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A large nitrogen supply from the stable mineral-associated soil organic matter fraction

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Abstract

Soil organic matter (SOM) mineralization and nitrogen (N) release are key biogeochemical processes for which the relative contribution of particulate (POM) and mineral-associated organic matter (MAOM) fractions is poorly understood. MAOM is generally considered to be a more stable fraction that contains most of the soil organic N, whereas POM is more readily decomposable and contains less N. Here, we measured variations in the potentially mineralizable N from each SOM fraction across three contrasting land-uses (forest, pasture, and croplands) and two different grazing managements (rotational and continuous grazing). Contrary to expectations, we found that the MAOM fraction consistently supplied more N than the POM fraction during SOM mineralization in all land-uses evaluated. Across our environmental gradient, potentially mineralizable N from POM increased with the carbon (C) concentration and C/N ratio of POM, while potentially mineralizable N from MAOM increased with the C concentration of MAOM but decreased with clay content. Our work suggests that MAOM contributions to short-term N mineralization and N supply to plants have been undervalued.

Keywords Particulate organic matter · Land-use change · Nutrient cycling

Introduction

Soil carbon (C) sequestration is claimed to be a relevant nature-based strategy for climate change mitigation (Griscom et al. 2017). However, soil C sequestration strategies should avoid excessive nitrogen (N) levels that may generate local contamination (Cotrufo et al. 2019). This requires well-substantiated knowledge about soil organic C and N cycling in natural (forests and grasslands) and transformed ecosystems (croplands and pastures). However, the processes governing soil organic matter cycling are still not well-understood (Yu et al. 2022; Börger et al. 2022). Separating soil organic matter into particulate organic matter (POM) and mineral-associated organic matter (MAOM) is fundamental for understanding these processes (Daly et al. 2021). POM is largely made up of lightweight plant fragments that are relatively undecomposed, whereas MAOM consists of single molecules or microscopic plant or microbial derived fragments of organic material that are chemically or physically associated with soil minerals. MAOM has greater protection from microbial decomposition through this association, whereas POM has relatively less. Consequently, POM has a faster cycling rate (~ years),

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whereas MAOM has a slower cycling rate (decades-centuries) (Lavallee et al. 2020).

The characteristics of these two contrasting soil organic matter fractions usually lead to the assumption that N mineralization occurs mainly from the POM fraction, while the MAOM fraction is a relatively stable pool that plays only a minor role in short-term N mineralization and N supply to plants (Haynes 2005). However, recent studies have suggested that MAOM-N could be destabilized by root exudates and mineralized in the shorter-term (Keiluweit et al. 2015; Jilling et al. 2021). Furthermore, MAOM is typically the largest fraction of soil organic C—storing the majority of C in mineral soils globally (Sokol et al. 2022)—and has the lowest C/N ratio (Lavallee et al. 2020), thus constituting a large potential source of N. Nevertheless, POM and MAOM contributions to total short-term soil organic N mineralization remain a critical knowledge gap affected by N mineralization rates and the relative pool size of each fraction.

Decomposition dynamics of total soil organic matter can be explored by incubating different soil fractions and measuring the sum of its mineralization products (Bimüller et al. 2014). Potentially mineralizable N (N_0) represents the maximum amount of N that soil can supply to the solution under optimum environmental conditions and is usually estimated by aerobic incubations over ~41 weeks, but can be accurately estimated by N released after a 7-day anaerobic incubation (Nan) (Schomberg et al. 2009; Reussi Calvo et al. 2018). Nan has been widely used to estimate the size of the labile organic matter pool of bulk soils (Williams et al. 2007; Sainz Rozas et al. 2008; Clark et al. 2019), but has not been used to assess the POM and MAOM labilities until now. Some studies show that POM and MAOM are not homogeneous in terms of turnover rates, and labile organic compounds have been found in both fractions (von Lützow et al. 2007). In this study, we present to our knowledge the first measurements of N released from the POM and MAOM fractions using a modified Nan measurement procedure to assess the size of the labile N pool in each fraction separately.

