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Patterns of denitrification rates in European alluvial soils under various hydrological regimes

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SUMMARY

1. Denitrification in floodplain soils is one of the main biological processes emitting and reducing nitrous oxide, a greenhouse gas, and the main process responsible for the buffering capacity of riparian zones against diffuse nitrate pollution.
2. The aim of this study was to measure denitrification rates under a wide range of current climatic conditions and hydrological regimes in Europe (from latitude 64°N to latitude 42°N and from longitude 2°W to longitude 25°E), in order to determine the response patterns of this microbial process under different climatic and hydrological conditions, and to identify denitrification proxies robust enough to be used at the European scale.
3. Denitrification activity was significant in all the floodplain soils studied whatever the latitude. However, we found an increase in rates of an order of magnitude from high to mid latitudes. Maximum rates (above 30 g N m^{-2} $month^{-1}$) were measured in the maritime conditions of the Trent floodplain. These rates are similar to mineralisation rates measured in alluvial soils and of the same order of magnitude as the amount of N stored in herbaceous plants in alluvial soils.
4. We used Multivariate Adaptative Regression Splines to relate the response variable denitrification with five relevant predictors, namely soil moisture, temperature, silt plus clay, nitrate content and herbaceous plant biomass.
5. Soil moisture, temperature, and nitrate were the three main control variables of microbial denitrification in alluvial soils in decreasing order of importance.
6. The model developed for denitrification with interaction effects outperformed a pure additive model. Soil moisture was involved in all interactions, emphasising its importance in predicting denitrification.
7. These results are discussed in the context of scenarios for future change in European hydrological regimes.

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Introduction

Worldwide predicted temperature increases for the 21st century range between 1.4 and 4.7 °C (Richards, 1993; IPCC, 2001). Although the importance of temperature in regulating physiological processes is unquestionable, predicting the relationship between an ecological process and temperature is complicated. As the Earth warms, a general intensification of the hydrological cycle is expected to occur (Miller & Russell, 1992). Precipitation, evapotranspiration and runoff are all expected to increase together with the extreme of floods and droughts (Loaiciga *et al.*, 1996). For instance, drastic changes are expected in Bangladesh with a shift in the timing of flood distribution and an increase in their magnitude and duration (Mirza, 2002; Mirza, Warrick & Ericksen, 2003). Consequently, considerable effort is being placed into modelling change in hydrological regimes (Bailey, 1976; Najjar *et al.*, 2000; Chang, Evans & Easterling, 2001; Pabich, Valiela & Hemond, 2001; Roy *et al.*, 2001; Stone *et al.*, 2001; Burlando & Rosso, 2002; Benito, Diez-Herrero & Villalta, 2003). However, global-scale generalisations of the relationships between climate change and extreme floods is difficult because climate (Nakagawa *et al.*, 2003) and hydrological responses vary regionally (Knox, 1993). For instance, Knox (1993) reported in a 7000-year geological study of the Upper Mississippi River that small changes in the mean annual temperature (1–2 °C) and mean annual precipitation (10–20%) can dramatically change the magnitude of floods.

Several papers have already addressed the water resources implications of global warming, including Falkenmark *et al.* (1998), Lettenmaier *et al.* (1999), Jackson *et al.* (2001) and Middelkoop *et al.* (2001). Yet very few authors have considered the ecological impact of climate change on river ecosystems (Poff, 2002). However, the functioning of rivers and their floodplains depends to a large extent on periodic flooding; the intensity, timing, frequency and duration of these events are essential to maintain a mosaic of habitats (Benke *et al.*, 2000) and high productivity both in rivers and in their floodplains (Junk, Bayley & Sparks, 1989; Naiman & Décamps, 1997). The high productivity of river ecosystems is largely because of riparian zones that control energy, nutrients and organic matter fluxes, both in longitudinal (Schlosser & Karr, 1981; Pinay *et al.*, 2000) and in lateral directions (Peterjohn & Correll, 1984; Haycock, Pinay & Walker, 1993). However the existence of riparian zones is also largely controlled by the timing and duration of flood events (Salo *et al.*, 1986; Gregory *et al.*, 1991; Conner & Day, 1992; Clawson, Lockaby & Rummer, 2001). More specifically, water regime changes, through alteration of the frequency, duration and period of occurrence of water levels, directly affect nutrient cycling in alluvial soils by controlling the duration of oxic and anoxic phases (Patrick & Tusnem, 1972; Ponnamperuma, 1972; Keeney, 1973) and, in turn, affect nitrogen end-products and availability (Hefting *et al.*, 2004).

In Europe, scenarios of change in hydrological regime forecast an overall increase in the inter-annual variability of runoff, an increase in the average annual runoff in northern Europe and a decrease in the south (Arnell, 1999). Moreover, the timing and duration of high and low flow events may shift, especially in the eastern part of the continent. Ultimately, these changes will affect the rates of nitrogen cycling in riparian wetlands and their plant productivity. In this context, we focused on denitrification in floodplain soils, one of the microbial processes involved in nitrogen cycling. This process is interesting for several reasons. First, it is very sensitive to the redox status of the soils and sediments, which is controlled by the hydrological regime of the rivers (Knowles, 1982). High rates have been measured in floodplain soils (Johnston, 1991; Groffman, Gold & Simmons, 1992; Pinay *et al.*, 2000). Secondly, it is one of the main biological processes emitting and reducing nitrous oxide, a greenhouse gas (Groffman, Gold & Jacinthe, 1998; Blitcher-Mathiesen & Hoffmann, 1999; Hefting, Bobbink & Caluwe, 2003). Thirdly, it has proved to be the main process responsible for the buffering capacities of riparian zones against nitrate diffuse pollution (Peterjohn & Correll, 1984; Pinay, Roques & Fabre, 1993; Haycock *et al.*, 1997; Sabater *et al.*, 2003).

