the vertical extensions of the terrestrial ecosystem will be delimited by the top of the vegetation and the depth to which roots and other organisms penetrate into the regolith (*9*). Vertical dimensions, defined in this manner, can expand or contract depending on the growth potential of present or succeeding communities. Thus, volumetric changes with time can be considered—for example, those associated with primary and secondary succession or with cliseral changes.

The Ecosystem and Biogeochemical Cycling

The terrestrial ecosystem participates in the various larger biogeochemical cycles of the earth through a system of inputs and outputs. Biogeochemical input in forest or field ecosystems may be derived from three major sources: geologic, meteorologic, and biologic. Geologic input is here defined as dissolved or particulate matter carried into the system by moving water or colluvial action, or both. Depositions of the products of erosion or mass wasting and ions dissolved in incoming seepage water are examples of geologic input. Meteorologic input enters the ecosystem through the atmosphere and is composed of additions of gaseous materials and of dissolved or particulate matter in precipitation, dust, and other wind-borne materials. Chemicals in gaseous form fixed by biologic activity within the ecosystem are considered to be meteorologic input. Biological input results from animal activity and is made up of depositions of materials originally gathered elsewhere; examples are fecal material of animals whose food was gathered outside the system, or fertilizers intentionally added by man.

Chemicals may leave the ecosystem in the form of dissolved or particulate matter in moving water or colluvium, or both (geologic output); through the diffusion or transport of gases or particulate matter by wind (meteorologic output); or as a result of the activity of animals, including man (biologic output).

Nutrients are found in four compartments within the terrestrial ecosystem: in the atmosphere, in the pool of available nutrients in the soil, in organic materials (biota and organic debris), and in soil and rock minerals (Fig. 1). The atmospheric compartment includes all atoms or molecules in gaseous form in both the below-ground and the above-ground portions of the ecosystem. The pool of available nutrients in the soil consists of all ions adsorbed on the clay-humus complex or dissolved in the soil solution. The organic compartment includes all atoms incorporated in living organisms and in their dead remains. (The distinction between living and dead is sometimes hard to make, particularly in the case of woody perennial plants.) The soil-rock compartment is comprised of elements incorporated in primary and secondary minerals, including the more readily decomposable minerals that enter into equilibrium reactions with the available nutrients.

The degree to which a nutrient circulates within a terrestrial ecosystem is determined, in part, by its physical state. Gases are easily moved by random forces of diffusion and air circulation; consequently, nutrients with a prominent gaseous phase tend not to cycle within the boundaries of a particular ecosystem but, rather, to be continually lost and replaced from outside. On the other hand, elements without a prominent gaseous phase may show considerable intrasystem cycling between the available-nutrient, organic, and soil-rock compartments (Fig. 1). This internal cycle results from (i) the uptake of nutrients by plants, (ii) the release of nutrients from plants by direct leaching, (iii) the release of nutrients from organic matter by biological decomposition, and (iv) equilibrium reactions that convert insoluble chemical forms in the soil-rock compartment to soluble forms in the available-nutrient compartment, and vice versa.

Available nutrients not only enter the ecosystem from outside but are added by the action of physical, chemical, and biological weathering of rock and soil minerals already within the system. Although some ions are continually withdrawn from the available-nutrient compartment, forming secondary minerals in the soil and rocks, for most nutrient elements there is a net movement out of the soil-rock compartment. As the ecosystem is gradually lowered in place by erosion or by the downward growth of roots, new supplies of residual rock or other parent material are included; in some systems these materials may also be added as geologic input.

