Control of C,N,P distribution in soils of riparian forests

G. Pinay, A. Fabre, Ph. Vervier and F. Gazelle
Centre d'Ecologie des Ressources Renouvelables C.N.R.S. 29, rue Jeanne Marvig, 31055 Toulouse cedex France

Abstract

It is now well accepted that riparian forests have an important role in regulating upstream/downstream flow of matter and energy in river ecosystems. Since geomorphic processes determine the structure of channels and floodplains, we have investigated whether different geomorphic features of riparian forests had any effects on the ability of their soils to retain nutrients and organic carbon. Willow riparian forests were chosen within the annual floodplain of the Garonne River, southwest France, to represent two different geomorphic types. Erosional types of riparian forests (E-type) were characterized by sand deposition on their soils because of high current velocity which hampered fine particle deposition. Depositional types of riparian forests (D-type) were characterized by slower overflow velocity; consequently silt and clay were dominant in their soils. Soil samples were taken at the end of the vegetation growth period, coinciding with low water levels prior to annual floods. Erosion and sedimentation processes affected the distribution of total C,N, and P contents in riparian forest soils, since they were significantly correlated with soil grain size. D-type riparian forest soils act as a sink for upstream/downstream nutrients and carbon flows during floods through accumulation of total C,N and P from year to year. In contrast, E-type riparian forests act as potential nutrient sources during high water periods, since they may release from their soils large amounts of easily available C, N and P into the river. These results demonstrate that nutrients and carbon retention ability of riparian forests soils should be analyzed through their geomorphic features rather than by their vegetation composition. Even if they belong to the same vegetation succession, riparian forests should not be considered as a homogeneous buffering system for upstream/downstream flows of nutrients and organic carbon.

Introduction

Riparian zones have been defined from many perspectives and for many purposes since Hynes (1975) first identified the importance of the river valley in the functioning of running water. The importance of the riparian zone far exceeds their areal extent because of the intricate linkages between terrestrial and aquatic ecosystems and their central location within watersheds. From an ecological perspective, their roles and functions and their application for river management have been well studied (Petersen *et al.* 1987). For instance, buffer capacities of riparian areas regarding nutrient fluxes between drainage basins and rivers is now well documented (Schlosser & Karr 1981; Lowrance *et al.* 1984; Peterjohn & Correl 1984; Jacobs & Gilliam 1985; Pinay & Décamps 1988). It is now well accepted that riparian
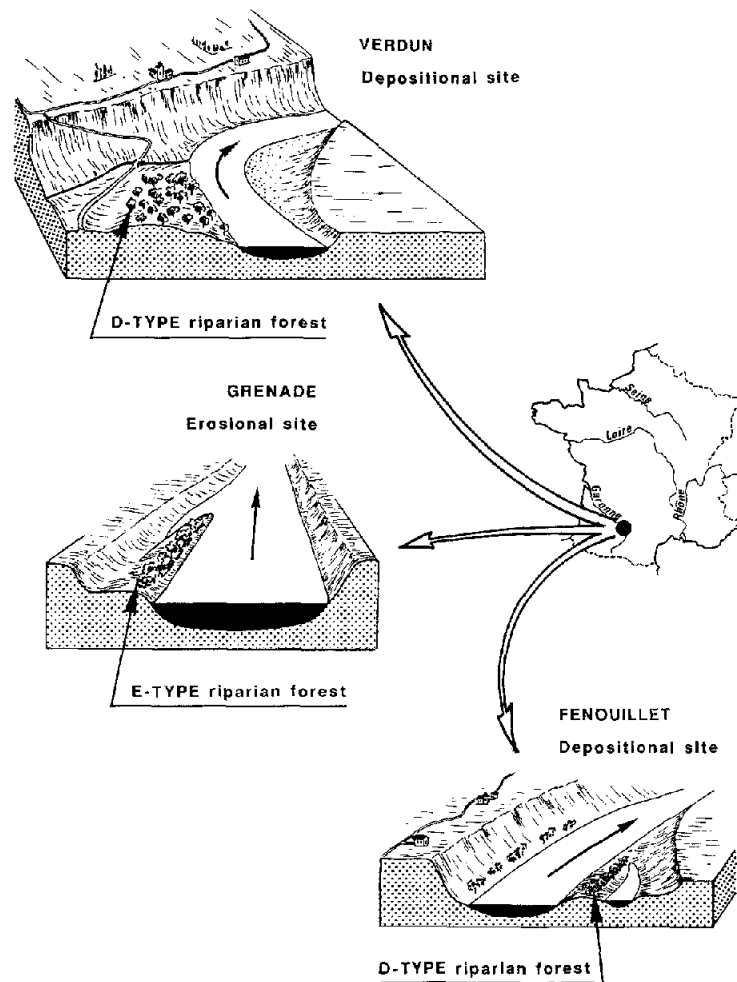
Fig. 1. Localization of the study sites in the Garonne River floodplain.

vegetation controls the quantity, quality and timing of allochthonous organic matter to streams (Cummins 1974). The high productivity of riverine vegetation has been also well documented (Brinson *et al.* 1980; Howard-Williams 1985; Megonigal & Day 1988). Yet, one lacks to know the importance of riverine vegetation in supplying organic matter to larger rivers, in comparison with numerous studies focused on streams (see Bird & Kaushik (1981) for a review).