The aims of this study were: (i) to measure denitrification rates in floodplain soils under a wide range of current climatic conditions and hydrological regimes across Europe, (ii) to determine the response patterns of this microbial process under these different climatic conditions, (iii) to identify denitrification proxies robust enough to be used at the European scale, and (iv) to discuss the possible changes in denitrification activity in floodplain soils under forecast climate change scenarios.

Methods

Study sites

We selected seven rivers in Europe to encompass a large range of climatic and hydrological regimes from maritime to continental regions (Fig. 1; Table 1): the Vindel River in the North of Sweden (64°N) and the Helge River in the South of Sweden (56°N), the River Trent in the U.K. (52°N near Nottingham), the Aar

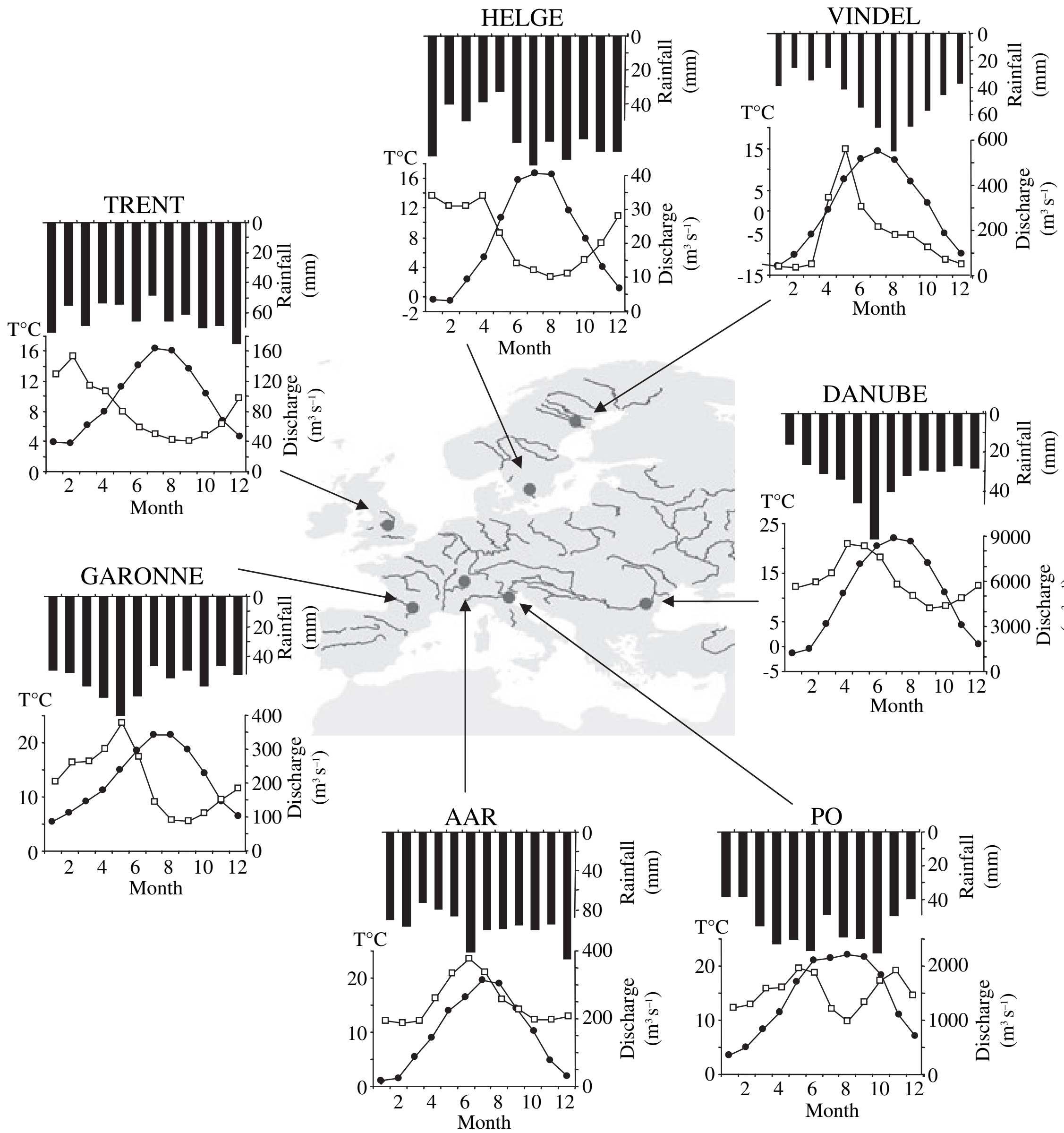

Fig. 1 Map of the rivers under study in Europe. The dots refer to the study areas along the different rivers. Small panels present the mean monthly soil temperature (black dots), mean monthly river discharge (open square) and average monthly precipitation (black bars) for each study site.

Table 1 Main characteristics of the rivers under study

	Aar	Danube	Garonne	Helge	Po	Trent	Vindel
Latitude N	47	42	44	56	44	52	64
Mean annual temp. (°C)	8.1	10.6	13.1	6.7	14.5	10.0	1.3
Mean January temp. (°C)	1.0	−1.3	5.5	−0.6	4	3.9	−12.8
Mean July temp. (°C)	17.6	22.0	21.5	16.7	26	16.5	14.4
Mean annual precipitation (mm)	1169	408	671	698	664	766	585
Month of max. precipitation	Nov.	Jun.	May	Jul.	Oct.	Dec.	Aug.
Mean (mm)	80	65	80	77	71	80	88
Month of min. precipitation	Mar.	Jan.	Jul.	May	Feb.	Jul.	Apr.
Mean (mm)	72	16	46	33	38	48	25
Mean daily discharge ($m^3\ s^{-1}$)	247	6032	202	22	1500	81	180
Month of max. discharge	Jun.	Apr.	May	Apr.	May	Feb.	Jun.
Mean ($m^3\ s^{-1}$)	686	8473	378	34	1960	153	562
Month of min. discharge	Dec.	Sep.	Sep.	Aug.	Aug.	Sep.	Mar.
Mean ($m^3\ s^{-1}$)	62	4231	86	10	971	40	34