Hydrologic-Cycle, Nutrient-Cycle Interaction

At many points, nutrient cycles may be strongly geared to the hydrologic cycle. Nutrient input and output are directly related to the amounts of water that move into and out of an ecosystem, as emphasized by the "leaching" and "flushing" concepts of Pearsall (*10*), Dahl (*11*), and Ratcliffe (*12*), while temporal and absolute limits of biogeochemical activities within the system are markedly influenced by the hydrologic regime. Biologic uptake of nutrients by plants and release of nutrients by biological decomposition are closely related to the pattern of water availability. Potential levels of biomass within the system are determined in large measure by precipitation characteristics. Similarly, the nature and rate of weathering and soil formation are influenced by the hydrologic regime, since water is essential to the major chemical weathering processes [ion exchange, hydrolysis, solution, diffusion, oxidation-reduction, and adsorption and swelling (*13*)].

Biogeochemical Studies of Ecosystems

Although study of nutrient input, nutrient output, and weathering is necessary for an understanding of field and forest ecosystems (*6*), ecologists, foresters, and pedologists have generally focused attention on the internal characteristics alone. Thus, considerable information has been accumulated on uptake, retention, and release of nutrients by the biota of ecosystems, and on soil-nutrient relationships (see, for example, *6, 14*). Rarely are these internal characteristics of the ecosystem correlated with input and output data, yet all these parameters are necessary for the construction of nutrient budgets of particular ecosystems, and for establishing the relationship of the smaller system to the biosphere.

Quantitative data on input-output relationships are at best spotty. There are many data on nutrient output due to harvesting of vegetation, but for particular natural ecosystems there are only sporadic data on nutrient input in precipitation, or on nutrient output in drainage waters (*6*). Recently, small lysimeters have been used successfully in the measurement of nutrient dynamics within the soil profile and in the measurement of nutrient losses in drainage water (*15*). The lysimeter technique seems to be well suited for studying ecosystems characterized by coarse-textured soils with a relatively low field capacity (*16*), high porosity, and no surface runoff. For most ecosystems, however, lysimeters are probably of limited value for measuring *total* nutrient output because (i) they are of questionable accuracy when used in rocky or markedly uneven ground, (ii) they cannot evaluate nutrient losses in surface waters, and (iii) their installation requires considerable disturbance of the soil profile.

The lack of information on the nutrient-input, nutrient-output relationships of ecosystems is apparently related to two considerations: (i) integrated studies of ecosystems tend to fall into an intellectual "no man's land" between traditional concepts of ecology, geology, and pedology; (ii) more important, the measurement of nutrient input and output requires measurement of hydrologic input and output. Unquestionably this lack of quantitative information is related to the difficulties encountered in measuring nutrients entering or leaving an ecosystem in seepage water or in sheet or rill flow, and to the high cost, in time and money, of obtaining continuous measurements of the more conventional hydrologic parameters of precipitation and stream flow. In many systems the problem is further complicated by the fact that much water may leave by way of deep seepage, eventually appearing in another drainage system; direct measurement of loss of water and nutrients by this route is virtually impossible.

Small-Watershed Approach to Biogeochemical Cycling

In some ecosystems the nutrient-cycle, hydrologic-cycle interaction can be turned to good advantage in the study of nutrient budgets, erosion, and weathering. This is particularly so if an ecosystem meets two specifications: (i) if the ecosystem is a watershed, and (ii) if the watershed is underlain by a tight bedrock or other impermeable base, such as permafrost. Given these conditions, for chemical elements without a gaseous form at biological temperatures, it is possible to construct nutrient budgets showing input, output, and net loss or gain from the system. These data provide estimates of weathering and erosion.

If the ecosystem were a small watershed, input would be limited to meteorologic and biologic origins. Geologic input, as defined above, need not be considered because there would be no transfer of alluvial or colluvial material between adjacent watersheds. Although materials might be moved within the ecosystem by alluvial or colluvial forces, these materials would originate within the ecosystem.

When the input and output of dust or windblown materials is negligible (this is certainly not the case in some systems), meteorologic input can be measured from a combination of hydrologic and precipitation-chemistry parameters. From periodic measurements of the elements contained in precipitation and from continuous measurements of precipitation entering a watershed of known area, one may calculate the temporal input of an element in terms of grams per hectare. Noncoincidence of the topographic divide of the watershed and the phreatic divide may introduce a small error (*17*).

