Biogeochemistry **50:** 163–182, 2000.

Geomorphic control of denitrification in large river floodplain soils

G. PINAY[1], V.J. BLACK[2], A.M. PLANTY-TABACCHI[3], B. GUMIERO[4] & H. DÉCAMPS[3]
[1]*UMR ECOBIO, University Rennes I, Campus de Beaulieu, F-35042 Rennes cedex, France;* [2]*Department of Geography, University of Loughborough, United Kingdom;* [3]*CESAC CNRS, 29 rue Jeanne Marvig, 31055 Toulouse cedex, France;* [4]*Department of Biology, University of Bologna, Italy*

Received 28 October 1999; accepted 16 December 1999

Key words: denitrification, floodplain, large river nitrogen, riparian forest, soils

Abstract. In this manuscript we investigated the relationships between the microbiological denitrification process in river alluvial soils with structures and patterns of the floodplain visible at a larger scale. We hypothesised that both topography and soil grain size represent pertinent environmental factors to forecast denitrification activity in river floodplain. The study was conducted in 15 alluvial sites along a 30 km long stretch of the Garonne River, a seventh-order stream of the south west of France. Sites were selected to encompass the widest range possible of average annual flood duration (0.04 to 29 days) and frequency (return period from 0.6 to 7 years). On an annual basis, we found that average denitrification rates did not show any significant trend along the flood frequency gradient. Although during the study the flood frequency and duration was higher than the calculated average, we did not find any relationship between flood duration and denitrification enzyme activity. If flood events do not last long enough to maintain waterlogging conditions conducive to sustain denitrification activity for long periods, they indirectly affect the spatial distribution of denitrification activity through the sorting out of sediment deposits. Indeed, we found a significant relationship between denitrification rates in the floodplain soils and their texture; highest rates were measured in fine textured soils with high silt + clay content. Below a threshold of 65% of silt and clay content, the floodplain soils did not present any significant denitrification rates. Above that threshold denitrification increased linearly. These results demonstrate that alluvial soil texture is a landscape scale factor which has a significant effect on denitrification in floodplains.

Introduction

River systems and their riparian zones can be viewed as open ecosystems dynamically linked longitudinally, laterally and vertically by hydrologic and geomorphic processes occurring within a temporal hierarchy (Ward 1989). These processes operate in three large geomorphic provinces of a river catchment, i.e., the erosional, transitional, and depositional provinces (Sullivan et al. 1987). The erosional province corresponds to the steep headwaters of the upper course. It is characterized by high gradient channels (>4%) that are structurally constrained by V-shaped valleys which permits minor lateral movements. The transitional province occurs in the river valley with channel gradients ranging from 1 to 4% where considerable transport of suspended sediments of small size (0.2 to 250 mm diameter) can occur. It corresponds generally to the middle course of a river. The deposition province, downstream from the transitional province, exhibits channels that are low gradient (<1%), unconstrained and shallow. The channels which are commonly unstable or multi-thread channels, exhibit high rates of deposition of fine sediments (<0.2 mm diameter), and the development of fragmented or dispersed riparian corridors (Tabacchi et al. 1998). Along the two lowest provinces, i.e. transitional and depositional, river floodplains have been recognized as important sinks for storing sediments and associated nutrients mobilized from upstream catchments (He & Walling 1997). Energy and matter fluxes alongside large river systems are mainly oriented from the river to the floodplain since most of the deposition of suspended sediment during periods of inundation is associated with overbank flood deposits (Grubaugh & Anderson 1989; Brunet et al. 1994). These transfers of energy and biotic or abiotic matters are largely under the control of flood duration, frequency and magnitude which create a mosaic of geomorphic surfaces influencing the spatial pattern and successional development of riparian vegetation (Salo et al. 1986; Roberts & Ludwig 1991). Indeed, these fluxes of energy and matter via flood deposits are responsible for the high nutrient cycling capacity of floodplain soils compared to upland ecosystems and play an important role in the control of upstream/downstream fluxes of nutrients (Brinson et al. 1984; Mulholland 1992).

Flooding directly affects nutrient cycling in alluvial soils by controlling the duration of oxic and anoxic phases (Ponnamperuma 1972; Keeney 1973; Patrick 1982). For instance it was found that the net nitrogen mineralization rate was 4 times greater in a spring-flooded marsh than in a nonflooded one (Neill 1995) and that alternate aerobic and anaerobic conditions enhance organic matter decomposition and nitrogen loss through denitrification in flooded soils (Reddy & Patrick 1975; Groffman & Tiedje 1988). Flooding duration is controlled by local topography; low areas are flooded more often and longer than higher ones, producing large variations in biogeochemical patterns at a meter scale (Pinay et al. 1989; Pinay & Naiman 1991). Flooding also indirectly affects nutrient cycling in floodplain soils by influencing the soil structure and texture through sediment deposits. Hence, floodplain and stream channel geomorphic and hydrologic processes influence the sorting of flood sediment deposits on a grain size basis creating a mosaic of soils of different textures. The control of soil texture on nitrogen cycling has already been documented in forests (Pastor et al. 1984; McClaugherty et al. 1985), alluvial forest (Pinay et al. 1995), coastal forest (Seely et al. 1998), shortgrass steppe (Schimel et al. 1985), desert ecosystems (Schlesinger et al. 1996) or grassland (Parton et al. 1988). The proportion of soil C and N present in the microbial biomass is also related to soil texture since the proportion of C and N in microbial biomass in coarse-textured soils is found to be smaller than in fine-textured ones (Amato & Ladd 1992; Hassink 1994).

In relation to N cycling in floodplain soils, it is important to forecast bacterial denitrification activity which is a key process since it constitutes a major sink of nitrate, and as such is involved in the control of nitrogen fluxes along river systems. For instance Pinay et al. (1995) found that denitrification rates were of the same order of magnitude than N mineralization one, and that nitrogen denitrified on a year basis represented up to 70% of the nitrogen deposited during floods. Yet, the pulse characteristic of flood events render predictive models of N cycling in floodplain soils, difficult to build up. Moreover, the development of predictive models necessitates finding a link between processes occuring at a microbial scale and landscape patterns visible at the floodplain scale. For instance, the role of soil moisture, nitrate concentration and available carbon in regulating this microbial process is now well documented (Rolston et al. 1984; Myrold & Tiedje 1985; Davidson & Swank 1986). Yet, none of these 3 factors could significantly explain the variation of the denitrification rates at the floodplain scale (Groffman & Tiedje 1989).

The objective of the paper is to relate the denitrification process which occurs in micro-sites to structures and patterns visible at larger scales. We hypothezise that topography and soil grain size represent pertinent environmental factors at the landscape scale to predict denitrification activity in a river floodplain. On one hand, local floodplain topography governs the duration of flood in a given stretch and in turn should influence soil redox conditions, with topographically low sites being more subject to the anaerobic conditions which are conducive to denitrification. On the other hand, soil texture, which influences soil water holding capacity, should create a range of responses in term of waterlogging duration after flood and rainfall events. Waterlogging durations are expected to be longer in fine textured floodplain soils and should result in higher denitrification rates.

