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Seasonal and storm dynamics of the hyporheic zone of a 4th-order mountain stream. II: Nitrogen cycling

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Abstract. The objective of this study was to quantify subsurface nitrogen fluxes between a riparian forest and a 4th-order mountain stream, McRae Creek, for each season of the year and during storms. A network of wells was installed on a gravel bar and a portion of the adjacent floodplain between 1989 and 1992. Water samples were collected to monitor dissolved nitrogen concentrations. Advected channel water and ground water were enriched in nitrogen relative to the stream; thus, subsurface flow was a net source of nitrogen to the stream in all seasons of the year and during both base-flow periods and storms. Estimates of the flux of advected channel water and the discharge of ground water were combined with changes in mean nitrogen concentrations along subsurface flow paths to estimate nitrogen inputs to the stream. Discharge of ground water from the conifer-dominated floodplain was the largest source of nitrogen added to the stream; however, more than 50% of this nitrogen was dissolved organic nitrogen. In contrast, two-thirds of the nitrogen from the alder-dominated gravel bar was inorganic. Net nitrogen fluxes from the gravel bar to the stream were lowest during the summer when water table elevations were low. Net fluxes of nitrogen from the gravel bar to the stream were largest during the fall, especially at peak flow during storms when interstitial water in the gravel bar was enriched in NO_3^-. The estimated annual flux of nitrogen from the riparian forest to McRae Creek was 1.9 g/m^2 of streambed, of which 1.0 g/m^2 was inorganic. Estimated net annual flux was large relative to the estimated input of nitrogen in litterfall, or the nitrogen required to support estimated rates of primary productivity.

Key words: hyporheic zone, nutrient dynamics, nitrogen cycling, riparian forest, ground water, hydrologic exchange, hydrology.

The interaction between subsurface fluxes of water, solutes, and biogeochemical processes may be of critical importance in nutrient-limited streams if the subsurface is either a source or a sink for limiting resources, or if it is the primary location for the biogeochemical transformation of nutrients cycling through the stream ecosystem. The importance of these subsurface processes to the stream ecosystem will be determined by the quantity of nutrients added to the stream, the element in question, and the chemical form of the added nutrients. In addition, both seasonal timing and location of these inputs will influence whether added nutrients are retained within the stream reach or exported. Nutrient retention will, in turn, be determined by the interactions between the hydrological and biological systems.

Primary productivity in 3rd-order and larger streams in the Cascade Mountains is often nitrogen limited (Gregory 1980); thus the transport of dissolved nitrogen in subsurface flows, as well as subsurface biogeochemical processes, may be of special importance in these streams. Exchange flows of advected channel water lead to longer residence times of stream water and dissolved nitrogen within the stream reach, longer contact time of stream water with sediments (Bencala et al. 1993, Stanford and Ward 1993), and increased opportunity for biogeochemical transformation of nitrogen (Hynes 1983, Grimm and Fisher 1984, Lock et al. 1984, Mickleburgh et al. 1984, Duff and Triska 1990, Triska et al. 1990). Nitrogen is transported with well-aerated channel water into the hyporheic zone (Triska et al. 1989b), where dissolved organic nitrogen (DON) is mineralized and ammonium (NH_4^+-N) is nitrified (Triska et al. 1990, Holmes et al. 1994, Jones et al. 1995). Inorganic forms of nitrogen may be taken up by plants, immobilized by microorganisms, or returned to the stream wherever advected channel water is discharged from the aquifer.

Exchange flows of advected channel water and the discharge of ground water transport nitrogen from riparian ecosystems to streams, augmenting the quantity of nutrients available to the stream ecosystem (Coats et al. 1976, Triska et al. 1984, Kim et al. 1992). Water may leach nitrogen from shallow rooting zones or rainfall may leach nitrogen from the soil into the ground water or hyporheic water. Nitrogen-fixing red alder, an early successional species (Worthington 1965, Bollen and Lu 1968), colonizes frequently flooded or recently disturbed surfaces along the banks of larger streams in the Cascade Mountains and may contribute significant quantities of nitrogen to the soil and subsurface water. Advection of channel water through the soil and alluvial sediment beneath riparian alders could leach nitrogen from the rooting zone and transport it to the stream (Coats et al. 1976) because water tables are commonly shallow in these locations.

The objective of our study was to quantify subsurface nitrogen fluxes between a riparian forest and an adjacent 4th-order mountain stream. We monitored changes in dissolved nitrogen concentrations in subsurface water among seasons and during storms, and used these data to infer the effect of both leaching of nitrogen from the riparian forest and the effect of biochemical transformations of nitrogen transported through the groundwater and hyporheic zones. Estimates of subsurface water fluxes (Wondzell and Swanson 1996) were combined with measured changes in mean nitrogen concentrations along subsurface flow paths to quantify the net flux of nitrogen between the riparian forest and the adjacent stream.

Study Site

The study site was on McRae Creek, a 4th-order stream within the Lookout Creek catchment and the H.J. Andrews Experimental Forest in the western Cascade Mountains of Oregon, USA (44°10′N, 122°15′W). The drainage area above the study site is 1400 ha, and most of the catchment is forested. Elevation within the catchment ranges from 600 m at the study site to 1600 m along the drainage divide. Average annual precipitation is approximately 2500 mm, falling mainly between November and March (Bierlmaier and McKee 1989). Summers are typically dry, and base flow discharge gradually decreases to reach an annual minimum in late September.

McRae Creek was not gauged; therefore, to estimate McRae Creek discharge we used records from Mack Creek which is 4.5 km away. We assumed that unit area discharges would be similar for the two catchments (Gordon et al. 1992) and multiplied Mack Creek discharge by the ratio in size between the two catchments (1.6). Estimated stream discharge was highly variable over the study period, ranging from a low of 100 L/s during September and October, to 600 L/s during baseflow periods throughout the winter; peak storm flows in fall and winter exceeded 5000 L/s. These estimates may be inaccurate because stream discharge often does not increase linearly with watershed area, especially during storms (Dunne and Leopold 1978). However, stream stage at McRae Creek was highly correlated with stream discharge at Mack Creek (n = 93, r^2 = 0.92) over the ranges observed, suggesting that channel routing of water through these two watersheds was similar. Thus, the estimation error should be small, even in storms.