Losses from this watershed ecosystem would be limited to geologic and biologic output. Given an impermeable base, geologic output (losses due to erosion) would consist of dissolved and particulate matter in either stream water or seepage water moving downhill above the impermeable base. Although downhill mass movement may occur within the system, the products of this movement are delivered to the stream bed, whence they are removed by erosion and stream transportation.

Geologic output can be estimated from hydrologic and chemical measurements. A weir, anchored to the bedrock (Fig. 2), will force all drainage water from the watershed to flow over the notch, where the volume and rate of flow can be measured. These data, in combination with periodic measures of dissolved and particulate matter in the outflowing water, provide an estimate of geologic output which may be expressed as grams of an element lost per hectare of watershed.

The nutrient budget for a single element in the watershed ecosystem may be expressed as follows: (meteorologic input + biologic input) − (geologic output + biologic output) = net loss or gain. This equation may be further simplified if the ecosystem meets a third specification—if it is part of a much larger, more or less homogeneous, vegetation unit. Biological output would tend to balance biological input if the ecosystem contained no special attraction or deterrent for animal populations moving at random through the larger vegetation system, randomly acquiring or discharging nutrients. On this assumption, the nutrient budget for a single system would become: (meteorologic input per hectare) − (geologic output per hectare) = net gain or loss per hectare. This fundamental relationship provides basic data for an integrated study of ecosystem dynamics.

Small Watersheds for Ecosystem Research

The relationship of the individual terrestrial ecosystem to biogeochemical cycles of the biosphere can be established by the small-watershed approach. Data on input and output of nutrients provide direct measurements of this relationship, while data on net loss provide, as explained below, an indirect measure of weathering rates for soil and rock minerals in relatively undisturbed ecosystems.

The small watershed may be used for experiments at the ecosystem level. This has been shown by numerous experiments concerned with hydrologic relationships (see, for example, *18*). Thus, it is possible to test the effects of various experimental treatments on the relationship of the individual ecosystem to the biospheric nutrient cycles. Experiments can be designed to determine whether logging, burning, or use of pesticides or herbicides have an appreciable effect on net nutrient losses from the system. This information is not generally available at the ecosystem level.

