Ann. Limnol. - Int. J. Lim. 2006, 42 (1), 43-52

Nitrogen dynamics in rural streams : differences between geomorphologic units**

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Nitrogen dynamics were investigated in the top centimeters of bottom sediment in three different geomorphologic units (riffles, sand bars, pools) and along two contrasted reaches (nitrogen-rich, nitrogen-poor) of a rural stream. Some predictions of links between geomorphology and processes were verified: (i) hydrological exchanges and nitrification were lower in pools than in riffles and bars, whereas (ii) ammonification and denitrification were higher in pools. Studies of denitrification potential in six other reaches of three N-rich streams support these conclusions and demonstrate that pools are spots of high microbial activity in streams.

Keywords : river, sediments, hydrological exchanges, hyporheic zone, denitrification.

Introduction

Nutrient cycling in rivers is largely dependent on biogeochemical processes that mostly occur at water-sediment interface (Newbold et al. 1982, Elwood et al. 1983). Many studies demonstrated that rivers exchange water with their sediments (Vaux 1968, Hendricks & White 1991, Stanford & Ward 1993) and pointed out the central role of these vertical exchanges in chemical and biological processes. When surface water infiltrates inside bottom sediment, dissolved oxygen is brought to the biofilms that cover particles and aerobic processes are stimulated. In contrast, when infiltration of surface water is reduced, oxygen disappeared rapidly, anaerobic processes can take place, and Nitrogen dynamics is modified (Dahm et al. 1987).

Most studies focussed on nitrogen-poor desert streams (Fisher 1977, Grimm & Fisher 1984, Grimm 1987, Valett et al. 1990, Valett et al. 1994, Holmes et al. 1996) or on mountain streams (Mulholland 1992, Mulholland et al. 2000, Peterson et al. 2001), but few works focussed on nitrogen dynamics and microbial activities in disturbed streams (Hill 1983, Christiensen et al. 1990, Hill et al. 1998), although human activities in rural streams have altered the nutrient budgets and sediment grain size characteristics (Vitousek et al. 1997) that both modify nitrogen dynamics. In the same way, most results have been obtained for deep sediments (from 20 to 100 cm deep) (Triska et al. 1990, Valett et al. 1990, Wroblicky et al. 1998) or for different type of substrates (rocky bottom, debris dams) (Coleman & Dahm 1990, Munn & Meyer 1990), but few studies focussed on nitrogen dynamics and microbial activities in the first centimetres of sandy bottom sediments. At shallow depth, the local characteristics of the stream bed (i.e. the geomorphologic units) may affect the nitrogen cycling because the spatial structure of bed sediment controls the heterogeneity of water velocity and vertical exchanges.

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** A study presented at the 47th congress of the French Limnological Association (AFL), 2004, Besançon, France. Guest Editor : Odile Fossati.

Article available at http://www.limnology-journal.org or http://dx.doi.org/10.1051/limn/2006005

Table 1. Predicted influence of geomorphologic units (riffles-bars versus pools) on hydrological and biological processes in shallow interstitial habitats of streams.

	Riffles and bars	Pools	References
Vertical exchanges	High (infiltration and restitution)	Low (poor water exchange)	Mermillot-Blondin et al. 2000
Oxygen availability	High -medium (surface water infiltration)	Low (microbial respiration)	Hall 1986 Kemp & Dodds 2001 Hendricks 1993
NH_4 dynamics	Export and oxidation of the NH_4	Accumulation of the produced NH_4	Dahm et al. 1987 Lefebvre et al 2004
Nitrification	Stimulated (aerobic conditions)	Inhibited (anaerobic conditions)	Dahm et al. 1987 Hendricks 1993
Denitrification	Inhibited (oxygen still available)	Stimulated (lack of available oxygen)	Boulton et al. 1998 Dahm et al. 1998 Garcia-Ruiz et al. 1998

Some effects of geomorphology on the processes that occur in shallow sediment can be predicted from bibliographic sources (Table 1): hydrological exchanges will be reduced in pools because of fine sediment deposition (Mermillot-Blondin et al. 2000), nitrification will follow the same trend due to oxygen depletion (Hall 1986, Kemp & Dodds 2001), ammonium produced by ammonification will accumulate inside sediments (Lefebvre et al. 2004), while nitrate will disappear because of a high denitrification (Dahm et al. 1987). Reverse predictions can be made for riffles and sand bars, where vertical exchanges and oxygenation are higher (Hendricks 1993), nitrification stimulated by the available oxygen, ammonium will be both oxidized and flush out of the sediments (Lefebvre et al. 2004), while nitrate content will be similar or slightly higher than in surface water (Christiensen et al. 1990).

