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Chapter 4

TOPOGRAPHIC FACTORS OF NITROUS OXIDE EMISSION

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ABSTRACT

Topography influences soil processes, and the use of topographic data to model and predict the spatial distribution of soil properties is widely reported. We studied an effect of topography on nitrous oxide emission under different climatic and hydrologic conditions in a typical agroecosystem using digital terrain modelling. The agrosystem is located in the Canadian prairies. For the study site, three data sets were used: (1) eighteen local, regional, and combined topographic variables, viz. slope steepness and aspect, twelve land surface curvatures (i.e., horizontal, vertical, accumulation, difference, ring, minimal, maximal, mean, Gaussian, unsphericity, horizontal excess, and vertical excess curvatures), catchment and dispersive areas, topographic and stream power indices; (2) soil environmental attributes: soil gravimetric moisture and soil bulk density; and (3) attributes of soil microbial activity: most probable number of denitrifiers, microbial biomass carbon content, denitrifier enzyme activity, nitrous oxide flux, denitrification rate, and microbial respiration rate. Rank multiple correlation and multiple linear regression were used as statistical analyses.

In wetter soil conditions, topographically-controlled and gravity-driven supply of nutritive materials to microbiota increased the denitrification rate. Its spatial differentiation was mostly affected by redistribution and accumulation of soil moisture and soil organic matter down the slope according to relative position of a point in the landscape. The nitrous oxide emission was affected by variation in soil moisture and organic matter due to the local geometry of a slope. The microbial biomass, number of denitrifiers, and microbial respiration depended on both the local geometry of a slope and relative position of a point in the landscape. In drier soil conditions, although denitrification persisted, it was reduced and did not depend on the spatial distribution of soil moisture and thus land surface morphology. This may result from a reduction in soil moisture below a critical level sufficient for transient induction of denitrification but not sufficient to preserve spatial patterns of the denitrification according to relief.

INTRODUCTION

Denitrification, a process of biological conversion of NO_3^- into N_2O and N_2 gases (Payne, 1981), is important for understanding N dynamics at regional and global scales (Mishustin and Shilnikova, 1971; Khalil and Rasmussen, 1992), and contribution of N_2O emission into climate fluctuation, stratospheric ozone depletion, and photochemical air pollution (Conrad, 1996; Kester et al., 1997; Cheneby et al., 1998; Meixner and Eugster, 1999). Agronomically, denitrification is of concern because it is responsible for most of the nitrogen loss from fall-applied fertilizers (Grant, 1991). It has been estimated that 30% of nitrogen fertilizer applied to agricultural soils is lost to the atmosphere because of the activity of denitrifying bacteria (Murray et al., 1989).

Topography is the recognised state factor of the soil development (Huggett, 1975; Gerrard, 1981; Huggett and Cheesman, 2002). It is common knowledge that topography effects significantly the spatial distribution of soil moisture, temperature, and organic matter (Beven and Kirkby, 1979; Romanova et al., 1983; Burt and Butcher, 1985; Moore et al., 1993; Florinsky and Kuryakova, 2000; Florinsky et al., 2002). At the same time, soil moisture, soil temperature and soil organic matter are acknowledged to be among the most important soil physiochemical properties influencing population dynamics, activity and ecology of the soil microbiota (Stotzky, 1997). Denitrification is influenced by soil water content, and the distribution of denitrifying activity is anticipated to respond to hydrological differences in a landscape (Groffman and Hanson, 1997). It was demonstrated that denitrification depends on characteristics of topography (Table 1) at a landscape scale (Whelan and Gandolfi, 2002; Florinsky et al., 2004; Boyer et al., 2006). In particular, Beaujouan et al. (2002) found that the highest denitrification rates occurred in concave areas and downslopes. In northern grasslands of North America, downslopes and depressions were marked by the highest rates of N_2 and N_2O emission comparing with up- and midslopes (Pennock et al., 1992; Van Kessel et al., 1993; Corré et al., 1996; Yates et al., 2006).

In this chapter, we describe the effect of topography on the activity of denitrifiers under different humidity conditions in northern grasslands at a landscape scale using digital terrain modelling.

STUDY SITE

The study site is located about 260 km west of the city of Winnipeg, Manitoba, Canada, near the town of Minnedosa (about 50°14'43" N, 99°50'34" W). The site measures 1,680 by 820 m, and the maximum elevation difference is about 13 m (Figure 1a). It is situated in the Newdale Plain at an elevation of about 580 m above sea level. The site is representative of a broad region of undulating-to-hummocky glacial till landscapes in Western Canada (Clayton et al., 1977).

Table 1. Definitions, formulae, and interpretations of some topographic variables (Florinsky, 1998; Shary et al., 2002)

Variable and unit	Definition, formula, and interpretation
Local Topographic Variables	
Slope steepness (G), °	Angle between a tangent plane and a horizontal one at a given point on the land surface. A measure of the velocity of substance flows. In particular, G controls runoff, soil loss< and soil moisture: as G increases, velocity of water flow and slope area increase, so the rainfall received per unit area and its infiltration decrease, whereas the runoff and an evaporation area increase, and hence soil moisture decreases. $G = \arctan\sqrt{p^2 + q^2}$
Slope aspect (A), °	Angle clockwise from north to a projection of an external normal vector to a horizontal plane at a given point on the land surface. A measure of the direction of substance flows. In association with G, A controls insolation and evapotranspiration. $A = \arctan(q/p)$
Vertical curvature (k_v), m^{-1}	A curvature of a normal section of the land surface by a plane, including gravity acceleration vector at a given point. k_v is a measure of relative deceleration and acceleration of flows. Overland and intrasoil lateral flows are decelerated when $k_v < 0$, and are accelerated when $k_v > 0$. k_v is one of the determining local factors of the dynamics of overland and intrasoil water. k_v influences soil moisture, pH, thickness of soil horizons, organic matter, etc. k_v can be used to map accumulation, transit and dissipation zones of the land surface. $k_v = -\frac{p^2 r + 2pqs + q^2 t}{(p^2 + q^2)\sqrt{(1 + p^2 + q^2)^3}}$
Horizontal curvature (k_h), m^{-1}	A curvature of a normal section of the land surface which is orthogonal to the section of vertical curvature at a given point on the land surface. k_h is a measure of flow convergence and divergence. Overland and intrasoil lateral flows are converged when $k_h < 0$, and are diverged when $k_h > 0$. k_h is one of the determining local factors of the dynamics of overland and intrasoil water. k_h influences soil moisture, pH, thickness of soil horizons, organic matter, etc. k_h can be used to map accumulation, transit, and dissipation zones of the land surface. $k_h = -\frac{q^2 r - 2pqs + p^2 t}{(p^2 + q^2)\sqrt{1 + p^2 + q^2}}$
Gaussian curvature (K), m^{-2}	A product of maximum curvature and minimum curvature. According to *Teorema egregium* by Gauss, K of a surface retains its values after bending the surface without breaking, stretching, and compressing. $K = k_{\min} k_{\max} = \frac{rt - s^2}{(1 + p^2 + q^2)^2}$

