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Nitrogen cycling in two riparian forest soils under different geomorphic conditions

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Abstract. At the floodplain scale, spatial pattern and successional development of riparian vegetation are under the control of geomorphic processes. The geomorphic and hydraulic characteristics of stream channels affect the sorting of organic material and inorganic sediment through erosion/sedimentation during floods. In turn, the proportion of fine sediments fractions differs by location within a given community of riparian forest succession. In this paper we tested the effect of geomorphic features of floodplains, through soil grain size sorting, on the nitrogen cycling in riparian forest soils. Two typical riparian forests formed by vertical accretion deposits from repeated addition of sediments from overbank flow have been chosen along the River Garonne, southwest France. These riparian forests had equivalent vegetation, flood frequency and duration, differing only in soil grain size composition: one riparian forest had sandy soils and the other had loamy soils. The evolution of the main soil physical and chemical parameters as well as denitrification (DNT), N uptake (N_U) and mineralization (N_M) rates were measured monthly over a period of 13 months in the two study sites. The loamy riparian forest presented a better physical retention of suspended matter during floods. Moreover, *in situ* denitrification rates (DNT) and N uptake by plants (N_U) measured in the loamy riparian forest soils were significantly greater than in the sandy soils. Although DNT and N_U could be in competition for available nitrogen, the peak rates of these two processes did not occur at the same period of the year, N_U being more important during the dry season when DNT was minimum, while DNT rates were maximum following the spring floods. N retention by uptake (N_U) and loss by DNT represented together the equivalent of 32% of total organic nitrogen deposited during floods on the sandy riparian forest soils and 70% on the loamy ones. These significant differences between the two sites show that, at the landscape level, one should not estimate the rates of N_U and DNT, in riparian forests soils only on the basis of vegetation, but should take also into account the geomorphic features of the floodplain.

Key words: denitrification, floodplain, flood, river, sediment

Introduction

Flood duration, frequency and magnitude determine the spatial pattern and successional development of riparian vegetation (Bell & Sipp 1975; Salo et al. 1986; Nilsson 1987; Roberts & Ludwig 1991). In return, riparian forests present a high sediment retention capacity during floods (Schlosser & Karr 1981; Lowrance et al. 1986; Cooper et al. 1987; Grubaugh & Anderson 1989; Brunet et al. 1993). In fact, the interface position of riparian forests between terrestrial and aquatic ecosystems gives them an important role in the regulation and transfer of inorganic and organic matter from the drainage basin to the surface waters (see Malanson 1993) for an exhaustive review). It has been also demonstrated that riparian forests buffer the lateral nitrate inflow from groundwater in very different hydrogeological conditions (Peterjohn & Correll 1984; Jacobs & Gilliam 1985; Pinay & Labroue 1986; Cooper 1990; Duff & Triska 1990; Haycock & Pinay 1993).

The high nutrient cycling capacity of riparian forests compared to upland ecosystems is probably the consequence of their open structure to fluvial sources via flood deposits and to lateral fluxes of nutrients from the drainage basin (Brinson 1977; Brinson et al. 1980; Peterson & Rolfe 1982; Megonigal & Day 1988). Just as the hyporheic zone is important in regulating nutrient concentration in stream water (Grimm & Fisher 1984; Ford & Naiman 1989; Vervier et al. 1993), the high-nutrient assimilative capacity of alluvial forests also plays an important role in controlling upstream/downstream fluxes of nutrients (Brinson et al. 1981; 1984; Mulholland 1992).

Among the factors influencing nitrogen assimilative capacity within forests, the importance of soil texture has been well studied by Pastor et al. (1984) and McClaugherty et al. (1985) who found an increase in nitrogen cycling rates along a soil texture gradient from sand to silt clay loam in old-growth forest stands. They hypothesized that these changes were due to change in litter quality because of species replacement along the soil texture gradient. This hypothesis has been verified in several soil catenas (Schimel et al. 1985; Gosz & White 1986; Burke 1989; Groffman et al. 1993).

Geomorphic and hydraulic characteristics of stream channels and floodplains condition the sorting of sediment through erosion and/or sedimentation during floods. This induces a mosaic of different soil textures that interacts with vegetation development during succession (Sollins et al. 1985). The purpose of this paper is to examine how different geomorphic features between two similar riparian forest communities influence nitrogen cycling rate, and in turn, the nitrogen assimilative capacity of the riparian forests.

Study area

Two riparian forests were chosen for our study along the Garonne River, downstream of the city of Toulouse, southwest France (Fig. 1). The Garonne River has its source in the Pyrénées. Study site is a seventh-order channel draining 10,000 km^2. Channel slope is 0.1% in the study area. It presents a

