

# 14

## Nutrient Cycles and Responses to Disturbance

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### Overview

- This chapter examines the cycling of nitrogen (N), phosphorus (P), and sulfur (S) in stream and river corridors of the Pacific coastal ecoregion under natural and managed conditions.

- In its inorganic form, nitrogen occurs primarily as nitrate ( $\text{NO}_3^-$ ) and ammonium ( $\text{NH}_4^+$ ). Microbially mediated transformations between these species generally move in the direction  $\text{NH}_4^+$  to  $\text{NO}_3^-$  through the process of nitrification. Under anoxic conditions,  $\text{NO}_3^-$  may be further transformed through microbially mediated denitrification into molecules of nitrogen ( $\text{N}_2$ ) and nitrous oxide ( $\text{N}_2\text{O}$ ). Both  $\text{NO}_3^-$  and  $\text{NH}_4^+$  are assimilated by organisms into amino acids and other organic molecules.

- Sulfur occurs as sulfate ( $\text{SO}_4^{2-}$ ) and sulfide ( $\text{S}^{2-}$ ) in its inorganic form, but only  $\text{SO}_4^{2-}$  is available for assimilation by organisms. As with N, the occurrence of  $\text{SO}_4^{2-}$  versus  $\text{S}^{2-}$  depends on redox conditions and microbially mediated reactions, with  $\text{S}^{2-}$  dominating reduced environments and  $\text{SO}_4^{2-}$  dominating oxidized environments.

- Phosphorus is unique relative to nitrogen and sulfur in that it has no redox chemistry. It remains in the (P-O) state in both organic and inorganic forms. In its dissolved inorganic form, it occurs as orthophosphate ( $\text{PO}_4^{3-}$ ), whereas in its organic form it occurs as P-O, bound into larger organic molecules. Phosphorus is also important to organisms in the inor-

ganic form of apatite ( $\text{Ca}_5[\text{PO}_4]_3\text{F}$ ), which forms an essential part of teeth and bones.

- Because these elements are essential nutrients for living organisms, their natural distributions are strongly influenced by biological, as well as chemical and physical processes. Forest plants and microbes are instrumental in the initial uptake of nitrogen from atmospheric sources, and phosphorus and sulfur from geologic sources, and forest to stream transfers are the primary pathways by which these elements are input to river corridors.

- Once in the river corridor, these elements follow a convoluted downstream course, which includes cycling between organic and inorganic forms, chemical species transformations in response to changing redox conditions, sorptive partitioning onto particulate surfaces, movement into and out of streamside soils, and periods of immobilization and storage. The specific course of these reactions and physical trajectories varies mainly as a function of hydrologic regime, temperature, and biological community composition.

- Concentrations and fluxes of nitrogen, phosphorus, and sulfur change in response to changing stream discharge. Fluxes increase with increasing discharge, but concentrations are less predictable and correlations may be positive or negative, depending on the season. Hydrologic exchange between the channel and its hyporheic zone significantly impacts nitrogen, phosphorus, and sulfur cycling, owing to the intensification of biological and sorptive processes in streamside soils and sediments and

to the temporary storage of these elements in hyporheic water.

- Temperature influences elemental distributions mainly by controlling rates of microbial processing.

- The composition of the biological community strongly controls cycling reactions by regulating nutrient uptake and regeneration rates. Pacific salmon (*Oncorhynchus* spp.) act as a net source of marine derived nutrients to the river system, whereas beaver (*Castor canadensis*) strongly influence cycling reactions by modifying the physical structure and hydrologic characteristics of the corridor.

- Natural and anthropogenic disturbances disrupt nutrient cycles by altering the nature of controlling processes (i.e., hydrologic regime, temperature, and biological community).

- Direct logging of river corridors for silvicultural and agricultural purposes profoundly impacts nutrient cycling, although the severity of the impact depends on the logging technique used. In general, dissolved and particulate nutrient concentrations tend to temporarily increase following logging, with  $\text{NO}_3^-$  showing the greatest increase among the measured parameters.

- Forest fertilization using urea (NH<sub>2</sub>-N) may temporarily increase stream nitrogen concentrations by nearly two orders of magnitude, but such concentration spikes are significantly reduced when unfertilized buffer strips are left along stream channels.

- Urbanization also tends to increase nutrient inputs to river corridors while reducing the capacity of the riverine biological community to uptake excess nutrients.

- Fire strongly disrupts nutrient cycles in river corridors, but the net effects on nutrient budgets are difficult to predict. Large amounts of nitrogen may be volatilized as ammonia (NH<sub>3</sub>) during the fire, but rainfall on ash tends to flush increased concentrations into the soil and stream systems.

- Climate change is now an acknowledged phenomenon which is predicted to intensify during the next century. Its impacts on riverine nutrient cycles will come mainly through altered hydrologic regimes, temperatures, and biological communities. Among the few

specific predictions are decreased food quality of leaf litter because of decreased leaf nitrogen content and increased soil organic matter decomposition rates with concomitant decreases in stream inputs.

## Introduction

Rivers are fundamental components of regional and global biogeochemical cycles, acting as both transport pathways and sites of elemental transformations. Coastal rivers of the Pacific Northwest form a particularly dynamic link between the region's highly productive temperate forests and nearby marine ecosystems. Nutrients derived from forests are accumulated in rivers and transferred downstream to estuarine systems. This transfer, however, is highly dynamic as transported nutrients participate in a variety of chemical and biological interactions. These interactions are dominated by sequential processes of biological uptake, remineralization, and microbially mediated redox transformations. An atom of a nutrient species may pass through the sequence of uptake and mineralization many times during its downstream journey, repeatedly cycling between organic and inorganic molecular species.

Three elements of key importance to the structural and physiological requirements of the biota of the river corridor are nitrogen (N), phosphorus (P), and sulfur (S). Under natural conditions, riverine cycles of nitrogen, phosphorus, and sulfur are intricately woven into the overall ecological balance of coastal forest ecosystems. Together, climate and geology produce the soils and moisture regimes that support the forests of the region. The forests, in turn, regulate the initial uptake of nitrogen, phosphorus, and sulfur from atmospheric and geologic sources. These elements are then cycled repeatedly through the forest's trophic system, the components of which are adapted to conserve and retain nutrients. Biological processes exert a primary control on the natural distributions of nitrogen, phosphorus, and sulfur in the recycling nutrient pool, but other abiotic processes such as adsorption to the surfaces of soil minerals also serve to retain nutrients.

The efficiency of nutrient retention in the forest ecosystem is not 100 percent, however, and a small quantity of nitrogen, phosphorus, and sulfur is continually input to streams and rivers. The bulk of these inputs occur through hydrologic flowpaths such as groundwater baseflow, storm flow, and canopy throughfall; biological pathways such as direct litterfall and lateral movement from the adjacent forest floor; and inorganic material flowpaths such as landslides and bank erosion.

A natural disturbance regime is part of healthy forest and river ecosystems (Naiman et al. 1992). Disturbances such as landslides and wildfires promote a more resilient and productive system by introducing heterogeneity. The key to maintaining disturbance as a healthy rather than detrimental influence is to separate events in space and time so as not to overwhelm an ecosystem's natural capacity to recover. In the heavily managed watersheds of the coastal ecoregion, disturbance has become more frequent and intense. Where watersheds have become urbanized, unnatural pressures are more or less continuous. Scientists and managers alike are faced with the challenge of understanding the beneficial aspects of disturbance on nutrient cycles and developing methods of assessing and minimizing the detrimental effects.

This chapter explores the cycling of nitrogen, phosphorus, and sulfur in rivers of the Pacific coastal ecoregion at several levels. It begins by describing the forms and concentrations of nitrogen, phosphorus, and sulfur encountered in riverine systems, the fundamental reactions involved in their cycles, and the principal input and output pathways determining their budgets. Next, it examines the principal biological and environmental variables influencing the direction and rate of cycling processes. Finally, some attention is devoted to the effects of natural and anthropogenic disturbances in temperate forest watersheds, where disturbance amounts to a sudden change in one or more of the variables controlling the course and rate of cycling. Responses of nutrient cycling in Pacific coastal watersheds to disturbances such as deforestation for silvicultural and agricultural purposes, urbanization, and fire are considered.

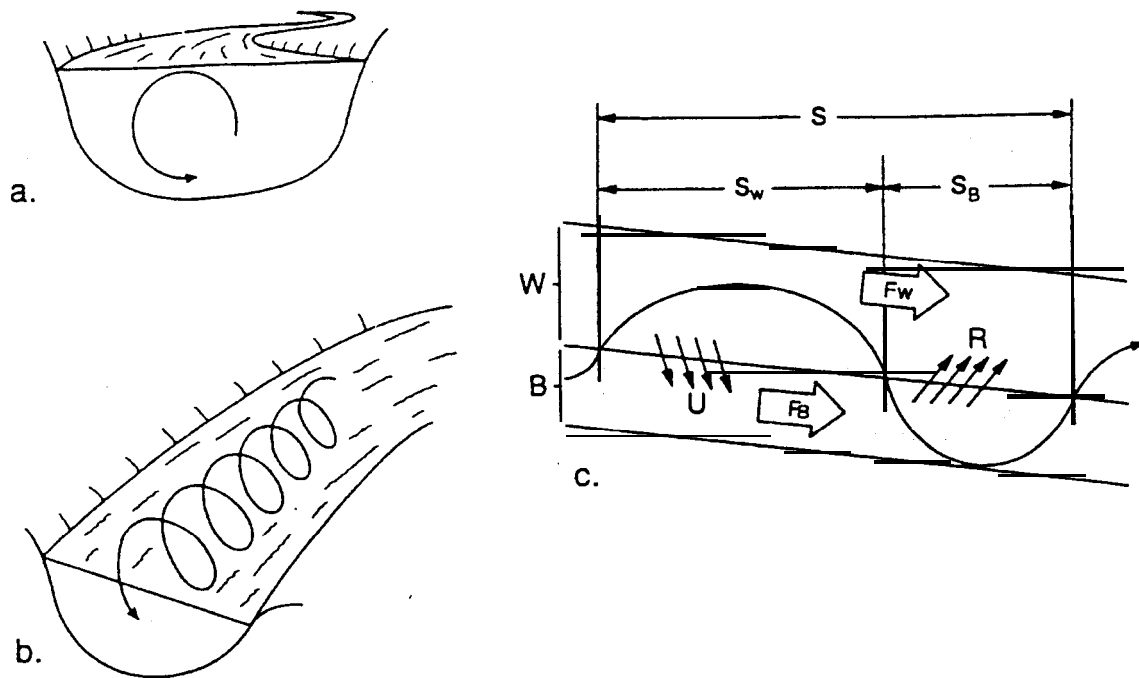
The potential responses of these cycles to changes in global climate are also considered. The goal is to clarify the relationships between disturbances and underlying cycling processes, thereby conveying a more process-based understanding of the consequences of watershed management decisions.

