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Variables controlling denitrification from earthworm casts and soil in permanent pastures

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Summary. Denitrification (using the acetylene block method) was determined in earthworm casts and soils from permanent, drained or undrained pasture plots fertilized with 0 or 200 kg N ha^{-1} year^{-1} as ammonium nitrate. Rates of N_2O production from soil cores were about three times higher from the fertilized than from the unfertilized plots while drainage had a relatively small effect. Denitrification rates from casts were 3–5 times higher than those from soil irrespective of the drainage treatment. Casts generally had higher NO_3^-, NH_4^+, and moisture contents, and higher microbial respiration rates than soil. Rates of N_2O production were determined primarily by NO_3^- supply, secondarily by moisture; available C did not appear to limit denitrification in these pastures. Estimates of the potential contribution of casts to denitrification ranges from 10.1% of 29.3 kg ha^{-1} year^{-1} from the unfertilized, drained plot to 22% of 82.5 kg ha^{-1} year^{-1} from the fertilized undrained plot.

Key words: Denitrification – Earthworms – Casts – Pasture – Rate determinants – Acetylene blockage technique

Denitrification is an important route of N losses from agricultural systems (Ryden 1986; Scholefield et al. 1988) but the number of rate determinants and the interactions between them have made it very difficult to predict fluxes. The proximate variables regulating denitrification are the availability of labile C and NO_3^- (Myrold and Tiedje 1985; Parkin 1987; Lalisse-Grundman et al. 1988; Van Klemput et al. 1988) and low O_2 tensions or anaerobic conditions (Bremner and Blackmer 1981; Aulakh et al. 1987; Klemedtsson et al. 1988). Indirect, or more distal factors, which affect the development of anaerobic microsites include temperature, organic matter content, soil texture, and rainfall. As the spatial scale of the investigation increases denitrification rates are generally related to these distal factors (Groffman et al. 1988). A major source of variation in flux estimates is the fine spatial scale at which conditions for denitrification may be optimized (Folorunso and Rolston 1984; Christensen and Tiedje 1988). Field estimates of N_2O production usually involve bulking soils to reduce this variation as the location of microsite "hot spots" cannot generally be identified. Earthworm casts, however, have been shown to constitute important microsites for denitrification (Svensson et al. 1986; Knight et al. 1989; Elliott et al. 1990) and hence contribute to the spatial variability of these fluxes from soils. The present paper reports measurements of NO_3^-, moisture, and available C as potential rate determinants of denitrification in casts and soils from permanent pastures. Microbial respiration is used as a measure of available C since Burford and Bremner (1975), Reddy et al. (1982), and Burton and Beauchamp (1985) suggest that it is correlated with water-soluble C. The potential contribution of cast material to denitrification losses from the pastures is also estimated.

Materials and methods

The studies were carried out within the Rowden experimental plots at the Institute for Grassland and Environmental Research (formerly IGAP), North Wyke, Okehampton, Devon. Each plot is hydrologically isolated and is fertilized with 0, 200 or 400 kg N ha^{-1} year^{-1} as ammonium nitrate. A second series of plots, with and without fertilizer treatments, has been drained using mole drains 0.5 m deep and 2 m apart. The soil is a pelostagnogley of the Hallsworth series with an A horizon of approximately 0.3 m depth. Annual rainfall is about 1000 mm and grass growth may continue throughout the winter period since mean soil temperatures rarely fall below 4°C.

Samples were collected from plots fertilized with 0 or 200 kg N ha^{-1} year^{-1} which were undrained or drained. Three areas of 1 m^2 each were pegged out on each of the four plots at the beginning of October 1988 (referred to as the autumn series). At weekly intervals, for a period of 9 weeks, all the surface cast material within these quadrats was collected. Soil cores (15 mm diameter by 50 mm deep) were also taken at random outside the quadrats as controls. A second series of determinations (winter) was made for 8 weeks from January 1989.

