moon, and they suggest that any convection inside the moon is most likely weak and cannot induce large stresses in the lunar lithosphere.

M. NAFI TOKSÖZ
NEAL R. GOINS, C. H. CHENG
Department of Earth and Planetary Sciences, Massachusetts Institute of Technology, Cambridge 02139

References and Notes

1. D. R. Lammlein, G. V. Latham, J. Dorman, Y. Nakamura, M. Ewing, *Rev. Geophys. Space Phys.* **12**, 1 (1974); G. Latham, M. Ewing, J. Dorman, D. Lammlein, F. Press, N. Toksöz, G. Sutton, F. Duennebier, Y. Nakamura, *Science* **174**, 687 (1971); Y. Nakamura, J. Dorman, F. Duennebier, M. Ewing, D. Lammlein, G. Latham, *Geochim. Cosmochim. Acta* **3** (Suppl. 5), 2883 (1974).
2. A. E. H. Love, *Some Problems of Geodynamics* (Dover, New York, 1967), p. 180; H. Takeuchi, *Trans. Am. Geophys. Union* **31**, 651 (1950); J. C. Harrison, *J. Geophys. Res.* **68**, 4269 (1963); W. M. Kaula, *ibid.*, p. 4959. The equation for Brown's theory can be found in the *Explanatory Supplement to the Astronomical Ephemeris and the American Ephemeris and Nautical Almanac* (Her Majesty's Stationery Office, London, 1961).
3. M. N. Toksöz *et al.*, *Rev. Geophys. Space Phys.* **12**, 539 (1974); A. M. Dainty, N. R. Goins, M. N. Toksöz, *Geochim. Cosmochim. Acta* **3** (Suppl. 6), 2887 (1975); A. M. Dainty and M. N. Toksöz, *Geochim. Cosmochim. Acta* (Suppl. 7), in press; Y. Nakamura, G. Latham, D. Lammlein, M. Ewing, F. Duennebier, J. Dorman, *Geophys. Res. Lett.* **1**, 137 (1974).
4. D. R. Lammlein, *Geochim. Cosmochim. Acta* (Suppl. 7), in press; R. Meissner, J. Voss, H. J. Kaestle, *Moon* **6**, 292 (1973).
5. T. H. Heaton, *Geophys. J. R. Astron. Soc.* **43**, 307 (1975); F. W. Klein, *ibid.* **45**, 245 (1976).
6. Moonquake catalogs used in this study were prepared at the University of Texas (Galveston) by Drs. G. Latham, J. Dorman, D. Lammlein, F. Duennebier, and Y. Nakamura. We thank Dr. Nakamura for many valuable suggestions at various stages of this work. This research was supported under NASA contract NAS9-12334 and grant NSG-7081.

23 August 1976; revised 23 November 1976

Nitrogen Budget for an Aggrading Northern Hardwood Forest Ecosystem

Abstract. *Long-term analyses of the structure and function of a northern hardwood ecosystem have resulted in measurement of the salient features of the nitrogen cycle. These data allow an evaluation of the importance of the various components and provide a framework for more efficient forest management.*

Nitrogen is one of the most important limiting nutrients for ecosystem production. Only now is it becoming apparent that our finite energy resources may serve as a limit for the widespread and often indiscriminate application of nitrogenous fertilizer, which was commonplace in the recent past. This realization has led to a more careful consideration of the nitrogen cycle in natural ecosystems, for it is apparent that before we can use natural sources of nitrogen more efficiently or learn how to add nitrogenous fertilizer more effectively, we must understand the nitrogen cycle in nature. Thus, the biogeochemistry of nitrogen is becoming one of the most intensively studied aspects of ecology.

Measurement of the nitrogen cycle is no small task. It requires sophisticated techniques, a well-designed model for identifying gaps, and years of careful and perceptive measurement. The data and deductions presented in this report represent the distillation of 13 years of work—literally thousands of chemical analyses of precipitation and stream water and of plant and animal tissue. For more than a decade, researchers at the Hubbard Brook Experimental Forest in the White Mountains of New Hampshire have been working to quantify the structure and function of various terrestrial and aquatic ecosystems and to determine the relationships between forested watershed ecosystems and the larger biogeochemical cycles of the earth (*1*).