## The Basics of Nitrogen, Phosphorus, and Sulfur Cycling

*Webster's Seventh New Collegiate Dictionary* defines cycling as "a course or series of events or phenomena that recur regularly and usually lead back to the starting point" (Figure 14.1a). *Biogeochemical cycling*, as used in ecosystem sciences, generally refers more broadly to a whole set of processes involving the element of interest, including physical transport and storage, changes in form (organic vs inorganic, solute vs particulate), and chemical transformations in elemental speciation (oxidation state, complexation) and association (adsorption). Cycling in the literal sense does occur, however, if the "starting point" is considered a chemical form rather than physical point.

## Nutrient Spiraling

In riverine ecosystems, transport is clearly an important component of all biogeochemical cycles, but because of the unidirectional nature of river flow, the completion of a cycle does not return an atom to its physical starting point. Instead, the atom is displaced some distance downstream, thereby stretching the visualized circular cycle into the shape of a spiral (Figure 14.1b). The concept of nutrient spiraling was developed in the late 1970s and early 1980s (Webster and Patten 1979, Newbold et al. 1982, Elwood et al. 1983) and remains a useful framework in which to examine the cycling of nutrients in rivers. According to the concept, one idealized cycle is completed when a nutrient atom has, in sequence, been taken up by an organism from a dissolved available state, passed through the food chain, and returned to a dissolved available state for reutilization



**FIGURE 14.1.** Schematic representations of nutrient spiraling. (a) Simple cycling with no consideration of transport. (b) Combined cycling and transport, with resulting spiral form. (c) Representation of spiraling between inorganic (dissolved in water column, W) and organic (bound in organisms or organic detritus, B) compartments. **Spiraling length (S)** is the total downstream distance over which a cycle is com-

pleted;  $S_w$  and  $S_B$  are the downstream distances over which nutrients are transported in the inorganic and organic forms, respectively.  $F_w$  and  $F_B$  represent the downstream fluxes in each compartment per unit width of channel, and  $U$  and  $R$  represent areal rates of nutrient uptake and regeneration (from Newbold 1992. Reprinted by permission of Blackwell Science, Inc.)

(Newbold et al. 1982). Two particularly important qualities of the concept are that it explicitly considers the longitudinal connectedness of river corridors, and it provides a simple quantitative framework in which to evaluate system variables such as productivity, remineralization, and nutrient limitation.

*Spiraling length (S)*, the longitudinal distance in the concept. For any nutrient (n),  $S_n$  is represented by the basic equation

$$S_n = Vt_c,$$

where  $V$  is the average downstream velocity of the nutrient atom and  $t_c$  is the average time required for the nutrient atom to complete one cycle. The uptake ( $U$ ) and regeneration ( $R$ ) of nutrients by the biotic community of the stream are critical terms in determining spiraling lengths (Figure 14.1c). Under ideal conditions, when  $U = R$ ,  $S$  may be expressed by as a simple

function of a nutrient's biotic uptake rate ( $U$ , in mass/area/time) and its total downstream flux per unit width ( $F_t$ , in mass/length/time) in the inorganic and organic forms:

$$S = \dagger \frac{F_t}{U} \quad (14.1)$$

For a more detailed quantitative development of the concept and a discussion of its applicability to questions of nutrient limitation and nutrient retention, the reader is referred to Newbold (1992). The general concept of nutrient spiraling is also useful because it can be effectively incorporated into larger riverine ecosystem theories such as the river continuum concept (Vannote et al. 1980) serial discontinuity concept (Ward and Stanford 1983), patch dynamics concept (Pringle et al. 1988) flood pulse concept (Junk et al. 1989), and riverine productivity model (Thorp and Delong 1994).

## Natural Forms, Distributions, and Transformations

Nitrogen, phosphorus, and sulfur occur in a variety of chemical forms which alternate as cycling reactions proceed (Table 14.1; Figure 14.2). In keeping with the idealized cycle presented in the previous paragraph, the first step in the cycle is biological uptake (assimilation) of these elements in their dissolved available states. In the cases of nitrogen and sulfur, assimilation is almost always accompanied by a decrease in the oxidation state of the element. The main exception is the assimilation of ammonium ( $\text{NH}_4^+$ ), which involves no redox reactions. Phosphorus occurs in only one oxidation state (+5), so redox reactions do not directly influence its cycling.

Nitrogen is available to plants primarily in the form of nitrate ( $\text{NO}_3^-$ ) and ammonium ( $\text{NH}_4^+$ ) (Figure 14.2a). Certain plants that contain symbiotic nitrogen-fixing bacteria (*Rhizobium*) in their roots are able to utilize gaseous nitrogen ( $\text{N}_2$ ) directly. Red alder (*Alnus rubra*) is one such plant in the Northwest that is particularly important. Nitrogen-fixing bacteria also have been identified in association with decaying wood in streams (Buckley and Triska 1978). Triska et al. (1989a) measured the uptake of  $\text{NO}_3^-$  injected into the stream channel of Little Lost Man Creek in northern California. Over the course of their 10-day injection experiment, approximately 19% of injected  $\text{NO}_3^-$  was taken up by the stream's biota, which amounted to an average uptake rate of  $26 \text{ mg/m}^2/\text{d}$ . Uptake rates were greatest during daylight hours but continued through the night.

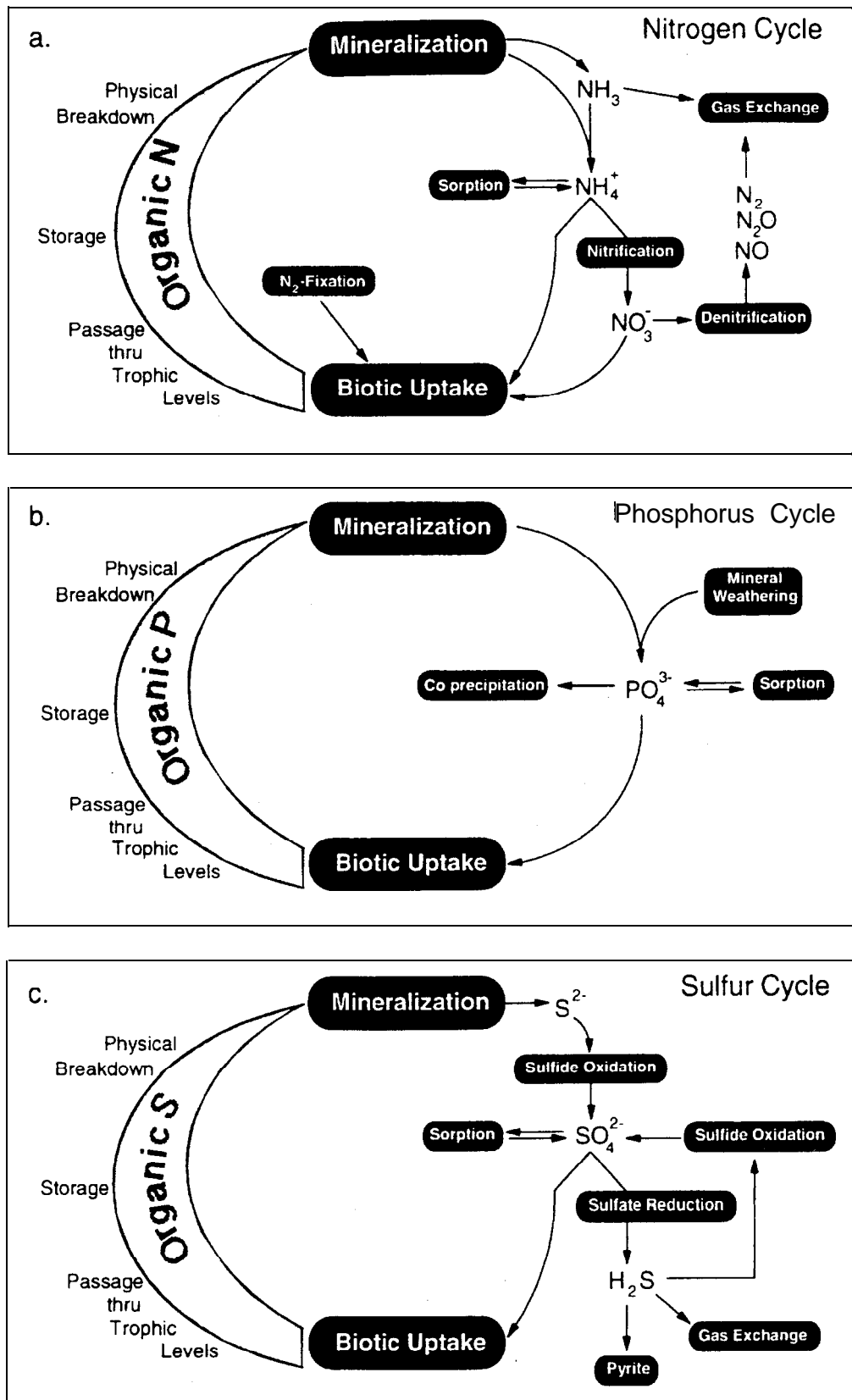
Phosphorus is available to plants in the form of orthophosphate ( $\text{PO}_4^{3-}$ ), which is also the only inorganic form in which phosphorus occurs in appreciable amounts (Figure 14.2b). Gregory (1978) examined isotopically labeled ( $^{32}\text{P}$ )  $\text{PO}_4^{3-}$  uptake by primary producers in Mack Creek, Oregon, and found epilithic algae to exhibit higher  $\text{PO}_4^{3-}$  uptake rates than either filamentous algae or riparian vegetation. He noted, however, that because of its larger standing crop, riparian vegetation may assimilate larger amounts of  $\text{PO}_4^{3-}$ .

Sulfur is available in the form of sulfate ( $\text{SO}_4^{2-}$ ), which is the predominant dissolved inorganic form of sulfur in oxygenated river waters (Figure 14.2c). Rates of  $\text{SO}_4^{2-}$  uptake have not been measured in Pacific coastal rivers. Animals, of course, can only acquire these elements by ingesting them in an already organic form. This may occur several times as the organically bound element makes its way through the food chain.

