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Agroforestry enhances the capacity of deep tropical soils to act as nutrient sinks and biogeochemical buffers, thereby improving internal nutrient recycling - insights from incubation experiments

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Abstract. The understanding of the interactions between the lower and upper compartments of the Critical Zone (CZ) is of major importance to the maintenance of life across continental landscapes. The extent to which deep root uptake supplies nutrients from depth and redistributes them to the entire ecosystem remains unknown. Identifying the processes at stake and quantifying their effects on nutrients cycles is of paramount importance for assessing ecosystem resilience and designing management practices enhancing biologically mediated CZ processes in agrosystems. The impact of depth and land-use on the decomposition of soil organic matter (SOM; roots free soil) and fine roots (<2 mm) was investigated for a tropical conventional irrigated agriculture plot and an agroforestry one, at two depths (0-15 cm and between 8 and 10 m), through soil incubations in small lysimeters over a period of 115 days. Dynamics of CO_2 and major soluble species (NO_3^-, SO_4^{2-}, PO_4^{3-}, Na^+, Ca^{2+}, Mg^{2+}, K^+, DOC and DIC) were monitored over the whole incubation period using sodium hydroxide traps and free pore water extraction at each time step, respectively. Soil initial and final C, N and exchangeable stocks were also characterized. During the 115 days that lasted this experiment, more than 90% of the C fluxes were released as CO_2 for all treatments. However, the final cumulative fluxes varied depending on soil depth and land use, both for the decomposition of SOM and for that of fine roots, with a potential priming in soils under conventional agriculture and a legacy effect in agroforestry soils. Cation and anion fluxes varied primarily with depth and could be classified into three groups based on their extraction dynamics: (1) Na and K, preferentially leached from the CEC; (2) nitrate and sulfate, mostly related to OM biological processes i.e. either production of microbial necromass (roots free soils) or immobilization in microbes' biomass (soils with root OM added), and were mainly compensated in terms of charges by Ca and Mg release; (3) phosphate with a significant impact of the sampling

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interval on its extraction due to the interaction between phosphates and soil mineral surfaces. However, at equivalent rates of root decomposition, subsoils retained N, S, P, K, and Ca more effectively than topsoils, and this retention was generally stronger under agroforestry than under conventional irrigated agriculture, without perennial deep rooting. Overall, this study supports the view that agroforestry enhances the capacity of deep tropical soils to act as nutrient sinks and biogeochemical buffers, thereby improving internal nutrient recycling and potentially increasing the resilience of the agrosystem. It also highlights the importance of taking into account the multiple correlations among the various major elements found in interaction in soil pore solutions into modeling for estimating soil carbon stocks in these tropical soils.

1 Introduction

Processes linking lower and upper parts of the Critical Zone (CZ) are crucial for sustaining life on continents (Anderson, 2019; Porder, 2019). Ecosystem services provided by eco- or agrosystems, such as primary production and regulation of nutrient and water cycles cannot be properly understood and predicted by focusing only on shallow topsoil horizons (Maeght et al., 2013; Germon et al. 2016). It is increasingly acknowledged that deep roots likely fulfill essential functions, impacting water and geochemical cycles, plant ecophysiology and community ecology not only in natural forests (Harper and Tibbett, 2013; Robin et al., 2019) but also in tree plantations (Germon et al., 2020). While our knowledge on plant root systems has considerably improved in the past few decades, with the development of new methodologies, it is still mostly limited to the topsoil horizons. Most of the published root profiles are majorly truncated (Schenk and Jackson, 2002), which is particularly problematic in tropical ecosystems where soils are globally deep (e.g. Braun et al., 2012). Many tropical regions have undergone long lasting chemical weathering for millions of years resulting in decameter thick and deeply weathered saprolite layers (Vitousek, 1984). Relatively thin (8 – 25 cm) nutrient rich topsoil layers often overlay extremely thick (up to >50 m meters) nutrient-depleted and deeply weathered subsoil or saprolite layers (Zauyah et al., 2010; Reichenbach et al., 2025). The turnover of organic carbon in tropical soils is comparatively rapid due to favorable climatic conditions, with high mean annual temperature (MAT) fostering biological activity and moisture regimes (MAP) ranging from permanently humid to strongly seasonal (Davidson and Janssens, 2006; Powers et al., 2011; Nottingham et al., 2015).

Deep horizons of soils are also understudied. The average depth considered for soil studies globally accounts for only 27 cm (Yost and Hartemink, 2020). However, subsoils (>30 cm) can store more than 50% of the global SOC and could be very sensitive to environmental perturbations such as land-use change or warming (Jobbágy and Jackson, 2000; Rumpel and Kögel-Knabner, 2011; Bellè et al., 2022). Carbon inputs to the subsoil arise from multiple sources, including dissolved organic matter (OM), root-derived compounds, and particulate materials transported from surface horizons (Marin-Spiotta et al., 2011). Yet the relative contribution of each remains poorly constrained. Depth profiles of elemental and isotopic composition—such as decreasing C/N ratios and increasing $\delta^{13}C$ values—along with molecular analyses (Kramer and Gleixner, 2008; Krüger et al., 2024), indicate that microbial products constitute a larger fraction of subsoil OM compared to plant-derived compounds.

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Subsoil OM exhibits extremely long turnover times, often ranging from 1,000 to over 10,000 years (Henneron et al., 2022), but the underlying causes of this persistence are not fully understood. Possible explanations include reduced microbial activity due to suboptimal environmental conditions, nutrient or energy limitations, and restricted substrate accessibility resulting from low OM density or strong associations with mineral surfaces and lack of oxygen (Pei et al., 2025). Microbial biomass typically declines with depth, accompanied by shifts in community composition toward greater substrate specialization (Hsiao et al., 2018; Xu et al., 2021). Emerging evidence points to energy limitation as key factors regulating subsoil carbon dynamics both in terms of quantity and quality of the OM available (Spohn and Chodak, 2015).

Roots contribute to soil OM (Rasse et al., 2005), in particular to deep soil horizons (Rumpel and Kögel-Knabner, 2011; Siegwart et al., 2023a). Root-derived carbon is retained in soils far more efficiently than aboveground inputs such as leaves and needles. Isotopic evidence and biomarker comparisons consistently demonstrate the predominance of root-derived molecular structures within soil OM and the incorporation of root-origin carbon into soil microbial biomass (Werth and Kuzyakov, 2008; Pries et al., 2018). This preferential stabilization likely reflects multiple mechanisms: much of the aboveground litter is mineralized within the surface layer, whereas root-derived organic compounds and mycorrhizal inputs have greater potential for physico-chemical association with mineral particles. Moreover, changes in the physico-chemical properties of the soil and root architecture result in a vertical and lateral succession of highly heterogeneous microenvironments for soil organisms, with depth acting as an environmental gradient (Siegwart et al., 2023c). Consequently, the characteristics of microbial communities (functionality, abundance) differ significantly between topsoils and subsoils, implying different mechanisms of organic compound degradation (Abiven et al., 2005).

Roots inputs are strongly connected to the C plant allocation and to the land use. Agroforestry is a land use characterised by high root derived inputs, because of tree roots adding carbon to both topsoils and subsoils (Siegwart et al., 2022; 2023b; 2023c). Roots are typically more abundant in agroforestry systems because trees and crops together create denser, deeper, and more continuous belowground biomass than annual monocultures, and management tends to reduce disturbance so roots OM can accumulate over time. This intensified and stratified rooting reflects both species diversity (trees, crops, understory) and adaptive responses to competition for water and nutrients (Siegwart et al., 2023b). Roots decay dynamics and associated nutrient release are then expected to differ according to land use and soil properties, including within the soil profile itself between topsoils and subsoils (Siegwart et al., 2022).

The decomposition of roots, and more generally of fresh organic OM does not have only implications on the C dynamics. Indeed, most of the element dynamics are modified by the decomposition processes. Nitrogen cycle is strongly affected, as a large part of the organic input N is organised by microbes, and depending on the initial C:N ratio of the material, a fraction is released as mineral nitrogen in the soil (Mary et al., 1993). Most of the elements, like phosphorus, calcium, potassium are released from the fresh input and interact with the soil exchange sites, either with the variable and fixed charges, or leached further down when not retained to the organo-mineral associations (Rowley et al., 2018). The dynamics of these different

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elements during decomposition remain poorly studied. Elements like calcium or magnesium seem to be released very rapidly from the OM (Ranjbar and Jalali, 2012), while elements like P require the decomposition of organic compounds like phospholipids or nucleic acids, which require more time. In a recent study looking at very particular organic inputs (mammal corpses), Taylor et al. (2023) proposed groups of elements according to their behaviour: Na, K, P, S mostly came from the added OM and their persistence in soil depended on solubility (P), soil exchange complex (Na and K) and microbial degradation (S). Ca, Mg, Mn, Se, B concentrations in soil could not be explained by organic inputs alone, and so also partially come from the soil exchange complex and solubilization as a result of soil acidification. This categorisation highlights that the release of the different elements is not only related to the organic (animal in this case) decomposition itself, but also the complex interactions between the elements and the soil during biogeochemical processes of OM decomposition.

