

Factors Controlling Denitrification in a Chihuahuan Desert Ecosystem

William T. Peterjohn* and William H. Schlesinger

ABSTRACT

Denitrification may be an important pathway for N loss from desert ecosystems. Few studies, however, have investigated the factors limiting this process in a desert environment. A factorial experiment was conducted to determine the factors controlling denitrification in the northern Chihuahuan Desert. Specifically, we measured the response of denitrification to additions of water, C, N, and C + N. Soil cores were collected from four vegetation zones along an alluvial piedmont. Dry cores were subjected to five treatments: (i) water; (ii) water + NO₃; (iii) water + C; (iv) water + NO₃ + C; and (v) a control (no additions). When denitrification rates were averaged across vegetation zones and patch types (between or under vegetation), the following treatment effects were significantly different: water + NO₃ + C >>> water + NO₃ = water >> water + C > control. These results indicate that denitrification at this site is limited by the availability of water. In wet soil cores, C additions immobilized available NO₃ and suppressed denitrification. When water + NO₃ + C was added (C/N = 22), however, denitrification was significantly greater than when water + NO₃ were added. This result indicates that C and N interact to control denitrification in wet desert soils. No evidence for an overall NO₃ limitation in moist cores was found. Surprisingly, denitrification rates in wet cores of nutrient-poor desert soils (≈32.9 ng N cm⁻² h⁻¹) were similar to those measured in the nutrient-rich soils of temperate and tropical forests. When extrapolated to an annual rate, denitrification for this site is 7.22 kg N ha⁻¹ yr⁻¹. Extreme drying-wetting cycles common in desert ecosystems may account for the high rates observed.

ARID AND SEMIARID LANDS occupy about one-third of the terrestrial surface of the earth and appear to be increasing at an estimated rate of 6 million ha yr⁻¹ (Brown et al., 1988). A 17% increase in desert lands may also accompany the climatic changes induced by a doubling of current CO₂ levels in the atmosphere (Emanuel et al., 1985; Manabe and Wetherald, 1986).

Due to their large expanse, arid ecosystems may have a significant impact on global processes (Schlesinger et al., 1990). For example, the high albedo, low evapotranspiration, and dust production of desert soils are thought to have significant effects on the global and local climate. In addition, 30% of the total gaseous emissions of N to the atmosphere from undisturbed terrestrial ecosystems may be derived from arid lands (Bowden, 1986). The loss of N gases such as N₂O and NH₃ from deserts may contribute to the depletion of stratospheric ozone (Cicerone, 1987), the global greenhouse effect (Dickinson and Cicerone, 1986), and the regulation of rainfall acidity (Warneck, 1988).

The loss of N from desert ecosystems also represents a loss of an important component of soil fertility. Desert plants respond to N additions (Sharifi et al., 1988; Fisher et al., 1988; Romney et al., 1978), and have very high N-use efficiencies (Lajtha, 1987). This fact, along with the presence of N-fixing shrubs, supports

the view that N is second only to water as the most important limiting factor in desert ecosystems.

The most important process responsible for the loss of N from desert ecosystems appears to be microbial denitrification. A N budget constructed for Curlew Valley in the Great Basin Desert of Utah suggested that 19 kg N ha⁻¹ yr⁻¹ (≈65% of N inputs) was lost by denitrification (West and Skujins, 1977). Denitrification during an aerobic incubation of Great Basin soil was also responsible for the loss of 75 to 81% of the N fixed by a cryptogamic crust (Skujins and Klubek, 1978) and 79 to 87% of added ¹⁵N-NH₄ (Klubek and Skujins, 1981). Studies in the Sonoran Desert have measured high denitrification rates (11.6 g N ha⁻¹ h⁻¹) from wet soil under the canopy of a N-fixing shrub (Virginia et al., 1982), and a 73 to 97% loss of added inorganic ¹⁵N after 1 yr under field conditions, presumably by denitrification (Westerman and Tucker, 1979).

Despite the apparent importance of denitrification in desert ecosystems, few actual measurements have been made, and only one study has investigated the factors limiting this process in a desert environment (Westerman and Tucker, 1978). Therefore, we performed a factorial experiment to investigate the factors limiting denitrification in a northern Chihuahuan Desert ecosystem. Specifically, we measured the response of denitrification to additions of water, C, N, and C + N.

MATERIALS AND METHODS

Site Description

This study was conducted along the permanent control transect of the Jornada LTER site in the northern Chihuahuan desert 40 km north-northeast of Las Cruces, NM (Fig. 1). The site is in the Jornada Del Muerto Valley of the Basin and Range physiographic province. In this region, parallel, fault block mountain ranges are skirted by alluvial piedmonts, or *bajadas*, that slope into endorheic basins. The basins often contain ephemeral or dry lakes called *playas*.