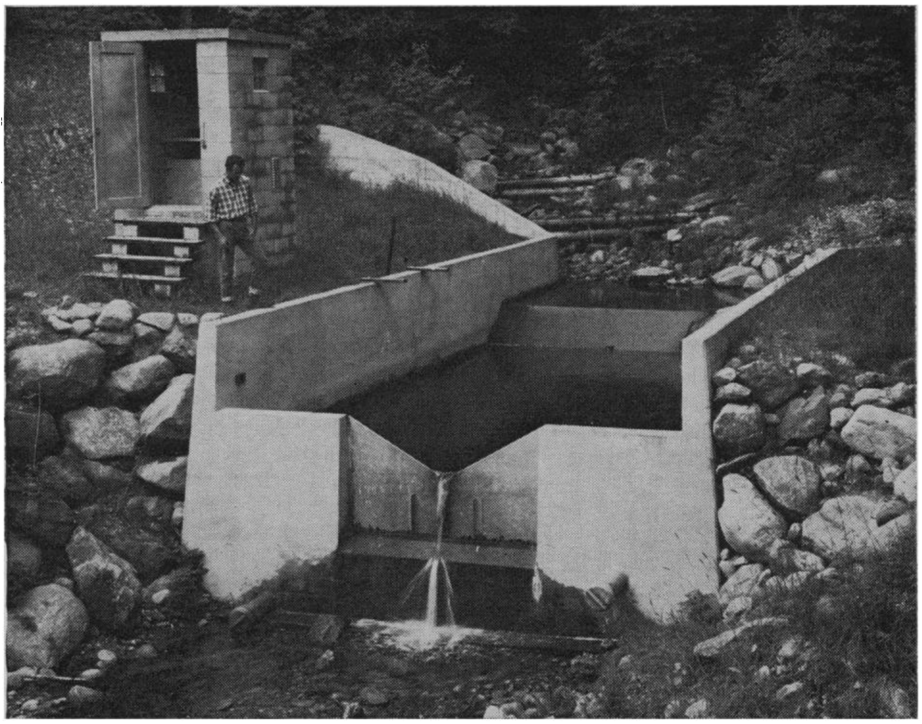

Fig. 2. A weir showing the v-notch, recording house, and ponding basin. [Courtesy of the Northeastern Forest Experiment Station]

The small watershed, with its measured parameters of hydrologic and chemical input, output, and net change, is an excellent vehicle for the study of interrelationships within a single ecosystem. Nutrient output may be related to hydrologic parameters such as seasonal and diurnal variations in stream flow, seasonal patterns of precipitation, individual rainstorms, and variations in evapotranspiration. Characteristics of the nutrient cycle may also be related to phenological events occurring within the ecosystem, such as leaf development, initiation of root growth, leaf fall, and litter turnover. In combination with current methods of biomass and nutrient analysis (see, for example, *6*), the small-watershed approach provides a comprehensive view of the status and behavior of individual elements within an individual ecosystem.

Weathering, or the rate at which an element bound in soil and rock minerals is made available, can be estimated from net losses of that element as calculated by the nutrient-budget method. Within the ecosystem (watershed), atoms of an element (one that lacks a gaseous form at ecosystem temperatures) may be located in (i) soil and rock minerals, (ii) the biota and organic debris, and (iii) the pool of available nutrients (Fig. 1). There is an intense intrasystem cycling between categories (ii) and (iii) as large quantities of ions are taken up by the vegetation each year and released by direct leaching or stepwise decomposition in the food chain. Ions are continually released to the intrasystem cycle by weathering of soil and rock material. Some of these ions, however, are reconstituted as secondary minerals. If an ecosystem is in a state of dynamic equilibrium, as the presence of climax forest would suggest (*19*), ionic levels in the intrasystem cycle must remain about the same for many years. Thus, in the climax ecosystem, net ion losses (output minus input) must be balanced by equivalent additions derived from weathering of soil and rock materials. Thus, net ionic losses from an undisturbed, relatively stable terrestrial ecosystem are a measure of weathering within the system. In a successional ecosystem (in which nutrients are accumulating in biomass and organic debris over the course of years), the rate at which an ion is released by weathering must equal its rate of net loss from the ecosystem plus its rate of net accumulation in the biota and organic debris (Fig. 1).

The watershed model allows comparison in relative importance of solution and suspended bed load in removing nutrients from an ecosystem.

Table 1. Budgets for dissolved cations in watershed No. 3 (42.4 hectares) for the period June 1963 to June 1964.

Cation	Input (kg/hectare)	Output (kg/hectare)	Net change (kg/hectare)
Calcium	3.0	7.7	−4.7
Sodium	1.0	6.3	−5.3
Magnesium	0.7	2.5	−1.8

Nutrient matter can be removed from an ecosystem by three forms of transportation in streams: in solution in the stream water, as inorganic and organic suspended load kept in motion by turbulent flow, and as inorganic and organic bed load slid or rolled along the stream bottom (*20*). Solution losses may be measured, as described above, from stream-flow data and periodic measurements of dissolved substances in the stream. Part of the losses of suspended matter may be estimated from stream-flow data and periodic measurements of particulate matter obtained by straining or filtering stream water as it comes over the weir. The remaining suspended matter and all of the bed load may be measured above the weir, where these materials collect in the ponding basin (Fig. 2). These comparative measurements should be of interest not only to the ecologist concerned with ecosystem dynamics but also, since stream transportation is one of the important aspects of fluvial denudation, to geologists.

