
6 Biological Processes and Catchment Studies

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6.1 INTRODUCTION

This evaluation of biological processes studied in the small catchments is restricted to biological variables that might influence the groundwater and surface water of the catchment with implicating effects on the whole ecosystem. Biological reactions taking part within populations or organisms in a shorter time perspective might be processes difficult to evaluate on an ecosystem basis. Also, very few catchment studies have focused on such biological processes.

Catchments are influenced by physical, chemical and biological processes in many different ways:

1. Weathering processes are controlled by radiation, temperature, humidity and water chemistry and above all by the original composition of the bedrock, soil structure and chemistry, where organic matter might also be of importance.
2. Deposition of water, gases, nitrogen and other elements in precipitation and dry fallout influences weathering, leaching and productivity processes both in vegetation and soil.
3. Biological processes are directed by all the above-mentioned variables and interact with many of them, but they are also governed by genetic variation and evolution mechanisms. The vegetation has an important regulating effect on the hydrological cycle in the catchment by evapotranspiration. Also, biological processes in other ecosystems including streams, lakes and the sea, might be affected by changes in the catchment.

Principal biological processes studied on an ecosystem level in forested catchments have been primary productivity and nutrient balance including the effects of leaching of nutrients and organic matter from forest canopies and different soil horizons, forest damage, decomposition and the chemistry of groundwater and surface water. Some studies have also been carried out on evapotranspiration in whole catchments. Historical data are of utmost importance in understanding long-term changes within catchments; organic sediments in swamp forests, streams and lakes (pollen, plankton species, chemistry) have been investigated.



6.2 LONG-TERM CHANGES IN CATCHMENTS

6.2.1 PALAEOECOLOGICAL STUDIES

To understand ongoing processes in catchments we should start looking backwards in time (Hultberg, 1985a). In the temperate zone of the Northern Hemisphere most existing catchments were last glaciated about 12 000 years ago, when warmer climate appeared causing deglaciation. Results from a pair of catchments in New England, USA (Ford, 1990), illustrate the importance of chemical changes in the long term, coupled to simultaneous changes in biota. Ford used palaeoecological methods to test the hypothesis of natural long-term ecosystem acidification. The structure and population dynamics of terrestrial communities associated with the two watersheds in the post-glacial period were inferred through pollen analysis of lake sediments. The history of the aquatic communities and limnological conditions were investigated through the stratigraphy of siliceous microfossils, particularly diatoms and chrysophytes. Chemical analyses of fractionated sediments indicated historical change in the inputs of major elements including aluminium, manganese, iron, silicon and calcium. The analyses revealed patterns of biogeochemical cycling relating to weathering and soil formation, which related the historical dynamics of the terrestrial and aquatic communities.

Already 10 000 years ago, Al appeared bound to organic matter in the sediments of Cone Pond, a catchment with thin till deposits, indicating slightly acid soil conditions and leaching of humus. About 8000–5500 years ago, a peak in Al concentrations was obvious, simultaneously with a lower Ca/organic matter ratio. These values were associated with increased forest growth of birch, hemlock and hardwoods. At this time the lake also became more acid, which was reflected by decreased presence of planktonic diatoms. The latter were totally replaced by benthic diatoms 5000–2000 years ago. The pH was estimated to be lower than 5.0 about 2000 years ago when spruce recolonized the catchment. Spruce was also one of the first tree invaders, together with aspen, birch and pine about 10 000 years ago. Chemical analyses of the lake sediments indicated that Al, Fe, Mn and Si all appeared simultaneously 10 000–8000 years ago, accompanied by organic sediments. The ratio of Si/Al decreased significantly 2000 years ago, indicating some influence of spruce on the soil chemistry and leaching processes, probably affecting an easily dissolved aluminosilicate complex.

The other catchment, South King Pond, differed from Cone Pond by being richer in calcium in the sediments and the soils of the thicker till deposits within the catchment. The same pollen record was found in the sediments, indicating similar vegetation development in the surroundings. However, judging from the diatom analyses and the chemistry of the sediments there was no indication of change in pH of either soils or lake water. Obviously this catchment had enough resilience to resist slow natural acidification.

From pollen analyses of sediments deposited over the last 500 years in SW Sweden it was shown that the invasion of spruce took place predominantly during

the last 200 years (Wallin and Renberg, 1985). However, major changes in the populations of diatoms, fish and other organisms did not appear until around 1960 (Renberg and Hellberg, 1982; Hultberg, 1985b), this coincided with high deposition rates of strong mineral acids from air pollutants (Renberg and Wallin 1985; Andersson and Olsson, 1985). Sediment chemistry revealed concurrently increased concentrations of iron, chromium, nickel, vanadium, copper and lead. Cadmium and zinc showed distinct maximum values during 1950–70, but decreased after 1980, probably as an effect of pH-differences in the sediments (Renberg, 1985).

Reconstruction of long-term changes of catchment chemistry and biology provides good background for evaluation of the rapid forest ecosystem changes within industrialized countries in the last 50 years.

6.2.2 LONG-TERM MONITORING

Long-term integrated monitoring (IM), has started in many countries, including the USA, Canada, the Nordic countries (Nordic Council of Ministers 1988; 1989) and several other European countries. Within the framework of the Economic Commission of Europe (ECE), a pilot programme has started as a network of sites with IM in small catchments (Söderman, 1990).

Apart from measuring air chemistry, deposition of chemical elements and runoff water chemistry, a large effort must be put into biological monitoring. The terrestrial portion of the ECE programme is centered on determining alterations to the structure and function of vegetation, especially in relation to internal nutrient fluxes of forest stands and of the catchment (litterfall, decomposition, throughfall and soil water (Figure 6.1). Comprehensive quantitative and qualitative ecological inventories of the flora include descriptions of productivity, vitality and fertility as well as phenological and behavioural aberrations (discoloration of leaves and needles, defoliation of trees, structural deformations, sprouting, etc.).

It is planned to explore physiological, biochemical and micromorphological characters of vegetation for high resolution, high specificity indicators. This line of research is exemplified by ultrastructural studies of needle tissues that are sensitive to ozone and other air pollutants (Ratsep, 1990). Increasingly, attention is being focused on changes in functional interactions of vegetation with other biota, such as herbivores, pathogens and fungal and bacterial symbionts. Mycorrhiza/fine root and other rhizosphere associations are possibly being damaged as a result of air pollutants; decreases in soil respiration, soil enzyme activity and macrofungal sporophore production might reflect this, indicating a loss of species and decrease of decomposer biomass.

Critical processes for nutrient balance in a catchment include decomposition, nitrogen transformations (nitrogen fixation, ammonification, nitrification, denitrification), mineralization of other nutrients and the cycling of energy which all are directly or indirectly microbially mediated. Evaluation of the structure and function