Table 1. (Continued)

Variable and unit	Definition, formula, and interpretation
Mean curvature (H), m^{-1}	A half-sum of curvatures of two orthogonal normal sections of the land surface at a given point. H presents flow convergence and relative deceleration with equal weights. Therefore, H can be more representative topographic attribute than k_h and k_v in relation to description of landscape processes. $$H = \frac{1}{2}(k_{\min} + k_{\max}) = \frac{1}{2}(k_h + k_v) = -\frac{(1+q^2)r - 2pqs + (1+p^2)t}{2\sqrt{(1+p^2+q^2)^3}}$$
Difference curvature (E), m^{-1}	A half-difference of vertical and horizontal curvatures. There are two mechanisms of flow accumulation, convergence and deceleration, are controlled by k_h and k_v, correspondingly. E describes which accumulation mechanism is more active at a given point of the land surface. $$E = \frac{1}{2}(k_v - k_h) = \frac{(q^2 r - 2pqs + p^2 t)(1+p^2+q^2) - (p^2 r + 2pqs + q^2 t)}{2(p^2+q^2)\sqrt{(1+p^2+q^2)^3}}$$
Accumulation curvature (K_a), m^{-2}	K_a is a measure of the probable degree of flow accumulation. In combination with H, K_a is used to map accumulation, transit, and dissipation zones of the land surface. $$K_a = k_h k_v = \frac{(q^2 r - 2pqs + p^2 t)(p^2 r + 2pqs + q^2 t)}{[(p^2+q^2)(1+p^2+q^2)]^2}$$
Unsphericity (M), m^{-1}	$M = 0$ on a sphere, so values of M show the extent to which the form of the land surface is non-spherical. $$M = \frac{1}{2}(k_{\max} - k_{\min}) = \sqrt{H^2 - K}$$
Ring curvature (K_r), m^{-2}	$K_r = 0$ for a radially symmetrical landform with a vertical axis of symmetry. $$K_r = k_{he} k_{ve} = M^2 - E^2 = \left[\frac{(p^2 - q^2)s - pq(r-t)}{(p^2+q^2)(1+p^2+q^2)}\right]^2$$
Horizontal excess curvature (k_{he}), m^{-1}	k_{he} describes to what extent k_h is larger than k_{min}. $$k_{he} = k_h - k_{\min} = M - E$$
Vertical excess curvature (k_{ve}), m^{-1}	k_{ve} describes to what extent k_v is larger than k_{min}. $$k_{ve} = k_v - k_{\min} = M + E$$
Minimum curvature (k_{min}), m^{-1}	A curvature of a normal section with the smallest value of curvature among all normal sections at a given point of the land surface. $k_{min} > 0$ describes hills, whereas $k_{min} < 0$ describes valleys. $$k_{\min} = H - M$$
Maximum curvature (k_{max}), m^{-1}	A curvature of a normal section with the largest value of curvature among all normal sections at a given point of the land surface. $k_{max} > 0$ describes ridges, whereas $k_{max} < 0$ describes depressions. $$k_{\max} = H + M$$

Variable and unit	Definition, formula, and interpretation
Regional Topographic Variables	
Catchment area (*CA*), m^2	An area of a closed figure formed by a contour intercept including a given point on the land surface and two flow lines coming from an upslope zone to the ends of the contour intercept. A measure of the contributing area. In particular, *CA* controls soil moisture: the amount of moisture per unit area increases along a slope from top to bottom, due to additional moisture contributed from upslope units. Thus, as *CA* increases, soil moisture content also increases. *CA* can play a more dominant role in the control of soil water redistribution than k_h, k_v, and *H*, since *CA* considers the location of a site in the landscape.
Dispersive area (*DA*), m^2	An area of a closed figure formed by a contour intercept including a given point on the land surface and two flow lines going downslope from the ends of the contour intercept. Dispersive area measures a downslope area potentially exposed by flows passing through a given point on the land surface.
Combined Topographic Variables	
Topographic index (*TI*)	A measure of the extent of flow accumulation. *TI* can be used to describe the spatial distribution of the soil moisture and related landscape processes. As *CA* increases and *G* decreases, *TI* and soil moisture content increase. This can lead to higher correlations of soil moisture with *TI* than with *CA* and *G*. $TI = \ln(CA/G)$
Stream power index (*SI*)	*SI* can be used to describe potential flow erosion and related landscape processes. As *CA* and *G* increase, the amount of water contributed by upslope areas and the velocity of water flow increase, hence *SI* and erosion risk increase. $SI = CA \cdot G$