Once incorporated by plants and animals, each of these elements serves vital metabolic and structural functions. Nitrogen is a component of all amino acids and therefore proteins. In this form it contributes to many functions, including structural support, movement, and defense against foreign substances. As a component of enzymes it catalyzes chemical reactions in cells. Nitrogen also occurs in alkaloids and urea  $\text{CO}(\text{NH}_2)_2$ . Organic forms of phosphorus include such important molecules as nucleic acids (RNA and DNA), adenosine triphosphate (ATP), and phospholipids (components of cell membranes). As a component of bones and teeth, phosphorus occurs with calcium (Ca) as the mineral apatite

TABLE 14.1. Species of nitrogen (N), phosphorus (P), and sulfur (S) encountered in river corridors.

Aqueous	Gas	Mineral	Organic
$\text{NO}_2^-$ (nitrite), $\text{NO}_3^-$ (nitrate)	$\text{N}_2$ , (nitrogen), $\text{N}_2\text{O}$ (nitrous oxide)	—	CO-HN, (amines)
$\text{NH}_4^+$ (ammonium)	NO (nitrogen oxide), NH <sub>3</sub> (ammonia)	—	$\text{CH}_2\text{-NH}_2$ (amides)
$\text{PO}_4^{3-}$ (phosphate)	—	$\text{Ca}_5(\text{PO}_4)_3\text{F}$ (apatite)	P-O,
$\text{SO}_4^{2-}$ (sulfate),	$\text{H}_2\text{S}$ (hydrogen sulfide)	FeS (pyrite)	$\text{CH}_2\text{-SH}$ (thiol)
$\text{HS}^-$ (hydrogen sulfide)	—	—	$\text{CH}_3\text{-S-CH}_3$ (sulfide)
$\text{S}^{2-}$ (sulfide)	—	—	-SS- (disulfide)



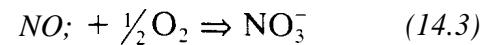
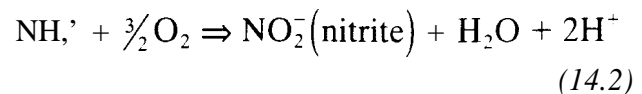
**FIGURE 14.2.** (a) nitrogen, (b) phosphorus, and (c) sulfur cycling. Element species are shown along with processes determining their concentrations and compositions.

(Ca<sub>5</sub>[PO<sub>4</sub>]<sub>3</sub>F). Sulfur is less abundant than nitrogen and phosphorus in living organisms, but nevertheless it serves essential functions as a component of two amino acids (cysteine and methionine) and several other less abundant molecules. Occurrence in living tissue represents the intersection point in the cycles of nitrogen, phosphorus, and sulfur. In the organic form, these elements co-occur in more or less constant proportions, roughly 35 : 2 : 1 in plants (Campbell 1990).

At the time of death, decomposition and mineralization reactions combine to transform nitrogen, phosphorus, and sulfur back into inorganic forms. These reactions rely on the action of heterotrophic bacteria and fungi who utilize reduced carbon as an energy source and liberate organically bound nitrogen, phosphorus, and sulfur in the process. Nitrogen emerges from these reactions in the form of ammonia (NH<sub>3</sub>) and NH<sub>4</sub><sup>+</sup> (Figure 14.2a). Although some of the NH<sub>3</sub> may volatilize (Freney et al. 1983), in the acidic waters common to the Pacific coastal ecoregion, most rapidly reacts with free protons (H<sup>+</sup>) to produce NH<sub>4</sub><sup>+</sup>. At this point, remineralized nitrogen is available for reutilization by organisms and the idealized cycle is effectively complete.

Various other energy-producing reactions may occur prior to nitrogen reassimilation. In anaerobic waters, NH<sub>4</sub><sup>+</sup> remains the stable form of dissolved inorganic nitrogen, but in aerobic river waters its concentrations are generally low. In Pacific coastal rivers and streams, natural concentrations of NH<sub>3</sub> are generally less than 1mM, but in oxygen depleted hyporheic waters adjacent to the stream concentrations may exceed 20mM. Another factor contributing to low ambient concentrations of NH<sub>4</sub><sup>+</sup> is its adsorption to cation-exchange sites on streambed sediments and adjacent hyporheic soils. At Little Lost Man Creek, California, Triska et al. (1994) reported concentrations of exchangeable NH<sub>3</sub> ranging from 10meq/100g sediment in the stream channel to 115 meq/100g soil in the hyporheic zone 18m inland of the channel.

Under aerobic conditions, NH<sub>4</sub><sup>+</sup> is oxidized to NO<sub>3</sub><sup>-</sup> in a two-step *nitrification* process which may be represented as follows:



These reactions are carried out by autotrophic bacteria of the genera *Nitrosomonas* and *Nitrobacter*, respectively. There are several possible intermediate compounds, the most important of which is nitrous oxide (N<sub>2</sub>O), a greenhouse gas that may be lost from the ecosystem by gas exchange. Nitrate is relatively unreactive with organic or mineral surfaces. Thus, upon entering aqueous environments it moves freely downstream until taken up once more by the biota or transformed through redox reactions. In Pacific coastal rivers, natural concentrations of NO<sub>3</sub><sup>-</sup> range from near 0 to 30mM.

If NO<sub>3</sub><sup>-</sup> is transported into an anoxic zone, such as generally occurs in streambed sediments, the hyporheic zone, or some micro-zone within a particle of degrading organic matter, it may be reduced by *denitrification* to N<sub>2</sub>. The gases NO (nitrogen oxide) and N<sub>2</sub>O are also byproducts of denitrification. These gases are generally lost from the ecosystem, thereby balancing the N<sub>2</sub> input via nitrogen-fixation (Jaffe 1992). The hyporheic zone is a particularly important site of denitrification reactions (Triska et al. 1993). In the hyporheic zone of Little Lost Man Creek, Duff and Triska (1990) reported increasing rates of denitrification with increasing distance from the stream channel and decreasing amounts of dissolved oxygen.

Phosphorus released from decomposing organic matter reenters the aquatic ecosystem as PO<sub>4</sub><sup>3-</sup> (Figure 14.2b). Natural concentrations of PO<sub>4</sub><sup>3-</sup> in Pacific coastal streams and rivers are generally less than 1mM (see Chapter 4). At neutral or acidic pH, PO<sub>4</sub><sup>3-</sup> is generally bonded to one or two hydrogen (H) atoms in the forms of phosphoric acids, HPO<sub>4</sub><sup>2-</sup> and H<sub>2</sub>PO<sub>4</sub><sup>2-</sup>. Like the first NH<sub>3</sub> to emerge from the organic form, this PO<sub>4</sub><sup>3-</sup> is immediately available for reutilization and the idealized cycle is complete. However, again several reactions may occur before reassimilation. Concentrations remain low in natural riverine systems due to strong

*adsorptive* reactions with iron ( $\text{FeO}_x$ ) and aluminum oxides ( $\text{AlO}_x$ ) and clay minerals. These adsorption reactions, along with *coprecipitation* reactions with Fe III, Ca, and Al, make  $\text{PO}_4^{3-}$  biologically unavailable to organisms. Because of adsorption, coprecipitation, and biotic assimilation, total phosphorus concentrations in river corridors are generally dominated by particulate forms of the element. This is especially true where phosphate minerals such as apatite occur.

Sulfur liberated from decomposing organic matter reenters the inorganic form as sulfide ( $\text{S}^{2-}$ ), but is quickly oxidized to  $\text{SO}_4^{2-}$  (*sulfide oxidation*) and is again available for reutilization (Figure 14.2c). The behavior of  $\text{SO}_4^{2-}$  at this stage is similar to that of  $\text{NO}_3^-$ , in that it too is rather inert and moves more or less freely with the flowing water, although not as freely as  $\text{NO}_3^-$ . Sulfate has not been analyzed in many Pacific coastal rivers but, where data are available, concentrations range from 10 to 30 mM (see Chapter 4). When  $\text{SO}_4^{2-}$  is transported into an anaerobic zone, it is reduced (*sulfate reduction*) by the action of heterotrophic bacteria to hydrogen sulfide ( $\text{H}_2\text{S}$ ). The  $\text{H}_2\text{S}$  produced may then react with  $\text{Fe}^{2+}$  to form the mineral pyrite ( $\text{FeS}_2$ ), or it may be transported back into an aerobic zone where it reacts spontaneously with oxygen and is oxidized back to  $\text{SO}_4^{2-}$  (Chen and Morris 1972).

As breakdown and mineralization reactions proceed, a fraction of the organically bound nitrogen, phosphorus, and sulfur persists in the refractory residual pool of particulate organic matter (POM). Coarse POM ( $>63 \mu\text{m}$ ) is often identifiable as fragments of plant litter, but fine POM is composed largely of molecularly unidentifiable and refractory organic matter termed *humins* (Hatcher and Spiker 1988). Fine POM remineralizes over long periods (months to years) and is subject to physical processes of transport and storage, as well as abiotic sorptive reactions with other organic matter or mineral surfaces.

The great variety of transformations involving nitrogen, phosphorus, and sulfur adds considerable complexity to the idealized representation of cycling within the nutrient spiraling concept (Figure 14.2a-c). Moreover, rivers

are open systems, where nitrogen, phosphorus, and sulfur are continually exchanged with adjoining terrestrial and atmospheric systems and output to the ocean. These input and output fluxes are examined more closely in the following section.

## Input-Output Pathways and Riverine Budgets

Nitrogen, phosphorus, and sulfur enter riverine ecosystems via several hydrological, geological, and biological flowpaths (Figure 14.3). Fluxes along these flowpaths are reported as mass per area of river surface per unit time (e.g.,  $\text{kg/m}^2/\text{s}$ ) or mass per distance of river length per time ( $\text{kg/m/s}$ ). Total fluxes to the river are **calculated** by multiplying these values by the total area or length of the river, respectively. Similarly, exports from the river may be reported in these units when considering lateral flowpaths like gas exchange, but exports associated with river discharge are reported simply as mass per time (e.g.,  $\text{kg/s}$ ). Groundwater baseflow is a continuous hydrologic flowpath, while stormflow and canopy throughfall are episodic and strongly seasonal. Geologic flowpaths, such as erosion, also are episodic and largely associated with seasonal precipitation patterns. The biological pathways of direct litterfall from the overhanging forest canopy and lateral movement from the adjacent forest floor are seasonally variable but continuous throughout the year. All input flowpaths are active along the entire length of river systems. Their relative importance, however, may vary in response to changing geomorphology, riparian plant communities, and channel size. Output pathways are less numerous than input pathways. Clearly the dominant pathway is river discharge to estuaries, but nitrogen and sulfur are also lost along the river's length via gas exchange ( $\text{N}_2$ ,  $\text{N}_2\text{O}$ ,  $\text{NO}$ ,  $\text{H}_2\text{S}$ ) with the atmosphere (Figure 14.3).