Since geomorphic processes, riparian vegetation and aquatic biota are intimately linked in the river ecosystem, overlying terrestrial vegetation is not the only key factor determining the standing stocks of carbon, nitrogen and phosphorus available for river functioning. At the floodplain scale, spatial pattern and successional development of riparian vegetation are under the control of geomorphic processes (Salo *et al.* 1986). The geomorphic and hydraulic characteristics of stream channels condition the sorting of organic material and inorganic sediment through erosion/sedimentation during floods. In turn, the proportion of fine sediments in different density fractions differs by location within a given community of riparian forest succession (Sollins *et al.* 1985). Peterson and Rolfe (1982) have found that nutrient pools were higher in floodplain soils than in upland ones. However, little is known about the effects of the flood-induced changes in soil properties on the function of riparian forest vis à vis their retention role (source vs sink) in the upstream/downstream flow of nutrients and carbon
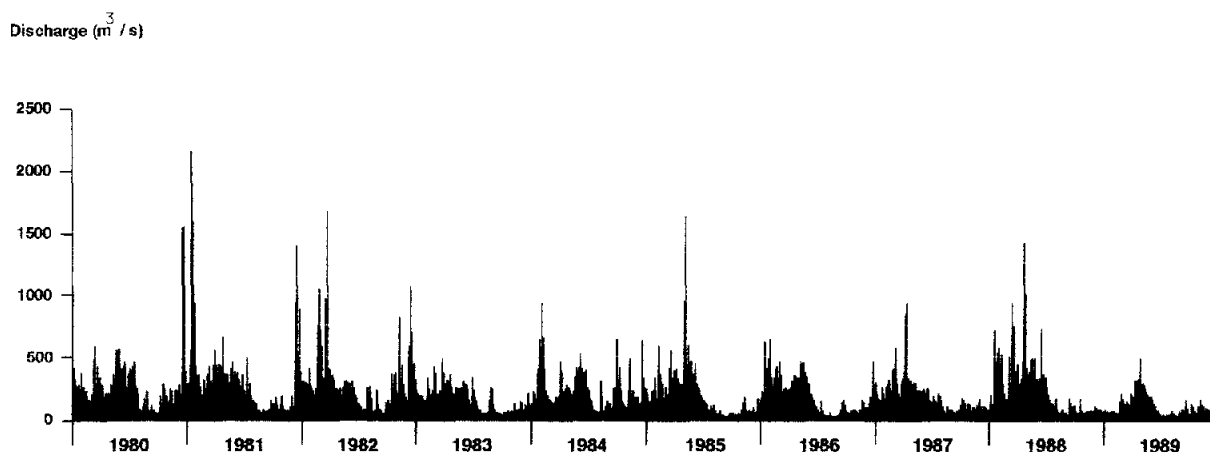
Discharge (m^3 / s)

Fig. 2. Flow regime of the Garonne River at Verdun between 1980 and 1989.

in river ecosystem. The aim of this study is to evaluate the effect of erosional/depositional processes, on soil C,N,P distribution in willow (*Salix alba*) riparian forest and their potential availability for the river.

Study sites

Three riparian forests were chosen for our study along a 30 km stretch of the Garonne River, downstream from the city of Toulouse, southwest France (Fig. 1). The River Garonne has its source in the Pyrénées mountains (altitude 2850 m) and drains ten thousand km^2 up to Toulouse. In the stretch under study the Garonne River is an order 7 stream. The slope of its riverbed is 0.1‰. It presents a pluvial-nival regime (Fig. 2) with maximum discharges (over 500 m^3/s) in spring (precipitation and snow melting), which entail erosion/sedimentation processes in the river floodplain, with fewer periods of severe land/water interactions in winter (precipitation). The low water period generally lasts from August to October, with discharge down to 20 m^3/s, while the mean annual discharge flowing through the stretch under study is 200 m^3/s.

The riparian forests Fenouillet, Grenade and Verdun were chosen to represent two different geomorphologic types (Fig. 1), typical in the stretch of the Garonne River under study (SMEPAG 1989). Erosional type of riparian forest (E-type) is

represented by Grenade, situated in a straight stretch. During floods, high current velocity (0.1 m/sec) entails erosional processes which remove soil litter and hamper fine particle deposition. Its soils are dominated by sand accumulation (Table 1). Depositional type of riparian forest (D-type) is represented by Fenouillet and Verdun, situated in a more protected area where overflow velocity is slower (0.05 m/sec). Although they differ in geomorphology, these two types of riparian sites are at the same altitude (140 m) along the Garonne riverbanks and are subject to the same flood duration and frequency (Table 1). During low water period, soil moisture is controlled by soil texture and precipitation, since the groundwater table oscillates between 0.5 m and 3.0 m (Pautou & Décamps 1985). Moreover, the vegetative cover associated with this submersion pattern is composed of a homogeneous willow stand (*Salix alba*), typical of the Garonne floodplain (Pautou & Décamps 1985; Décamps *et al.* 1988).

Materials and methods

Soil samples were taken in September 1989, during low water period, at the end of the vegetation growth and prior to litter fall. In each of the three study sites, 30 samples of the upper 10-cm of soil (after the litter was discarded), were taken every 5 meters (at the same elevation), along transects

Table 1. Mean characteristics of the study sites.

| Granulometry | E-type site | | D-type sites | | | |
| | Grenade | | Fenouillet | | Verdun | |
	%	SD	%	SD	%	SD
Sand	49.37	7.11	19.41	8.83	14.43	6.76
Silt coarse	16.13	4.80	22.46	5.34	24.40	5.14
Silt fine	26.66	7.67	53.05	9.84	53.22	12.24
Clay	7.85	6.91	5.08	1.54	7.95	5.54
PH	7.70	0.15	7.92	0.08	7.98	0.08

Submersion

Frequency — 4.2. times a year

Duration — (average over ten years) 2.8 days

maximum 12 days

Vegetation

Community — Willow stand (Salix alba)

Litterfall — 5.23 tons/ha

parallel to the river bank (20 meters from the river bank). After collection, all samples were stored at 4°C until they could be processed, within 48 hours.

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 fresh:dry mass and percent moisture by mass (MOIST). Soil pH was determined on air-dried soils in 2.5:1 (liter:kilogram) water.

Total organic carbon (TOC) was determined by combustion of air-dried subsamples with a Carmhograph 8. Ten grams of fresh soils 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 g). Aliquots of the filtered solutions were used for the determination of "extractable glucose equivalent" (EGE), considered as an index of carbon availability (Stanford *et al.* 1975; Reddy *et al.* 1982), by the phenol method (Dubois *et al.* 1956).