The study consisted in two complementary experiments. The aims were in a first step (1) to examine the intensity of the vertical hydrological exchanges between surface and interstitial waters in three different geomorphologic units (riffle, sand bar, and pool), (2) to identify the microbial processes associated to the nitrogen cycling in the three geomorphologic units of two contrasted reaches of the same river (one N-rich and one N-poor reach), and in a second step (3) to verify the observed pattern of denitrification potential in riffle-pool sequences in six other stream reaches.

Study site

The studies were carried out on rivers located in an agricultural landscape near Pleine-Fougères (Brittany, France : 48°4'N; 1°3'W; Fig. 1), the sector is a part of a Long-Term Ecological Research (LTER). In the first study, two reaches (100 m long ; noted F and W) of dif-

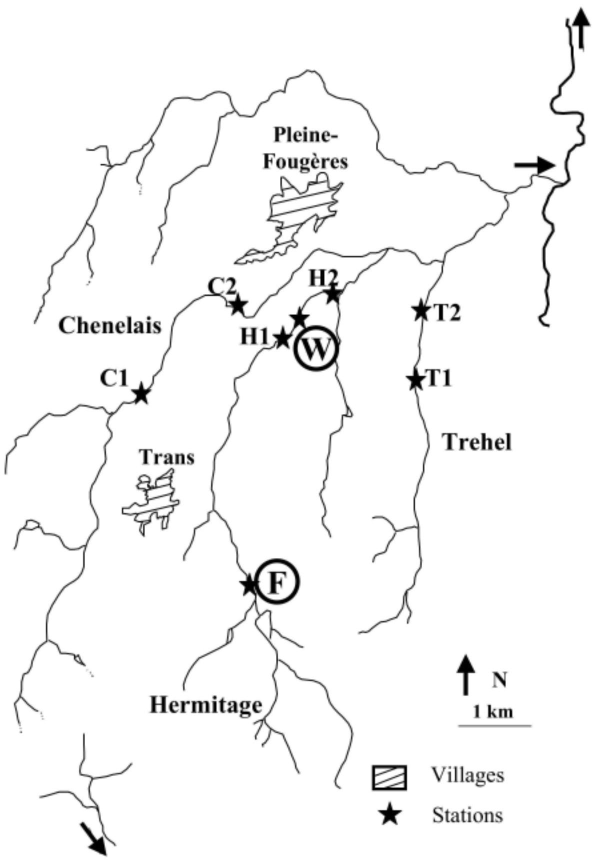

Fig. 1. Map of studied area with the localization of the studies reaches in the first (F and W) and second (C1, C2, H1, H2, T1, and T2) studies.

ferent trophic levels were studied in the Petit Hermitage stream. Both reaches consisted in meander successions in a wooded area. Reach F (1.5 m wide for 40 l.s^{-1}) was fed by springs and flows through semi-natural forest (low level of nutrients). Reach W (2 m wide for 80 l.s^{-1}) was located 6 km downstream in a wetland surrounded by agricultural landscape (grassland, wheat and maize, high level of nutrients). In the second study, six reaches of three different streams were investigated to test the patterns observed in the first study: the Chenelais (C1; 1.4 m wide for 25 l.s^{-1}, and C2; 1.6 m wide for 30 l.s^{-1}), the Petit Hermitage, on both sides of the site W (H1 and H2; 2 m wide for 80 l.s-1), and the Trehel River (reaches T1 and T2; 1.2 m wide for 25 l.s^{-1}). The streambed of these six reaches consisted of riffle-pool sequences and the reaches were surrounded by agricultural area. Streams were all sampled during low water period, in summer 2001 (first study, F and W reaches) and summer 2002 (second study, C, H, and T reaches).

Methods

Streambed topography (for site F and W) was established along 50 transects (2 m step) where orientation, width and depth (at 3 points) were measured with a theodolite, because GPS could not be used under the dense canopy. In each reach, the streambed consisted in a sequence of geomorphologic units: riffles, pools, and sand bars (Fig. 2). Three riffles, three bars, and three pools were sampled in each reach. Interstitial water was sampled at 6 points in each riffle and sand bar (3 in downwelling zone, n=9, and 3 in upwelling zone, n=9) and at 3 points in each pool (n=9). To sample shallow interstitial water (5cm deep in the sediments), we used a modified syringe (60 ml) fixed to a pipette tip (10 cm long) screened on 2 cm. Oxygen content (WTW OXY92), temperature, electrical conductivity (WTW LF92), pH (pH-meter : IQ, Scientific Instrument) were measured in both surface and interstitial water. To locate downwelling and upwelling zones, Vertical Hydraulic Gradient (VHG; Lee & Cherry 1978) was measured in mini-piezometers (1 m long and 1.7 cm diameter) at 10 cm deep inside sediments, due to technical limit (Boulton 1993). VHG was calculated using water levels inside (interstitial water) and outside (surface water) the mini-piezometers and ex-