The permanent control transect of the Jornada LTER site extends northeast for 2700 m from the eastern slope of Mount Summerford to a small playa. The transect parallels the slope of an alluvial bajada and crosses five geomorphic surfaces (Gile et al., 1981; Lajtha and Schlesinger, 1988). The soils along the bajada are derived from the weathered monzonitic bedrock of Mount Summerford and form a chronosequence from younger (≈3040 yr BP) high-elevation soils, to older (≈25 660 yr BP) low-elevation soils (Lajtha and Schlesinger, 1988). Soils near the base of Mount Summerford are Hawkeye (sandy, mixed, thermic Torriorthentic Haplustoll) and Aladdin (coarse-loamy, mixed, thermic Torriorthentic Haplustoll). The mid- and lower-piedmont soils are Dona Ana (fine-loamy, mixed, thermic Typic Haplargid), Onite (coarse-loamy, mixed, thermic Typic Haplargid), Berino (fine-loamy, mixed, thermic Typic Haplargid), and Bucklebar (fine-loamy, mixed, thermic Typic Haplargid), and the playa soil is Dalby (fine, montmorillonitic, thermic Typic Torrtent) (Wierenga et al., 1987; Gile, 1981).

The Jornada LTER site control transect crosses seven vegetation zones (Wierenga et al., 1987). Starting on the rocky slopes of Mount Summerford, the transect crosses a narrow

W.T. Peterjohn, The Ecosystems Center, Marine Biological Lab., Woods Hole, MA 02543; and W.H. Schlesinger, Dep. of Botany and Geology, Duke Univ., Durham, NC 27706. Received 23 July 1990.
*Corresponding author.

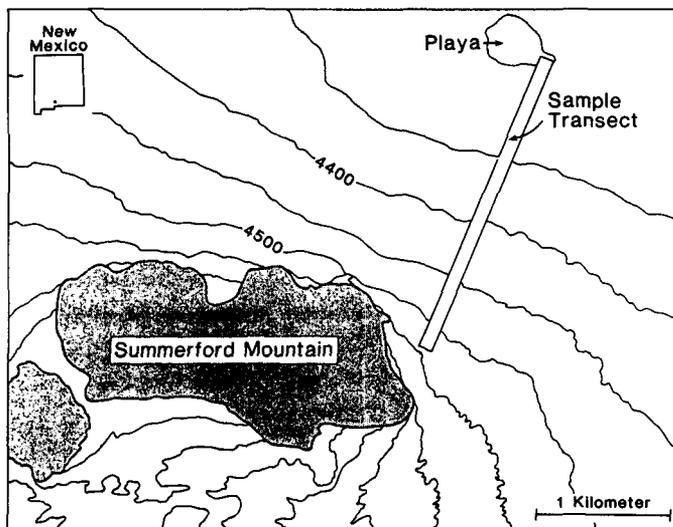


Fig. 1. Location of the study site and sample transect. Contour intervals are 15.24 m (50 ft).

shrubland dominated by turpentine bush (*Ericamera laricifolia* Gray) followed by two upper grassland communities dominated by black gramma (*Bouteloua eriopoda* Torr.) and fluffgrass (*Erioneuron pulchellum* H.B.K.). Downslope, the transect crosses a creosotebush (*Larrea tridentata* DC.) shrubland that grades into a wide lower grassland community dominated by red threeawn [*Aristida purpurea* var. *longiseta* (Steud.)] Finally, the transect crosses a narrow shrubland dominated by honey mesquite (*Prosopis glandulosa* Torr.) and ends in a grassy playa dominated by vine mesquite (*Panicum obtusum* H.B.K.).

The Jornada LTER site has an arid climate. The mean annual rainfall is 230 mm, of which 53% occurs between 1 July and 30 September (U.S. Department of Commerce, 1965). Yearly pan evaporation in nearby Las Cruces, NM, averages 239 cm (Kunkel et al., 1988). The mean annual temperature is 14.8 °C. The highest maximum monthly temperature is 35 °C occurring in July and the lowest is 13.4 °C occurring in December and January (U.S. Department of Commerce, 1965).

Field Sampling Design and Protocol

For this study, we sampled four vegetation zones along the LTER control transect: the upper grassland, creosotebush shrubland, lower grassland, and playa. These zones correspond directly to those identified by Wierenga et al. (1987) except that the two upper grassland communities were combined into one zone. Within each vegetation zone, we collected samples along five equally spaced 100-m transects (Fig. 2). The distance between sample transects was directly proportional to the width of each vegetation zone and so varied between zones. Sample transects were aligned perpendicular to the LTER control transect and were oriented in an east-southeasterly direction. Along each sample transect we collected two intact soil cores at 20-m intervals: one from beneath the nearest patch of the dominant vegetation type (grass clump or creosotebush) and the other from the nearest bare area. An equal number of cores were collected from between and under vegetation in order to examine the spatial variability caused by islands of soil fertility (Barth and Klemmedson, 1978; Charley and West, 1975, 1977). In total, 200 soil cores were collected; 50 were obtained from each vegetation zone (25 under vegetation and 25 between vegetation).