Approximately 10 g (fresh mass) of each sample was extracted with 150 ml of 2 mol/L KCl. The extract was filtered and analyzed for NH_4-N and NO_3-N with a Technicon Autoanalyser (Technicon 1976). NO_2-N form of inorganic nitrogen has not

been taken into account since it presented low and constant values whatever the site considered. Nitrogen mineralization potential (NMNL) was performed on fresh subsamples by anaerobic incubation for 7 days at 40°C (Waring & Bremner 1964). The potential of nitrogen mineralization (NMNL), is considered as an index of nitrogen availability in forest ecosystems (Waring & Bremner 1964; Keeney 1980; Powers 1980). Total nitrogen (TN) was determined by digestion of air-dried subsamples following Kjeldahl method (Bremner 1965). Denitrification (DNT) was assayed by a static core acetylene inhibition technique (Yoshinari & Knowles 1976). Intact cores (length 10 cm, diameter 3 cm) were capped with rubber serum stoppers and then amended with acetone-free acetylene to bring core atmosphere concentrations to 10 KPa (10% V/V) acetylene and 90 KPa air. Head space samples were removed from all cores and stored in evacuated collection tubes. Gas samples were analyzed via gas chromatography (GC Varian 3300) equipped with electron captur detector (ECD [63]Ni) and Porapak Q columns.

Total phosphorus (TP) was determined by ignition and subsequent extraction with 1N H_2SO_4 and total inorganic phosphorus (Pi) by extraction of unignited samples with 1N H_2SO_4. The difference

Table 2. Soil characteristics in D-type and E-type riparian forests.

Parameter	Units	E-type N = 30		D-type N = 60	
		Mean ± 95% CL	SD	Mean ± 95% CL	SD
Moisture	%	17.2 ± 1.04	2.80	25.1 ± 1.37	5.30
pH	pH unit	7.7 ± 0.06	0.15	8.0 ± 0.02	0.09
Carbon					
TOC	mg/g of dry soil	22.3 ± 1.96	5.26	33.4 ± 0.82	3.19
EGE	μg/g of dry soil	21.5 ± 2.10	5.63	8.8 ± 1.48	5.74
Nitrogen					
TN	mg/g of dry soil	1.5 ± 0.12	0.32	2.6 ± 0.09	0.33
NH4-N	μg/g of dry soil	9.4 ± 0.33	0.89	20.0 ± 3.22	12.48
NO3-N	μg/g of dry soil	12.4 ± 3.79	10.16	32.0 ± 5.57	21.58
NMNL	μg/g of dry soil	61.3 ± 8.76	23.50	67.7 ± 8.19	31.71
DNT	ng N/g of dry soil/h	0.4 ± 0.18	0.47	4.1 ± 1.84	7.12
NMNL/TN	%	39.0 ± 3.21	8.60	26.6 ± 3.23	12.50
Phosphorus					
PT	μg/g of dry soil	668 ± 12.00	82.60	808 ± 20.90	82.60
Pi	μg/g of dry soil	374 ± 11.67	31.30	561 ± 17.51	67.80
Po	μg/g of dry soil	293 ± 13.38	35.90	246 ± 13.79	53.40
MLPi	μg/g of dry soil	68 ± 2.98	8.00	40 ± 2.61	10.10

between TP and Pi gives estimation of organic phosphorus (Po) (Saunders & Williams 1955). Soluble inorganic phosphorus in sodium bicarbonate solution at pH 8.5 was extracted according to Olsen *et al.* (1954). This form of inorganic phosphorus is generally considered as moderate labile Pi (MLPi).

Linear correlation coefficients, univariate (ANOVA) and multivariate (MANOVA) analyses of variance were performed using Systat software (Wilkinson 1990). For all reported results we considered only high significant differences at P < 0.01 (Elliott 1977).

Results

The two types of riparian forests under study differ in geomorphology. D-type riparian forests are affected by sedimentation processes which lead to silt deposition on their soils (Table 1), while in E-type forest soils sand deposition dominates. Thus grain size of E-type soils differs significantly in its sand and fine silt composition from D-type ones (MANOVA P < 0.001).