In the context of global changes, the issue of alterations in biogeochemical cycles of nutrients in deep tropical soils remains largely unaddressed. It is estimated that increased aridity linked to climate change would cause the carbon, nitrogen and phosphorus cycles to become decoupled, and could have an even more negative impact on plant nutrition and ecosystem services in arid environments (Delgado-Baquerizo et al., 2013). The impact of agricultural practices and the presence of trees on the dynamics of nutrients and micronutrients, and their interactions with the OM cycle, is also a key issue. Some studies conducted in contexts of soil salinisation or carbonation have shown that the dynamics of OM mineralisation can be controlled by processes involving calcium (Setia et al., 2010), and that, conversely, the mobility and speciation of calcium depend on the status of soil organic matter (SOM) (Rowley et al., 2018). In particular, the question of the role of root-derived OM from trees in the nutrient and micronutrient cycles is worth considering.

The objective of this study was to assess the impact of the decomposition of SOM and roots on nutrient retention or leaching in tropical soils, and more specifically to investigate how the soil regulates these fluxes as a function of soil depth and land use. To this end, we studied the dynamics of soluble chemical elements—namely the nutrients N, P, K, and S, as well as Na, Ca, Mg —during the mineralization of SOM and roots in soil samples from two South-Indian farm plots: one under conventional irrigated agriculture and the other under irrigated agroforestry. Our main hypothesis was that agroforestry soils, which already experienced root OM inputs under field conditions, would be more able to decompose soil OM and fine roots. A second hypothesis was that SOM mineralization would depend on soil depth and so we considered both top- and subsoils

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for each land use. These dynamics were followed throughout a 115-day soil incubation experiment in lysimeters which allowed to survey the respiration and nutrients dynamics.

2 Material and methods

2.1 Study site

Sampling sites are located in the Berambadi cultivated experimental catchment (84km², 11°46'N, 76°35'E), which is part of the Kabini Critical Zone Observatory and SNO M-TROPICS since 2010 (Sekhar et al., 2016; https://mtropics.obs-mip.fr/natural-environment/site-india/). The Berambadi catchment is located in the semi-arid part of the climatic gradient induced by the Western Gaths, where the rainfall drops from 5000 mm.yr^{-1} to 500 mm.yr^{-1} within less than 100 km. The rainfall in the catchment ranges from 900 mm.yr^{-1} at the East (upstream), to 700 mm.yr^{-1} at the East (outlet). The soils considered in this study are deep polycyclic soils which have developed at the expense of previously weathered and transported alluvium deposited likely during the Quaternary period (i.e., allochthonous deposits of Precambrian materials from gneiss and mafic lithologies)). Processes behind the development of current horizons are ferralitization with relative accumulation of Fe- and Al- oxyhydroxydes (i.e., plinthic horizon), long term bioturbation (e.g., roots and faunal activity), clay leaching, pedological carbonates dynamics with different features (e.g., calcrete, rhizoliths) and redox processes (deep horizon seasonally waterlogged and presenting stagnant features). The saprolite formed in situ lies below 900 cm. Despite their initial ferralitic nature, the soils are generally clayey-sandy, calcareous mainly for the topsoil above 2 m depth with a pH (H_2O) above 8. Cation exchange capacity (CEC) ranges from 4 to 18 cmol+.kg^{-1} depending on the horizon. The exchangeable fraction is dominated by Ca but the proportion of Na can be significant and reach 25% in depth. In the first 2 m, clay proportion increases with depth, which would bring these soils closer to the chromic luvisols described by Bourgeon in 1992 and documented more recently by Gunnell et al. in 2024.

Crops grown on these soils are diversified (banana, cabbage, onion, garlic, turmeric, maize…) and rotated on small plots irrigated using the local groundwater drawn from bore wells. Groundwater table depth ranges seasonally from 10 to 30 m. The majority of the plots follow three annual rotations, with sometimes two mixed crops. The crops are regularly amended with mineral fertilizers, but also with sediment dug from nearby reservoirs. Some plots are co-planted with trees (e.g., mango, teak) which are harvested for fruit and/or timber.

2.2 Soil sampling and analysis

Soils were collected in June 2022 from observation wells 10 m deep and 1.5 m diameter. One well is located in a groundwater-irrigated plot without trees, in which short-cycle crops grow (Conventional Plot, further referred as 'CP'), the other in a neighbouring groundwater-irrigated plot, with similar type of crops but bordered by a line of 30 years-old teak trees (*Tectona*

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grandis), further referred as Agroforestry or 'AF'. Teak trees are 12 m tall with a trunk circumference comprised between 1 m and 1.10 m and a canopy diameter of around 10 m. Both observation wells are approximately 30 m away from each other and the center of the AF well is located at around 2 m from teak tree line. The soil samples were composite, meaning they were collected from a 2 m² area corresponding to the area excavated for the construction of the wells.. They were dried at 40°C for a week, decompacted and sieved at 2 mm. Incubated samples came from the topsoil at 0-15 cm depth in the ploughed horizon for both wells (further referred as 'topsoils'), and from the deepest stagnic horizon located above the saprolite at 980-1010 cm for AF and 780-890 cm for CP (further referred as 'subsoils'). All the experiments and analyses were performed on the fine earth fraction (<2mm).

Soil granulometry, pH (H_2O) and plant-available-P were determined at the Laboratoire d'Analyse des Sols at Arras. Initial and final CEC of soils were measured by the modified cobaltihexamine method (Ciesielski et al., 1997) and the chemical composition of the exchangeable cations (Ca^{2+}, Mg^{2+}, K^+, Na^+) was determined by ICPOES at GET, Toulouse. Total phosphorus (P_{tot}) was determined with an ICPMS iCapQ ThermoFisher at Service d'Analyse des Roches et Minéraux (SARM, Nancy), with a detection limit of 0.04 $g.kg^{-1}$. Total carbon (C_{tot}) and nitrogen (N_{tot}) content in soils and roots were measured at GET using a CHNS analyzer Thermo for soil organic (C_{org}) and inorganic carbon (C_{inorg}). For C_{inorg} determination soil samples were heated at a temperature of 500°C for 1 hour. C_{org} content was then calculated through the difference between C_{tot} and C_{inorg}. The detection limit for both N and C was 0.2 $g.kg^{-1}$.

Granulometry and its evolution between the two horizons considered in this study were similar for both sites, with the clay fraction slightly higher in topsoil than in subsoil samples, around 350 and 250 $g.kg^{-1}$, respectively. The sand fraction was more abundant in CP (520 $g.kg^{-1}$ in topsoil and 650 $g.kg^{-1}$ in subsoil) than in AF (450 $g.kg^{-1}$ in topsoil and 425 $g.kg^{-1}$ in subsoil) (Table 1). CEC followed broadly the same trend as the clay content, and ranged in AF from 18.7 $cmol+.kg^{-1}$ in topsoil to 13.4 $cmol+.kg^{-1}$ in subsoil. CEC was more homogeneous in CP, from 15.6 to 14.3 $cmol+.kg^{-1}$, respectively for top- and subsoil samples. CEC composition was dominated by exchangeable Ca in both topsoils (63-70% of total cations) and equally by Ca and Mg in subsoils (34-44% and 39% of total cations, respectively). The proportion of exchangeable K in CEC was higher in topsoils (5-10%) than in subsoils (2-3%) while exchangeable Na exhibited an opposite trend (0.8-5% in topsoil and 13-25% in subsoil) (Table 3). Plant-available phosphorus was only detectable in topsoils. Its content was 0.046 $g.kg^{-1}$ in AF and 0.051 $g.kg^{-1}$ in CP, which represented 12 % and 10 % of the total phosphorus, respectively (Table 2). As for plant-available phosphorus, Ntot was only detectable in topsoils, with similar initial amounts between CP and AF (0.7-0.8 $g.kg^{-1}$) (Table 2). Corg content in AF evolved from 9 $g.kg^{-1}$ in the surface layer to lower than the detection limit (0.2 $g.kg^{-1}$) at depth and in CP from 7 $g.kg^{-1}$ to 0.2 $g.kg^{-1}$. The C/N ratio of topsoils was 11-12. Cinorg decreased with depth in AF from 0.7 $g.kg^{-1}$ to 0.2 $g.kg^{-1}$ of soil and in CP from 0.6 $g.kg^{-1}$ to 0.4 $g.kg^{-1}$ of soil (Table 2).