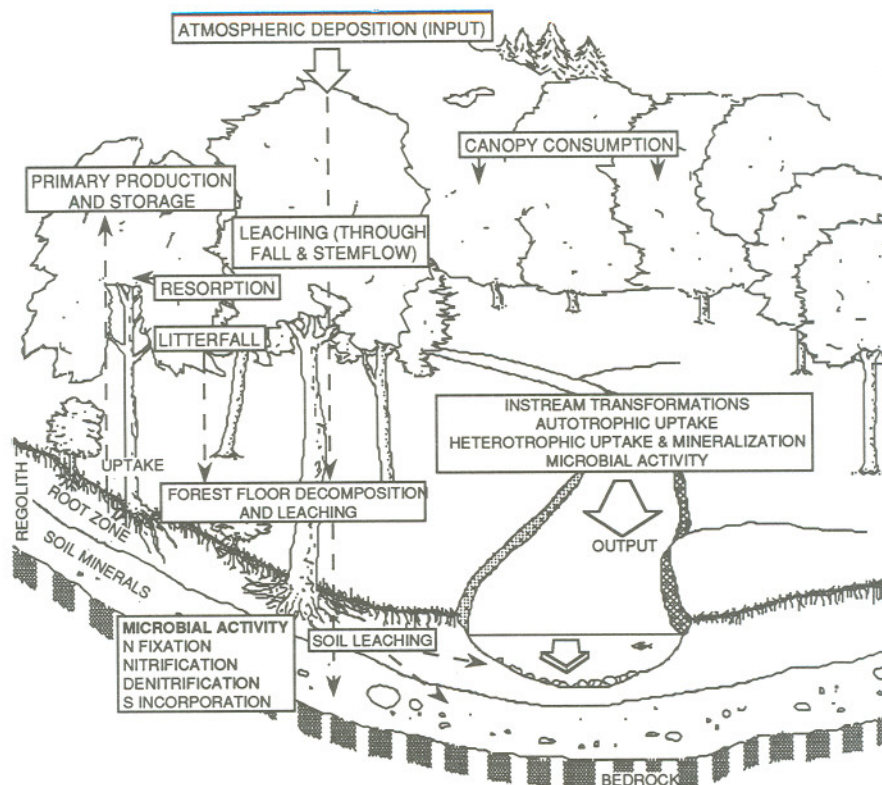


Figure 6.1 Schematic illustration of the biogeochemical processes of importance in long-term research of a watershed (Swank, 1986).

of microbial and other biotic communities in forest soils is extremely relevant for understanding of biogeochemical linkages in small catchments. In catchments with relatively large bodies of surface water, limnological processes assume greater importance in proportion to terrestrial processes.

6.3 PRIMARY PRODUCTIVITY AND NUTRIENT CYCLING IN CATCHMENTS

Although much initial work on catchments focused on hydrological questions, the utilization of these systems for investigating biogeochemical relationships, including anthropogenic influences, became apparent in the 1960s (Bormann and Likens, 1969). In the USA, two focal points for biogeochemical research have been the catchments at Hubbard Brook Experimental Forest in the White Mountains of

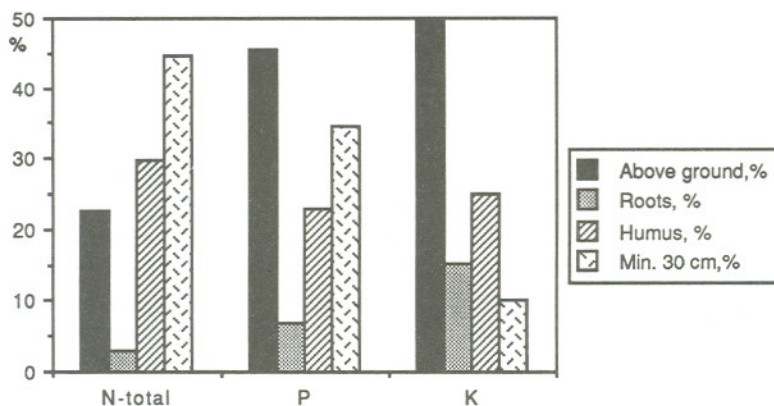


Figure 6.2 Relative distribution of nitrogen, phosphorus and potassium in a forested ecosystem of the boreal zone (average values from Rosén, 1982 are used). Total amounts for the different fractions are given, except for in the mineral soil down to 30 cm depth, where exchangeable amounts are given for P and K.

New Hampshire (Likens *et al.*, 1977) and Coweeta Hydrologic Laboratory, located in the southern Appalachians of North Carolina (Johnson and Swank, 1973). The interest in acidic deposition resulted in the development of intensive investigations of a large number of watersheds in North America and Europe.

Coupling primary productivity with biogeochemical cycles has been a central theme of many catchment studies in temperate forests (Likens *et al.*, 1977; Sollins *et al.*, 1980; Swank and Crossley, 1988; Johnson and Van Hook, 1989). In some cases, ecosystems' resistance and resilience associated with harvesting have been linked directly with net primary production and storage of nutrients in vegetation (Swank and Waide, 1980). For example, catchment research at Coweeta has shown that following clearcutting in mixed deciduous forests, the early successional forest vegetation promotes rapid recovery of biogeochemical cycles due to high rates of net primary production (NPP) and immobilization of nutrients in successional vegetation. Only three years after cutting, above-ground NPP of the prolific hardwood sprout, herb and vine growth was about 80% of the NPP of the original mature hardwood forest, while some nutrients in NPP equalled or exceeded values for the mature forest (Boring *et al.*, 1988). The regulating effects of primary production on nutrient cycles have been illustrated in other catchment studies for northern hardwood forests (Marks, 1974; Bicknell, 1979) and northwest coniferous forests (Gholz *et al.*, 1985) although patterns vary across ecosystems, partly due to rapidity of regrowth.

The nutrient cycles of a catchment are to a large extent determined by biota, especially by the primary production of plants and by microbial decomposition. Severe losses from the ecosystem of important nutrients, e.g. Ca, Mg, K and P, are expected to lower the productivity when occurring in the root zone (Hornung,

1990). Most nutrients available for circulation in a temperate forested ecosystem are found in the tree layer or in the accumulated organic matter of the soil (Rosén, 1982). This is especially true for the most important macronutrients (C, N, P, K, Ca, Mg and S). Nitrogen is almost completely bound to organic matter and when it is mineralized it is either leached as nitrate or assimilated and immobilized by organisms in the soil. Including the humus horizon, the soil organic matter contains the largest pool of nitrogen in a boreal forest (Figure 6.2). For phosphorus and potassium this pool of organic matter is also of importance, but in a boreal forest a relatively higher amount is in the living biomass. The long-term soil development slowly proceeds towards a lower rate of weathering in the root zone and relatively higher amounts in the circulation of the ecosystem (Hornung, 1990).

Wet and dry deposited elements are intercepted in the canopy, where ion exchange might occur. The canopy plays the dominant role in a number of processes: a chemical ion exchange on positions of the leaf surface; diffusion into or out of the leaf; active uptake of nitrogen, mainly ammonium; excretion, emission or leaching of elements, and especially of organic compounds (Schaefer and Reiners, 1990). A distinction must be made between dry deposition to deciduous and coniferous forests; a red spruce forest might show dry deposition levels 50–100% higher than a beech forest (Matzner and Meiwes, 1989; Ivens, 1990), due to a higher leaf area index during the whole year in the former forest. Soil processes which may appear to be purely chemical in the soil are affected by biota; both weathering and leaching are affected by the growth of roots, their mineral uptake and release of acid ions, by organic matter and mineralization. Important processes mediated by biota are the direct uptake of dissolved nutrients by roots or microorganisms, and the elemental accumulation in humus.

In order to understand significant changes in nutrient fluxes inside the catchment caused by biota, it is necessary to measure total biomass and the yearly production, amounts of organic matter in the soil, as well as nutrient contents, yearly uptake and litterfall (Nihlgård, 1989a). Measurements of throughfall, stemflow and soil water flow inside forest stands must also be undertaken. Most information exists about these processes on an ecosystem level, and less on a catchment basis. Some principles for the behaviour of different elements connected to biota in catchments are reviewed below.