There were other significant differences (ANOVA, P < 0.01) between the erosional (E-type) and depositional (D-type) riparian forest soils (Table 2). The depositional type had a higher concentration in total carbon (TOC), nitrogen (TN) and phosphorus (PT), with values averaging respectively 33.5 mg.g^{-1}, 2.58 mg.g^{-1} and 808 μg.g^{-1} of dry soil for TOC, TN and PT. These values were significantly different from those measured in E-type soils since they averaged only 22.3 mg.g^{-1} for TOC, 1.54 mg.g^{-1} for TN and 668 μg.g^{-1} for PT. Moreover, in D-type forest soils, inorganic forms of nitrogen (ammonium NH$_4$-N and nitrate NO$_3$-N) had also higher concentrations than in E-type forest soils. Soil NH$_4$-N concentration averaged 20.0 mg.g^{-1} of dry soil in D-type soils compared to 9.4 mg.g^{-1} in E-type ones, while soil NO$_3$-N concentration averaged 32.0 mg.g^{-1} of dry soil in D-type soils compared to 12.4 mg.g^{-1} in E-type ones. Denitrification activity (DNT) was also significantly higher in D-type soils (4.1 ng N.g^{-1} of dry soil.h^{-1}) than in E-type ones (0.4 ng N.g^{-1} of dry soil.h^{-1}). Furthermore, average soil concentration of inorganic phosphorus (Pi) was signifi-
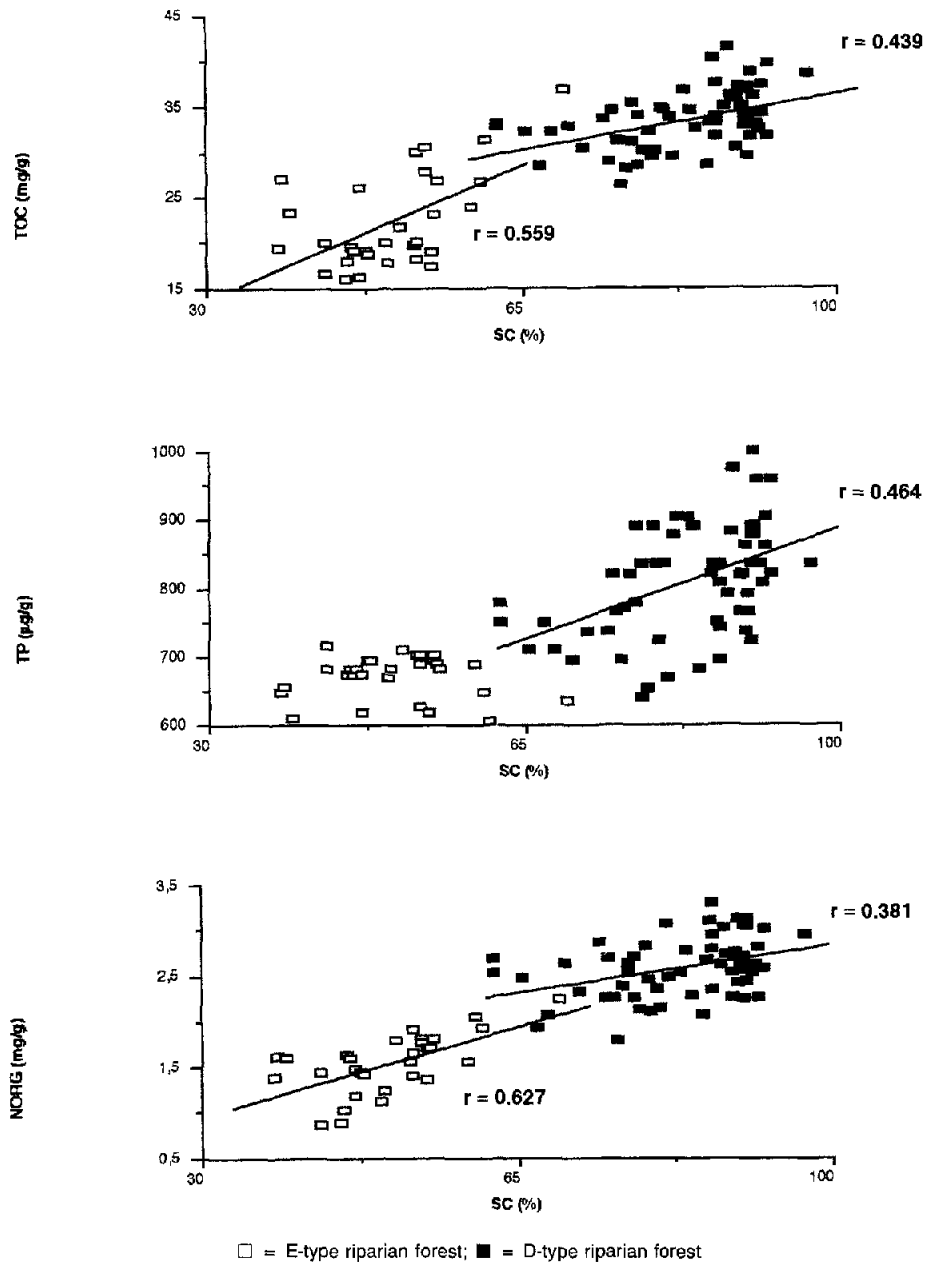
126

Fig. 3. Relationships between percentage of Silt + Clay content (SC), total organic carbon (TOC), total nitrogen (TN) and total phosphorus (TP) in D-type and E-type riparian forest soils.

cantly higher in D-type riparian forest soils (561 μg.g^{-1} of dry soil) than in E-type ones (374 μg.g^{-1} of dry soil).

Soils of erosional type of riparian forests have higher contents in labile and easily utilizable forms of carbon (EGE) with an average of 21.5 μg.g^{-1} of dry soil compared to 8.8 μg.g^{-1} in D-type soils.

Moreover, labile phosphorus (MLPi) average concentration in E-type soils were also higher (68 μg.g^{-1} of dry soil) than in D-type soils (average: 40 μg.g^{-1} of dry soil). In addition, organic phosphorus (Po) average concentration in E-type soils (293 μg.g^{-1} of dry soil) was significantly different (P < 0.01) from D-type one (246 μg.g^{-1} of dry soil).
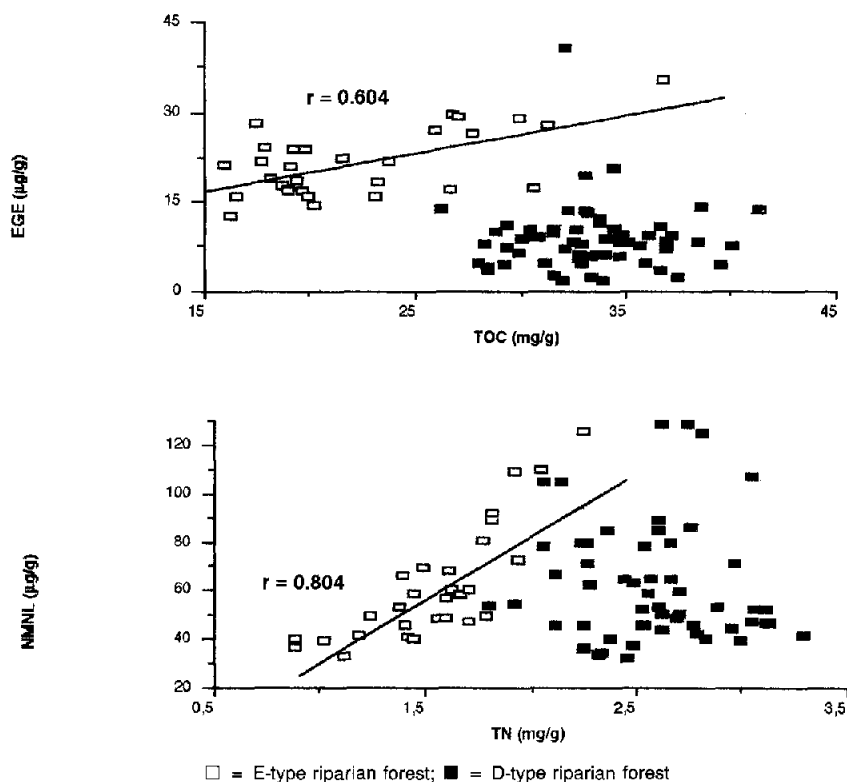
Fig. 4. Correlation between total organic carbon (TOC) and extractable glucose equivalent (EGE) and between total nitrogen (TN) and nitrogen potential of mineralization (NMNL) in D-type and E-type riparian forest soils.

