

Plant and Soil 202: 125–131, 1998. © 1998 Kluwer Academic Publishers. Printed in the Netherlands.

# Soil nitrogen dynamics in northeastern Patagonia steppe under different precipitation regimes

M.J. Mazzarino<sup>1</sup>, M.B. Bertiller<sup>2</sup>, C. Sain<sup>2</sup>, P. Satti<sup>1</sup> and F. Coronato<sup>2</sup>

<sup>1</sup>Centro Regional Universitario Bariloche (Univ.Nac.Comahue), 8400-Bariloche, Argentina<sup>\*</sup> and <sup>2</sup>Centro Nacional Patagónico (CENPAT-CONICET), 9120-Puerto Madryn, Argentina

Received 1 July 1997. Accepted in revised form 21 April 1998

Key words: arid Patagonia steppe, N mineralization-immobilization, water availability

## Abstract

Small-scale heterogeneity of plant cover and highly variable precipitation events in dry regions can strongly influence N dynamics. We evaluated the differences in N availability (Ni), N mineralization (Nmin), flush of microbial-N (N-MF) and soil moisture (SM) at 0-20 cm depth among four types of patches characteristic of heavily grazed areas in the northeastern Patagonia steppe of Larrea divaricata and Stipa spp. Soil samples were taken monthly during two years of differing annual precipitation (178 mm in 1994 and 325 mm in 1995). Ni and SM were also measured at 20-40 cm depth. Additionally, we estimated the potential N mineralization (pNmin) during two months in both winter and summer in laboratory incubations at 20% soil moisture and 25 °C. Sampled patches included: undisturbed patches of shrubs and perennial grasses (GSP), incipient patches of Larrea divaricata and perennial grasses (IGSP), incipient patches of the perennial grass Stipa tenuis (GP), and bare soil (BS). Mineralization rates were much higher during the wet year, and higher in GSP and IGSP than in GP and BS. The prevailing form of Ni was  $NH_4^+$ –N, but pulses of  $NO_3^-$ –N were measured in field incubations when SM was higher than 10%; NO<sub>3</sub> –N was also the main form of Ni in pNmin assays. Flush of microbial-N depended mainly on plant cover, following the sequence: GSP>IGSP>GP=BS. It was not correlated with soil moisture, except in the GSP patches, and exhibited lower values during the wet year. Available N (as  $NH_4^+$ –N) was higher in the subsurface than in the surface samples during the wet year. The relative importance of N-MF and Nmin as indicators of spatial and temporal changes in N dynamics, and the role of deep-rooted shrubs in the recovery of soil N fertility, are discussed.

#### Introduction

The Patagonian steppe of *Larrea divaricata* and *Stipa* spp. is characterized by 'islands of soil fertility' which have significant effects on the patterns of microbial activity and nutrient availability (Rostagno et al., 1991), as has been often observed in other arid and semiarid regions (e.g. Charley and West, 1977; Schlesinger et al., 1990). We previously found in northeastern Patagonia during a dry year, that (i) available N and flush of microbial-N were greater in the soil beneath undisturbed patches of vegetation than in bare soil interspaces, (ii) recolonization of bare soil by shrubs and

\* FAX No: +54 94422111.

E-mail: mmazzari@crub.uncoma.edu.ar

grasses led to the recovery of the labile-N fraction, and (iii) ammonium dominated the N economy under field conditions, while mineralization proceeded to nitrification under favourable soil moisture in laboratory incubations (Mazzarino et al., 1996). Based on these results, we concluded that the dynamics of soil N varied under different vegetation canopies and was regulated mainly by soil moisture.