A technique which has proven particularly informative in investigating ecosystem nutrient cycles is the construction of input-output budgets. Budgets are calculated by subtracting the sum of output fluxes from the sum of input fluxes. Differences in the fluxes reflect net ecosystem processes such as nutrient accumulation

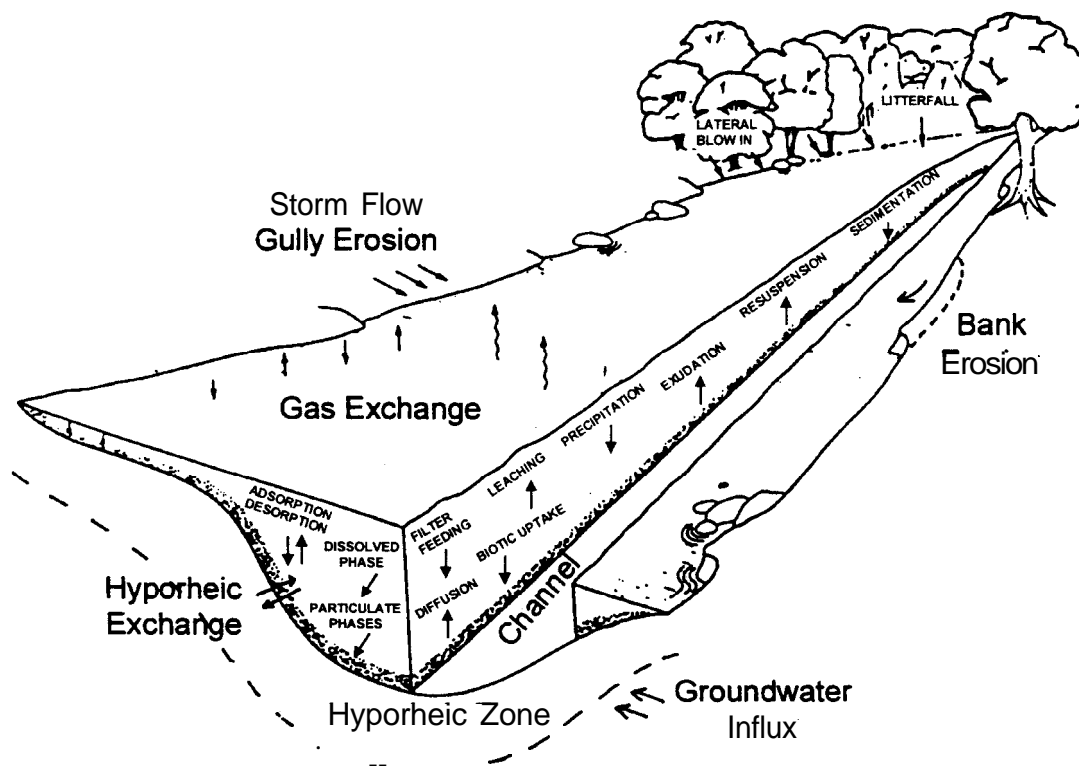


FIGURE 14.3. Physical, chemical, and biological pathways and processes impacting nitrogen (N), phosphorus (P), and sulfur (S) cycling in Pacific coastal

streams and rivers (modified from Meyer et al. 1988 with permission).

or depletion. Nutrient budgets are most often constructed at the scale of the entire watershed, where precipitation represents the dominant input and stream and groundwater discharges the dominant outputs (Likens et al. 1977). Budgets such as this have been constructed for nitrogen, phosphorus, sulfur and other elements in several Pacific coastal watersheds (Fredriksen et al. 1975, Scrivener 1975, Feller and Kimmins 1979, Larson 1979).

Unfortunately, budgets for the streams themselves are rarely determined. One exception is the work of Triska et al. (1984), who constructed such a budget for nitrogen in a small stream in the western Cascades of Oregon (H.J. Andrews Experimental Forest, Watershed 10). By considering input-output flux pathways and nitrogen forms individually, these researchers succeeded in developing a detailed stream budget which also shed light on internal ecosystem processes. For the two years of data they reported, 74% of nitrogen input to the stream was in the dissolved form through groundwater baseflow and canopy throughfall, 21% of input occurred through litterfall and

lateral movement, and the remaining 5% of input occurred through  $N_2$  fixation within the stream channel (Table 14.2). Overall, more than 90% of the nitrogen input to the stream was organic and derived from biotic sources in the surrounding forest. Inputs of dissolved inorganic nitrogen ( $NO_3^-$ ,  $NO_2^-$ ,  $NH_4^+$ ) accounted for less than 5% of nitrogen inputs. Total nitrogen inputs exceeded total outputs by 34%, indicating significant retention of nitrogen within the stream ecosystem during the period of the study. The greatest degree of retention and processing was in the pool of nitrogen held in leaf and needle litter. Only 13% of nitrogen input as leaf and needle litter exited the watershed in a recognizable form, indicating that 87% was either mineralized, leached into dissolved form, or broken down into unrecognizable fine POM. Of the nitrogen input as wood, only 40% was output from the reach. The remaining 60% was retained in the stream, mostly in storage, but some fraction also contributed to the growing pool of fine POM. Fine POM is more easily transported in the stream system, and although it is more refractory, it

TABLE 14.2. Nitrogen budget for Watershed 10 at the H.J. Andrews Experimental Forest.

Pathway	Form	g/m <sup>2</sup>	% Total
Nitrogen inputs			
Groundwater baseflow	NO <sub>3</sub> <sup>-</sup> -N (nitrate)	0.50	3
	DON (dissolved organic nitrogen)	10.56	69
Throughfall	Organic	0.30	2
Litterfall	Organic	1.35	9
Lateral movement	Mixed	1.78	12
In-stream N <sub>2</sub> -fixation	Organic	0.76	5
Total		15.25	100
Nitrogen outputs			
Stream discharge	NO <sub>3</sub> <sup>-</sup> -N (nitrate)	0.43	4
	DON (dissolved organic nitrogen)	8.38	74
	LPON (large particulate organic nitrogen)	0.87	7
	FPON (fine particulate organic nitrogen)	1.66	15
Denitrification	N <sub>2</sub> (nitrogen), N <sub>2</sub> O (nitrus oxide)	2	7
	Total	11.36	100

From Triska et al. 1984.

constitutes an important input of nitrogen and other nutrients to downstream reaches. Magnitudes of nitrogen loss via gas exchange were not quantified, but they were assumed to be minimal (Triska et al. 1984).

Although comprehensive stream budgets have not been constructed for phosphorus and sulfur in the Pacific coastal ecoregion, within the organic forms, phosphorus and sulfur budgets are expected to be similar to that of nitrogen. Organic forms input via litterfall and lateral movement are largely retained in the stream channel. It may be, however, that fluxes

of inorganic phosphorus and sulfur are proportionally more important than those for N. This prediction stems from two important points; phosphorus and sulfur occur in organic matter in smaller concentrations than nitrogen, and, whereas the ultimate source of nitrogen is the atmosphere and all sources to the stream depend on plant-derived nitrogen, both phosphorus and sulfur have geological sources, which release these elements through mineral weathering.

Table 14.3 summarizes the forms of nitrogen, phosphorus, and sulfur encountered in riverine

TABLE 14.3. Summary of reactions impacting nitrogen (N), phosphorus (P), and sulfur (S) cycling.

Process/reaction	Reactant(s)	Product(s)	Mediator
Assimilation	NO <sub>3</sub> <sup>-</sup> (nitrate), NH <sub>4</sub> <sup>+</sup> (ammonium) PO <sub>4</sub> <sup>3-</sup> (phosphate), SO <sub>4</sub> <sup>2-</sup> (sulfate)	Organic N, P, S	Plants, fungi, bacteria
Mineralization	Organic N, P, S	NH <sub>3</sub> (ammonia), NH <sub>4</sub> <sup>+</sup> , PO <sub>4</sub> <sup>3-</sup> , S <sup>2-</sup> (sulfide)	Bacteria, fungi
Nitrification	NH <sub>3</sub>	NO <sub>2</sub> <sup>-</sup> (nitrite), NO <sub>3</sub> <sup>-</sup>	Bacteria
Denitrification	NO <sub>3</sub> <sup>-</sup>	N <sub>2</sub> , N <sub>2</sub> O (nitrous oxide), NO (nitrogen oxide)	Bacteria
Sulfate reduction	SO <sub>4</sub> <sup>2-</sup>	H <sub>2</sub> S (hydrogen sulfide)	Bacteria
Sulfide oxidation	S <sup>2-</sup>	SO <sub>4</sub> <sup>2-</sup>	Bacteria
Adsorption	NH <sub>4</sub> <sup>+</sup> , PO <sub>4</sub> <sup>3-</sup> Organic N, P, S	Sorbed forms	Abiotic
Coprecipitation	PO <sub>4</sub> <sup>3-</sup> , S <sup>2-</sup>	Amorphous Fe (iron) and Al (aluminum) oxides, FeS (iron sulfide)	Abiotic

systems, the fundamental reactions involved in their biogeochemical cycles, and the principal input and output pathways determining their budgets. The environmental variables determining the course and rate of these cycles are treated next.

## Controlling Variables in Nitrogen, Phosphorus, and Sulfur Cycling

The natural distributions and cycling of nitrogen, phosphorus, and sulfur in riverine ecosystems are determined by the balance of inputs, internal processing, and outputs. These factors, in turn, respond to an interrelated suite of environmental variables including the hydrologic regime, temperature (air and water), and the composition and activity of the biological community. In the Pacific coastal ecoregion, relatively strong gradients in these variables occur with changing altitude, latitude, and season.