River in Switzerland (47°N near Meienried), the Garonne River in Southern France (near Toulouse 44°N), the Po River in Northern Italy (near Pontelagoscuro 43°N) and the Danube in Romania (Near Braïla 42°N). In maritime areas, such as the River Trent, the flow regime reflects the seasonal variability in rainfall and evapotranspiration. In continental areas, such as the Danube, the peak runoff season corresponds to snowmelt. Between these two extremes, there exist many mixed regimes representing local climatic conditions (Arnell, 1999). For instance, northern (Vindel River, Helge River) and Alpine regions of Europe (Aar River) have a snow-dominated flow regime, while the Garonne and the Po Rivers are influenced both by snowmelt, respectively from the Pyrenees and the Alps mountains, and by the balance of a rainfall and evapotranspiration.

The riparian zones studied were located in the annually flooded alluvial reaches of each river. The main source of nutrient input to the riparian floodplain originated from flood deposits. In most cases, the study sites were forested and included similar species or genera at each site. The most common genera were willow (*Salix*), alder (*Alnus*), oak (*Quercus*), elm (*Ulmus*), and poplar (*Populus*). The main genera of the understorey varied between regions: *Carex* and *Calamagrostis* in the Vindel River, *Phragmites* and *Deschampsia* in the Helge River, *Urtica* and *Phragmites* in the Aar River, *Urtica* and *Impatiens* in the Trent and the Garonne rivers, *Solidago* and *Urtica* in the Po River, *Agrostis* and *Bidens* in the Danube River. At the Swedish sites, the soils were typical podzols, which were regularly flooded. At the other sites, the soils belonged to the Fluvents series of alluvial entisoils.

Measurements and analyses

River discharge and rainfall were monitored at hydrometric stations near each of the study sites in each country. Within each river valley, 5 to 10 forested riparian locations were selected in different geomorphologic contexts but at the same relative altitude to ensure similar flooding duration and frequency. This sampling effort represents altogether about 2500 different samples collected between 1996 and 1999. At each location, three plots, each of 1 m^2, were chosen monthly. At each site, aboveground herbaceous vegetation was harvested monthly (except when soil was frozen) and oven-dried at 60 °C to determine the dry mass. Soil temperature was measured hourly using a datalogger (Tinytalk II; Gemini Dataloggers, Chichester, U.K., range −10 to +40 °C).

A composite soil sample was collected in each quadrat from the upper 10 cm of soil, the most biologically active zone, after the litter was discarded. A subsample was oven-dried for 24 h at 105 °C to determine fresh and dry mass and percentage moisture. Percentage of sand was determined by sieving (50 μm mesh) after pretreating the samples with hydrogen peroxide and dispersal with sodium hexametaphosphate solution (Day, 1965). Ten grams (fresh mass) of each soil sample was extracted with 150 mL of 2 M KCl. The extract was filtered and analysed for NO_3-N with a Technicon Autoanalyzer (Technicon, 1976). Nitrate is expressed in g N-NO_3 m^{-2} of soil.

Denitrification was assayed by the static core acetylene inhibition method (Yoshinari & Knowles, 1976). Nine intact cores (length 10 cm, diameter 5 cm) collected monthly or every 2 months 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. These cores were incubated at field temperature for periods of between 1 and 4 h, and the rate of denitrification calculated as the rate of nitrous oxide (N_2O) accumulation in the head space in 4 h. Head-space gas samples were removed from all cores, stored in evacuated collection tubes (Venoject; Terumo Scientific, Rutherford, NJ, U.S.A.), sent to Toulouse, and subsequently analysed within a few days using a gas chromatograph (GC Varian 3300, Palo Alto, CA, U.S.A.) equipped with an electron capture detector (ECD ^{63}Ni) and Porapak Q columns. Results are expressed in g N m^{-2} month^{-1} with the assumption that the value measured is somehow representative of the 2 weeks before and 2 weeks after the sampling time. Even though it is well known that the acetylene block method has some problems, we consider it to be a reasonably robust method, especially for riparian soils with moderate or high nitrate fluxes such as riparian soils (see Groffman *et al.*, in press, for a review). Therefore it provides a fair estimate of denitrification rates when applied to short-term essays and allows inter-sites comparisons.

Statistical analyses

We used Multivariate Adaptative Regression Splines (MARS) to relate the response variable denitrification with five relevant predictors, namely soil silt and clay (SC, %), herbaceous plant biomass (HPB, g dry mass m^{-2}), soil moisture (SM, %), g N-NO_3 (m^{-2}) and temperature (°C). Introduced by Friedman (1991), MARS approximates the underlying relationship between the response variable and the predictors using a set of adaptative piecewise linear regressions called basis functions (BFs). A typical BF is $\max(0,x - c)$ [resp. $\max(0,c - x)$] taking values x (resp. $-x$) for all values of x greater (resp. lower) than some threshold c and 0 otherwise. The constant c is usually referred to as knot where a change in the slope of the BF occurs. The MARS algorithm searches for the optimal combination of BFs and therefore allows maximum flexibility in describing any functional (including non-linear) form of the response variable. Two features of MARS were important for our purpose. First, MARS provides a hierarchy regarding the importance of covariates as predictors of denitrification. This ranking of variables is based on the goodness-of-fit of models from which all terms involving the predictor under investigation are dropped, where the goodness-of-fit is measured by the generalised cross-validation (GCV) value. The lower the GCV is, the better the model is supported by the data. Secondly, MARS is able to explore complex relationships by automatically deciding whether a predictor enters additively or interacts with another predictor in the model for the response variable. MARS models were fitted using the MARS software (Salford Systems, http://www.salford-systems.com/mars.php). Because results produced by MARS can be affected by multicollinearity in the set of explanatory variables, we first checked that the predictors were non-linearly correlated using standard Pearson correlations and a principal component analysis (results not shown).