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The cast and soil material was returned to the laboratory and the total wet weight of the casts was determined. Aliquots of 5 g casts or soil were weighed into 30-ml serum bottles, taking care to maintain the macro-aggregate structure of the material. The bottles were then fitted with caps which had been drilled so that the butyl rubber seal could be used as an injection septum. C_2H_2 was injected into each bottle to 10 KPa (ca. 10%, v : v) and the samples were incubated at 10°C for 24 h. After incubation the headspace volume of each bottle was sampled and analysed for N_2O using a Pye-Unicam Series 104 gas-liquid chromatograph fitted with a ^{63}Ni electron detector at 300°C. The column (2.2 m) was packed with Poropak Q and maintained at 55°C with the N_2 carrier gas flowing at a rate of 40 ml min^{-1}. After the N_2O analysis was complete, the cast and soil material was dried at 40°C for 48 h to avoid mineral-N losses (Allen et al. 1974) and dry weights and moisture contents were calculated. Estimates of N_2O production were corrected for dissolved N_2O (Moraghan and Buresh 1977) and rates of denitrification were calculated as $\mu g\ N\ g^{-1}$ (dry weight) day^{-1}.

CO_2 production by the cast and soil material during incubation was determined as a measure of available C. A second series of 5 g aliquots was prepared and a vial containing 4 ml 0.1 M KOH was introduced into each serum bottle before it was sealed. Bottles without casts or soil material were used as controls. The bottles were incubated at 25°C for 24 h, after which the vials were removed and titrated against 0.1 M HCl using a capillary microburette (Anderson 1973).

Samples of soil and casts used for N_2O determinations were rehydrated in 1 M KCl and shaken for 1 1/2 h. The solutions were then filtered (Whatman 42 ashless filter paper) and analysed colorimetrically for nitrate and ammonium concentrations (by the sulphanilamide/copper hydrazine and alkaline phenate/nitroprusside methods, respectively) using a Bemas autoanalyser (Burkhard Instruments, UK). Results were expressed as NO_3^--N or NH_4^+-N concentrations ($\mu g\ N\ g^{-1}$ dry weight).

Data for N_2O production were $\log_{10}$ transformed (Parkin and Robinson 1989), and percentage moisture contents were arcsin transformed, to normalize distributions in calculations for analysis of variance, Student's *t*-tests and correlation coefficients. The values for NO_3^--N presented here were obtained by summing the NO_3^--N determined by extraction and N losses through denitrification, in order to give an estimate of initial NO_3^- contents in the cast and soil material.

Results

Mean rates of denitrification for the autumn and winter periods are shown in Fig. 1 A and B, with data given for CO_2 production, NO_3^- and NH_4^+ concentrations, and moisture contents for the autumn period. The general trends were closely similar for both data sets except that the NO_3^- and NH_4^+ concentrations were much lower during the winter period.

N_2O production

Rates of N_2O production were generally three times higher from casts than soil, irrespective of fertilizer treatment, drainage regime or season. Both casts and soil from the fertilized plots produced two to three times more N_2O than samples from the unfertilized plots. Mean rates of denitrification from casts ranged between 0.2 and 0.9 $\mu g\ N\ g^{-1}$ (dry weight) day^{-1} during the autumn period and from 0.3 to 1.1 $\mu g\ N\ g^{-1}$ (dry weight) day^{-1} during the winter period. Mean rates for the soil were 0.05–0.3 $\mu g\ N\ g^{-1}$ (dry weight) day^{-1} during the autumn and 0.1–0.4 $\mu g\ N\ g^{-1}$ (dry weight) day^{-1} during the winter. Denitrification rates in both cast and soil material from both fertilized and unfertilized plots were unaffected by the drainage regimen.

NO_3^- concentrations

NO_3^--N concentrations in the autumn (Fig. 1 C) were two to three times higher in casts than soil in the fertilized, undrained and drained plots. In the drained, unfertilized plot, NO_3^--N concentrations were five times higher in casts than soil although in the unfertilized, undrained plot there were no significant differences between materials. The casts contained similar NO_3^--N concentrations of 3.5–4.0 $\mu g\ N\ g^{-1}$ dry weight in the fertilized, drained and undrained plots, but casts from the undrained, unfertilized plot had significantly lower concentrations ($t = 2.62$, $P = 0.02$) than casts from the drained, unfertilized plot.

Concentrations of NO_3^--N were generally lower during the winter than during the autumn, ranging from 0.29 to 1.11 $\mu g\ N\ g^{-1}$ dry weight in casts and 0.12–0.36 $\mu g\ N\ g^{-1}$ dry weight in soil material. NO_3^- concentrations were significantly higher in cast than soil material from both fertilized plots but not from either unfertilized plot. NO_3^- concentrations were also higher in casts and soil from fertilized plots than from unfertilized plots, except in soil from the undrained, fertilized and unfertilized plots where concentrations were similar.