Vinton and Burke (1995) suggested that in semiarid ecosystems the presence or absence of plant cover is more important to soil nutrient dynamics than the particular species forming the canopy, because decomposition and nutrient availability are primarily limited by water. As in other arid ecosystems, annual precipitation in northeastern Patagonia, and consequently soil water availability, are highly variable among years (Barros and Rivero, 1982). A strong variation in N dynamics in terms of quantity of mineralizable N and the

years (Fisher et al., 1987). Studies on N dynamics under field conditions in arid environments are scarce and have mostly referred to potential mineralization under controlled conditions or to estimates of microbial biomass N at points in time (Mazzarino et al., 1996). *In situ* studies of N mineralization rates in arid soils are time consuming and difficult to interpret and compare due to the low values usually obtained and to the lack of a standard procedure (Hook and Burke, 1995).

rate of N mineralization may then be expected among

In the present work, we compared the spatial and temporal (intra- and interannual) variations of *in situ* monthly estimates of N availability, mineralization and flush of microbial-N in a heavily grazed steppe characteristic of range conditions in northeastern Patagonia. Our main objectives were to study the changes in soil N dynamics under different types of plant cover during two years with different amount of annual precipitation, and to identify the variables related to such changes.

### Materials and methods

The study site is located in northeastern Patagonia (Argentina), 40 km W from Puerto Madryn (42°39' S, 65°23' W, 115 m.a.s.l.). The average annual temperature is 13.7 °C and the average annual precipitation is 188 mm with high mean inter-annual variations. Soils are a complex of Typic Palaeorthid-Typic Calciorthid with low SOM (0.60-0.74% organic C) and total N contents ranging from 0.08 to 0.10% in the upper 20 cm, the lowest C and N contents corresponding to bare soil, and the highest to undisturbed vegetation patches (Mazzarino et al., 1996). In the upper soil (0-10 cm), coarser texture characterizes the vegetated patches (4-6% clay content vs. 7-8% in bare soil) (Rostagno et al., 1991). The vegetation corresponds to the steppe of Larrea divaricata and Stipa spp. with characteristic patches of perennial grasses and shrubs (GSP), incipient patches of Larrea divaricata with a ring of perennial grasses (IGSP), patches of four or more bunches of the perennial grass Stipa tenuis (GP), and patches of bare soil without vegetation representing 40-60% of the total surface (BS).

The study area was about 2 ha and representative of a heavily grazed *Larrea divaricata* and *Stipa* spp.

steppe; it was excluded from grazing from September 1993. Ten vegetation patches of each type and ten areas of bare soil were randomly selected. Each month, four patches among them were selected randomly for replication, and sampled between January 1994 and February 1996. At each sampling date, soil samples (0–20 cm depth) were taken at the periphery of each vegetation patch and at the center of each area of bare soil.

In situ N mineralization (Nmin) was determined in samples taken with PVC tubes (intact cores), 15 cm high and 5.5 cm diameter, sealed in polyethylene bags, and incubated during 30 d in the field (Binkley et al., 1992). Initial and incubated samples were analyzed for inorganic N ( $NH_4^+$ -N and  $NO_3^-$ -N) in fresh soil samples extracted with 2 *M* KCl. Net Nmin was estimated as the difference between  $NH_4^+$ -N+ $NO_3^-$ -N in the incubated minus the initial samples. Nitrogen availability (Ni) corresponded to the inorganic N content in the initial samples. Soil moisture (SM) was determined gravimetrically.

The flush of microbial-N (N-MF) was assessed using a modification of the chloroform fumigation– incubation technique (Vitousek and Matson, 1985). Liquid chloroform (1 mL) was added directly to 50g fresh soil samples, stirred and left in sealed beakers during 20 h. Afterwards chloroform was removed and samples were incubated at 20% soil moisture (w/w) for 10 d at about 20–25 °C. Samples were extracted with 2 *M* KCl and analyzed for NH<sub>4</sub><sup>+</sup>–N. No attempt was made to express N-MF in terms of microbial biomass, since reported values of recovery factors are extremely variable ( $k_N = 0.41-0.68$ ) depending on the N content of soil microorganisms (Carter and Rennie, 1984; McGill et al., 1986).

Nitrogen availability and SM were also measured at 20–40 cm depth.