Although the potential of mineralization (NMNL) is not significantly different (P > 0.1) between the two types of soils, the availability of nitrogen potentially mineralizable (NMNL/TN) is significantly higher (P < 0.01) in the E-type soils than in the D-type ones (Table 2).

Total nitrogen (TN) and total carbon (TOC) in the soil samples were significantly correlated (P < 0.01) with soil grain size (SC) in D-type as well as in E-type riparian forest soils (Fig. 3). Moreover, total phosphorus was correlated with soil grain size (SC) only in D-type soils (Fig. 3).

Qualitative characterization of total carbon (TOC) and total nitrogen (TN) in the two types of riparian soils was evaluated through the relationship existing between TOC and extractible glucose equivalent (EGE), and between TN and potential of nitrogen mineralization (NMNL). Erosional soils had significant correlations (r = 0.604, P < 0.01) between TOC and EGE and between TN and NMNL (r = 0.804, P < 0.01), while D-type soils do

not present any correlation at P > 0.1 (Fig. 4). For a wide range of TOC content, D-type soils provide low and rather constant extractible glucose equivalent (EGE), while potential of nitrogen mineralization is highly variable for a given total nitrogen content.

Soil moisture content (MOIST), inorganic forms of nitrogen (NH_4-N, NO_3-N), and rate of denitrification do not present any correlation with soil grain size in both soil types (Fig. 5). High values of ammonium (NH_4-N), positively correlated with soil moisture (r = 0.453, P < 0.01), were measured in D-type soils sampled after a storm event (Fig. 5). Moreover, in situ denitrification process has shown some activity only in these moist D-type soils.

Discussion

Riparian forests evolve in response to dynamic interactions between the river channel and the floodplain (White 1979; Pautou & Décamps 1985). In
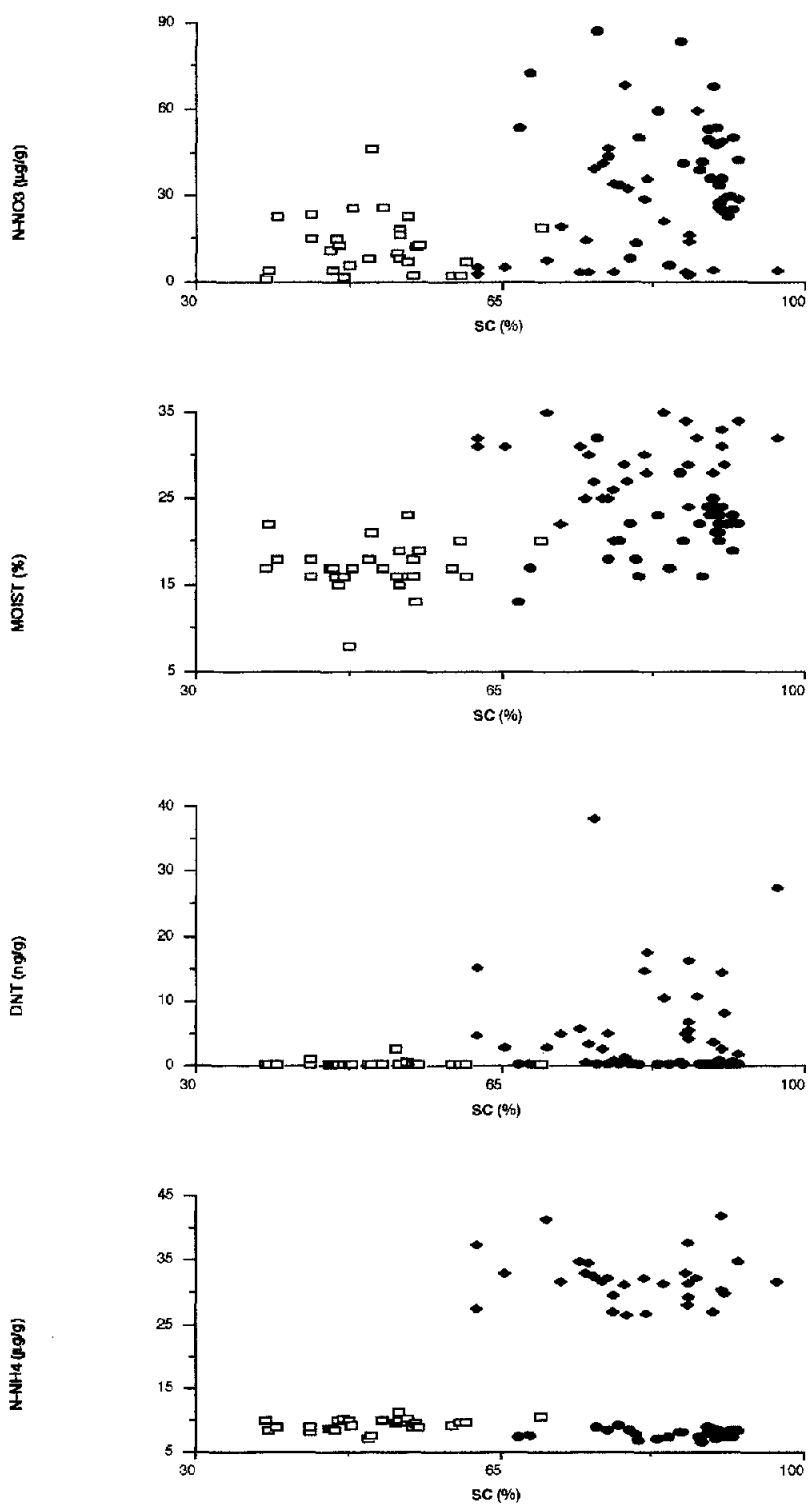
128