NH_4^+ concentrations

Concentrations of NH_4^+-N in casts were higher on the unfertilized than the fertilized plots (Fig. 1 D). Soil concentrations were similar for all treatments, except for the fertilized, undrained plot where concentrations were lower. Only casts and soil from the unfertilized, drained plot showed significant differences in NH_4^+ concentrations ($t = 3.88$, $P \leq 0.01$). Mean values ranged between 0.20 and 0.32 $mg\ N\ g^{-1}$ (dry weight).

During the winter period levels of NH_4^+-N were similar in both materials and in all plots. Only the fertilized, drained plot showed any significant difference, with casts containing higher concentrations than soil ($t = 2.74$, $P = 0.01$). Mean values ranged between 0.17 and 0.25 $mg\ N\ g^{-1}$ (dry weight).

Moisture content

Moisture contents during the autumn were significantly higher in casts than soil by 8–10% on the fertilized plots and by about 3% on the unfertilized plots (Fig. 1 E). Casts from the fertilized plots were 2–5% wetter than casts from the unfertilized plots, but the soils showed the reverse trend with higher moisture contents on the unfertilized plots.

During the winter casts material was generally wetter than soil, except on the unfertilized, drained plot where levels were similar. Cast material was significantly wetter ($t = 6.98$, $P \leq 0.001$) on the fertilized, drained plot than on the unfertilized, drained plot. Soil, however, was wetter on the unfertilized, drained plot ($t = 2.88$, $P = 0.007$). There was no significant difference between the moisture contents of soil material on the unfertilized and fertilized, drained plots.