In selected months of austral summer (December 1994 and January 1995) and winter (July and August 1995), potential N mineralization (pNmin) was estimated by incubating surface soil samples in the laboratory for 30 d at 25 °C and 20% soil moisture (w/w). In summer of 1997 (February and March), pN-min was again estimated with soil samples from 0–20 and 20–40 cm depth.

Ammonium was analyzed by the indophenol bluemethod (adapting Wiener Lab kits for 'Uremia') and  $NO_3^-$ –N by copperized Cd reduction (Keeney and Nelson, 1982). All results were expressed on the basis of oven-dried (105 °C) soil weight.



*Figure 1.* (a) Monthly precipitation events and soil temperatures at both sampling depths. (b) Soil moisture at 0-20 cm under different patches depths. (c) Soil moisture at 20-40 cm under different patches depths Treatment codes: GSP, border of vegetated patches with perennial grasses and shrubs; IGSP, incipient patches of *Larrea divaricata* and perennial grasses; GP, patches of few bunches of the perennial grass *Stipa tenuis*; BS, bare soil.

Analysis of variance (ANOVA) and Duncan's analysis of significance for P < 0.05 were used to determine significant differences among patches and years. Pearson's correlation coefficients among variables for each patch (CORR) were also calculated (SAS Inst., 1988).

## Results

The amount and intensity of precipitation events varied widely during the sampling period, mean annual precipitation being 178 mm in 1994 and 311 mm in 1995. Soil temperatures were quite similar for both years (Figure 1a). Accordingly, soil moisture (SM) was higher in 1995 than in 1994 at both depths, and significantly higher at 20–40 cm than at the surface (Table 1). During 1995, soil moisture was higher than 6% on 8 dates at 0–20 cm and higher than 9% on 6



*Figure 2. In situ* measurements: (a) mineralized N at 0–20 cm; (b) available N as  $NH_4^+$ –N+ $NO_3^-$ –N at 0–20 cm; (c) available N as  $NH_4^+$ –N+ $NO_3^-$ –N at 20–40 cm and (d) flush of microbial-N at 0–20 cm. Codes as in Figure 1.

dates at 20–40 cm; during 1994, these ranges were only observed on 3 and 2 dates, respectively (Figure 1b, c).

Net N mineralization rates (Nmin) were almost negligible during 1994 and net N immobilization frequently occurred. Values of Nmin were less than 3.5 mg kg<sup>-1</sup> 30 d<sup>-1</sup>. In contrast, frequent pulses of Nmin, ranging from 4 to 8 mg kg<sup>-1</sup> 30 d<sup>-1</sup>, were measured in 1995 in the patches with mixed canopies (GSP = IGSP

*Table 1.* Mean values of soil moisture (SM), available N (Ni), available nitrate ( $NO_3^--N$ ), net N mineralization (Nmin) and flush of microbial N (N- MF) during 1994 and 1995. Common letters indicate no significant differences (P < 0.05): capital letters between years for the same treatment, and small letters among treatments over the same year. Treatment codes: GSP, border of patches with perennial grasses and shrubs; IGSP, incipient patches of *Larrea divaricata* and perennial grasses; GP, patches of perennial grass *Stipa tenuis*; BS, bare soil

Depth 0–20 cm				Depth 20–40 cm				
	SM	Ni	$NO_3^N$	Nmin	N-MF	SM	Ni	$NO_3^N$
Treatments	(%)	$(mg kg^{-1})$	(as % Ni)	$(mg kg^{-1} 30 d^{-1})$	$(mg kg^{-1})$	(%)	$(mg kg^{-1})$	(as % Ni)
January 1994–January 1995								
GSP	4.3 Bb	4.8 Aa	27	0.14 Ba	18.6 Ba	5.9 Ba	2.4 Aa	24
IGSP	4.4 Bab	4.1 Ab	22	-0.05 Ba	15.3 Ab	6.2 Ba	2.3 Ba	20
GP	4.8 Ba	3.6 Ac	19	0.17 Ba	13.2 Ac	6.2 Ba	2.2 Ba	23
BS	4.5 Bab	4.0 Abc	23	0.10 Ba	11.5 Ac	6.0 Ba	2.3 Aa	22
Mean	4.5	4.1	-	0.09	14.7	6.1	2.3	_
January 1995–January 1996								
GSP	5.7 Ab	3.8 Ba	37	1.74 Aa	23.1 Aa	7.5 Ac	2.9 Ab	14
IGSP	5.9 Aab	2.7 Bbc	24	1.74 Aa	13.1 Bb	8.2 Ab	3.3 Aab	8
GP	6.3 Aa	2.5 Bc	30	1.57 Aab	11.4 Bc	8.8 Aa	3.5 Aa	8
BS	6.0 Aab	3.0 Bb	32	0.89 Ab	10.4 Bc	7.9 Abc	3.0 Ab	11
Mean	6.0	3.0	_	1.5	14.5	8.1	3.2	-