A model was developed for these deciduous, northern hardwood ecosystems to facilitate the collection, analysis, and interpretation of diverse field data (*1*). Utilizing this model and the small watershed technique, it was possible to measure input and output of chemicals and water and to construct quantitative nutrient budgets for natural ecosystems. Six small drainage areas tributary to Hubbard Brook were the watershed ecosystems chosen for study (*1*). This report presents our current understanding of the nitrogen budget (Fig. 1) for one of these forested watershed ecosystems, watershed 6.

The forest on watershed 6 is about 55 years old and is dominated by sugar maple (*Acer saccharum* Marsh.), American beech (*Fagus grandifolia* Ehrh.), and yellow birch (*Betula alleghaniensis* Britt.) (*2*). The mean basal area of the forest is 24 m^2/ha, net primary production is 1040 g (dry weight) per square meter per year, and living and dead biomass accumulation is 393 g m^{-2} $year^{-1}$ (*3, 4*). The ecosystem is thus aggrading, with an annual net accumulation of biomass.

The area of watershed 6 is 13.2 ha. Climate is generally humid-continental with short, cool summers and long, cold winters. Precipitation averages about 130 cm/year and is distributed evenly throughout the year. A deep snowpack is characteristic of wintertime and soil frost is uncommon. Streamflow averages about 80 cm/year, with about 54 percent of the annual streamflow occurring during the months of March, April, and May as the snowpack melts. Bedrock and till are derived from the granitic Littleton and Kinsman formations. The thin, acidic soils are mostly well-drained podzols (haplorthods) with a thick (3 to 15 cm) organic layer at the surface. Detailed information on topography, geology, soils, hydrology, and climatic conditions have been reported elsewhere (*1, 5, 6*).

The pattern of nitrogen accumulation and transfer within the aggrading ecosystem (*7–14*) is of particular interest since it may be severely altered by disturbance (for example, clear-cutting). Understanding the pattern is thus vital to facilitating recovery processes after cutting. Several important features of the nitrogen cycle emerge from an analysis of the overall pattern (Fig. 1), and these are in general agreement with those reported for other deciduous forest ecosystems (*15, 16*).

1) Natural forested ecosystems tend to accumulate and cycle large amounts of nitrogen (*1, 6, 17*).

2) Some 68 percent of the nitrogen that is added to the ecosystem each year is from nitrogen fixation. Thirty-two percent is added in bulk precipitation, and little, if any, is added by weathering.

3) Of the estimated 20.7 kg/ha entering the system each year, about 81 percent is held or accreted within the ecosystem.

4) Of the 83.5 kg/ha added to the inorganic pool within the ecosystem, only a small fraction, 5 percent, leaks out of the system in streamflow.

5) Of the 119 kg of nitrogen estimated to be used in growth processes by plants, 33 percent is withdrawn from storage locations within the living plants in the spring and utilized in growth, and a like amount is withdrawn from the leaves and stored in more permanent tissues shortly before leaf senescence in the autumn.

6) Of the nitrogen accreted into long-term storage, some 54 percent is added to living biomass, while 46 percent is stored in organic matter of the forest floor.

7) Root exudation, for the first time quantitatively estimated for an entire ecosystem, releases about 1 percent of the inorganic nitrogen made available by net mineralization.

8) Most of the nitrogen in a northern hardwood forest ecosystem, approximately 90 percent, is in soil organic matter; about 0.5 percent exists as available