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Table 1: Initial and final pH and initial soil granulometry of fine earth (<2mm). Both soil granulometry and pH(H2O) were determined at the Laboratoire d'Analyse des Sols at Arras (France) for the initial values (t=0) and final pH(H2O) values were determined at GET, Toulouse. Standard deviations for pH(H2O) t=115 represent the triplicate variability, except for AF subsoil which was only duplicated.

Site	Depth (cm)	Roots (g $C_{org}.kg^{-1}$)	pH(H2O)		Clay (<2 µm) ($g.kg^{-1}$)	Silts (2-50 µm) ($g.kg^{-1}$)	Sands (50-2000 µm) ($g.kg^{-1}$)
			t=0 (n=1)	t=115 (n=3)	t=0 (n=1)	t=0 (n=1)	t=0 (n=1)
AF	0-15	0	**7.6**	**7.8** ± 0.0	**351**	**203**	**446**
		4.34		**7.7** ± 0.2			
	980-1010	0 (n=2)	**8.6**	**8.9** ± 0.0	**270**	**89**	**641**
		4.34		**8.6** ± 0.1			
CP	0-15	0	**8.2**	**8.2** ± 0.1	**335**	**145**	**520**
		4.34		**8.1** ± 0.1			
	780-890	0	**8.6**	**8.9** ± 0.1	**243**	**105**	**652**
		4.34		**8.5** ± 0.1			

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Table 2: Initial and final elemental composition of fine earth (<2mm). C_{tot} and N_{tot} content in soils were measured at GET using a CHNS analyzer Thermo for soil organic (C_{org}) and inorganic carbon (C_{inorg}). The detection limit for both N and C was 0.2 g.kg^{-1}. P_{tot} was determined with an ICPMS iCapQ ThermoFisher at Service d'Analyse des Roches et Minéraux (SARM, Nancy), with a detection limit of 0.04 g.kg^{-1}. Plant-available-P were determined at the Laboratoire d'Analyse des Sols at Arras. Standard deviations at 115 days represent the triplicate variability, except for AF subsoil which was only duplicated.

Site	Depth (cm)	Roots (g Corg.kg-1)	Corg (g.kg-1)		Cinorg (g.kg-1)		Ntot (g.kg-1)		Ptot (g.kg-1)	P Plant available (g.kg-1)
			t=0 Thermo (n=1)	t=115 Thermo (n=3)	t=0 Thermo (n=1)	t=115 Thermo (n=3)	t=0 (n=1)	t=115 (n=3)	t=0 (n=1)	t=0 POlsen (n=1)
AF	0-15	0	9.8	9.2 ± 0.2	0.3	<0.2	1.3	1.0 ± 0.0	0.4	0.05
		4.34		11.8 ± 0.4		<0.2		1.2 ± 0.1		
	980-1010	0 (n=2)	0.2	0.3 ± 0.1	<0.2	<0.2	<0.2	<0.2	<0.04	<0.002
		4.34		1.7 ± 0.3		0.2 ± 0.1		0.2 ± 0.0		
CP	0-15	0	7.2	7.0 ± 0.1	0.2	0.2 ± 0.2		0.8 ± 0.0	0.5	0.05
		4.34		9.4 ± 0.4		<0.2		0.9 ± 0.0		
	780-890	0	0.4	0.3 ± 0.1	<0.2	0.4 ± 0.3	<0.2	<0.2	<0.04	<0.002
		4.34		1.2 ± 0.4		0.2 ± 0.1		0.2 ± 0.0		

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Table 3: Initial and final exchangeable stocks of fine earth (<2mm). Initial and final CEC of soils were measured by the modified cobaltihexamine method and the chemical composition of the exchangeable cations (Ca^{2+}, Mg^{2+}, K^+, Na^+) was determined by ICPOES at GET, Toulouse. In the last column, the cations sum was calculated based on the soil exchangeable fraction measurements in terms of positive charges. Standard deviations at 115 days represent the triplicate variability, except for AF subsoil which was only duplicated.

Site	Depth (cm)	Roots (g $C_{org}.kg^{-1}$)	CEC (cmol+.kg^{-1})		Soil exchangeable fraction (cmol.kg^{-1})								Cations sum (cmol+.kg^{-1})	
					Ca^{2+}		Mg^{2+}		Na^+		K^+			
			t=0 (n=1)	t=115 (n=3)	t=0 (n=1)	t=115 (n=3)	t=0 (n=1)	t=115 (n=3)	t=0 (n=1)	t=115 (n=3)	t=0 (n=1)	t=115 (n=3)	t=0 (n=1)	t=115 (n=3)
AF	0-15	0	18.3	19.3 ± 0.4	5.82	5.64 ± 0.13	1.97	3.00 ± 0.06	0.07	0.07 ± 0.00	0.40	0.53 ± 0.01	16.1	17.8 ± 0.1
		4.34		19.9 ± 0.0		5.76 ± 0.03		3.12 ± 0.04		0.14 ± 0.02		0.71 ± 0.01		18.6 ± 0.0
	980-1010	0 (n=2)	13.4	19.4 ± 0.3	2.01	3.28 ± 0.05	2.28	5.20 ± 0.15	1.44	1.32 ± 0.01	0.14	0.19 ± 0.00	10.2	18.5 ± 0.2
		4.34		19.5 ± 0.4		3.22 ± 0.03		5.24 ± 0.07		1.40 ± 0.02		0.29 ± 0.01		18.5 ± 0.1
CP	0-15	0	15.6	15.9 ± 0.1	4.59	4.39 ± 0.04	1.54	2.53 ± 0.02	0.33	0.14 ± 0.01	0.73	0.74 ± 0.02	13.2	14.6 ± 0.1
		4.34		16.5 ± 0.3		4.43 ± 0.07		2.71 ± 0.05		0.26 ± 0.02		0.94 ± 0.02		15.4 ± 0.1
	780-890	0	14.3	17.8 ± 0.2	2.63	3.83 ± 0.09	2.34	4.27 ± 0.09	0.77	0.58 ± 0.02	0.19	0.27 ± 0.01	10.8	17.1 ± 0.1
		4.34		18.3 ± 0.5		3.69 ± 0.08		4.63 ± 0.15		0.51 ± 0.03		0.35 ± 0.02		17.5 ± 0.2

2.3 Root sampling and analysis

Teak roots were collected during the digging of the AF well. They were manually and systematically picked from each soil layer over an area of 1 m^2, then sorted according to three diameter size classes (fine 0-2 mm, medium 2-10 mm and coarse >10 mm) before being washed with ultrapure water and dried for a week at 40°C. Fine roots inorganic composition was determined by ICP-MS after acid digestion with a microwave oven at GET, Toulouse, while C and N were measured with a CNHS analyzer Thermo, also at GET. Carbon content in roots was 430 $g.kg^{-1}$, N content 15 $g.kg^{-1}$ (C:N ratio = 29) and P content 1.5 $g.kg^{-1}$. Other element contents were dominated in decreasing order by Ca, K, Mg (Table 4).

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Table 4: Fine Roots (<2mm) elemental composition. Fine roots inorganic composition was determined by ICP-MS after acid digestion with a microwave oven at GET, Toulouse, while C and N were measured with a CNHS analyzer Thermo, also at GET.