The small-watershed approach provides invaluable baseline information for the investigation of stream biology. Life-history studies of stream organisms, population studies, and shifts in community structure and diversity might be correlated with the measured physical and chemical parameters of drainage streams. Analyses of uptake, release, and transport of various nutrients by stream organisms could be made. Moreover, the vegetation of a watershed and the stream draining it are an inseparable unit functionally, and it would be of great interest to obtain information on the biological interaction between them.

Sites for Watershed Studies

Small watersheds meeting the conditions outlined above are probably common. However, even if the desired conditions are met, the investigator studying nutrient cycling is faced with the task of initiating a hydrologic study before he can attack his major problem. This is a time-consuming and expensive procedure, involving construction and maintenance of weirs, establishment of a precipitation network, and continuous collection of records, as well as land rental fees and possible road construction costs. A practical solution to this problem is inauguration of nutrient cycling studies at established hydrologic laboratories, where the required conditions exist and where hydrologic parameters are being measured and data are available.

The feasibility of this approach is demonstrated by our study at the Hubbard Brook Experimental Forest in West Thornton, New Hampshire. There, with the support of the National Science Foundation and the excellent cooperation of the Northeastern Forest Experiment Station, we are studying nutrient cycling and ecosystem dynamics on six small monitored watersheds. We have accumulated data on weathering rates, input, output, and the annual budget of several ions in this northern hardwood ecosystem. Also, studies of biomass, phenology, productivity, annual rates of nutrient turnover, and other factors are being made in one undisturbed watershed and in one in which conditions are being experimentally modified.

Preliminary data on input, output, and net change for three cations are presented in Table 1. These results allow us to add some numerical values to our ecosystem model (Fig. 3). For the calcium cycle, for example, input would be about 3 kilograms per hectare, while output (erosion) is estimated to be about 7.9 kilograms per hectare. Of this latter amount, 98 percent (7.7 kilograms per hectare) is lost in the form of dissolved substances in the stream water, while first approximations indicate that 2 percent is lost as calcium incorporated in organic matter flushed out of the ecosystem. On the basis of assumptions discussed above, it is estimated that the net amount of calcium lost, approximately 5 kilograms per hectare, is replaced by calcium released from soil and rock minerals by weathering. Hence 5 kilograms of calcium per hectare is added to the system each year by weathering.

As yet we have not measured the calcium content of the soil and vegetation or the annual uptake and release of calcium by the biota. From Ovington's data (*6*), for a beech forest in West England, which must be of about the same magnitude as values for our forest in New Hampshire, we see that 203 kilograms of calcium per hectare are localized in the trees and litter, while 365 kilograms per hectare represent exchangeable calcium in the soil. This gives a total of 568 kilograms of calcium per hectare in organic matter or as available nutrient. Assuming that our forest (Fig. 3) contains a similar amount of calcium, we estimate that a net annual loss of 5 kilograms