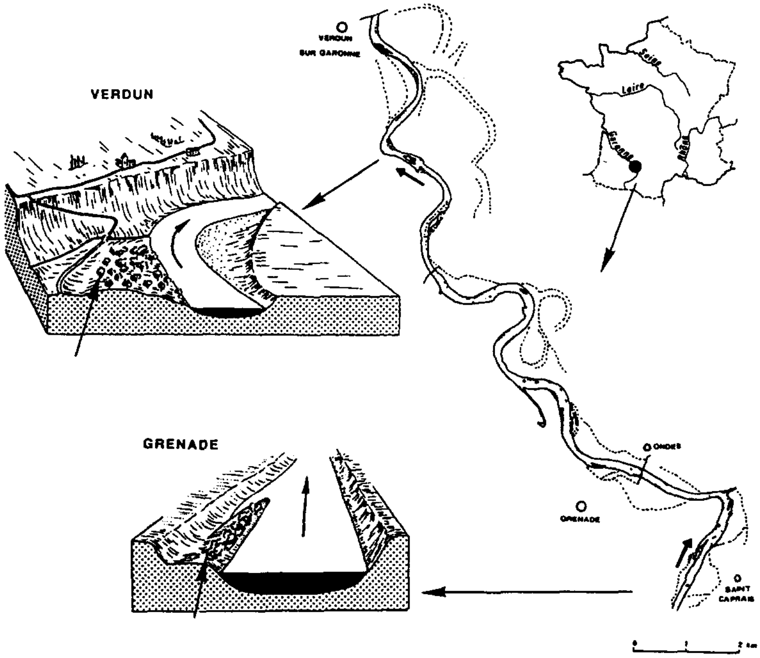

Fig. 1. Location of the two study sites along the Garonne River. Dashed lines represent the old channels which are reinundated during floods.

pluvial-nival regime with maximum discharge in spring due to precipitation and snow melt (up to 4350 $m^3 s^{-1}$ in 1952). The low water period generally lasts from August to October, with discharge down to 20 $m^3 s^{-1}$, while the average annual discharge in the stretch under study is 200 $m^3 s^{-1}$.

The Garonne River exhibits a typical irregular meandering feature in the reach under study, where the natural migration of meander bars is accompanied by the lateral accretion of sediment over the floodplain. The two study sites represented two different geomorphic types (Pinay et al. 1992), typical in the stretch of the Garonne River under study (Smepag 1989; Steiger 1991). These two sites lay at the same altitude (140 m) and are subject to the same flood duration and frequency which was monitored during the study period (Table 1). These two sites were flooded by a discharge of the Garonne River greater than 500 $m^3 s^{-1}$ which occurs approximately 4 times a year, with a 3 day duration per event, on an average over thirty years. During the 13 months of the study the two sites were flooded two times (with a peak discharge of 963 $m^3 s^{-1}$ in March 26, 1991; and 1510 $m^3 s^{-1}$ in May 10, 1991). Due to the proximity of the sites to the river channel, groundwater level in both sites was under the control of the surface water

Table 1. Main characteristics of the two riparian forests

		Grenade		Verdun	
Submersion					
Average over 30 years					
Frequency		4.2 times a year			
Duration		2.8 days (maximum 12 days)			
During the study period					
Frequency		2 times			
Duration		March, 3 days May, 8 days			
Vegetation					
Tree community		*Salix alba* with *Populus alba, Fraxinus exelsior & Ulmus campestris*		*Populus nigra* with *Salix alba*	
Understorey		*Ranunculus acris* *Viola odorata* *Lamium purpureum* *Arum italicum*		*Urtica dioïca* *Ranunculus acris* *Lamium purpureum* *Arum italicum*	
Particle size distribution		SD	%	%	SD
Sand	2000–50 μm	43.6	7.1	14.4	6.8
Silt coarse	50–20 μm	21.8	4.8	24.5	5.1
Silt fine	20–2 μm	26.7	7.7	53.2	12.2
Clay	<2 μm	7.9	6.9	7.9	5.5
Soil pH		7.7	0.15	8.0	0.08
C/N		10.9	0.38	13.8	0.94

level fluctuation of the Garonne River. Thus, in both sites the groundwater level dropped 50 cm below the soil surface within a few days after the floods had receded. However, the two riparian forests differed by their soil grain size which reflected their geomorphic location within the river stretch. The Verdun riparian forest was subject to slow overflow velocity (<0.05 m s^{-1}) which allowed deposition of fine sediment. Silt plus clay content averaged 85.6% (Table 1). This percentage of fine sediment was significantly higher ($P < 0.001$) than in the Grenade riparian forest. The latter was situated in a straight stretch of the Garonne River corridor, where high overflow velocity

(>0.1 m s^{-1}) removed soil litter, reduced fine particle deposition and led to deposition of coarser sediment (silt+clay = 56.4%).

The two riparian forest soils belong to the Fluvents series of alluvial entisoils. Soil trenches were dug in both the sites to estimate the soil profiles. Both the sites belonged to the same river terrace underlain with coarse alluvial gravel deposits. In the Verdun site the soil had a depth of about two meters; the Grenade site had a depth of about 50 cm.

Vegetation in the two study sites was typical of vegetation stands of floodplains in southwest France (Tabacchi et al. 1990; Tabacchi 1992) and was composed of willows (*Salix alba*), and poplar stands (*Populus nigra*), and a few ash trees (*Fraxinus exelsior*). Chauvet (1987) and Chauvet & Jean-Louis (1988) have found that the amount of litterfall and the litter decomposition rates among these tree species are not significantly different but high compared to other forest ecosystems.