Grasslands and dry forests face land degradation and are often overlooked in sustainable development (Barral et al. 2020; Bardgett et al. 2021). The conversion of natural forests to arable croplands or implanted pastures, as well as grassland disturbance through overgrazing, has a drastic impact on soil organic matter dynamics, leading to substantial soil C losses and greenhouse gas emissions (IPCC 2019). In this study, we conducted a “living lab” experiment using a paired sampling strategy to assess soil organic matter dynamics under contrasting land-uses, including grasslands (under two grazing managements), forests, croplands, and pastures. Our objective was to evaluate the following: (i) the contributions of particulate organic matter (POM) and mineral-associated organic matter (MAOM) to total labile N, considering varying POM and MAOM stocks and qualities (e.g., forest soils are expected to have a higher proportion of POM and higher C/N ratios compared to soils with herbaceous vegetation, such as croplands, pastures, and grasslands); (ii) the environmental factors controlling N mineralization in different soil fractions; and (iii) the effects of land-use and grazing management on the quantities and qualities of POM and MAOM.

Materials and methods

Study sites

The study was conducted in two contrasting regions: the Argentine Semiarid Chaco and the Uruguayan Grasslands. The Argentine Semiarid Chaco Region is a vast plain located in the north-central part of the country, covered by a mosaic of dry forests, shrublands, grasslands, pastures, and croplands (Barral et al. 2020). The main soils of the study area are Mollisols and Entisols, with silty-loam and loam textures (INTA 1990). The mean annual temperature is 20°C and mean annual precipitation ranges from 450 to 700 mm and is concentrated from November to April followed by a long dry season from May to September (Bucher 1982). The Rio de la Plata grasslands is a vast region of natural grasslands, encompassing Uruguay, southern Brazil, and central Argentina (Soriano 1991). Most of the Uruguayan territory was originally covered by natural grasslands, but only about half of them currently remains. The region has a humid temperate-subtropical climate without a dry season and with the general appearance of prairies, savannahs, and steppes. The mean annual temperature is 17.5°C, and mean annual precipitation is around 1200 mm and is distributed throughout the year.

Twenty-four sites were evaluated, eight in the Argentine Semiarid Chaco (between 26.01° S; 61.32° W and 26.9° S; 61.98° W) and fourteen in the Uruguayan Grasslands (between 31.29° S; 56.12° W and 34.38° S; 54.61° W). At each site of Semiarid Chaco, three adjacent plots with native forest, pasture, and cropland were sampled. Two paired adjacent plots with continuous and rotational grazing were sampled at each site in the Uruguayan Grasslands. In total, 52 plots were sampled, 24 in the Semiarid Chaco, and 28 in the Uruguayan Grasslands.

Field sampling and lab analyses

Soil samples were collected using a 2-cm-diameter soil corer, taking composite samples (with 20 to 30 subsamples) at two soil depths: 0–5 and 5–20 cm in Semiarid Chaco and 0–5 and 5–10 cm in the Uruguayan grasslands. Soil samples were oven dried at 30°C and sieved through 2-mm mesh, identifiable plant material was eliminated manually, and soil was stored until fractionation and analysis.

Dry soil samples were physically fractionated into POM and MAOM (Cambardella and Elliott 1992). Briefly, 10 g of 2 mm sieved soil was shaken overnight (18 h) in 30 ml 5% hexametaphosphate dispersing solution. The dispersed soil was then sieved through 53-µm mesh. The material retained in the sieve contained the POM, and the slurry that passed through the sieve contained the MAOM. Both fractions were collected in beakers. The beaker containing the POM was dried in an oven at 60 °C until reaching a constant weight. Five milliliters of calcium chloride (2 N concentration) was added to the beaker containing the MAOM to precipitate solids out of the solution. After 24 h, the supernatant was carefully removed with a vacuum pump, and the beaker was placed in an oven at 60°C until reaching a constant weight. Once weighed, the POM and MAOM were ground with a mortar.

Soil texture determination was carried out by the hydrometer method (Bouyoucos 1962) for soil samples from Argentine Semiarid Chaco. For the sites of Uruguayan Grasslands, sand contents were measured for each sample by wet sieving with a 53-micron sieve. Clay and silt contents were then estimated based on sand contents and soil map databases in each region.

N released after a 7-day anaerobic incubation (Nan) was determined as described by Keeney (Keeney 1983), but using POM and MAOM fractions instead bulk soil. Thus, 5 g of POM and MAOM recovered from fractionation was placed inside test tubes (150 mm high × 16 mm in diameter), and the remaining volume was filled with distilled water. They were hermetically capped, ensuring an anaerobic condition, and incubated for 7 days at 40°C. At the end of the incubation, ammonium-N content was determined by steam distillation (Keeney and Nelson 1983).