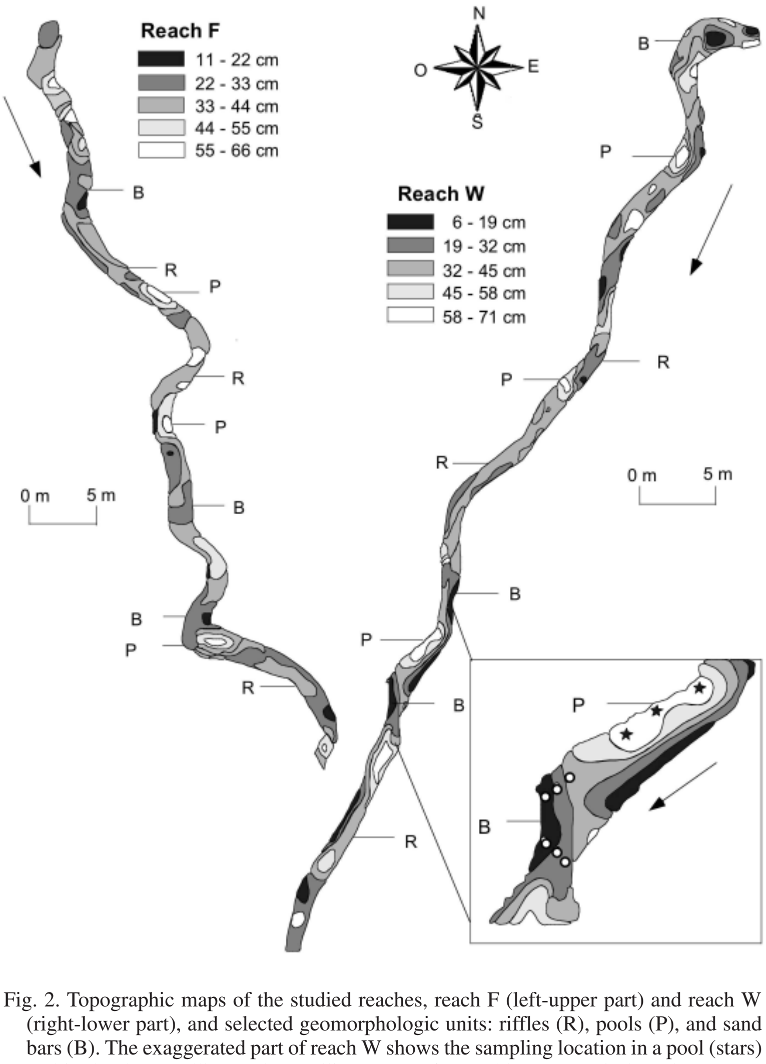

Fig. 2. Topographic maps of the studied reaches, reach F (left-upper part) and reach W (right-lower part), and selected geomorphologic units: riffles (R), pools (P), and sand bars (B). The exaggerated part of reach W shows the sampling location in a pool (stars) and in the downwelling and upwelling zones of a sand bar (open circle). Fine arrows beside streams indicates the flow direction.

pressed in percent of the sampling depth (Winter et al. 1988, Hendricks & White 1991). The first five centimetres of sediments were then sampled using a Plexiglas core (30 cm long and 4 cm diameter). Groundwater was sampled in 3 piezometers pushed at 1m deep in the stream bank. In the six reaches of the second study, surface water was sampled in triplicate, and shallow sediments were picked-up with cores in three riffles at 6 points (3 in downwelling zone and 3 in upwelling zone), and at 3 points in three pools. The water and sediments were stored in 250 ml polyethylene boxes, washed with river water and placed in cool box.

Water samples were filtered (Whatman GF/C) before analysis by colorimetric methods: blue-indophenol for ammonium (NH_4-N; Rossum & Villaruz 1963) and diazotation for nitrite (NO_2-N; Barnes & Kollard 1951), using a Uvikon XS spectrophotometer to read optical densities. Nitrate concentrations were measured using an automated cadmium reduction method (NO_3-N; APHA, 1976). Seven sediment size classes were measured on dry sediments (48 hours at 105°C) by sieving with 65, 125, 250, 500, 1000 and 2000 µm. The D50 (equivalent diameter at 50 % cumulative frequency) were calculated for each sampling point.