Materials and methods

The two riparian forest soils were sampled monthly between October 1990 and November 1991. Within each forest, 52 sampling sites of one square meter were selected randomly and labelled. In order to avoid the risk of pseudoreplication (Hurlbert 1984) four sampling sites were chosen randomly each month in each riparian forest to constitute the 4 replicates on which soil *in situ* incubations and analyses were performed. Soil analysis focused on the surface ten centimetres which correspond 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. All the results were expressed per square meter of soil, corresponding to a ten centimetre thick layer, using the soil bulk density.

The upper 10 cm of soil were taken after the litter was discarded. After collection, all samples were stored at 4 °C until they could be processed, within 24 h. 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 h at 105 °C in order to determine fresh and dry mass and percent moisture (MOIST) by mass. In order to extract soluble organic carbon, in each sampling site 3 subsamples of ten grams of fresh soil were treated with 20 ml of deionized water and filtered through a pre-washed 0.45 μm filter after 30 min shaking and 20 min centrifugation (8000 $\times$ g). Aliquots of the filtered solutions were used for the determination of "extractable glucose equivalent" (EGE) by the phenol method (Dubois et al. 1956) considered as an index of carbon availability (Stanford et al. 1975; Reddy et al. 1982).

Ten grams (fresh mass) of each soil sample were extracted with 150 ml of 2 mol l^{-1} KCl. The extract was filtered and analyzed for NH_4-N and NO_3-N with a Technicon Autoanalyser (Technicon 1976). The nitrite form (NO_2-N) of inorganic nitrogen was not taken into account 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 following 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 a static core acetylene inhibition method (Yoshinari & Knowles 1976). Three intact cores (length 10 cm, diameter 3 cm) collected monthly from each of the four sampling sites of each riparian forest 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. Denitrification rate was calculated as the rate of nitrous oxide (N_2O) accumulation in the head space between 4 and 8 h incubation in the laboratory at the field temperature. Bulk density of each core was measured in order to express denitrification results on an areal basis. Head space samples were removed from all cores and stored in evacuated collection tubes (Venoject, Terumo Scientific N.J.). Gas samples were analyzed via gas chromatography (GC Varian 3300) equipped with an electron capture detector (ECD ^{63}Ni) and Porapak Q columns. Estimates of annual N loss to denitrification were calculated by extrapolating measured rates during the period between sampling dates.

Denitrification enzyme activity was measured in six soil samples from each of the four sampling sites by transforming them into a slurry followed by anaerobic incubation in closed flasks for 8 h at average soil temperature (10 °C). Acetylene was added in the same proportion as for *in situ* denitrification. Three of the soil suspensions were amended with nitrate, 10 μg NO_3-N g^{-1} (soil fresh wt basis) following Smith and Tiedje's (1979) procedure, referred to denitrification enzyme activity with N amendment (DEA_{+N}). Three other soil subsamples were amended with nitrate (10 μg NO_3-N g^{-1}, soil fresh wt basis) plus glucose (4 mg C g^{-1}, soil fresh wt basis) referred to denitrification enzyme activity with C and N amendment (DEA_{C+N}).

Estimation of nitrogen mineralization, losses, and uptake by understorey vegetation were obtained by a method proposed by Raison et al. (1987) using sequential coring and *in situ* incubation of soils in four sampling sites chosen randomly in each riparian forest. Net mineralization of N (N_M) in riparian forest soils was calculated from measured changes in the mineral-N content of largely undisturbed soil isolated inside capped pvc tubes *in situ*. The tubes were 10 cm long and 10 cm in diameter, allowing air to pass through as proposed by Adams et al. (1989) but preventing leaching. After one month of incubation nitrogen content (total mineral N) in the incubated cores ($n_{e(t+1)c}$) was compared to the bare soil content at the beginning of the incubation ($N_{b(t)}$): $N_M = N_{e(t+1)c} - N_{b(t)}$. Since microbial immobilization of NH_4-N and NO_3-N is not determined, this method allows only the determination of net mineralization. Net nitrification (NITR) was estimated from measured changes in the NO_3-N content during exposure in the same undisturbed soil cores.

Four other open PVC tubes were used in the same sampling sites to estimate N losses through leaching. Leaching of mineral-N (N_L) was assessed by comparing the quantity of mineral-N present in covered ($N_{e(t+1)c}$) and open cores ($N_{e(t+1)o}$) at the end of each exposure period (i.e., one month): $N_L = N_{e(t+1)c} - N_{e(t+1)o}$. The deficit in mineral-N in open cores represented an upper limit for leaching losses, because of the absence of uptake of water and N by roots inside cores (Raison et al. 1987).

Since we did not find significant differences in soil moisture content between soils inside and outside open tubes, we hypothesized that the rates of net ammonification and nitrification were the same for soils inside and outside tubes; hence, the amount of mineral-N taken up by vegetation (N_U) during the exposure period (one month) is given by comparing the quantity of mineral-N present in the open tube after one month of incubation ($N_{e(t+1)o}$) and the bare soil at the end of the incubation ($N_{b(t+1)}$): $N_U = N_{e(t+1)o} - N_{b(t+1)}$. This corresponds only to plant uptake because microbial uptake was not prevented by any of the treatments.