Carbon and N concentrations were measured using a C–N analyzer coupled to an isotope mass spectrometer. Soil samples from Argentine Semiarid Chaco were analyzed at *Laboratorio de Isótopos Estables en Ciencias Ambientales, Argentina* using an Thermo Scientific DELTA V Advantage coupled via the ConFlo IV interface to a Flash 2000 Elemental Analyzer, and soil samples from Uruguayan Grasslands were analyzed at the *Stable Isotope Facility* located in University of California, Davis campus, in the Department of Plant Sciences using an Elementar Vario EL Cube or Micro Cube elemental analyzer. C, N, and Nan concentrations (g g soil^{-1}) were also expressed in mg ha^{-1} (for C and N), and kg ha^{-1} (for Nan), using the following equation:

$$y = (Fw/Sw) * x * BD * depth \tag{1}$$

where y is the amount of C, N (mg ha^{-1}) or Nan (kg ha^{-1}) in the POM or MAOM fraction, Fw is soil fraction weight (g), Sw is total soil weight (g), x is C, N, or Nan concentration of the POM or MAOM fraction, and depth is the considered soil depth (cm). For Nan, y was divided by 1000 to convert mg into kg. Soil bulk density could be affected by land-use/managements changes (Davidson and Ackerman 1993). Therefore, to report C, N, and Nan in an equivalent soil mass, soil sampling depths under croplands, pastures, and rotational grazing were corrected using the following equation (Solomon et al. 2002):

$$Depth = \left(BD_{reference}/BD_{converted}\right) * z \tag{2}$$

where $BD_{reference}$ is the bulk density (g cm^{-3}) of the reference land-use/management (forest in the Argentine Semiarid Chaco and continuous grazing in the Uruguayan Grasslands), $BD_{converted}$ is the bulk density (g cm^{-3}) of the converted land-use, and z is the sampled soil depth (cm). The bulk density was calculated by dividing the total dry weight by the total volume (volume of each soil core multiplied by the number of subsamples in the composite sample). For native Chaco forests, we used bulk density values reported previously for the same sites that by Villarino et al. (2017) that were also corrected to an equivalent soil mass.

Data analysis

Statistical analyses were performed with the R software (R Core Team 2022). C and N stocks, and Nan fluxes were compared across land-uses/managements using linear mixed effects models. Land-use in Argentine Semiarid Chaco (forest, pasture, and cropland) and Uruguayan grassland grazing management (continuous and rotational) were fitted as fixed effects, while the sampling site was fitted as a random effect. Models were fitted using the R package *lme4* (Bates et al. 2015). When the *p* values of the analysis of deviance table (Type II Wald chi-square tests) were less than 0.05, marginal means were estimated using the *emmeans* R package (Lenth 2022). Finally, the letter display of all pair-wise comparisons was done using the *cld* function of the *multcomp* R package (Hothorn et al. 2008). The same procedure was carried out for Nan/N, Nan/C, and C/N comparisons across land-uses/managements and soil fractions.

Linear models using the *lm* function of R (R Core Team 2022) were fitted to assess the relationships between POM-Nan with POM-C and POM-C/N, and between MAOM-Nan with MAOM-C and clay percentage.

Result and discussion

Relative contribution of labile N from POM and MAOM fractions

Contrary to expectations, we found that most of the potentially mineralizable N in soil comes from the MAOM fraction, across all contrasting land-uses or -managements evaluated

(Fig. 1). Although most soil organic N is known to be stored in the MAOM fraction (von Lützow et al. 2007; Lavallee et al. 2020; Sokol et al. 2022), its availability to microorganisms is poorly known and was generally presumed to be low. However, our results show that the MAOM fraction can supply more than 50% of the N released by SOM mineralization, and that its relative contribution increases with land-use intensification (Fig. 1). However, the amount of potentially mineralizable N per gram of N in the soil (i.e., the Nan/N ratio) was higher in the POM than in the MAOM fraction in all land-uses and regions (Table 1), suggesting that the POM fraction is a labile and less stable fraction, but usually of smaller pool size. Therefore, the MAOM fraction is a large N supplier to the soil solution because it stores most soil N and its larger size overcompensates for its lower concentration of labile or more easily mineralizable N.