Site	Roots type	Depth (cm)	C ($g.g^{-1}$)	N ($g.g^{-1}$)	P ($mg.kg^{-1}$)	Ca ($mg.kg^{-1}$)	Mg ($mg.kg^{-1}$)	Na ($mg.kg^{-1}$)	K ($mg.kg^{-1}$)
AF	FR (<2 mm)	15-30	0.43	0.015	1508	9175	3443	1613	7558

2.4 Incubation setup

Soils were incubated in the lab for 115 days in small lysimeters with a sintered base allowing the extraction of free pore water, hereinafter referred to as 'leachate', during the course of the experiment (González-Domínguez et al., 2017). Lysimeters were maintained in the dark at a controlled temperature of 20°C. An aliquot of 80 g homogenized topsoil or 100 g homogenized of subsoil was placed in each vial, moistened up to field capacity and left 4 days at 25°C in order to pre-incubate the soils. Teak fine roots collected between 15 and 30 cm of the agroforestry plot were added to half of the vials (treatment root '+R') at a rate of 1% of the soil mass, i.e., 0.8 g for topsoil and 1 g for subsoils corresponding to an addition of 4.34 g $C_{org}.kg^{-1}$ of soil (Table 2). Each lysimeter was then placed in a sealed container along with a vial containing water to prevent soil evaporation, and a vial containing 20 mL of 1 M NaOH to trap the CO_2 emitted. The amount of CO_2 flux emitted at each time step was then calculated from the difference between initial and final NaOH conductivity (Wollum II and Gomez, 1970; Abiven and Andreoli, 2014). NaOH solution was renewed after each CO_2 sampling, and the concentration of atmospheric CO_2 in the container was estimated from a container without soil (blank). Leachates were collected at each CO_2 sampling step by adding a volume of ultrapure water equivalent to the moisture content at field capacity (15 mL for topsoil and 20 mL for subsoils) followed by vacuum filtration. Soil moisture was monitored by weighing the vials. The amount of leachate extracted was also monitored in order to calculate the associated chemical fluxes. NaOH traps and leachates were collected 14 times at 1, 2, 3, 6, 9, 13, 17, 21, 28, 36, 43, 69, 92 and 115 days after the beginning of the incubation. Non-cumulative fluxes extracted at each time step will further be referred to as 'instantaneous fluxes'. The comparison of the respective effects of land use, soil depth and the presence/absence of roots on soil respiration and related chemical fluxes implied eight experimental configurations, each triplicated, except one set up for which the glass vial was broken and the sample lost (deep soil without any roots added in AF).

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Teak root decomposition rates and associated dynamics were estimated by subtracting the organic matter mineralization rates of soils without roots to those in which roots were added. With this calculation, we did not separate the decomposition of the root itself and the priming effect its addition induced. The corresponding values of C emitted as CO_2 ($C\text{-}CO_2$) were then compared to the initial carbon content of the roots (Table 4), thus assuming that priming effect was negligible compared to the root decomposition.

Chemical composition of leachates was determined with an ion chromatograph Dionex ICS 2000 for the major anions and with an ICP-OES AMETEK SPECTRO for the major cations. The total dissolved organic carbon (DOC) was determined with a Shimadzu TOC 5000 analyzer at GET. Since the volume recovered at each step was limited (<20ml), default alkalinity fluxes ($C\text{-}HCO_3^-$) were estimated by default for each replicate as the difference between the cationic and the anionic charges expressed in charge equivalent ($\mu eq.g^{-1}$ of soil) (Drever, 1997). The accuracy of this approach was further tested by merging, for each of the 8 experiments, the integrality of replicates and time steps and titrating the composite solution with a Mettler Toledo autotitrator. Alkalinity of composite leachate solutions were found to be close to their anionic charge default (Tables S3). Initial steps corresponding to 0, 1 and 2 days of incubation were not included in the analysis of leachate compositions because they corresponded to the dissolution of the salts initially present as soil pore water. These salts were particularly rich in Cl^-, NO_3^-, Na^+ and induced concentrations that were orders of magnitude higher than those of the solutes released during the incubation itself. Carbon fluxes will be presented in $mg.g^{-1}$ of soil, but associated fluxes will be presented in $\mu mol.g^{-1}$ of soil in order to compare the stoichiometry of leached chemical species.

2.5 Root sampling and analysis

Normal data distribution was assessed by the Shapiro-Wilk test and the homogeneity of variances by the Levene test. After confirming that data were normally distributed, analysis of variance (ANOVA) with subsequent multiple comparison Tukey HSD tests were performed on linear mixed models with the replicates as a random factor to analyze the effect of depth and land use on C mineralization dynamics and leachate chemical composition using the statistical software R (R software 2023, version 4.3.2). The level of significance of statistical tests was $p < 0.05$ in this study.

3 Results and discussion

Given the contrasting composition and land uses of the incubated soil samples, their reactivity during the experiment should also show different trends. We first describe and discuss the dynamics of respiration and of dissolved fluxes extracted from the soil without roots added. Then, we focus on the dynamics of root decomposition and its impact on dissolved fluxes mobility.

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3.1 Soils without roots

3.1.1 Respiration dynamics and dissolved carbon fluxes

Cumulative carbon fluxes emitted as CO_2 after 115 days of incubation differed according to soil depth and land use. Overall, topsoils exhibited higher respiration than in subsoils. In CP, the topsoil respiration was almost four times higher than in subsoil (topsoil: 1.1 ± 0.1 mg C-CO_2.g^{-1} of soil / subsoil: 0.3 ± 0.1 mg C-CO_2.g^{-1} of soil). For AF, the differences were smaller and not significant due to the variability among the AF subsoil replicates (topsoil: 1.3 ± 0.1 mg C-CO_2.g^{-1} of soil / subsoil: 0.8 ± 0.4 mg C-CO_2.g^{-1} of soil) (Fig.1 (A)). AF variability could result from the presence of fine roots in the soil samples which, although removed during sampling, left small-scale heterogeneity in a sample with such a low organic matter content, including microbial biomass (Rasse et al., 2005; Angst et al., 2016; Siegwart et al., 2023). For both sites the respiration values observed were rather low when compared with the literature for equivalent tropical soils (Abiven et al., 2005). In both topsoils, C-CO_2 fluxes represented about 15% of the initial C_{org} stocks. They represented a large proportion of the subsoils organic carbon (AF: 7.4E3 ± 3.9E3 mg C-CO_2.g^{-1} of C_{org} / CP: 1.4E3 ± 3.2E2 mg C-CO_2.g^{-1} of C_{org}). However, it was not feasible, as for topsoils, to accurately estimate the C_{org} stocks in subsoils and the associated percentage of C-CO_2 emitted relative to the initial C_{org} content since the C contents in subsoils were close to the detection limit. The uncertainty regarding the C_{org} stocks in subsoils is thus very high. The greater degradability of subsoil carbon could be due to changes in the physical and chemical conditions (moisture, redox) of the soil between the natural environment and incubation, including the sample preparation phases (drying and sieving) (Salomé et al., 2010).

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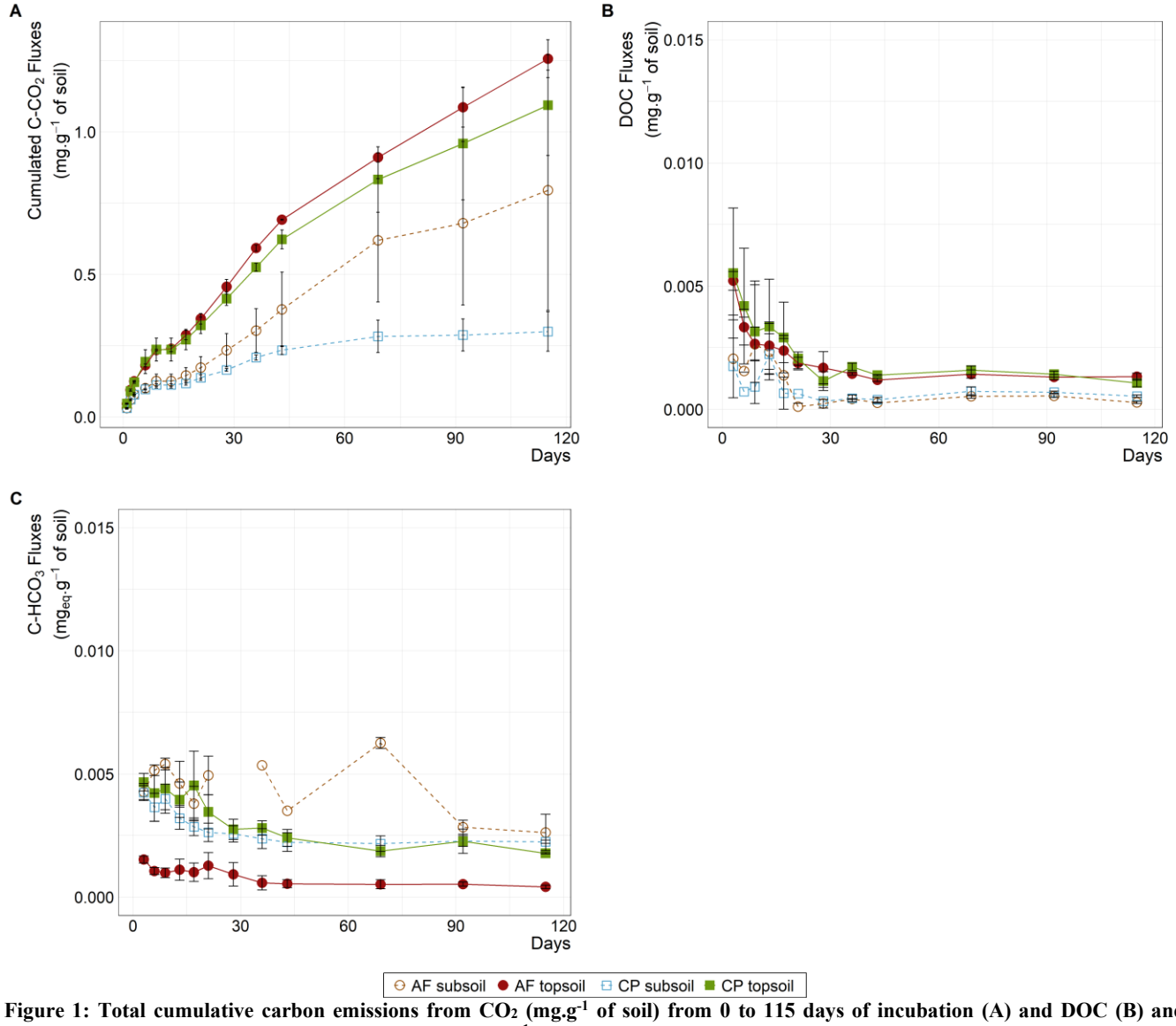