Sediment deposition during floods in each of the two riparian forests was estimated using nine patches of eight flat smooth plates (0.06 m^{-2}) randomly dispersed on the riparian sites. These sediment traps were collected after each flood event and sediment was removed from plates. Sediment deposition values obtained on the sediment traps were averaged and expressed by square meter of riparian soil. Total organic nitrogen (TON) deposited during floods was estimated by averaging the amounts obtained in the sediment traps after each flood event. The soil organic nitrogen stock was estimated by averaging the amount estimated monthly in each riparian forest. The annual budget of nitrogen cycling for the studied processes was calculated by summing the monthly measurements on a yearly basis.

Water level and discharge of the River Garonne were provided by the French Navigation Service (Service Hydrologique Centralisateur). Air temperature and precipitation records were provided by the French National Meteorological Service.

For all the reported results we considered differences significant at $P < 0.05$.

Results

Sediments deposited during the two floods which occurred during the study period differed significantly in their quantity and quality (Table 2). On March 26, the Garonne River discharge reached 963 $m^3\ s^{-1}$ (flood recurrence interval of 1.4 year; Steiger 1991). The amount of sediment deposited did not differ significantly between the two riparian forest sites, while the organic carbon composition of sediments deposited in Verdun (37.7 mg g^{-1} dry sediment) was significantly higher than in Grenade (30.8 mg g^{-1}; $P < 0.01$). On May 10, the Garonne River discharge reached 1510 $m^3\ s^{-1}$ (flood recurrence interval of 2.2 years; Steiger 1991). The amount of sediment deposited in Grenade (23.2 kg m^{-2}) was significantly higher ($P < 0.01$) than in Verdun (13.8 kg m^{-2}). Moreover, the amounts of sediment deposited in both Grenade and Verdun during the May flood were significantly higher than those deposited in March ($P < 0.001$). However total organic nitrogen and carbon content of May sediments in both sites (Table 2) were significantly lower than those deposited in March ($P < 0.001$). Nevertheless organic carbon and nitrogen per gram of dry sediment deposited in Verdun were significantly higher ($P < 0.001$) than those deposited in Grenade.

Soil temperature in the two riparian forests ranged between 1.1 and 20.1 °C at the ten centimetre depth with an average of 11.5 °C between October 1990 and November 1991 (Table 3). Monthly average air temperature ranged between 5.7 and 30.9 °C with a mean value of 17.5 °C. Precipitation occurred all year, but was greatest in autumn (October 1990 and November 1991). The annual precipitation was 748.8 mm m^{-2}, and based on a 20-year record, it was considered as a normal year.

Soil moisture, significantly higher in Verdun than in Grenade ($P < 0.05$) throughout the study period, increased in both sites during the flood periods (Fig. 2a), and remained high at Verdun's. Soil NH_4-N concentration did not present any significant difference among sites and increased similarly after the flood events and in late summer in both sites (Fig. 2b). NO_3-N increased sharply in summer at Verdun site while it remained at a significantly lower ($P < 0.05$) and more stable level at Grenade (Fig. 2c). Total organic nitrogen (TON) remained stable throughout the study period in Verdun soils while it decreased constantly after the flood events in Grenade (Fig. 2d). Total organic carbon (TOC) did not present any trend at either site throughout the study period (Fig. 2e). Potential mineralization of soil organic nitrogen (NMP) presented high values after the flood events and during the litter-

Table 2. Quantities and organic C and N content of the sediments deposited during the two flood events. (* significantly different at $P < 0.05$)

		Grenade		Verdun	
		X	SE	X	SE
March 1991	N = 72				
Dry sediment	(kg/m^2)	7.3	[1.37]	6.6	[0.34]
Organic C	(g/m^2)	205*	[33.01]	247.1*	[12.10]
Organic C	(mg/g dry sed.)	30.8*	[2.32]	37.7*	[0.45]
Organic N	(g/m^2)	21.3	[3.54]	25.1	[1.29]
Organic N	(mg/g dry sed.)	3.2	[0.27]	3.8	[0.04]
May 1991	N = 72				
Dry sediment	(kg/m^2)	23.2*	[2.97]	13.8*	[0.85]
Organic C	(g/m^2)	410.5	[31.9]	477.1	[24.87]
Organic C	(mg/g dry sed.)	18.8*	[1.33]	34.7*	[0.49]
Organic N	(g/m^2)	28.4	[2.80]	38.8	[1.42]
Organic N	(mg/g dry sed.)	1.3*	[0.08]	2.9*	[0.13]

Table 3. Climatic characteristics and soil temperature in the two study sites during the period under study

	Monthly precipitation (mm)	Air T °C	Soil temperature T °C	
			Verdun	Grenade
October 1990	120.9	20.1	14.8	14.8
November	54.3	12.3	14.5	14.5
December	51.0	5.7	5.5	5.5
January 1991	23.1	8.3	4.5	3.3
February	34.2	9.4	1.1	2.2
March	52.9	16.2	9.7	9.2
April	54.1	16.2	11.2	11.5
May	45.9	19.0	12.3	12.5
June	52.5	23.0	13.5	14.0
July	31.9	28.1	18.0	18.1
August	30.3	30.9	19.7	20.1
September	61.6	26.7	15.9	16.6
October	34.6	16.8	11.0	11.2
November	101.5	12.7	9.5	9.8
Annual precipitation (mm)	748.8			
Mean T °C		17.5	11.5	11.6