Study area

Fifteen riparian sites were chosen in the floodplain of the Garonne River along a 30 km long stretch, downstream of the city of Toulouse, southwest France

44° Lat N (Figure 1). All sites were selected within the 10y floodplain, with the maximum altitude difference between the lowest and the highest sites being 5 m. In this stretch the river meanders and the natural migration of meander bars is accompanied by the lateral accretion of sediment over the floodplain. In the study site the river is a seventh-order channel draining 10,000 km^2. The altitude of the reach is about 140 meters above sea level and channel slope is 0.1%. The Garonne River which has its source in the Pyrénées mountains (2850 m) has maximum discharge in spring (March to May) due to precipitation and snow melt (up to 4350 m^3 sec^{-1} in 1952). The low water period generally lasts from August to October, with discharge down to 20 m^3 sec^{-1}, while the average annual discharge in the stretch under study is 200 m^3 sec^{-1}.

Sites were selected to encompass the widest range possible of flood duration and frequency and to include different geomorphic features typical of the study reach (Smepag 1989; Steiger 1991). Soils in all sites had low clay content (5.6 to 11.6%) but their silt and sand content varied widely according to their geomorphic location (Table 1). The soils belonged to the Fluvents series of alluvial entisoils and were layered beneath having coarse alluvial gravel deposits at various depths (from 60 cm to 2 meters). The vegetation community was typical of vegetation stands of French floodplains (Tabacchi et al. 1990; Tabacchi 1992) and was dominated by *Populus nigra, Salix alba*, *Rubus caesius*, *Urtica dioica*, *Carex maxima* and *Phalaris arundinacea*. The amount of litterfall and the litter decomposition rates of the tree species found in the fifteen sites were high compared to other forest ecosystems but do not differ from one another (Chauvet 1989; Chauvet & Jean-Louis 1988).

Materials and methods

At each of the 15 study sites, 3 different sampling areas (1 m^2 each) were selected during each of the 6 sampling periods that occured between April 1993 and June 1994. Soil analysis focused on the surface ten centimeters which corresponds to the most active zone in a biological sense (i.e. maximum root concentration) and also to the zone which is most subject to the mechanical processes of erosion and deposition on a yearly basis. In each area the upper 10 cm of soil were taken using a hand auger after the litter was removed. Samples were stored at 4 °C and processed within 24 h. Soil bulk density (D_b) was measured by oven drying at 105 °C for 24 h a given volume of soil (251 cm^3). The bulk density was then calculated using the formula:

$$D_b = \text{dry mass of soil/total volume of soil.}$$

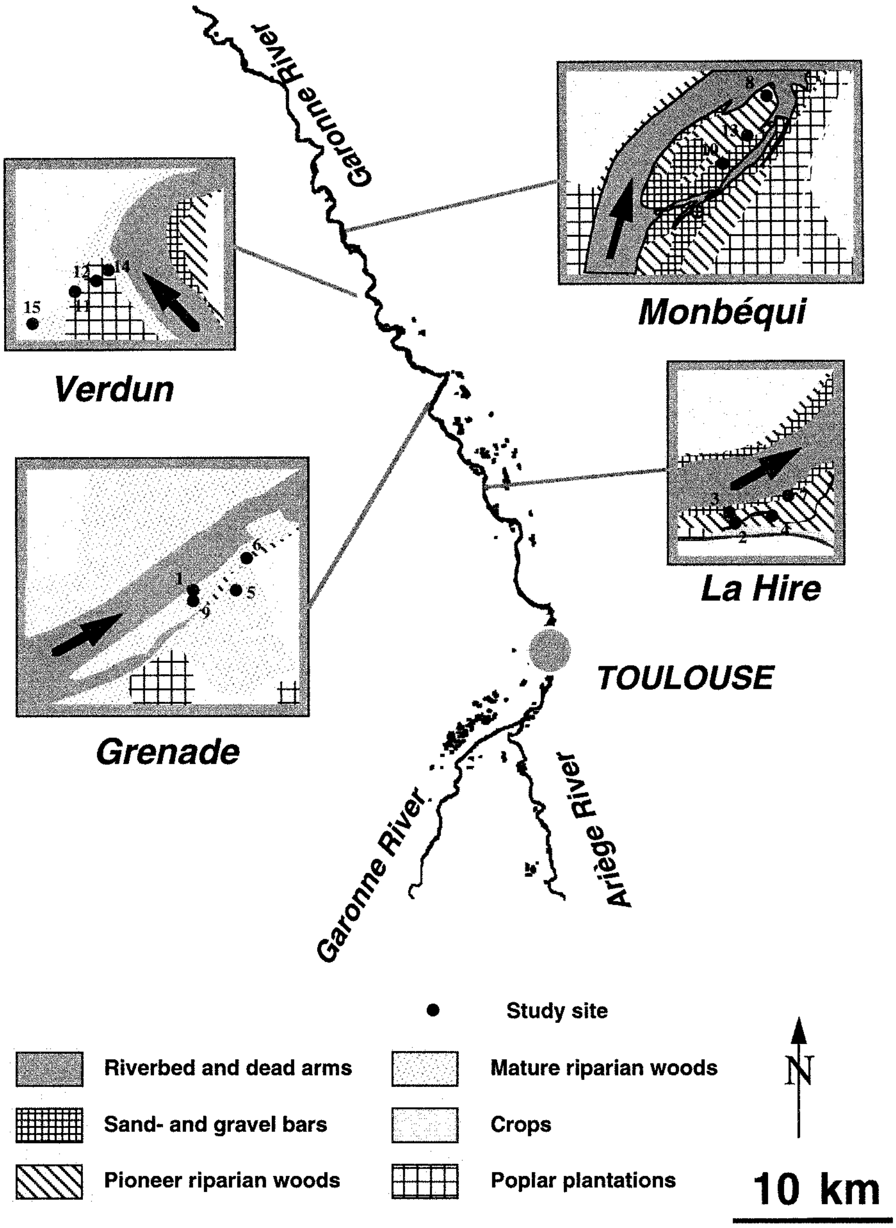

Figure 1. Geographic situation of the study sites along the Garonne River.

Table 1. Main characteristics of the study sites.

Site	Texture			Flood				
	Clay (%) $<2\ \mu$m	Silt (%) 2–50 μm	Sand (%) 50–2000 μm	Overbank discharge $m^3\ s^{-1}$	Return period (year)	Mean annual duration 1972–1994	Duration during the study period (days)	Events during the study period
1	7	25	68	442	0.6	29	70	15
2	7	36	57	1000	1.1	3.5	6	5
3	7	42	51	1000	1.1	3.5	6	5
4	7	47	48	2600	7	0.04	0	0
5	8	47	47	600	0.7	11.9	23	8
6	9	55	36	471	0.6	24.6	53	12
7	9	59	32	1000	1.1	3.5	6	5
8	9	60	31	471	0.6	24.6	53	12
9	10	62	28	2000	3	0.3	1	1
10	10	62	28	2000	3	0.3	1	1
11	10	64	26	700	0.8	8.0	17	6
12	11	63	26	700	0.8	8.0	17	6
13	11	64	25	2600	7	0.04	0	0
14	11	66	23	471	0.6	24.6	53	12
15	12	67	21	1200	1.4	2.2	2	2

Soil porosity was calculated by the formula $S_t = 100*(1 - D_b/P_p)$ where P_p was the particle density which we assumed to be equal to 2.65 g cm^{-3} (Vomocil 1965). Soil grain-size was determined by the Pipette Sampling Method (Day 1965), pre-treating the samples with hydrogen peroxide and dispersing with sodium hexametaphosphate solution. Soil subsamples were oven-dried for 24 hours at 105 °C in order to determine dry mass and percent moisture (P_w). Water filled Pore Space (WFPS) was calculated using the formula:

$$\%\ \mathrm{WFPS} = P_w/S_t.$$

Ten grams (fresh mass) of each soil sample were extracted with 150 ml of 2 M KCl. The extract was filtered and analysed for NH_4-N, NO_2-N and NO_3-N with a Technicon Autoanalyzer (Technicon 1976). Nitrate concentration was calculated by substracting nitrite value from the nitrate one. Nitrite data is not discussed in this study since it presented low and constant values at all sites considered. Nitrogen mineralization potential (nmp) was determined on fresh subsamples by anaerobic incubation for 7 days at 40 °C (Waring & Bremner 1964). Total organic nitrogen (ton) was determined by digestion of air-dried subsamples using the Kjeldahl method (Bremner 1965). Total organic carbon (toc) was determined using a high-temperature induction furnace (Carmhograph 8 Wösthoff, Bochum Germany).