Ammonification and nitrification were roughly estimated using local increase of their products (i.e. ammonium and nitrate, respectively), whereas denitrification was measured in laboratory. The potential for denitrification enzyme activity (DEA) was estimated in laboratory by acetylene inhibition technique (Yoshinari & Knowles 1976). Fresh sediments were placed under anoxic conditions by replacing air with N_2. Each sample was saturated with distilled water amended with 10 µg N-NO3.g^{-1} fresh sediments and 4 mg.glucose g^{-1} fresh sediments, that correspond to optimal conditions for the potential denitrification (Smith & Tiedje 1979). Acetone-free acetylene was added to each flask to bring flask atmosphere at 10 kPa acetylene and 90 kPa air (% V/V). Incubations (8 hours) were made at laboratory temperature and flasks were shaken frequently. The rate of denitrification was expressed as the rate of N_2O gas released per gram of dried sediments per hour. Gas samples were analysed by gas chromatography (Chrompack 9001).

Most variables were analysed using non-parametric tests, because data were not normally distributed, even after log-transformation. Chemical characteristics of interstitial water, sediment, and microbial activities were compared using Kruskal-Wallis ANOVA of rank (H), and Mann-Whitney test (z), using Statistica software (5.5 Statsoft Inc., 1994). The spearman correlation was used to test the relation between microbial activity and sediment grain size. Levels of probability are noted in the text: $P<0.1$ (+), $P<0.05$ (*), $P<0.01$ (**) and $P<0.001$ (***).

Results

Initial investigations of reaches F and W

In the surface water, electrical conductivity (EC), pH and nitrate (NO_3-N) concentrations were significantly lower in reach F than in reach W, whereas dissolved oxygen (DO) and ammonium (NH_4-N) concentrations were similar in both sites. Similar differences were observed for EC, pH and NO_3-N concentration in the interstitial water, but in this case DO and NH_4-N concentrations were higher in reach F than in reach W (Table 2).

In the interstitial water of both reaches, pH and DO content were significantly lower than in surface water, whereas NH_4-N concentrations were higher in interstitial water than in surface (Table 2). NO_3-N concentrations were similar in both water types in reach F, but lower in the interstitial water in reach W (Table 2).

Table 2. Electrical conductivity (EC), pH values, dissolved oxygen (DO), nitrate (NO_3-N) and ammonium (NH_4-N) concentrations in surface (n = 3) and interstitial (n = 6) water of the reaches F and W, and results of Mann-Withney test's between reaches (reach F vs. reach W; line test) and water type (surface vs. interstitial water; column test - means ± S.D.).

Physico-chemical variables	Water type	Reach F	Reach W	Test
EC (µS.cm^{-1})	Surface	146 ± 0.57	257 ± 0.95	*z = -3.6****
	Interstitial	156 ± 11.7	291 ± 17.0	*z = -8.1****
	Test	*N.S.*	N.S.	
pH	Surface	6.8 ± 0.11	7.5 ± 0.04	*z = -3.6****
	Interstitial	6.2 ± 0.07	6.9 ± 0.04	*z = -8.1****
	Test	z = 4.1***	z = 4.6***	
DO (mg.l^{-1})	Surface	8.8 ± 0.14	8.1 ± 0.11	*N.S.*
	Interstitial	2.2 ± 0.14	1.6 ± 0.32	*z = 3.2****
	Test	z = 4.7***	z = 3.8***	
NO_3-N (mg.l^{-1})	Surface	0.34 ± 0.02	5.7 ± 0.11	*z = -3.6****
	Interstitial	0.38 ± 0.12	3.8 ± 0.64	*z = -7.9****
	Test	N.S.	z = 3.8***	
NH_4-N (mg.l^{-1})	Surface	0.05 ± 0.01	0.07 ± 0.01	*N.S.*
	Interstitial	0.27 ± 0.07	0.12 ± 0.03	*z = 4.0****
	Test	z = -4.0***	z = -2.3***	

In both reaches F and W, the Vertical Hydraulic Gradients (VHG) were close to zero in pools (Fig. 3A), but significantly different to zero in downwelling and upwelling zones of riffles (z = -3.5***, for both sites). Similar differences were observed for sand bars in reach W (z = -3.6***), whereas in reach F the upwelling of interstitial water dominated both upstream and downstream-ends of sand bars, with a high local variability (VHG varied from - 45 to + 72%).