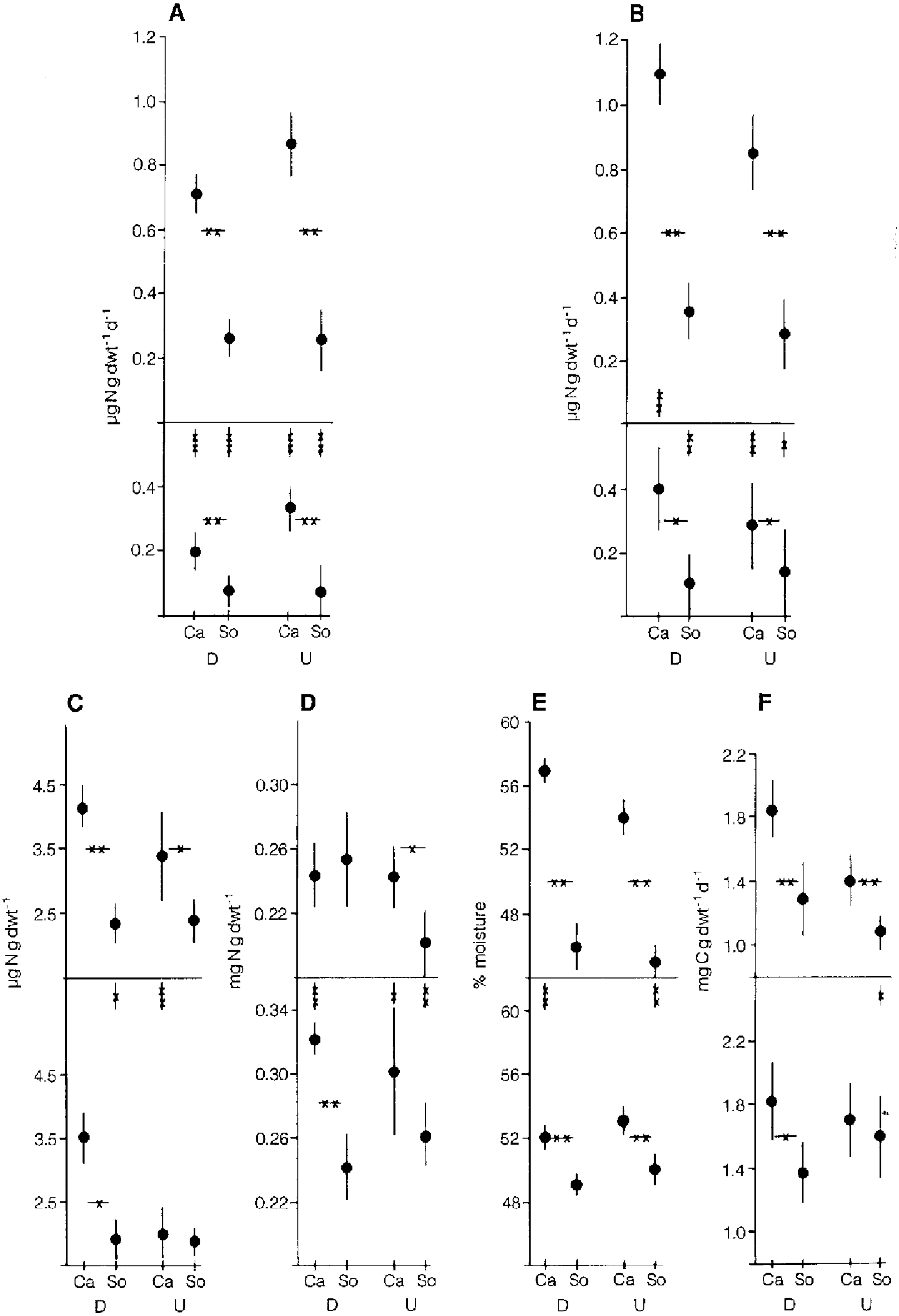

Fig. A–F. Rates of N_2O production from casts (Ca) and soil (So) in pastures during autumn (**A**) and winter (**B**) periods, with values for NO_3^- (**C**) and NH_4^+ (**D**) concentrations, moisture (**E**) and CO_2 efflux (**F**) during the autumn. The pastures were either unfertilized (lower section of each figure) or were fertilized with 200 kg N ha^{-1} year^{-1} (upper section of each figure) and were drained (D) or undrained (U). Statistically significant differences between casts and soil within the same plot are shown or horizontal bars, and differences between the same material in the fertilized and unfertilized plots are shown on vertical bars (* $0.01 < P \leq 0.05$; ** $0.001 < P \leq 0.01$; *** $P \leq 0.001$). Values shown are means ± SE

CO_2

Rates of CO_2 production followed similar trends to the other variables, with higher rates in cast material than soil during the autumn (Fig. 1 F). Only the unfertilized, undrained plot showed little difference between cast and soil material. Data for CO_2 production are not presented for the winter as the trends were similar to those in the autumn and the statistical analysis (see below) showed no significant relationships between CO_2 production and denitrification.

Correlations between denitrification and rate determinants

Correlations between rates of N_2O and CO_2 production, concentrations of mineral-N species, and moisture contents were not significant for soils. Production of N_2O in casts was correlated with NH_4^+ ($r = 0.5$, $P = 0.03$) and the moisture content ($r = 0.5$, $P = 0.03$) on both unfertilized plots, and with NO_3^- on both fertilized plots ($r = 0.6$, $P = 0.01$). On the fertilized and drained plot N_2O production showed a higher correlation ($r = 0.7$, $P \leq 0.01$) with the moisture content. No significant correlation was found between N_2O and CO_2 production.

No correlation was found between N_2O production and NH_4^+-N concentrations for casts over the winter period. N_2O was, however, correlated with NO_3^--N on both drained, fertilized and unfertilized plots ($r = 0.5$, $P = 0.03$) and with moisture on the fertilized, undrained plot ($r = 0.6$, $P = 0.01$).

Relative importance of rate determinants

The results of analyses of variance of main effects (drainage, fertilizer and material) and co-variates (NO_3^--N, CO_2, and moisture) for the autumn data set are shown in Table 1a. The effects of drainage, CO_2, and interactions, with the exception of drainage×material (cast or soil), were not significant. A second analysis of variance excluding non-significant variables (Table 1b) showed that material, moisture content, and the interactions moisture×material were the main determinants of denitrification rates during the autumn.

The same procedure was used for analysis of the winter data set. The results in Table 2a show that only fertilizer, material and NO_3^--N were significant. Further analysis using these variables showed that material and NO_3 regulated denitrification during the winter.