The study site was 100 m long and 80 m wide and lay along the eastern bank of an unconstrained stream reach (Fig. 1). A complex of landforms is present within the study site, including a recently formed gravel bar, older floodplain surfaces, and terraces. Sediment of the gravel bar and the stream channel is a poorly sorted mix of sand, gravel, cobbles, and boulders more than 1.5 m in depth. A layer of rounded, stream-worked cobbles and boulders, 10 to 50 cm in diameter, is present at 1 to 3 m depth within the floodplain. The sediment overlying this layer varies in texture from loam to fine sand. A small seep is present along the boundary between the terrace and floodplain, but is not gauged. There is no surface flow from this seep in late summer. Flows increase in the winter rainy season, and peak during storms.

Subsurface flow in the shallow aquifer adjacent to McRae Creek is complex (Fig. 1), with water from several sources flowing in a complex flow net (Wondzell and Swanson 1996). We follow the terminology of Triska et al. (1989b) when describing these flows. The exchange of surface and interstitial water is exchange flow, and stream water flowing into the aquifer is advected channel water. Ground water refers to subsurface water from other sources. We do not

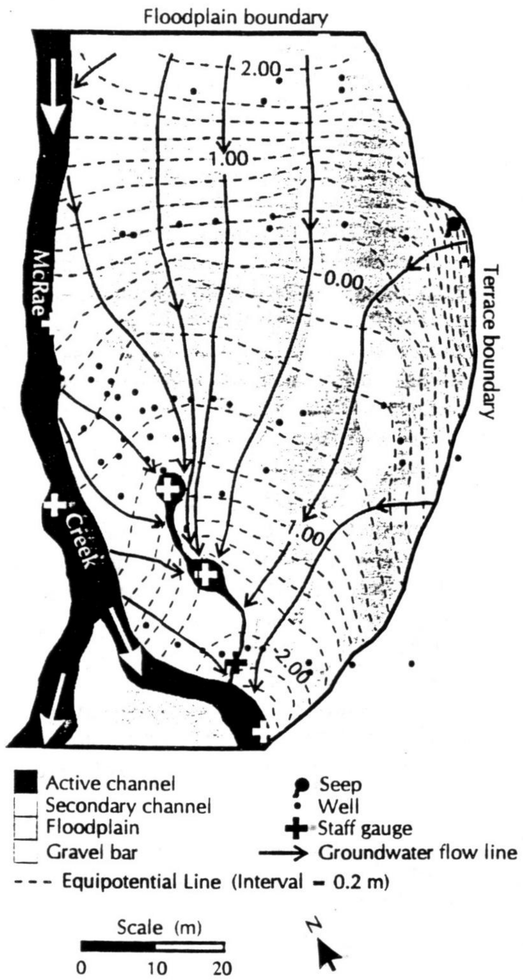


FIG. 1. McRae Creek study site showing landforms and well locations. Piezometric surface and groundwater flow lines for winter base flow are from Wondzell and Swanson (1996).

differentiate between soil water draining from adjacent hillslopes and that in deep aquifers. The zone beneath and to the side of the stream, where subsurface water is a mixture of at least 10% advected channel water and ground water, is the hyporheic zone. The hyporheic zone does not extend into the streamside aquifer in zones of groundwater discharge, but is >10 m wide in zones where exchange flow is dominant.

Methods

Wells and well transects

Two types of well were used in this study: observation wells to measure water table elevations and sample wells to collect interstitial water. Casings for observation wells were made from PVC pipe and screened by drilling 0.32-cm-diameter holes into the bottom 50 cm of each PVC pipe, at an approximate density of 1 hole/cm^2. Casings for sample wells were constructed from 45-cm lengths of 2.54-cm-diameter, porous, high density polyethylene pipe (HDPE) with a mean pore diameter of 20 μm. A length of PVC pipe was added to extend the casing above the ground surface.

All wells were driven by hand because the study site had no road access. Large cobbles and boulders throughout the study site hindered well placement so that the deepest wells penetrated only 2.5 m below the ground surface. Wherever possible, wells were placed in holes driven at least 50 cm below the surface of the water table at summer baseflow. Holes were back filled with the soil originally removed, and, if necessary, additional fill was taken from nearby soil pits or recent root-throw pits. Following installation of the wells, back fill was washed and entrained sediments were removed from the well casing by repeated pumping.

A single transect of wells was established during late summer in 1989 as a pilot study. Additional transects of wells were installed during the summer of 1990 and a further 18 wells were established on, and adjacent to, the gravel bar during 1991 and 1992. Nine sample wells were placed adjacent to observation wells so that water-table levels could be measured concurrently with the collection of water samples during storms. During the summer of 1991, about half of the observation wells were retrofitted with evacuation tubes so that water samples could be collected over a much larger area during baseflow periods.

Water samples and chemical analyses

Water samples were collected from wells to compare changes in dissolved nitrogen concentrations among seasons and within storms. Sampling was concentrated from mid summer to early fall and during fall storms. Samples were also collected in mid winter, in early spring, and during a single late-winter storm. Water-table depths were recorded from observation wells less than 24 h before collecting base flow water samples, after which wells were pumped dry and allowed to refill before samples were collected. Dissolved oxygen and temperature were also measured in each observation well using a YSI Model 51A dissolved oxygen meter and a YSI probe in 1991 and 1992. Water samples were collected from the sample wells during storms because observation wells were used to monitor changes in water-table levels, and withdrawing water to collect samples would have changed the water level in the wells. Twenty-four hours before a forecasted storm, all sample wells were pumped dry and allowed to refill. Wells were not re-evacuated between sample collections during a storm.

Samples were filtered with acid washed glass microfibre filters (Whatman GF/C, retention of 1.2 μm). The analysis for total Kjeldahl nitrogen (TKN) generally followed the Kjeldahl procedure using a H_2SO_4 digestant and $CuSO_4$/KCl catalyst, but with Nessler finish (Greenberg et al. 1980). NO_3^- and NH_4^+ were analyzed on an Technicon Autoanalyzer II. The analysis for NO_3^- (procedure 418F, Greenberg et al. 1980) was modified following Technicon's Industrial Method No. 100–70W distributed in 1973 (Technicon Industrial Systems, Tarrytown, New York 10591). The analysis for NH_4^+ followed procedure 417F of Greenberg et al. (1980). DON was the difference between TKN and NH_4^+. Total dissolved nitrogen (TDN) was the sum of NO_3^-, NH_4^+, and DON.