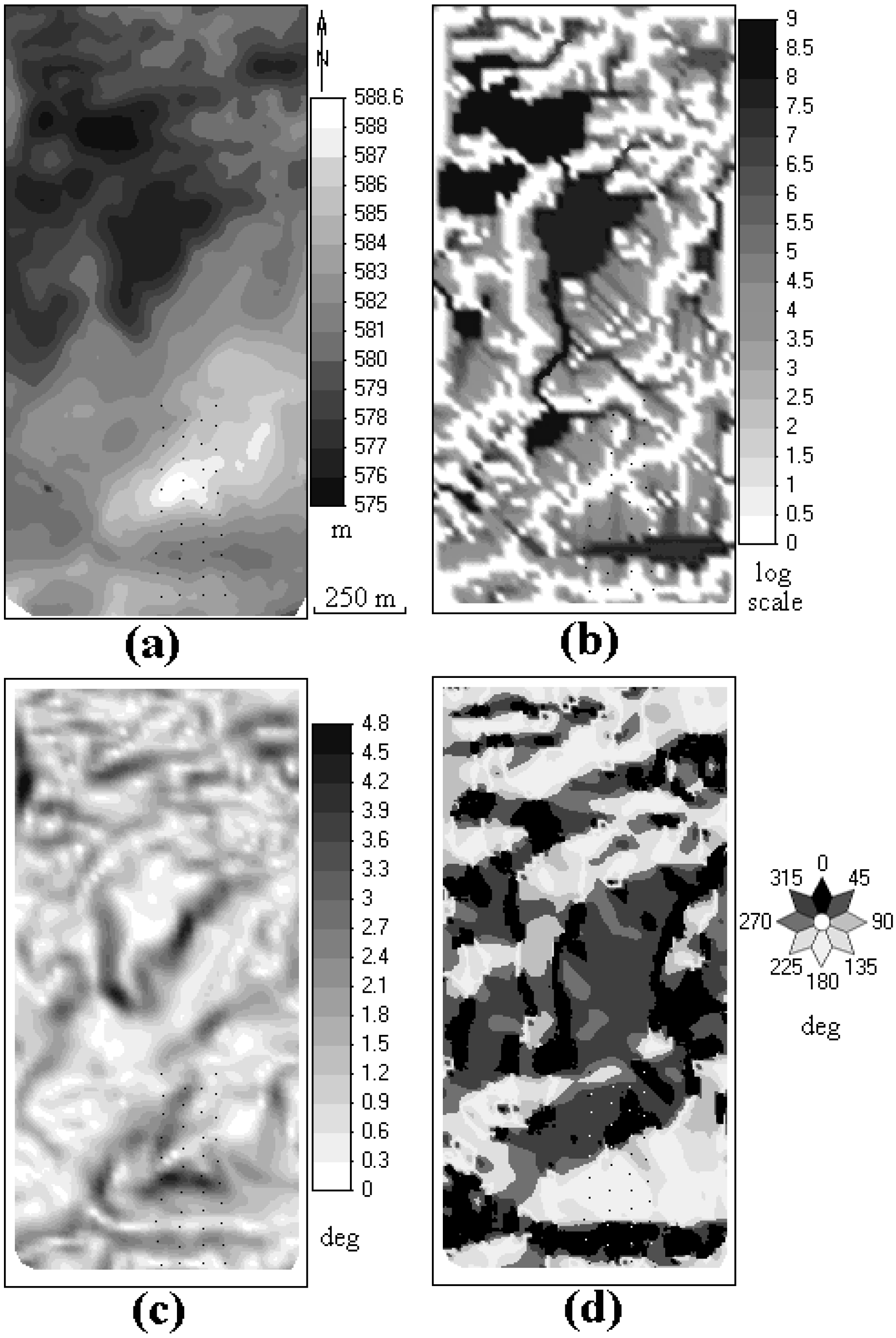
$p = \frac{\partial z}{\partial x}$, $q = \frac{\partial z}{\partial y}$, $r = \frac{\partial^2 z}{\partial x^2}$, $s = \frac{\partial^2 z}{\partial x \partial y}$, and $t = \frac{\partial^2 z}{\partial y^2}$ for the elevation given by $z = f(x, y)$; x and y are Cartesian co-ordinates.

The site is located within a continental climate zone with warm summers and prolonged, cold winters. Mean annual temperature is 2.5°C, mean summer temperature is 16°C, mean winter temperature is -11°C. Mean annual precipitation is 460 mm including 310 mm of rainfall and 150 mm of snowfall.

The parent material consists of loamy textured glacial till deposits (Clayton et al., 1977). For the most part, soils at the site are Black Chernozems (Soil Classification Working Group, 1998). The Newdale Orthic and Cordova Calcareous series were predominant on well-drained crests and midslopes. The Beresford and Varcoe Gleyed Carbonated Rego series were indicative of imperfectly drained downslopes, often in association with the Angusville Gleyed Eluviated series. The Drokan Gleysols series predominate in poorly drained depressions (Bergstrom et al., 2001b). The site is located in the aspen parkland of the Canadian prairies, the northern extension of open grasslands in the Great Plains of North America. Native vegetation of willows (*Salix sp.*), aspen (*Populus tremuloides*), and sedges (*Carex sp.*) surrounds water-saturated depressions.

The site is a conventional tilled field cultivated by a deep-tiller, with one pass in autumn and one or two passes in spring. Historically, crops have included wheat (*Triticum aestivum*

L.), barley (*Hordeum vulgare* L.), oats (*Avena sativa* L.), rape (*Brassica napus*), and flax (*Linum usitatissimum* L.) (Bergstrom et al., 2001a). The site was cropped to rape in 2000 and wheat in 2001.



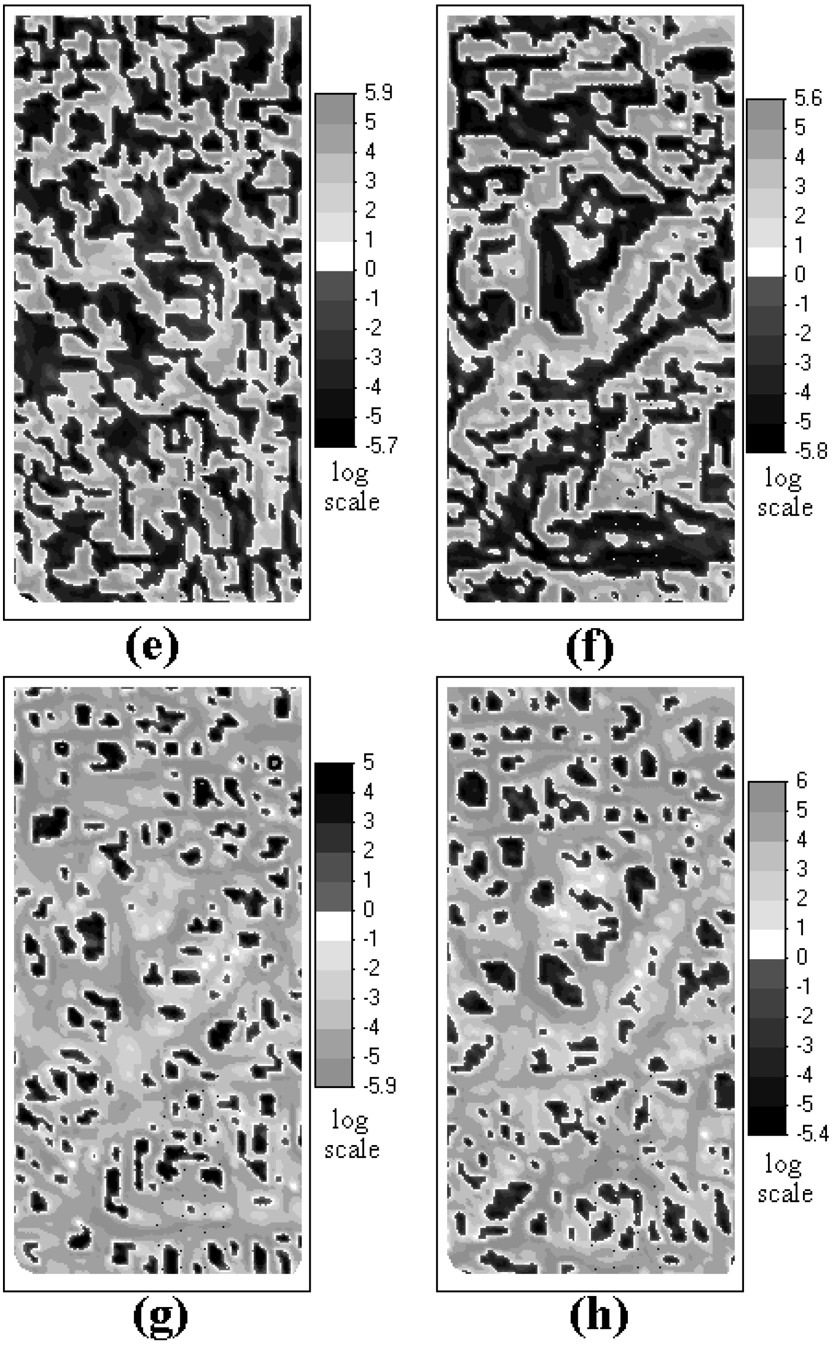


Figure 1. The study site, topographic variables: (a) elevation, (b) catchment area, (c) slope steepness, (d) slope aspect, (e) horizontal curvature, (f) vertical curvature, (g) minimal curvature, (h) maximal curvature. Points indicate sampling sites.