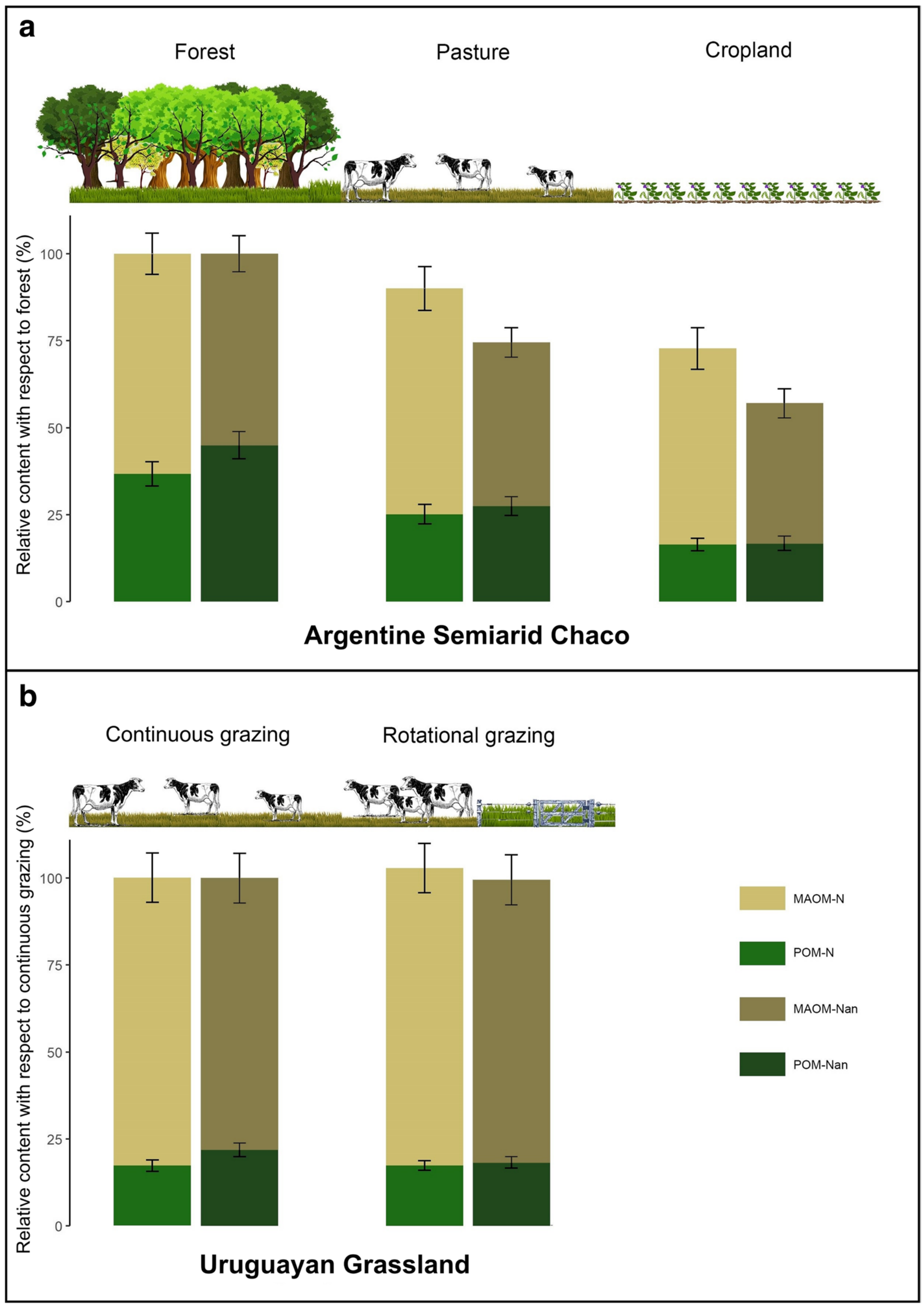

Fig. 1 Relative stock of nitrogen (N) and potentially mineralizable N, estimated by N released after a 7-day anaerobic incubation (Nan) in particulate organic matter (POM) and mineral-associated organic matter (MAOM). Relative N and Nan were calculated with respect to the N and Nan stocks under the respective reference conditions—i.e., forest in Argentine Semiarid Chaco region (**a**) and continuous grazing in Uruguayan Grasslands (**b**). The legend shown in panel b refers to both panels