### Hydrologic Regime

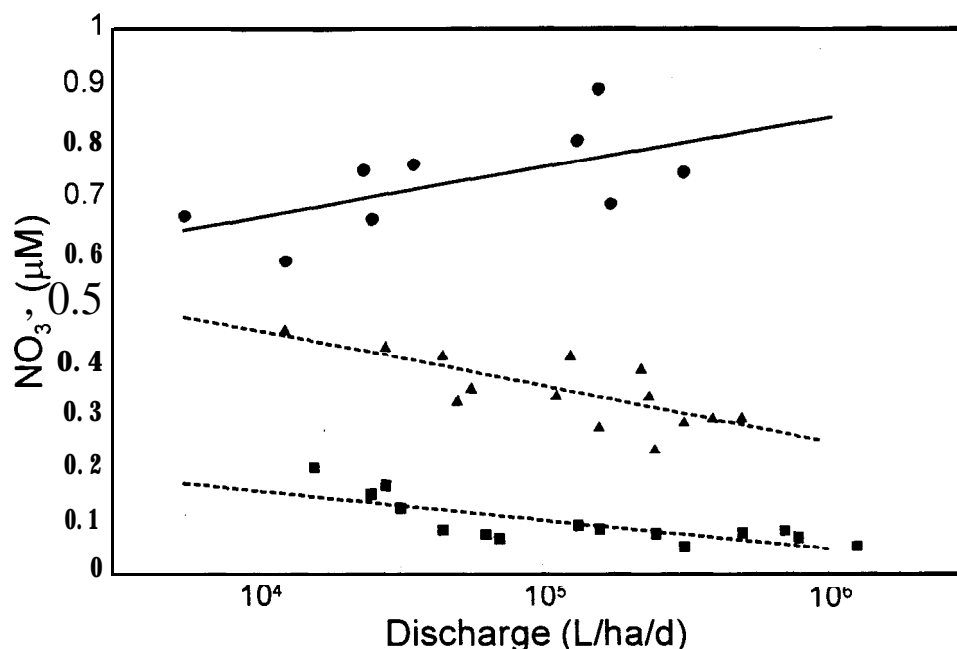
Hydrologic regimes permeate every facet of nitrogen, phosphorus, and sulfur cycling, because of the primary role of water as a transport medium and solvent. Water also reduces gas diffusion rates, thereby promoting anoxia in organic-rich bed sediments or hyporheic soils where oxygen consumption exceeds oxygen influx rates. While biological processes mainly vary seasonally and diurnally, hydrologic regimes vary on the scale of individual storm events. Sudden increases in river discharge (freshets) wash in large amounts of organic and inorganic debris, flush out areas of stagnant surface water and groundwater, and generally stir up the system. The flushing action of freshets may even aerate previously anoxic zones. Precipitation feeding the increased discharge washes the tree canopy and transfers the leached material to the river by direct throughfall or overland flow pathways. During the course of a freshet, concentrations of sus-

pended matter in the river swell and both dissolved and particulate loads increase (Bilby and Bisson 1992). Less dramatic seasonal patterns in hydrologic regime also occur. Increased baseflow during the winter rainy season produces wetlands and wider channels. The degree of seasonality in discharge and the intensity of freshets varies geographically with latitude. Thus, multi-temporal variations in hydrologic regime are superimposed on geographic variations, producing complex patterns of variability (see Chapter 3).

It is not easy to predict how dissolved inorganic nitrogen, phosphorus, and sulfur concentrations will respond to increasing discharge. In order for concentrations to rise, storm waters must dissolve more nutrients (per liter) than baseflow waters. This is the case during autumn freshets when new rains dissolve nutrients that have accumulated in the forest canopy, forest floor, and upper soil horizons during the preceding dry season. Later in the rainy season, however, after the forest has been repeatedly washed by winter rains, the discharge relationship breaks down or becomes negative (representing dilution by storm water).

Clear correlations between discharge and nitrogen, phosphorus, and sulfur concentrations in undisturbed Pacific coastal rivers are rare. Positive correlations between discharge and concentrations of  $\text{NO}_3^-$  (Scrivener 1975),  $\text{SO}_4^{2-}$  (Scrivener 1975, Feller and Kimmins 1979) and  $\text{PO}_4^{3-}$  (Fredriksen 1975, Gall 1986) have been reported, but they are not consistent in time or between studies. Scrivener (1975) reported positive correlations between  $\text{NO}_3^-$  and discharge only during autumn freshets; later in the autumn and winter the relationship became negative (Figure 14.4). Similarly, both Scrivener (1975) and Feller and Kimmins (1979) reported positive correlations between discharge and  $\text{SO}_4^{2-}$  only on select occasions; otherwise correlations were unclear or negative. No data are available concerning correlations between discharge and dissolved organic forms of these elements.

Regardless of the significance of concentration-discharge relationships, overall fluxes of dissolved and particulate inorganic and organic



**FIGURE 14.4.** Nitrate ( $\text{NO}_3^-$ ) concentrations as a function of discharge during three freshets at Carnation Creek, British Columbia, Canada (●; October 12-14, 1973, A; October 18-20, 1973, and ■; February 5-14, 1974). Trends illustrate the positive correlation between  $[\text{NO}_3^-]$  and discharge at the beginning of the

rainy season and the subsequent negative correlation. The positive correlation is thought to result from the flushing of accumulated  $\text{NO}_3^-$  from plants and soils, whereas the later negative trend results from dilution of baseflow stream water by low- $\text{NO}_3^-$  storm runoff (modified from Scrivener 1982).

nitrogen, phosphorus, and sulfur tend to increase with increasing flow. High flows create higher energy environments in rivers which suspend and transport previously deposited sediment and organic particulate material (Chapter 2). These materials, along with their associated nutrients, are carried downstream until energy levels decrease and they are again deposited. When plant litter and soils eroded from the adjacent hillslopes are added to this in-stream derived load, increases in downstream fluxes of particulate matter may become substantial.

Hydrological characteristics determine the dimensions of the hyporheic zone, the area beneath and adjacent to the channel where stream water mixes with upland groundwater. Many chemical and biological processes which play a key role in controlling the nutrient dynamics of stream systems occur in the hyporheic zone (Chapter 16). The size of the zone within which these processes may operate depends on the interaction between exchange flow out of the river channel and groundwater inflow from up-

lands. Upland groundwater influxes are controlled by upland water table gradients and the permeability of upland soils. Similarly, exchange between a river and its hyporheic zone is strongly dependent upon channel hydraulics (i.e., pressure gradients) and the grain size of channel bed sediments. In general, irregularities in stream channel shape and coarse bed sediments promote exchange. During tracer injection experiments at Little Lost Man Creek in northern California, Triska et al. (1989b) found hyporheic water 10m from the stream channel to contain 47 to 76% stream water, with the remaining water derived from upland groundwater inputs. Triska et al. (1989b) estimated nominal travel times ranging from 5 to 19 days for stream derived water to reach the 10-m distance. This illustrates the role of the hyporheic zone as a transient storage point for stream water during downstream transport, but from a nutrient standpoint, the hyporheic zone may very well be a final sink for  $\text{NO}_3^-$  and  $\text{SO}_4^{2-}$  which may be reduced to  $\text{N}_2$  and  $\text{H}_2\text{S}$ , respectively, and released to the atmosphere. Slow

water movement through the hyporheic zone, coupled with biotic uptake by riparian vegetation (Gregory 1978), greatly reduces nutrient spiraling lengths relative to those exhibited by atoms of the same nutrient in the open water of the channel.

## Temperature

Temperature is a fundamental variable in many of the processes involved in nutrient cycling. It varies daily and seasonally as well as along latitudinal and altitudinal geographic gradients. Naiman and Anderson (1996) reported mean annual water temperatures which decreased from 15 °C in central California to about 3°C in south-central Alaska. Above 48°N latitude, mean annual minimum temperatures drop to below 0°C, while at the southern extreme of the ecoregion mean annual maximum temperatures exceed 25°C. The diurnal range in temperatures decreases with increasing latitude.

Changing temperatures impact the biotic and abiotic processes that govern nutrient movement through riverine systems. As temperatures increase, so does microbial activity. This leads to higher rates of plant litter processing and higher rates of redox reactions. These reactions increase rates of both nutrient mineralization and uptake, depending upon the reaction considered. Plant metabolism is also accelerated by increasing temperatures, thereby increasing nutrient uptake. The metabolic rate of invertebrates, fishes and other cold-blooded stream animals increases with temperature, necessitating increased rates of food intake, and thus nutrient assimilation, and increased elimination of waste products. In cold-water streams ( $\leq 1-2$  °C), an interesting condition may develop where bacterial activity is shut down but algal production is not (J. Stockner, personal communication).

## Biological Community Composition

The biological community occupying the river corridor plays a key role in nearly every aspect of nitrogen, phosphorus, and sulfur cycling. It comprises not only channel communities and

processes, but also communities and processes in riparian zones, floodplains, and even the river's estuary. Plant litter from riparian and aquatic plants are major sources of nutrients to the river. Plants also remove and temporarily store an appreciable mass of these nutrients through uptake from channel and hyporheic waters (Chapter 12). Microbial communities mediate chemical transformations of nitrogen, phosphorus, and sulfur including dissimilatory-transformations and redox reactions as well as assimilatory uptake and biosynthesis (Meyer 1994). Riverine invertebrate and fish communities ingest various forms of organic matter and associated nutrients (Chapters 8, 9, and 15). These organisms subsequently release nutrients in waste products and as they decompose after death.

Susceptibility of litter to microbial decomposition and consumption by invertebrates varies by plant species, with important consequences for the availability of elements to higher trophic levels (Chapter 6). Input vectors for plant nutrients include direct litterfall (primarily autumn) as well as more stochastically driven lateral transport, lateral movement, and flooding of adjacent riparian zones. Herbaceous vegetation provides the most labile nutrient source to channel communities due to generally higher content of nitrogen phosphorus, and sulfur, and lower content of metabolically refractory structural tissues such as cellulose and lignin. The degree of direct nutrient availability for biosynthesis is termed "quality." Litter quality generally proceeds from annual herbaceous to deciduous to coniferous to woody debris. A natural, intact, riparian corridor provides a variety of litter types, which decompose at various rates and are introduced to the channel by a variety of seasonal and stochastic vectors. As a result, a significant mass of nutrients is almost always available in various states of decay to the channel community.