Results

European scale

We combined all the data from the different study sites, sampling locations and sampling dates to analyse the patterns of denitrification rates at the European scale. Several local studies have already shown that soil temperature, moisture and grain size influence denitrification rates. The objective here was to determine whether these simple parameters could be used as proxies of denitrification activity at the large scale; in other words, to find if they would be robust enough to encompass local, regional and seasonal variability. Our expectation was that denitrification activity would be positively correlated to alluvial SM and temperature. We found high variability in denitrification rates ranging from 0 to 30 g N m^{-2} month^{-1} (Fig. 2). Maximum denitrification activity was not found at maximum SM but between 50% and 80% (w/w) (Fig. 2a). The relationship between denitrification activity and soil grain size was not linear either (Fig. 2b). The highest denitrification activity was measured in soil with approximately 80% SC. A negative exponential relationship was found between soil nitrate content and

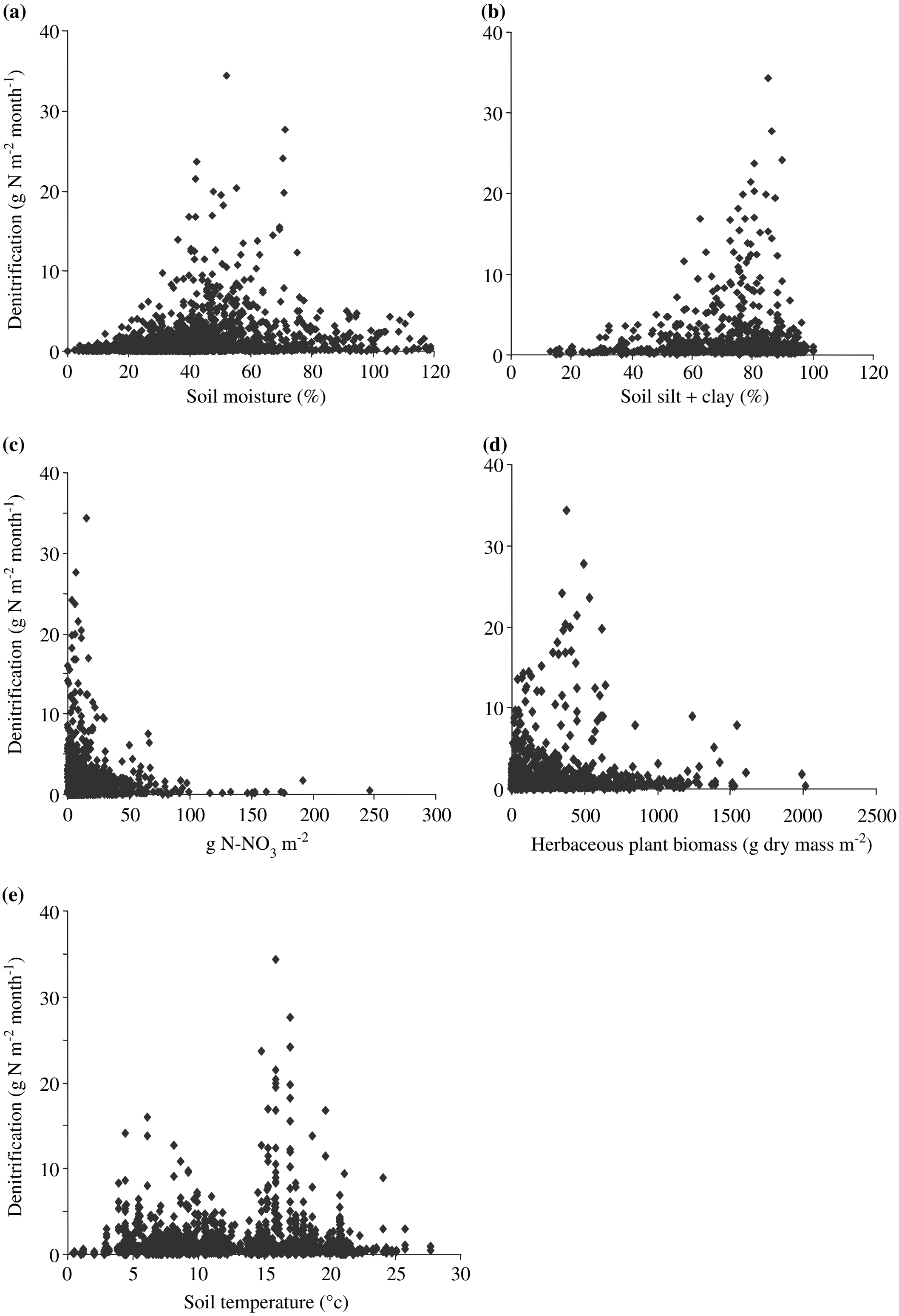

Fig. 2 Relationship between denitrification activity and alluvial soil variables. All the data from the different study sites were combined. Denitrification rates and (a) soil moisture, (b) soil texture expressed as percentage of silt and clay, (c) riparian soil nitrate content, (d) herbaceous plant biomass in the riparian sites, (e) soil temperature.

denitrification activity (Fig. 2c). High denitrification rates were measured in soils with low to medium nitrate concentration. Moreover, at this large scale of analysis there was also a negative exponential relationship between denitrification rates in alluvial soils and herbaceous biomass production (Fig. 2d). Highest denitrification activity was measured in soils with low herbaceous biomass production. At this European scale denitrification presented a bimodal pattern with high rates at both low (*c.* 5–10 °C) and intermediate (*c.* 15–20 °C) soil temperature (Fig. 2e).