Table 1 Ratios (%) between potentially mineralizable nitrogen (Nan), soil organic nitrogen (N) and soil organic carbon (C), within particulate organic matter (POM) and mineral-associated organic matter (MAOM) fractions across different land-uses

Region	Ratio	Land-use/management	POM	MAOM
Argentine Semiarid Chaco	Nan/N	Forest	3.37 ±0.22 A a	2.31 ±0.14 B a
		Pasture	3.18 ±0.45 A a	1.94 ±0.09 B b
		Cropland	2.67 ±0.23 A a	1.93 ±0.09 B b
	Nan/C	Forest	0.29 ±0.01 A a	0.28 ±0.02 A a
		Pasture	0.26 ±0.03 A a	0.23 ±0.01 A b
		Cropland	0.24 ±0.01 A a	0.23 ±0.01 A b
	C/N	Forest	11.7 ±0.23 A a	8.4 ±0.18 B a
		Pasture	12.0 ±0.34 A a	8.3 ±0.30 B a
		Cropland	11.1 ±0.58 A a	8.4 ±0.27 B a
Uruguayan Grasslands	Nan/N	Grassland CG	6.79 ±0.72 A a	4.91 ±0.44 B a
		Grassland RG	5.39 ±0.43 A b	4.70 ±0.25 A a
	Nan/C	Grassland CG	0.45 ±0.04 A a	0.48 ±0.05 A a
		Grassland RG	0.38 ±0.04 A b	0.47 ±0.03 B a
	C/N	Grassland CG	14.7 ±0.59 A a	10.2 ±0.19 B a
		Grassland RG	14.7 ±0.64 A a	10.3 ±0.12 B a

Different capital letters indicate significant differences (p <0.05) between POM and MAOM for the same land-use/management, and different lowercase letters indicate significant differences between land-uses in Argentine Semiarid Chaco and land management in Uruguayan Grassland. *CG* continuous grazing, *RG* rotational grazing

MAOM is more resistant to mineralization than POM. However, Nan fluxes per gram of C (Nan/C) were similar between fractions (Table 1). It is likely that the higher N concentration in MAOM fraction (i.e., lower C/N) (Table 1) is offsetting its lower mineralization rates. Therefore, a smaller amount of organic matter (which is richer in N concentration) is mineralized in the MAOM, whereas a larger amount of organic matter (which is poorer in N concentration) is mineralized in the POM, thus producing a similar Nan/C ratio between MAOM and POM fractions.

Controls of potentially mineralizable N in the POM and MAOM fractions

When considering all sites from the Semiarid Chaco and Uruguayan Grasslands, we found that Nan increased with C concentrations, both in the POM and in the MAOM (Fig. 2). However, POM-Nan linearly increased with POM-C while MAOM-Nan showed a logarithmic relationship with MAOM-C, suggesting that other factors constrain N mineralization at high MAOM-C contents. High MAOM-C