Figure 1: Total cumulative carbon emissions from CO_2 (mg.g^{-1} of soil) from 0 to 115 days of incubation (A) and DOC (B) and theoretical C-HCO_3^- (C) fluxes in the leachates (mg eq-.g^{-1} of soil) from 3 to 115 days of incubation in soils without any roots added. DOC fluxes were directly measured in the leachates at each time step. C-HCO_3^- fluxes were estimated based on the difference between the cations and anions sums at each time step. Error bars represent the triplicate variability, except for AF subsoil which was only duplicated.

Mineralisation dynamics could be described in three phases: (1) an intense production of CO_2 during 5-6 days, (2) a plateau when mineralisation of organic matter was minimal (6 to 21 days) and (3) a slow but steady mineralisation, strongly varying depending on the depth and land-use, until the end of the experiment (115 days). CP subsoil showed a dynamic that was expected for a subsoil with a mineralization that stopped quite early (around 43 days) when possibly all the resources in the soil were exhausted. On the contrary, AF subsoils presented an intermediate dynamic between both topsoils and CP subsoil with a continuously positive mineralisation rate until the end of the incubation (Fig.1 (A)). In experiments like incubations,

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such dynamics are usually smoother (Sierra et al., 2015). Since experimental conditions were constant and similar for all treatments, these phases may correspond to an evolution of the biological dynamics and/or activity. The second phase may have involved microbial communities that require time to develop, following K strategist dynamics (Kallenbach et al., 2015; Don et al., 2017; Sokol et al., 2022). Such dynamics were not visible for CP subsoil treatment, indicating that these communities may not play an important role under these conditions.

DOC instantaneous fluxes extracted as leachate varied with depth, but not with land use (Fig. 1 (B)). In topsoils, it accounted for 2-3% of the C-CO_2 fluxes and 0.4% of the C_{org}, while in subsoils it ranged between 5 (CP) and 12% (AF) of the C-CO_2 ones. Most of the DOC was extracted during the first 30 days of the incubation with fluxes decreasing quickly and then stabilizing until the end. During that last phase, fluxes were higher in topsoils (AF: 1.3E-3 ± 0.1E-3 mg.g^{-1} of soil / CP: 1.1E-3 ± 0.1E-3 mg.g^{-1} of soil) compared to subsoils (AF: 2.7E-4 ± 0.5E-4 mg.g^{-1} of soil / CP: 5.3E-4 ± 0.5E-4 mg.g^{-1} of soil). The fraction extracted at the beginning of the incubation corresponds to the labile C stocks initially present in the soils, and the product of the decomposition, leading to the production of microbial derived organic matter (Kalbitz et al., 2000; Kaiser and Kalbitz, 2012). In the second phase of the incubation, less decomposition (indicated by lower respiration rates) led to lower DOC production and consumption by soil microbes. Indeed, the rise in DOC flux between 6 and 21 days corresponded to the plateau of C-CO_2 production. This evolution was even stronger for subsoils than topsoils, which had a longer plateau phase. The sodicity of subsoils (see section "Soil sampling and analysis) may also explain a greater solubility of organic matter in these soils (Mavi et al., 2012).

C-HCO_3^- instantaneous fluxes revealed a strong influence of land use, at both depths (Fig.1 (C), Table S3). Theoretical alkalinity calculated over the whole incubation period was higher in AF subsoil than in topsoil (topsoils: 1.1E-2 mg eq- C-HCO_3^-.g^{-1} of soil/ subsoils: 4.4E-2 mg eq- C-HCO_3^-.g^{-1} of soil), while it was in the same range at both depth for CP (topsoils: 3.7E-2 mg eq- C-HCO_3^-.g^{-1} of soil/ subsoils: 3.3E-2 mg eq- C-HCO_3^-.g^{-1} of soil). Total alkalinity extracted corresponded to 1-3% of the C-CO_2 emissions in topsoils, to 6-11% in subsoils and accounted for 2-8% of the C_{inorg} in CP and AF topsoils and for 22% of the AF subsoil. These differences in terms of dissolution dynamics could be explained by pH differences between AF and CP topsoils, pH being around 0.6 lower in AF than in CP (Table 1).

3.1.2 Initial and final soil elemental stocks

Initial C_{org} contents were 7.2-9.8 g.kg^{-1} in topsoils and 0.2-0.4 g.kg^{-1} in subsoils, and remained in the same range after 115 days of incubation. The C_{inorg} contents remained close to the detection limit between the beginning and the end of the incubation (Table 2). Nitrogen, phosphorus and sulfur are brought to topsoil as fertilizers, and are mostly associated with soil organic matter. Both CP and AF topsoils are heavily supplied with nitrogen, mainly in the form of urea. In topsoils, total phosphorus (0.37-0.52 g P.kg^{-1} of soil) results from phosphate fertilizers, mainly in the form of hydroxyapatite. Approximately 10% of the total P stock was Plant-available. At depth, both P_{tot} and Plant-available P were below the detection limits of 0.04 and 0.002 g P.kg^{-1} of soil, respectively, so it was not possible to estimate the corresponding stocks. The variations in the measured N_{tot}

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stocks before and after the experiment were small and fall within the detection limit of the analyser for both top- and sub-soils (Table 2).

The CEC remained stable between the beginning and the end of the incubation in topsoils, but rose in subsoils (AF: +6 cmol+.kg^{-1} / CP: +4 cmol+.kg^{-1}) (Table 3). In absence of significant C_{org} content in subsoils, the increase of CEC could only result from physico-chemical processes. Such an increase is poorly documented in the literature. Renault et al. (2009), in their work on the incorporation of vinasse into ferralsols, also observe an increase in CEC which they attribute to alternating periods of oxidation and reduction. Indeed, the reduction of the structural iron initially contained in smectites would be responsible for an increase in the surface charge of waterlogged soils (Stucki et al., 1984; Favre et al., 2002, 2006). Another hypothesis could be the preferential release of exchangeable Na and/or K by initially low-concentrated solutions, as it is in the control sample from the incubation experiments conducted by Kanang et al. (2025). Exchange selectivity is a key process governing the dynamics of cations and, more broadly, of nutrients in the soil (Comerford, 2005). It depends on physico-chemical conditions (e.g. pH, presence of carbonates, quantity of exchangeable charges, physico-chemistry of the solution). Studies show that the exchange of monovalent cations for divalent cations at exchange sites is responsible for an increase in soil CEC (e.g., Rhue and Mansell, 1988; Appel et al., 2003).