Data analysis

Samples were categorized by location, season, and a storm index variable. Samples from wells were grouped by landforms, and grab samples from surface water were assigned to the stream, tributary, or secondary channel. Samples from early fall, collected before the start of the rainy season, were grouped with summer samples. Each season was subdivided into periods of base flow or storm flow using hydrographs of either stream discharge or well records of water-table elevations. Storms were further subdivided by the rising leg, crest, and falling leg of the stream hydrograph.

Dissolved nitrogen concentrations were ln transformed to fit a normal distribution. Analysis of variance was used to test for significant differences in nitrogen and oxygen concentrations among seasons within each landform, and among landforms within each season. Significant differences ($p < 0.1$) between each pairwise combination of seasons or landforms were further analyzed with a Least Squares Means Test. Means and standard errors of the mean were back transformed for graphical presentation. Back-transformed standard errors are not evenly distributed above and below the mean; therefore, only the upper (larger) standard error is shown.

Estimates of subsurface fluxes of water and nitrogen

Subsurface water flux for each season of the year was estimated from model simulations. Discharge records collected between 1979 and 1992 from Mack Creek were used to separate periods of base-flow discharge from periods of storm flow, and the number of days of base-flow discharge during each season was estimated. A base-flow hydrograph of the water year was constructed by averaging the daily mean discharge (storm days excluded) over the 13-y period of record. Regression equations (Wondzell and Swanson 1996) relating subsurface flux to stream discharge were used to estimate the mean subsurface-water flux through the study site for each day of the year under base-flow conditions (Table 1).

Scaling up estimates of subsurface flux during storms to estimate total annual storm flux was problematic. Only one storm was simulated. However, this 6-d period was a sequence of three small

TABLE 1. Mean seasonal flux (m^3/h) of stream water (McRae Creek), advected channel water through the gravel bar (Gravel bar), and ground water through the floodplain (Floodplain) during base flow and storms.

Season	McRae Creek	Gravel bar	Flood-plain
Winter (22 Dec–15 Mar)			
Baseflow—58.2 d	1773	3.05	1.66
Storm—25.8 d	5871	3.40	2.36
Spring (16 Mar–31 May)			
Baseflow—55.4 d	1837	3.09	1.68
Storm—21.6 d	4312	3.44	2.39
Summer (1 June–23 Oct)			
Baseflow—138.3 d	901	2.57	1.30
Storm—7.7 d	2352	2.86	1.83
Fall (24 Oct–21 Dec)			
Baseflow—35.0 d	1571	2.94	1.57
Storm—23.0 d	4353	3.28	2.25

storms spaced 6–24 hours apart, which could be treated as three separate sub-storms to represent the flow conditions that may occur during small, intermediate, and large storms. We made a linear extrapolation from the drainage rates of ground water from the floodplain during the final 24 h of the transient simulation, or the period between 54 and 78 h when little precipitation fell. We assumed that the change in drainage rate would be constant for the entire falling leg, and made a linear extrapolation to estimate the length of time that subsurface flows were influenced by precipitation from each of the three sub-storm periods. We underestimated actual storm fluxes because the response is non-linear, and changes in drainage rate slow as the water table nears steady state elevation. Each sub-storm was subdivided into a rising leg, crest, and falling leg. Water sample data showed that peak nitrogen concentrations lasted for a period of only a few hours at the peak of storm discharge. Thus, we defined the period of peak discharge as lasting for 25% of the length of the storm and centered on the time of peak discharge. We then calculated the area under the curve to estimate the subsurface flux for the rising leg, crest and falling leg of the hydrograph within each storm class.

Discharge records collected between 1979 and 1992 from Mack Creek were used to estimate the number of days of storm discharge and the frequencies of small, intermediate, and large storms during each season of the year. The number of storm days during each season was multiplied by the proportion of storms in each size class and by the subsurface flux estimated for storms of each size class to estimate subsurface flux (Table 1). Separate estimates were made for the rising leg, crest, and falling leg of the hydrograph.

Concentrations of NH_4^+, NO_3^-, DON, and TDN were multiplied by the estimated subsurface flux of water to estimate the flux of nitrogen through the subsurface. Water samples collected in the spring were not analyzed for DON. Therefore, we used the winter mean concentration of DON to estimate spring fluxes. Our estimates of nitrogen fluxes are based directly on the fluxes of subsurface water predicted from a numerical groundwater flow model. The assumptions made to model groundwater flow at our study site, and the sources of uncertainty in the model predictions, are presented in Wondzell and Swanson (1996). The mean concentration of each form of nitrogen in stream water was subtracted from the concentration in advected channel water to correct for nitrogen transported into the subsurface by advective flow. The net flux of nitrogen from both the floodplain and from the gravel bar was estimated for both base-flow periods and storm-flow periods in each season of the year.

Results

Nitrogen dynamics

Grab samples from McRae Creek and a tributary channel were dominated by DON during all seasons of the year (Fig. 2). The secondary channel was the only source of surface water not dominated by DON; however, this channel was not connected to the stream, but rather, surface flow was fed by the discharge of ground water and advected channel water. DON was dominant at all sample locations in winter (Fig. 2).

Mean concentration of NO_3^- was significantly greater in samples from the gravel bar than in the stream during summer (Fig. 2). Mean concentration of dissolved O_2 in stream water (10.0 mg/L) was significantly greater than in wells on the gravel bar (5.5 mg/L). Water samples collected from floodplain wells had mean concentrations of NH_4^+ and TDN significantly greater than samples collected from other locations (Fig. 2). Dissolved oxygen concentrations were very low in many floodplain wells (<2.0 mg/L) and the mean concentration in floodplain wells (4.1 mg/L) was significantly lower than in the stream.

Concentrations of NO_3^- and NH_4^+ were higher in samples from the gravel bar than in those from the stream during fall base flow. NO_3^- concentrations increased significantly in samples collected from McRae Creek and from gravel-bar wells during storms (Fig. 3). The observed concentration of NO_3^--N in gravel bar wells averaged 78 μg/L for the short period during peak flow, a 5-fold increase over fall base-flow concentrations. Nitrogen concentrations in samples collected from floodplain wells during fall base flow were lower than during summer (Fig. 2) but changed rapidly during storms (Fig. 3). NH_4^+ concentrations in samples collected during storms were significantly lower than those collected during fall base flow, but concentrations of DON were significantly higher.