Soil cores were collected over an 8-d period during the dry season by driving 6.35×20 cm coring tubes into the soil

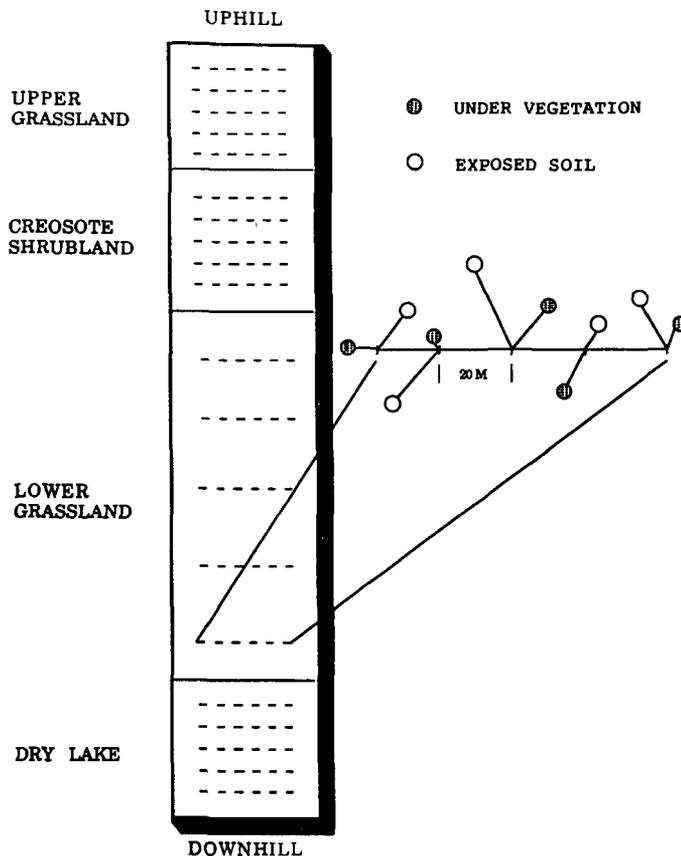


Fig. 2. Sampling design used to collect intact soil cores. Samples were collected at 20-m intervals from under the canopy of the closest patch of dominant vegetation and from the closest patch of exposed soil.

with a sledgehammer. Coring tubes were constructed from schedule 40 polyvinyl chloride pipe that had been perforated with about ≈ 50 2-mm holes. The perforations facilitated gas diffusion (Burton and Beauchamp, 1984) and the large volume of the soil core ensured reliable estimates of natural denitrification rates (Parkin et al., 1987). Coring tubes were fitted with a steel cutting shoe on one end and a steel cap on the other before being driven into the ground. Surface litter was removed prior to sampling. To minimize disturbance to the soil core, the inside diameter of the cutting shoe was slightly less than the coring tube (Swallow et al., 1987). The length of the soil core relative to the length of the coring apparatus was used to determine soil compaction. Compaction ranged from 4 to 7% and appeared to depend on soil texture. After each coring tube was excavated, a plastic lid was placed over each end and the whole core was encased in two layers of undyed nylon stocking material. No rainfall occurred for an extended period prior to the time of sampling, which resulted in soils ranging in moisture content from about 0.01 to 0.08 kg kg⁻¹. Cores were returned to the laboratory on the day of collection and were stored in their dry condition for <10 d.

Laboratory Procedures and Analyses

To determine the factors limiting denitrification in this ecosystem, a factorial experiment using the intact soil cores was conducted in the laboratory. We randomly assigned five replicate soil cores from each vegetation zone and patch type (between and under vegetation) to one of five treatments. The five treatments consisted of: (i) 100 mL of distilled water (equivalent to a 31.5-mm rainstorm); (ii) 100 mL of a so-

lution containing 134.8 mg N L⁻¹ as KNO₃ ($\approx 4 \times$ background NO₃-N levels); (iii) 100 mL of a solution containing 2.94 g C L⁻¹ as dextrose ($\approx 4 \times$ background available-C levels); (iv) 100 mL of a solution containing both C and N in the same amounts used in Treatments 2 and 3 (C/N = 21.8); and (v) a control with no additions to the dry soil.

The experiment was run in four batches, each consisting of the 50 cores from a given vegetation zone. For each batch of samples, all soil cores were allowed to acclimate to treatment conditions for 24 h before denitrification rates were measured.

