

Long term ^{15}N studies in a catena of the shortgrass steppe

J.A. DELGADO¹, A.R. MOSIER¹, D.W. VALENTINE², D.S. SCHIMEL^{2,3}
& W.J. PARTON²

¹USDA, Agricultural Research Service, Fort Collins, CO 80522, USA; ²Natural Resource Ecology Laboratory, Colorado State University, Fort Collins, CO 80523, USA; ³National Center for Atmospheric Research, Boulder, CO 80307, USA

Received 3 February 1995; accepted 13 September 1995

Key words: nitrogen, particulate organic matter, nutrient cycling, grassland

Abstract. A set of long term ^{15}N studies was initiated during the summers of 1981 and 1982 on the backslope and footslope, respectively, of a catena in the shortgrass steppe of northeastern Colorado. Microplots labeled with ^{15}N urea were sampled for ^{15}N and total N content in 1981 and 1982 and again in 1992. In November, 1982, 100% of the added N was recovered in the soil-plant system of the finer-textured footslope, compared to 39% in the coarser-textured backslope microplots. Ten years later, ^{15}N recovery of the applied N decreased at both topographic positions to 85% in the footslope and 29% in the backslope. Average losses since the time of application were $3.5 \text{ g N m}^{-2}\text{yr}^{-1}$ in the backslope and $0.8 \text{ g N m}^{-2}\text{yr}^{-1}$ in the footslope. In 1992, soil organic matter was physically fractionated into particulate (POM) and mineral associated (MAON) fractions and 21-day mineralization incubations were conducted to assess the relative amounts of ^{15}N that were in the slow, passive and active soil organic matter pools, respectively, of the two soils. Our findings confirm the assumptions that POM represents a large portion of the slow organic compartment and that the MAON represents a large fraction of the passive compartment defined in the Century model. The N located in the MAON had the lowest availability for plant uptake. Isotopic data were consistent with textural effects and with the Century model compartmentalization of soil organic N based on the residence time of the organic N.

Introduction

Net primary production in semiarid grasslands is regulated by the availability of moisture and nitrogen (Parton et al. 1987; Sala et al. 1988), but there are few studies of the long term fate of N added to shortgrass steppe. The two ^{15}N pulse-labeling studies that have been conducted in the Colorado shortgrass steppe provide apparently contradictory results. Clark's (1977) low-N addition study indicated that a loamy sand textured grassland soil had a very tight internal N cycle from which little added N was lost over a 5-year period. Schimel et al. (1986), found that approximately 61% of the N added to a sandy loam textured soil (catena backslope) was not recovered in the soil or plants of plots fertilized with ^{15}N -labeled urea a year earlier. In a finer (loam) textured soil (catena, footslope) in the same study, they found no

measurable N loss 4-months after adding urea. These two studies suggest that methodological and soil textural differences may affect our understanding of N dynamics in this system.

Clark (1977) applied a small amount of N, 2.58 g N m^{-2} of KNO_3 , to plots during mid May when blue grama (*Bouteloua gracilis* Lag.) would normally be actively growing. Clark concluded that ^{15}N added to soil and immobilized in plant material during the first growing season is either retained or quickly recycled to the plant in the next several growing seasons. Nitrogen is slowly transferred to soil humus, thus limiting loss of added N. In Clark's study the added N was quickly immobilized and no large pools of additional mineral N persisted in ^{15}N treated soils. Schimel et al. (1986) applied 53.5 g of urea N m^{-2} to the catena backslope in August, 1981, and to the footslope in July, 1982, during times when moisture stress can limit blue grama growth (Monson et al. 1986). Schimel et al. (1986), found high concentrations of mineral N in ^{15}N treated soils, and observed a rapid loss of nitrate (NO_3^-) during the first year following urea additions in the backslope soil. In the finer-textured footslope soil, they recovered all of the urea-N added after 4 months. About 40% of the added N was present in the soil as inorganic N at that time. The Clark (1977) and Schimel et al. (1986) results suggest that a longer-term analysis is needed to determine if losses of added N continued after the added N was incorporated into organic constituents of the catena soil-plant system.