In situ denitrification (dnt) was assayed by the static core acetylene inhibition method (Yoshinari & Knowles 1976). Nine intact cores (length 10 cm, diameter 5 cm) collected during the 6 sampling periods from each of the 15 sites were capped with rubber serum stoppers and then amended with acetone-free acetylene to bring core atmosphere concentration to 10 KPa (10% V/V) acetylene and 90 KPa air. Samples were incubated at field temperature, and denitrification rate was calculated as the rate of nitrous oxide (N_2O) accumulation in the head space between 1 and 4 h. Head space samples were removed from all cores and stored in evacuated collection tubes (Venoject, Terumo Scientific N.J). Gas samples were analysed via gas chromatography (GC Varian 3300) equipped with an electron capture detector (ECD ^{63}Ni) and Porapak Q columns.

Denitrification enzyme activity was measured at each sampling period using Smith and Tiedje's (1979) procedure. Three subsamples from each of these sites were amended with nitrate (10 μg NO_3-N.g^{-1}, soil fresh wt basis) and referred to as DEA_{+N}, and 3 sub-samples were amended with C + N (10 μg NO_3-N.g^{-1} and 4 mg C-glucose.g^{-1}, soil fresh wt basis), referred to as DEA_{C+N}. Acetylene was added and samples were made anoxic by flushing with N_2 and incubated for 8 h at mean soil temperature (10 °C).

Water level and discharge of the Garonne River were provided by the French Navigation Service (Service Hydrologique Centralisateur). The determination of the overbank discharge in the different sites was estimated after biweekly field survey over a year period. Soil moisture in the 15 sites was measured at two week intervals using the procedure described above. Soil temperature was measured continuously with a temperature datalogger (Tinytalk II) and precipitation records were provided by the French National Meteorological Service for a site situated 15 km from the study area.

Results

Overbank discharge in the selected sites, ranged from 442 m^3–2600 m^3 sec^{-1} corresponding to return period of 0.6–7 years (Table 1). In the most frequently inundated site (1), the longest flooded period in the last 22 years was 50 days and the average flood duration for the same period was 29 days per year (Table 1) corresponding to flood events of short duration. Except for the highest sites, i.e. 4 and 13, which have not been flooded during the study period, the other sites have been more often flooded and for a longer period of time than the average calculated over the last 22 years period. Average soil moisture was significantly correlated (r^2 = 0.54; $p < 0.01$) to soil silt + clay content. We calculated the water filled porosity of the soils from their percentage of water measured at two week intervals. On an annual basis, water filled porosity of all the studied soils was above 60% of their soil total porosity for at least 100 days. Yet, no significant relationship was found between the average annual duration of flood events on the floodplain sites and the annual number of days their soils exhibited water filled porosity above 60% (Figure 2(A)). Since average annual duration of flood events is related to soil elevation, there seems to be no significant relationship between soil elevation and waterlogging conditions. Moreover, there were no significant relationship between average annual duration of flood event and silt + clay content of surface soils. However, we found a significant positive linear relationship ($r^2 = 0.64$; $p < 0.01$) between soil silt + clay content and the annual number of days during which its water filled porosity was above 60% (Figure 2(B)).

On an annual basis, average denitrification rates did not show any significant trend along the flood frequency gradient (Figure 2(C)) while they presented an exponential pattern when plotted against the soil silt + clay content (Figure 2(D)). The denitrification enzyme activity of the denitrifying population presented a larger response (Figure 2(E and F)) when incubated anaerobically with glucose and nitrate (DEA_{C+N}), compared to incubation with nitrate alone (DEA_{+N}). Moreover, highest rates (up to 150 ng N g^{-1} dry soil h^{-1}) were measured on fine textured soils with glucose and nitrate (Figure 2(F)). As with *in situ* denitrification, DEA was not related to flood frequency (Figure 2(E)).

Soil ammonia and nitrate exhibited similar concentrations with annual average values ranging from 14.2 to 25.6 μg N-NH_4 g^{-1} dry soil (Figure 3(A and B)) for ammonia and from 1.9 to 20.2 μg N-NO_3 g^{-1} dry soil for nitrate (Figure 3(C and D)). Ammonia concentrations presented large variation and did not show any significant trend on an annual basis, either along the flood duration transect, nor against the silt + clay gradient. Annual average soil nitrate concentrations were not significantly correlated with silt + clay content either (Figure 3(D)). Soil organic nitrogen mineralization potential (Figure 3(E and F)) presented a significant positive correlation with soil silt + clay content ($r^2 = 0.54$; $p < 0.01$) but did not show any significant relationship with the average annual flood duration (Figure 3(E)). Soil organic carbon and nitrogen concentrations were significantly correlated with soil silt + clay content with respectively $r^2 = 0.67$; $p < 0.01$, and $r^2 = 0.55$; $p < 0.01$ (Figure 4(B and D)). Moreover, the ratio of carbon to nitrogen in the study sites ranged between 10 and 20 and were negatively correlated with soil grain size ($r^2 = 0.44$; $P < 0.01$), underlining that small particle sediments are organic-rich and of high quality (Figure 4(F)). However, they did not present any significant trend along the average annual flood duration gradient (Figure 4(E)).

On a seasonal basis, soil ammonia concentration was low in spring and summer (between 3 and 7 μg N-NH_4 g^{-1} of dry soil; Figure 5(A–C, F))