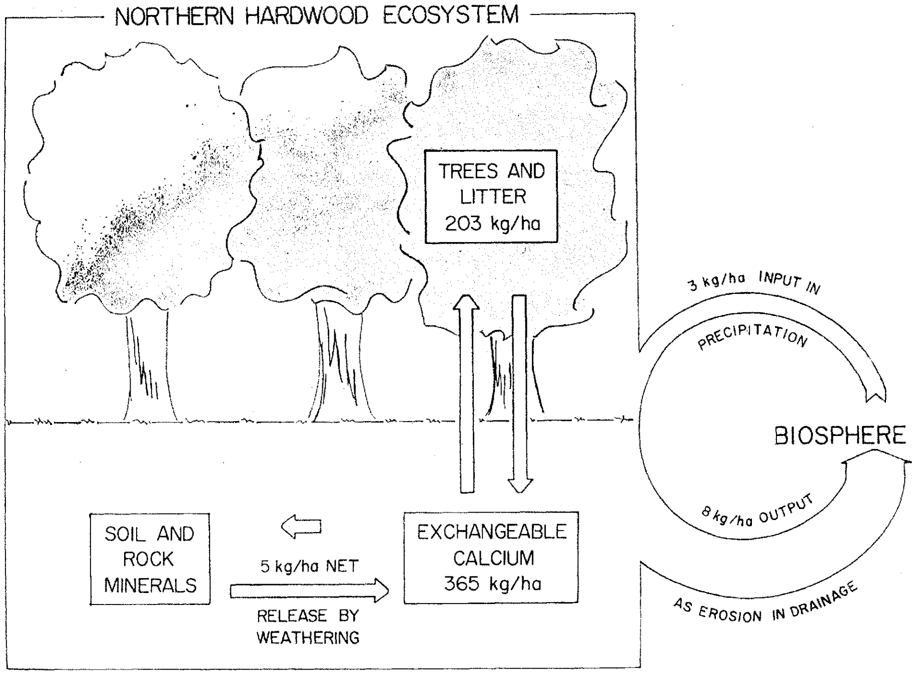

Fig. 3. Estimated parameters for the calcium cycle in an undisturbed northern hardwood ecosystem in central New Hampshire. [Data on trees, litter, and exchangeable calcium from Ovington (*6*)]

per hectare would represent only nine-tenths of 1 percent of the total. This suggests a remarkable ability of these undisturbed systems to entrap and hold nutrients. However, if these calculations were based on actual amounts of calcium circulated each year rather than on the total, the percentage losses would be higher.

On its completion, the Hubbard Brook study will have yielded estimates, for individual elements, of many of the parameters and flux rates represented in the nutrient cycle shown in Fig. 1. These data will increase our understanding of fundamental nutrient relationships of undisturbed northern hardwood forests, and they will provide baseline information from which we can judge the effects on nutrient cycling of such practices as cutting, burning, and the application of pesticides.

Studies similar to these at Hubbard Brook could be established elsewhere in the United States. There are thousands of gaged watersheds operated by private and public interests (*17*), and some of these must meet the proposed requirements. On selected watersheds, cooperative studies could be made by the agencies or organizations controlling the watershed and university-based investigators interested in biogeochemical cycling. Just such cooperation, between federal agencies and universities, has been urged by the Task Group on Coordinated Water Resources Research (*21*).

Cooperative studies of this type have the advantage of providing a useful exchange of ideas between scientists in diverse fields who are working on the same ecosystem. The studies would provide a larger yield of information on a single system, the prospect of new concepts arising from the available information, and a greater scientific yield per dollar invested. Finally, cooperative studies would make available, for interpretation from the standpoint of nutrient cycling, an invaluable record of past hydrologic performance and, in some cases, of the responses of watersheds to experimental manipulation.

Conclusion

The small-watershed approach to problems of nutrient cycling has these advantages. (i) The small watershed is a natural unit of suitable size for intensive study of nutrient cycling at the ecosystem level. (ii) It provides a means of reducing to a minimum, or virtually eliminating, the effect of the difficult-to-measure variables of geologic input and nutrient losses in deep seepage. Control of these variables makes possible accurate measurement of nutrient input and output (erosion) and therefore establishes the relationship of the smaller ecosystem to the larger biospheric cycles. (iii) The small-watershed approach provides a method whereby such important parameters as nutrient release from minerals (weathering) and annual nutrient budgets may be calculated. (iv) It provides a means of studying the interrelationships between the biota and the hydrologic cycle, various nutrient cycles, and energy flow in a single system. (v) Finally, with the small-watershed system we can test the effect of various land-management practices or environmental pollutants on nutrient cycling in natural systems.