Parton et al. (1987) used the Century model to predict aboveground plant production and soil C and N levels across a range of soil textures in Great Plains grasslands. The Century model assumes that soil organic N is contained in three compartments with different residence times. An active compartment has a turnover time of 1 to 5 years and consists mainly of microbes, microbial products, and organic N. A slow compartment is more resistant to decomposition and has an intermediate turnover time of 20 to 40 years. A third compartment is the passive pool, which is chemically recalcitrant and perhaps also physically protected. The passive compartment has a turnover time of 200 to 1500 years. Part of the active fraction is readily mineralized. An estimate of the N derived from this active fraction, which would include turnover of microbial biomass and easily mineralized soil organic matter, can be made through short term mineralization studies (Clark 1977; Parton et al. 1987).

The slow and passive soil N compartments of soil organic matter can be separated by a physical technique (Cambardella & Elliott 1992). This separation technique divides soil organic matter into particulate organic matter (POM) and a mineral associated soluble fraction (MAON). Cambardella and Elliott found that the N located in the POM is susceptible to losses when

grassland sites were cultivated but the organic N passing through the sieve and associated with the soil mineral particles (MAON) was relatively stable, physically protected, and not affected by cultivation. They suggested that the POM fraction represents a large portion of the slow compartment and the MAON fraction represents a large portion of the passive compartment as conceptualized by Parton et al. (1987).

Fortunately the Schimel et al. (1986) study was designed with enough ^{15}N -fertilized microplots to allow for five samplings at later dates. In this paper, we report the analysis of soil and plants in a set of these ^{15}N treated microplots 10 years after the last set of microplots was analyzed by Schimel et al. (1986) in November, 1982.

In addition to quantifying the total ^{15}N remaining in the soil and plants within the ^{15}N treated microplots, we determined the amount of ^{15}N in two organic matter fractions, as defined by Cambardella & Elliott (1992). We also conducted short-term mineralization studies on soils from the ^{15}N -labeled microplots to determine the amount of ^{15}N in the pools of readily available soil organic N. These analyses show the amount of applied N incorporated into the active, slow and passive soil organic N pools as described by the Century model (Parton et al. 1987).

The objectives of our study were: 1) to determine the amount of ^{15}N that remained in the plant and soil fractions within ^{15}N -fertilized microplots established in 1981 and 1982; and 2) to determine how this ^{15}N was compartmentalized in the POM and MAON and in readily mineralizable organic matter in two catena soils of differing textures.

Materials and methods

Study area

This study was conducted at the U.S. Department of Agriculture/Agricultural Research Service Central Plains Experimental Range (CPER) which is located 56 km north east of Fort Collins, Colorado (Latitude $40^{\circ}48'23''$ N, longitude $104^{\circ}45'15''$ W). In August 1981 and July 1982, ^{15}N studies were initiated on the backslope and footslope, respectively, of a catena. Microplots were made by driving stainless-steel cylinders (10-cm-diameter by 40-cm-long) 38 cm into the ground, inside a cattle exclosure that was established in 1980. These microplots were fertilized with $53.5 \text{ g N-urea m}^{-2}$ (10 atom% ^{15}N). The first set of samples was collected during 1981 and 1982 in the backslope and during 1982 at the footslope (Schimel et al. 1986). Soil properties are presented in Table 1. Detailed soil, vegetation, and initial ^{15}N application and sampling procedures are found in Schimel et al. (1985 & 1986).

Table 1. Properties for surface 15 cm of catena soils¹.

Site	Clay	Organic C	Organic N	N Mineralized "in situ"
	%	$\mu\text{g g}^{-1}$	$\mu\text{g g}^{-1}$	kg N ha y^{-1}
Backslope	15	5700	665	41
Footslope	27	20400	1937	55

¹ Schimel et al., (1985 & 1986).