N losses from the pasture by denitrification

Values for potential N losses through denitrification were calculated from mean casting rates and mean N_2O production rates (Table 3). Annual rates of casting were based on observations that earthworms only produce surface casts for about 26 weeks of the year. Extreme weather conditions often prevented casting during the summer and winter months. Denitrification from soil, however, was calculated assuming that N losses potentially occur over the whole year.

The results show that denitrification in soil from the fertilized plots accounted for 41% and 48% of the applied fertilizer for the drained and undrained plots, respectively. Estimates of denitrification rates in cast material ranged from 2.97 – 6.98 kg N ha^{-1} $year^{-1}$ in the unfertilized plots to 10.23 – 18.70 kg ha^{-1} $year^{-1}$ in the fertilized plots, the drained plot representing the lower value in each case. Hence, the contribution from casts to the total fluxes could be as high as 10.1% of 29.3 kg ha^{-1} $year^{-1}$ from the unfertilized, undrained plot to 22.5% of 82.5 kg ha^{-1} $year^{-1}$ from the fertilized, undrained plot.

Discussion

The most striking feature of these results is that mean denitrification rates were three times higher from casts

Table 1. Analysis of variance for factors and co-factors affecting denitrification in earthworm casts and soil over the autumn period

Factor/co-factor	Degrees of freedom	Variance ratio (*F*)	Significance (*P*)
Analysis of main effects and co-variables			
Fertilizer	1	28.51	<0.001
Drainage	1	0.00	NS
Material	1	7.53	NS
Drainage × fertilizer	1	1.57	NS
Fertilizer × material	1	1.23	NS
Drainage × fertilizer × material	1	3.59	NS
NO_3^-	1	4.77	0.03
Moisture	1	3.91	NS
CO_2	1	0.97	NS
Error	90		
Analysis excluding non-significant effects			
Material	1	29.47	<0.001
Moisture	1	8.82	0.004
Material × moisture	1	34.93	<0.001
Error	122		

Table 2. Analysis of variance for factors and co-factors affecting denitrification in earthworm casts and soil over the winter period

Factor/co-factor	Degrees of freedom	Variance ratio (*F*)	Significance (*P*)
Analysis of main effects and co-variables			
Fertilizer	1	39.82	<0.001
Drainage	1	1.30	NS
Material	1	4.81	0.03
Drainage × fertilizer	1	0.53	NS
Drainage × material	1	0.05	NS
Fertilizer × material	1	0.02	NS
Drainage × fertilizer × material	1	0.39	NS
NO_3^-	1	7.92	0.006
Moisture	1	2.34	NS
Error	130		
Analysis excluding non-significant effects			
Fertilizer	1	39.92	<0.001
Material	1	15.02	<0.001
Nitrate	1	8.55	0.004
Fertilizer × material	1	0.25	NS
Error	139		

Table 3. Mean rates of casting and denitrification for a 9-week period in autumn 1988 followed by an 8-week period in winter 1989

	Cast production			Denitrification						
	Daily (g m^{-2} day^{-1})		Annual (t ha^{-1} $year^{-1}$)	Daily (µg N g^{-1} day^{-1})				Annual (kg N ha^{-1} $year^{-1}$)		Total (kg N ha^{-1})
	Autumn	Winter		Autumn		Winter		Cast	Soil	
				Cast	Soil	Cast	Soil			
No fertilizer										
Drained	5.16	5.68	9.89	0.20	0.07	0.40	0.12	2.97	26.35	29.32 (10.1)
Undrained	8.37	7.73	14.69	0.33	0.07	0.29	0.15	6.98	30.51	37.49 (18.6)
200 kg N ha^{-1} $year^{-1}$										
Drained	3.48	8.69	11.37	0.71	0.26	1.10	0.36	10.23	85.99	96.22 (10.6)
Undrained	8.50	15.50	21.50	0.87	0.26	0.86	0.29	18.70	63.80	82.50 (22.5)

Values are calculated for cast turnover per year; estimated annual rates of denitrification are also shown. Soil mass to a depth of 0.1 m was calculated using a mean value for bulk density of 0.76 g cm^{-3}. Values in parentheses indicate percentage contribution of casts to total denitrification

than soil and three times higher from the fertilized than the unfertilized plots.

The main factors accounting for these differences in denitrification rates were NO_3^- availability and moisture content, as shown by other studies in agricultural grassland systems (Myrold and Tiedje 1985; Lalisse-Grundman et al. 1988). Differences between casts and soil can be explained in terms of the ecology of the earthworm species in relation to the main plot treatments.