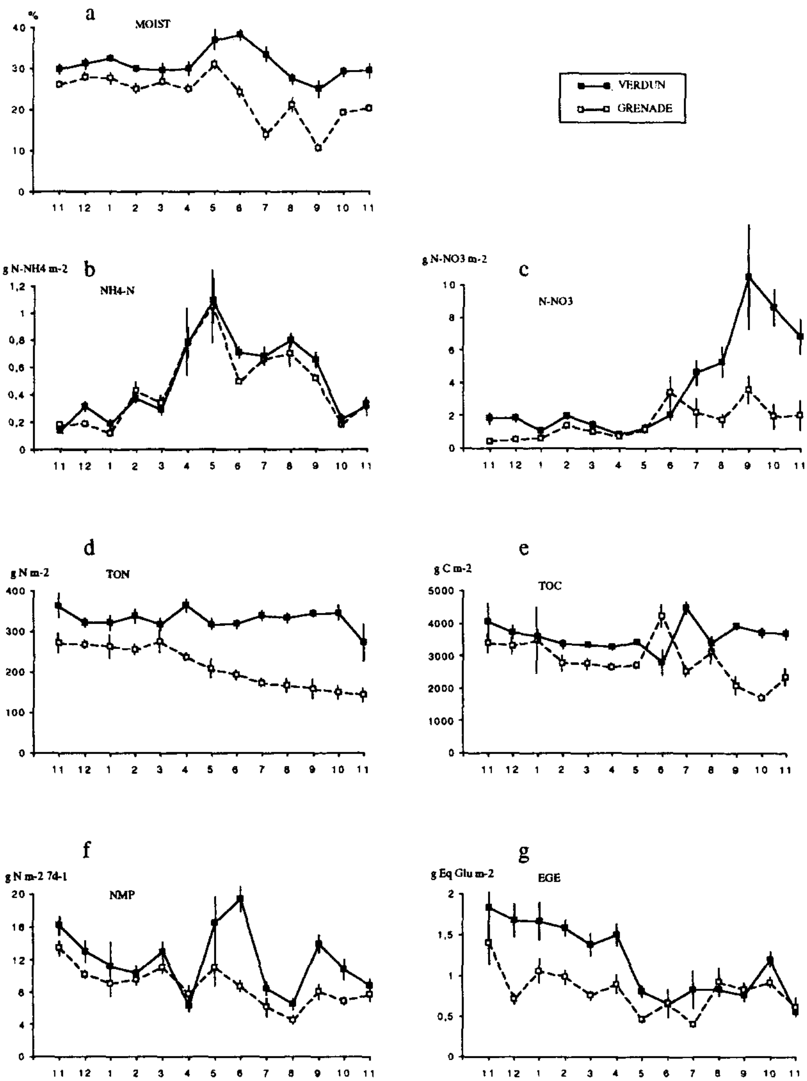

Fig. 2. Comparison of the monthly variations of the soil moisture and the main soil biochemical parameters in the two riparian forests. a) soil moisture (MOIST); b) soil ammonium concentration (NH_4-N); c) soil nitrate concentration (NO_3-N); d) total organic nitrogen (TON); e) total organic carbon (TOC); f) nitrogen mineralization potential (NMP); g) equivalent glucose extraction (EGE).

fall period at Verdun (Fig. 2f). Although the peak values were significantly lower in Grenade ($P < 0.05$), evolution of NMP presented the same pattern. Soil Extractable Glucose Equivalent (EGE) presented significantly higher values in Verdun ($P < 0.05$) from December 1990 until April 1991, and then