¹⁵N sampling

In November, 1992, we collected four ¹⁵N-urea-treated and two non-treated (background) microplots from each catena position. Each microplot was excavated and separated into six soil depths, 0–2.5, 2.5–5, 5–7.5, 7.5–10, 10–20, and 20–40 cm. Deep cores were taken for recovery of the added N at depths of 40–60 cm below the soil surface at each slope position. Coarse roots were separated from soils at each depth by sieving through a one-mm screen. Analysis of N and ¹⁵N was performed using a Carlo Erba automated N analyzer coupled to a VG-903 isotope ratio mass spectrometer using Europa Scientific methodology (Burke et al. 1990).

Dynamics of the added N are based on the ¹⁵N-isotope recovery values. Equations used in these calculations follow:

- (1) Recovery of the added N (gNm^{-2}) = (Recovery of ¹⁵N excess (gNm^{-2}) \div ¹⁵N excess of the added N-urea (0.10)).
- (2) Recovery of ¹⁵N excess (gNm^{-2}) = (Total N content \bullet Atom% ¹⁵N excess).
- (3) Atom% ¹⁵N excess = (Atom% ¹⁵N (treated microplot sample) – Atom% ¹⁵N (average 2 non-treated microplots samples) at the specific soil depth increment).

Statistical analyses for the 1992 data were performed using t-tests (TTEST procedure of SAS (SAS Institute 1988). Confidence intervals (95%) were used to test the differences between the recovery of the added N in 1982 and 1992.

Physical fractionation and mineralization of the soil organic N

Physical fractionation of the soil organic matter was conducted as described by Cambardella and Elliott (1992). Ten-gram subsamples of air-dried soils were dispersed in 30 mL of five g L^{-1} sodium hexametaphosphate by shaking for 15 h on a reciprocal shaker. POM was collected on a sieve (53 μm) and

Table 2. Total Nitrogen content recovered¹ in 1982 and 1992 following the addition of 53.5 g N-urea m⁻² (10 atom% ¹⁵N) to a backslope in 1981 and to a footslope in 1982.

Footslope		Backslope	
Month/Year	g N m ⁻²	Month/Year	g N m ⁻²
		1/82	*48.3
		5/82	*44.5
		6/82	*45.0
8/82	*53.5	7/82	*29.0 ^a
11/82	*53.5	11/82	*20.9 ^b
11/92	45.5 ^c	11/92	15.5 ^c

* Schimel et al. (1986)

¹ Recovered N = ¹⁵N recovered ÷ 0.10

^a Less than the 6/82 N recovery ($P < 0.05$)

^b Less than the 7/82 N recovery ($P < 0.05$)

^c Less than the 11/82 N recovery ($P < 0.05$)

rinsed several times with distilled water. The soil slurry passing through the sieve, containing the MAON, was dried in a forced-air oven at 50 °C, weighed, and ground with a mortar and pestle before N and ¹⁵N contents were determined. The N and ¹⁵N in the POM was obtained by difference from the total organic N in the soil: POM = Total Soil Organic N in soil – MAON (Cambardella & Elliott 1992).

Laboratory mineralization studies were conducted to measure the atom% ¹⁵N excess in N mineralized. The N mineralized in this assay is derived from the active soil organic matter compartment described in the Century model (Parton et al. 1987). Air dry soils from each depth increment were moistened to field capacity and incubated aerobically for 21 days at 28 °C in the dark, followed by extraction with 2N KCl. The NO₃⁻ and ammonium (NH₄⁺) contents of the extract were determined colorimetrically by automated flow injection analysis, and ¹⁵N content of each N component was determined by mass spectrometric analysis of diffused extracts (Burke et al. 1990).

Results and discussion

Changes in recovery of the added N, November 1982–November 1992

In November 1982, 39% of the N added in August 1981 was recovered from backslope microplots (Schimel et al. 1985; Table 2). During the following decade the backslope continued losing the added N, but at a decreased rate. In

Table 3. Nitrogen content, atom % ^{15}N excess, and % of the added N that was recovered in different components of the catena footslope and backslope positions in 1992

Compartment	Footslope			Backslope		
	g N m^{-2}	Atom% ^{15}N Excess	% ¹	g N m^{-2}	Atom% ^{15}N Excess	% ¹
Crowns	11	4.13	8	8	1.62	2
Roots	11	2.78	6	7	1.53	2
Shoots	5	2.80	3	2	1.00	1
Litter	8	2.57	4	4	0.93	1
SON ²	1108	0.31	64	754	0.17	24
POM ³	379	0.53	37	200	0.27	10
MAON ⁴	729	0.22	27	554	0.14	14

¹ Amount of N recovered as % of the amount applied (53.5 g N m^{-2}).