Nitrogen concentrations were much lower in winter than in summer or fall (Fig. 2). As before,

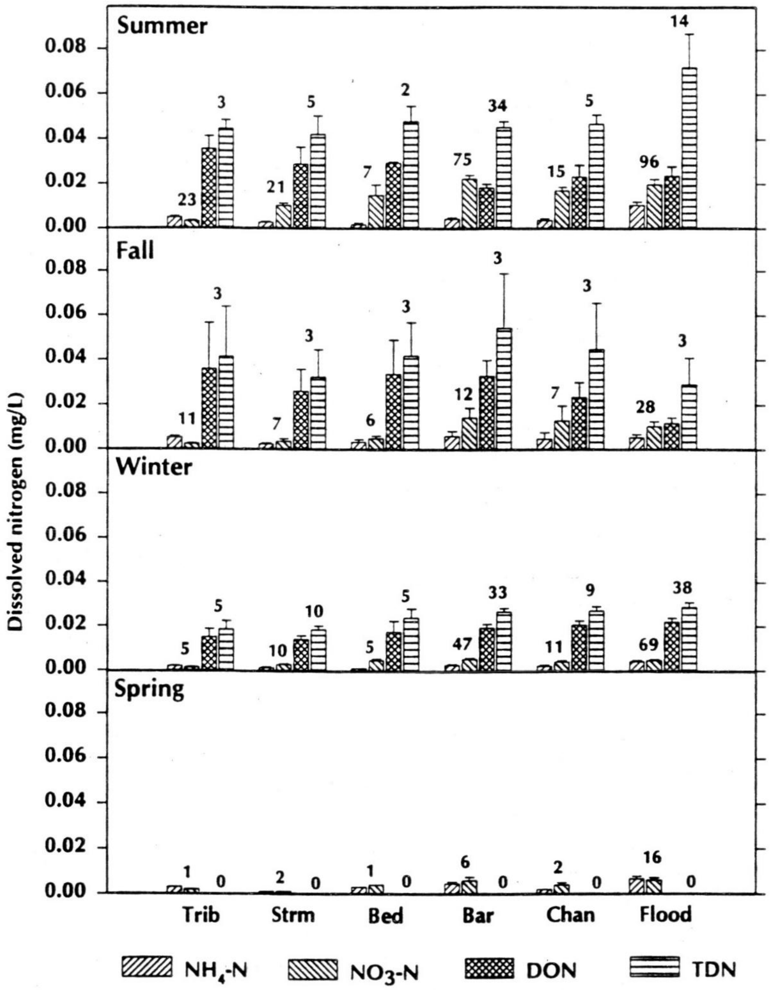


FIG. 2. Mean (+1 SE) dissolved nitrogen concentrations for tributary (Trib), McRae Creek (Strm), streambed (Bed), gravel bar (Bar), secondary channel (Chan), and floodplain (Flood) for each season of the year. Sample sizes are shown above pairs of bars; they are equal for NH_4^+-N and NO_3^--N, and for DON and TDN. Means and standard errors were calculated from ln transformed data and back transformed before graphing.

concentrations of NH_4^+, NO_3^-, and TDN were significantly higher in samples collected from gravel-bar wells than in samples collected from the stream. Mean dissolved nitrogen concentrations in samples collected from floodplain wells were also significantly greater than concentrations observed in samples from either stream or tributary. There were no significant changes in concentrations of dissolved nitrogen in samples collected during a single late-winter storm in March 1993 (Fig. 4). Spring base flow samples were from a single date and analyzed for only NH_4^+ and NO_3^-. Observed nitrogen concentrations were similar to those during winter base flow (Fig. 2).

Nitrogen flux

Subsurface flow was a net source of nitrogen to the stream in all seasons and during both base flow and storms because ground water and advected channel water were enriched in nitrogen, relative to the stream (Fig. 5). Fluxes were dominated by DON in winter and spring, whereas NH_4^+ and NO_3^- were more important in summer and fall. The lowest net flux was from the gravel bar in summer. The greatest flux occurred during fall storms and was dominated by fluxes of nitrate from the gravel bar to the stream in advected channel water. Organic nitrogen dissolved

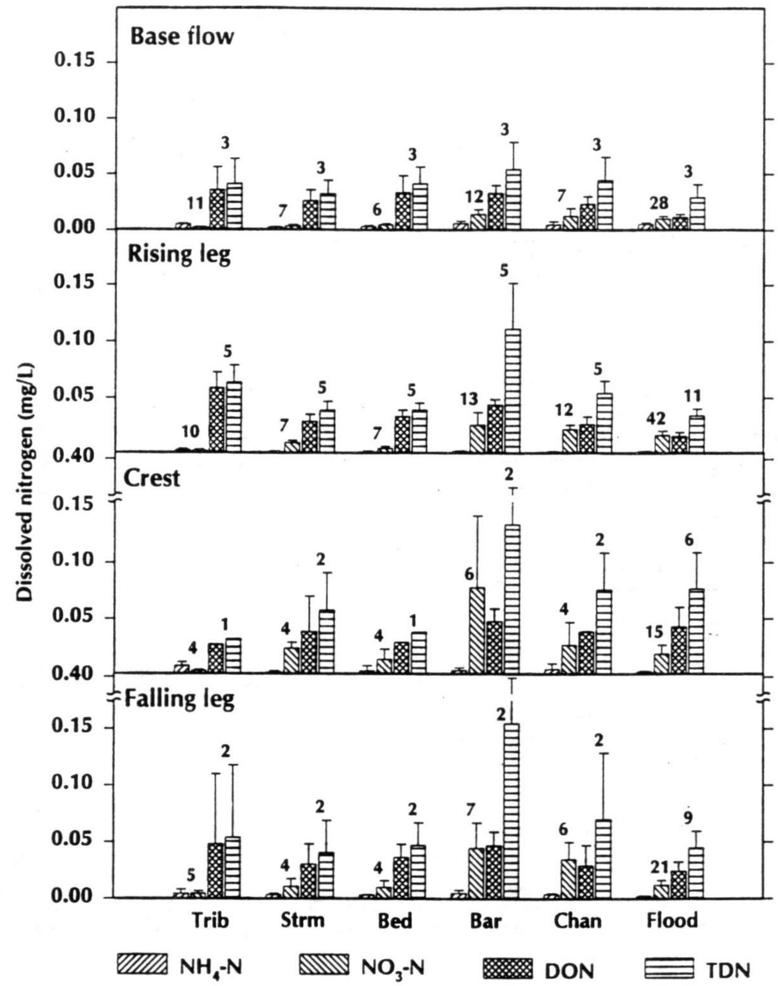


FIG. 3. Mean (+1 SE) dissolved nitrogen concentrations for tributary (Trib), McRae Creek (Strm), streambed in streamside well (Bed), gravel bar (Bar), secondary channel (Chan), and floodplain (Flood) during fall storms. Sample sizes are shown above pairs of bars; they are equal for NH_4^+-N and NO_3^--N, and for DON and TDN. Means and standard errors were calculated from ln transformed data and back transformed before graphing.