The BFs selected by the MARS analysis, in terms of soil SC (%), HPB (g dry mass m^{-2}), SM (%), nitrate (N, g $N\text{-}NO_3$ m^{-2}) and temperature (TEMP, °C) were as follows:

$$\begin{aligned}
&BF1 = \max(0, SM - 77.390),\\
&BF2 = \max(0, 77.390 - SM),\\
&BF3 = \max(0, N - 1.660),\\
&BF4 = \max(0, 1.660 - N),\\
&BF6 = \max(0, 17.000 - TEMP),\\
&BF7 = \max(0, SM - 56.310) \times BF6,\\
&BF9 = \max(0, SM - 75.120) \times BF3,\\
&BF11 = \max(0, SM - 58.310),\\
&BF13 = \max(0, TEMP - 15.780) \times BF11,\\
&BF14 = \max(0, 15.780 - TEMP) \times BF11,\\
&BF15 = \max(0, HPB + 0.120690 \times 10^{-4}),
\end{aligned}$$

and the final model for denitrification is:

$$\begin{aligned}
\text{Denitrification} = {} & 55.127 + 3.531 \times BF1 - 0.728\\
& \times BF2 + 31.947 \times BF - 1.471 \times BF6\\
& - 0.950 \times BF7 - 1.789 \times BF9\\
& + 3.554 \times BF13 + 1.159 \times BF14\\
& - 0.010 \times BF15.
\end{aligned}$$

From this equation, it is clear that a model with interaction effects outperformed a pure additive model, which is confirmed by the difference in GCV of the two models, 493.562 versus 529.599 respectively. Interestingly, the explanatory variable SM was involved in all interactions through BFs BF7, BF9 and BF11, emphasising its importance in predicting denitrification. In Table 2 we present the ranking of predictors for denitrification by order of importance (%), defined by the relative importance of predictors when compared with the best one (SM here). This confirms that SM was the most important variable determining denitrification, and to a lesser extent, in order of importance, temperature, nitrate, then marginally HPB. It is interesting to note that soil texture (SC content) did not play any role in the final model.

Table 2 Ranking of predictors for denitrification by order of importance

Predictor	Importance (%)	−GCV
SM	100.00	719.98
TEMP	78.35	632.55
N	68.04	598.37
HPB	13.71	497.82
SSC	0.00	493.56

The predictors are soil moisture (SM), temperature (TEMP), nitrate (N), herbaceous plant biomass (HPB), and soil texture (SSC). −GCV is the loss in generalised cross-validation when all basis functions involving the corresponding predictor are removed from the final model. Importance is the relative importance of predictors when compared with the best one (SM here).

River scale

The relationship between denitrification activity and alluvial soil temperature was re-analysed at the local scale, considering the denitrification patterns river by river (Fig. 3). The lowest denitrification rates were measured in the Vindel and the Helge alluvial soils but they were of the same order of magnitude as the values obtained at the other sites. Different seasonal patterns were found across Europe: in the Vindel, Helge, Aar and Danube rivers, corresponding respectively to cold, high latitude, high altitude and continental sites, denitrification rates were greater at the higher temperatures characteristic of the period from mid spring to late summer. In these sites, no significant denitrification rates were measured at times of low temperature. In the Trent, Garonne and Po rivers, corresponding respectively to oceanic and warm temperate climates, denitrification rates showed a bimodal pattern, being higher at both high and low (i.e. 3–5 °C) soil temperatures.

Detailed analysis of the temporal pattern of denitrification in the Garonne alluvial soils, for instance, revealed that both rainfall and flood events can trigger microbial activity (Fig. 4). High denitrification rates were measured when soil temperature was high and rainfall was moderate (Fig. 4a). However, during high-water periods and various rainfall events, high denitrification rates were also measured even at times of low soil temperature (Fig. 4b). Similarly, rainfall