After sealing the soil cores in airtight chambers constructed of 7.62 \times 21 cm polyvinyl chloride pipe, the denitrification rates were measured using the acetylene block technique (Tiedje et al., 1989; Parkin et al., 1987, 1984; Parkin, 1987). The top of each chamber was fitted with a rubber septum to allow gas samples to be taken. We injected enough CaC₂-generated C₂H₂ into each chamber to achieve a C₂H₂ partial pressure of ≈ 10 kPa. The C₂H₂ was circulated by pumping with a 60-mL syringe, and then an initial 20-mL sample was taken. Following the initial sampling, the remaining overpressure in each chamber was vented through a syringe needle to the atmosphere. After 10 h, 20 mL of N₂ was injected into each chamber, circulated by syringe pumping, and a final sample was taken. The linearity of the denitrification rate was determined for four soil cores by sampling four times during a 10-h period. Gas samples and certified standards of N₂O were stored for later analysis in 12-mL evacuated vials.

After the final gas sample was collected, the headspace volume with the core in place and the mass of each soil core were measured. A subsample of the soil was also taken for water-content determination. The headspace volume of each chamber with the core in place was determined by injecting 50 mL of air and measuring the pressure increase with a pressure transducer (Parkin et al., 1984). The headspace volume was ≈ 450 mL. The percentage of water in the soil samples was determined gravimetrically after drying for > 24 h at 110 °C.

Gas samples were analyzed for N₂O using a Varian 3700 gas chromatograph (Varian Associates, Sunnyvale, CA) equipped with a ⁶³Ni electron-capture detector. The oven temperature was 40 °C, and the carrier gas was 5% methane in Ar flowing at 27 mL min⁻¹. The detector temperature was set at either 210 or 270 °C, depending on the sensitivity required (Hall and Burford, 1976). To achieve compound separation, a 0.9-m stainless steel "stripper" column was connected in series by a 10-port valve to a 1.8-m analytical column. Both columns were packed with Porapak Q (0.15–0.18 mm; Waters Associates, Milford, MA).

Denitrification rates were calculated by multiplying the headspace volume with the core in place by the change in N₂O concentration, and then dividing the result by the time period. Concentrations were corrected for dissolved N₂O (Tiedje, 1982) and for the dilution caused by injecting N before the final samples were taken.

Statistical Analysis

Field measurements of denitrification using intact soil cores are often lognormally distributed (Parkin et al., 1988). Our measurements closely approximated a lognormal distribution so rates were log-transformed before being subjected to a three-way ANOVA, followed by Tukey's multiple comparison of the means.

Negative rates of denitrification were measured in four of the control (dry) cores that were close to the limits of detection (≈ 0.0674 ng N g⁻¹ d⁻¹). To overcome the problems encountered when analyzing lognormally distributed variables containing negative values, three different approaches were used. These included: (i) assigning all negative rates