Nitrogen is an element controlled in nature basically by organisms. The most important input in non-industrial regions is nitrogen fixation, but in most parts of Europe the deposition rate today is high enough to make dry and wet deposition the most important source. Ammonium and nitrate nitrogen in precipitation behave differently in the catchment; most ammonium is taken up by the canopy at low deposition rates ($<5 \text{ kg ha}^{-1} \text{ year}^{-1}$) and nitrate may pass the canopy but almost no ionic nitrogen will appear in runoff (Malanchuk and Nilsson, 1989). High deposition rates ($> 20 \text{ kg ha}^{-1} \text{ year}^{-1}$), however, might cause substantial transfer of both ammonium and nitrate in throughfall (Grennfelt *et al.*, 1985). After continuous high deposition of nitrogen, nitrate may also appear in catchment runoff (Malanchuk and Nilsson, 1989; Weissen *et al.*, 1988). The latter situation indicates

that nitrogen is no longer the limiting element to plants of the catchment, and also that microorganisms seem to be unable to assimilate the excess nitrate. In areas with high nitrogen deposition both vegetation and epiphytes are reported to change; nitrate-demanding species appear and ordinary epiphytic lichens are replaced by green algae (Nihlgård, 1985; Falkengren-Grerup, 1989). Also, the amino acid accumulation pattern might change in the trees. Microorganisms in the soil temporarily immobilize nitrogen by accumulation in their biomass. They might also use nitrate as an electron acceptor in denitrification processes.

Phosphorus is usually conserved in the internal fluxes of the ecosystem and the catchment. Both input and output are low compared to its use in the ecosystem.

Leaching of high amounts of K, Mn, Ca and Mg from the canopy has been observed. Most of these elements show lower concentrations in the soil water solution (Bergquist, 1987) and in the runoff; they are obviously taken up by the plant roots quite quickly again. Ca and Mn both seem to be easily weathered in acid forest soils and are leached out from the catchments (Nilsson and Bergquist, 1983).

Many heavy metals brought to the catchment as air pollutants are accumulated in the organic matter. Pb and Cu are continuously accumulated in the upper soil horizon. An average deposition figure, including throughfall and litterfall, of $1.5 \text{ g Pb m}^{-2} \text{ year}^{-1}$ (Bergquist, 1987) and corresponding total amounts in the humus of forests in southernmost Sweden of about 15 g Pb m^{-2} , indicates a considerable accumulation rate, as air transport of Pb is the only input. Cd, Cr, Ni, V and Zn are also accumulated, but at lower rates than Pb and Cu. Accumulation in the long run must lead to increased risk that toxic levels for decomposing organisms will be reached. The leaching process of Hg from catchments is known to be correlated with the humus content in the runoff water (Iverfeldt and Johansson, 1988), indicating that organic matter is very important for mercury's mobilization, as it is for many other metals.

Acidification, caused by deposition of extra hydronium ions (free or as ammonium ions) to the catchment, might cause increased leaching of the dominating macroelements—calcium, magnesium and potassium. In combination with high nitrogen deposition, nutrient imbalance appears in forests within a few decades (Weissen *et al.*, 1988). Especially P/N, Mg/N and K/N ratios seem to decrease in the leaves of plants with increasing acidity of the soils (Nihlgård, 1989b). Decreased pH follows and the concomitant increased dissolution of aluminium might soon affect the pH deeper in the soil (Nilsson, 1985). Liming with Ca-Mg carbonate (dolomite) slowly increases the pH of the soil, and after some years also the pH of runoff surface water (Nihlgård and Pålsson, 1988, and unpubl. data).

A lot of uncertainty still exists concerning the natural nutrient circulation within the different ecosystems of the same catchment, e.g. the importance of internal transport from ecosystems situated higher in the catchment to those situated lower, and the local accumulation of organic matter and elements in areas with a high groundwater table. The stability of the pool of organic matter, directed by accumulation and decomposition processes, to a large extent determines the nutrient cycles of some elements within the catchment.

6.4 MICROBIAL REGULATION IN CATCHMENTS

The regulation of biogeochemical cycles by microbial populations is of most direct importance in the cycling of N, S, P and C. Much of the ecosystem pool of these elements resides as organic forms in forest floor and mineral soil compartments. These organic complexes are subjected to microbial transformations which regulate NO_3^- , SO_4^{2-} and PO_4^{3-} dynamics and availability which, in turn, indirectly influences the movement of other solutes through maintenance of ionic balances of solutions (Johnson *et al.*, 1979; Vitousek, 1984). However, quantification of the role of microbial processes in biogeochemical cycles even at the small catchment scale is not well established. This gap is due in part to the large spatial and temporal variability in processes involving C and N, and in part due to lack of *in situ* studies in the case of S and P. In addition, the consideration of the roles of

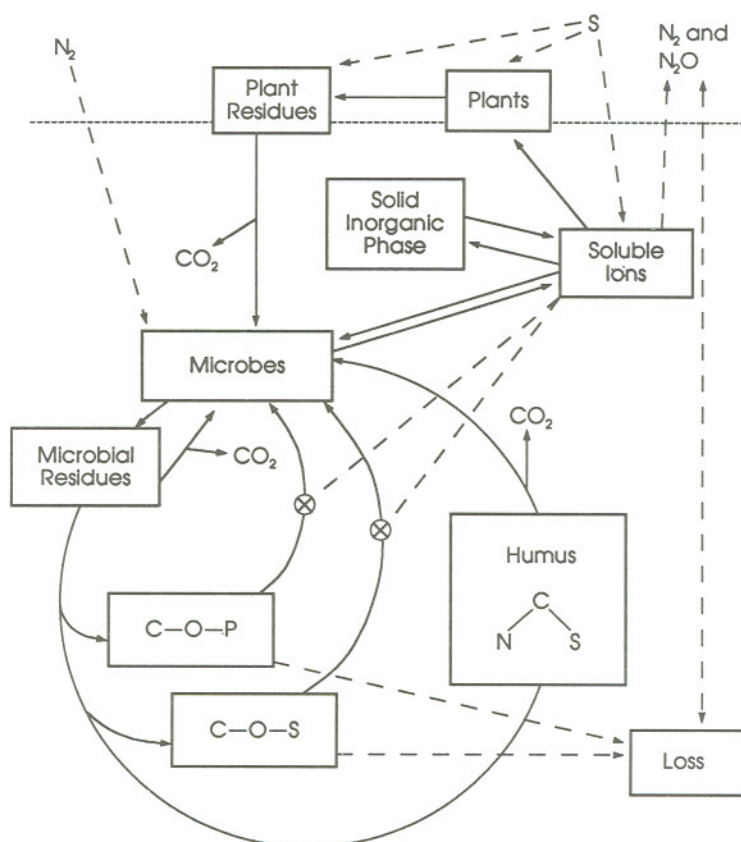


Figure 6.3 A tentative model illustrating decomposition interactions (after McGill and Cole, 1981; reproduced by permission of Elsevier Science Publishers BV.).

microbes in the metabolism of N, S, P and C has often focused on individual elements with less attention to elemental interactions. However, models such as that proposed by McGill and Cole (1981) for grasslands, should have general applicability (Figure 6.3). Some of the relationships in these models have been included in simulations of soil elemental transformations (Hunt and Parton, 1986).

6.4.1 NITROGEN

Since N is a nutrient that frequently limits forest productivity, there is an abundance of literature on the N cycle and its transformations (Clark and Rosswall, 1981; Söderlund and Rosswall, 1982; Carlyle, 1986). The major N transformations and fluxes are given in Figure 6.4. Processes of dinitrogen fixation, mineralization, immobilization and nitrification have received the most attention but there is a paucity of information on denitrification. The status and fluxes of N in forest ecosystems are strongly regulated by rates of N mineralization and immobilization.