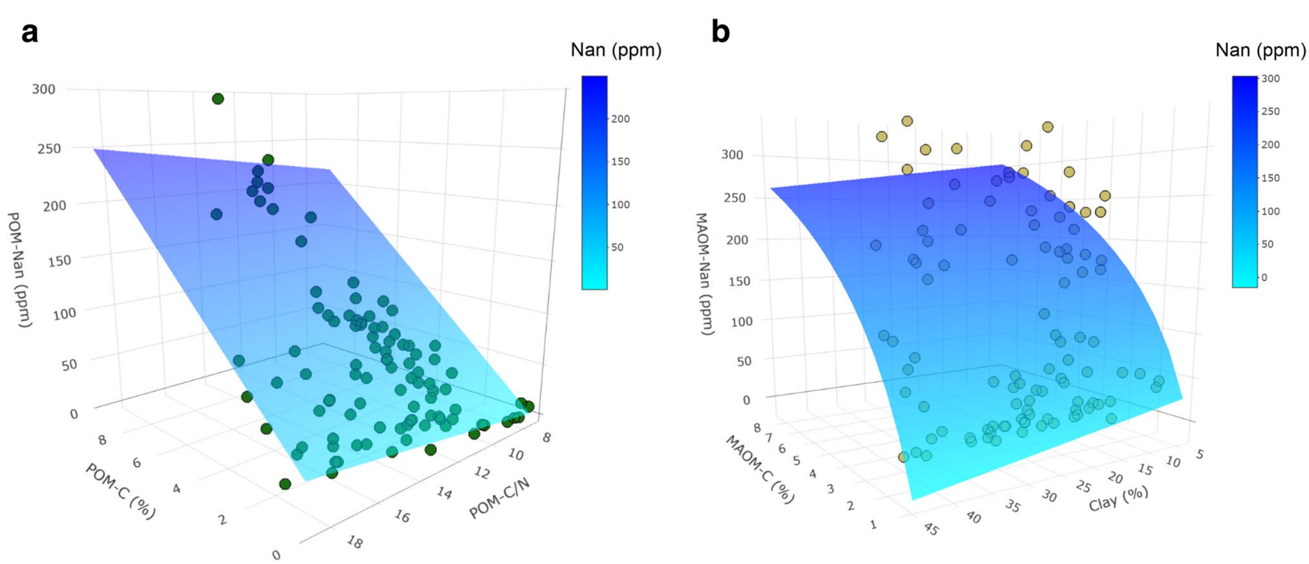

Fig. 2 Relationships for particulate organic matter (POM) (**a**) and mineral-associated organic matter (MAOM) (**b**) between nitrogen released after a 7-day anaerobic incubation (Nan), organic C, C/N ratio, and clay percentage. Summary of fitted models is shown in Table 2

contents found in some soils could be due to the existence of strong bonds between minerals and organic matter that prevent its mineralization. Therefore, more soil C does not necessarily imply more C available for microorganisms.

The C/N ratios and clay percentages were also associated with POM-Nan and MAOM-Nan fluxes, respectively (Fig. 2, Table 2). Mineralization kinetics and its controlling factors are expected to differ between fractions due to their different nature and associated protection mechanisms (Lavallee et al. 2020). In the POM fraction, we expected a negative relationship between Nan and C/N ratios, because lower C/N ratios reflect higher SOM quality and therefore should lead to higher Nan supply. However, an opposite and significant relationship was found for the POM fraction ($p < 0.001$, Table 2). The POM-C/N ranged from 7 to 19 (Fig. 2) and thus were always below the 20 threshold, where N starts limiting decomposition (Cleveland and Liptzin 2007), suggesting that POM is likely a C-limited substrate for microorganisms. As POM-C/N increases, relatively more C is available to support microbial growth and activities, enhancing decomposition and N releases from POM. In agreement with us, Pan et al. (2023) found that under C-limited conditions, microbes use C-rich molecules more efficiently than N-rich molecules, because with the formers they can meet their C demand, and N is then rapidly released as NH_4^+ and NO_3^- in short time frames. Energy (i.e., the amount of C), rather N, could be limiting microbial growth and POM mineralization, explaining the positive relationship between POM-C/N and POM-Nan. On the other hand, the negative relationship between MAOM-Nan and clay percentage was expected since more clay implies more binding sites that could retain N and prevent mineralization. A recent study also found that net N mineralization decreased with increasing clay/C ratios (Soinne et al. 2021).

Land-use and grazing management effects on POM and MAOM fractions

In the Argentine Semiarid Chaco, land-use intensification decreased POM-C and POM-N stocks and POM-Nan fluxes, as well as MAOM-Nan fluxes, but only small decreases were observed in MAOM-C and MAOM-N stocks (Fig. 3). These results are consistent with previous studies showing that POM stocks are highly vulnerable to land-use intensification while MAOM stocks are less sensitive and relatively more stable (Six et al. 2002). The MAOM-Nan/MAOM-N ratios decreased under pastures or crops as compared to native forests (Table 1). POM-Nan/POM-N ratios also showed a similar trend, though not statistically significant (Table 1). These results can be explained by the differential levels of protection from decomposition between POM and MAOM. Due to the low physical protection of POM (only occluded in large aggregates) (Lavallee et al. 2020), land-use intensification may strongly affect both POM-N stocks and POM-Nan fluxes. Hence, POM-Nan/POM-N ratio may remain relatively constant (Table 1). In contrast, the high physical-chemical protection of MAOM prevents mineralization of N stocks, and only the labile pools of MAOM were affected by land-use intensification, causing the reduction in the MAOM-Nan/MAOM-N ratio.