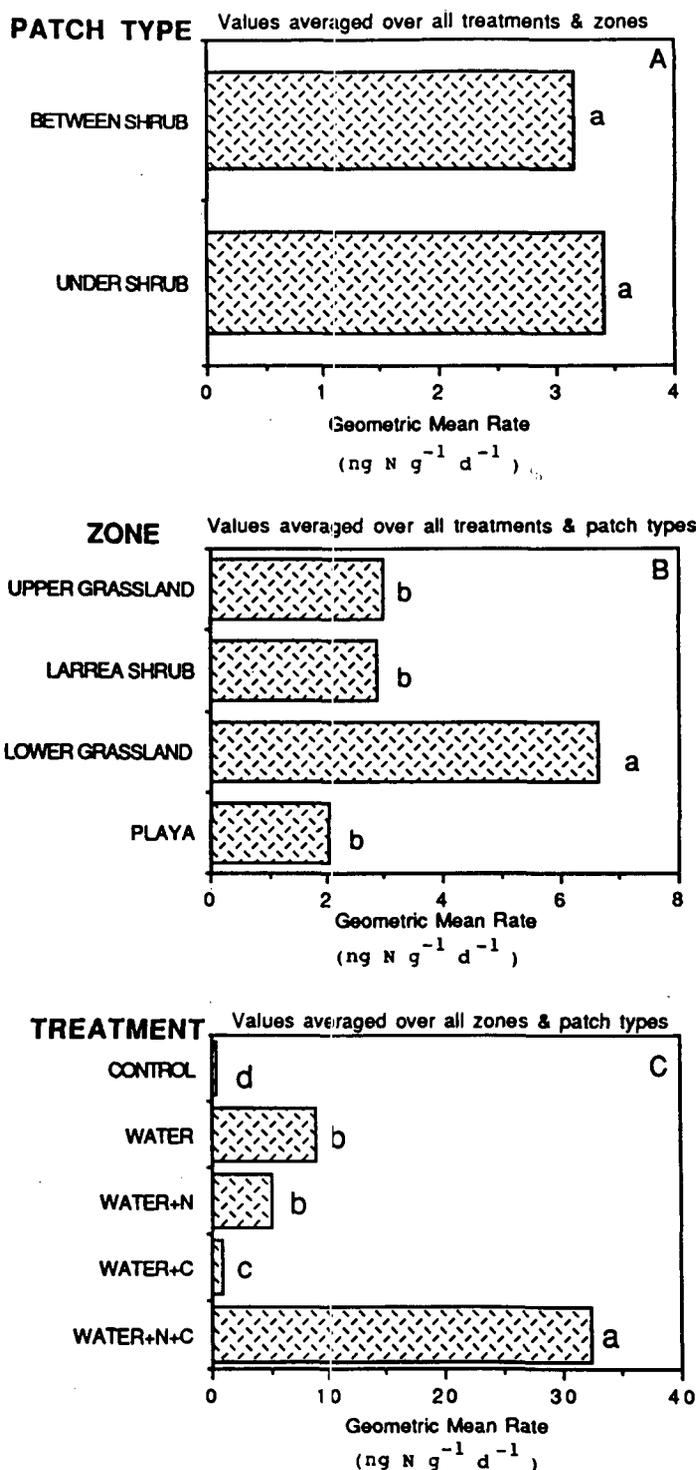


Fig. 3. Main patch type (A), zone (B), and treatment (C) effects from the three-way analysis of variance. Bars with different letters indicate significant differences ($P < 0.05$).

the estimated detection limit; (ii) removing the negative values from the data set; and (iii) adding a constant value to all rates that was sufficient to remove negative values without changing the lognormal character of the distribution (D. Burdick, 1990, personal communication). The ANOVA from all three approaches was similar, so only the first approach will be considered here.

To estimate the population mean for the denitrification

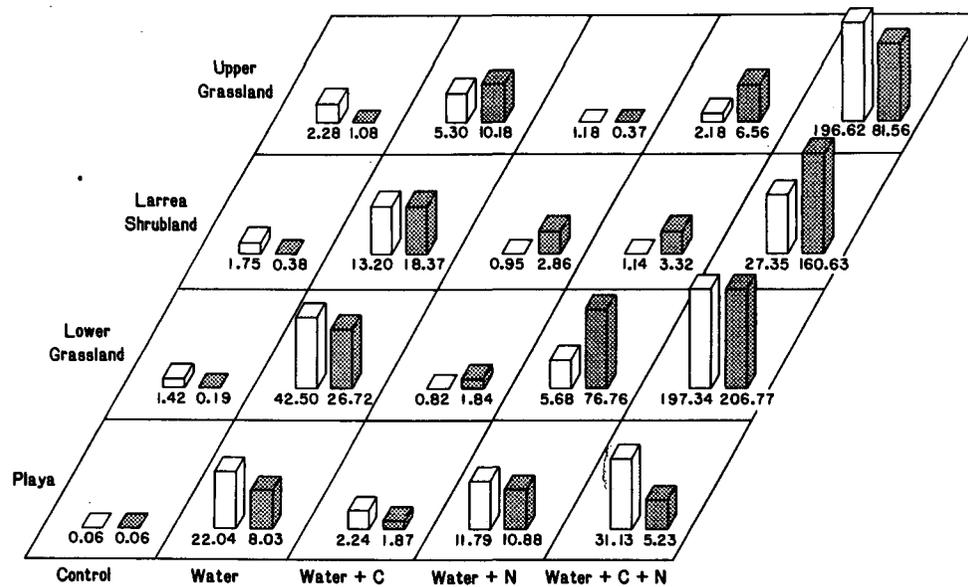


Fig. 4. Arithmetic mean denitrification rates ($\text{ng N g}^{-1} \text{d}^{-1}$) for all treatment-zone-patch type interactions. Bars are scaled logarithmically. Shaded bars are for samples under vegetation and unshaded bars are for samples taken between vegetation.

rates of the untransformed data, we used the uniformly minimum variance unbiased estimator (Gilbert, 1987), which is preferred when the coefficient of variation of the untransformed variable is > 1.0 (Parkin et al., 1988).

RESULTS

The three-way ANOVA revealed that the main treatment and vegetation-zone effects were significant ($P < 0.05$), and that the main patch-type effect (between or under vegetation) was not significant. All two-way interactions in the ANOVA were significant ($P < 0.05$), indicating that the effect of each factor on denitrification depended on the level of the other factors. The three-way interaction term in the ANOVA was not significant. Cores showed relatively linear denitrification rates during the 10-h incubation period, and the average coefficient of determination (r^2) for all four curves were 0.95 (Peterjohn, 1990).