MATERIAL AND METHODS

Field Sampling

A plot was selected within the study site to include a typical soil catena (Bergstrom et al., 2001b). The plot measures about 500 by 200 m with a difference in elevations of about 8 m (Figure 1a). Soil samples were collected along four parallel transects about 500 m long, each about 50 m apart. There were 10 sampling points along transects spaced at intervals of approximately 50 m, for a total of 40 sampling points in the plot (Figure 1). This design allowed us to measure and describe variations of soil properties within the catena. Each of the 40 points was previously georeferenced with horizontal accuracy of 0.03 m by a global positioning system (GPS receivers Trimble TSC1 Asset Surveyors) (Bergstrom et al., 2001b).

We sampled two sets of soil attributes. First, there were two environmental properties influencing soil microbial activity: gravimetric soil moisture (%), and soil bulk density (gcm^{-3}). Second, there were six indices of soil microbial activity: most probable number of denitrifiers, microbial biomass carbon, denitrifier enzyme activity, denitrification rate, microbial respiration rate, and N_2O flux (Table 2).

Table 2. Interpretations of soil microbial variables

Variable	Interpretation
Most probable number of denitrifiers, $\#_{organisms}\, g_{soil}^{-1}$	A measure of the number of denitrifiers in the soil.
Microbial biomass carbon, $\mu g_C\, g_{soil}^{-1}$	A measure of the microbial biomass expressed as carbon.
Denitrifier enzyme activity, $\mu g_N\, g_{soil}^{-1} h^{-1}$	A measure of the amount of denitrifying enzymes in the soil.
Denitrification rate, $\mu g_N\, g_{soil}^{-1} h^{-1}$	A measure of the total gas N production from the soil.
Microbial respiration rate, $\mu g_{CO_2}\, g_{soil}^{-1} h^{-1}$	A measure of the rate of the total microbial respiration in the soil.
N_2O flux, $ng_{N_2O}\, m^{-2} s^{-1}$	A measure of the rate of N_2O emission from the soil.

Sampling of all soil attributes took place at two times, July 2000 and July 2001, to assay the effect of topography on the activity of denitrifiers in different hydrologic situations. The 2000 sampling date occurred during a period of elevated rainfall, the 2001 sampling occurred following a period of limited rainfall. Monthly precipitation of 133 and 26 mm was observed in July 2000 and July 2001, correspondingly, at the nearest weather station in the city of Brandon located 40 km southward of the site.

Soil samples were collected using aluminum soil cores 5 cm in diameter and 5 cm of height. Depth of sampling was approximately 0.1 m because each core pressed into the ground passed surface litter and discontinuities (about 2 cm). To allow direct comparison, analyses were conducted on a single sub-sample taken from each soil core within 1 h of collection. Measurements were made sequentially (microbial respiration, denitrification, then denitrifier enzyme activity) within 48 h of sampling.

To minimize an impact of temporal variability of denitrification and storage of samples, collection of soil core and N_2O flux measurements occurred simultaneously. N_2O flux was estimated using vented static chambers (Hutchinson and Mosier, 1981). Chambers were inserted within 1 m of each sample point. After 1 h of accumulation, a 15-mL gas sample was taken of each chamber by a syringe and injected into 10-mL Vacutainers^{TM} and returned to the laboratory for analysis (Burton et al., 2000).

Laboratory Methods

Soil moisture was determined by drying 10-g soil subsamples at 105°C for 24 h (Topp, 1993). Bulk density was calculated from the moist weight of soil, water content and volume of the core (Culley, 1993).

Microbial biomass C was determined using fumigation-direct extraction (Voroney et al., 1993). Two 15-g samples were weighed into square French bottles. One sample was extracted immediately using 30 mL 0.5 M K_2SO_4. The second sample was fumigated for 24 h under chloroform atmosphere, and then extracted. Filtrate was analysed for C using Technicon Auto-analyzer (Industrial Method #455-76W/A).

The most probable number of denitrifiers was determined with a modified method of Tiedje (1994). Aliquots (0.5 mL) of serial dilutions from 10^{-3} to 10^{-6} were added to 4.5 mL of sterile nutrient broth in 10-mL Vacutainers^{TM}. They were incubated for approximately 7 days at 25°C. Denitrifier presence was determined by measuring N_2O accumulation in the headspace using a Varian 3800 gas chromatograph.

To measure denitrifying enzyme activity, we applied a modified method of Beauchamp and Bergstrom (1993). Soil (5 g) was incubated at ambient temperature with 4 mL of buffer solution under a helium/acetylene atmosphere in 20-mL headspace vials. The buffer solution consisted of 10 mM glucose, 10 mM KNO_3, and 50 mM K_2HPO_4. N_2O in the headspace was measured at 30-min intervals using a Varian 3800 gas chromatograph.

To measure denitrification rate, we used a modified method of Beauchamp and Bergstrom (1993). Soil (5 g) was incubated in ambient temperature in 20-mL headspace vials containing atmospheric air and 10% acetylene. After 24 h, headspace was analysed for N_2O concentration using a Varian 3800 gas chromatograph. The acetylene blocks the conversion of N_2O to N_2 (the last step of denitrification), so in this case the N_2O production is a reasonable equivalent to the evolution of N_2O and N_2 without addition of acetylene. Therefore, the rate of N_2O accumulation can be used as a proxy for total denitrification ($N_2O + N_2$). This is not analogous to the measurements of the N_2O flux *in situ* (see above) when the conversion of N_2O to N_2 can proceed.

To measure microbial respiration rate, we used a modified method of Zibilske (1994). Soil (5 g) was incubated at ambient temperature in 20-mL headspace vials for 2 h, after which time the headspace was sampled, and CO_2 concentration determined by a Varian 3800 gas chromatograph.