² Soil organic N (SON), 0–60 cm; inorganic N was less than 1 mg kg^{-1} . SON = POM + MAON.

³ Particulate Organic Matter (POM), 0–60 cm.

⁴ Organic N associated with the soil mineral particles (MAON), 0–60 cm.

November 1992, ^{15}N recovery was 29% of that added (Table 2). In contrast, in November 1982, no measurable loss of added N was detected in the footslope microplots (Table 2), recovery of the added N in the footslope had decreased to 85% by 1992 (Tables 2 & 3). In November 1982, about 40% of the added N was present as NO_3^- and NH_4^+ . Since no analyses were made on the N-amended microplots during the intervening ten years, we do not know if this mineral N was ever taken up by plants or microbes or if the mineral N was lost from the system via leaching or denitrification. In 1982 6.0 g N m^{-2} of added N was contained in plant material and 33 g N m^{-2} was contained in soil organic matter (Schimel et al. 1986); in 1992 11.2 and 34.2 g N m^{-2} were contained in these fractions, respectively. Average losses since the time of application were greater from the backslope ($3.5 \text{ g N m}^{-2} \text{ y}^{-1}$) than from the footslope ($0.8 \text{ g N m}^{-2} \text{ y}^{-1}$).

During the two weeks following the urea application, 27% of the N applied was lost as NH_3 in the backslope while a 0–2% was loss as NH_3 in the footslope (Schimel et al. 1986). Monitoring $^{15}\text{NO}_3^-$ in the soil profile suggested that at the coarse-textured backslope a significant amount of $^{15}\text{NO}_3^-$ leached below the cylinder and probably moved laterally down slope (Schimel et al. 1986).

Although about one third of the ^{15}N in the soil organic matter was recovered in the top 5 cm of the soil profiles in both catena positions, there was measurable ^{15}N below the microplot cylinders at each position (Table 4). The

Table 4. Total soil organic N (SON), % of soil organic N associated with the soil mineral particles (MAON), and the mean atom% ^{15}N excess ± 1 std of the N in the particulate organic matter (POM) the MAON and the mineralized N (MN) by depth.

Bottom Depth(cm)	SON gNm^{-2}	MAON (%)	SON	MAON	^{15}N atom% excess		MN
					-----	-----	
					Footslope		
2.5	52 \pm 14	43	1.235 \pm 0.085	1.205 \pm 0.084	1.262 \pm 0.112		2.210 \pm 0.318
5.0	67 \pm 5	59	0.666 \pm 0.093	0.574 \pm 0.083	0.812 \pm 0.091		1.594 \pm 0.475
7.5	63 \pm 20	57	0.610 \pm 0.094	0.424 \pm 0.061	0.870 \pm 0.141		1.935 \pm 0.577
10.0	73 \pm 6	60	0.504 \pm 0.099	0.317 \pm 0.052	0.783 \pm 0.175		1.729 \pm 0.460
20.0	239 \pm 23	63	0.352 \pm 0.062	0.219 \pm 0.034	0.598 \pm 0.152		1.652 \pm 0.435
40.0	376 \pm 25	71	0.156 \pm 0.057	0.092 \pm 0.027	0.316 \pm 0.031		1.234 \pm 0.428
60.0	238 \pm 3	71	0.079 \pm 0.001	0.052 \pm 0.020	0.135 \pm 0.015		0.876 \pm 0.595
					Backslope		
2.5	35 \pm 13	61	0.640 \pm 0.095	0.629 \pm 0.135	0.776 \pm 0.391		1.019 \pm 0.156
5.0	39 \pm 4	63	0.501 \pm 0.127	0.496 \pm 0.124	0.512 \pm 0.130		1.099 \pm 0.107
7.5	33 \pm 6	58	0.441 \pm 0.100	0.302 \pm 0.217	0.557 \pm 0.137		1.054 \pm 0.341
10.0	34 \pm 7	73	0.362 \pm 0.069	0.299 \pm 0.079	0.526 \pm 0.063		1.106 \pm 0.359
20.0	134 \pm 18	75	0.225 \pm 0.068	0.167 \pm 0.019	0.438 \pm 0.148		0.854 \pm 0.219
40.0	256 \pm 57	76	0.085 \pm 0.023	0.063 \pm 0.021	0.167 \pm 0.050		0.494 \pm 0.200
60.0	223 \pm 58	73	0.047 \pm 0.009	0.034 \pm 0.006	0.087 \pm 0.021		0.263 \pm 0.048