The evolution of exchangeable elemental stocks differed mainly according to depth. First, exchangeable Na stocks were depleted in CP at both depths with losses ranging between 25 and 50% during the incubation (Table 3, Fig.2 (A) and (B)). However, for AF, stocks being initially much lower than in CP, they remained quite stable with losses ranging between 0-10% (Table 3, Fig.2 (A) and (B)). Then, for Mg and K, at both depths final stocks were higher than initial ones (between +25% and +125% of the initial stocks). Initial and final topsoil stocks of Ca were identical while in the subsoils, stocks after incubation increased by nearly 50% for both AF and CP (Table 3, Fig.2 (A) and (B)). As a result, the relative proportion of cationic charges in the exchangeable pool evolved significantly during the incubation. In topsoils, Mg rose by 9 to 11% and tended to compensate for the 8 to 9% loss of Ca. In subsoils, the relative gain of Mg (+9 to 13 %) offset both Na (-7 to -12%) and Ca (-1 to -2%) losses (Fig.3).

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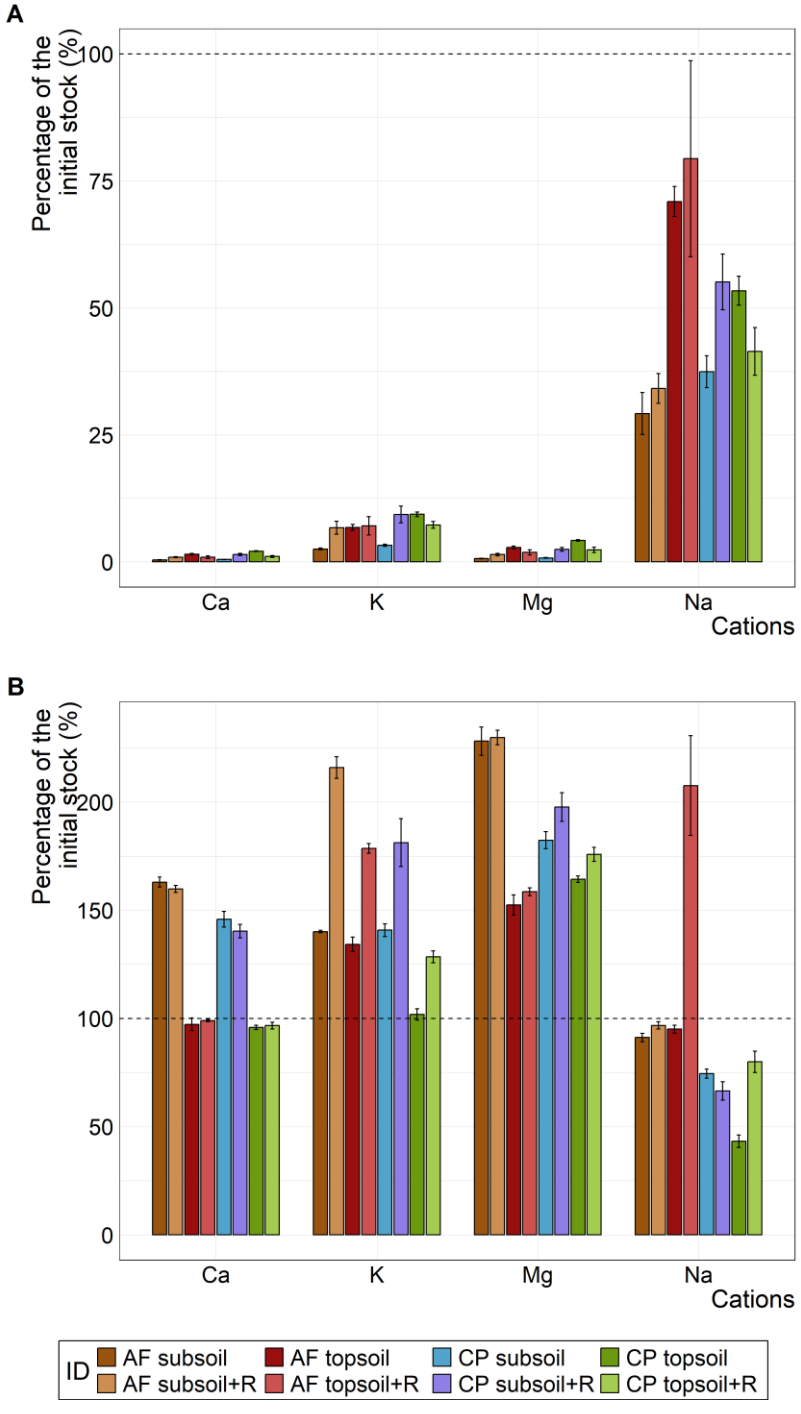

Figure 2: Total cumulative cations fluxes extracted in leachates between 3 and 115 days of incubation (A) and measured in the soil exchangeable stock at 115 days (B), both expressed by percentage of the initial soil exchangeable stock. The black dashed line represents the limit of 100% of the initial exchangeable stock. Error bars represent the triplicate variability, except for AF subsoil which was only duplicated.

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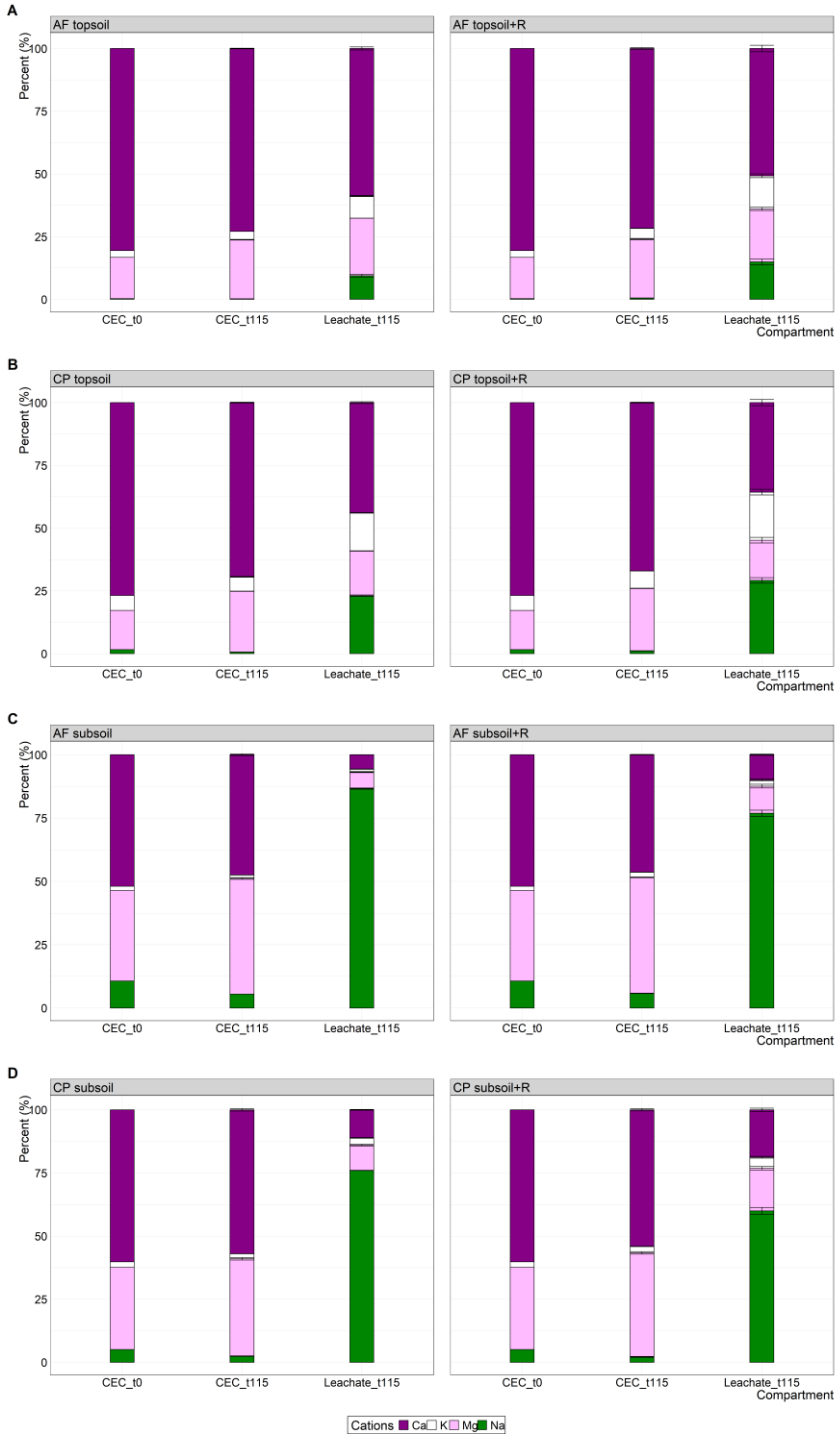

Figure 3: Initial (t0) and final cumulative(t115) 100% standardized stocks of cations in the soil exchangeable fraction (CEC) and the leachates for both soils without and with roots added: (A) AF topsoils, (B) CP topsoils, (C) AF subsoils and (D) CP subsoils. Error bars for CEC_t115 and Leachate t115 represent the triplicate variability, except for AF subsoil which was only duplicated.