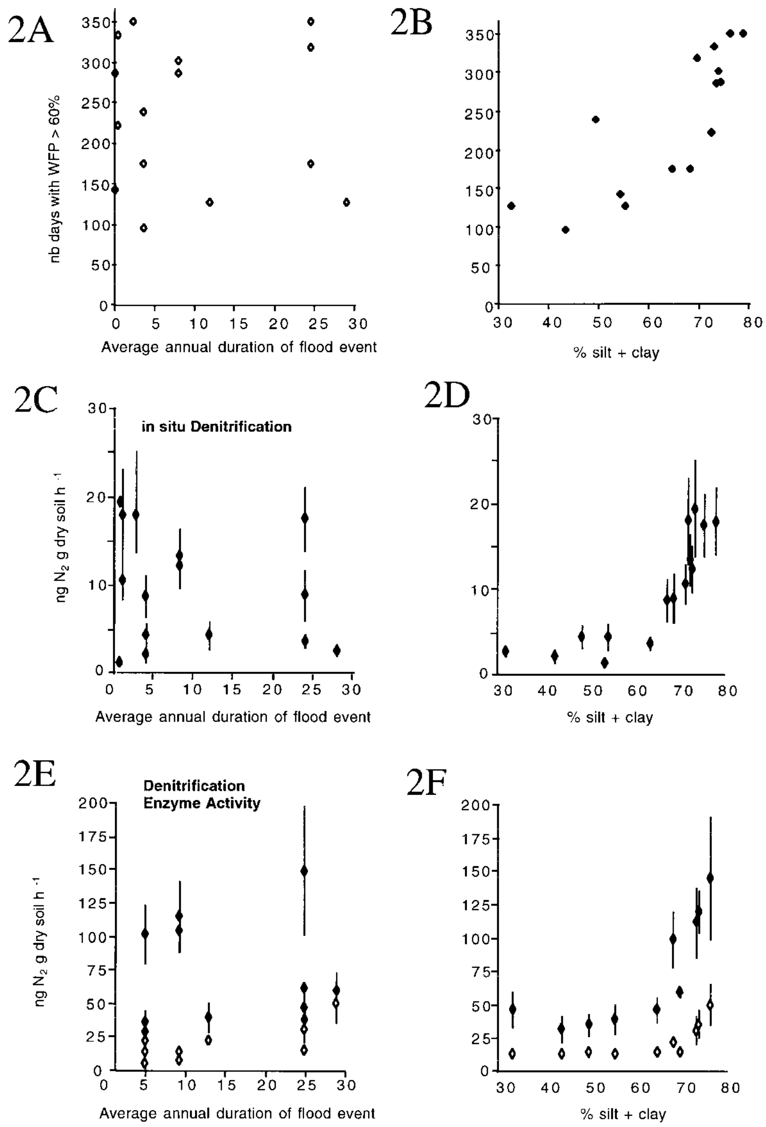

Figure 2. Relationship between floodplain soil topography represented as their annual duration of flood event, and the number of days during which the soils present a water filled porosity above 60% (2(A)), the annual average of in situ denitrification rates (2(C)), and the soil denitrification enzyme activity (2(E)). Relationship between soil silt + clay content and the number of days during which their water filled porosity was above 60% (2(B)), the annual average of in situ denitrification (2(D)) and the soil denitrification enzyme activity (2(F)). In Figure 2(E) and 2(F) open circles represent the anaerobiosis and nitrate treatment (DEA_N) while the closed circles represent the anaerobiosis and nitrate and glucose treatment (DEA_{CN}). Vertical bars represent the standard deviation of the mean.

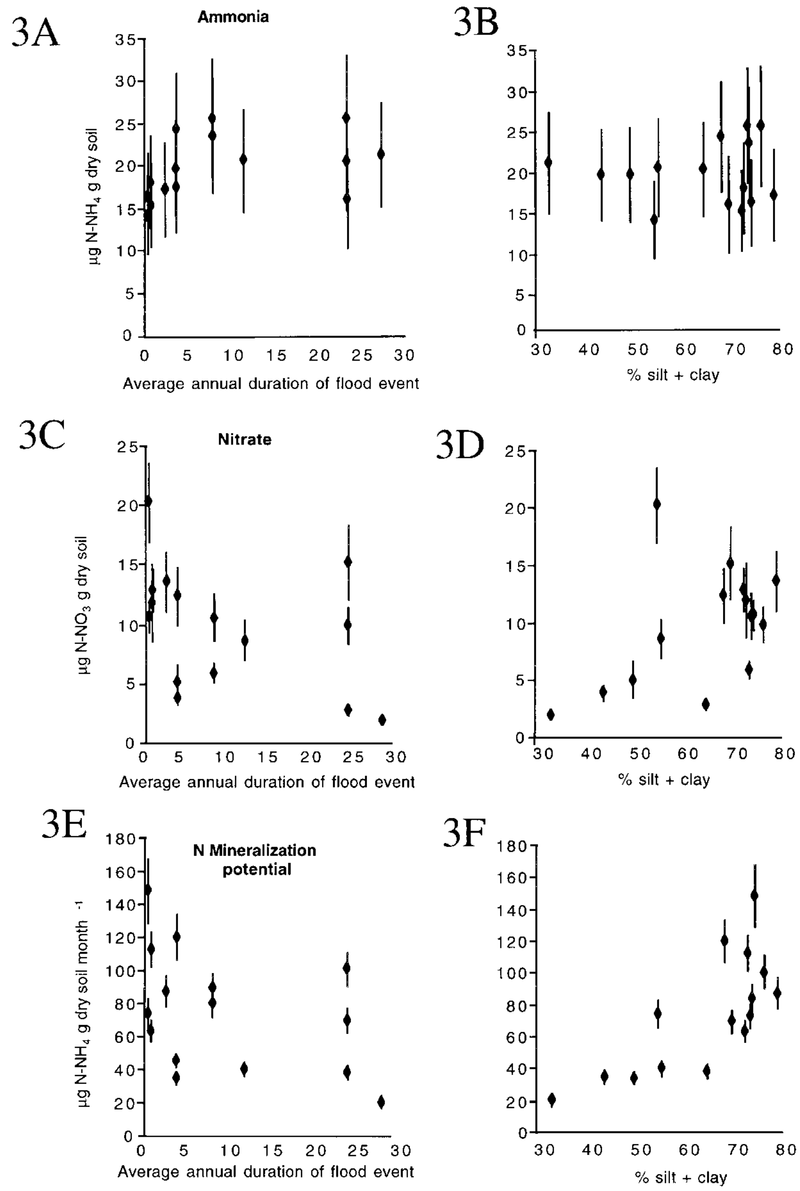

Figure 3. Relationship between floodplain soil topography represented as their annual duration of flood event, and average annual soil ammonia concentration (3(A)), the annual average of soil nitrate concentration (3(C)), and annual average of mineralization potential (3(E)). Relationship between soil silt + clay content and average annual soil ammonia concentration (3(B)), the annual average of soil nitrate concentration (3(D)) and annual average of mineralization potential (3(F)). Vertical bars represent the standard deviation of the mean.