depth of 40–60 cm contained, 5.4 and 7.6% of the recovered ^{15}N at footslope and backslope positions, respectively. Recovery of ^{15}N below the microplot insertion depth indicates downward transport of part of the surface-applied urea over time. Two possible mechanisms of N transport to this depth are NO_3^- leaching and translocation through plant root systems. We cannot determine the mechanism of movement within the soil profile.

The difference in N recovery between topographic positions may be explained by the difference in soil clay content, rate of N accumulation in organic matter and microbial biomass, and microbial activity (Tables 1 & 3) in the two soils. The clay content of the backslope soil is 15% compared to about 27% in the footslope. Since there is generally a direct relationship between soil clay content and the protection of soil organic matter from microbial mineralization (Paul & Van Veen 1978; Van Veen & Paul 1981; Parton et al. 1987), the turnover of organic matter would be expected to be lower in the footslope soil. Schimel et al. (1985) found that the higher soil carbon content in the footslope reflects the trends in carbon input to the soil which may result in higher N immobilization (Table 1). The amount of added N found in soil organic matter was 11.4 and 33.0 g N m $^{-2}$ in the backslope and footslope soils, respectively, in 1982 compared to 12.8 and 34.2 g N m $^{-2}$, respectively, ten years later. The combined effect of the clay content, rate of N accumulation in the organic matter and microbial biomass, and microbial activity explains the higher recovery in the footslope than in the backslope one decade after N additions (Tables 2, 3 & 4).

The small N losses observed from both catena positions from 1982–1992 may be due to a variety of possible mechanisms. Trace gas studies were conducted in similar positions along the catena during 1981 and 1982, on plots that received N-urea similar to the amount applied to our ^{15}N treated microplots (Mosier et al. 1985; Parton et al. 1988) and were renewed in 1990 (Mosier et al. 1991; Mosier et al. 1994). Microbial activity that generated leaks in the N cycle through emissions of N_2O was increased by large N additions. Higher N_2O emissions were measured one decade after the N was added in both catena positions. Recent studies at another site about one km from our catena showed that N additions 5-years earlier increased N_2O and NO losses in a coarse-textured soil (Scholes et al. 1994). Nitrous oxide losses account for less than 5% of N input from atmospheric deposition, and thus probably a very small fraction of the ^{15}N added in 1982. The losses of NO are larger (Scholes et al. 1994), but insufficient data are available from the site to calculate annual emission rates.

Denitrification and N loss through emission of dinitrogen has probably not played a significant role in ^{15}N measured losses, mainly because these soils generally are not waterlogged (Mosier et al. 1981; Parton et al. 1988;

Clark & Woodmansee 1991). Removal of ^{15}N by small rodents, by wind from the microplot, by leaching of NO_3^- , or by ammonia volatilization from plants were not measured. Losses by these mechanisms are likely to be small, but collectively they may contribute to the observed loss of applied N from the catena during the decade.

Clark (1977) may have found high ^{15}N retention during a four-year period because most of the $2.6 \text{ g } ^{15}\text{N-NO}_3^-$ (80 atom%) applied was rapidly absorbed by plants. The larger amount of N added by Schimel et al. (1986) probably exceeded the capacity of the plant and microbial populations to immediately assimilate the added N, and thus mineral N was susceptible to leaching and other loss processes.