The results for the main effects of the ANOVA are presented in Fig. 3. Geometric means are plotted in this figure because they are the measure of central tendency that is tested when lognormally distributed variables are log-transformed and subjected to ANOVA procedures (Snedecor and Cochran, 1972).

High concentrations of soil nutrients (islands of fertility) are often present under the canopy of desert plants. When denitrification rates were averaged across all treatments and vegetation zones, however, there was no significant difference between the rates measured in different soil patch types (i.e., soil beneath or between the canopy of vegetation; Fig. 3a). To determine if this result was due only to a differential response to the various treatments, a two-way ANOVA was performed using the denitrification rates of soil cores that received only water. This also showed no significant island-of-fertility effect. The effect of patch type depended on the treatment and vegetation zone (Fig. 4). For example, when only the control cores were considered, the mean denitrification rates were lower under vegetation than in the exposed soil be-

tween vegetation. This was not the case for the other treatments.

When denitrification rates were averaged across all treatments and patch types, the rate in the lower grassland was significantly higher than the rates in any of the other vegetation zones (Fig. 3b). When only the soil cores that received water were considered, this effect was still significant ($P < 0.05$). In this case, the geometric mean of the denitrification rates in the lower grassland ($21.55 \text{ ng N g}^{-1} \text{d}^{-1}$) was about twice the mean for the playa samples ($10.39 \text{ ng N g}^{-1} \text{d}^{-1}$), and about four times the geometric mean for both the creosotebush shrubland ($5.56 \text{ ng N g}^{-1} \text{d}^{-1}$) and upper grassland ($5.21 \text{ ng N g}^{-1} \text{d}^{-1}$). The effect of the vegetation zone depended on the treatment and patch type (Fig. 4). For example, soils that received water + C + N had the highest mean denitrification rate in the lower grassland vegetation zone. This pattern, however, was not seen consistently in other treatments.

When denitrification rates were averaged across all vegetation zones and patch types (between or under vegetation), the following treatment effects were significantly different: water + NO_3^- + C $\gg \gg$ water + NO_3^- = water \gg water + C $>$ control (Fig. 3c). The response of denitrification to the different treatments, however, depended on the vegetation zone and the vegetative patch type (Fig. 4). For example, the denitrification rate in the playa decreased or only slightly increased in response to the water + C + N treatment (relative to the water treatment), whereas a large increase in the denitrification rate was observed in all other vegetation zones.

DISCUSSION

The lack of a significant island-of-fertility effect on the rate of denitrification in this desert site was unexpected. Virginia et al. (1982) found a strong island-of-fertility effect for denitrification in a Sonoran Desert site, and Peterjohn (1990) found an island-of-fertility effect for the denitrification enzyme content in wet

soils from the Jornada. The study by Virginia et al. (1982) is probably an extreme case, since the shrub used was a N fixer, honey mesquite, and the differences in enzyme content found by Peterjohn (1990) do not reflect differences that can occur in enzyme activity. The exact reason for the lack of an island-of-fertility effect is unknown. It is likely, however, that the high spatial variability usually associated with field measurements of denitrification masked other differences (Folorunso and Rolston, 1984; Robertson and Tiedje, 1984; Burton and Beauchamp, 1984; Parkin et al., 1985, 1987). For example, when the denitrification rates for cores receiving only water were averaged, the coefficient of variation for the untransformed values was 130.32 and 107.61% for between and under vegetation, respectively.

The highest overall rate of denitrification was found in the lower grassland. It is the widest of the four vegetation zones, and therefore contributes the most to estimates of the denitrification rate for the entire site. It is interesting that the rates in the lower grassland were higher than those measured in the playa. The playa has a substantially higher nutrient and denitrification-enzyme content, and higher rates of potential mineralization and nitrification when compared with the other vegetation zones (Peterjohn, 1990). The differences between the playa and lower grassland may be due to texture-induced differences in soil water potential. The water potential of a soil, rather than the water content, regulates the degree of microbial activity (Skujins, 1984), and the water content required to achieve a typical wet-season water potential (-0.05 MPa) is three times higher in the playa ($\approx 27\%$) than in the lower grassland ($\approx 9\%$; Peterjohn, 1990). Therefore, the standard addition of water that was made to all cores (100mL) resulted in large differences in water availability and microbial activity in these zones.