The N_2O flux samples were analysed using a Varian 3800 gas chromatograph (Burton et al., 2000).

Digital Terrain Modelling

An irregular digital elevation model (DEM) of the study site based on 7,193 points was constructed with a GPS technique (Bergstrom et al., 2001b). Single-frequency Trimble 4600LS Surveyors were mounted on all-terrain vehicles; data were collected cinematically (Clark and Lee, 1998). Vertical and horizontal accuracy of the DEM was 0.05 and 0.03 m, respectively.

The irregular DEM was converted into a regular one by the Delaunay triangulation and piecewise smooth interpolation (Watson, 1992). The grid interval of the regular DEM was 20 m, corresponding to typical sizes of topographic elements within the site. Digital models of fourteen local topographic attributes – G, A, k_h, k_v, H, K, k_{min}, k_{max}, K_a, E, K_r, k_{ve}, k_{he}, and M (Table 1) – were calculated by the method of Evans (1980). The method of Martz and De Jong (1988) was applied to calculate a digital model of two regional topographic variable – *CA* and *DA* (Table 1), as well as digital models of two combined attributes: *TI* and *SI* (Table 1). The grid interval of all derived digital terrain models (DTMs) was 20 m (Figure 1). Then we used smooth interpolation of these DTMs to determine values of elevation (z) and all derived secondary topographic attributes at each of the sampling points.

Digital terrain modelling and mapping of topographic attributes were performed by LandLord 4.0 software (Florinsky et al., 1995).

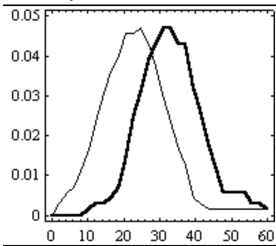
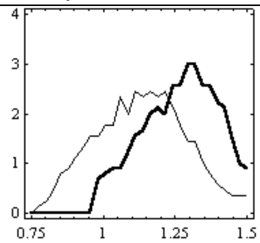
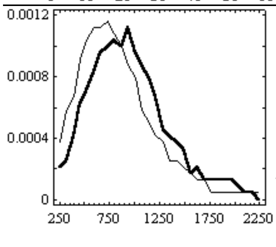
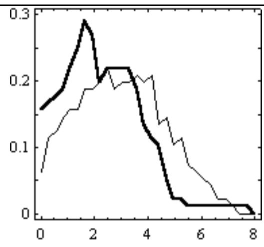
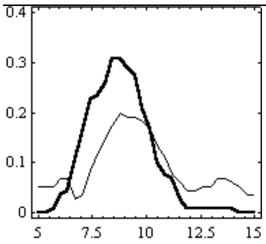
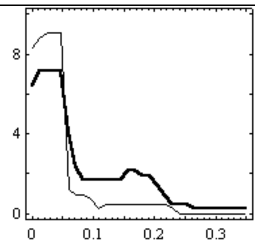
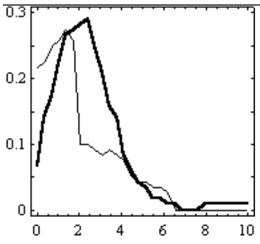
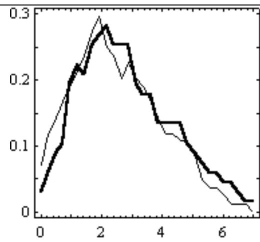
Statistical Analyses

To assess distinctions in statistical distributions of the soil samples due to different hydrologic situations in 2000 and 2001, we carried out three procedures. First, we plotted density traces for each soil variable using 40-point samples (Table 3). The density traces were constructed using an unweighted boxcar method with an interval of 30% of an x-axis width. Second, mean ($\bar{x}$), standard deviation (s), and standard error of the mean ($s_{\bar{x}}$) were determined for each soil variable (Table 3). Third, to estimate whether two distributions of each soil property measured in the wetter and drier soil conditions are different, we applied the Kolmogorov-Smirnov two-sample test (Daniel, 1978) to each soil property (Table 3). According to the Kolmogorov-Smirnov test, if the test statistic $D > D_{0.05}$, one can assume that there is a statistically significant difference between the two distributions at the 95% confidence level. $D_{0.05} = 0.300$ for $n = m = 40$ (Daniel, 1978). To estimate distinctions in the spatial distribution of the soil properties within the plot due to different hydrologic conditions, the coefficient of variation (CV) was determined (Table 3) for each soil variable.

To estimate a topographic representativeness of the plot relative to the entire area of the site (Figure 1), we applied the Kolmogorov-Smirnov two-sample test and plotted density traces for each topographic variable within the plot and site using 40- and 3,193-point samples, correspondingly (Florinsky et al., 2004).

Since A is a circular variable, it cannot be used in linear statistical analysis. The most common approach is to analyse $\sin A$ and $\cos A$ rather than A (King et al., 1999). Since most of soil and topographic attributes are marked by non-normal distributions, we calculated the Spearman rank correlation pairwise coefficients to measure the strength of association between soil environmental and microbial properties (Table 4), and between soil and topographic attributes (Table 5). 40-point samples were used in these analyses.

Table 3. Density traces and statistics for soil attributes in the wetter and drier conditions

Density trace		2000	2001	Density trace		2000	2001
	Gravimetric moisture, %				Bulk density, $g cm^{-3}$		
	min	19.0	9.8		min	1.07	0.87
	max	57.0	52.2		max	1.51	1.41
	av	33.3	23.2		av	1.27	1.13
	s	7.1	7.6		*s*	0.12	0.14
	CV	21	33		CV	9	13
	DN (P)	0.650 (0.00)			DN (P)	0.475 (0.00)	
	Microbial biomass C, $\mu g_C g^{-1}_{soil}$				Denitrifier enzyme activity, $\mu g_N g^{-1}_{soil} h^{-1}$		
	min	316.2	257.0		min	0.58	0.60
	max	1907.2	2053.8		max	6.75	6.24
	av	926.8	803.8		av	2.25	2.92
	s	364.7	361.8		*s*	1.36	1.56
	CV	39	45		CV	60	54
	DN (P)	0.225 (0.26)			DN (P)	0.300 (0.05)	
	Most probable number, $\#_{organisms} g^{-1}_{soil}$				Denitrification rate, $\mu g_N g^{-1}_{soil} h^{-1}$		
	min	1055	140		min	0.00	0.00
	max	293919	3004033		max	0.32	0.18
	av	15305	238778		av	0.06	0.01
	s	45753	631857		*s*	0.08	0.04
	CV	299	265		CV	136	276
	DN (P)	0.325 (0.03)			DN (P)	0.550 (0.00)	
	Respiration rate, $\mu g_{CO2} g^{-1}_{soil} h^{-1}$				N_2O flux, $ng_{N2O} m^{-2} s^{-1}$		
	min	0.27	0.14		min	0	0.92
	max	9.21	5.04		max	643.35	327.64
	av	2.39	1.40		av	41.99	31.51
	s	1.50	1.54		*s*	113.35	58.60
	CV	63	110		CV	270	186
	DN (P)	0.575 (0.00)			DN (P)	0.138 (0.89)	

Heavy and thin lines describe samples collected in 2000 and 2001, correspondingly.