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3.1.3 Leached N, S and P fluxes

Nitrogen ($N\text{-}NO_3^-$) and sulfur ($S\text{-}SO_4^{2-}$) instantaneous fluxes extracted during incubation varied strongly depending on depth, regardless of land use. In subsoils, both $N\text{-}NO_3^-$ and $S\text{-}SO_4^{2-}$ fluxes remained close to zero during the whole incubation (Fig.4 (A) and (B)), which was expected considering that subsoils had a very low C_{org} content (Table 2). The total amount of $N\text{-}NO_3^-$ extracted during the incubation was around 2.0 ± 0.1 µmol.g^{-1} of soil (AF) 1.7 ± 0.1 µmol.g^{-1} of soil (CP) in topsoils and of 8.5E-3 ± 2.3E-3 µmol.g^{-1} of soil (AF) 32.6E-3 ± 7.0E-3 µmol.g^{-1} of soil (CP) in subsoils (Table S1) corresponding to 2% of the initial topsoil N_{tot} stocks and less than 1% of the subsoil ones (Table 2). The total amount of $S\text{-}SO_4^{2-}$ extracted from topsoils was around one order lower than nitrogen ones (Fig.4 (A) and (B), Table S1). Both $N\text{-}NO_3^-$ and $S\text{-}SO_4^{2-}$ fluxes rose significantly during the incubation period following a three steps/bump dynamic similar as the one observed for CO2, especially after 43 days which also corresponded to the last phase of $C\text{-}CO_2$ production, when it started to slow down (Fig.1 (A) and Fig.4 (A) and (B)). These dynamics could be linked to SOM decomposition and changes in soil microbes' community structure or physiological shifts within the existing communities because a production of nitrates linked with a decline in soil respiration could be explained by the production of microbial necromass (Marschner and Kalbitz, 2003; Miltner et al., 2009; Cotrufo et al., 2013; Kallenbach et al., 2015). It makes sense that N and S were following similar dynamics because both biogeochemical cycles are closely related. As C, N and S being major compounds of SOM, the amount of soil organic S is closely linked to SOC and N_{tot} levels (Edwards, 1998; Wilhelm Scherer, 2009; Zhou et al., 2025).

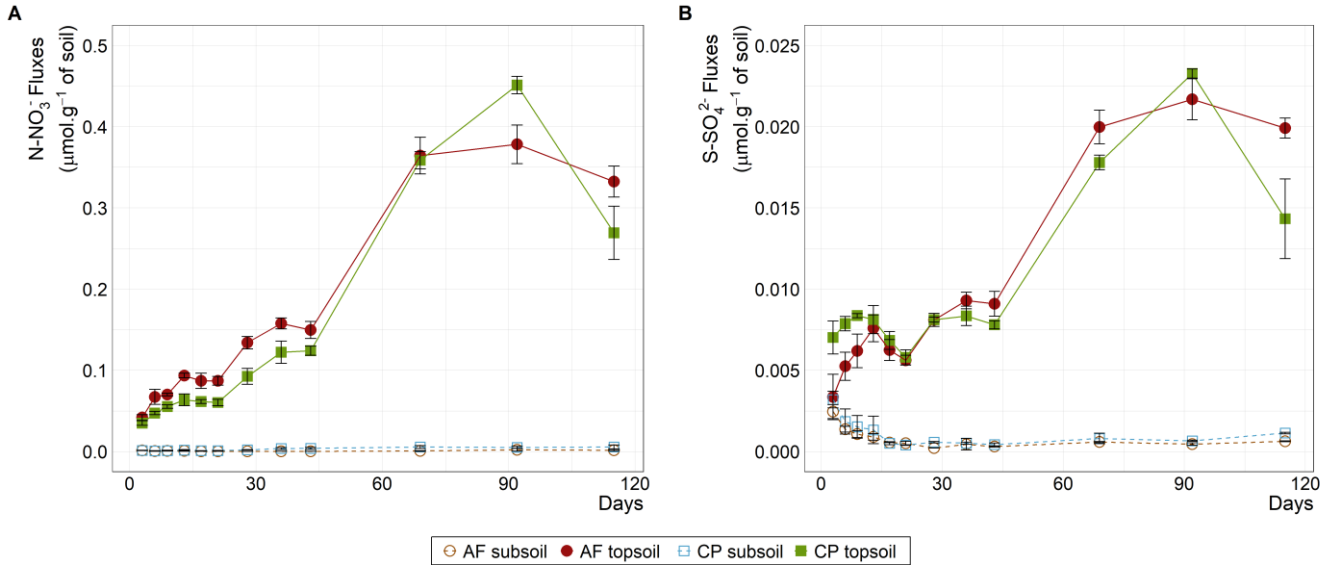

Figure 4: Nitrogen fluxes from $NO3^-$ (A) and sulfur fluxes from SO_4^{2-} (B) measured in the leachates (µmol.g^{-1} of soil) from 3 to 115 days of incubation in soils without any roots added. Fluxes were directly measured in the leachates at each time step. Error bars represent the triplicate variability, except for AF subsoil which was only duplicated.

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As for nitrogen and sulfur, phosphorus ($P\text{-}PO_4^{3-}$) instantaneous fluxes did not differ by land use, but only by depth. The total amount of $P\text{-}PO_4^{3-}$ extracted during the 115 days of incubation was around 0.1 ± 0.0 µmol.g^{-1} of soil (AF and CP) in topsoils and of 7.2E-3 ± 1.9E-3 µmol.g^{-1} of soil (AF), 11.8E-3 ± 5.2E-3 µmol.g^{-1} of soil (CP) in subsoils (**Table S1**), corresponding to 1% of the total initial topsoil phosphorus stocks and 7% of the Plant-available one (**Table 2**). For subsoils, given the initial levels of total and plant-available P, which were under the detection limits, it was expected that fluxes would be very low. In terms of dynamics, significant variations were only observed in subsoils in which fluxes rose to 3E-3 µmol.g^{-1} of soil between 26 and 36 days and then quickly depleted again around 0 µmol.g^{-1} of soil in less than 10 days. In topsoils, they tended to decrease from 43 days (**Fig.5**).