Fig. 5. Relationships between percentage of silt + clay content (SC), soil moisture (MOIST), inorganic forms of nitrogen (NH_4-N, NO_3-N) and rate of denitrification in D-type and E-type riparian forest soils.

turn, riverine wetlands markedly regulate the hydrology, since they constitute a retention system vis à vis upstream-downstream flow of matter and energy in river landscape (Schlosser & Karr 1981; Brinson et al. 1983; Pinay et al. 1990). However, the results obtained in the Garonne River's floodplain lead one to reconsider the retention capacity of the riparian areas vis à vis nutrient fluxes in fluvial landscape as a function of their geomorphic situation.

Geomorphic pattern, through erosion/sedimentation processes exert control directly on total C,N, and P accumulation in riparian soils. The highly significant correlation between soil grain size and total C,N, and P contents in the upper soil level of the riparian forests under study confirms the important role of erosion/sedimentation processes in soil nutrient distribution (Fig. 3). D-type soils are characterized by fine sediment deposits (Table 1). Their protected situation vis à vis high current velocity during floods prevents them from litter stratum scouring and favors in situ accumulation of organic matter (Table 2). Since vegetation cover and litterfall are not significantly different between E and D-types of riparian forests (Chauvet 1989), the erosional situation of E-type forests during floods, which hampers organic matter accumulation from year to year, explains their low TOC, TN and TP contents compared to D-type sites where deposition during floods enhances organic matter accretion (Table 2). Total phosphorus distribution follows different patterns in E and D-type soils (Fig. 3). The lack of correlation between TP content and soil grain size (SC) in E-type forest soils can be related to the fact that an important part of phosphorus (mainly Pi) in floodplains comes from suspended matter deposits (Walling & Webb 1987). Since E-type forests are submitted to high current velocity during flood, only coarse suspended matter, poor and relatively constant in phosphorus (Chauvet & Fabre 1990), are uniformly deposited and hide any correlation with grain size distribution.

The importance of soil texture has been already demonstrated in toposequence of floodplain soils (Bell & Sipp 1975; Peterson & Rolfe 1982; Pinay et al. 1989; Walke 1989), in sediments (Syers et al.

1969; Dong et al. 1983), as well as in other terrestrial ecosystems (Rashid 1977; Quesnel & Lavkulich 1980; Schimel et al. 1985; Burke 1989). Here, the pattern of distribution of grain size, and in turn of total C,N,P content is not only the result of gravity like in toposequence, but the geomorphic structure of the stretch of the river.

Geomorphic pattern, through erosion/sedimentation processes induces directly and indirectly a higher availability of available carbon (EGE), nitrogen (NMNL/TN) and phosphorus (MLPi) in the erosional type of riparian soils (Table 2). Moreover, accumulation of labile P (MLPi) in E-type soils represses the mineralization of organic phosphorus (Po) which in turn accumulates as well (McGill & Cole 1981).

Directly, annual rejuvenation of erosional type of riparian soils by high current velocity during floods hampers the accumulation of organic matter from year to year. High significant correlations between TOC and EGE on the one hand, and TN and NMNL on the other hand in E-type soils (Fig. 4) suggest that organic matter remaining in E-type soils is still fresh and of high potential of availability.

Indirectly, erosion/sedimentation processes act by creating different soil moisture conditions related to soil texture, and in turn, condition nutrient cycling (Pastor and Post 1986). Due to their silty texture, D-type soils are subject to frequent wetting and drying cycles, which enhances microbiological activities (Reddy and Patrick 1975; Lund and Goksoyr 1980; Orchard and Cook 1983). This hypothesis of higher microbiological activity in D-type soils than in E-type ones is in accordance with Odum (1979) who envisioned that the abrasive flooding acts as stressor, depressing biological activity. This could explain the lower content of available carbon and phosphorus in D-type soils than in E-type, since it may have been already assimilated. Depositional type of riparian forest soils present not only temporal alternance of wet/dry cycles and the resultant aerobic/anaerobic functioning, but also spatial variations since they can present anaerobic microsites within an aerobic environment (Fluhler et al. 1976; Pinay and Décamps 1988). Simultaneous presence of high values of nitrates and am-

130

monium, as well as significant denitrification rates in D-type sites sampled after a storm event (Fig. 5) confirm the existence of this spatial functional heterogeneity in D-type soils due to their poorly drained capacity (Groffman and Tiedje 1989a, 1989b).

The large qualitative heterogeneity of total organic carbon and total nitrogen in D-type soils revealed by the absence of correlation (P > 0.1) between TOC and EGE and between TN and NMNL (Fig. 4), can be attributed, to the existence of this spatio-temporal functional heterogeneity (i.e., aerobic/anaerobic), and to the accumulation process occuring from year to year, which leads to the accumulation of different maturation levels of organic matter more or less refractory.

Conclusion

Erosion and sedimentation processes affect the distribution of total C,N and P contents, as well as their availability in riparian forest soils. Depositional type of riparian forests, rich in fine grain size sediments, act as a nutrient sink for upstream/downstream flow within the fluvial landscape since they accumulate total C,N and P from year to year. Erosional type of riparian forests, present large contents of carbon, nitrogen and phosphorus of high microbiological availability like extractable glucose equivalent (EGE), organic nitrogen easily mineralizable (NMNL/TN) and labile phosphorus (MLPi). High contents of easily available C,N and P in E-type soils, at the end of the vegetation growth period coupled to their geomorphic situation, where erosional processes dominate, confer to these E-type willow riparian forests a predominant role in river functioning, since they act as nutrient sources during high water periods.