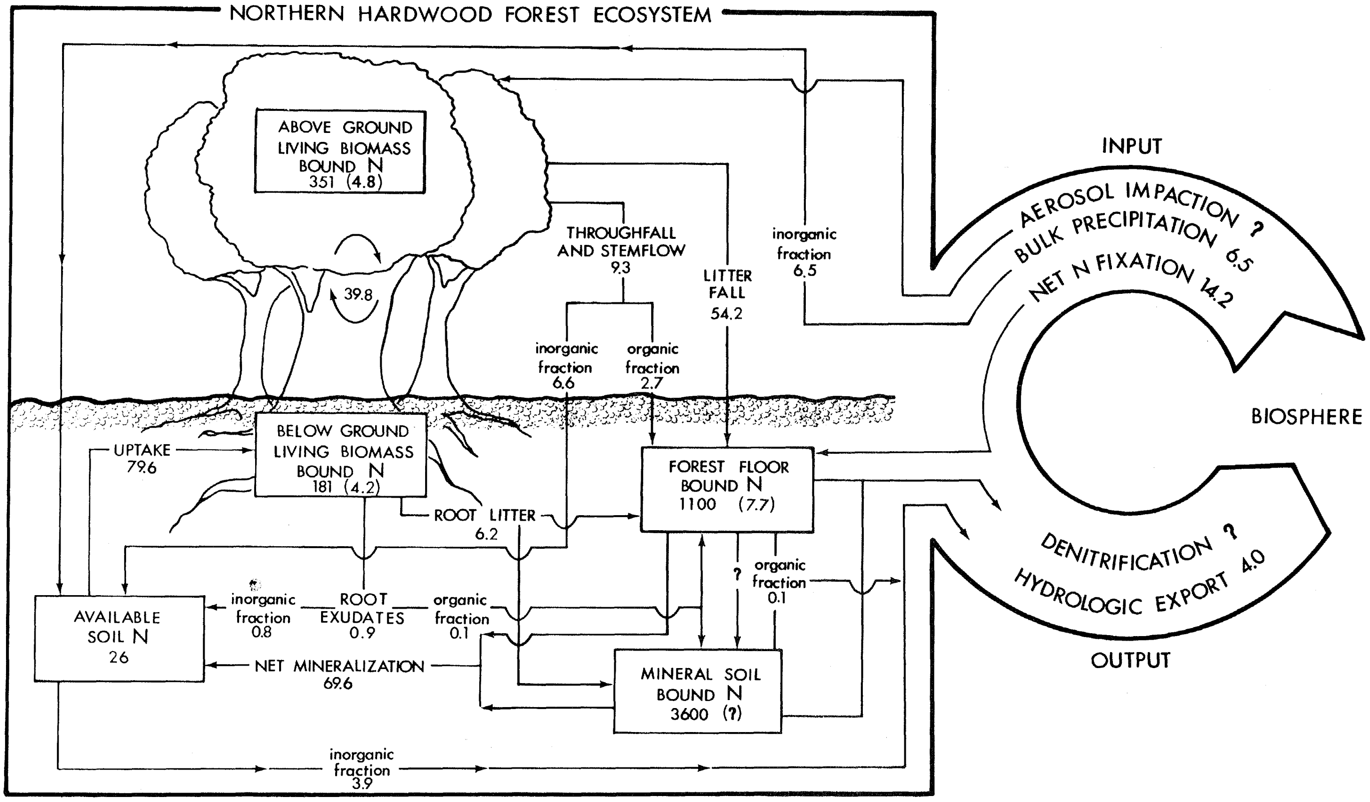

Fig. 1. Annual nitrogen budget for an undisturbed northern hardwood forest ecosystem at Hubbard Brook. The values in boxes are in kilograms of nitrogen per hectare. The rate of accretion of each pool (in parentheses) and all transfer rates are expressed in kilograms of nitrogen per hectare per year.

nitrogen in the soil; and the remaining nitrogen, approximately 9.5 percent, is in the vegetation.

These data support the view that retranslocation of nitrogen from tree leaves to woody tissue before leaf senescence is an important characteristic of nitrogen cycling in temperate ecosystems dominated by perennial plants (*16*, *18*). Retranslocation is apparently involved in maintaining a relatively mobile pool of nitrogen within the living biomass of the ecosystem. This internal source, not susceptible to loss from the ecosystem through streamflow, may provide the vegetation with a buffer against periodic short-term fluctuations in available soil nitrogen.

To balance the budget, we estimate 14.2 kg/ha of nitrogen fixation. This value is similar to that reported for a hardwood forest in North Carolina (*16*). Although we have detected no symbiotic nitrogen fixers, and the soil conditions (cool and acid) do not seem conducive to the free-living nitrogen fixers so familiar in agricultural systems, studies under way show nitrogen fixation by microorganisms associated with decaying wood (*19*).

When compared with other nitrogen budgets that we have developed for recently disturbed (experimentally cut and commercially cut) northern hardwood forest ecosystems (*17*), the nitrogen budget for our aggrading forest system is "tight." Further, the nitrogen budget supports the contention that both annual uptake by living vegetation and annual accretion of nitrogen in woody biomass play important roles in promoting tight nutrient cycling in northern hardwood forest ecosystems (*17*, *20*).