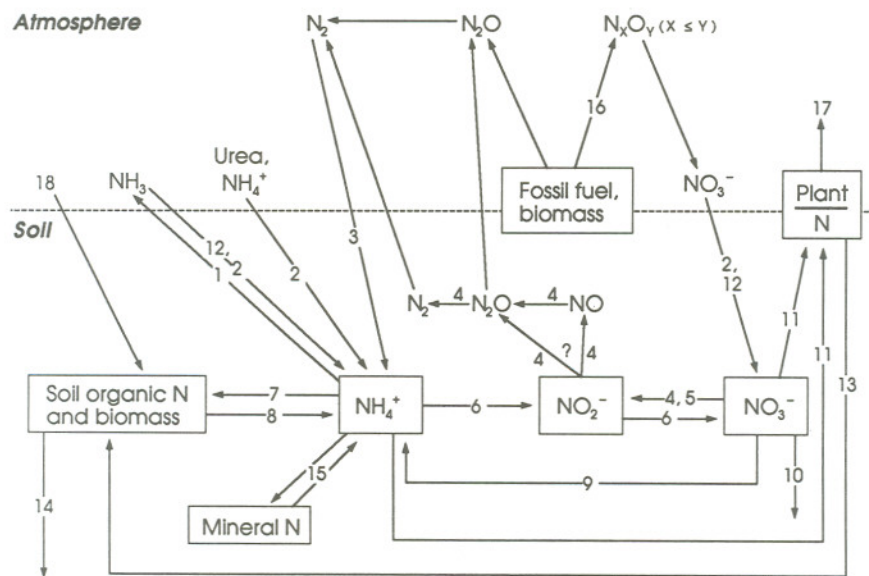


Figure 6.4 A nitrogen model illustrating fluxes of nitrogen in a terrestrial ecosystem (after Smith and Rice, 1986; reproduced by permission of Martinus Nijhoff).

Explanation of the fluxes: 1, NH_3 volatilization; 2, Fertilization; 3, N_2 -fixation; 4, Denitrification; 5, NO_3^- respiration; 6, Nitrification; 7, Immobilization; 8, Mineralization; 9, Assimilatory and dissimilatory NO_3^- reduction to NH_4^+ ; 10, Leaching; 11, Plant uptake; 12, Atmospheric deposition; 13, Residue composition, exudation; 14, Soil erosion; 15, NH_4^+ fixation and release by minerals; 16, Combustion; 17, Crop harvest and grazing; 18, Addition of organics.

The influences of these processes on biogeochemical cycles at a catchment scale have been demonstrated in experiments at Hubbard Brook Experimental Forest (HBEF), New Hampshire, USA and Coweeta, North Carolina, USA. Over a three-year period after clearcutting a hardwood forest at Hubbard Brook, forest-floor organic matter decreased by 10800 kg ha^{-1} , soil organic matter declined by 18900 kg ha^{-1} and net N loss from the soil was estimated to be 472 kg ha^{-1} with an increased export of inorganic N in the stream of 337 kg ha^{-1} (Bormann and Likens, 1979). Recently, the N and C content at HBEF have been reassessed and it has been established that the previous analyses may have substantially underestimated the N and C content of the forest floor and mineral soil (Huntington *et al.*, 1988). Nevertheless, the responses associated with the clearcutting were attributed to accelerated rates of decomposition induced by favourable temperature-moisture-nutrient conditions and enhanced nitrification rates. Increased availability and loss of NO_3^- also increased the loss of cations from the ecosystem (Likens *et al.*, 1977). This early experiment also included herbicide treatment to suppress the growth for the first two years after cutting. More recently in the autumn of 1983 and spring of 1984, a similar experiment without herbicides was repeated with a commercial whole-tree harvest (Bowden and Bormann, 1986; Lawrence *et al.*, 1987). As in the earlier experiment, the removal of the vegetation sink resulted in stimulation of nitrification and, hence, accelerated nitrate and H^+ leaching from the autumn of 1984 through the spring of 1987 compared to a reference watershed (Mitchell *et al.*, 1989). However, after a high initial pulse of nitrate loss there was a decrease in leaching which was likely attributable to vegetation regrowth and concomitant increased demand.

Significant alteration of nitrogen fluxes has been observed in a clearcut and logging experiment at Coweeta. In the first three years after logging, soil N mineralization increased by about 25% and nitrification increased by 200%; however, only a small fraction of available soil N was exported from the catchment via stream water (Waide *et al.*, 1988). Ecosystem retention was due partly to rapid revegetation and high rates of N uptake and partly to microbial immobilization. In other studies of an age sequence of clearcut and control hardwood forests in Indiana, greater mineralization rates were observed in only a four-year-old clearcut, but rates for control forests were inherently high (Matson and Vitousek, 1981). In loblolly pine in the southeastern USA, forest harvesting stimulated mineralization, but N losses from the system were low because microbial populations immobilized most of the mineralized N (Vitousek and Matson, 1985). Further evidence for the importance of the balance between mineralization and immobilization in regulating N losses in other ecosystems is given by Hornbeck *et al.* (1986). It is apparent that nitrification rates and associated nitrate losses differ tremendously across forest ecosystems due to a number of sources of variation.

There is increasing concern that increased anthropogenic inputs of N coupled with forest maturation may lead to the phenomenon of nitrogen saturation where N inputs exceed the demand of both the vegetation and the microbes, which results

in nitrification and nitrate leaching (Aber *et al.*, 1989; Chapter 11, this volume). It has been shown that N losses from ecosystems are highly variable, but generally sites in North America and northern Scandinavia show loss rates of N of $<1.4 \text{ kg ha}^{-1} \text{ year}^{-1}$ whereas sites in southern Scandinavia and Central Europe exhibit loss rates often $>7 \text{ kg ha}^{-1} \text{ year}^{-1}$. In South Sweden, this situation is also coupled to low P/N ratios in the foliage, indicating nutritional imbalance. The role of biotic regulation of NO_3^- flux is manifested in its episodic pulses to surface waters in the winter and spring in many sites (Driscoll *et al.*, 1989).

Fixation of dinitrogen to ammonia in forest ecosystems can occur on and/or in a variety of forest substrates including plant canopies and stems, epiphytic plant compartments, wood, litter, soil and roots (Dawson, 1983). This reductive process is performed by free-living microorganisms and various microbial symbionts including *Rhizobium* species. A recent review of the magnitude of N inputs to forest ecosystems by fixation (Boring *et al.*, 1988) indicates that non-symbiotic fixation ranges from <1 to $5 \text{ kg N ha}^{-1} \text{ year}^{-1}$ and symbiotic fixation ranges from about 10 to $160 \text{ kg N ha}^{-1} \text{ year}^{-1}$ in early successional ecosystems where N-fixing species are present. In catchment level studies at Coweeta, the chronological sequence of N pools and accretion in stands of black locust, a woody legume, were examined (Boring and Swank, 1984). The net average annual rates of N accretion were 48, 75 and $33 \text{ kg ha}^{-1} \text{ year}^{-1}$ for stand ages 4, 17 and 38 years, respectively, which usually exceeded values of mixed hardwood stands at Coweeta. Nitrogen fixation by black locust increased soil NO_3^- concentrations which could affect transport of other solutes. Furthermore, black locust litter has a low C : N ratio which could increase decomposition rates and accelerate mineralization of other elements. Some of the major gaps in our understanding of the role of dinitrogen fixation and recommendations for future research are identified by Boring *et al.* (1988).