Geomorphic processes and features determine the structure of stream channels and floodplains. The resulting mosaic of geomorphic surfaces determine the spatial pattern of riparian forests and their retention capacity vis à vis upstream/downstream flow of energy and matter in river landscapes. Riparian forests, even if they belong to the same given vegetation succession like willow stand, should not be considered as a homogeneous buffering system.

These willow riparian forests lying under different geomorphic features do not only present differences in nutrients and carbon content of their soils, but present also significant differences regarding the quality of these nutrients.

Hydrogeomorphic processes such as high flood events (i.e. over 2000 m³/s in the Garonne River's reach under study, Fig. 2) can be viewed as disturbance events from a nutrient retention perspective since they can alter the physical structure and biological functioning of riparian forest soils on episodic time scale. Such high flood event occuring naturally with a ten years frequency in the Garonne River will provoke mesoform processes like channel migration, which will induce changes in the sequence of sedimentary deposits, and in turn will affect the retention capacity of the riparian areas. For instance, due to channel migration, depositional type of forest may become subject to preferential erosion processes which will lead to a large release in the river of organic matter and nutrients accumulated for several years, while a E-type forest may become a D-type one, where accumulation processes will predominate.

These natural changes may be reversible in the course of the channel evolution, since another high flood event may revert the reach to previous conditions. Any anthropomorphic impoundment, such as river channelization, which often includes bank stabilization, will alter irreversibly the hydraulic and morphologic characteristics of the river reach and in turn its nutrient retention capacity.

Literature cited

Bell, D.T. and Sipp, S.K. 1975. The litter stratum in the streamside forest ecosystem. Oikos. 26: 391–397.

Bird, G.A. and Kaushik, N.K. 1981. Coarse particulate organic matter in streams. *In* Perspectives in Running Water Ecology. pp. 41–68. Edited by M.A. Lock and D.D. Williams. Plenum Press, New York.

Bremner, J.M. 1965. Total nitrogen. *In* Methods of Soil Analysis. pp. 1149–1178. Edited by C.A. Black. Agronomy 9.

Brinson, M.M., Bradshaw, H.D., Holmes, R.N. and Elkins J.B. Jr. 1980. Litterfall, stemflow and throughfall nutrient fluxes in an alluvial swamp forest. Ecology. 61(4): 827–835.

Brinson, M.M., Bradshaw, H.D. and Holmes, R.N. 1983. Significance of floodplain sediments in nutrient exchange between a stream and its floodplain. *In* "Dynamics of Lotic Ecosystems". 494 p. Edited by T.D. Fontaine and S.M. Bartel. Ann Arbor Science, Michigan, USA.

Burke, I.C. 1989. Control of nitrogen mineralization in a Sagebrush Steppe Landscape. Ecology. 70(4): 1115–1126.

Chauvet, E. 1989. Production, flux et décomposition des litières en milieu alluvial. Dynamique et rôle des hyphomycètes aquatiques dans le processus de décomposition. Thèse de Doctorat d'Etat. Université Paul Sabatier. Toulouse. pp. 243.

Chauvet, E. and Fabre, A. 1990. Dynamics of seston constituents in the Ariège and Garonne rivers (France). Hydrobiologia 192: 183–190.

Cummins, K.W. 1974. Structure and function of stream ecosystems. BioScience 24: 631–641.

Day, P.R. 1965. Particle fractionation and particle-size analysis. *In* "Methods of Soil Analysis". pp. 545–567. Edited by C.A. Black. Agronomy 9.

Décamps, H., Fortuné, M., Gazelle, F. and Pautou, G. 1988. Historical influence of man on the riparian dynamics in a fluvial landscape. Landscape Ecology 1: 163–173.

Dong, A., Simsiman, G.V. and Chesters, G. 1983. Particle-size distribution and phosphorus levels in soil, sediment, and urban dust and dirt samples from the Menomonee River Watershed, Wisconsin, USA. Water Res. 17(5): 569–577.

Dubois, M., Gilles, K.A., Hamilton, J.K., Rebers, P.A. and Smith, F. 1956. Colorimetric method for determination of sugars and related substances. Analyt. Chem. 28: 350–356.

Elliott, J.M. 1977. Some methods for the statistical analysis of benthic invertebrates. FBA Publ. N° 25.

Flühler, H., Stolzy, L.H. and Ardakani, M.S. 1976. A statistical approach to define soils aeration in respect to denitrification. Soil Science 122(2): 115–123.

Groffman, P.M. and Tiedje, J.M. 1989a. Denitrification in north temperate forest soils: relationships between denitrification and environmental factors at the landscape scale. Soil Biol. Biochem. 21(5): 621–626.

Groffman, P.M. and Tiedje, J.M. 1989b. Denitrification in north temperate forest soils: spatial and temporal patterns at the landscape and seasonal scales. Soil Biol. Biochem. 21(5): 613–620.

Howard-Williams, C. 1985. Cycling and retention of nitrogen and phosphorus in wetlands. A theoretical and applied perspective. Freshwater Biology 15: 391–431.

Hynes, H.B.N. 1975. The stream and its valley. Verh. Int. Ver. Limnol. 19: 1–15.

Jacobs, T.C. and Gilliam, J.W. 1985. Riparian losses of nitrate from agricultural drainage waters. J. Environ. Qual. 14(4): 472–478.

Keeney, D.R. 1980. Prediction of soil nitrogen availability in forest ecosystems: a literature review. Forest Sci. 26(1): 159–171.

Lowrance, R.R., Todd, R.L. and Asmussen, L.E. 1984. Nutrient cycling in an agricultural watershed: II streamflow and artificial drainage. J. Environ. Qual. 13(1): 27–32.

Lund, V. and Goksoyr, J. 1980. Effects of water fluctuations on microbial mass and activity in soil. Microb. Ecol. 6: 115–123.

McGill, W.B. and Cole, F.S. 1981. Comparative aspects of cycling of organic C,N, S and P through soil organic matter. Geoderma 26: 267–286.