The predominant deforestation method in Argentine Semiarid Chaco involves land clearing with heavy bulldozers, burning the remaining vegetation, and plowing down the residues, resulting in significant soil changes including soil aeration, roots removal, and surface exposure to precipitation, wind, and solar radiation (Villarino et al. 2017). These changes have various detrimental effects on soil organic matter storage that can explain observed depletion in pastures and croplands (Fig. 3). Furthermore, N fertilization in croplands and pastures strongly influences the below-ground community and C and N dynamics (e.g., narrower C:N ratios from N fertilizer could accelerate organic matter mineralization) (Kim et al. 2022).

In the Uruguayan Grasslands, no significant differences in C and N stocks and Nan fluxes of POM and MAOM fractions were found after changes in grazing management, although changes in Nan/N ratios of both fractions were like those observed for the Chaco Forests after intensification (Fig. 3 and Table 1). This was expected because grazing management changes are

Table 2 Summary of linear models fitted for the relationships between nitrogen released after a 7-day anaerobic incubation (Nan) with organic C and C/N ratio in the particulate organic matter (POM) and between Nan with organic C and clay percentage in the mineral-associated organic matter (MAOM) (Fig. 3)

Fitted model	Adjusted R^2	Coefficients	Estimate	p value
POM-Nan ~ POM-C (%) + POM-C/N	0.84	Intercept	−23.58	0.07
		POM-C (%)	23.96	2.0E−16
		POM-C/N	2.86	0.00231
MAOM-Nan ~ log(MAOM-C (%)) + Clay (%)	0.74	Intercept	22.45	0.19
		log(MAOM-C (%))	132.45	2.0E−16
		Clay (%)	−1.01	0.04