Denitrification, a dissimilatory pathway of nitrate reduction into nitrogen oxides and dinitrogen, is performed by a wide variety of microorganisms (Wollum and Davey, 1975). Until the recent development of the acetylene-inhibition technique (Ryden *et al.*, 1979; Tiedje, 1982), studies in forest soils were hindered by methodological limitations. Measurable rates of N_2O production have been observed in many forest soils but the magnitude of rates shows substantial variation. In a study involving nine forested sites, Robertson and Tiedje (1984) found the highest rates of N_2O production in soils of recently cut or mature (>100 years) hardwood stands and extrapolation of rates on the most active sites indicated a loss of $2.12 \text{ kg N ha}^{-1} \text{ month}^{-1}$. In soils of the three pine stands examined, N_2O production was much lower. In another study in seven natural stands of both deciduous and coniferous forests (Goodroad and Keeney, 1984), N_2O production was estimated to range from 0.2 to 2.1 kg N ha^{-1} for time increments of five to nine months. From Central Europe experiencing high nitrogen deposition, values of N_2O emission of $2\text{--}7 \text{ kg ha}^{-1} \text{ year}^{-1}$ were reported, with the lowest values on limed plots (Brumme *et al.*, 1989). Studies on forested catchments at Coweeta indicated that potential denitrification

in soils of undisturbed and recent clearcut hardwood forests ranged from 1 to 5 kg N ha⁻¹ year⁻¹ (Swank, 1986). More recent *in situ* studies at Coweeta using improved methods suggest that the N₂O loss from mixed deciduous forests at this site was less than 0.4 kg ha⁻¹ year⁻¹ (Davidson and Swank, 1986). Bowden and Bormann (1986) found for the whole-tree harvesting experiment described previously for Hubbard Brook, that this had a small effect on the N dynamics at the site. Similarly, in his review of gaseous N emissions from ecosystems, Bowden concluded that gaseous losses of N (Table 5.1 from Bowden, 1986) generally do not markedly contribute to ecosystem N dynamics except under conditions of disturbance and/or the presence of high concentrations of grazing mammals. All *in situ* studies of denitrification in forest soils have shown large spatial and temporal variability in response to varying soil characteristics such as acidity, temperature, moisture, oxygen, ambient NO₃⁻ and available C.

Extrapolations of site-specific short-term measurements to a catchment scale are tenuous at best. Quantification of denitrification at an ecosystem level will require intense experimental efforts in combination with modelling. However, initial findings suggest the process is more important in forest soils than originally perceived.

6.4.2 SULPHUR

Microbial transformations are as important in the S cycle of forest ecosystems as in the N cycle. The sulphur cycle with specific reference to forested ecosystems has been extensively reviewed (Fitzgerald and Johnson, 1982; Johnson, 1984, 1986; Swank *et al.*, 1985; Mitchell *et al.*, 1992a). The major sulphur pools and transformations are depicted in Figure 6.5. Similar to N, most of the S pool is found in organic form in forest floor and soil compartments. However, unlike N there are important abiotic processes, especially sulphate sorption processes, which play a critical role in regulating sulphate dynamics of catchments.

In many forest ecosystems the short-term, annual S dynamics appear to be primarily regulated by sulphate adsorption processes (Mitchell *et al.*, 1992b; Rochelle *et al.*, 1987). An example of this was shown in the Hubbard Brook whole-tree harvesting experiment where the decrease in sulphate output from the watershed was attributed to sulphate adsorption which was enhanced by soil acidification from nitrification (Mitchell *et al.*, 1989). However, the role of microbial immobilization/mineralization processes may be important in regulating the long-term accumulation of the large organic S pools. The role of organic S accumulation in affecting the reversibility of S retention (Harrison *et al.*, 1989) in forested ecosystems, especially those which have been subject to accelerated inputs from atmospheric deposition, has yet to be ascertained (Mitchell *et al.*, 1992a).

Biological pathways of S movement have been a topic of research at Coweeta because sulphate is a major constituent of acid precipitation in the region (Swank and Waide, 1988) and catchment level studies of S inputs and outputs show apparent accumulations of 6 to 9 kg ha⁻¹ year⁻¹ in mixed hardwood forests (Swank *et al.*,

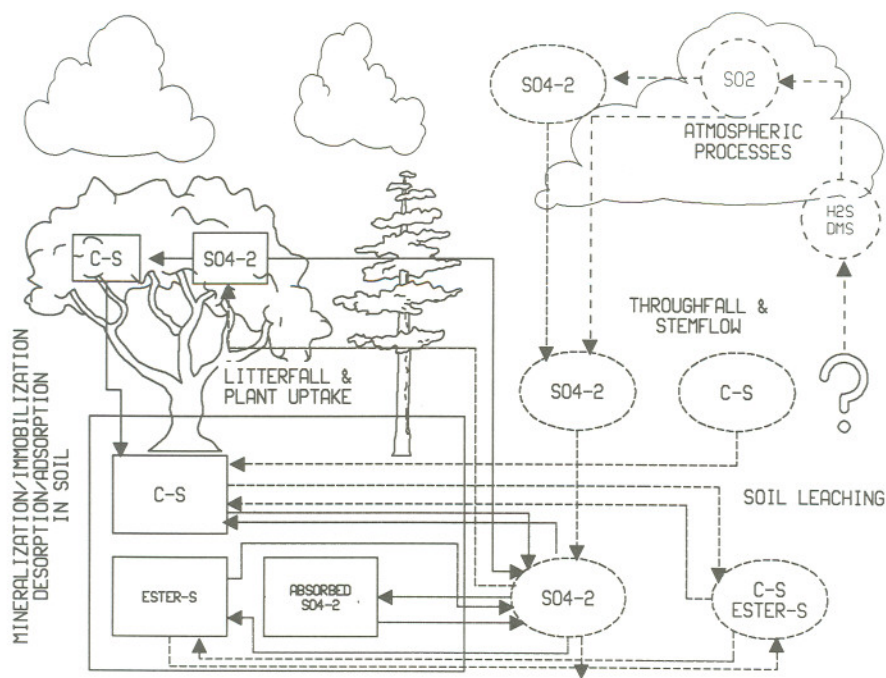


Figure 6.5 A model illustrating fluxes of sulphur in a forest ecosystem (from Mitchell *et al.*, 1992a; reproduced by permission of SCOPE).

1984). Furthermore, analysis of long-term stream chemistry records for undisturbed hardwood forests at Coweeta shows increasing sulphate concentrations and initial stream water acidification (Swank and Waide, 1988). Coupling physico-chemical processes of sulphate adsorption/desorption with biological dynamics is needed to interpret catchment responses. Plant sulpholipids are subject to mineralization and the release of the mobile sulphate anion (Strickland *et al.*, 1984). Moreover, additional studies have shown that microbial metabolism transforms a substantial portion of released sulphate into organic matter (Strickland and Fitzgerald, 1983). Conversion of sulphate-S to organic S immobilizes the anion and potentially reduces soil cation leaching. However, processes of S mineralization and incorporation proceed rapidly in response to several factors including temperature, moisture, and exogenous sulphate availability in soils and water. It is the balance between the rates of these processes that determines the biological contributions to sulphate availability. A partial review of S research conducted in undisturbed mixed hardwood forests at Coweeta is given by Fitzgerald *et al.* (1988).

6.4.3 PHOSPHORUS

The microbial regulation of P is tightly coupled to soil development and the change of P pools from the predominance of primary inorganic P (e.g. apatite) to that of organic P, secondary P minerals and occluded P as has been described by Walker and Syers (1976) and is illustrated in Figure 6.6a. Forests developing over different soil series have different amounts and fractions of these P components (Figure 6.6b).