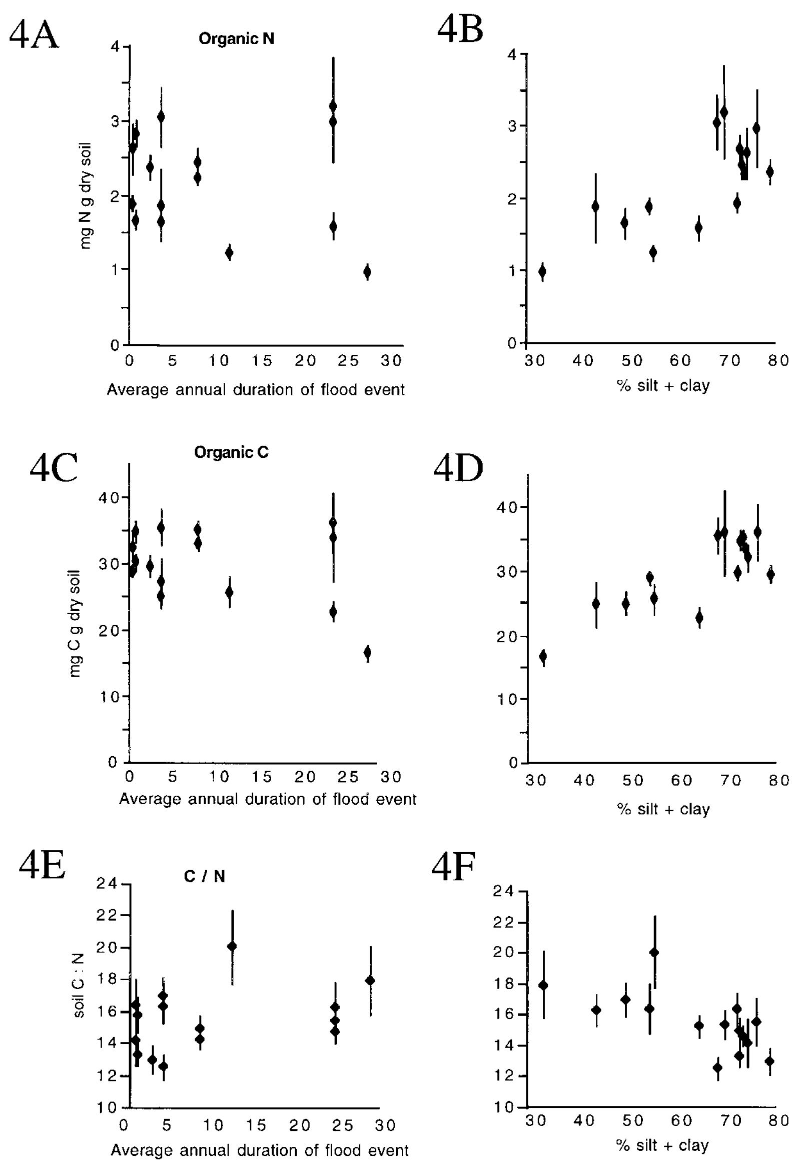

Figure 4. Relationship between floodplain soil topography represented as their annual duration of flood event, and average annual soil organic nitrogen concentration (4(A)), the annual average of soil organic carbon concentration (4(C)), and annual average of C/N ratio (4(E)). Relationship between soil silt + clay content and average annual soil organic nitrogen concentration (3(B)), the annual average of soil organic carbon concentration (3(D)) and annual average of soil C/N ratio (3(F)). Vertical bars represent the standard deviation of the mean.

but increased ten fold (between 54 and 74 μg N-NH$_4$ g^{-1} of dry soil) in autumn (Figure 5(D)). There was no significant relationship between ammonia concentration and soil grain size during these periods. The winter sampling was done on February 15th 1994 (Figure 5(E)), two days after a flood event which peaked at 1100 m^3 sec^{-1}, flooding all study sites except the five highest ones (4, 9, 10, 13 and 15). Flooded sites had high ammonia concentrations (between 47 and 55 μg N-NH$_4$ g^{-1} of dry soil), whereas nonflooded sites had low ammonia concentrations (between 12 an 16 μg N-NH$_4$ g^{-1} of dry soil (Figure 5(E)).

Rates of *in situ* denitrification (DNT) were low in alluvial soils with low silt + clay content (up to 60%) whatever the season (Figure 6). DNT rates were significantly higher (up to 30 ng N g^{-1} dry soil h^{-1}) in fine textured soils, i.e., soils with more than 65% of silt + clay, except in August 1993 (Figure 6(C)) where they remained low most probably because of the low soil moisture concentration during this period. Anaerobic incubation with nitrate amendment did not significantly increase the denitrification rates (DNT$_{+N}$), except in August (Figure 7). This increase in summer might be the result of the combined effect of nitrate addition, moisture increase in the slurry and anaerobiosis. This experiment cannot clearly determine the respective role of each of these effects in the case of August sampling. However, the absence of significant effect of anaerobiosis and nitrate addition during the other sampling dates demonstrate that these two factors were not the limiting factors of denitrification (Figure 7). In contrast, anaerobic incubation with carbon and nitrate amendments increased significantly the denitrification rates (DNT$_{+CN}$) both in coarse and fine texture soils, suggesting that organic carbon was the limiting factor of denitrification in alluvial soils. Highest potential rates (up to 530 ng N g^{-1} dry soil h^{-1}) were measured in February 1994 (Figure 7(E)), a few days after a flood event. Yet, even during this period available carbon was the most limiting factor of denitrification. The pattern observed in the relationship between *in situ* denitrification and soil grain size remained: the fine textured soils presented significantly higher rates than coarse ones. Moreover, the difference between the two treatments (plus N and plus C + N) was significantly higher in the fine textured soils than in the coarse ones.

Discussion

Our first hypothesis was that alluvial soil elevation above the river was a pertinent environmental factor to forecast denitrification activity at the flood-plain landscape scale. The rationale was that lower grounds would be subject to higher flood duration and frequency which would lead to longer soil

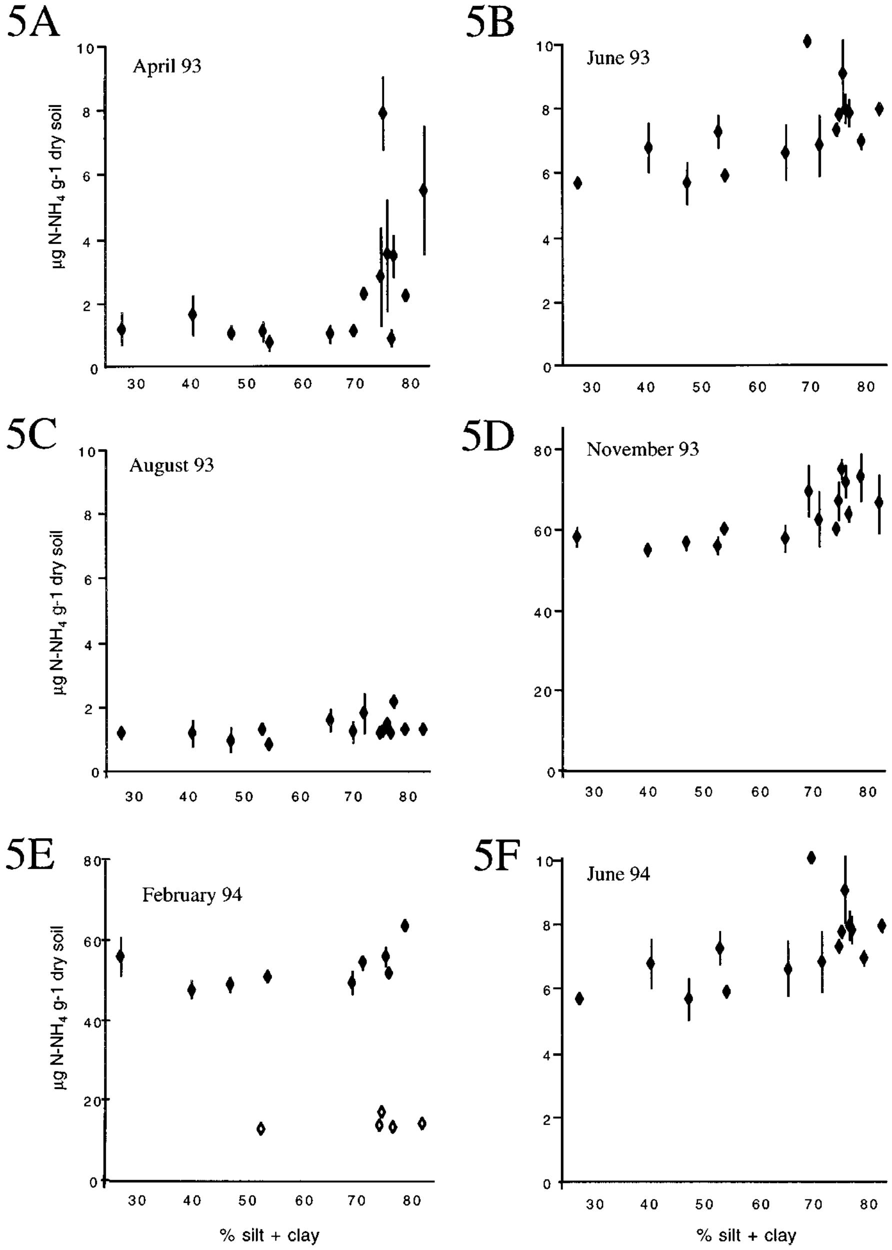

Figure 5. Seasonal pattern of the relationship between soil silt + clay content and soil ammonia concentration. In Figure 5(E) open circles represent the sites nonaffected by the February flood event while the closed ones represent the sites which have been inundated. Vertical bars represent the standard deviation of the mean. Note that in 5(D) and 5(E), the y-axis is 8 times higher.