References and Notes

1. L. C. Cole, *Sci. Amer.* **198**, 83 (Apr. 1958).
2. E. P. Odum, *Ecology* (Holt, Rinehart, and Winston, New York, 1963).
3. R. Revelle, W. Broecker, H. Craig, C. D. Keeling, J. Smagorinsky, in *Restoring the Quality of Our Environment* (Government Printing Office, Washington, D.C., 1965), pp. 111–133.
4. L. C. Cole, *Saturday Rev.* (7 May 1966).
5. E. P. Odum, *Fundamentals of Ecology* (Saunders, Philadelphia, 1959).
6. J. D. Ovington, in *Advances in Ecological Research*, J. B. Cragg, Ed. (Academic Press, New York, 1962), vol. 1.
7. A. G. Tansley, *Ecology* **16**, 284 (1935).
8. L. B. Slobodkin, *Growth and Regulation of Animal Populations* (Holt, Rinehart, and Winston, New York, 1961).
9. H. O. Buckman and N. C. Brady, *The Nature and Properties of Soils* (Macmillan, New York, 1960).
10. W. H. Pearsall, *Mountains and Moorlands* (Collins, London, 1950).
11. E. Dahl, "Rondane. Mountain vegetation in South Norway and its relation to the environment," *Skrifter Norske Videnskaps-Akad. Oslo I, Mat. Naturv. Kl. 1956* (1956).
12. D. A. Ratcliffe, *J. Ecol.* **47**, 371 (1959).
13. C. Bould, in *Plant Physiology, A Treatise*, F. C. Steward, Ed. (Academic Press, New York, 1963), vol. 3.
14. J. R. Bray and E. Gorham, in *Advances in Ecological Research*, J. B. Cragg, Ed. (Academic Press, New York, 1964), vol. 2; K. J. Mustanoja and A. L. Leaf, *Botan. Rev.* **31**, 151 (1965).
15. D. W. Cole and S. P. Gessel, *Soil Sci. Soc. Amer. Proc.* **25**, 321 (1961); ———, in *Forest-Soil Relationships in North America*, C. T. Youngberg, Ed. (Oregon State Univ. Press, Corvallis, 1965).
16. D. W. Cole, *Soil Sci.* **85**, 293 (1958).
17. C. O. Wisler and E. F. Brater, *Hydrology* (Wiley, New York, 1959).
18. R. E. Dils, *A Guide to the Coweeta Hydrologic Laboratory* (Southeastern Forest Experimental Station, Asheville, N.C., 1957).

→ R. H. Whittaker, *Ecol. Monographs* **23**, 41 (1953).

20. A. N. Strahler, *The Earth Sciences* (Harper and Row, New York, 1963).
21. R. Revelle, *Science* **142**, 1027 (1963).
22. Financial support was provided by National Science Foundation grants GB 1144 and GB 4169. We thank J. Cantlon, N. M. Johnson, R. C. Reynolds, R. H. Whittaker, and G. W. Woodwell for critical comments and suggestions during preparation of the manuscript.

Where Is Biology Taking Us?

Robert S. Morison

Others in this symposium (*1*) have described the expected improvement in our knowledge of perception, cognition, and learning, and have shown how these improvements can be expected to facilitate the educational process. It remains for me to try to identify some of the long-term practical consequences of these trends, so that we can prepare ourselves to exploit the advantages and minimize the dangers which accompany any advance in knowledge or technique. As formal education improves in effectiveness, it seems natural to suppose that its public image will continue to be enhanced. We in the United States have always held institutionalized education in high respect and, second only to our Soviet friends, have looked to it to solve all manner of individual and social evils. As it becomes more and more capable of actually doing so, its prestige must necessarily continue to increase concomitantly. What, then, are the probable consequences of the increased prestige of institutionalized education? No doubt there will be a considerable number, but I should like to look particularly at its effect on more traditional ways of transmitting accumulated experience to a new generation and to lay before you my reasons for believing that, as public recognition of formal education continues to rise,

---

The author is director of the Division of Biological Sciences, Cornell University, Ithaca, New York. This article is adapted from a lecture presented in October 1966 at the California Institute of Technology, Pasadena, on the occasion of the Institute's 75th Anniversary Convocation.