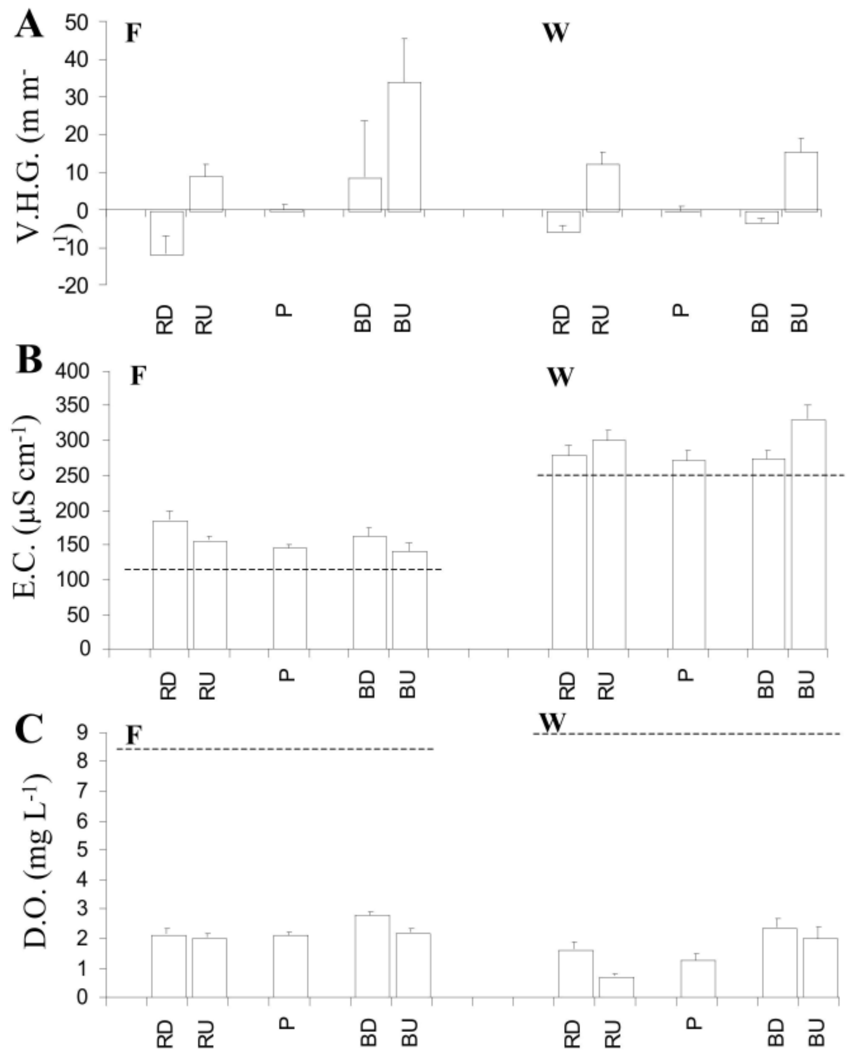

Fig. 3. Vertical Hydraulic Gradient (V.H.G. - A) measured at 10 cm deep in sediments, specific conductance (E.C. - B) and concentration of dissolved Oxygen (D.O. - C) measured in the surface water (horizontal dashed line) and at 5 cm deep in the sediment (bars). Geomorphologic units: pools (P), riffles and sand bars in downwelling and upwelling zones (RD, RU and BD, BU) for sites F and W (means ± S.D. ; n = 9).

Electrical conductivity (EC) decreased from downwelling to upwelling zones in riffles and bars of site F, but increased from downwelling to upwelling in site W (Fig. 3B). In both reaches, the EC measured in the upwelling water was similar to groundwater (80 $\mu S.cm^{-1}$ and 500 $\mu S.cm^{-1}$, in F and W respectively).

In both reaches, Oxygen contents were slightly higher in downwelling zones of sand bars than in pools (H = 9.1*** and H = 9.4*** for reach F and W respectively), and rather similar between upwelling zones and pools (Fig. 3C). A reverse pattern was observed for ammonium (Fig. 4C) with high concentrations in pools and upwelling zones of sand bars in reach F (H = 8.8***), and in upwelling zones of riffles in reach W (H = 7.7**).

Nitrate contents in pools were significantly lower than in riffles (z = 4.1*** for reach F and $z = 1.6^{+}$, for reach W) and sand bars (z = 4.0*** for reach F and z = 2.9*** for reach W). In riffles and sand bars, nitrate content decreased from downwelling to upwelling in reach W, and increased in reach F (Fig. 4A).