The applications of these results to problems of industrial forestry are potentially important and numerous. For example, replacement of nitrogen reserves after clear-cutting is essential to avert a long-term decline in forest productivity and to reestablish biotic control of hydrology and biogeochemistry. Thus it is tempting to couple an appraisal of the nitrogen loss from timber harvest with calculations of nitrogen replacement rates in assessing the impact of harvest rotation time on nutrient recovery for the ecosystem. We suggest, however, that the problem is more complicated and that such an approach is too simplistic. Not only does harvesting remove nutrients in wood products, it frequently accelerates nutrient loss by other pathways, such as erosion and solution (*21*). Rates of replacement by nitrogen fixation or rates of loss by denitrification may also change drastically during recovery following harvest. Such variables make simple answers questionable and suggest that these aspects of the nitrogen cycle should receive high research priority, especially in light of the increasing demands for the utilization of hardwoods and the development of techniques for harvesting whole trees (*21*).

F. H. Bormann
School of Forestry and Environmental Studies, Yale University, New Haven, Connecticut 06511
G. E. Likens
Section of Ecology and Systematics, Cornell University, Ithaca, New York 14853
J. M. Melillo
Ecosystem Center, Marine Biological Laboratory, Woods Hole, Massachusetts 02543

References and Notes

1. F. H. Bormann and G. E. Likens, *Science* **155**, 424 (1967); G. E. Likens, F. H. Bormann, N. M. Johnson, R. S. Pierce, *Ecology* **48**, 772 (1967); N. M. Johnson, G. E. Likens, F. H. Bormann, R. S. Pierce, *Geochim. Cosmochim. Acta* **32**, 531 (1968); D. W. Fisher, A. W. Gambell, G. E. Likens, F. H. Bormann, *Water Resour. Res.* **4**, 1115 (1968); G. E. Likens, F. H. Bormann, R. S. Pierce, D. W. Fisher, *Proceedings of the Brussels Symposium on Productivity of Forest Ecosystems*, P. Duvigneaud, Ed. (Unesco, Paris, 1971), pp. 553–563; G. E. Likens and F. H. Bormann, *Ecosystem Structure and Function*, J. Wiens, Ed. (Oregon State Univ. Press, Corvallis, 1972), pp. 25 → J. E. Hobbie and G. E. Likens, *Limnol. Oceanogr.* **18**, 734 (1973); F. H. Bormann, G. E. Likens, T. G. Siccama, R. S. Pierce, J. S. Eaton, *Ecol. Monogr.* **44**, 225 (1974); G. E. Likens and F. H. Bormann, *BioScience* **24**, 447 (1974).
2. F. H. Bormann, T. G. Siccama, G. E. Likens, R. H. Whittaker, *Ecol. Monogr.* **40**, 373 (1970).

→ R. H. Whittaker, F. H. Bormann, G. E. Likens, T. G. Siccama, *ibid.* **44**, 233 (1974).
4. W. W. Covington, thesis, Yale University (1976).
5. C. A. Federer, *U.S. For. Res. Note NE-167* (1973).
6. G. E. Likens, F. H. Bormann, R. S. Pierce, J. S. Eaton, N. M. Johnson, *Biogeochemistry of a Forested Ecosystem* (Springer-Verlag, New York, 1977).
7. Nitrogen in aboveground and belowground living biomass pools is calculated from biomass estimated by dimensional analysis (*3, 4*) and nitrogen concentrations representative of vegetative components of the ecosystem (*8*). Organically bound nitrogen in the forest floor and mineral soil to a combined depth of 45 cm is calculated from depth, bulk density, and Kjeldahl nitrogen analyses (*9*). Available nitrogen content is calculated from depth, bulk density, and ammonium, nitrite, and nitrate analyses of the soil to a depth of 38 cm (*10*).

Values for nitrogen accretion in living biomass are calculated from annual woody biomass increments estimated by dimensional analyses (*3, 4*), data on woody litter (*11*), and Kjeldahl nitrogen analyses (*8, 10, 11*). Nitrogen accretion in the forest floor is estimated by using samples obtained from a successional sequence of northern hardwood stands ranging in age from 3 to about 200 years (*4*). Nitrogen accretion in the mineral soil is assumed to be near zero.

Since the ecosystem is a small watershed with a watertight bedrock, the only significant nongaseous loss of nitrogen occurs as dissolved or particulate matter in water draining from the system (*1*). The average annual nitrogen export in stream water is based on 10 years of direct measurement (*6*). Gaseous loss of nitrogen resulting from denitrification is unmeasured, but is assumed to be small since the soils are acid (*p*H 3.9 to 4.5), well drained, and low in nitrate production (*9, 10*). These conditions are apparently not conducive to denitrification (*12*); however, incubation of KNO_3-amended soils from Hubbard Brook in a helium atmosphere for 5 weeks at 25°C suggests that these soils have a potential for denitrification (L. H. Wullstein, unpublished data).