in stream water (DON_{st}) and transported into the gravel bar with advected channel water appeared to be transformed into NO_3^- in summer, but this transformation was not observed in other seasons (Fig. 5). If the McRae Creek study site is representative of the mix of landforms and forest types in unconstrained stream reaches along the stream network, and assuming that fluxes from both sides of the valley floor were similar, then an estimated 1.9 g N was added to each m^2 of streambed area via subsurface flow each year (1.9 g m^{-2} streambed yr^{-1}), and an additional 0.2 g m^{-2} streambed yr^{-1} of NO_3^--N was returned to the stream from the transformation of DON_{st} within the gravel bar.

Discussion

Gravel bar and hyporheic zone

A source of nitrogen.—Preferential drainage through a secondary channel maintains an extensive lateral hyporheic zone beneath the gravel bar at our study site (Fig. 1 and Wondzell and Swanson 1996). In summer, the hyporheic zone appeared to be hydrologically isolated from al-

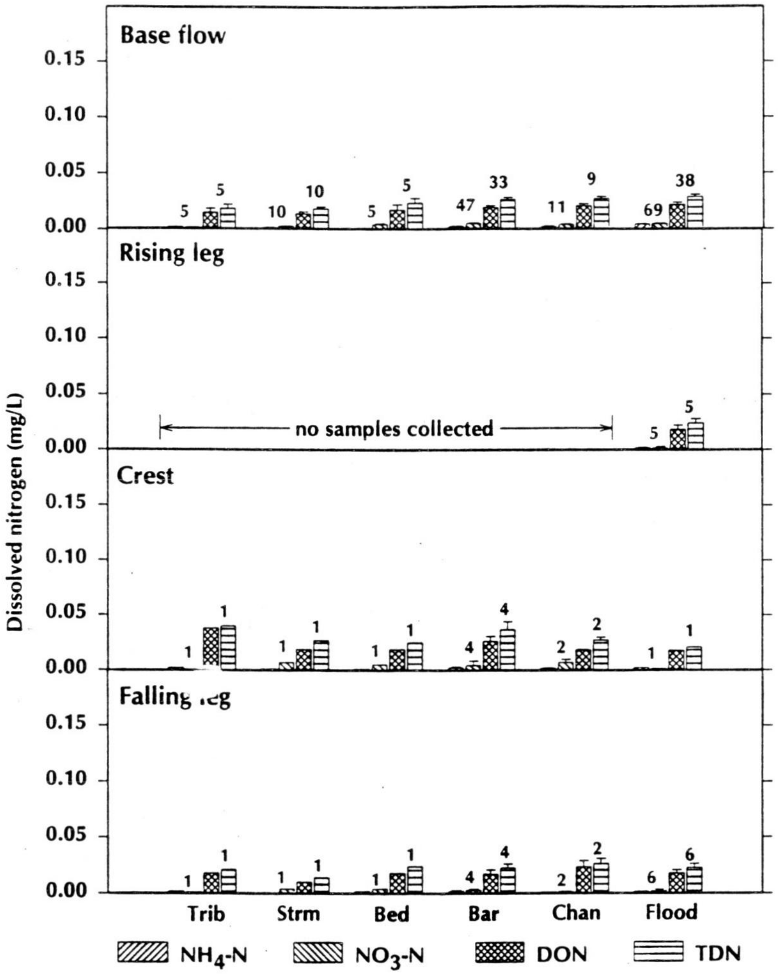


FIG. 4. Mean (+1 SE) dissolved nitrogen concentrations for tributary (Trib), McRae Creek (Strm), streambed in streamside well (Bed), gravel bar (Bar), secondary channel (Chan), and floodplain (Flood) during a winter storm. Sample sizes are shown above pairs of bars; they are equal for NH_4^+-N and NO_3^--N, and for DON and TDN. Means and standard errors were calculated from ln transformed data and back transformed before graphing.

ders growing on the gravel bar because the water table was lower than their rooting depth. Further, there was little rain to leach nitrogen from the overlying soil. Consequently, the exchange flow of advected channel water through the gravel bar was not a significant source of nitrogen to the stream in summer (Fig. 6A). The hyporheic zone was hydrologically reconnected to the riparian forest ecosystem at the onset of the rainy season because of percolation of precipitation through the soil profile and because the water table rises into the rooting zone of alders on the gravel bar. Gravel bars appeared to be a significant source of NO_3^- for the stream during fall (Fig. 5). Exchange flows of advected channel water transported nitrogen, especially NO_3^-, from the gravel bar to the stream (Fig. 6B). Fresh inputs of organic matter from leaf fall, and perhaps fine root turnover, could produce high levels of NO_3^- if labile organic nitrogen was mineralized and nitrified.

We observed large changes in concentrations of dissolved nitrogen in advected channel water between the rising leg, crest, and falling leg of storm hydrographs (Fig. 3), a time scale of 10s of hours. However, we estimate that the mean residence time for water in the gravel bar would be approximately 9 d given the predicted fluxes