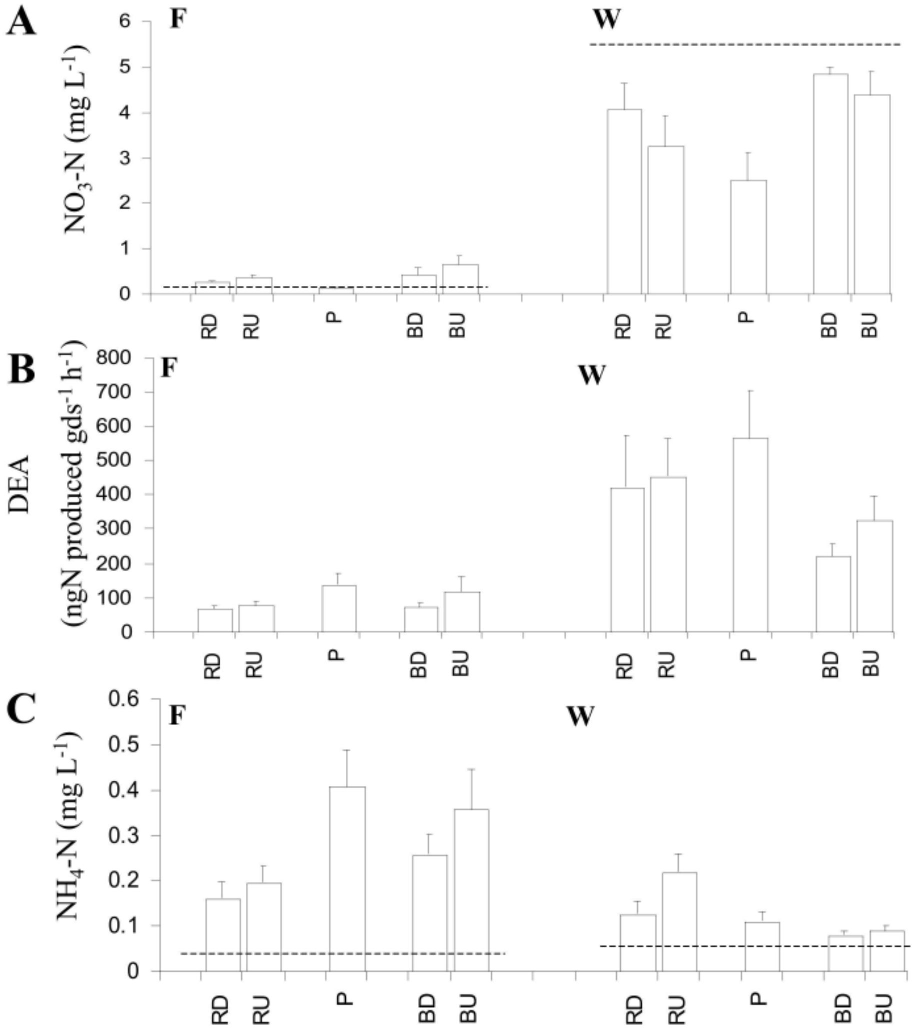

Fig. 4. Concentration of nitrate-N (A) and ammonium-N (C) measured in surface water (horizontal dashed line) and interstitial water (bars), and denitrification enzyme activity (DEA, B) measured in shallow sediments cores for each geomorphologic unit: pools (P), riffles and sand bars in downwelling and upwelling zones (RD, RU and BD, BU) for sites F and W (means ± S.D. ; n = 9).

Fine sediment content did not significantly varied between reaches, but accumulations of fine sediment were observed in the pools of the reach F (z = 2.06* compared to riffles) and in the upwelling zones of riffles in reach W (z = -2.52** compared to bars). In contrast, the microbial activities associated to the sediment varied between the two reaches. Whatever the geomorphologic unit considered, the potential denitrification was lower in reach F than in reach W (z = -7.0*** ; Fig. 4B). In both reaches, this activity was higher in pools than in sand bars (z = 1.9+ for reach F). The potential denitrification was negatively correlated with the D50 of the sediment (r = -0.47*** for reach F and r = -0.38*** for reach W; i.e. the denitrification increased with the fine sediment content) and with the available dissolved Oxygen (r = -0.79*** for reach F and r = -0.77*** for reach W; i.e. the denitrification increased with the hypoxia).

Nitrogen dynamics in riffles and pools of the six other reaches

Each reach of the second study had high nitrate concentrations in the surface water. The nitrate contents were typical for agricultural N-rich streams varying from 5.4 ± 0.01 $mg.l^{-1}$ (for H1-H2) to 8.3 ± 0.2 $mg.l^{-1}$ (for C1-C2) and even 9.6 ± 0.09 $mg.l^{-1}$ (for T1-T2), whereas ammonium concentrations were similar for all sites (below 0.1 $mg.l^{-1}$). The D50 of the sediment was higher in riffles than in pools of three of the six studied reaches (i.e. the fine sediment accumulated in pools, Table 3) in the three other reaches sediment characteristics were similar in riffles and pools.