Microbial fixation of nitrogen and nitrogen in bulk precipitation are the two major inputs considered. Microbial fixation of nitrogen is estimated by difference: annual nitrogen fixation = (annual nitrogen accretion of the system + annual hydrologic export of nitrogen) − (annual precipitation input of nitrogen). The value we report is actually an estimate of net fixation: net fixation equals fixation minus denitrification. Our estimate of net fixation is based on the average of two different periods of biomass accretion (1956 to 1960 and 1961 to 1965). If we used these as separate periods, estimated nitrogen-fixation would range from 10.9 to 17.2 kg ha^{-1} $year^{-1}$. Inorganic nitrogen in bulk precipitation (wet and dry deposition) has been measured directly for 10 years and mean annual input is used (*6*). Based on a relatively few measurements, there apparently are negligible amounts of organic nitrogen in precipitation at Hubbard Brook.

Another possible source of nitrogen input for the ecosystem is gaseous uptake of ammonia or impaction of nitrogenous aerosols (such as ammonium sulfate) on vegetation surfaces. Preliminary evidence suggests that these inputs are small compared to the nitrogen fixed by microbial activity. Since our estimate of net microbial fixation of nitrogen for the ecosystem is obtained by difference, uptake of gaseous or impacted nitrogen would reduce the estimate for fixation.

Direct measurements of the movement of nitrogen in stemflow and throughfall (*13*), root exudates (*14*), and aboveground litter (*10, 11*) were made, and root litter (*3, 4, 10*) was estimated. Annual uptake of nitrogen by all of the plants from the soil is estimated from the sum of the nitrogen incorporated in annual woody biomass accretion and the nitrogen transferred annually from living vegetation to the soil through stemflow and throughfall, root exudates, aboveground litter, and root litter.

In the soil, transformation of organically bound nitrogen to inorganic nitrogen (available soil nitrogen) is referred to as gross N-mineralization. Only that portion of the gross not used by soil microorganisms (that is, net N-mineralization) is potentially available to the ecosystem's vascular plants. Annual net N-mineralization is estimated by difference: annual net N-mineralization = (annual nitrogen uptake by plants + annual hydrologic export of inorganic nitrogen) − (annual precipitation input of inorganic nitrogen + annual transfer of inorganic nitrogen in stemflow and throughfall + annual transfer of inorganic nitrogen in root exudates). In estimating net N-mineralization, it is assumed that all inorganic nitrogen entering the soil as precipitation input, stemflow and throughfall, and root exudates moves directly into the available soil nitrogen pool. If this inorganic nitrogen entering the soil were first taken up by soil microorganisms and then mineralized, our net N-mineralization estimate would be larger.