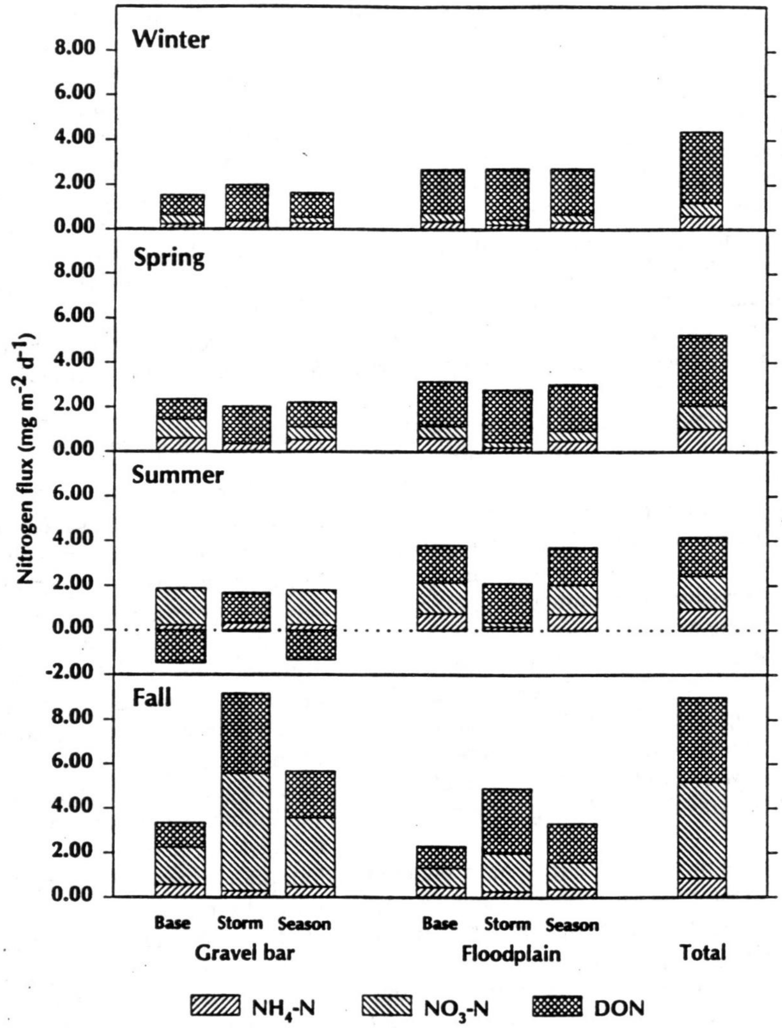


FIG. 5. Nitrogen flux into the stream from the gravel bar, the floodplain, and from both landforms combined (Total). Estimates are for base-flow periods (Base), storms, or the entire season (Season) for each landform. Seasonal totals (Total) are the sum of seasonal fluxes from both the gravel bar and floodplain. Note that DON in advected channel water transformed to NO_3^- in the gravel bar during summer is negative, resulting in a net flux of zero. The total shown for the summer does not include this DON or NO_3^-.

during the period of peak flow (Wondzell and Swanson 1996). Consequently, a simple replacement of the nitrogen-poor water with nitrogen-rich water during storms cannot explain the rapid changes in dissolved nitrogen. Our measurements could have been biased because nitrogen concentrations in shallow wells close to the roots of red alders may have been higher for a short period when water-table elevations crested, but then decreased quickly as nitrogen-rich and nitrogen-poor water was mixed within the gravel bar. Alternatively, a relatively small volume of water within larger pore spaces could turn over much more rapidly than the rest of the water within the gravel bar. Similar flow systems, in which "macropore flow" occurs, have been documented for forest soils (Bevin and Germann 1982, Seyfried and Rao 1987, Sollins and Radulovich 1988).

Nitrogen fluxes were dominated by DON during the winter and spring (Fig. 6C) and little change was observed during a late winter storm, even though the water table was high and the hyporheic zone remained hydrologically connected to the riparian forest. Concentrations of NH_4^+ and NO_3^- were low in both the floodplain and gravel bar at this time of year. We suggest that continued flushing of the soil profile throughout the rainy season either depleted existing pools of mobile nitrogen or exceeded the rate at which mineralization and nitrification replenished these pools. Certainly, most vascular plants are dormant during winter, so fresh inputs of labile organic matter would not be expected and cold temperatures would reduce the rates of microbial activity.

A site for nitrogen transformations.—Although the gravel bar was not a source of added nitrogen for the stream ecosystem in summer, it appeared to be an important site for the transformation of DON_{st} to NO_3^- (Fig. 6A). Concentrations of NO_3^- along flow paths through the gravel bar increased in summer (Fig. 2), probably through the mineralization of organic nitrogen and subsequent nitrification. Stream water was the most likely source of DON, and this hypothesis is supported by the trend of decreasing DON and the concurrent loss of dissolved O_2 along the flow path of advected channel water through the gravel bar during summer base flow.

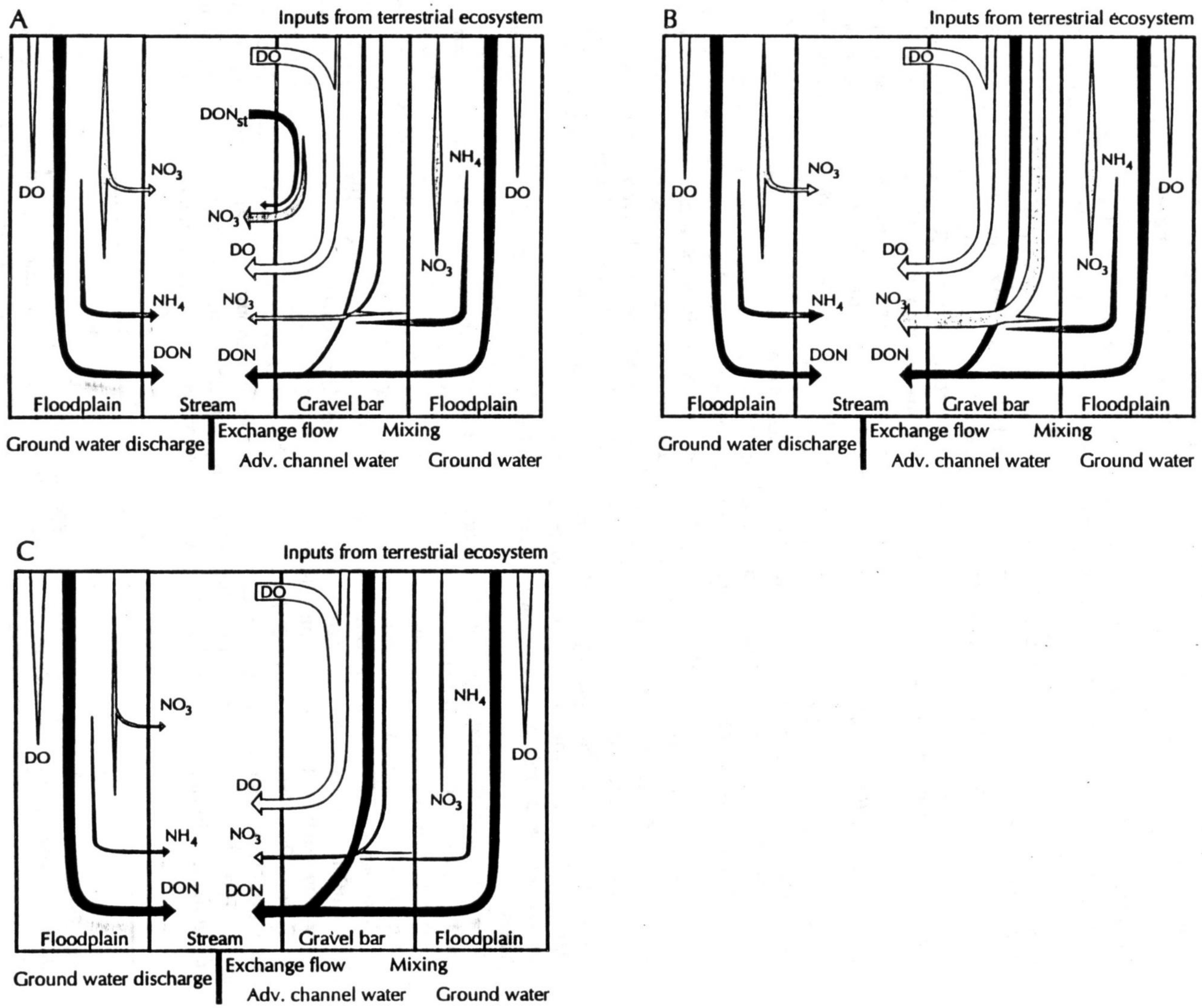
The increase in NO_3^- also may have resulted from the transformation of particulate organic nitrogen (PON) transported from the stream into the subsurface, or leaching from the soil above. However, if PON was the ultimate source of the increased NO_3^-, then TDN also should have increased with distance from the stream, but this was not observed (Fig. 2). We cannot rule out the possibility of alternative sources of nitrogen; however, if alternative sources existed, then some combination of plant uptake, immobilization, or denitrification prevented accumulation of TDN in the gravel bar along the flow path of advected channel water. Further, it is unlikely that nitrogen was lost through denitrification because water in the gravel bar was well aerated.