The potential denitrification reached similar values in all streams. In these N-rich rivers, the geomorphologic effect was predominant: the potential denitrification was significantly higher in pools than in riffles units in the Chenelais and the Petit Hermitage streams (Table 3). No significant difference was observed in the reach T1, and the microbial activity was significantly higher in riffles sediments in the reach T2. The potential denitrification was negatively correlated with the D50 (r = -0.34*, for all reaches plotted together).

Discussion

This study highlights three major results: 1) similar hydrological exchanges were observed in similar geomorphologic units, particularly with low or no vertical exchanges in pools, 2) nitrogen dynamics in river sediment was directly linked to these vertical exchanges,

Table 3. Rates of denitrification potential (DEA) and medium sediment grain size (D50) in riffles and pools sediments of the 6 studied reaches (Chenelais - C1 and C2, Hermitage - H1 and H2, Trehel - T1 and T2), and results of Mann-Withney test's between geomorphologic units (means ± S.D.; n=3).

Station	Geomorphologic Units & Mann-Withney test	DEA ($ngN_2.gds^{-1}.h^{-1}$)	D50
C 1	Riffles	137 (± 50)	901 (± 236)
	Pools	263 (± 74)	545 (± 124)
	Test	*z = -1.52⁺*	*z = 1.52⁺*
C 2	Riffles	172 (± 37)	1203 (± 315)
	Pools	421 (± 132)	1461 (± 645)
	Test	*z = -1.52⁺*	*N.S.*
H 1	Riffles	196 (± 79)	1633 (± 186)
	Pools	574 (± 126)	365 (± 176)
	Test	*z = -1.96**	*z = 1.96**
H 2	Riffles	101 (± 11)	1005 (± 292)
	Pools	185 (± 18)	1205 (± 277)
	Test	*z = -1.96**	*N.S.*
T 1	Riffles	224 (± 67)	1036 (± 57)
	Pools	247 (± 19)	569 (± 243)
	Test	*N.S.*	*z = 1.96**
T 2	Riffles	335 (± 12)	1174 (± 413)
	Pools	215 (± 10)	1429 (± 419)
	Test	*z = 1.96**	*N.S.*

3) streambed geomorphology was responsible for variations in the denitrification potential of interstitial habitats.

Hydrological processes in geomorphologic units

Meandering rivers with sandy and gravely sediment are generally characterized by a succession of shallow (riffles and sand bars) and deep (pools) areas (Keller & Melhorn 1978). Many hydraulic mechanisms may interact to build and maintain this succession: stream water velocity, flow pattern (especially secondary channels), shear stress which control channel morphometry and sediment erosion, transport, and deposition. Spatial variation of water velocity, with high and low current areas, controls the necessary alternation of erosion and deposition (Yalin 1971). Changes in near-bed turbulence induced at the beginning of shallow-depth sequences create differences in sediment entrainment (shear stress); these enhance and maintain the sequence through a form of feedback process (Clifford 1993a, 1993b). Thus, the longitudinal succession of different geomorphologic units is related to the longitudinal oscillations in the velocity field of turbulent flow (Knighton 1998). This development is also due to the convergence and divergence of flow along the channel, combined with secondary circulation currents (e.g. surface flow divergence over shallow area favours the deposition of largest sediments; Keller & Melhorn 1973). The combination of these mechanisms explains the dominance of fine sediments in pool and bars, and the dominance of coarse particle in riffles. Both, the longitudinal variation of water depth and the grain size of sediment govern vertical hydrological exchanges: they are reduced or absent in pools and pronounced in riffle and bars. These latter units show similar hydrological pattern with surface water infiltration upstream and interstitial water upwelling downstream (Figure 3A). Similar patterns were observed in many streams with riffle-pool sequences (Vaux 1968, Triska et al. 1990, Valett et al. 1990, Hendricks & White 1991, Stanford & Ward 1993, Wroblicky et al. 1998).

The direction of water exchanges is controlled by the river topography and by the shape of the valley. Constrained areas induce stronger groundwater upwelling through the streambed than in unconstrained ones (Creuzé-des-Chatelliers et al. 1994, Woessner 2000). The high variability of VHG observed in the upstream parts of sand bars in site F is an illustration of this phenomenon: some bars are located at the foot of the hill slope and are subjected to massive groundwater inputs. This explains the difference between sites F and W with respect to the electric conductivity of the upwelling zone (low at site F and high at site W), which is influenced by the surrounding groundwater (Figure 3B).