At the height of the growing season, leaf tissue in this northern hardwood forest ecosystem has a nitrogen content of approximately 70 kg/ha. During senescence, the amount of nitrogen in the leaves decreases precipitously. Fresh leaf litter contains only about 30 kg/ha. Of the various pathways by which nitrogen may be removed from the leaves, it is concluded that during senescence almost 40 kg/ha is retranslocated from the leaves to the woody tissue of the hardwoods (D. F. Ryan, unpublished data). Retranslocation is estimated by difference: annual retranslocation of nitrogen = (nitrogen content of leaves prior to senescence) − (nitrogen content of leaf litter + nitrogen in throughfall and stemflow during senescence). In estimating retranslocation it is assumed that there is no aerosol impaction of nitrogen on leaf surfaces, no direct uptake of gaseous nitrogen by leaves, and no loss of gaseous nitrogen from leaves.
8. G. E. Likens and F. H. Bormann, *Yale Univ. Sch. For. Bull. 79* (1970).
9. A. S. Dominski, thesis, Yale University (1971).
10. J. M. Melillo, thesis, Yale University (1977).
11. J. R. Gosz, G. E. Likens, F. H. Bormann, *Ecology* **53**, 769 (1972).
12. M. Alexander, *Soil Microbiology* (Wiley, New York, 1961).
13. J. S. Eaton, G. E. Likens, F. H. Bormann, *J. Ecol.* **61**, 495 (1973).
14. W. H. Smith, *Ecology* **57**, 324 (1976). Smith considers root exudate estimates as conservative since they are based on one class of roots.
15. P. Duvigneaud and S. Senaeyer-DeSmet, in *Analysis of Temperate Forest Ecosystems*, D. E. Reichle, Ed. (Springer-Verlag, New York, 1970), pp. 199–225.
16. G. S. Henderson and W. F. Harris, in *Forest Soils and Land Management*, B. Bernier and C. H. Winget, Eds. (Université Laval, Quebec, 1973), pp. 179–193; J. E. Mitchell, J. B. Waide, R. L. Todd, in *Mineral Cycling in Southeastern Ecosystems*, F. G. Howell, J. B. Gentry, M. H. Smith, Eds. (Energy Research and Development Administration, Washington, D.C., 1975), p. 41; R. L. Todd, J. B. Waide, B. W. Cornaby, in *ibid.*, p. 729.
17. F. H. Bormann, G. E. Likens, D. Fisher, R. S. Pierce, *Science* **159**, 882 (1968); W. H. Smith, F. H. Bormann, G. E. Likens, *Soil Sci.* **106**, 471 (1968); G. E. Likens and F. H. Bormann, in *Proceedings of the First International Congress on Ecology* (Centre for Agricultural Publications and Documentation, Wageningen, Netherlands, 1974), pp. 330–335; ______, N. M. Johnson, *Science* **163**, 1205 (1968); __ →., D. W. Fisher, R. S. Pierce, *Ecol. Monogr.* **40**, 23 (1970).
18. G. L. Switzer and L. E. Nelson, *Soil Sci. Soc. Am. Proc.* **36**, 143 (1973).
19. J. P. Roskoski, thesis, Yale University (1977).
20. P. M. Vitousek and W. A. Reiners, *BioScience* **25**, 376 (1975).
21. R. S. Pierce, C. W. Martin, C. C. Reeves, G. E. Likens, F. H. Bormann, in *Symposium on Watersheds in Transition* (American Water Resources Association and Colorado State University, Fort Collins, 1972), pp. 285–295.

22. This is a contribution to the Hubbard Brook Ecosystem Study. Financial support was provided by the National Science Foundation. This work was conducted at the Hubbard Brook Experimental Forest in cooperation with the U.S. Forest Service.

16 August 1976; revised 3 December 1976

Chainlike Formation of Particle Deposits in Fluid-Particle Separation

Abstract. *A theory is proposed for the formation and growth of particle dendrites on a collector placed in an aerosol or hydrosol stream. It is based on the interplay of two intrinsic properties of suspended particles: (i) their finite size and (ii) the randomness of the location of individual particles in the fluid stream. The results of simulations based on this theory resemble those obtained from experiments.*

The transfer of solid particles from a flowing stream to a surface plays an important part in many physical and biological processes, such as the filtration of fluid-particle suspension, the deposition of inhaled particles, and the accumulation of particles on the walls of the arterial tree. The deposition rate depends on, among other factors, the ratio of the particle size to the characteristic length of the collector. When this size ratio is sufficiently large, the collector surface is markedly altered as the particle deposit accumulates. The change in the surface structure, in turn, affects the rate of subsequent deposition. The dynamic aspect of the collector surface clearly has significant effects on the deposition process.

The manner in which the particle deposit forms on the collector surface is strongly influenced by two intrinsic properties of suspended particles: (i) their finite size and (ii) the randomness of the location of individual particles in the fluid stream. The purpose of this report is to explain how the interplay of these two intrinsic properties leads to the formation of chainlike particle dendrites on a collector such as a fiber in air filtration.

The structure of solid particle deposits on fibers has been observed by a number of investigators (*1*). Although various filtration theories have been developed

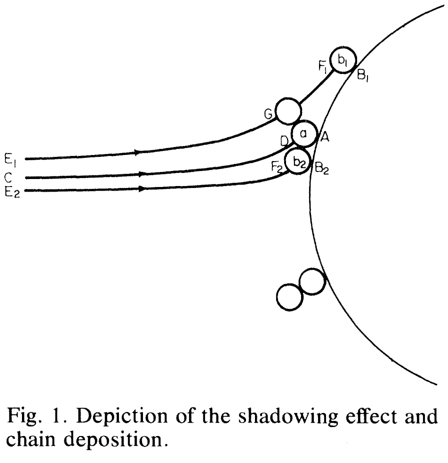

Fig. 1. Depiction of the shadowing effect and chain deposition.