 $\geq$  GP  $\geq$  BS) (Table 1, Figure 2a); net immobilization was less frequent than in 1994.

In the surface soil, mean available N, mainly found as  $NH_4^+$ –N, decreased from 4.1 mg kg<sup>-1</sup> in 1994 to 3.0 mg kg<sup>-1</sup> in 1995. The reverse was observed at 20–40 cm depth where values were 2.3 and 3.2 mg kg<sup>-1</sup>, respectively. Available N was significantly higher in the surface soil of GSP than in the other patches (Table 1, Figure 2b, c). Although  $NH_4^+$ –N was the predominant form of Ni under field conditions, two pulses of  $NO_3^-$ – N (6–8 mg kg<sup>-1</sup>) were observed during the wet year within the *in situ* incubation tubes coinciding with SM pulses >10%, and were significantly higher in GSP than in the other patches (Figure 3).

Potential N mineralization in 0–20 cm depth soil was significantly higher in GSP than in the other patches (Tables 2 and 3). At 20–40 cm depth, it varied markedly among patches depending on the date analyzed: in February, pNmin was significantly higher in IGSP and GP and in March in GSP and BS (Table 3).

The flush of microbial-N was significantly different among patches as follows: GSP > IGSP > GP = BSin both years. Significant differences in N-MF were observed between years in all patches. During the wet year, it increased in GSP and decreased in BS, GP and IGSP (Table 1, Figure 2d).



*Figure 3. In situ* measurements: (a)  $NH_4^+$ –N at 30 d; (b) Average soil moisture at 0–20 cm and  $NO_3^-$ –N at 30 d. Codes as in Figure 1.

	Summer		Winter		
	pNmin	$NO_3^N$	pNmin	$NO_3^N$	
Patches	$(mg kg^{-1} 30 d^{-1})$	(%)	$(mg kg^{-1} 30 d^{-1})$	(%)	
GSP	9.2a	91	14.1a	82	
IGSP	7.5ab	94	6.6b	81	
GP	6.4bc	89	5.4b	84	
BS	4.7c	85	5.4b	86	

*Table 2.* Potential N mineralization (pNmin) in samples incubated under favourable laboratory conditions during 30 d, and percentage of Ni as  $NO_3^-$ -N at 30 d. Results correspond to means of December 1994–January 1995 (summer) and July–August 1995 (winter) values

*Table 3.* Potential N mineralization (pNmin) (mg kg<sup>-1</sup> 30 d<sup>-1</sup>) of samples taken in February and March of year 1997 at two depths

	0–20 cm		20–40 cm	
Patches	February	March	February	March
GSP	11.3a	15.6a	2.4b	4.5a
IGSP	6.2b	7.1b	4.0a	2.1b
GP	4.6b	0.9d	4.0a	-0.8c
BS	1.6c	4.9c	1.0c	3.5ab
Mean NO <sub>3</sub> –N (as % of Ni) at 30 d	96	95	94	91
Mean soil moisture (%) at 0 d	8.0	14.5	5.8	15.8

Net Nmin was positively correlated with SM in GSP and IGSP. A significant negative correlation was found between Ni at 0–20 cm and Nmin in all patches, and between Ni at 0–20 cm and SM in GSP. The flush of microbial-N was not significantly correlated with any of these variables (Table 4).