Nutrients such as nitrogen, assimilated by microbial decomposers, can actually increase the nutrient capital of decomposing litter as refractory structural components such as cellulose and lignin are partially digested. The result is a lowering of the carbon to nitrogen (C : N) ratio in decomposing litter which improves

food quality for litter consuming invertebrates known as shredders. This improvement in food quality is termed *conditioning*. The conditioning process is especially important in Pacific coastal streams where much of the litter is refractory. Anderson and Grafius (1975) demonstrated the importance of conditioning time on decay and consumption of red alder litter and Sedell et al. (1975) reported similar findings on needle litter in Oregon streams. Triska and Buckley (1978) reported increases in nitrogen capital during decomposition of Douglas-fir (*Pseudotsuga menziesii*) litter from six Oregon coastal and Cascade streams. They also reported that invertebrate biomass associated with litter packs tended to be greatest on litter with the lowest C:N ratio.

Nutrient uptake from channel water supports primary production (photosynthesis) by both benthic (periphyton) and planktonic algae (Chapter 7). In oligotrophic waters primary production can result in large diel shifts in nutrient concentration under low-flow conditions. The magnitude of diel shifts depends on stream order because channel width determines canopy cover, and heavy shading inhibits photosynthesis. Gregory (1979) reported virtually no  $\text{NO}_3^-$  uptake on a 1st-order stream in the Oregon Cascades but a greater than 80%  $\text{NO}_3^-$

decrease from midnight concentration in a 5th-order stream (Figure 14.5). Thus primary production by benthic algae can be a significant mechanism for dissolved nutrient retention. Nutrient transformation into tissue also produces an important food resource to grazer invertebrates, which are themselves a major link in the lotic food chain. Egesta from grazer and shredder invertebrates constitutes effective breakdown and repackaging of nutrients in particulate organic forms which are more transportable in the river current. Conversely, uptake of dissolved nutrients by algae or decomposers promotes retention. The result is a balance between transport and retention which directly determines the structure and function of riverine communities.

Symbiotic relationships between microbes and higher plants such as exists with nitrogen fixation can have important consequences for nutrient input into Pacific coastal streams and rivers. As mentioned previously, red alder roots often contain nodules infected with an actinomycete-like endophyte which facilitates nitrogen fixation. In the Coast Range of Washington, Oregon, and northern California, alder often invades following clear-cutting. Because alder lives long, it can make significant long-term contributions to the nitrogen capital of

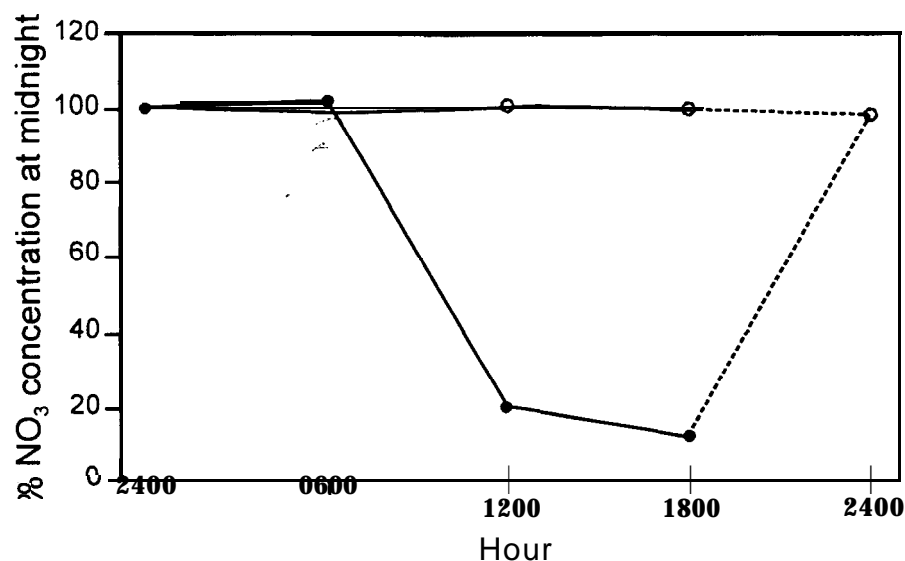


FIGURE 14.5. Percentage change from midnight concentration of nitrate in a summer-derived sample from 1st-order (○; Watershed 10) and 5th-order (●;

Lookout Creek) streams from the H.J. Andrews Experimental Forest (modified from Gregory 1979)

affected watersheds and ultimately to the streams draining them.

Between 1975 and 1985 the role of nitrogen fixation by alder was examined as a potential substitute for urea fertilization (Atkinson and Hamilton 1978, Miller and Murray 1979). The average annual accumulation of nitrogen by fixation varies by site, stand age, and duration of significant fixation. In the Cedar River watershed in Washington, annual nitrogen accumulation in a 38-year old stand was estimated at 85.3 kg/ha/yr (Cole et al. 1978). Fixation at sites in the Coast Range of Oregon vary from 11 to 45 kg/ha/yr (Berg and Doerksen 1975), although rates as high as 320kg/ha/yr (Newton et al. 1968) have been reported. Nitrogen accretion does not occur indefinitely. Cromack et al. (1979) estimated long-term accretion after 500 years was no greater than that of 15 years because fixation slows as nitrogen accumulates in soils, while denitrification and transport to the watershed's stream gradually balance fixation and atmospheric inputs.

Transport of nitrogen from fixation-enriched hillslopes can be a long-term source of both particulate and dissolved nitrogen to the adjacent aquatic environment. Direct litter input by alder can be an enhanced source of nitrogen to channel microbial and invertebrate communities since it typically has a higher nitrogen content than most other litter species. The initial nitrogen content of red alder litter typically exceeds 2%, whereas that of other common litter species like bigleaf maple (*Acer macrophyllum*), vine maple (*Acer circinatum*), and needle litter of Douglas-fir, and western hemlock (*Tsuga heterophylla*) is approximately 0.5% (Triska et al. 1975). Alder dominated riparian areas can also promote elevated dissolved nitrogen concentrations in stream water. Goldman (1961) noted that alder-lined (*Alnus tenuifolia*) springs on the east side of Castle Lake, California, averaged 10 times the  $\text{NO}_3^-$  concentration of west shore springs which lacked alder. He reported that the enhanced nitrogen input increased primary production in Castle Lake. Triska et al. (1994) analyzed for interstitial dissolved inorganic nitrogen and  $\text{NH}_4^+$  sorption in riparian sediments beneath

the water table at Little Lost Man Creek, California. Their study reach included a 25-year old, alder standing clear cut along the stream's west bank and old-growth forest along the east bank. Nitrate concentrations were typically far higher in riparian groundwater beneath the clear-cut bank than beneath the old-growth. Concentrations were highest during the late fall-to-spring rainy season when transport of infiltrated precipitation is high. At summer the base-flow  $\text{NO}_3^-$  concentration of stream water was significantly lower upstream of the alder-dominated clear-cut (Triska et al. 1995), and increased dramatically within short reaches along the clear-cut (Triska et al. 1989a).

Both beaver (*Castor canadensis* and Pacific salmon (*Oncorhynchus* spp.) influence the biogeochemistry of watersheds in the Pacific coastal ecoregion. The abundance of these animals, however, is much reduced from historical levels throughout much of the region (Johnson and Chance 1974, Nehlsen et al. 1991), reducing their influence on the chemical processes of streams and rivers. Nevertheless, investigations on the impact of beaver and salmon on nutrient dynamics in systems where these animals are abundant indicates they can have a very significant effect (Brickell and Goring 1970, Naiman et al. 1988).

Five species of Pacific salmon die after spawning once. As a result, these anadromous fishes transport nutrients and organic matter from the north Pacific Ocean to streams and rivers of the coastal ecoregion. The species utilize different parts of the watershed for spawning and spawn at different times of the year, thereby distributing the input of nutrients provided by the carcasses both temporally and spatially.

Spawning sockeye (*Oncorhynchus nerka*) and pink (*Oncorhynchus gorbuscha*) salmon affect stream water chemistry.  $\text{NO}_3^-$  concentration increased four-fold and organic nitrogen concentration increased three-fold for a month following spawning by pink salmon (Brickell and Goring 1970). In Lake Dalnee, British Columbia, 26% of the annual phosphorus input is provided by spawning sockeye salmon in the lake's inlet stream (Krokhin 1968). Richey et al.

(1975) found that spawning kokanee salmon (landlocked sockeye salmon) contributed 44 kg/yr of phosphorus to a small tributary of Lake Tahoe, California. Increased phosphorus concentrations in the stream water and a consequent algal bloom were attributed to the spawning fish.

There appear to be several pathways by which nutrients released by decomposing salmon may be assimilated into the stream ecosystem. Richey et al. (1975) found that autotrophic production utilized much of the phosphorus released during decomposition of kokanee salmon carcasses. Bilby et al. (1996) examined the contribution of spawning coho salmon (*Oncorhynchus kisutch*) to a small stream system in western Washington using nitrogen and carbon stable isotopes. They found that up to 30% of the nitrogen and 39% of the carbon in the stream biota was contributed by the spawning salmon (Table 14.4). Autotrophic uptake accounted for very little assimilation of the nitrogen or carbon released during decomposition of the carcasses. Sorption onto the streambed substrate of dissolved organic matter released by the rotting car-

**TABLE 14.4.** Percent of nitrogen (N) and carbon (C) contributed by spawning salmon to riparian vegetation and aquatic biota of a small stream in western Washington. Approximately 350 coho salmon (*Oncorhynchus kisutch*) per km of channel length spawned at the study site. Proportions of marine-derived nutrients were determined using stable isotope analysis.

Sample type	% Marine N	% Marine C
Riparian foliage	17.5	0
Epilithic organic matter	20.7	25.2
Grazers	24.8	29.2
Shredders	23.8	0
Collector-gatherers	14.4	29.4
Invertebrate predators	10.9	27.5
Age 0 cutthroat trout ( <i>Oncorhynchus clarki</i> )	18.5	23.4
Age 1 and 2 cutthroat trout	25.6	24.8
Age 0 coho salmon ( <i>O. kisutch</i> )	30.6	39.5

Data taken from Bilby et al. (1996).

**TABLE 14.5.** Historical and present levels of nutrients delivered from streams in the Willapa Bay drainage of Washington by spawning salmon (*Oncorhynchus* spp.). Historical values assume no harvest of returning fish

	Historical	Present
	(kg/km of stream length)	
Biomass	1.110	86
Nitrogen	111	9.0
Phosphorus	4.0	0.3

cases, heterotrophic uptake, and direct consumption of the carcasses by insects and juvenile fishes inhabiting the stream were the primary pathways of incorporation.