^{15}N in active, slow and passive soil organic matter fractions after a decade of N transformations

Ten and eleven years after adding ^{15}N -labeled urea to catena microplots in footslope and backslope locations, respectively, all components of the soil-plant system in the footslope had higher atom% ^{15}N excess values than those at the backslope ($P < 0.01$; Table 3).

At both sites the plant and litter compartments had a higher atom% ^{15}N excess than the atom% ^{15}N excess of the soil organic N ($P < 0.01$; Table 3). This is consistent with the observation of Clark (1977), who found that added ^{15}N was taken up by plant during the first growing season and retained in the different plant compartments or quickly recycled into new plant growth.

To determine where the N added was located in the organic matter of the soil at the two catena positions with respect to active, slow and passive pools, we conducted a short-term mineralization study and a fractionation study. We estimated the ^{15}N content of the active fraction of the soil organic matter from 21-day mineralizations of soils from each depth increment (Table 4). The atom % ^{15}N excess of mineralized N integrated over the 60-cm soil profile was 1.95 in the footslope and 0.95 in the backslope. The similarity of atom % ^{15}N excess in the active N pool and in the plant component of each location further confirms Clark's conclusions that plant N is derived mainly from plant internal translocation and mineralization of easily decomposable organic materials.

Detrital roots and plant litter form part of the POM. At both sites the POM had a higher ^{15}N enrichment, integrated over the soil profile, than the MAON (Table 3). The ^{15}N enrichment was, however, not different between the POM and MAON in the surface 5 cm of soil from the two slope positions.

At both sites the MAON contained about 70% of the soil organic N but had lower atom% ^{15}N excess than the POM (Table 3). The higher ^{15}N enrichment in the more active POM fraction is indicative of tight N-cycling between plants

and POM. It also shows that N located in the MAON has a low probability of reentering a plant. Otherwise, after a decade of N transformations the atom% ^{15}N excess in the plant compartments would have been lower than we observed.

The descending order of the atom% ^{15}N excess of root > mineralized N > POM > MAON, agreed with the results of Black & Wight (1979), who found that N applications greater than 33 gNm^{-2} in an eastern Montana grassland increased plant biomass production and N uptake, eight years later. They concluded that this residual effect was due to uptake of the mineralized N that came from the initial N immobilized in root material.

Conclusions

The footslope soil showed a higher capacity to assimilate and retain N, as 85% of the added N was recovered after 10 years compared to 29% recovered after 11 years in the backslope ($P < 0.01$). Measured ^{15}N losses, during the last decade, contrast with Clark's, (1977) 100% recovery, but are consistent with losses of ^{15}N measured by Schimel et al. (1986). The ^{15}N enrichment values of the mineralized N > POM > MAON suggest that although microbial processes generate N leaks in the system, they also play an important role in retaining and recycling the added N. Isotopic data in this study are consistent with soil textural effects found at the shortgrass steppe by Schimel et al. (1986) and Parton et al. (1987). The relation between high clay content and high N retention suggests that organically bound N is more stable and better protected in association with the clay fraction.

The ^{15}N recovery and atom% ^{15}N excess values support the conceptual fractionation of soil organic matter devised by Parton et al. (1987) in the Century model. The atom% ^{15}N excess values of the mineralized N > POM > MAON, support the observation that the interaction between the active and slow compartments plays a vital role in recycling N into plants. The POM appears to represent a large portion of the slow organic compartment while the MAON represents a large fraction of the passive pool (Cambardella & Elliott 1992).

Schimel et al. (1986) concluded that the grassland system was either gaining N or was in balance between the N outputs and inputs. Clark's (1977) data suggest that since little N input escapes from the grassland soil, organic N must be accumulating. Over the last decade the loss rates have been higher from a coarse texture than from a finer texture soil. Data from future sampling times at this site should provide additional information about the dynamics of the soil organic N compartments and the balance of N inputs

and outputs in order to further evaluate Schimel et al.'s (1986) and Clark's (1977) conclusions.

Acknowledgements

We thank Mary F. Smith, Susan J. Crookall, and Becky Riggle for their technical assistance. This research was initially supported by the National Science Foundation grant DEB-7906009 and was a contribution from the Shortgrass Steppe Long Term Ecological Research Program (NSF BSR-8114822); recent work was supported by the United States Department of Agriculture, Agricultural Research Service.