The replicate variability for each variable and sampling date was as follows: 2–30% for SM, 4–40% for N-MF, and 4–60% for Nmin. Only when Nmin was <1 mg kg<sup>-1</sup>, some values were  $\geq$ 80%

## Discussion

In the Patagonia steppe as in other arid ecosystems, net N mineralization depends on water availability. While almost negligible during the dry year, it showed several significantly higher pulses in all treatments during the wet year. However, significant correlations with soil moisture were only found in the vegetated patches with mixed canopies, i.e. undisturbed patches (GSP) and incipient patches of *Larrea divaricata* (IGSP). In both years, available N was mainly in the form of ammonium-N, but nitrate-N increased during field incubations when soil moisture was higher than 10%. This confirms previous suggestions of Kovda et al. (1979) that nitrification is inhibited when soil moisture is <10%. In laboratory incubations, under favourable temperature and soil moisture conditions, mineralization was higher than in the field and proceeded to nitrification. Rates of *in situ* N mineralization (Nmin) also depended on the quality and/or quantity of the mineralizable substrate. Both under field and laboratory conditions, the highest rates corresponded to the undisturbed patches with mixed canopies (GSP).

An indicator of substrate quality is given by the microbial-N, considered as a regulator of N dynamics in arid and mesic environments (e.g., Garcia and Rice, 1994; Robertson et al., 1988). Microbial biomass acts as a sink and source of nutrients and represents the chief component of the active soil organic matter pool (McGill et al., 1986). As a sink, microbial biomass constitutes a mechanism of conserving N, reducing losses by leaching or denitrification (Garcia and Rice, 1994; Vitousek and Matson, 1985). However, N retained in the microbial biomass occurs in labile, i.e. easily mineralizable, forms. In arid-semiarid environments, microbial mortality during a dry period may account for 40% or more of the gross Nmin produced during subsequent wet periods (Bernhard-Reversat, 1982; Mazzarino et al., 1991).

Microbial biomass-N levels depend mainly on carbon sources which are usually limiting in aridsemiarid ecosystems (Gallardo and Schlesinger, 1992; Mazzarino et al., 1991; West and Skujins, 1978), and are obviously higher under vegetated patches. Shortterm fluctuations of microbial-N are associated with

Variables	GSP	IGSP	GP	BS
Nmin/Ni <sub>0-20</sub>	-0.47*	-0.53**	-0.53**	-0.64***
Nmin/ SM <sub>0-20</sub>	0.65***	0.39*	0.25 n.s.	0.12 n.s.
Ni <sub>0-20</sub> /SM <sub>0-20</sub>	-0.49**	-0.31 n.s.	-0.31 n.s.	–0.11 n.s.
N-MF/Nmin	0.20 n.s.	0.08 n.s.	0.10 n.s.	0.29 n.s.
N-MF/ Ni <sub>0-20</sub>	-0.01 n.s.	0.23 n.s.	-0.06 n.s.	-0.20 n.s.
N-MF/ $SM_{0-20}$	-0.13 n.s.	-0.09 n.s.	0.06 n.s.	-0.12 n.s.

*Table 4.* Pearson's correlation coefficients among variables for each treatment. Asterisks indicate significant correlation between the two variables at 0.05 (\*), 0.01 (\*\*) and 0.001 (\*\*\*) probability levels; n.s., not significant. Treatment codes as in Table 1

litterfall, the translocation of N and carbohydrates from above- to below-ground organs, and mainly with root responses to drying-rewetting cycles (Abbadie et al., 1992; Garcia and Rice, 1994). In the present work, the flush of microbial-N (N-MF) was higher in GSP during both years, but differences widened during the wet year due to the increase in GSP and the decrease in all other patches. Considering N-MF as an indicator of both the pool of labile N and of a mechanism to conserve N, our results suggest that in periods of higher microbial activity (higher Nmin), this pool/mechanism was increased in the GSP soil, but could not be maintained in all other patches. Whereas, Nmin was dependent on water availability, N-MF remained relatively constant, even during the dry year, and was not correlated significantly with soil moisture content. This implies that microorganisms were capable of surviving dry periods of short duration, although there was a decrease in their activity (Mazzarino et al., 1991).