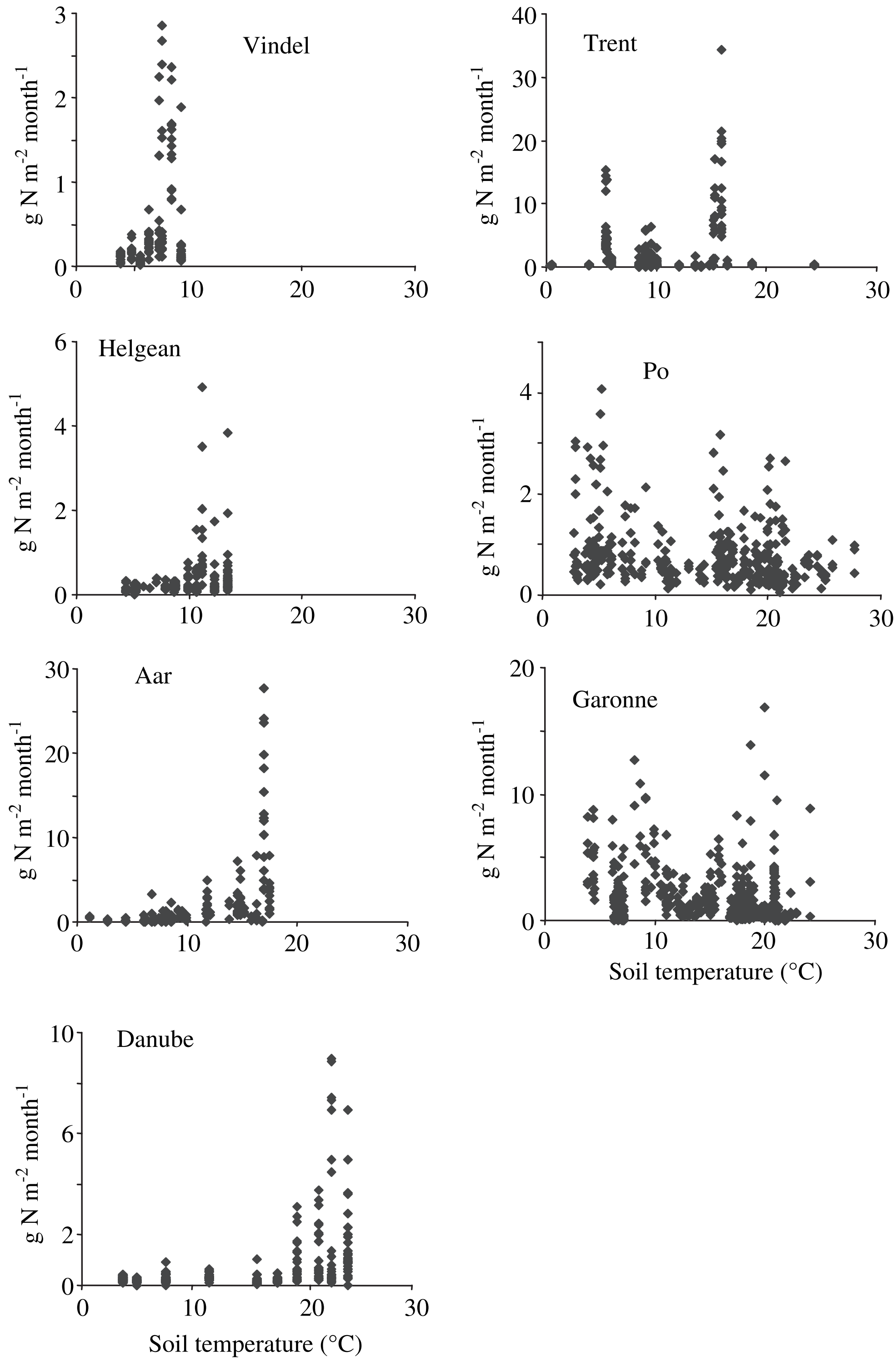

Fig. 3 Relationship between riparian soil temperature and denitrification activity in the different rivers under study.

and flood events can cause high denitrification rates in the alluvial soils of the Po River (Fig. 5) under a wide range of soil temperatures (from 5 to 20 °C). Even a relatively brief rainfall event (100 mm in two days in June; Fig. 5d, box 2) in an otherwise dry period can trigger high denitrification rates.

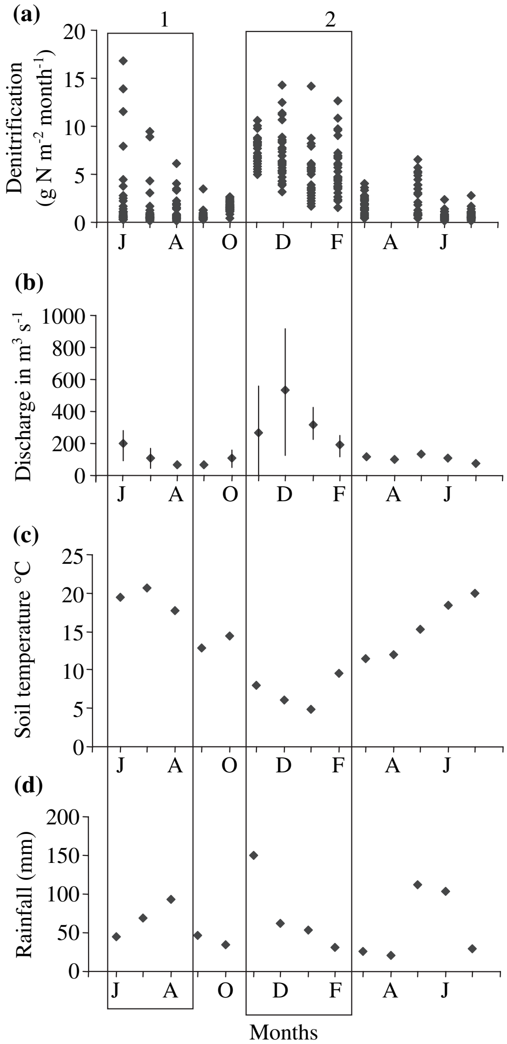

Fig. 4 (a) Monthly denitrification activity in the soils of the Garonne riparian zones. (b) Monthly variations of the Garonne River discharge. (c) Monthly variations of the riparian soil temperature. (d) Monthly variations of rainfall in the study sites along the Garonne River. Box 1 underlines a period with moderate rainfall and high soil temperature. Box 2 underlines a high water period with low soil temperature.

Discussion

Patterns of denitrification activity and controlling factors at the European scale

Denitrification activity was significant in all the floodplain soils at all latitudes. However, we found a difference in rates of an order of magnitude from high to mid latitudes. Maximum rates (above 30 g N m^{-2} $month^{-1}$) were measured under the maritime conditions of the Trent floodplain. These rates are in accordance with those measured in other wetland sites (Merrill & Zak, 1992; Pinay *et al.*, 1993; Naiman *et al.*, 1994; Johnston, Bridgham & Schubauer-Breigan, 2001; Pinay *et al.*, 2003).

Soil moisture. The most important control variable was SM, which is determined by hydrological events. In the MARS analysis, SM was involved in all interactions through BFs BF7, BF9 and BF11, emphasising its importance in predicting denitrification. Flooding frequency and duration are controlled by local topography, low areas being flooded more frequently and for longer periods than higher ones, producing large variations in biogeochemical patterns at the metre scale (Pinay *et al.*, 1989; Pinay & Naiman, 1991). Biogeochemical processes, especially involving nitrogen, are sensitive to the oxidation status of the soil. For instance, ammonification of organic nitrogen can be realised both under aerobic and anaerobic conditions. The nitrification process, which is strictly aerobic, can occur only in aerated soils or sediments. As a consequence, in permanently anaerobic conditions organic nitrogen mineralisation processes result in the accumulation of ammonia.