It is believed that the organic P in soils is derived not from the accumulation of plant and animal residues, but rather by microbial synthesis reactions. Much of the organic P occurs in ester linkages (up to 60%) with lesser amounts in other forms (Stewart and McKercher, 1982). Also, there is a small loss of P due to leaching losses, which range from as little as $7 \text{ g ha}^{-1} \text{ year}^{-1}$ at Hubbard Brook (Wood *et al.*, 1984) to up to $500 \text{ g ha}^{-1} \text{ year}^{-1}$ for a glacial outwash in New Zealand (Walker and Syers, 1976). Loss rates generally are greatest in young, base-rich

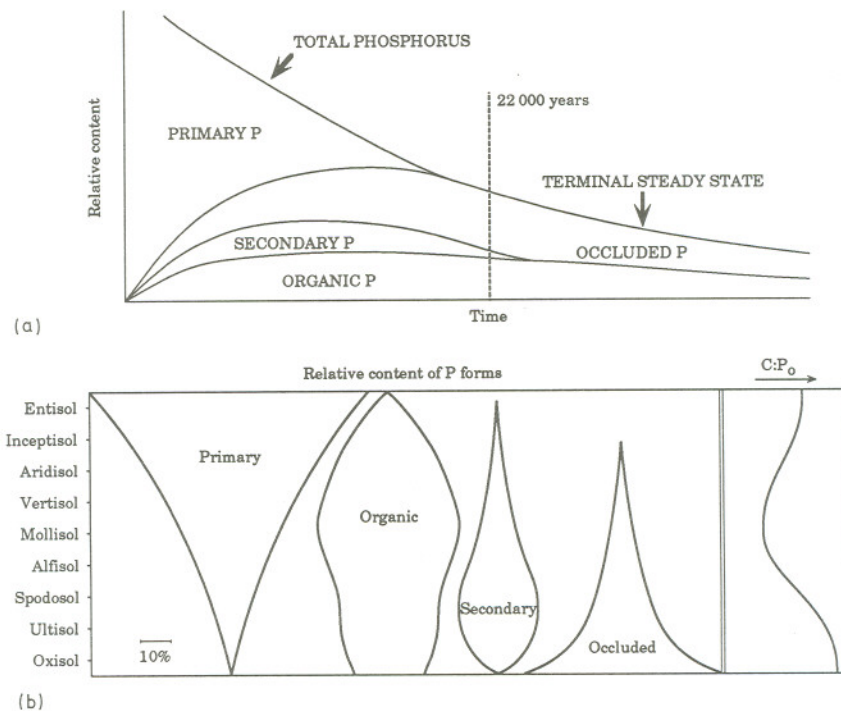


Figure 6.6(a) The long-term relative development of different phosphorus fractions in an ecosystem; (b) the relative contents of these fractions in different soil types. Also, the idealized carbon to organic P ratios ($C:P_o$) are illustrated (from Smeck, 1985; reproduced by permission of *Geoderma* (Elsevier Science Publishers BV))

soils and lowest in acidic soils ($\text{pH} < 5.0$) with high concentrations of sesquioxides, which may fix phosphate. Thus, soils at intermediate stages of soil development have the highest availability of P, which is partly regulated by microbial mineralization processes.

Soil processes controlling the cycling and availability of P are less well understood compared to N, C and S cycles. Annual P budgets have been estimated for a number of temperate forests (Wood, 1980; Monk and Day, 1988; Johnson and Henderson, 1989), but soil P turnover is usually calculated from net annual uptake requirements of the vegetation. There is scant information on the relative contributions of mineral and organic sources of P and no direct evidence of the importance of biological control of long-term P availability in temperate forests. Tight biological control of P cycling in the forest floor of some tropical forests is assumed (Stark and Jordan, 1978). Wood (1980) suggested that biological processes dominated P movement in surface horizons of a Spodosol soil underlying a northern hardwood forest, while inorganic P adsorption was maximum in the B horizon. In contrast, Walbridge *et al.* (1991) found that biological and geochemical P subcycles were not vertically stratified in Haploid and Dystrochrept soils underlying a hardwood forest at Coweeta. Plant roots, soil microorganisms and P-sorbing minerals all reach maximum concentrations in the forest floor or near-surface mineral horizons, and strongly compete for PO_4^{3-} in solution. *In situ* studies using ^{35}P as a tracer are currently in progress to assess the relative importance of microbial immobilization, plant/mycorrhizal uptake and mineral adsorption on P dynamics. Such information is most relevant to an assessment of plant productivity, because catchment research indicates that P is strongly conserved in forest ecosystems (Swank and Waide, 1980) and P export is little altered even with severe disturbance (Swank, 1988).

6.4.4 CARBON

Obviously the fates of N, S and P are tightly coupled not only with each other, but also with C dynamics of soils (Anderson, 1988). For example, it has been suggested that the leaching of dissolved organic species of N, S and P contributes to the accumulation of these elements in mineral soil (Mitchell *et al.*, 1989; Schoenau and Bettany, 1987). This leaching of organics is an important component of soil formation of Spodosols (Ugolini *et al.*, 1977) which are common especially in northern, coniferous watersheds. These elemental linkages are commonly used for predicting whether an element is mineralized or mobilized (Paul and Clark, 1989; Swift *et al.*, 1979). This approach has been most commonly used for predicting the relationships between C and N mineralization rates although other factors such as lignin content must also be considered (Aber and Melillo, 1982). Not only do carbon constituents form major soil fractions of N, S and P, but organic constituents play a major role in regulating the availability and dynamics of many other elements (McKeague *et al.*, 1986; Stevenson, 1986).

6.5 WITHIN-STREAM BIOLOGICAL FACTORS

Small, first- to third-order streams represent 86% of the total stream length in the United States (Leopold *et al.*, 1964). These small streams are closely linked with biogeochemical processes in the riparian zone and with the upslope terrestrial system. Solutes exported to a stream from the landscape are subjected to additional biological, chemical and physical processes during downstream transport (Figure 6.7). These processes influence dissolved and particulate nutrient transport and the eventual enrichment of downstream systems. Studies in forested basins have shown that nutrient uptake lengths in headwater streams are very short due to heterotrophic and autotrophic uptake and release of nutrient and macroinvertebrate egestion of particles (Mulholland *et al.*, 1985; Munn, 1989; Webster *et al.*, 1991).

Aquatic biology in relation to nutrient dynamics has been a topic of intensive effort at Coweeta for decades (Wallace, 1988) and several examples are used to illustrate the influence of biota on nutrient transformations. In one study, within-stream depletion of NO_3^- -N was attributed to denitrification in stream sediments

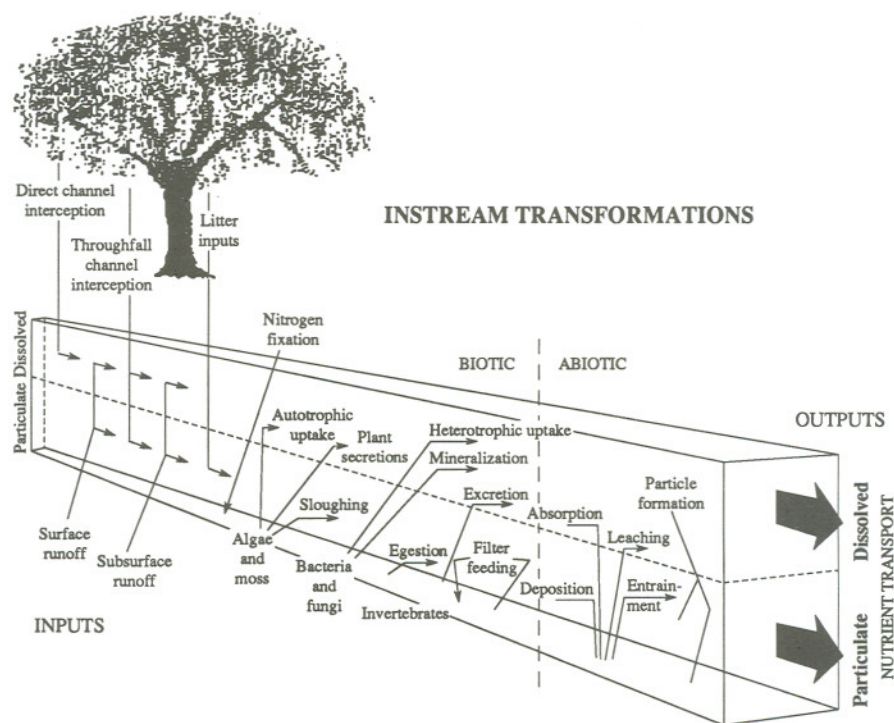


Figure 6.7 A variety of processes can potentially affect solute dynamics within small woodland streams (from Webster and Swank, 1985).