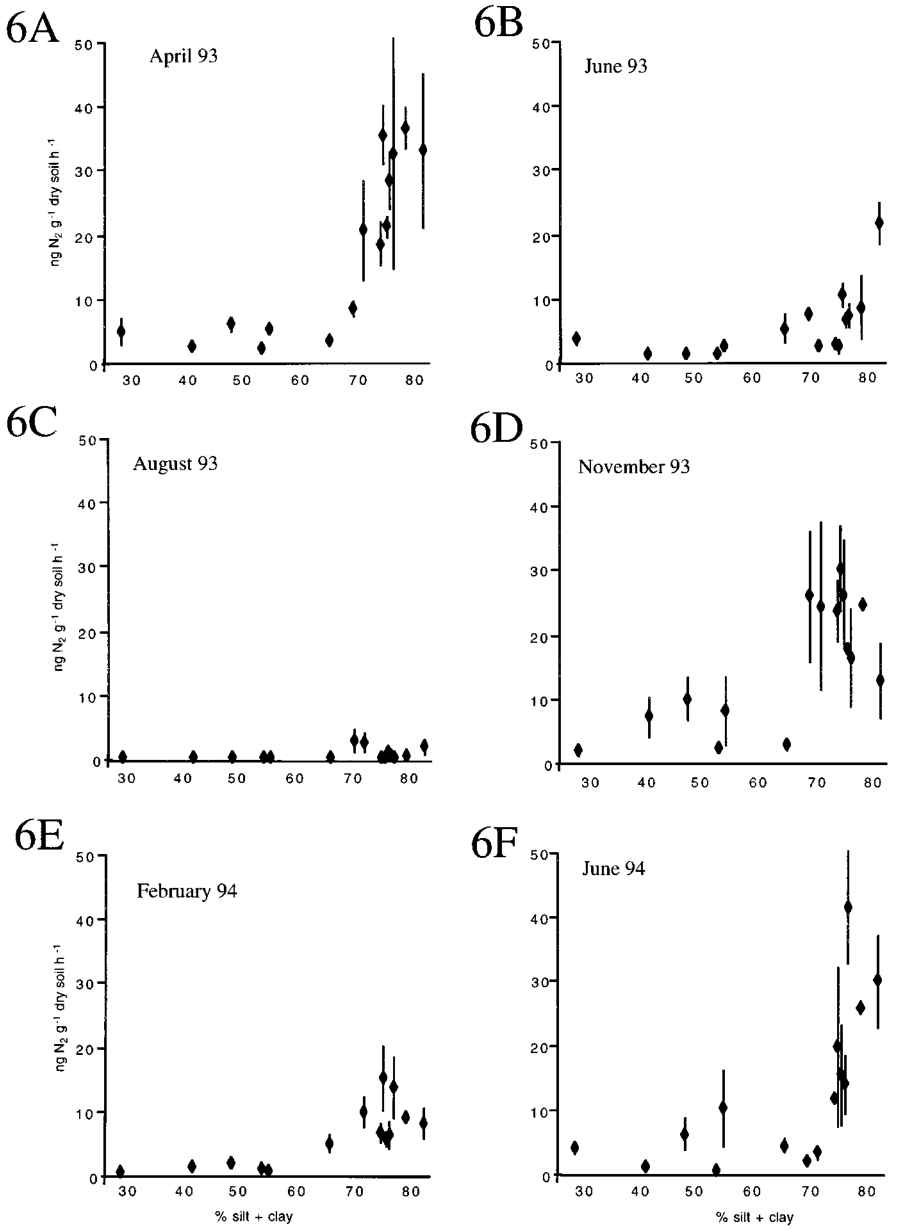

Figure 6. Seasonal pattern of the relationship between soil silt + clay content and rates of in situ denitrification. Vertical bars represent the standard deviation of the mean.

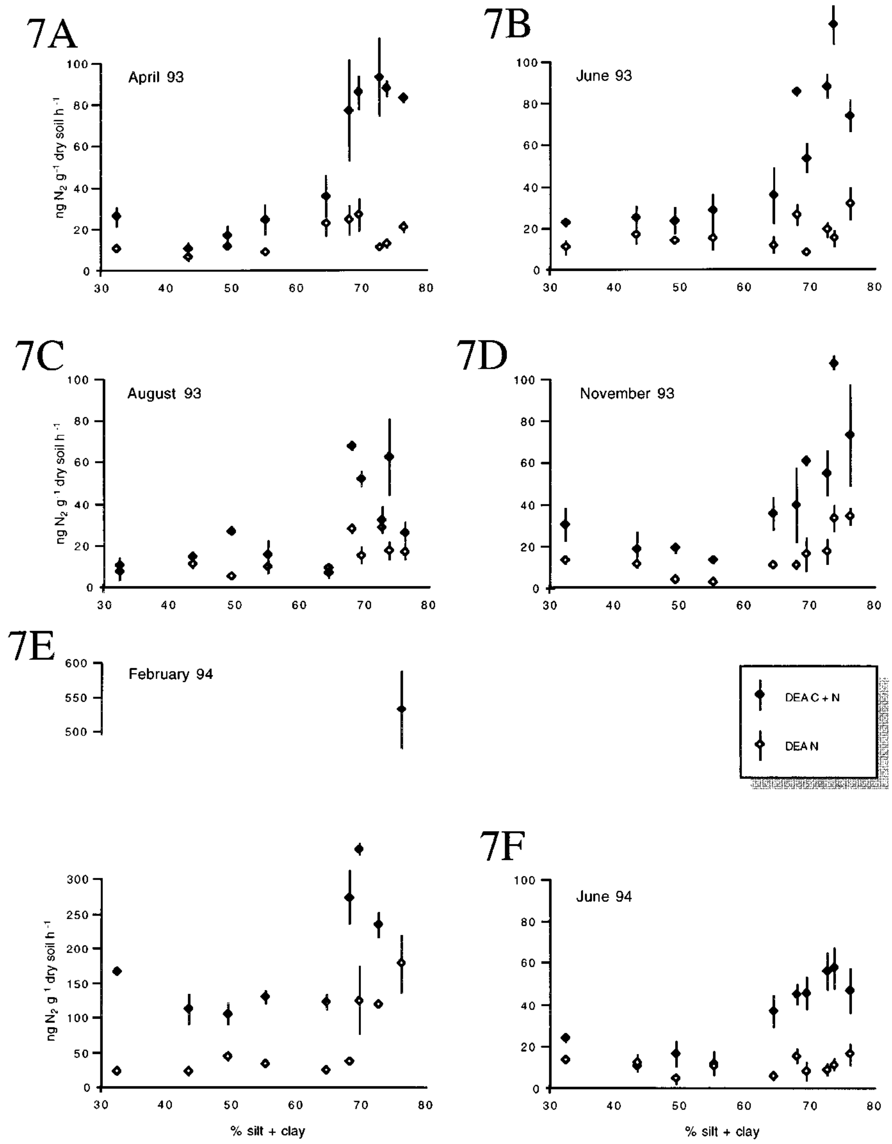

Figure 7. Seasonal pattern of the relationship between soil silt + clay content and denitrification enzyme activity. Open circles represent the anaerobiosis and nitrate treatment (DEA_N) while the closed circles represent the anaerobiosis and nitrate and glucose treatment (DEA_{CN}). Vertical bars represent the standard deviation of the mean.