The experimental plots were permanent pastures which were grazed during the summer months to maintain a constant sward height. On the fertilized plots between five and eight cattle were required to maintain sward height compared with three to six head on the unfertilized plots where grass growth was slower. The effects of these stocking densities are important when considering the quality of the food resources available to the earthworms. Dung coverage of the fertilized plots was calculated as 550 m^2 or 5.5% of the total plot area compared with 360 m^2 or 3.5% of the unfertilized plots (Richards and Wolton 1976) during the growing season. Hence, the effect of the fertilizer was to increase the input of dung as well as to improve the quality and quantity of herbage production. The high input of these resources to the soil may account for the absence of any C limitation to denitrification, in contrast to findings from other studies (Myrold and Tiedje 1985; Wheatley and Williams 1989).

The main species of earthworm casting on the surface of the soil in the North Wyke plots was *Lumbricus rubellus*, which is active in the organic horizons, and *Aporrectodea caliginosa*, which also occurs in mineral soil horizons (Edwards and Lofty 1977). In these soils, however, high water tables in the winter force *A. caliginosa* to the surface horizons (D. Knight, unpublished data). Both species selectively ingest organic matter with *L. rubellus* exploiting less decomposed material such as dung (Bolton and Phillipson 1976). The casts produced by the earthworms are high in labile organic N and C, resulting in higher rates of N and C mineralization relative to the bulk soil (Lunt and Jacobson 1944; Reddy et al. 1982; Syers et al. 1979; Scheu 1987). The generally higher moisture content of the casts and their particular physical properties also results in an greater prevalence of anaerobic conditions and more complete reduction of NO_3^- to N_2 than in the surrounding soil (Elliott et al. 1990).

The results of the present study support the findings of other workers who have identified the variables that directly control denitrification (Groffman et al. 1988) and indicate the relative importance of these variables to denitrification rates from pasture systems. In the autumn the growth of grass slows as the days become shorter. N mineralization in warm soil is then in excess of plant demand and denitrification is determined by water saturation of soil pores. During warm winter and spring conditions in Devon, however, leaching of mineral N by high rainfall, and continued grass growth acting as a sink for slower rates of N mineralization, results in a switch to NO_3^- limitation of denitrification. Earthworms are often active throughout these periods in Devon and we have shown that they influence the spatial heterogeneity of denitrification in a pasture and may make a significant contribution to the total gaseous N losses from these systems. Maximum effects were recorded in the fertilized (200 kg N ha^{-1} $year^{-1}$), where surface casts from worm populations of 173 m^{-2} (Elliott et al. 1990) were estimated to have contributed 22.5% of 82.5 kg N m^{-2} $year^{-1}$ lost through denitrification, a value closely similar to estimates of denitrification losses from this plot of 90 kg N m^{-2} $year^{-1}$ reported by Garwood (1988). The similarity of these independent estimates of total denitrification provides support for our methodology and for the extrapolation of these results to indicate the potential magnitude of earthworm effects on gaseous N losses from these pastures.

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References

Allan SE, Grimshaw HM, Parkinson JA, Quamsby C (1974) Chemical analysis of ecological materials. Blackwell, Oxford

Anderson JM (1973) Carbon dioxide evolution from two temperate deciduous woodland soils. J Appl Ecol 10:361–379

Aulakh MS, Rennie DA, Paul EA (1987) Acetylene and N-serve effects upon nitrous oxide emissions from ammonium and nitrate treated soil under aerobic and anaerobic conditions. Soil Biol Biochem 16:351–356

Bremner JM, Blackmer AM (1981) Terrestrial nitrification as a source of atmospheric nitrous oxide. In: Delwiche CC (ed) Denitrification, nitrification and atmospheric nitrous oxide. Wiley, New York, pp 151–190

Bolton PJ, Phillipson J (1976) Burrowing, feeding, egestion and energy budgets of *Allolobophora rosca* (Savigny) (Lumbricidae). Oecologia (Berlin) 23:225–245

Burford JR, Bremner JM (1975) Relationships between the denitrification capacity of soils and the total water soluble and readily decomposable soil organic matter. Soil Biol Biochem 7:389–394

Burton DL, Beauchamp EG (1985) Denitrification rate relationships with soil parameters in the field. Commun Soil Sci Plant Anal 16:539–549