The main treatment effects reveal several important properties about denitrification at this desert site. First, the control (dry) soil cores had significantly lower rates of denitrification than those that received water. This indicates that denitrification is limited by the availability of water, and that only very low rates can be expected during the dry season. Secondly, the addition of a large amount of available C in addition to water significantly decreased the rate of denitrification when compared with the addition of water alone. This indicates that microbial immobilization of available N caused denitrification to be N-limited in the presence of abundant available C. Laboratory experiments have demonstrated that added C decreases the production of denitrifying enzymes in these soils (Peterjohn, 1990), so it is likely that the decrease observed in the field cores was due to an inhibition of denitrifying enzyme production. Thirdly, no significant difference was found between the rate of denitrification in cores receiving water + N and those receiving water alone. This indicates that denitrification in wet soils is not limited by the availability of NO_3 . Finally, soil cores that received water + C + N had significantly higher rates of denitrification, when averaged across all vegetation zones and patch types, than all other treatments. This indicates that there is

a strong C/N interactive effect that controls the rate of denitrification at this desert site.

To synthesize the results for the main treatment effects, we offer a conceptual model that is consistent with the results of the factorial experiment (Fig. 5). The model relates the denitrification rate to the ratio of available C to available N, and is divided into three regions: (i) a region where the C/N ratio is low and microbial growth and activity is limited by the availability of C; (ii) a region where the C/N ratio is high and microbial growth and activity is limited by N availability; and (iii) a region where neither C or N availability limit microbial growth and activity. In this experiment it appears that denitrification in the wet soil cores was strongly limited by available C. This theory is supported by the lack of any N limitation on denitrification and the observed increase in the denitrification rate when both C and N were added to the soil. The low denitrification rate observed when water + C was added to soil cores was probably due to a N limitation of denitrification caused by vigorous microbial immobilization of available N in the presence of abundant C (i.e., high C/N ratio). The average C/N ratio in these soils is 8.0 (Peterjohn, 1990).

Factors controlling denitrification in Sonoran Desert soils have been investigated in both laboratory and field studies (Westerman and Tucker, 1978, 1979). In a laboratory experiment, soils from three depths were incubated at two temperatures for 5, 10, or 15 d under different combinations of N, C, and moisture contents (Westerman and Tucker 1978). In these experiments, N was added in the form of KNO_3 and available C was added in the form of glucose. The soils were incubated in unsealed containers, allowing them to experience a drying cycle. In these soils, N loss increased 16% when the temperature was increased from 27 to 37 °C, and increased 22% when C was added along with supplementary N, even though the C/N ratio was 150. Immobilization of N was also enhanced by the addition of C. Other factors had little effect on N losses.

In a separate laboratory experiment, Westerman and Tucker (1978) investigated the effect of a range of C/N ratios (10 to 45) on the fate of ^{15}N after 5-d incubations at 37 °C and 8% moisture content. In this experiment, increasing the C/N ratio was found to enhance microbial immobilization of N and decrease the pool of available NO_3 . Surprisingly, however, increasing the C/N ratio did not decrease N loss. This result, and the enhanced N loss from the first experiment when the C/N ratio was 150, contrast strongly with our observations in the Chihuahuan Desert, where additions of C alone always reduced the rate of denitrification.

In a field study conducted by Westerman and Tucker (1979), varying amounts and forms of ^{15}N were added to isolated soil columns either alone or in combination with wheat (*Triticum aestivum* L.) straw. The soil cores were incubated in situ for either 3 or 12 mo. During this experiment, most of the rainfall (32.5 mm) and N loss occurred during about the first 3 mo. This indicates that N loss was closely associated with water availability. Loss of added N varied from 73 to 94% when only inorganic N was added. Additions of wheat

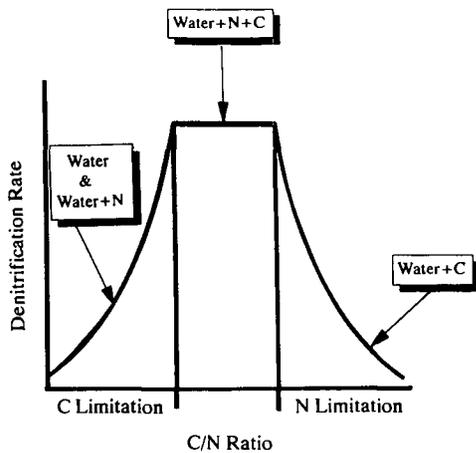


Fig. 5. Conceptual model to explain the main treatment effects of the factorial experiment.

straw lowered N losses due to enhanced immobilization of N. These results are similar to our observations in the Chihuahuan Desert.

Thus, studies in both the Sonoran and Chihuahuan Deserts found that water is an important factor limiting denitrification, and that a C/N interaction appears to have a significant effect on denitrification. The exact nature of this interactive effect varies, however, and may depend on the nature of the soil, C source, and the experimental conditions.