Other processes such as nitrogen dissimilation or denitrification are strictly anaerobic, requiring saturated soils to operate. Therefore the end products of nitrogen cycling in riparian soils are directly controlled by the ground water table with important implications for floodplain productivity. Even so, maximum denitrification activity was not found at soil saturation but between 60% and 80% of maximum SM. This can be explained by the fact that partial waterlogging conditions favour the co-existence of aerobic and anaerobic sites at the soil micro-scale. This, in turn, allows the occurrence in nearby microsites of both strictly aerobic and anaerobic biogeochemical processes involved in the nitrogen cycle, enhancing organic matter decomposition and nitrogen loss through denitrification in flooded soils (Reddy & Patrick, 1975; Groffman & Tiedje, 1988). Moreover, alternate aerobic and anaerobic conditions triggered by short-term periodicity of flood-drainage cycles or short rainfall events will produce similar results and therefore enhance the process of denitrification, provided soil temperature is above 0 °C.

Soil temperature The second most important control variable, as confirmed by the MARS analysis, was soil

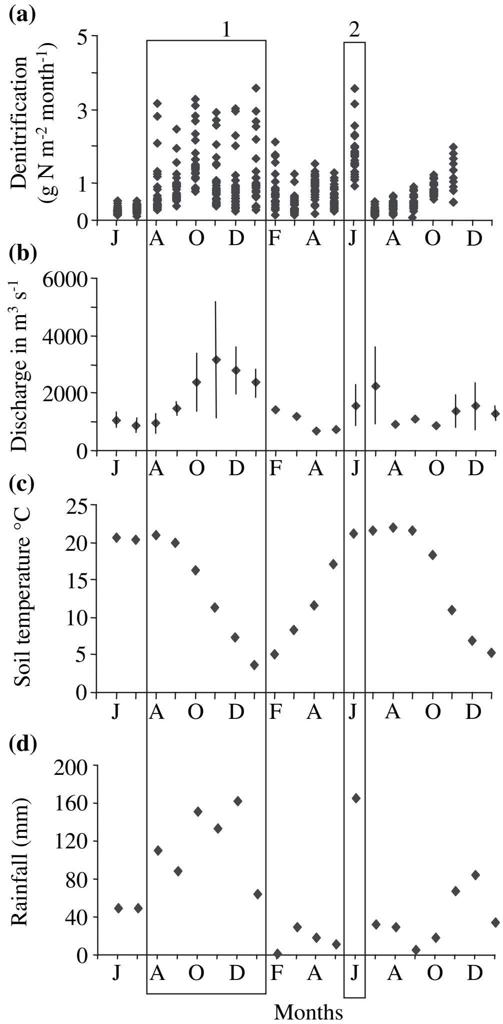

Fig. 5 (a) Monthly denitrification activity in the soils of the Po riparian zones. (b) Monthly variations of the Po River discharge. (c) Monthly variations of the riparian soil temperature. (d) Monthly variations of rainfall in the study sites along the Po River. Box 1 underlines a period with rainfall and floods. Box 2 underlines summer rainfall event.

temperature. At the European scale denitrification presented a bimodal pattern with high rates at both low and intermediate soil temperatures. It was found that in cold winter regions (i.e. high latitudes: Vindel and Helge Rivers), high altitudes (Aar River) and continental regions (Danube River), very low temperatures during the winter period limit microbial activity in general and denitrification in particular. Therefore, no hydrological event, flood or rainfall, triggered any significant denitrification activity during these low-temperature periods. Under milder winter conditions (i.e. Trent, Garonne and Po Rivers), denitrification rates could be significant throughout the year. Flooding or rainfall could cause high denitrification rates by controlling waterlogging conditions in the alluvial soils and the duration of oxic and anoxic phases (Ponnamperuma, 1972; Keeney, 1973; Patrick, 1982).

Nitrate. The third control variable on denitrification after soil temperature and SM, confirmed by the MARS analysis, was soil nitrate concentration. At the microbial scale, nitrate is a limiting factor for denitrification. Yet, the global negative relationship between denitrification activity and soil nitrate content reveals that nitrate can be used as a proxy to determine whether denitrification occurs in alluvial soils. However, low or medium soil nitrate concentrations do not provide much information on the rate of nitrogen turnover in alluvial soils because we measured a wide range of denitrification rates under these soil nitrate concentration. High denitrification rates measured in soils with low nitrate concentration suggest that denitrification rates are of the same order of magnitude as N mineralisation rates. See Johnston (1991) for a review.

Herbaceous plant biomass. Competition between plant growth and denitrification for N uptake in floodplain soils entails a negative exponential relationship between HPB and denitrification. Plant biomass was a significant variable in the denitrification model developed by the MARS procedure. Given that HPB contains an average of 2% N, the N denitrified in alluvial soil is about the same order of magnitude as the N stored in herbaceous plants. However, denitrification constitutes a true removal of N as the end products are in gaseous form (Knowles, 1982). Consequently denitrification represents a significant loss of nitrogen from floodplain systems and its increase could limit plant biomass production.

Soil texture. Denitrification activity was low in alluvial soils with a low percentage of SC. Above a threshold of about 60% of SC we measured the highest rates of denitrification activity. This threshold was found whatever the site considered. Interestingly, at this European scale, SC content was not found in our model to be a significant variable to estimate denitrification in alluvial soils. Yet, the role of soil texture in controlling nitrogen cycling has already been documented in forests (Pastor *et al.*, 1984; McClaugherty, Pastor & Aber, 1985), coastal forests (Seely, Lajtha & Salvucci, 1998), short-grass steppe (Schimel, Stillwell & Woodmansee, 1985), desert ecosystems (Schlesinger *et al.*, 1996) and grassland (Parton, Mosier & Schimel, 1988). We also know that flooding indirectly affects nutrient cycling and especially denitrification in floodplain soils by influencing soil structure and texture through sediment deposits (Pinay, Ruffinoni & Fabre, 1995; Pinay *et al.*, 2000). Hence, locally, floodplain and stream channel hydromorphological processes influence the sorting of flood deposits by grain size, creating a mosaic of soils of different textures. However, sediment texture does not seem to be an important variable at the European scale.