Christensen S, Tiedje JM (1988) Denitrification in the field: Analysis of spatial and temporal variability. In: Jenkinson DS, Smith K (eds) Nitrogen efficiency in agricultural soils. Elsevier, London, pp 295–305

Edwards CA, Lofty JR (1977) Biology of earthworms. Chapman and Hall, London

Elliott PW, Knight D, Anderson JM (1990) Denitrification from earthworm casts and soil from pastures under different fertilizer and drainage regimes. Soil Biol Biochem 22:601–605

Folorunso DA, Rolston DE (1984) Spatial variability of field measured denitrification gas fluxes. Soil Scx Soc Am J 48:1214–1219

Garwood EA (1988) Water deficiency and excess in grassland: The implications for grass production and for the efficiency of use of N. In: Wilkins RJ (ed) Nitrogen and water use by grassland. AFRC, Hurley, pp 24–41

Groffman PM, Tiedje JM, Robertson GP, Christensen S (1988) Denitrification at different temporal and geographical scales: Proximal and distal controls. Proceedings of Symposium on Advances in Nitrogen Cycling. In: Wilson JR (ed) Commonwealth Agricultural Bureau International, Wallingford, pp 174–192

Klemedtsson L, Svensson BH, Rosswall T (1988) Relationship between soil moisture content and nitrous oxide production during nitrification and denitrification. Biol Fertil Soils 6:106–111

Knight D, Elliott PW, Anderson JM (1989) Effects of earthworms upon transformations and movement of organic matter applied to agricultural soils. In: Hansen JA, Henrikson K (eds) Nitrogen and organic wastes applied to soil. Academic Press, London, pp 59–80

Lalisse-Grundman G, Brunel B, Chalamet A (1988) Denitrification in a cultivated soil: Optimal glucose and nitrate concentrations. Soil Biol Biochem 20:839–844

Lunt HA, Jacobson HGM (1944) The chemical composition of earthworm casts. Soil Sci 58:367–375

Moraghan JT, Buresh R (1977) Correction for dissolved oxide in nitrogen studies. Soil Sci Soc Am J 41:1201–1202

Myrold DD, Tiedje JM (1985) Establishment of denitrification capacity in soil: Effects of carbon, nitrate and water. Soil Biol Biochem 17:819–822

Parkin T (1987) Soil microsites as a source of denitrification variability. Soil Sci Soc Am J 51:1194–1199

Parkin TB, Robinson JA (1989) Stochastic models of soil denitrification. Appl Env Microbiol 55:72–77

Reddy KR, Rao PSC, Jessup RE (1982) The effect of carbon mineralization on denitrification kinetics in mineral and organic soils. Soil Sci Soc Am J 46:62–68

Richards IR, Wolton KM (1976) The spatial distribution of excreta under intensive cattle grazing. J Br Grassl Soc 31:89–92

Ryden JC (1986) Gaseous loss of nitrogen from grassland. In: van der Meer HC, Ryden JC, Ennik GC (eds) Nitrogen fluxes in intensive grassland systems. Martinus Nijoff, The Hague, pp 59–73

Scheu S (1987) Microbial activity and nutrient dynamics in earthworm casts. Biol Fertil Soils 5:230–234

Scholefield D, Garwood EA, Titchen NM (1988) The potential of management practices for reducing losses of nitrogen from grazed pastures. In: Jenkinson DS, Smith K (eds) Nitrogen efficiency in agricultural soils. Elsevier, London, pp 220–230

Svensson BH, Bostrum U, Klemedtsson L (1986) Potential for higher rates of denitrification in earthworm casts than the surrounding soil. Biol Fertil Soils 2:147–149

Syers JK, Sharpley AN, Keeney DR (1979) Cycling of nitrogen by surface casting earthworms in a pasture ecosystem. Soil Biol Biochem 11:181–185

Van Klemput O, Abbound S, Baert L (1988) Denitrification and interactions between its intermediate compounds. In: Jenkinson DS, Smith K (eds) Nitrogen efficiency in agricultural soils. Elsevier, London, pp 302–311

Wheatley RE, Williams BL (1989) Seasonal changes in rates of potential denitrification in poorly drained, reseeded blanket peat. Soil Biol Biochem 21:355–360