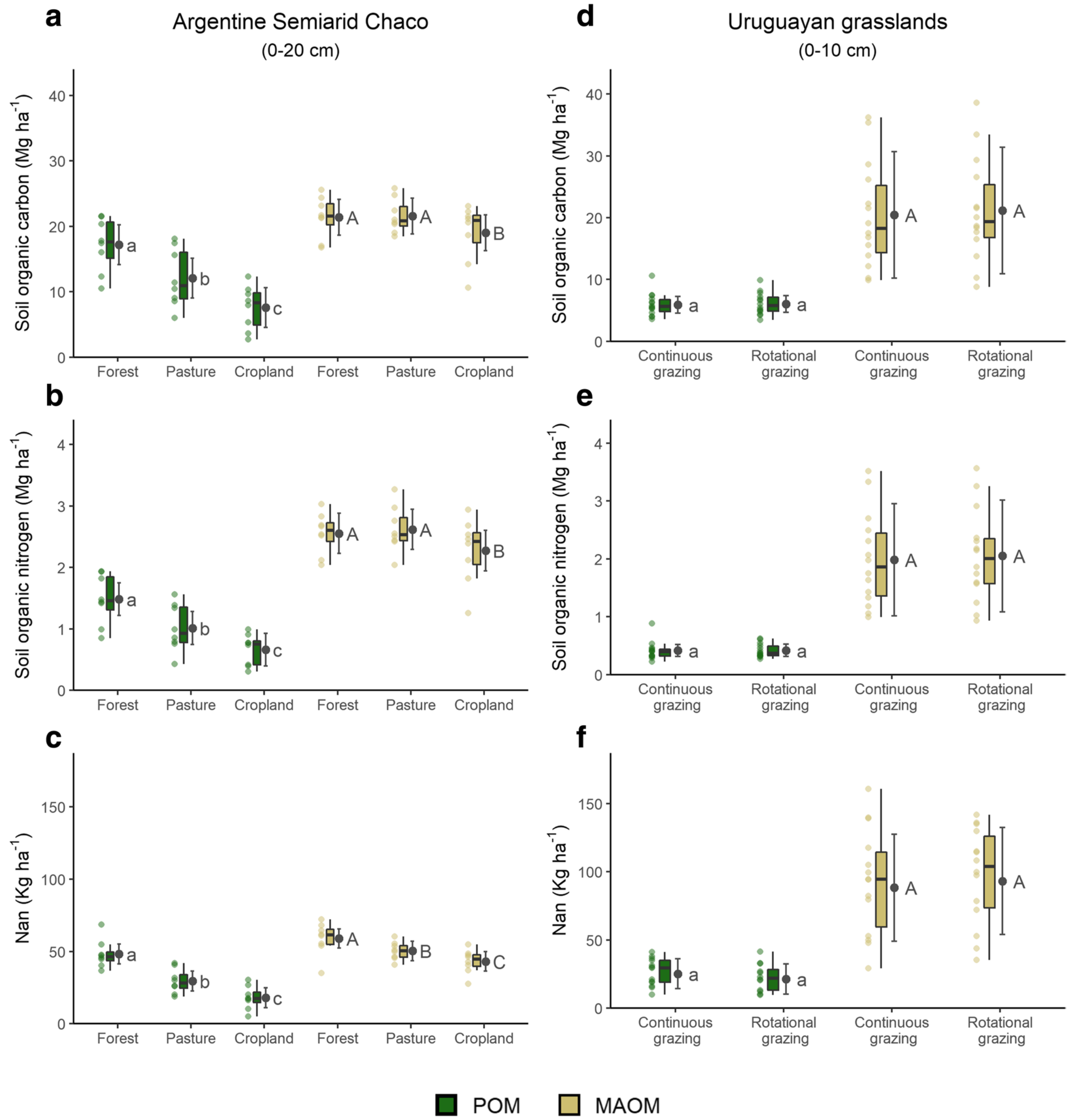

Fig. 3 Soil organic carbon and nitrogen stocks, and potentially mineralizable nitrogen (Nan; released after a 7-day anaerobic incubation), in particulate organic matter (POM, green boxes) and mineral-associated organic matter (MAOM, golden boxes), across land-use intensification gradients in Argentine Semiarid Chaco (**a**, **b**, and **c**) and Uruguayan Grasslands (**d**, **e**, and **f**). Boxes represent the interquartile distance, horizontal lines indicate the median, and whiskers indicate the maximum and minimum non-outlier values. Values were outliers when at least 1.5 interquartile ranges below the first quartile or above the third quartile. Green and golden dots represent raw data, gray dots and error bars represent means ± 95% confidence interval. Means with different letters (lowercase for POM comparison and uppercase for MAOM comparison) are significantly different (Tukey's test, 5% significance level)

subtler than land-use changes studied in the Argentine Semiarid Chaco forests. However, and in agreement with our results from Chaco, land-use intensification (i.e., when grazing management changed from continuous to rotational grazing) decreased Nan/N ratios in the POM fraction ($p = 0.01$). Altogether, these results suggest that Nan/N ratios are sensitive to changes in the quality of the organic matter present in each fraction and therefore describe its heterogeneity in terms of its decomposability and nitrogen supply. Large changes in the sizes of the fractions may obscure changes in the Nan/N ratio, but smaller changes, such as changes in biomass inputs or changes in biomass quality, are expected to mainly affect N fluxes and hence the Nan/N ratio.

Conclusions

Our study demonstrates that MAOM plays an important role in short-term N mineralization and N supply to plants (Fig. 1). Our results challenge the idea that MAOM is a homogeneous, slow-cycling fraction and support the concept that both POM and MAOM are heterogeneous fractions containing labile compounds. Therefore, both fractions, but especially MAOM, should be monitored, because land-use changes or management practices may affect them differently and agricultural decisions, such as fertilization and crop rotations, depend strongly on soil N dynamics and N supplied by both fractions. The POM fraction has been proposed as a good soil-health indicator (Haynes 2005), but MAOM has received less attention (Yu et al. 2022). However, MAOM-Nan is a promising indicator of soil health because it is relevant (it is related to the soil nutrient supply) sensitive (it consistently detects rapid or large changes in SOM dynamics), informative (allows inferences about land-use management), and is measured by a relatively easy, low-cost laboratory technique (Lehmann et al. 2020). Although Nan measurements require a week of incubation, which could limit the use of MAOM-Nan for short-term agricultural decisions (days), these measurements in both soil fractions are still useful for planning, designing, and managing agricultural production systems in the medium to long-term scales (seasons to decades). Future research is needed to explore other potential methods to characterize POM and MAOM's internal heterogeneity, in particular their short-term decomposition and its relative contribution to plant N supply in contrasting managed and natural ecosystems.

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Data Availability Data will be made available on request.

Declarations

Conflict of interest The authors declare no competing interests.

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