Possible changes in denitrification activity patterns under a climatic change scenario

Bacterial denitrification activity is a key process in the cycling of N in floodplain soils as it constitutes a major sink for nitrate, and as such is involved in the control of nitrogen fluxes along river systems. The denitrification rates measured in this pan-European study confirm also that this process is important in a wide range of climatic conditions. Yet, the construction of predictive models of N cycling in floodplain soils is extremely difficult because of the often episodic nature of flood and rainfall events. Moreover, the development of predictive models necessitates that a link be established between processes occurring at a microbial scale and landscape patterns visible at the floodplain scale. For instance, although the role of SM, nitrate concentration and available carbon in regulating this microbial process is now well documented, these three factors do not explain fully the variation in the denitrification rates observed at the floodplain scale. Indeed, we found that the main driving factors of microbial denitrification in alluvial soils were SM, temperature and to a lesser extent soil nitrate concentration. These factors were also identified in laboratory experiments (Rolston, Rao & Davidson, 1984; Myrold & Tiedje, 1985; Davidson & Swank, 1986) but they might well be affected by global change (Shaver *et al.*, 2000; Georgakakos & Smith, 2001). Indeed, geomorphologic and hydrological processes can be altered both from the upslope by land use/land cover change and via river discharge changes (Nilsson & Berggren, 2000; Nijssen *et al.*, 2001; Burt *et al.*, 2002; Pinay, Clement & Naiman, 2002) while temperature should rise under atmospheric carbon dioxide concentration increase (IPCC, 2001). Yet there remains a major difficulty under climate change scenarios to estimate the resulting hydrological changes as the modelling of their components (i.e. precipitation, evapotranspiration, SM and runoff) is considerably less reliable than, for instance, modelling temperature and pressure (Jones & Woo, 2002). Moreover, the effect of a change in climate on the natural hydrological system is frequently non-linear due to the existence of critical thresholds (Arnell, 2000). For instance, even as the Earth as a whole continues to warm gradually, large regions may experience a rapid shift into colder climate (Peterson *et al.*, 2002).

Despite these uncertainties, there is evidence from Quaternary records that the impacts of climate change on fluvial dynamics are more marked in the upper reaches of river networks (Veldkamp & Tebbens, 2001). Therefore, signs of hydrological changes caused by climate change are expected to be less marked in the lower part of the Danube River than in the other study sites. The four scenarios of climatic change, namely UKHI (Mitchell *et al.*, 1990); UKTR (Murphy & Mitchell, 1994), CCC (Boer, McFarlane & Lazare, 1992), GHGx, (Johns, Carnell & Crossley, 1997), used by Arnell (1999) to evaluate the hydrological change in Europe, consistently assume an increase of precipitation and average annual runoff in northern Europe and a decrease of both precipitation and runoff in southern Europe. In cold regions, the timing of flow through the year should be unaffected but we can expect an increase in the spring streamflow peak in response to an increase in winter precipitation stored as snow (Nijssen *et al.*, 2001). This should potentially trigger increases in both rates and durations of denitrification in alluvial soils such as in the Vindel River in Northern Sweden. A temperature rise will reduce snow cover at the margin between maritime and continental regimes, which will reduce spring flow and increase winter flows in these areas. This shift in the high-water period could reduce denitrification activity as waterlogging would occur under colder temperature conditions in areas such as the Helge River region in the southern part of Sweden. In maritime regions such as in the Trent valley in the U.K., an increase in both the frequency and the magnitude of flooding events is expected (Reynard, Prudhomme & Crooks, 2001).

While there is still no firm evidence of a change in flooding trends caused by climate change, a number of studies have suggested that rainfall has become more variable and that rainfall intensity and frequency has increased (Osborn & Hulme, 2002; Robson, 2002; Burt & Horton, 2003). This increase in rainfall variability should increase the frequency of aerobic–anaerobic cycles in alluvial soils and therefore increase denitrification activity. A higher frequency of wet–dry cycles might increase the proportion of N_2O emission by denitrification and contribute to an increase in the greenhouse effect (Blitcher-Mathiesen & Hoffmann, 1999; Jacinthe, Dick & Brown, 2000). In warmer regions such as those represented by the Garonne River in south-west France and the Po River in northern Italy, a decrease in annual rainfall is expected together with an increase in heavy summer rainfall events. Our results show that these alluvial soils are highly reactive to such short-term rain events, which result in high rates of denitrification activity. One can expect that an increase in the frequency of these summer rainfall events would increase the loss of nitrogen from alluvial soils during the vegetated period, and this may increase competition for N and, in turn, alter the productivity of these riparian zones.

New challenges

It is now recognised that the importance of indirect effects of climate change such as hydrological changes on the structure and function of ecosystems may be more influential than the increase in temperature *per se* (Vitousek, 1994; Pace & Groffman, 1998). In this study we have shown that microbial denitrification, an important process of N cycling in alluvial soils, had a pattern of activity which varied widely with regional climatic context. Even so, it was possible to identify the main controlling variables of denitrification at the European scale, namely SM and temperature, and provide a model to forecast denitrification in alluvial soils which could be used to predict the response of these soils to climatic and anthropogenic changes. For instance, two-thirds of freshwater flowing to the oceans is obstructed by large dams (Nilsson & Berggren, 2000). This is especially true in the Northern Hemisphere and particularly in Europe and North America. Thus, it is possible that hydraulic engineering has produced both local and global-scale impacts on the terrestrial water cycle (Vörösmarty & Sahagian, 2000). The new challenge today is to decouple the relative impact of direct human intervention from those effects caused by climate change and determine the consequences of hydrological variations fostered by climate change on the resistance and resilience of biogeochemical cycles in river systems.

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