To find models fitting the data on soil microbial properties measured within the plot, the 'best' combinations of predictors (G, sin$A$, cos$A$, k_h, k_v, H, K, k_{min}, k_{max}, K_a, E, K_r, k_{ve}, k_{he}, M, ln(CA), TI, and SI) were chosen by stepwise multiple regression (Seber, 1977) using 40-point samples (Tables 6 and 7). Based on the Kolmogorov-Smirnov and Watson statistics, hypotheses about statistically significant differences in distributions of topographic variables within the plot and site may be rejected for sin$A$, cos$A$, k_h, k_v, H, K, k_{min}, k_{max}, K_a, E, K_r, k_{ve}, k_{he}, and M, whereas may not be rejected for z, G, and CA (Florinsky et al, 2004).

Table 4. Pairwise coefficients of the Spearman rank correlation between indices of soil microbial activity and soil environmental properties in the wetter and drier conditions

Index of soil microbial activity	Soil environmental property			
	Gravimetric moisture		Bulk density	
	2000	2001	2000	2001
Most probable number	0.29	–	-0.32	–
Microbial biomass carbon	0.70	0.65	-0.66	-0.29
Denitrifier enzyme activity	0.53	–	–	–
Denitrification rate	0.36	–	–	–
Microbial respiration rate	0.33	–	–	–
N_2O flux	0.47	–	-0.40	–

n = 40; $P \leq 0.07$ for statistically significant correlations; dashes are statistically non-significant correlations.

Table 5. Rank correlations between soil properties and topographic variables in the wetter and drier conditions

Soil property	Topographic attribute										
	Year	*z*	*G*	sin*A*	k_v	*H*	k_{min}	k_{max}	*CA*	*TI*	*SI*
Gravimetric moisture	2000	-0.51	–	–	-0.60	-0.48	-0.33	-0.43	0.42	0.53	0.34
	2001	-0.50	–	–	-0.37	-0.31	–	-0.33	–	–	–
Bulk density	2000	0.53	0.35	–	0.65	0.57	0.36	0.58	-0.47	-0.65	-0.49
	2001	–	–	–	–	–	–	–	–	–	–
Most probable number	2000	–	-0.41	-0.40	–	–	–	–	–	–	–
	2001	–	–	–	–	–	–	–	–	–	–
Microbial biomass C	2000	-0.48	-0.30	–	-0.39	-0.32	–	-0.33	0.38	0.50	–
	2001	–	–	–	–	–	–	–	–	–	–
Denitrifier enzyme activity	2000	–	–	–	–	–	–	–	–	–	–
	2001	–	–	–	–	–	–	–	–	–	–
Denitrification rate	2000	–	–	–	–	–	–	–	0.52	0.46	0.40
	2001	–	–	–	–	–	–	–	–	–	–
Microbial respiration rate	2000	–	-0.40	–	–	–	–	–	–	–	–
	2001	–	–	–	–	–	–	–	–	–	–
N_2O flux	2000	–	–	–	-0.37	–	–	–	–	–	–
	2001	–	–	–	–	–	–	–	–	–	–

n = 40; $P \leq 0.05$ for statistically significant correlations; dashes are statistically non-significant correlations. There were no significant correlations between soil properties and the following topographic attributes: cosA, k_h, K, K_a, E, K_r, k_{ve}, k_{he}, and M.

Thus, the plot is generally representative of the site for the most topographic attributes, except for *z*, *G*, and *CA*. Indeed, the plot does not include values of *z*, *G*, and *CA* which are typical for bottoms and some slopes of depressions in the northern part of the site (Figure 1a-c). Thus, we derived predictive maps of denitrification rate and microbial biomass carbon of the entire area of the site, except for 'critical' depressions (Figure 2). The maps were obtained using digital models of topographic attributes (Figure 1) inserted into the corresponding regression equations as predictors (Tables 6 and 7).

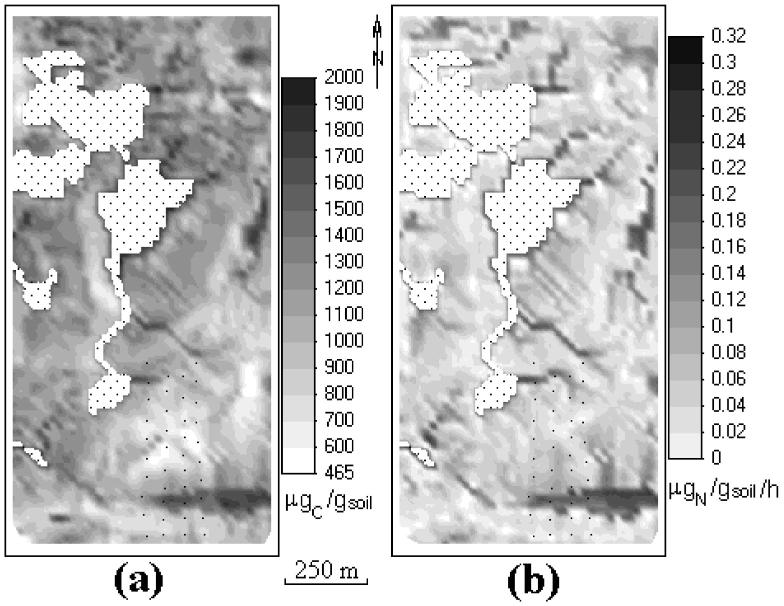


Figure 2. Prediction of the spatial distribution of soil microbial properties: (a) microbial biomass carbon in 2000, (b) denitrification rate in 2000. Points indicate sampling sites. Hatching indicates depressions omitted from the prediction.