waterlogging conditions conducive to higher denitrification rates. In fact no significant relationship was found between annual average duration of flood event and soil denitrification (Figure 2(C)). This can be explained by the short flood frequency and duration they encounter. Indeed, in most of the floodplain soils the duration of a flood event generally lasts between 1 and 4 days and the average total flood duration ranges from 0.3 to 26 days per year. Although this year the flood frequency and duration was higher than the calculated average (Table 1), we did not find any relationship between flood duration and denitrification enzyme activity (Figure 2(E)). DEA is considered as an integrative product of the denitrifying activity of a given soil (Groffman & Tiedje 1989). It corresponds to the potential denitrifying activity of the denitrifying bacteria population present in the soil. DEA varies very little over the course of the year relative to denitrification. The DEA data indicate that such short events cannot maintain anaerobic conditions long enough to be revealed with a two month sampling periodicity. Indeed, February sampling occured by chance two days after a flood event which reached the 10 lowest sites (Figure 5(E)). This flood event has increased by 5 fold the soil ammonia concentration of the flooded sites compared to the non flooded ones. This rise in ammonia concentration can be attributed to flood deposits since the flood did not significantly raise the water filled porosity of the lower sites compared to the upper ones not affected by the flood ($p < 0.01$). Yet, no measurement of flood deposits have been done to clearly confirm this hypothesis.

Our second hypothesis was that soil texture is a landscape scale factor which has a significant effect on denitrification. Indeed, we found a significant relationship between denitrification rates in the floodplain soils and their texture; highest rates were measured in fine textured soils with high silt + clay content (Figures 2(D) and 6). Yet, no significant relationship was found between average annual duration of flood event and soil texture. Other factors, such as direction and velocity of flood, are probably more important than the flood duration in influencing the sediment sorting. It was found that below a threshold of 65% of silt and clay content, the floodplain soils did not present any significant denitrification rates. Above that threshold denitrification increased linearly. These results confirm the importance of texture on soil nitrogen cycling processes and coroborate the significant positive relationship found between bacterial denitrification and soil percentage of silt and clay (Groffman & Tiedje 1989; Pinay et al. 1995). This positive relationship between fine textured soils and denitrification activity is due to the fact that a given water content will entail a higher percentage of water filled porosity in fine textured soils than in coarser ones (Granli & Bockman 1994). Hence a high percentage of water filled porosity will decrease the diffusion rate of oxygen, favor anaerobic conditions to develop, and in turn will increase denitrification (Parkin & Tiedje 1984). Several studies reported that soil denitrification was negligible below 60% of water filled capacity (Aulakh & Rennie 1985; Grundmann & Rolston 1987). Above that threshold a significant positive correlation has been reported between denitrification rate and soil water content (Groffman & Tiedje 1991; Parsons et al. 1991). Indeed, we found a significant relationship between soil percentage of silt and clay and the number of days they present a WFP $>60\%$ (Figure 2(B)). Fine textured soils, i.e., with silt and clay content $>65\%$, exhibit a WSP $>60\%$ for at least half of the year. This high WFP has been maintained in fine textured soils by precipitation events. The low WFP in August which corresponds to the dry summer period explain the low denitrification rates measured. Nevertheless, the high denitrification potential measured during this period (Figure 7) stresses that denitrifying bacteria are still present and potentially active under such dry conditions.

The DEA results do not allow us to evaluate the role of anaerobiosis since all our experiments were performed under oxygen free conditions. Anaerobiosis + nitrate addition (DEA_N) did not increase significantly the denitrification activity of the floodplain soils except during the winter period, i.e., February (Figure 7(E)). Moreover, the addition of glucose did not increase the potential rates of the coarser sites. This confirms the limiting microbial denitrification activity of coarse textured soils on an annual basis, except during the wet winter period. The significant response of fine textured soils to glucose addition revealed that their denitrifying population is high and limited by organic carbon availability, even though these silty sites have higher organic matter concentration of higher quality (high organic carbon and low C/N, Figure 4(D) and 4(F)).

Conclusion

Large river floodplains such as the Garonne present a mosaïc of soil texture which is under the control of both the geomorphic features of the floodplain and flood events. If flood events do not last long enough to maintain waterlogging conditions conducive to sustain denitrification activity for long periods, they indirectly affect the spatial distribution of denitrification activity through the sorting out of sediment deposits. Hence, the fate of flood water movements on the floodplain, i.e. direction, current, distance from the main channel, influence the texture type of sediment deposits and in turn affects the denitrification activity. Until now, the modelization and regionalization of alluvial soil microbial processes was based mainly on soil topography and flood duration. The indirect relationship found between landscape patterns and denitrifying microbial process opens new possibilities to evaluate denitrification rates of alluvial soils according to a given geomorphic feature which is measurable at a larger scale. Even though a given spatial pattern of alluvial soil grain size mosaic can vary temporarily, following extreme hydrological events such as high floods, the analyses of alluvial soil texture profiles will provide some insights to evaluate retrospectively the consequences of the changes of alluvial geomorphic patterns on the denitrification activity.

Acknowledgements

We would like to thank R.M. Holmes for his constructive comments on an earlier version of the manuscript. This work was supported by an European Union grant from the Environment and Climate Programme on European River Margins (ERMAS), contract No EV5V-CT92-0100.

References

Amato M & Ladd JN (1992) Decomposition of 14C-labelled glucose and legume material in soils: Properties influencing the accumulation of organic residue C and microbial biomass C. Soil Biol. Biochem. 24: 455-464

Aulakh MS & Rennie DA (1985) Gaseous nitrogen losses from conventional and chemical summerfallow. Canad. J. Soil Sci. 65(1): 195–203.

Bremner JM (1965) Total nitrogen. In: Black CA (Ed) Methods of Soil Analysis, Vol. 9 (pp 1149–1178). Agronomy

Brinson MM, Bradshaw HD & Kane ES (1984) Nutrient assimilative capacity of an alluvial flood plain swamp. Journal of Applied Ecology 21: 1041–1057

Brunet RC, Pinay G, Gazelle F & Roques L (1994) The role of floodplain and riparian zone in suspended matter and nitrogen retention in the Adour River, southwest France. Regul. Rivers Res. Manag. 9: 55–63

Chauvet E (1989) Production, flux et décomposition des litières en milieu alluvial. Dynamique et rôle des hyphomycètes aquatiques dans le processus de décomposition. PhD Thesis, Université Paul Sabatier, Toulouse III, France

Chauvet E & Jean-Louis AM (1988) Production de litière de la ripisylve de la Garonne et apport au fleuve. Acta Oecologia, Oecologia Generalis 9: 265–279

Davidson EA & Swank WT (1986) Environmental parameters regulating gazeous nitrogen losses from two forested ecosystems via nitrification and denitrification. Appl. Environ. Microbiol. 52(6): 1287–1292