These vertical exchanges induce contrasted physico-chemical characteristics of interstitial water (Marmonier & Dole 1986, Hendricks & White 1991, Dole-Olivier & Marmonier 1992). High oxygen content in downwelling zone of riffles and bars is a consequence of surface water infiltration. The low oxygenation measured inside pool sediments is linked to poor vertical exchange and microbial respiration (Grimm & Fisher 1984, Jones 1995, Pusch 1997, Fellows et al. 2001).

Geomorphology and Nitrogen dynamics in river sediment

Most differences were observed between pools and the two others units. In pools, nitrate content was low whilst potential denitrification reached highest values (Fig. 4A & B). The sedimentation of organic and inorganic fine particles in pools may explain this nitrate depletion: fine sediments offer a large surface for the development of heterotrophic bacteria that consumed dissolved oxygen (Lock, 1993), and generated anaerobic micro-sites in which denitrification occurs (Hendricks 1993, Garcia-Ruiz et al. 1998, Steinhart et al. 2000). Negative correlations between denitrification and D50 and between denitrification and Oxygen content support this statement.

In riffles and bars, an Oxygen depletion was strong in reach W, where nitrate content decreased between downwelling and upwelling zone. In reach F, Oxygen content remained above 2 mg L^{-1} and nitrate increased between downwelling and upwelling zones. Denitrification processes may explain the nitrate depletion in reach W, whereas groundwater input and nitrification may explain the nitrate increase observed in the upwelling zone of site F. Similar nitrate increases in upwelling areas have been observed in other streams that drain oxygenated groundwater (Grimm & Fisher 1984, Dole-Olivier & Marmonier 1992). At site F, the oxygenation of the interstitial water seems to be high enough to limit denitrification (Table 2; Fig. 4B) and to support nitrification processes.

The pattern of the potential denitrification observed in the second set of rivers (Table 3) confirms the effect of geomorphology on the denitrification, that was negatively correlated to the medium sediment grain size. Garcia-Ruiz et al. (1998) observed a similar relationship in rivers of north-east England, where the denitrification potential increased in a downstream direction as the percentage of fine sediments increased. Fine sediment favour the microbial attachment and the formation of anoxic microenvironment (Hendricks 1993, Garcia-Ruiz et al. 1998, Steinhart et al. 2000). Hill et al. (1998) have also reported that denitrification was favoured in the shallow sediments of pool-units in a N-rich stream. These areas of slow moving water increase the residence time of channel water and favour nitrate retention.

Ammonium content followed a reverse pattern, with accumulation in pools and upwelling zones, especially at site F (Fig. 4C). This accumulation may have been due to biodegradation of organic matter by heterotrophic biofilms that resulted in ammonification, as already observed in pools behind debris dams (Dahm et al. 1987) and poor nitrification due to the low oxygen content. Ammonium is generally flushed out of river sediment by water exfiltration. In sandy rivers, this export is reduced because of weak vertical flow and to the adsorption of ammonium on fine sediment and biofilm (Triska et al. 1994). Increase of ammonium concentrations in pools and upwelling zones of the site F is a good illustration of ammonification process that took place in stream with forested watershed.

Conclusion

The proposed predictions (Table 1) were, in general, verified. The influence of geomorphology on vertical hydraulic exchanges was clear: few or no exchanges were observed in pools, where accumulation of ammonium and denitrification were most intensive. The increase of nitrate concentration in upwelling zones of riffles and bars was observed at site F only, where the surface water was nitrate limited and the denitrification potential was low. At site W, which is N-rich and where the fine fraction of sediment was dominant, the nitrate decreased because of the high denitrification potential. Finally, this general pattern was confirmed by results from four of the six additional reaches, which highlighted the importance of streambed sediment heterogeneity. Future studies of nutrient retention capacity at the reach scale should take sediment heterogeneity of the geomorphological units into consideration.

Acknowledgements

We thank G. H. Copp for the correction of an earlier draft of this paper. Thanks are also extended to Nathalie Josselin and Marie-Paule Briand for their help for field assistance and during laboratory analyses, to Michel Lefeuvre and Yves Picard for their technical assistance, and Danièle Jouanneau for the maps. This study was funded by grants from the “Conseil Supérieur de la Pêche” (Grant No. 00-899) and the “Action Concertée Incitative : Eau et Environnement” (French Research Ministry).

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