References

- Black AL & Wight JR (1979) Range Fertilization: Nitrogen and Phosphorous uptake and recovery over time. *J. Range Manage.* 32: 349–353
- Burke IC, Mosier AR, Porter LK & O'Deen WA (1990) Diffusion of soil extracts for nitrogen and nitrogen-15 analyses by automated combustion/mass spectrometry. *Soil Sci. Soc. Am. J.* 54: 1190–1192
- Cambardella CA & Elliott ET (1992) Particulate soil organic-matter changes across a grassland cultivation sequence. *Soil Sci. Soc. of Am. J.* 56: 777–783
- Clark FE (1977) Internal cycling of ¹⁵Nitrogen in a shortgrass prairie. *Ecology* 58: 1322–1332
- Clark FE & Woodmansee RG (1991) Nutrient Cycling. In: Coupland RT (Ed) *Ecosystems of the World 8A. Natural Grasslands. Introduction and Western Hemisphere* (pp 137–146). Elsevier, New York
- Monson RK, Sackschewsky MR & Williams GJ, III (1986) Field measurements of photosynthesis, water-use efficiency, and growth of *Agropyrum smithii* (C₃) and *Bouteloua gracilis* (C₄) in the Colorado shortgrass steppe. *Oecologia* 68: 400–409
- Mosier AR, Stillwell M, Parton WJ & Woodmansee RG (1981) Nitrous oxide emissions from a native shortgrass prairie. *Soil Sci. Soc. Am. J.* 45: 617–619
- Mosier AR & Parton WJ (1985) Denitrification in a shortgrass prairie: A modeling approach. In: Caldwell DE, Brierly JA & Brierly CL (Eds) *Planetary Ecology. Selected Papers from the Sixth International Symposium on Environmental Biogeochemistry* (pp 441–452) Van Nostrand Reinhold, New York
- Mosier A, Schimel D, Valentine D, Bronson K & Parton W (1991) Methane and nitrous oxide fluxes in native, fertilized and cultivated grasslands. *Nature*. 350: 330–332
- Mosier AR, Delgado JA, Follett RF, Cochran VL, & Valentine DW (1994) Methane and nitrous oxide flux in grasslands in Alaska, Colorado, and Puerto Rico. *EOS Supplement* 75: 151
- Parton WJ, Schimel DS, Cole CV & Ojima DS (1987) Analysis of factors controlling soil organic matter levels in Great Plains grasslands. *Soil Sci. Soc. Am. J.* 51: 1173–1179
- Parton WJ, Mosier AR & Schimel DS (1988) Rates and pathways of nitrous oxide production in a shortgrass steppe. *Biogeochemistry* 6: 45–58
- Paul EA & Van Veen J (1978) The use of tracers to determine the dynamic nature of organic matter. *Trans. Int. Congr. Soil Sci.*, 11th 3: 61–102
- Sala OE, Parton WJ, Joyce LA and Lauenroth WK (1988) Primary production of the central grassland region of the United States. *Ecology* 69: 40–45
- SAS Institute (1988) SAS/STAT user's guide. Version 6.03 ed. SAS Inst., Cary, NC

- Schimel DS, Stillwell MA & Woodmansee RG (1985) Biogeochemistry of C, N, and P in a soil catena of the shortgrass steppe. *Ecology* 66: 276–282
- Schimel DS, Parton WJ, Adamsen FJ, Woodmansee RG, Senft RL & Stillwell MA (1986) The role of cattle in the volatile loss of nitrogen from a shortgrass steppe. *Biogeochemistry* 2: 39–52
- Scholes MC, Martin RE, Mosier AR, Parton WJ & Ojima DS (1994) Water and temperature controls on NO and N₂O fluxes on soils in the Colorado short grass steppe. *EOS Supplement* 75: 151
- Van Veen JA & Paul EA (1981) Organic C dynamics in grassland soils. I. Background information and computer simulation. *Can. J. Soil Sci.* 61: 185–201