Table 6. Parameters and statistics of the regression equation for the microbial biomass carbon in 2000

Predictors		Estimate		Standard error	
Constant		30308.40		14667.70	
z		-50.12		25.05	
G		-109.74		64.17	
sin$A$		-162.89		90.34	
cos$A$		-70.37		69.46	
k_h		1418.17		853.89	
lnCA		165.64		72.51	
Source	Sum of squares	Df	Mean square	F-Ratio	P-Value
Model	2631810.00	6	438634.00	5.66	0.00
Residual	2555750.00	33	77447.10		
Total (Corr.)	5187560.00	39			
R^2		0.51			
Adjusted R^2		0.42			
Standard error of the estimate		278.29			
Mean absolute error		216.56			
Durbin-Watson statistic		2.26			

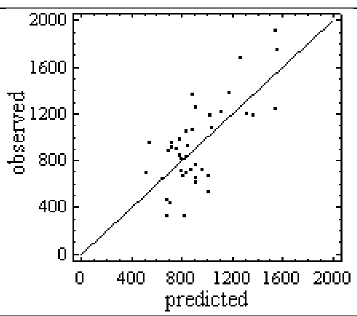
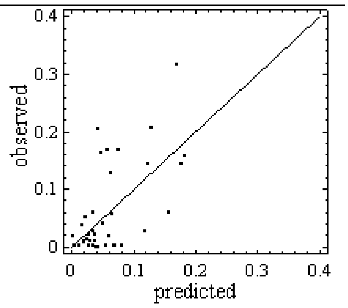


Table 7. Parameters and statistics of the regression equation for the denitrification rate in 2000

Predictors		Estimate		Standard error	
Constant		0.03		0.02	
sin*A*		-0.01		0.02	
cos*A*		-0.02		0.01	
k_v		0.19		0.21	
k_{max}		-0.12		0.26	
ln*CA*		0.06		0.01	
Source	Sum of squares	Df	Mean square	F-Ratio	P-Value
Model	0.10	5	0.02	4.51	0.00
Residual	0.14	34	0.00		
Total (Corr.)	0.24	39			
R^2		0.40			
Adjusted R^2		0.31			
Standard error of the estimate		0.06			
Mean absolute error		0.04			
Durbin-Watson statistic		1.43			



Statistical analysis was carried out by Statgraphics Plus 3.0 (© Statistical Graphics Corp., 1994-1997). Maps of predicted soil microbial properties (Figure 2) were produced by LandLord 4.0 software (Florinsky et al., 1995).

RESULTS

Different rainfall conditions in July 2000 and July 2001 resulted in different levels of soil water in the landscape: the means of soil moisture content in the plot differed by 10% in July 2000 and July 2001 (Table 3). In the wetter and drier soil conditions, there were strong differences in relationships between soil environmental and microbial properties (Table 4) as well as between soil properties and topographic attributes (Table 5).

Wetter Soil Conditions

The correlation analysis demonstrated significant dependence of all soil microbial variables, notably microbial biomass carbon and denitrification enzyme activity, on soil moisture in the wetter soil conditions of July 2000. Microbial biomass carbon, most probable number and N_2O flux also depended on the bulk density (Table 4).

These results are consistent with previous observations of the influence of soil moisture and bulk density on denitrification (Myrold and Tiedje, 1985; Groffman and Tiedje, 1989; Webster and Hopkins, 1996). Indeed, gravimetric moisture content and bulk density are indicative of aeration status in the soil. These parameters also influence the movement of water through soil and thereby the distribution of N and organic C, proximal regulators of denitrification. An increased water content (percent water-filled pores) and/or an increase in bulk density (decreased total porosity) will result in lower air-filled porosity and therefore a greater number of anaerobic sites in the soil, increasing the suitability of the environment to support denitrification. Bulk density influences the ratio of pore sizes and thus for a given water content, soils of lower bulk density will have a greater number of air-filled pores and therefore greater aerobic microbial activity. These trends were reflected in the positive and negative correlations of general soil microbial activity with soil moisture and bulk density, correspondingly, in the wetter soil conditions (Table 4).

There was a relatively strong influence of topography on the spatial distribution of soil moisture for the wetter soil conditions of July 2000 (Table 5). This was expected and supported by interpretations of topographic variables (Table 1) and previous results (Burt and Butcher, 1985; Florinsky and Kuryakova, 2000; Florinsky et al., 2002). Soil moisture was highest where values of k_v were negative (concave profiles), whereas values of *CA* were high. Detailed physical interpretation of these usual trends can be found elsewhere (Florinsky et al., 2002).

Correlations between bulk density and topographic attributes (Table 5) resulted from its dependence on soil moisture, soil texture, and soil organic matter usually distributed according to land surface morphology. Consequently, upslopes are marked by higher values of bulk density than downslopes and depressions within the plot.

A topographic influence on the spatial distribution of the soil organic carbon content, a proximal regulator of denitrification (Myrold and Tiedje, 1985), has been previously demonstrated at this site in the wetter soil conditions using the same sampling grid (Bergstrom et al., 2001b). This was expected and stems from the spatial differentiation of organic matter and moistening according to the land surface morphology (Moore et al., 1993; Arrouays et al., 1998; Florinsky et al., 2002).

All soil microbial properties (except denitrifier enzyme activity), in one way or another, depended on topographic variables in the wetter soil conditions (Tables 5). This was expected, as essential factors for denitrification, such as soil moisture, soil organic C, and bulk density depended on topographic attributes within the plot (see above). Microbial biomass C and denitrification rate depended basically on non-local and combined topographic variables, viz. *CA*, *TI*, and *SI* (Table 5). Microbial biomass C also depended on some local topographic variables, *z*, *G*, k_v, k_{max}, and *H*. N_2O flux was effected by k_v, whereas the number of denitrifiers and microbial respiration rate was influenced by *G* (Table 5). Correlations of soil microbial variables with regional and combined topographic attributes are positive, whereas they are negative with local topographic variables.

Thus, under the wetter soil conditions, spatial variability of the denitrification rate was mostly affected by redistribution and accumulation of soil moisture and soil organic matter due to their gain along a slope from top to bottom, that is, according to relative position of a point in the landscape. However, the N_2O emission was affected by the distribution of other attributes of the environment related to the local geometry of the slope. Both topographic factors of spatial redistribution and accumulation of soil moisture and organic matter influenced the microbial biomass, number of denitrifiers, and microbial respiration. Thus, topographically-controlled and gravity-driven aspects of the system increased the denitrification rate. These observations are consistent with previous observations that 'hot spots' of denitrification are associated with downslope positions (Pennock et al., 1992; Van Kessel et al., 1993; Corre et al., 1996).

Drier Soil Conditions

Based on the Kolmogorov-Smirnov statistics (Table 3), in the drier soil conditions there were marked decreases in soil moisture and bulk density, decreases in denitrification and microbial respiration rates, a slight increase of the number of denitrifiers, and no significant changes in microbial biomass C, denitrification enzyme activity, and N_2O flux (Table 3). Comparisons between the two sampling events demonstrated essential changes in the spatial differentiation of the soil properties. In the drier soil conditions, the CV values shown pronounced increases in variation of soil moisture, denitrification and microbial respiration rates, and a pronounced decrease in variation of the N_2O flux (Table 3). Correlations between indices of soil microbial activity and selected soil environmental properties became statistically insignificant in the drier soil conditions, except for the microbial biomass carbon (Table 4).