Mean values of N-MF were higher in the incipient patches of *Larrea divaricata* and perennial grasses (IGSP) than in the small grass patches (GP) and bare soil (BS), suggesting that shrub recolonization leads to a progressive recover of soil N fertility. As reported elsewhere, microbial-N (or N-MF) appears to be a good indicator of the spatial variation of the active soil organic matter pool (Garcia and Rice, 1994; Lynch and Panting, 1982; Ocio et al., 1991). As such, it might be used as an indicator of the magnitude of desertification in northeastern Patagonia, but requires further testing at sites under different intensities of disturbance. However, N-MF can not be used to assess temporal changes of N dynamics, for which Nmin represents a more reliable indicator.

Results on available N dynamics indicate a consistent pattern of accretion of Ni at 20-40 cm depth during the wet year. Leaching of available N from the surface is unlikely, since the main Ni form accumulated was  $NH_4^+$ –N. This would imply that N mineralization actually occurred at 20–40 cm, despite having been reported to be very low in arid-semiarid ecosystems (Bolton et al., 1990; Soudi et al., 1990). Our results indicate that Ni production under favourable conditions may range from 1 to 5 mg kg<sup>-1</sup> 30 d<sup>-1</sup> at 20–40 cm; these values represent a considerable amount of N when compared to the overall low values found in this ecosystem.

We concluded that in the NE Patagonian steppe: (i) rates of N mineralization increase during wet years in all patch types, but the flush of microbial-N, considered as an indicator of the labile-N pool and as a mechanism to conserve N, increases only in the undisturbed patches of vegetation, and (ii) the accumulation of available N and high water availability at depth would represent an advantage for deep-rooted shrubs. Compared to grasses, this could explain the faster recover of soil fertility under shrubs, confirming previous suggestions for arid Patagonia ecosystems by Bertiller et al. (1991) and Sala et al. (1989).

## Acknowledgement

We would like to thank F Laos and L Roselli for their helpful comments and assistance in the laboratory, and J Ares for manuscript revision. We also gratefully thank Wiener Lab. for providing the 'Uremia' kits. This research was funded by PID-CONICET 3112/92.

## References

- Abbadie L, Mariotti A and Menaut J C 1992 Independence of savanna grasses from soil organic matter for their nitrogen supply. Ecology 73, 608–613.
- Barros V and Rivero M 1982 Mapas de probabilidad de la precipitación en la Provincia del Chubut, Centro Nacional Patagónico (CONICET), Puerto Madryn s/n.
- Bernhard-Reversat F 1982 Biochemical cycle of nitrogen in a semiarid savanna. Oikos 38, 321–332.
- Bertiller M B, Beeskow A M and Coronato F 1991 Seasonal environmental variation and plant phenology in arid Patagonia (Argentina). J. Arid Environ. 21, 1–11.
- Binkley D, Bell R and Sollins P 1992 Comparison of methods for estimating soil N transformation in adjacent conifer and alderconifer forests. Can. J. For. Res. 22, 858–863.
- Bolton H Jr, Smith J L and Wildung R E 1990 Nitrogen mineralization potentials of shrub-steppe soils with different disturbance histories. Soil Sci. Soc. Am. J. 54, 887–891.
- Carter M R and Rennie D A 1984 Dynamics of soil microbial N under cero and shallow tillage for spring wheat, using 15 urea. Plant Soil 76, 157–164.
- Charley J L and West N E 1977 Micropatterns of N-mineralization activity in soils of some shrub dominated semidesert ecosystems of Utah. Soil. Biol. Biochem. 9, 357–365.
- Fisher F M, Parker L W, Anderson J P and Whitford W G 1987 Nitrogen mineralization in a desert soil: Interacting effects of soil moisture and nitrogen fertilizer. Soil Sci. Soc. Am. J. 51, 1033– 1041.
- Gallardo A and Schlesinger W H 1992 Carbon and nitrogen limitations of soil microbial biomass in desert ecosystems. Biogeochemistry 18, 1–17.
- Garcia F O and Rice C W 1994 Microbial biomass dynamics in tallgrass prairie. Soil Sci. Soc. Am. J. 58, 816–823.
- Hook P B and Burke I C 1995 Evaluation of methods for estimation of net nitrogen mineralization in semiarid grasslands. Soil Sci. Soc. Am. J. 59, 831–837.
- Keeney D R and Nelson D W 1982 Nitrogen-Inorganic Forms. In Methods of Soil Analysis. Part 2. 2nd edn. Series Agronomy 9. Eds. A L Page, R H Miller and D R Keeney. pp 643–698. ASA, SSSA, Madison, Wisconsin.
- Kovda V A, Samailova E M, Charley J L and Skujins J J 1979 Soil processes in arid lands. *In* Arid-Land Ecosystems. Vol. I. Eds. D W Goodall, R A Perry and K M W Howes. pp 439–470. Cambridge University Press, UK.