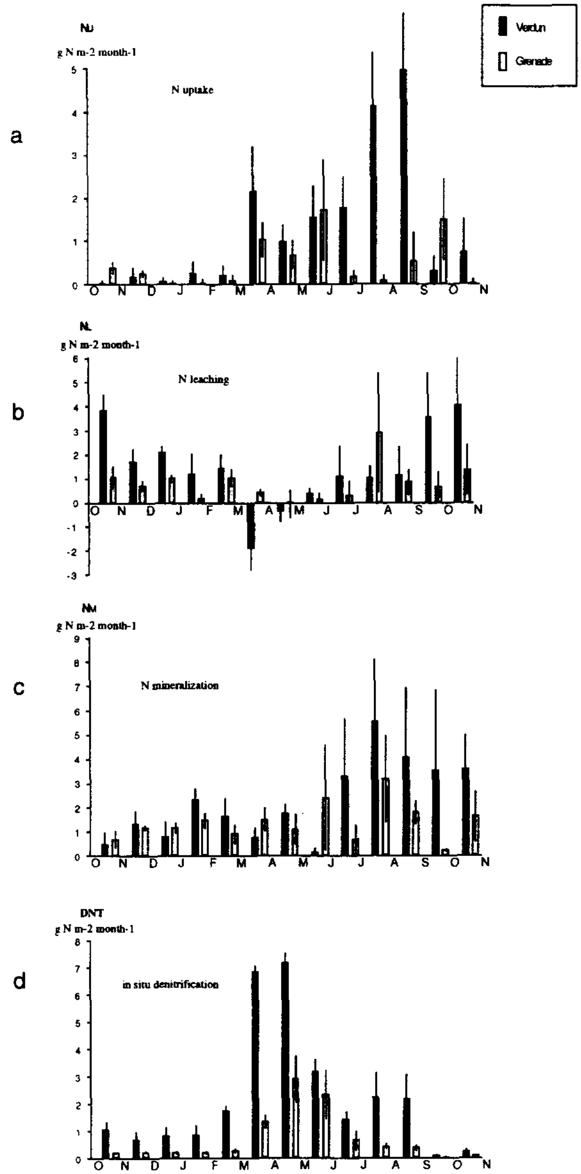

Fig. 3. Comparison of the monthly variation of the soil leaching and the three main biological processes involved in the nitrogen cycling in the two riparian forest soils. a) N uptake (N_U); b) N leaching (N_L); c) N mineralization (N_M); d) *in situ* denitrification (DNT).

decreased in both sites after the flood events (Fig. 2g). They then remained relatively constant and not significantly different throughout summer and fall 1991 at both sites.

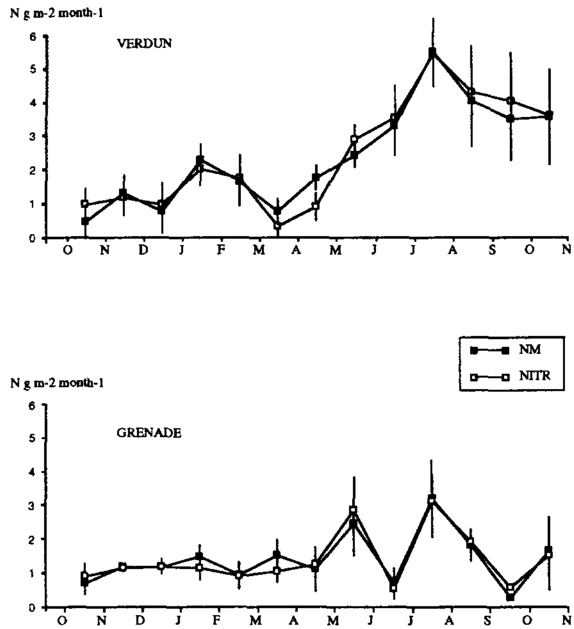

Fig. 4. Comparison between N mineralization (N_M) and nitrification (NITR) through time in the soils of the two riparian forests under study.

Uptake by vegetation occurred almost all the year round at both riparian forests (Fig. 3a). As expected, higher values were found between spring and autumn at both sites with a large within-site variability. However very low uptake values were found in Grenade during the summer season. Mineral nitrogen losses by leaching (N_L) estimated by the above-mentioned method (Raison et al. 1987) were higher in late summer and autumn in both riparian forest soils and did not differ significantly from each other (Fig. 3b). Because of the grain size difference between the two study sites, we expected that N_L should be significantly higher in Grenade than in Verdun; however this was not the case. Between March and May the low or negative estimates of N losses in both riparian sites constituted an experimental artifact since the open cores were filled with sediment deposits during the two flood events which occurred during this period.

Mineralization occurred all the year in both riparian forest soils (Fig. 3c). Although there was great variability within each riparian forest, highest averaged values were recorded during summer and autumn. On a monthly basis the two study sites did not differ significantly except between August and October, where N_M was higher in Verdun than in Grenade ($P < 0.05$). Net nitrification (NITR) and mineralization (N_M) followed the same monthly pat-

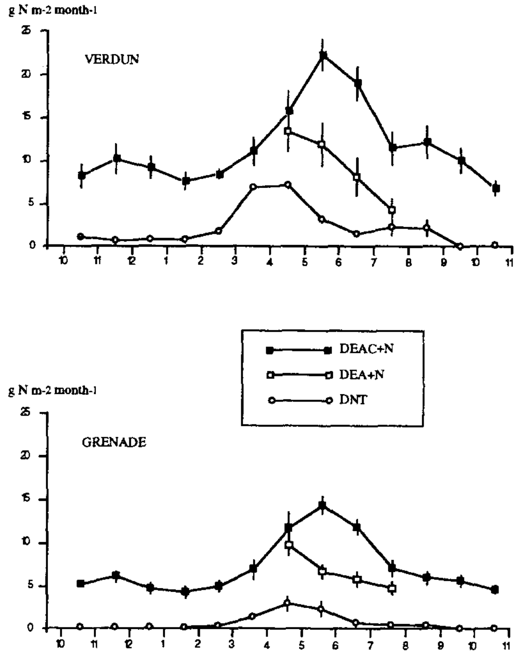

Fig. 5. Comparison between *in situ* denitrification (DNT) and denitrification enzyme activity (DEA_{C+N} and DEA_{+N}) in the two riparian forest soils through time.

tern (Fig. 4). Nitrification occurred all the year at both sites with a maximum in summer and autumn in Verdun. At both sites, nitrification was higher than mineralization between May and June. However, mineralization and nitrification were not significantly different on an annual basis in each site, indicating that the mineralization of organic nitrogen was accomplished to the nitrate stage.