(Swank and Caskey, 1982). Mass balance calculations within stream sections, combined with assays of potential denitrification in sediment cores, suggested a NO_3^- -N depletion of 2 to 4 kg year⁻¹. Studies in other stream ecosystems have also implicated denitrification in sediments as a significant mechanism of N loss (Hill, 1979, 1983), even in streams where NO_3^- -N concentrations are low (Wyer and Hill, 1984).

The forest surrounding most small streams provides heavy shade which usually limits primary production. At Coweeta, periphyton production is typically low with estimates of about 3 kg(dry weight) m⁻² year⁻¹ in streams draining undisturbed forests (Webster *et al.*, 1983). However, canopy removal associated with logging increased solar insolation of the stream and periphyton production increased to 84 g m⁻² year⁻¹ which provides a potential sink for NO_3^- and P.

Lacking significant primary production, leaves and small woody material from the surrounding environment are the major sources of energy to many forested headwater streams (Cummings, 1974). Stream fauna play an important role in the comminution of this particulate organic matter and the mineralization of nutrients (Webster, 1983). Webster and Patten (1979), for example, estimated that 80% of the leaf litter input to a small stream was ingested by macroinvertebrates. Other studies at Coweeta quantified the influence of detritus on K and Ca export in streams of three different ecosystems (Webster and Patten, 1979). The dissolved form accounts for more than 95% of the total export for these two cations in each ecosystem (Table 6.1). However, K and Ca excreted by detritivores frequently exceeded other forms of ion export. Meyer and Tate (1983) and Meyer and O'Hop

Table 6.1 Total annual stream export (kg year⁻¹) of potassium and calcium in various forms for three Coweeta ecosystems (after Webster and Patten, 1979)

	K			Ca		
	White pine Old field (WS 6)	Hardwood plantation (WS 17)	forest (WS 18)	White pine Old field (WS 6)	Hardwood plantation (WS 17)	forest (WS 18)
Total dissolved	65.26	66.68	86.41	122.83	84.95	121.82
Dissolved excretion (detritivores) ^a	0.14	0.1	0.28	0.71	0.66	0.94
Sediment	0.08	0.04	0.02	1.43	0.96	0.71
Large particulate organic matter	0.006	0.004	0.001	0.16	0.13	0.13
Fine particulate organic matter	—	—	—	0.36	0.24	0.006
Insect emergence and organism drift	0.002	0.002	0.003	0.014	0.007	0.006

From Effects of Watershed Perturbation on Stream Potassium and Calcium Dynamics by J.R. Webster and B.C. Patten, Ecology Monographs, 1979, 49, 51–72. Copyright © 1979 by Ecological Society of America. Reprinted by permission

^aIncludes excretion by insects and crayfish.

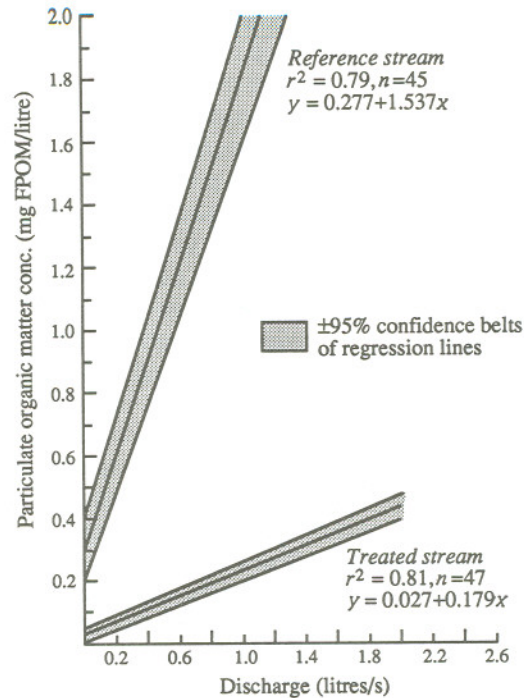


Figure 6.8 Regressions of suspended particulate organic matter vs. discharge in two first-order Coweeta streams following application of methoxychlor in the treated stream which reduced aquatic insect densities by more than 90%. Data represent low flow conditions, primarily in the autumn months (after Wallace *et al.*, 1982; reproduced by permission of Springer-Verlag).

(1983) found that macroinvertebrate shredders feeding on leaves could release 1 to 50 g m⁻² year⁻¹ of dissolved organic C (DOC) to stream water, which is a significant within-stream source of DOC during low flow periods.

Experimental evidence for the role of macroinvertebrate communities in regulating particulate organic matter transport is provided by Wallace *et al.* (1982, 1986, 1987) and Cuffney *et al.* (1984, 1990). In field stream experiments, the size of macroinvertebrate populations was reduced using the insecticide methoxychlor. Microbial respiration was not altered by the insecticide manipulation, but populations of shredders, large collectors and filter feeders were greatly reduced. Following treatment, detrital processing rates were reduced, benthic organic matter accumulated and there was a large reduction in fine particulate organic matter (FPOM) export (Figure 6.8). Additional research has shown the relative importance of biological vs. physical regulation of FPOM where insect manipulation accounted for 75% of observed decreased FPOM export compared to a 25% reduction associated with reduced discharge during a drought year with a >50 year

recurrence interval (Cuffney and Wallace, 1989). Clearly, invertebrate activity increases the supply of FPOM, DOM and nutrients in both upstream and downstream reaches.

6.6 HERBIVORE EFFECTS

6.6.1 INSECTS

The influence of insect populations on forest ecosystem processes is important both in the canopy and forest floor compartments. Canopy arthropods are postulated to act as regulators of forest primary production and nutrient cycling (Mattson and Addy, 1975). Other investigators have also suggested that herbivore activity alters nutrient uptake, translocation and leaching while enhancing microbial processes in the forest floor (Schowalter, 1981; Seastedt *et al.*, 1983). A substantial body of evidence has shown that forest floor invertebrates affect nutrient cycling both directly through digestion and assimilation of the litter (Gist and Crossley, 1975; Seastedt and Crossley, 1988) and indirectly through litter fragmentation, inoculation of litter with microflora, dissemination of fungal spores and physical mixing of soil and litter (Crossley, 1970; Gist and Crossley, 1975; Seastedt and Crossley, 1983; Seastedt and Tate, 1981).

Quantitative evidence that conclusively illustrates the influence of insect regulation of biogeochemical cycles on a small catchment scale is scarce. Perhaps some of the clearest demonstrations of functional, ecosystem-level consequences of forest defoliators are found in studies at Coweeta Hydrologic Laboratory in the southeastern United States (Swank *et al.*, 1981). An outbreak population of the fall cankerworm (*Alsophila pometaria*), a spring defoliator of hardwood forests, was observed on Watershed 27, a 38.8-ha control catchment in 1969. Defoliation progressed from higher elevations (1400 m) on the catchment towards lower elevations in ensuing years and peaked in 1974 when about 33% of the total leaf mass was consumed. During the period of chronic infestation, mean monthly concentrations of NO_3^- -N in stream water rose from the usual $10 \mu\text{g l}^{-1}$ background levels to over $50 \mu\text{g l}^{-1}$. Decline in the cankerworm population to endemic levels was accompanied by a return of NO_3^- -N concentrations towards baseline levels. Increased export of NO_3^- -N ranged from about $200 \text{ g ha}^{-1} \text{ year}^{-1}$ to $450 \text{ g ha}^{-1} \text{ year}^{-1}$ and more than 80% of the increased export occurred during the winter and spring months. Increased stream export of NO_3^- -N concomitant with fall cankerworm defoliation was also observed on two other nearby catchments, one at high elevation (Swank *et al.*, 1981).