131

- Lynch J M and Panting L M 1982 Effects of season, cultivation and nitrogen fertilizer on the size of the soil microbial biomass. J. Sci. Food Agric. 33, 249–252.
- Mazzarino M J, Bertiller M B, Sain C L, Laos F and Coronato F R 1996 Spatial patterns of nitrogen availability, mineralization and immobilization in northeastern Patagonia (Argentina). Arid Soil Res. Rehab. 10, 295–309.
- Mazzarino M J, Oliva L, Abril A and Acosta M 1991 Factors affecting nitrogen dynamics in a semiarid woodland (Dry Chaco, Argentina). Plant Soil 138, 85–98.
- McGill W B, Cannon K R, Robertson J A and Cook F D 1986 Dynamics of soil microbial biomass and water-soluble organic C in Breton L after 50 years of cropping to two rotations. Can. J. Soil Sci. 66, 1–19.
- Ocio J A, Brookes P C and Jenkinson D C 1991 Field incorporation of straw and its effects on soil microbial biomass and soil inorganic N. Soil Biol. Biochem. 23, 171–176.
- Robertson G P, Huston M A, Evans F C and Tiedje J M 1988 Spatial variability in a successional plant community: patterns of nitrogen availability. Ecology 69, 1517–1524.
- Rostagno C M, del Valle H H and Videla L 1991 The influence of shrubs on some chemical and physical properties of an aridic soil in north-eastern Patagonia, Argentina. J Arid Environ. 20, 179–188.
- Sala O E, Golluscio R A, Lauenroth W K and Soriano A 1989 Resource partitioning between shrubs and grasses in the Patagonian steppe. Oecologia 81, 501–505.
- SAS Inst. 1988 SAS/STAT User's Guide, Release 6.03 ed. SAS Institute Inc., Cary, NC.
- Schlesinger W H, Reynolds J F, Cunningham G L, Huenneke L F, Jarrell W M, Virginia R A and Whitford W G 1990 Biological feedbacks in global desertification. Science 247, 1043–1048.
- Soudi B, Sbai A and Chiang C N 1990 Nitrogen mineralization in semiarid soils of Morocco: Rate constant variation with depth. Soil Sci. Soc. Am. J. 54, 756–761.
- Vinton M A and Burke I C 1995 Interactions between individual plant species and soil nutrient status in shortgrass steppe. Ecology 76, 1116–1133.
- Vitousek P M and Matson P A 1985 Disturbance, N-availability and N-losses: An experimental study in an intensively managed loblolly pine plantation. Ecology 66, 1360–1376.
- West N E and Skujins J J 1978 Nitrogen in Desert Ecosystems. US/IBP Synthesis Ser. 9. Dowden, Hutchinson and Ross, Stroudsburg, PA.

Section editor: S Recous