Throughout the study period monthly *in situ* denitrification (DNT) was significantly higher in Verdun riparian forest soils than in Grenade ones ($P < 0.05$), except during the periods May–July and September–November (Fig. 3d). Highest *in situ* denitrification activity was measured in spring, corresponding to the flood period, in both riparian forest soils (Fig. 5). DEA_{C+N} was always significantly higher than *in situ* denitrification ($P < 0.05$), except in April in Verdun. Moreover, in Verdun, values of DEA_{C+N} were mostly significantly higher ($P < 0.05$) than those measured in Grenade, except between April and May. In both sites DEA_n was significantly lower than DEA_{C+N}, except also between April and May.

Annual *in situ* denitrification was significantly higher (about 3 times) at Verdun than at Grenade (Table 4). This true loss of nitrogen for the riparian ecosystem represented the equivalent of about 50% of the total input of the

Table 4. Annual rates of soil microbiological processes involved in nitrogen cycling compared to the soil nitrogen standing stock in the upper ten centimetres and the nitrogen deposited during the two flood events.

	Verdun		Grenade	
	N g m^{-2} y^{-1}	SE	N g m^{-2} y^{-1}	SE
Standing stock (N organic)	335	16.5	271	48.5
Flood deposit (N organic)	63.9	6.9	49.6	8.2
N Mineralization (N_M)	25.8	6.3	16.4	2.9
Nitrification (NITR)	28.2	3.5	16.4	4.1
N Leaching (N_L)	15.3	10.0	9.3	4.4
In situ denitrification (DNT)	28.5	3.1	9.4	4.2
Nitrogen uptake(N_U)	16.6	3.1	6.5	0.9

total nitrogen deposited during floods in Verdun, but only 20% at Grenade. N uptake was also significantly higher in Verdun than in Grenade. N retention by uptake (N_U) and loss by *in situ* denitrification (DNT) represented the equivalent of 70% of the total nitrogen deposited by floods in Verdun, and only 32% in Grenade.

Discussion

Influence of soil texture on nitrogen cycling

It is reasonable to assume that soil grain size affects the rates of microbiological processes involved in the nitrogen cycle through the effect of grain size on soil water holding capacity. Hence, the fact that loamy soils of Verdun supported for most of the year the highest rates of microbiological processes involved in nitrogen cycling, compared to those measured in Grenade sandy soils is in favour of this assumption. However, soil grain-size differences may not be the only reason. For instance the higher soil concentration of total organic carbon (TOC) and available carbon (EGE) in the Verdun site could also support a higher microbial activity.

In situ denitrification was almost always significantly higher in Verdun loamy soils than in Grenade sandy soils. On an annual basis, the amount of nitrate denitrified was three times higher. These results are in accordance with other studies on soil catenas (Groffman & Tiedje 1989a & b; Bowden et al. 1992) which underlined the importance of soil texture to the denitrification process. Fine textured soils had higher denitrification rates than coarser ones because their drainage capacities were poor and thus they became anaerobic more easily (Bremner & Blackmer 1979; Colbourn & Dowdell 1984; Chalamet 1985). Moreover, the high organic carbon availability in the fine textured soils of Verdun, partly provided by sediment deposits during floods could fuel heterotrophic processes such as denitrification.

The monthly course of mineralization rates presented the same pattern in both sites with a peak in summer and lower but measurable rates in winter. Mineralization rates measured on an annual basis were high, compared to those Pastor et al. (1984) and McClaugherty et al. (1985) found in other terrestrial forest soils. Moreover, since the containment period was long, i.e., one month, mineralization is probably underestimated (Adams et al. 1989). However mineralization rates were significantly higher in Verdun loamy soils. This difference could be explained by the difference in soil water holding capacities. Pastor et al. (1984) have found a correlation between N mineralization and soil texture. They explained it by the fact that low soil moisture could be limiting the growth of micro-organisms (Stanford & Epstein 1974; Matson & Vitousek 1981). The absence of differences between mineralization and nitrification most of the year, showed that the mineralization process was held up in the last stage, i.e., nitrate (NO_3-N). However, mineralization was significantly greater than nitrification in Verdun between March and May and significantly smaller between May and June. Ammonification was probably enhanced following the flood period by the input of organic nitrogen in sediment deposits. Then, nitrifiers drew on NH_4-N provided by allochthonous organic nitrogen deposition in April and May. The high nitrogen mineralization potential values (NMP) measured in May and June in Verdun support this hypothesis.

Plant uptake of nitrogen was measurable all the year in both sites, but it occurred mainly between spring and autumn. The Verdun site presented maximum rates in summer, while Grenade rates were very low. The dryness of Grenade soils during this period may explain this low nitrogen uptake rate. The rates estimated were high (Binkley & Vitousek 1989) but lower than mineralization. Nitrogen uptake contributed to the retention of 13 and 24% of the equivalent of N deposited during floods, in Grenade and Verdun respectively. However, we did not measure the microbial uptake which can be in the same range of magnitude as plant uptake (Smith & Paul 1990).