Megonigal, J.P. and Day, F.P. Jr. 1988. Organic matter dynamics in four seasonally flooded forest communities of the Dismal swamp. Am. J. Bot. 75(9): 1334–1343.

Odum, E.P. 1979. Ecological importance of the riparian zone. *In* "Strategies for Protection and Management of Floodplain Wetlands and Other Riparian Ecosystems". p. 2–4. Edited by P.P. Johnson and J.F. McCormick. USFSG Technical Report WO-12 Washington D.C..

Olsen, S.R., Cole, C.V., Watanabe, F.S. and Hawley, J.W. 1954. Estimation of available phosphorus in soils by extraction with sodium bicarbonate. U.S. Department of Agriculture. Circular 939.

Orchard, V.A. and Cook, F.J. 1983. Relationship between soil respiration and soil moisture. Soil Biol. Biochem. 15(4): 447–453.

Pastor, J. and Post, W.M. 1986. Influence of climate, soil moisture and succession on forest carbon and nitrogen cycles. Biogeochemistry 2: 3–27.

Pautou, G. and Décamps, H. 1985. Ecological interactions between the alluvial forests and hydrology of the upper Rhône. Archiv für Hydrobiol. 104(1): 13–37.

Peterjohn, W.T. and Correl, D.L. 1984. Nutrient dynamics in an agricultural watershed: observations on the role of a riparian forest. Ecology 65(5): 1466–1475.

Petersen, R.C. Jr., Madsen, B.L., Wilzback, M.A., Magadza, C.H.D., Paarlberg, A., Kullberg, A. and Cummins, K.W. 1987. Stream management: emerging global similarities. Ambio 6(4): 166–179.

Peterson, D.L. and Rolfe, G.L. 1982. Seasonal variation in nutrients of floodplain and upland forest soils of Central Illinois. Soil Sci. Soc. Am. J. 46: 1310–1315.

Pinay, G. and Décamps, H. 1988. The role of riparian woods in regulating nitrogen fluxes between the alluvial aquifer and surface water: a conceptual model. Regulated Rivers 2: 507–516.

Pinay, G., Décamps, H., Arlès, C. and Lacassin-Seres, M. 1989. Topographic influence on carbon and nitrogen dynamics in riverine woods. Archiv für Hydrobiologie 114(3): 401–414.

Pinay, G., Décamps, H., Chauvet, E. and Fustec, E. 1990. Functions of ecotones in fluvial systems. *In* "Ecology and Management of Aquatic Terrestrial Ecotones". p. 141–169.

Edited by R.J. Naiman and H. Décamps. Parthenon Press Publ.

Powers, R.F. 1980. Mineralizable soil nitrogen as an index of nitrogen availability to forest trees. Soil Sci. Soc. Am. J. 44: 1314−1320.

Quesnel, H.J. and Lavkulich, L.M. 1980. Nutrient variability of forest floors near Port Hardy. British Columbia. Canada. Can. J. Soil Sci. 60: 565−573.

Rashid, G.H. 1977. Dynamique de la minéralisation du carbone et de l'azote dans deux sols d'une caténa forestière: incidence de l'hydromorphie. Thèse de spécialité Doct. Ing. Paris Sud. pp. 123.

Reddy, K.R. and Patrick, W.H. Jr. 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.

Reddy, K.R., Rao, P.S.C and Jessup, R.E. 1982. The effect of carbon mineralization on denitrification kinetics in mineral and organic soils. Soil Sci. Soc. Am. J. 46: 62−68.

Salo, J., Kalliola, R., Häkkinen, I., Mäkinen, Y., Niemelä, P., Puhakka, M. and Coley, P.D. 1986. River dynamics and diversity of Amazon lowland forest. Nature 332: 245−258.

Saunders, W.M.H. and Williams, E.G. 1955. Observations on the determination of total organic phosphorus in soil. J. Soil. Sci. 6: 254−267.

Schimel, D., Stillwell, M.A., Woodmansee, R.G. 1985. Biochemistry of C,N and P in a soil catena of the shortgrass steppe. Ecology 66(1): 276−282.

Schlosser, I.J. and Karr, I.R. 1981. Water quality in agricultural watersheds: impact of riparian vegetation during baseflow. Wat. Res. Bull. 17: 233−240.

SMEPAG. 1989. Monographie des crues de la Garonne. C.A.C.G. Ed. pp 137.

Sollins, P., Glassman, C.A. and Dahm, C.N. 1985. Composition and possible origin of detrital material in streams. Ecology 66(1): 297−299.

Stanford, G., Vander Pol, R.A. and Dzienia, S. 1975. Denitrification rates in relation to total and extractable soil carbon. Soil Sci. Soc. Am. Proc. 39: 284−289.

Syers, J.K., Shah, R. and Walker, T.W. 1969. Fractionation of phosphorus in two alluvial soils and particle-size separates. Soil Science 108: 283−289.

Technicon Instrument Systems. 1976. Technicon methods guide. Technicon, Tarrytown, New York, U.S.A.

Walke, L.R. 1989. Soil nitrogen changes during primary succession on a flood plain in Alaska. U.S.A. Arct. Alp. Res. 21(4): 341−349.

Walling, D.E. and Webb, B.W. 1987. Suspended Load in Gravel-bed Rivers: UK Experience. In Sediment Transport in Gravel-bed Rivers. pp. 691−723. Edited by C.R. Thorne, J.C. Bathurst and R.D. Hey. John Wiley and Sons Ltd.

Waring, S.A. and Bremner, J.M. 1964. Ammonium production in soil under waterlogged conditions as an index of nitrogen availability. Nature 202: 951−952.

White, P.S. 1979. Pattern, process, and natural disturbance in vegetation. The Botanical Review 45: 229−299.

Wilkinson, H.M. 1990. Systat: the System for Statistics. Evanston IL. Systat Inc.

Yoshinari, T. and Knowles, R. 1976. Acetylene inhibition of nitrous oxide reduction by denitrifying bacteria. Biochem. Biophys. Res. Comm. 69: 705−710.