Unlike desert ecosystems, forest ecosystems often have enhanced denitrification rates associated with NO_3 additions (Groffman and Tiedje, 1989; Melillo et al., 1983; Robertson and Tiedje, 1988; Robertson et al., 1987; Davidson and Swank, 1987). Only one study (Davidson and Swank, 1987), however, has experimentally investigated factors other than NO_3 . This study found a strong N limitation and flooding (aeration) effect, and, except in soils with low C and high available N, only a small response to added C. Relative to desert ecosystems, most forest soils have higher C/N ratios (Post et al., 1985). So the limitation of denitrification by the availability of N in forests is in agreement with our conceptual model, and suggests that the model might apply across ecosystems.

In addition to investigating the factors that limit denitrification in a Chihuahuan Desert ecosystem, the results from this factorial experiment were used to compare denitrification rates in different terrestrial ecosystems (Table 1). Although few measurements have been made, it appears that young, aggrading ecosystems and coniferous forests tend to have lower denitrification rates than do recently disturbed forests, mature forests, and desert ecosystems (Groffman and Tiedje, 1989; Robertson and Tiedje, 1984; Robertson et al., 1987; Robertson and Tiedje, 1988; Virginia et al., 1982; this study). It is interesting to note that, when denitrification occurs in desert ecosystems, it takes place at rates comparable to more nutrient rich, temperate ecosystems.

Frequent periods of rapid wetting and drying are typical in desert soils (Parker et al., 1983; Young and Nobel, 1986; Schlesinger et al., 1987) and may account for the high denitrification rates exhibited in relatively nutrient poor desert soils. Freshly wetted soils often

Table 1. Comparison of the range of mean denitrification rates in different terrestrial ecosystems.

Mean Rate	Ecosystem	Conditions	References
ng N cm ⁻² h ⁻¹			
32.9	Chihuahuan Desert	31.5 mm H ₂ O	This study
2.0-116.0	Sonoran Desert	50 mm H ₂ O	Virginia et al., 1982
0.2-3.5	Temperate old field	unamended	Robertson et al., 1988
0.6-115.4	Temperate hardwood forest	unamended	Robertson and Tiedje, 1984 Groffman and Tiedje, 1989
0.7-5.1	Temperate coniferous forest	unamended	Robertson et al., 1987
<4.7-22.2	Tropical rain forest	unamended	Robertson and Tiedje, 1988

Table 2. Weighted average estimate of the annual denitrification rate.

Zone	Rate†	Weighting‡	Rate × weighting factor
	kg N ha ⁻¹ yr ⁻¹		
Upper grassland	2.31	0.1977	0.46
Creosote bush shrubland	4.28	0.1744	0.75
Lower grassland	10.48	0.5465	5.73
Playa	3.47	0.0814	0.28
Weighted average§ = 7.22 kg N ha ⁻¹ yr ⁻¹			

† Uniformly minimum variance unbiased estimates of denitrification rates for cores that received only water.

‡ The relative width of each zone.

§ Calculation assumes a 3-mo wet season and constant denitrification rate.

have high N and C availability (van Screven, 1967; Sorensen, 1974; Kieft et al., 1987) and associated high rates of denitrification (Myers and McGarity, 1971; Patten et al., 1980; Groffmann and Tiedje, 1988). The results from this study apply only to denitrification in freshly wetted soils, but we believe that significant denitrification in desert ecosystems occurs only after rainfall.

ESTIMATED ANNUAL DENITRIFICATION RATE

The annual denitrification rate for the study site was estimated using the weighted average of the universal minimum variance unbiased estimator (Parkin et al., 1988; Gilbert, 1987) for the areal rates of each vegetation zone. Only soil cores that received water were used, and the weighting factor was the relative width of each vegetation zone (Wierenga et al., 1987). Since >50% of the annual precipitation at this site occurs in a 3-mo interval, the value was prorated by the length of the rainy season. The final estimate was 7.22 kg N ha⁻¹ yr⁻¹ (Table 2) and is consistent with a recent estimate of the lower limit for total N loss from the deserts of the southwestern USA (2.32 kg N ha⁻¹ yr⁻¹; Peterjohn and Schlesinger, 1990). Estimated denitrification is about three times the annual dissolved-N inputs to this site (2.84 kg N ha⁻¹ yr⁻¹; Schlesinger, 1990 unpublished data), but the values for N input do not include particulate-N deposition or biological N fixation. Crawford and Gosz (1982) considered 10 kg N ha⁻¹ yr⁻¹ as a reasonable estimate for N input to deserts from all sources, which, if true for the Jornada

site, implies that denitrification losses may account for 70% of N inputs. Thus, denitrification appears to be an important pathway of N loss from this Chihuahuan Desert ecosystem. The actual magnitude and significance of denitrification at this desert site, however, will not be known conclusively until this process has been monitored in the field for several years.

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