Flood deposits and geomorphic features of the riparian forest

Episodic flood events transport most of the suspended matter on a long-term annual basis (Probst 1983; Chauvet & Fabre 1990). The quantity of deposited sediments represented 30.4 and 20.3 kg m^{-2} in Verdun and Grenade respectively for the two floods. These high values are similar to those that Brunet et al. (1993) reported for the Adour River of southwestern France. They are also within the range of what Lowrance et al. (1986) found in the riparian zone of a coastal plain watershed in Georgia, (USA). Floodplain soils, such as the ones we studied, are built up by vertical accretion deposits from repeated additions of sediments from overbank flow (Allen 1965). Geomorphic features of the floodplain condition the sorting of sediments on the basis of grain size. Sediment deposits were significantly different between the two riparian forests only during the May flood (1510 m^3 s^{-1}); however, the organic C and N contents associated with inorganic sediments differed for both depositional events between the two sites. In fact, the particulate organic matter transported during floods is preferentially associated with fine inorganic sediment, and is deposited when overbank velocity is low. Thus, although the total weight of sediment deposited per square meter was higher in Grenade during the May flood, the amount of TOC and TON deposited was significantly higher in Verdun. Consequently, due to its geomorphic position, the loamy riparian forest had a higher physical retention potential for suspended organic matter (SOM).

Importance of nitrogen retention and loss in riparian soils

Apart from the better physical retention of SOM, *in situ* denitrification (DNT) and vegetation uptake (N_U) were significantly more important in Verdun soils than in Grenade ones. N uptake represents an important retention process in riparian forests, and depends upon the age of the forest stand; a part of the N uptake will go back to the soil through litter (Peterson & Rolfe 1982); the proportion returning through litter being higher in older tree stands (Vitousek & Reiners 1975). *In situ* denitrification constitutes a true loss of N from the ecosystem since the end product is mainly N_2 (Knowles 1981). *In situ* denitrification and uptake rates were comparable on an annual basis. However, their peak rates did not occur at the same time period.

In situ denitrification in both riparian soils was high, but within the range of what Lowrance et al. (1985), Groffman & Tiedje (1989a & b), Merrill & Zak (1992), Groffman et al. (1993) and Pinay et al. (1993) measured in similar conditions, and what Peterjohn & Correll (1984) estimated to be lost by denitrification in riparian forests next to agricultural fields, using a mass balance analysis. *In situ* denitrification was measured in the top ten centimetre of soils which corresponded to the most active zone where all the conditions for denitrification to occur were met, i.e., moisture, organic carbon and nitrate content. Thus the rates expressed per m^{-2} were related to a depth of 10 cm. *In situ* denitrification was at a maximum following floods, when an important proportion of N release occurred, 60 and 69% of the annual totals in Verdun and Grenade, respectively. This process represented an important loss of total

N, since it varied between 20 and 50% of the amount deposited during floods, depending on the site considered. However the experimental design did not permit evaluation of the fraction of nitrogen deposited by floods that was denitrified, incorporated in the soil, or assimilated. The amount of nitrogen denitrified at these two sites was comparable although higher than the annual quantity of nitrogen provided by litterfall in similar riparian forests of the region (7.5 g m^{-2} y^{-1}; Chauvet 1989). N retention by uptake, together with N loss by *in situ* denitrification represented the equivalent of 32% of the TON deposited during floods in Grenade and 70% in Verdun.

Both riparian forest soils displayed higher denitrification potentials, i.e., DEA_{C+N} and DEA_{+N}, than those measured *in situ*, but with similar temporal pattern. Maximum DEA was measured between May and June which corresponded to the Garonne River flood period. These high denitrification potentials values were similar to those obtained by Wheatley & Williams (1989) in poorly drained blanket peat. However, it seems difficult to extrapolate real denitrification potential from these DEA measurements since these results constitute "potentials" where we forced the micro-organisms to operate under artificial condition of anaerobiosis and substrate availability. However, we can compare the results from these assays in a relative sense. Thus, except for April and May, DEA_{C+N} was higher than DEA_{+N} at both sites, suggesting that available organic carbon was also a limiting factor to denitrification. It appears that the timing between floods and plant phenology is crucial for *in situ* denitrification, since riparian vegetation provides litter of higher quality (Brinson et al. 1980; Chauvet 1989) which can fuel this microbiological process, if it is decomposed under anaerobic conditions.

Conclusion

Geomorphic processes determine the structure of floodplains and, at a landscape level, create a mosaic of geomorphic surfaces which influence the spatial pattern of riparian forests. In turn, these geomorphic features condition the physical retention capacity of suspended matter vis-à-vis upstream/ downstream flow and also affect the sorting of sediment and the associated suspended organic matter on a grain-size basis. Nitrogen retention by microbes is associated with the physical retention capacity of the riparian forests. This is confirmed by the highest rates of microbiological processes, including *in situ* denitrification and uptake, measured in the loamy soils, which also had higher TON sedimentation during floods, than sandy soils. Thus, episodic events, such as floods, have long-term effects on nitrogen cycling in riparian forest soils.

Although denitrification and vegetation uptake compete for nitrogen, these two processes do not peak at the same period of the year. N retention by vegetation uptake is more important during the dry season when denitrification is minimal, while maximum nitrogen loss by denitrification follows the flooding events. Hence, changes in the timing of phenology and flooding by climatic change or land use and river management could affect the ratio of N retention versus N loss in riparian forests.

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