Historically, many Pacific coastal watersheds supported large numbers of spawning salmon, often exceeding 100,000 fish in larger systems. Pacific salmon range in size from approximately 2kg for pink salmon, the smallest species, to greater than 20 kg for chinook salmon (*Oncorhynchus tshawytscha*). Therefore, the contribution of nitrogen and phosphorus from the fish was substantial (Table 14.5). The reduction in the numbers of naturally spawning salmon in many watersheds of the Pacific coastal ecoregion has led to a corresponding decrease in the delivery of nutrients and organic matter and a reduction in the productivity of these stream ecosystems. Many watersheds currently support salmon runs of less than 10% their historical size (Nehlsen et al. 1991). Reduction in the number of spawning fish not only reduces the number of juvenile fish to repopulate available habitat but also decreases the productivity of the stream, reducing its capacity to support future generations of salmon.

Beaver influence biogeochemical cycles of streams by changing the hydrologic regime and altering patterns and rates of organic matter and sediment transport. Impoundments created by beaver flood forest soils, creating anoxic conditions (Naiman et al. 1994). These conditions produce an increase in the amount of reduced nitrogen and conditions conducive to the release of nitrogen through denitrifica-

**TABLE 14.6.** Increase in the total amount of various nutrients in a 2563-ha area in Minnesota influenced by beaver (*Castor canadensis*). Few beaver were present in the watershed in the 1920s. The initial nutrient values assume all soils in the watershed exhibited levels similar to those currently displayed by non-flooded forest soils in the area.

Nutrient	% Increase after recovery of beaver population
Total N	72
NO <sub>3</sub> <sup>-</sup> -N	208
NH <sub>4</sub> <sup>+</sup> -N	295
Total P	43
SO <sub>4</sub> <sup>2-</sup>	82

Data from Naiman et al. (1994).

tion (Naiman et al. 1988, Triska et al. 1994). The impoundments also collect and retain large amounts of organic matter. Organic matter sources include the inundated forest, material carried into the pond by the stream and transported to the pond from the upslope forest by the beaver. Naiman et al. (1988) reported a three-fold increase in organic matter standing stock following impoundment of a stream by beaver. The nutrients contained in the organic matter increase the overall abundance of nutrients in systems where beaver are active (Table 14.6).

## Responses to Disturbance

Healthy riverine ecosystems are balanced systems, where inputs, outputs, and chemical transformations maintain nutrient concentrations within ranges appropriate for organisms living in the river. The preceding sections examined the current understanding of the biogeochemical cycling of nitrogen, phosphorus, and sulfur in Pacific coastal rivers, and although much remains to be learned, several fundamental linkages between cycling processes and other biophysical characteristics of river and forest systems have been elucidated. Change is clearly a fundamental component of the biogeochemistry of riverine ecosystems. These changes often cycle at various time scales (e.g.,

diurnal, seasonal, or interannual). However, infrequent severe disturbances also play a key role in maintaining the long-term diversity and productivity of riverine ecosystems (Naiman et al. 1992).

In many steep, headwater stream segments, debris flows are an important pathway by which sediment and large woody debris are transported to and down streams (Bisson et al. 1987). This is despite the fact that their recurrence frequency is estimated at once every 500 years (Swanson et al. 1982). Wildfires are another catastrophic event that causes widespread disruption of watershed processes in the short-term, but on longer time scales is beneficial to forest and stream ecosystems. **Wildfires** tend to be rare in the Pacific coastal ecoregion due to the wet climate. Hemstrom and Franklin (1982) estimate an average recurrence interval of once every 450 years. Although these events often result in mortality among organisms, over longer time scales they deliver much of the larger structural materials, such as large wood, to channels (Naiman et al. 1992). These large materials provide a great deal of structural heterogeneity to the stream, creating depositional sites for organic matter, sediments, and associated nutrients (Bilby 1981).

In many of the heavily managed and urbanized watersheds of the Pacific coastal ecoregion, natural disturbance regimes have been overridden by anthropogenic effects. This section examines these effects and their impacts on natural biogeochemical cycles.

## Forest Conversion and Management

Forest conversion to managed silviculture is the most widespread type of anthropogenic disturbance impacting rivers of the coastal ecoregion. Trees accumulate nutrients from primary atmospheric and geologic sources, supply organic nutrients to rivers, and remove nutrients from hyporheic and riparian groundwater. Their canopies control water temperature by providing shade and fallen trees significantly affect channel morphology. The roots of trees dampen the hydrograph of streams and rivers by absorbing infiltrating groundwater, and they

stabilize colluvium on hillslopes, thereby decreasing rates of erosion. Removal of trees along a river corridor disrupts each of these processes. Macroinvertebrate and fish communities may also be altered by logging activities (Newbold et al. 1980, Hartman and Scrivener 1990). Consequently, the biological drivers of nutrient cycling are affected at all trophic levels. Owing to the tight linkages between ecosystem processes in watersheds, disturbances at the streamside (and even on the hillslope) propagate throughout the system.

In one of the first studies of its kind in the Pacific coastal ecoregion, Brown et al. (1973) investigated the effects of logging on concentrations of  $\text{NO}_3^-$  and  $\text{PO}_4^{3-}$  in two streams of the Oregon Coast range. In the Deer Creek watershed, the forest was "patch cut," with 25% of the forest cut in three logging units; slash was burned in one of the three patches. Concentrations of  $\text{NO}_3^-$  and  $\text{PO}_4^{3-}$  had no significant response to this treatment. In the Needle Branch watershed, where the forest was fully clear cut and the slash burned, mean annual concentrations of  $\text{NO}_3^-$  in the stream increased 240% (from 13 to 31mM) and persisted at elevated concentrations for six years.  $\text{PO}_4^{3-}$  concentrations remained unchanged in both watersheds following logging. In a similar study, Fredriksen et al. (1975) reported data for three watersheds in the Oregon Cascades. Their results differed slightly from those of Brown et al. (1973) in that 25% patch cuts at Fox Creek and the South Umpqua Experimental Forest produced measurable increases in  $\text{NO}_3^-$  concentrations, and 100% clear-cutting at the H.J. Andrews Experimental Forest produced increased  $\text{PO}_4^{3-}$  concentrations in the first year following the cut. The pattern of increased  $\text{NO}_3^-$  and unchanged  $\text{PO}_4^{3-}$  concentrations was also reported at Carnation Creek on Vancouver Island (Scrivener 1982) and in other watersheds of the H.J. Andrews Experimental Forest (Martin and Harr 1989).

Differences in the responses of  $\text{NO}_3^-$  and  $\text{PO}_4^{3-}$  concentrations may stem in large part from the different surface reactivity of these species. Both are released in large amounts by burning and decomposing slash, and both remain in inorganic forms more readily due to the

decrease in uptake by trees. But  $\text{PO}_4^{3-}$  appears to be effectively immobilized in the system by adsorption to mineral surfaces, a process that does not affect  $\text{NO}_3^-$ . Data are not available concerning responses of stream concentrations of  $\text{SO}_4^{2-}$  or dissolved organic forms of nitrogen, phosphorus, or sulfur following logging, but one might expect temporary increases in these species as well. It should be noted that  $\text{NO}_3^-$  concentrations after logging have not been measured in excess of drinking water standards (700mM). Moreover, elevated nutrient concentrations and water temperatures at Carnation Creek produced no discernible increases in stream periphyton productivity (Shortreed and Stockner 1982).

Large increases in suspended sediment loads are a common response to logging activities (Figure 14.6). The increases are attributed in part to the removal of trees, but road construction appears to play an even larger role (Brown and Krygier 1971, Beschta 1978). In the four Oregon watersheds discussed in the preceding paragraph, maximum suspended sediment concentrations increased by as much as two orders of magnitude following logging (Fredriksen et al. 1975). The delivery to streams of nutrients bound to soil particles must also increase as a result of logging. However, no studies in the Pacific coastal ecoregion have specifically addressed these inputs. If the sediment generated by logging has the same nutrient content as sediment generated under undisturbed conditions, nutrient input by this pathway would increase in proportion with the increase in sediment delivery. However, the sources of sediment after logging are more diverse than those in an undisturbed situation and nutrient content may be different. The only certainty is that as suspended sediment loads increase, so will fluxes of particulate nitrogen, phosphorus, and sulfur. Revegetation is the most effective means of reducing increased sediment loads (Fredriksen et al. 1975).

Cutting of the riparian forest decreases nutrient inputs from direct litterfall. Input of litter to a stream flowing through a recently clear-cut area in western Washington averaged about 16 g/m<sup>2</sup>/yr ash-free dry weight (AFDW), whereas input to a nearby stream in an old-

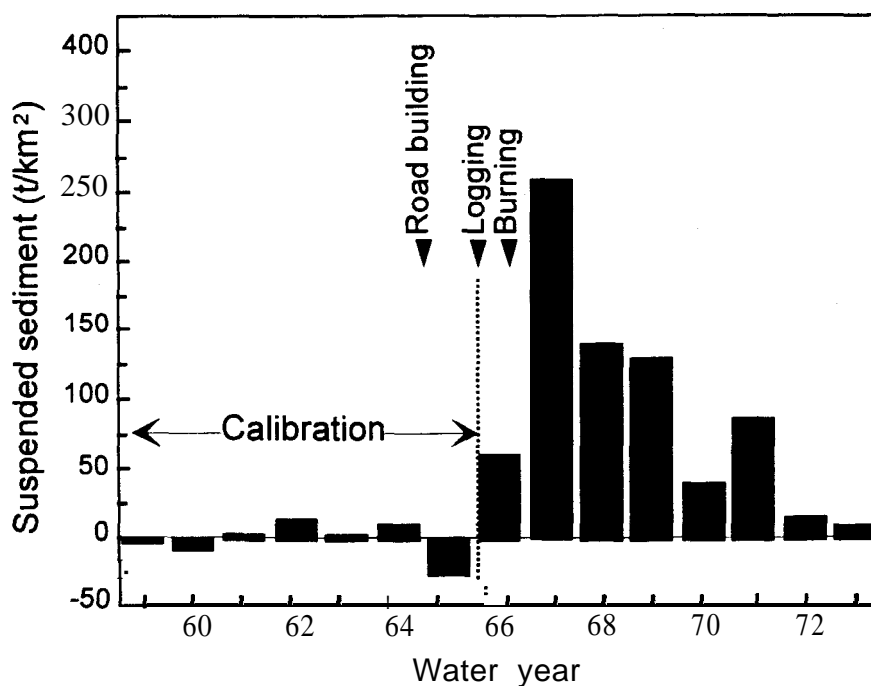


FIGURE 14.6. Suspended sediment yield in the Needle Branch watershed, western Oregon, before and after road building, 82% clear-cut logging, and burning (modified from Beschta 1978).

growth forest received about 230 g/m<sup>2</sup>/yr AFDW (Bilby and Bisson 1992).