We observed a decrease of topographic control of soil moisture in the drier July 2001, while associations of other soil properties with topographic attributes became insignificant (Table 5). It was not surprising that we found different correlations between soil and topographic attributes in the different years for the same area: this demonstrates a phenomenon of the temporal variability in topographic control of dynamic soil properties (Florinsky et al., 2002).

From the observed distribution of denitrification rate, it may be deduced that the denitrifier activity continued to persist under the drier soil conditions, but it was reduced and ceased to depend on the spatial distribution of soil moisture and thus land surface morphology. This likely reflects a transition of some critical level of soil moisture status, and the ability of denitrifiers to be effective aerobic heterotrophs under aerobic conditions. Soil moisture status was still sufficient for the activity of these organisms, but was no longer a dominant force in influencing their spatial patterns.

Regression-Based Prediction

In the wetter soil conditions, regression equations explained 51% of the variability of the microbial biomass carbon, and 40% of the variability of the denitrification rate (Tables 6 and 7). Predictive patterns of the denitrification rate and microbial biomass C (Figure 2) generally resemble the structure of some geomorphometric maps (Figure 1). Standard errors of the estimate (Tables 6 and 7) may be used to assess roughly the accuracy of the prediction outside the plot. We do not present regression equations with R^2 less than 0.35.

DISCUSSION

It is possible to conclude that for topography to control of the distribution of denitrifiers and their activity, the landscape must contain some sufficient amount of soil moisture. Physically this idea seems reasonable as the topographically-controlled gravity-driven lateral transport of substances generally acts through the medium of gravimetric soil water. Different aspects of this lateral transport affect distinct manifestations of the denitrifier population and its activity. Indeed, in the wetter soil conditions, topographically-controlled aspects of the system clearly increased the denitrification rate and denitrifier enzyme activity. Spatial differentiation of the denitrification rate and amount of denitrifying enzyme in the soil occurred according to relative position of a point in the landscape. The N_2O emission was influenced by the local geometry of a slope. The microbial biomass, number of denitrifiers, and microbial respiration were influenced by both topographic factors for spatial redistribution of soil moisture and organic matter. However, in the drier soil conditions, the various measures of denitrifier activity (denitrification rate and denitrifier enzyme activity) were reduced and ceased to depend on the spatial distribution of soil moisture and hence topography, reflecting a transition beyond a critical level of soil moisture status sufficient to allow transient denitrification to occur but not to allow the expression of spatial patterns of the denitrification according to relief.

In the drier soil conditions, the number of denitrifiers continued to depend on topography, while the denitrifier enzyme activity was essentially the same on both sampling dates, ceasing to be affected by relief (Tables 3 and 5). This result reinforces the view that under field conditions there is seldom a direct relationship between the number of denitrifiers and the amount of denitrifying enzyme in the soil (Parsons et al., 1991). This is because of the dual aerobic/anaerobic nature of the ecology and physiology of denitrifiers. The occurrence of denitrifying bacteria in any given habitat is primarily controlled by their ability to compete as heterotrophs rather than ability to denitrify (Groffman and Tiedje, 1989). The expression of denitrifying enzyme, however, is in response to anaerobic conditions and reflects soil aeration status.

The decrease in the denitrification rate without a significant change in the N_2O flux in the drier soil condition demonstrates, that in some situations, these parameters are independent even though denitrification is one of the primary processes producing N_2O. This independence reflects the role of denitrification as both a source and sink for N_2O as well as role of physical factors such as diffusion and solubility of N_2O in the soil profile at very high levels of water-filled porosity in determining the relative amount of N_2O lost to the atmosphere during denitrification. So, although total denitrification ($N_2O + N_2$) is lower in drier soils, the potential for N_2O to diffuse from the site of production, thus preventing further reduction to N_2 is greater because of higher air-filled porosity. This may increase the N_2O/N_2 ratio of the denitrification process and result in N_2O emissions from drier soils of similar magnitude to those from wetter soils (Webster and Hopkins, 1996). The decrease in denitrification rate without a significant change in the N_2O flux suggests that most of the N released was in the form of N_2O in the drier soil condition. This may reflect a greater rate of N_2O diffusion from the site of denitrification because of higher air-filled porosity under the drier condition. This is not always the case however as other researchers have observed that N_2O flux is a function of soil moisture content (van Kessel et al., 1993; Corre et al., 1996).

The lower topographic control of the spatial differentiation of the N_2O emission compared with other soil microbial variables in the wetter soil conditions as well as the disappearance of this control in the drier soil conditions (Table 5) may reflect the high temporal and spatial variability of this attribute (Parsons et al., 1991) plus the nature of N_2O production. Since N_2O production results from both autotrophic, aerobic processes (nitrification) and heterotrophic, anaerobic processes (denitrification) and is merely an intermediate in denitrification, it is not surprising that N_2O production and flux is highly variable and does not always reflect environmental pre-requisites of either of the microbial groups producing this gas.

The results reported here demonstrate no relationship between N_2O flux and landscape. This is in apparent contrast to observations in the Saskatchewan grasslands: Corré et al. (1996) found seasonally sustained associations between the highest rates of N_2O emission and downslopes. One possible explanation for the discrepancy is that the two systems simply behaved differently with respect to role of landscape. Whether due to pedogenic aspects of the site or site management, the processes responsible for N_2O production may have been different at the two sites. The two hydrologic conditions examined here are at the two extremes of the optimal water content for N_2O production of 40–80% water-filled pore spaces (Davidson, 1991).

The hydrologic condition during the 2000 sampling was at the upper end of the optimal region for N_2O production (mean water-filled pore space was 81%). At water-filled pore space ratios of this magnitude there is a shift from N_2O towards N_2 emission. Under the drier condition of 2001, the average water-filled pore space was 46%. In this situation, the primary source of N_2O is nitrification, rather than denitrification. This might explain why the N_2O production was not very different between the two years despite significant differences in water content. This also highlights the challenge in describing unique relationships between N_2O flux and soil environmental parameters.

CONCLUSION

In wetter soil conditions, topographically-controlled and gravity-driven supply of nutritive materials to microbiota increased the denitrification rate. Its spatial differentiation was mostly affected by redistribution and accumulation of soil moisture and soil organic matter down the slope according to relative position of a point in the landscape. The nitrous oxide emission was affected by variation in soil moisture and organic matter due to the local geometry of a slope. The microbial biomass, number of denitrifiers, and microbial respiration depended on both the local geometry of a slope and relative position of a point in the landscape.

In drier soil conditions, although denitrification persisted, it was reduced and did not depend on the spatial distribution of soil moisture and thus land surface morphology. This may result from a reduction in soil moisture below a critical level. This moisture level was sufficient for transient induction of denitrification but not sufficient to preserve spatial patterns of the denitrification according to relief.

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