We did not measure nitrogen transformations that occurred within the hyporheic zone of the immediate streambed. Large volumes of exchange flow would be expected in mountain streams where streams have a stepped morphology and sediments are coarse textured (Vaux 1962, Munn and Meyer 1988, Triska et al. 1989b, Grant et al. 1990, Harvey and Bencala 1993). However, the residence time of water within the streambed is also likely to be much shorter than in the adjacent gravel bar. Even so, small changes were observed between the concentration of nitrogen in the stream water and samples collected from a shallow well at the edge of the stream. Certainly, the cumulative influence of the streambed over the length of the stream network could be large. Thus, we must have underestimated the net flux of inorganic nitrogen resulting from biogeochemical transformations in the hyporheic zone in summer.

Floodplain and ground water

Discharge of ground water from the floodplain was a major subsurface source of nitrogen added to the stream ecosystem (Fig. 6). This nitrogen may have come either from the mobilization of nitrogen from organic matter co-deposited with sediments on the floodplain, or from leaching of the soil profile overlying the aquifer. Alternatively, this nitrogen may have been transported into the study site with water draining from adjacent hillslopes or from locations on the floodplain upstream of our study site. Unfortunately, we cannot separate the effect of biochemical processes occurring within the floodplain from the effect of nitrogen inputs from adjacent areas because wells were not located at the hillslope–floodplain boundary. A trend towards increasing concentrations of TDN with distance along flow paths through the floodplain would be expected if nitrogen were leached into ground water from overlying soil, or mobilized from organic matter deposited within the sediment of the floodplain. TDN concentrations did not increase, suggesting that these processes did not occur, or that plant uptake, immobilization, or denitrification prevented accumulation of nitrogen in the ground water along these flow paths.

Ground water from adjacent hillslopes may have been an important source of nitrogen. The ground water flux into the aquifer from the hillslopes accounted for ~15% of the total subsurface flow through the floodplain in summer and exceeded 40% during the winter wet season (Wondzell and Swanson 1996). Both the concentrations of nitrogen and the seasonal changes in concentrations were similar to those found by Sollins and McCorison (1981) in soil solution at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Inputs from terrestrial ecosystem
DO
DON$_{st}$
NO$_3$
NH$_4$
DO
NO$_3$
DO
DO
NO$_3$
NH$_4$
NO$_3$
DON
DON
Floodplain
Stream
Gravel bar
Floodplain
Ground water discharge
Exchange flow
Mixing
Adv. channel water
Ground water
B
Inputs from terrestrial ecosystem
DO
NO$_3$
NH$_4$
DO
DO
DO
NO$_3$
NH$_4$
NO$_3$
DON
DON
Floodplain
Stream
Gravel bar
Floodplain
Ground water discharge
Exchange flow
Mixing
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Ground water
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Inputs from terrestrial ecosystem
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NO$_3$
NH$_4$
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NO$_3$
DON
DON
Floodplain
Stream
Gravel bar
Floodplain
Ground water discharge
Exchange flow
Mixing
Adv. channel water
Ground water

2 m depth (below the rooting zone) in a nearby upland old-growth coniferous forest.

The DON concentrations in the ground water increased rapidly when water-table elevations crested during fall storms (Fig. 3). These data suggest that percolation of precipitation through the soil profile or the rise of the water table into the rooting zone of conifers leaches DON from the riparian forest at the onset of the rainy season (Fig. 6B). However, a simple replacement of nitrogen-poor water with nitrogen-rich water during storms cannot explain the changes in DON concentrations that took place on a time scale of 1–2 d because the mean turnover time of ground water in the floodplain was approximately 30 d (Wondzell and Swanson 1996).

Effect of seasonal timing and spatial location

The influence of added or regenerated nitrogen on the stream ecosystem will ultimately be determined by the ability of the stream to retain this nitrogen. Stream retention changes with seasons and with changes in hydrologic regime, and our data show that there are large differences in both the quantity and elemental form of nitrogen added to the stream among seasons and during storms. Consequently, inputs of nitrogen added from the terrestrial ecosystem may not always be retained by the stream ecosystem.

We expect that the greatest potential retention of added nitrogen in the stream would occur in summer. Periphyton uptake has been shown to be a major factor determining retention of nitrogen in streams (Triska et al. 1989a, Kim et al. 1992), and in summer, rates of gross primary production reach an annual maximum (Naiman and Sedell 1980, Triska et al. 1982, Bott et al. 1985). Both water velocity and stream discharge are small relative to the wetted perimeter of the stream during this season; thus the stream ecosystem would have the maximum potential to retain nitrogen. However, the hydrologic linkages between the stream and the terrestrial ecosystem at our study site are restricted in summer. Consequently, nitrogen added to the stream from the subsurface reaches an annual minimum, with negligible contributions from the gravel bar (Fig. 6A).