Overall fluxes of organic nutrients probably increase temporarily in streams following logging. Increased nutrient inputs due to higher amounts of sediment and dissolved nutrients delivered to the channel generally outweigh any decreased input of nutrients in litterfall. Outputs increase due to greater runoff, during both summer and winter (Harr et al. 1982, Harr 1986), and accelerated flushing of stored particulate matter from the streambed due to elimination of depositional sites as woody debris decomposes (Bilby 1981). Returning to the nutrient spiraling concept and equation (1), increased fluxes ( $F_i$ ) from logging will increase spiraling lengths ( $S$ ), unless there are commensurate increases in nutrient uptake ( $U$ ).

The degree of disturbance associated with deforestation is greatly dependent upon the method of logging employed and the geomorphology of the watershed. During the first half of this century little consideration was given to the impact of logging on stream systems, as economic pressures were the primary determinant in the design of management practices.

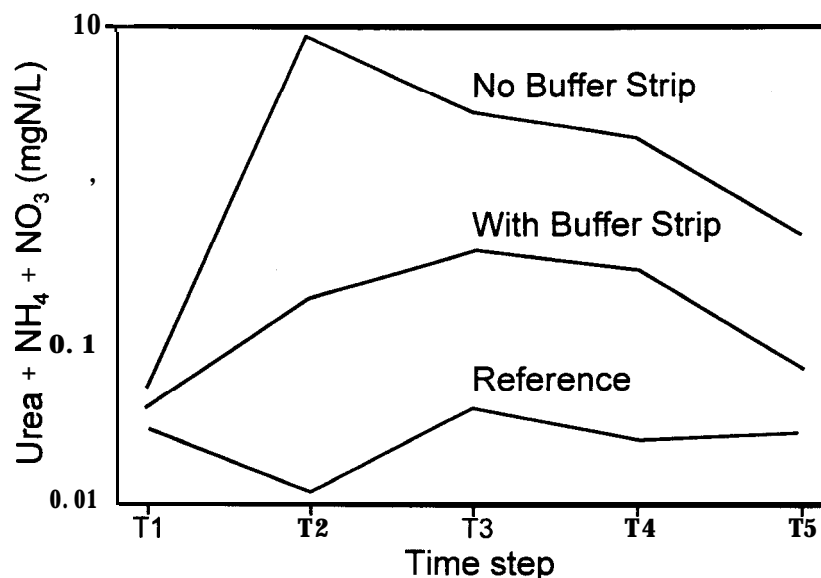
More recently, however, as knowledge of ecosystem functioning has improved and societal pressures for ecosystem protection have come into play, forest management has adopted new techniques which substantially reduce the degree of disturbance to river corridors. This trend continues today, as the latest management techniques aim to further minimize the degree of disturbance within the river corridors as well as on the surrounding hillslopes (Franklin 1992).

The effects of forest management are felt not only at the time of tree cutting. Continued management through replanting and regrowth also alters natural nutrient cycles. Nitrogen is most often the limiting nutrient in coniferous forests of the Pacific coastal ecoregion (Weetman et al. 1992). Consequently, for decades, foresters have applied urea pellets (-200 kg N/ha) to replanted stands every 5 to 10 years in order to enhance tree growth. While unfertilized buffers are established along larger streams, urea is often introduced directly into smaller systems. In the Mohun drainage basin on northern Vancouver Island, Perrin et al. (1984) compared the responses of stream nitrogen concentrations following forest fertilization in

catchments with and without buffer strips. Nitrogen in streams without buffer strips peaked at concentrations which were 20 times greater than those in streams with buffer strips (Figure 14.7). Both systems, however, had nitrogen concentrations in excess of those in unfertilized catchments. Bisson et al. (1992) reported nearly instantaneous increases in the concentration of dissolved organic nitrogen (DON) in stream water from two fertilized watersheds from western Washington (Louse and Ludwig Creeks). In Louse Creek, DON concentrations increased from less than 50mM to greater than 4000mM. Less dramatic, but equally rapid increases in DON were reported in two small tributaries to Lens Creek on southern Vancouver Island (Hetherington 1985). DON concentrations in both of these systems returned to near pre-fertilization levels within 3 to 10 days. By comparison, concentrations of inorganic nitrogen ( $\text{NH}_4$  and  $\text{NO}_3^-$ ) increased and remained elevated for weeks in the case of ammonia and up to a year or more in the case of nitrate. In another study

conducted in two southeastern Alaskan streams where only  $\text{NH}_4$  and  $\text{NO}_3^-$  were monitored following fertilization, stream concentrations responded in a similar fashion (Meehan et al. 1975).

Herbicides are often applied to reduce vegetation competing with young conifer trees in newly planted stands. Measures to protect streams from deleterious effects of herbicide contamination are built into procedures of application and, in general, these measures are quite effective (MacDonald et al. 1991), although herbicide residues are commonly detected in streams for a few days following application (Fredriksen et al. 1975). Nutrient concentrations in streamwater draining areas treated with herbicide often increase. Applications of the herbicide glyphosate (Roundup®) resulted in a doubling of  $\text{PO}_4^{3-}$  concentrations for one to two years (Hartman and Scrivener 1990). Concentrations of  $\text{NO}_3^-$  also increased, but only following large storm events. Hartman and Scrivener (1990) attribute the increase in  $\text{PO}_4^{3-}$  concentrations to leaching of



**FIGURE 14.7.** Mean concentrations of combined dissolved nitrogen (N) versus time in the Mohun drainage system of British Columbia, Canada, following application of urea fertilizer in two catchments. Stream dissolved nitrogen concentrations in catchments where a 50m buffer strip was left unfertilized remained significantly less than stream dissolved nitrogen concentrations in catchments not containing a 50m buffer strip that was left unfertil-

ized, but concentrations were still higher than in the reference catchments. Time steps are defined as follows: T1 encompasses an 8 month period prior to fertilization, T2 encompasses the first 3 days following fertilization, T3 encompasses days 4-18 following fertilization, T4 encompasses days 19-59 following fertilization, and T5 encompasses day 60 through the completion of the study (modified from Perrin et al. 1984).

the P-rich deciduous vegetation killed by the treatment.

## Urbanization and Agriculture

Converting forest land to agriculture or urban/suburban development dramatically alters natural nutrient cycles. In the Pacific coastal ecoregion, deforestation is the first step in land conversion, but instead of replanting trees, the forest is permanently removed. Furthermore, the channels of streams and rivers flowing through these areas are often engineered to guard against flooding and erosion, permanently destroying many of their natural geomorphologic features. In addition to the input pathways described earlier, sewage and industrial effluent from urban areas and fertilizers from agricultural fields and residential landscaping become major input pathways, raising nutrient concentrations to many times their natural concentrations. In response to the high nutrient levels and the associated high concentrations of organic matter, autotrophic and heterotrophic microbial communities bloom, and natural species compositions are severely disrupted. The consequences of all of these effects to water quality may be so severe that human health is directly threatened, especially given the presence of other toxins in these effluents. See Chapter 4 for a more detailed discussion of water quality.

## Fire

The occurrence of wildfires is one disturbance that has actually decreased as a result of management programs in Pacific coastal watersheds. The good and bad points of this reduction are a topic of considerable debate, and the effects on nutrient cycles are not clear. When fire sweeps through a watershed, large amounts of organically bound nutrients are mineralized and enter the soil column. In the case of nitrogen, however,  $\text{NH}_3$  volatilization during the fire may result in significant nitrogen losses from the ecosystem. Grier (1975) reported nitrogen losses of 97% from the forest floor and 33% from the A1 horizon of the mineral soil following a fire in the

Entiat valley of central Washington. The total loss amounted to 39% of the nitrogen stock in the ecosystem. These losses appear to have occurred almost entirely via volatilization, given that waters leaching the remaining ash layer contained undetectable amounts of nitrogen (Grier 1975). Volatilization losses of  $\text{PO}_4^{3-}$  and  $\text{SO}_4^{2-}$  are likely to be less important.

The net effect of severe fires is not completely unlike that of logging and slash burning. The forest is largely destroyed and large amounts of non-volatile nutrients (including base cations) are input to the soil. Destruction of the vegetation results in decreased rates of nutrient uptake, as well as decreased inputs of nutrients to streams from riparian vegetation. Woody debris within the streams may also be burned. Hillslope instability is possible, although not to the extent associated with improperly built roads. Likewise, the potential for forest regeneration is also very high, as seedlings profit from the mostly increased levels of available nutrients.

## Climate Change

The future course of global climate change is still far from clear, but there now appears to be general agreement that global atmospheric temperatures are rising and will continue to rise into the next century (Titus and Narayanan 1995, IPCC 1996). The most extreme ecosystem responses to climate change are expected in marginal or stressed systems, but the net effects are likely to be felt to some extent in all living systems. Possible impacts include changing patterns of rainfall (and therefore runoff), shifts in growing season temperatures, and changes in soil moisture levels. Increased fires as well as altered vegetation patterns are a concern (Risser 1992).

In an analysis not limited to the Northwest, Meyer and Pulliam (1992) considered various potential impacts of climate change to stream systems. Rising carbon dioxide ( $\text{CO}_2$ ) and anticipated rising temperatures may lead to changes in the food quality of litter as leaf nitrogen contents decrease. Increased plant metabolism may deplete nutrients in soil and

groundwater, and enhanced organic matter decomposition in warmer soils could reduce inputs of dissolved organic nutrient forms to streams. Overpeck et al. (1990) reasoned that increasing temperatures will alter the natural disturbance regimes of forests and streams. In southeastern Alaska, increasing air temperatures would probably lead to decreased water temperatures, as streams receive more runoff from melting glaciers (Oswood et al. 1992). Thus, there are many possible responses of nutrient cycles to a changing climate, but until our understanding of these responses improves, or until verifiable evidence of changed cycles appears, discussions will continue to be qualified by words like *may*, *could*, and *might*.

*Acknowledgments.* The authors thank John Stockner, Robert Beschta, and Robert Naiman for their careful reviews of the manuscript.

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