The elevated loss of NO_3^- -N illustrates that insect grazing can measurably alter biogeochemical cycles at the ecosystem level of organization. Process-level research conducted during the period of cankerworm defoliation of Watershed 27 showed the following changes in ecosystem structure and function: (i) substantial increases of frass inputs and associated elements to the forest floor; (ii) increases in

combined litter–soil metabolism and standing crops of total microbes and nitrifying bacteria; (iii) significant increases in pools of mineral N in upper soil horizons; (iv) decreased stemwood production, but increased leaf production; when taken together, an increase in total above-ground net primary production; (v) large increases in leaf litter fall; and (vi) seasonal increase in evapotranspiration and hence reductions in streamflow due to increased leaf area index (Swank *et al.*, 1981, 1988).

Additional evidence for insect regulation of biogeochemical cycles at the ecosystem level is found in a study of Watershed 6, which has been a site of long-term manipulative research and represents the most disturbed catchment in the Coweeta Basin. The mixed deciduous forest was converted to a grass cover and heavily limed and fertilized in 1960, maintained in grass through 1965 and then herbicided for a two-year period (Hibbert, 1969). Subsequently, no further treatment has been applied and the catchment has been allowed to revert to successional vegetation (Johnson and Swank, 1973). Over the period from 1972 to 1978, the period of herbaceous-to-forest succession, NO_3^- -N concentrations in streamwater declined from about 0.75 mg l^{-1} concurrent with a heavy infestation of the locust stem borer (*Megacyllens robiniae*) and rose to 0.90 mg l^{-1} in 1980 following major infestation by the locust borer. In the subsequent decade, NO_3^- -N concentrations have oscillated but remain elevated above previous time trend levels. Since black locust was the dominant woody species, the infestation was distributed over the entire catchment. Tree mortality was substantial with 21% mortality of black locust population by 1982, 18% with severe injury and many of the remaining stems with some evidence of canopy decline. A variety of hypotheses were investigated to explain the relationship between insect stress and increased NO_3^- loss from the ecosystem. Primary factors contributing to enhanced NO_3^- leaching were reduced uptake due to mortality, significant quantities of nitrogen-rich frass input to the forest floor, enrichment of inorganic and organic N in throughfall and stemflow, and accelerated decomposition of the forest floor with associated high rates of mineralization and nitrification (L.R. Boring and B. Haines, unpubl. data; Montagnini *et al.*, 1986).

Both of these small catchment studies represent some of the clearest demonstrations available of functional, ecosystem-level regulation of biogeochemical cycles by terrestrial insects under epidemic conditions. The nitrogen cycle and associated changes in NO_3^- fluxes serve as a sensitive indicator of ecosystem disturbance, partly because of biological transformations of this nutrient. In most cases, changes in concentrations of other solutes such as cations are difficult to detect because bed-rock mineralogy can easily mask small changes in streamwater ionic composition.

6.6.2 LARGE MAMMALS

Other catchment studies in the southern Appalachian Mountains have shown the influence of large mammals on forest biogeochemical cycles. Rooting by wild pigs (*Sus scrofa*) in a northern hardwood forest in the Great Smoky Mountains National Park accelerated leaching of Ca, P, Zn, Cu and Mg from leaf litter and soil, while

NO_3^- concentrations were also higher in soil, soil water and streamwater on rooted areas (Singer *et al.*, 1984). The observed NO_3^- responses were partly the net effect of changes in nitrogen transformation processes, and partly due to reduced nitrogen uptake and recycling through the elimination of the herbaceous vegetative layer by rooting activity (Swank, 1991).

Research on small streams in Alaska has shown linkages between terrestrial herbivory and aquatic food webs. Moose (*Alces alces* L.) browsing of birch tree leaves increased condensed tannic leaching rate, foliar N concentration and rate of mass loss (Irons *et al.*, 1991). These factors caused birch detritus, a primary energy input to the stream, to be processed more rapidly by stream biota which, in turn, could increase secondary production of stream consumers.

6.7 CONCLUSIONS AND RECOMMENDATIONS

The most important conclusions concerning biota and its importance for biogeochemical processes in catchments are as follows:

1. A catchment, including both the biotic and abiotic components, naturally changes over the long term, depending on climatic and soil conditions. Acidification is a natural process accompanying primary production in humid areas, but strongly accelerated by deposition of mineral acids and nitrogen.
2. Biota are extremely important for understanding the input-output figures of catchments. Organisms cause accumulation of organic matter and the nutrients most needed for production; these are kept in circulation in the ecosystem, usually with only minor losses when the ecosystem matures and is left undisturbed by man. Nitrogen, often a growth-limiting element, is almost entirely organically bound within the catchment.
3. Organic matter, alive or dead, changes the incoming precipitation with respect to both quantity and quality. This result of the presence of organisms in turn depends on a number of abiotic variables in climate and soil chemistry.
4. A great part of deposited heavy metals accumulated in the catchment, bound to organic matter. Runoff concentrations seem to be correlated to soil acidification and leaching of soluble humic substances.
5. Greater losses of nutrients may appear after disturbance by insects and larger herbivores, windfelling, etc.
6. Detritivores within streams have important effects on the amounts of transported organic matter.
7. Soil acidification, high nitrogen deposition, liming, clearfelling, agriculture, nitrogen fertilization and other anthropogenic influences may elicit immediate responses in runoff water. It is obvious that the terrestrial biota are not adapted to change rapidly to prevent leaching effects on the subsoil, groundwater and

stream water ecosystems. Some points for improvement concerning understanding of small catchments and biotic reactions are identified:

- (a) Quantitative estimates at a catchment scale are lacking on microbial transformations of nutrients in relation to nutrient availability, mobilization and loss. For example, denitrification is one of the key processes in the cycling of nitrogen, but there are few estimates of this process on a catchment basis.
- (b) Of special importance in understanding the internal ecosystem processes is to what degree the throughfall measurements reflect dry deposition and/or leaching of elements.
- (c) There is need for concurrent quantification of productivity and nutrient cycling processes on the same catchment for different forest ecosystems and a better understanding of forestry practice impacts on the nutritional "stability" of the catchment.
- (d) We are not very well aware of the different transport mechanisms between different communities of the same catchment and the accumulation rate of mineral elements.
- (e) Different heavy metals, of importance to both the catchment and the neighbouring ecosystems, behave very differently in accumulation and transport mechanisms. We still have very few estimates of their concentrations in catchment biota to understand whether the contents in biota derive from dissolution in the soil or from dry and wet deposition.
- (f) We need better information about "critical loads" of pollutants on a catchment basis, to understand to what extent biota might counteract nitrogen deposition, soil acidification and heavy metal accumulation under different climatic and environmental situations.
- (g) We want to answer the question of whether existing negative effects, especially of nitrate leaching, appear as a result of insufficient time for organisms to spread, evolve and adapt to a new chemical situation. How long will this process continue? Is it the land-use and/or the deposition climate that has to change in order to prevent high nitrogen losses? What is the regional danger for groundwater pollution if biota of the catchments are disturbed? We consider long-term monitoring/research of catchments as a necessary tool not only for understanding ongoing processes, but also for predicting future changes in our environment.

6.8 SUGGESTED READING

There is a large number of excellent books covering the scope of this chapter. Very useful volume on nitrogen and its importance is that of Malanchuk and Nilsson (1989), cycling of sulphur is covered in depth by Howarth *et al.* (1992) and Johnson and Lindberg (1992).

Catchment-oriented discussion of biological research is the main theme of the Swank and Crossley (1988) volume on ecological research at Coweeta. A similar extensive volume is devoted to research at Walker Branch Watershed (Johnson and Van Hook, 1989).

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