The greatest subsurface inputs of nitrogen added to the stream were from the exchange flow of advected channel water through the gravel bar during the fall, especially during early fall storms (Fig. 6B). The seasonal timing of these inputs may reduce their relative importance to the stream. Rates of primary production are reduced in fall and winter (Naiman and Sedell 1980, Triska et al. 1982, Bott et al. 1985) and we expect periphyton uptake also to be reduced. Further, the largest fluxes of nitrogen added to the stream occurred during periods of peak storm flow, further minimizing the potential for uptake. Increased water velocity and stream discharge during storms result in shorter residence times of water within the stream channel and higher ratios of water volume to wetted perimeter (Hill 1988). Thus, the ability of the stream to retain added nitrogen will likely be reduced in the fall, especially during storms.

The locations where advected channel water and ground water are discharged to the stream will also determine the importance of subsurface processes on nitrogen cycling within the stream. The primary location of subsurface discharge at our study site was into a secondary channel (Wondzell and Swanson 1996) that never received direct surface flow, even during storms. Nutrient-rich ground water and advected channel water upwells into this channel, feeding surface flow. Although discharge increases noticeably during storms, the ratio of water volume to perimeter was only a fraction of that of the

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FIG. 6. Flow paths of nitrogen and dissolved oxygen (DO) through the subsurface, changes due to biochemical transformations, and subsurface inputs of nitrogen to the stream for summer (A), fall (B), and winter or spring (C). Width of arrows is proportional to the magnitude of fluxes. Ground water is discharged directly to the stream in groundwater discharge zones where upwelling prevents exchange flows (left side), but mixes with advected channel water before reaching the stream where the hyporheic zone is extensive (right side). Arrows starting at the top of each panel represent inputs from terrestrial ecosystems, including both ground water inputs from adjacent areas and leaching from the overlying soil. The vertical axis represents length of flow path through the streamside aquifer.

stream channel. Both Rigler (1979) and Hill and Warwick (1987) showed that the uptake (or immobilization) of phosphorus and NH_4^+ were rapid in groundwater-fed springs within the riparian zone. Consequently, this secondary channel provides an environment where nitrogen may be retained, rather than lost downstream.

Importance of forest type/landform

Gravel bars colonized by red alder appeared to have a much greater effect on the cycling of nitrogen through the stream ecosystem than would be expected on the basis of their area within the catchment. We estimated that the annual flux of nitrogen from the alder-dominated gravel bar to the stream was 3.8 kg N/ha of forest, two-thirds of which was in inorganic forms. In contrast, only 1.3 kg N/ha of forest was leached from the conifer-dominated floodplain, of which more than 50% was in organic forms. This DON had presumably leached from the soils of the upland and riparian coniferous forest (Fig. 6). Much of this DON must have been in refractory forms to be transported through the soil and ground water without transformation, given that the residence time for ground water within the aquifer of the floodplain ranges between 30 and 90 days (Wondzell and Swanson 1996).

Our estimate of nitrogen flux from the alder-dominated gravel bar was much lower than leaching losses estimated for red alder stands in upland sites (Van Miegroet and Cole 1984, Binkley et al. 1994). Leaching losses may be related to both the pool size of soil nitrogen and nitrogen fixation by red alders. Neither the pool size nor the rate of fixation is known. Most of the nitrogen fixed in upland red alder stands accumulates in the soil (Bormann and DeBell 1981). The soils of the gravel bar are coarse textured and poorly developed, with little accumulation of organic matter at the surface. Nitrogen fixation rates may also be proportional to alder density (Bormann and Gordon 1984). Alder density on the gravel bar was low, and most trees were young and small, which might account for the small leaching losses observed in this study. Alders are often older and denser on other gravel bars along McRae Creek and other streams on the west slope of the Cascade Range. If leaching losses from these gravel bars equaled leaching losses estimated for upland stands, gravel bars colonized by red alder and located along the stream network may be more important to the stream nitrogen budget than this study would indicate.

Relative importance of subsurface nitrogen inputs to the stream ecosystem

The estimated annual input of TDN to McRae Creek from both groundwater discharge and the exchange flows of advected channel water was 1.9 g/m² of streambed, of which 1.0 g/m² was inorganic. This input was large relative to expected nitrogen inputs from other sources. Triska et al. (1984) estimated that nitrogen inputs from litterfall and nitrogen fixation supplied 4.2 g/m² of streambed in a nearby headwater catchment. We expected similar inputs of nitrogen from both litterfall and nitrogen fixation at McRae Creek because the forest canopy was closed, or nearly closed, over most of the studied reach. Therefore, estimated subsurface inputs of nitrogen to McRae Creek would equal 45% of the nitrogen input from litterfall and nitrogen fixation.

The estimated subsurface nitrogen input to McRae Creek was also large relative to the quantities of nitrogen required for primary productivity. Cummins et al. (1983) estimated that annual gross primary productivity (GPP) in 4th-order streams in the Oregon Cascades was 47.2 g C/m² of streambed. Assuming a C:N ratio of 8 (S. V. Gregory, Oregon State University, personal communication), the annual uptake of nitrogen would be 6.9 g/m² of streambed. We do not know metabolic respiration rates of primary producers in this study, but subsurface inputs could account for nearly 30% of the nitrogen required for GPP. Triska et al. (1989a) estimate that net primary productivity in Little Lost Man Creek, a 3rd-order stream in a similar environment, required 10.2 mg N m^{-2} d^{-1} to account for net primary production (NPP) in late summer. We estimated that subsurface inputs from both the gravel bar and floodplain averaged 4.2 mg N m^{-2} d^{-1} at our study site over the summer; however, DON inputs are of unknown biological availability. Inputs of dissolved inorganic nitrogen (DIN) averaged 2.4 mg m^{-2} d^{-1}. In addition, 1.5 mg DON_{st} m^{-2} d^{-1} was transformed into NO_3^- in the gravel bar. Assuming that NPP in McRae Creek is similar to that of Little Lost Man Creek, inputs of new and regenerated DIN would account for nearly 40% of the nitrogen required for primary productivity during summer.

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