Day PR (1965) Particle fractionation and particle-size analysis. In: Black CA (Ed) Methods of Soil Analysis, Vol. 9 (pp 545–567). Agronomy

Granli T & Bockman OC (1994) Nitrous oxide from agriculture. Norwegian J. Agricult. Sci. 12(128): 63–72

Groffman PM & Tiedje JM (1988) Denitrification hysteresis during wetting and drying cycles in soils. Soil Sci. Soc. Am. J. 52: 1626–1629

Groffman PM & Tiedje JM (1989) Denitrification in north temperate forest soils: Relationships between denitrification and environmental factors at the landscape scale. Soil Biol. Biochem. 21: 621–626

Groffman PM & Tiedje JM (1991) Relationships between denitrification, CO_2 production and air-filled porosity in soils of different texture and drainage. Soil Biol. Biochem. 23(3): 299–303

Grubaugh JW & Anderson RV (1989) Upper Mississippi River: Seasonal and floodplain forest influences on organic matter transport. Hydrobiologia 174: 235–244

Grundmann GL & Rolston DE (1987) A water function approximation to degree of anaerobiosis associated with denitrification. Soil Sci. 144(6): 437–441

Hassink J (1994) Effect of soil texture on the size of the microbial biomass and on the amount of C and N mineralized per unit of microbial biomass in Dutch grassland soils. Soil Biol. Biochem. 26(11): 1573–1581

He Q & Walling DE (1997) Spatial variability of the particle size composition of overbank floodplain deposits. Water Air Soil Pollut. 99: 71–80

Keeney DR (1973) The nitrogen cycle in sediment-water systems. J. Environ. Qual. 2(1): 15–29

McClaugherty CA, Pastor J & Aber JD (1985) Forest litter decomposition in relation to soil nitrogen dynamics and litter quality. Ecology 66(1): 266–275

Mulholland PJ (1992) Regulation of nutrient concentrations in a temperate forest stream: Roles of upland, riparian, and instream processes. Limnol. Oceanogr. 37(7): 1512–1526

Myrold DD & Tiedje JM (1985) Establishment of denitrification capacity in soils: Effects of carbon, nitrate and moisture. Soil Biol. Biochem. 17(6): 819–822

Neill C (1995) Seasonal flooding, nitrogen mineralization and nitrogen utilization in a prairie marsh. Biogeochemistry 30: 171–189

Parkin TB & Tiedje JM (1984) Application of a soil case method to investigate the effect of oxygen concentration on denitrification. Soil Biol. Biochem. 16(4): 331–331

Parton WJ, Mosier AR & Schimel DS (1988) Rates and pathways of nitrous oxide production in a shortgrass steppe. Biogeochemistry 6: 45–58

Parsons LL, Murray RE & Smith MS (1991) Soil denitrification dynamics: Spatial and temporal variations of enzyme activity, populations and nitrogen gas loss. Soil Sci. Soc. Am. J. 55: 90–95

Pastor J, Aber JD, McClaugherty CA & Melillo JM (1984) Aboveground production and N and P cycling along a nitrogen mineralization gradient on Blackhawk island, Wisconsin. Ecology 65(1): 256–268

Patrick WHJr (1982) Nitrogen transformations in submerged soils. In: Stevenson FJ (Ed) Nitrogen in Agricultural Soils, Vol. 22 (pp 449–465). Agronomy Monograph

Pinay G, Décamps H, Arles C & Lacassin-Seres M (1989) Topographic influence on carbon and nitrogen dynamics in riverine woods. Arch. Hydrobiol. 114(3): 401–414

Pinay G & Naiman RJ (1991) Short-term hydrologic variations and nitrogen dynamics in beaver created meadows. Arch. Hydrobiol. 123(2): 187–205

Pinay G, Ruffinoni C & Fabre A (1995) Nitrogen cycling in two riparian forest soils under different geomorphic conditions. Biogeochemistry 30(9): 9–29

Ponnamperuma FN (1972) The chemistry of submerged soils. Advances in Agronomy 24: 29–96

Reddy KR & Patrick WHJr (1975) Effect of alternate aerobic and anaerobic conditions on redox potential, organic matter decomposition and nitrogen loss in a flooded soil. Soil Biol. Biochem. 7: 87–94

Roberts J & Ludwig JA (1991) Riparian vegetation along current-exposure gradients in floodplain wetlands of the River Murray, Australia. J. Ecol. 79: 117–127

Rolston DE, Rao PSC, Davidson JM & Jessup RE (1984) Simulation of denitrification losses of nitrate fertilizer applied to uncropped, cropped and manure-amended field plots. Soil Sci. 137: 270–279

Salo J, Kalliola R, Häkkinen J, Mäkinen Y, Niemelä P, Puhakka M & Coley PB (1986) River dynamics and the diversity of Amazon lowland forest. Nature 332: 254–258

Schlesinger WH, Raikes JA, Hartley AE & Cross AF (1996) On the spatial pattern of soil nutrients in desert ecosystems. Ecology 77(2): 364–374

Schimel D, Stillwell MR & Woodmansee RG (1985) Biochemistry of C, N and P in a soil catena of the shortgrass steppe. Ecology 66(1): 276–282

Seely B, Lajtha K & Salvucci GD (1998) Transformation and retention of nitrogen in a coastal forest ecosystem. Biogeochemistry 42: 325–343

Smepag (1989) Monographie des crues de la Garonne. Compagnie d'Aménagement des Coteaux de Gascogne Ed

Smith JL & Tiedje JM (1979) Phases of denitrification following oxygen depletion in soils. Soil Biol. Biochem. 11: 261–267

Steiger J (1991) La dynamique fluviale de la Garonne entre Saint Caprais et Verdun sur Garonne. D.E.A. de Géographie et Aménagement, University of Toulouse le Mirail

Sullivan KT, Lisle CA, Dollof GE & Reid IM (1987) Stream channels: The links between forests and fishes. In: Salo EO & Cundy TW (Eds) Streamside Management: Forestry and Fishery Interactions. University of Washington, Institute of Forest Resources, Contribution No. 57, Seattle, WA.

Tabacchi E (1992) Variabilité des peuplements riverains de l'Adour. Influence de la dynamique fluviale à différentes échelles d'espace et de temps. PhD Dissertation, University of Toulouse III

Tabacchi E, Planty-Tabacchi AM & Décamps O (1990) Continuity and discontinuity of the riparian vegetation along a fluvial corridor. Landscape Ecol. 5: 9–20

Tabacchi E, Correll DL, Hauer R, Pinay G, Planty-Tabacchi AM & Wissmar RC (1998) Development, maintenance and role of riparian vegetation in the river landscape. Freshwater Biol. 40(1): 1–21

Technicon (1976) Technicon Instrument System. Technicon Method Guide. Technicon, Tarrytown, New York.

Vomocil JA (1965) Porosity. In: CA Black (Ed) Methods of Soil Analysis. Part 1: Physical and Mineralogical Properties, Including Statistics of Measurement and Sampling (pp 299–314). ASA Inc. Publ., Madison, WI, U.S.A.

Ward JV (1989) The four dimentional nature of lotic ecosystems. J. North Benthological America Society 8(1): 2–8

Waring SA & Bremner JM (1964) Ammonium production in soil under waterlogged conditions as an index of nitrogen availability. Nature 201: 951–952

Yoshinari T & Knowles R (1976) Acetylene inhibition of nitrous oxide reduction by denitrifying bacteria. Biochem. Biophys. Res. Comm. 69: 705–710