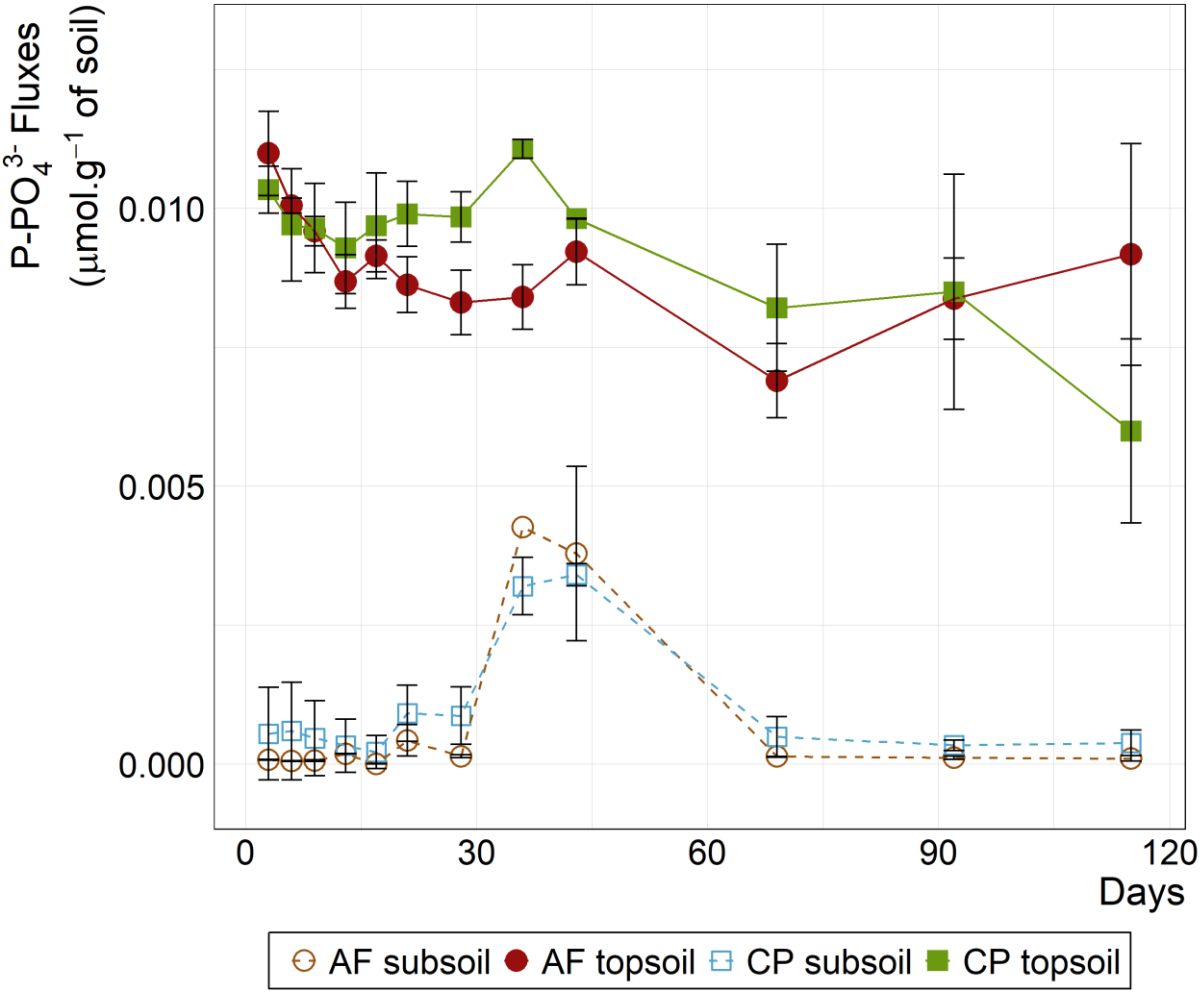

Figure 5: Phosphorus fluxes from PO_4^{3-} measured in the leachates (µmol.g^{-1} of soil) from 3 to 115 days of incubation in soils without any roots added. Fluxes were directly measured in the leachates at each time step. Error bars represent the triplicate variability, except for AF subsoil which was only duplicated.

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3.1.4 Leached cations

Total fluxes of cations extracted during the 115 days of incubation are presented in **Table S2**. Cation fluxes in leachates were dominated by Na in CP topsoil and both AF and CP subsoils and accounted for 43 and 90-95% of the fluxes, respectively. In AF topsoil, the cations fluxes were more balanced (**Fig.3**). Proportions of Na in leachates were strongly correlated to the absolute and relative stocks of Na in the CEC of the corresponding soils (**Fig.6 (A)**). This is not really surprising, because CEC is the only possible source of labile Na in these experimental conditions, and Na in calcareous soils is known to be the most weakly bound to clay minerals surfaces (e.g., Jalali et al., 2020). However, Na was over-represented in all leachates compared to its relative abundance in the CEC (**Table 3**). For instance, while in CP topsoil Na represented only 1% in the CEC, it contributed to 25% of the cations flux extracted (**Fig.3 (B)**). Conversely, Ca and Mg contributions in leachates were reduced as soon as the Na content in the CEC reached a few percent, as in CP topsoil (4.5% Na in CEC), while K, another monovalent cation, was still significantly leached, at least close to its proportion in CEC. In both subsoils with Na beyond 10% in CEC, the release of all three cations was inhibited (**Fig. 6 (A)**).

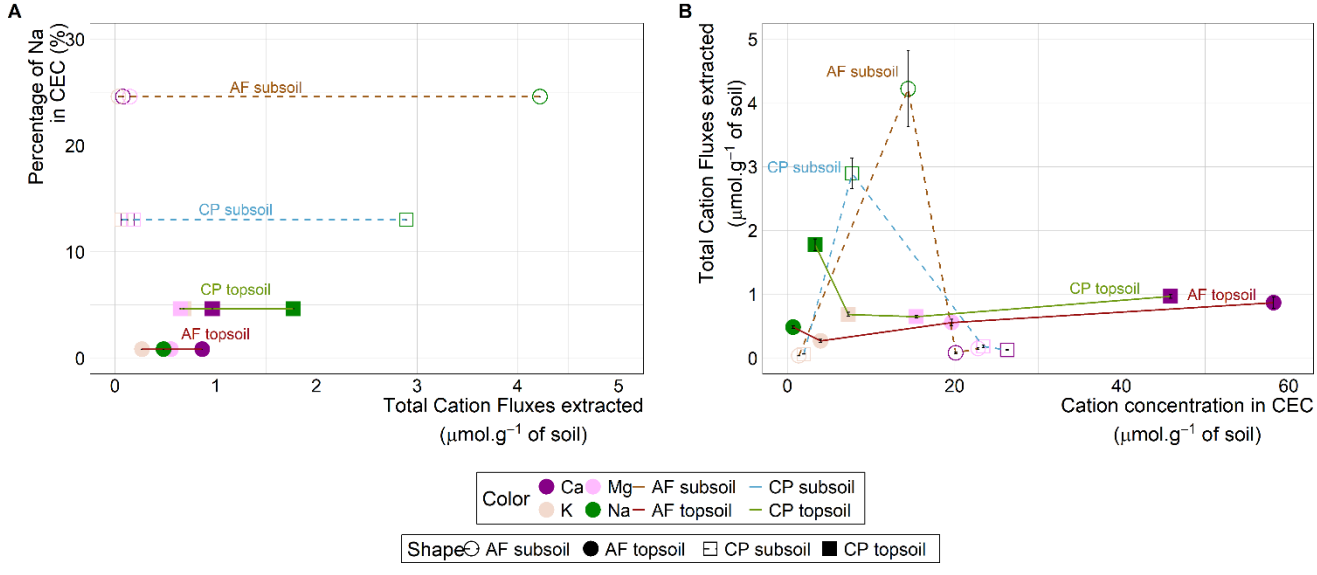

Figure 6: Relationship between the total cumulative flux of cations (Ca^{2+}, Mg^{2+}, Na^{+}, K^{+}) extracted from 3 to 115 days of incubation in soils without any roots added and (A) the proportion of Na in the initial CEC of the four soils analyzed (AF topsoils, AF subsoils, CP topsoils, CP subsoils) and (B) the content of cations in the CEC (µmol.g^{-1} of soil). Plain (topsoils) or dotted (subsoils) lines join the cations from the same soil. Error bars represent the triplicate variability, except for AF subsoil which was only duplicated.

As a conclusion, within our experimental conditions at least, we inferred that Na from CEC played a dominant role in adjusting the charge balance of porewater solutions and the exchange cations composition during incubation. When significantly present in the CEC, it controlled by default the nature of the cations released in solution. The content or proportion of exchangeable Ca, Mg and K in the CEC only played a secondary role in the fluxes exported in leachates (Fig.6 (B)). Ca was the least leached element from the CEC, even though it was the most abundant in the four soils analyzed (34 to 70% in molar proportion), and

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this low proportion of leaching may even be overestimated when soils contained calcium carbonates. Preferential Ca retention on clay minerals is consistent with the findings of DeSutter et al. (2006) and earlier authors, and Ca ion bonding in soil not only involves outer sphere complexes but may also be retained more strongly by soil components through inner sphere complexes (Rowley et al., 2018).

Analysis of the dynamics and intensity of cations instantaneous fluxes extracted during incubation made it possible to assess which cations indirectly balanced anions. The first phase of the incubation (43 days) was characterized by the intense leaching of Na from subsoils, irregular in AF subsoil, and decreasing with time for CP subsoil. This trend was also found, with a lower intensity, in topsoils (Fig.7 (D)). During these 43 days phase more than 80% of the Na flux was extracted, while less than 20% extracted in the last 70 days of the incubation. The temporal evolution of Na leachates from the subsoil was identical and of the same intensity as that of default alkalinity, which was by far the dominant anion (Fig.1 (C)). Anionic charges associated with alkalinity are neutralised by Na, both of which originate from the dissolution of residual sodium carbonate phases resulting from initial soil drying, or to the dissolution of calcium carbonate followed by a Ca-Na exchange within the CEC. In topsoils, the control on other cations by Na was less effective because of the lower Na content in the CEC (Table 3). However, the leaching dynamics of Na and alkalinity in CP topsoil were still similar (Fig.1 (C) and Fig.7 (D)).

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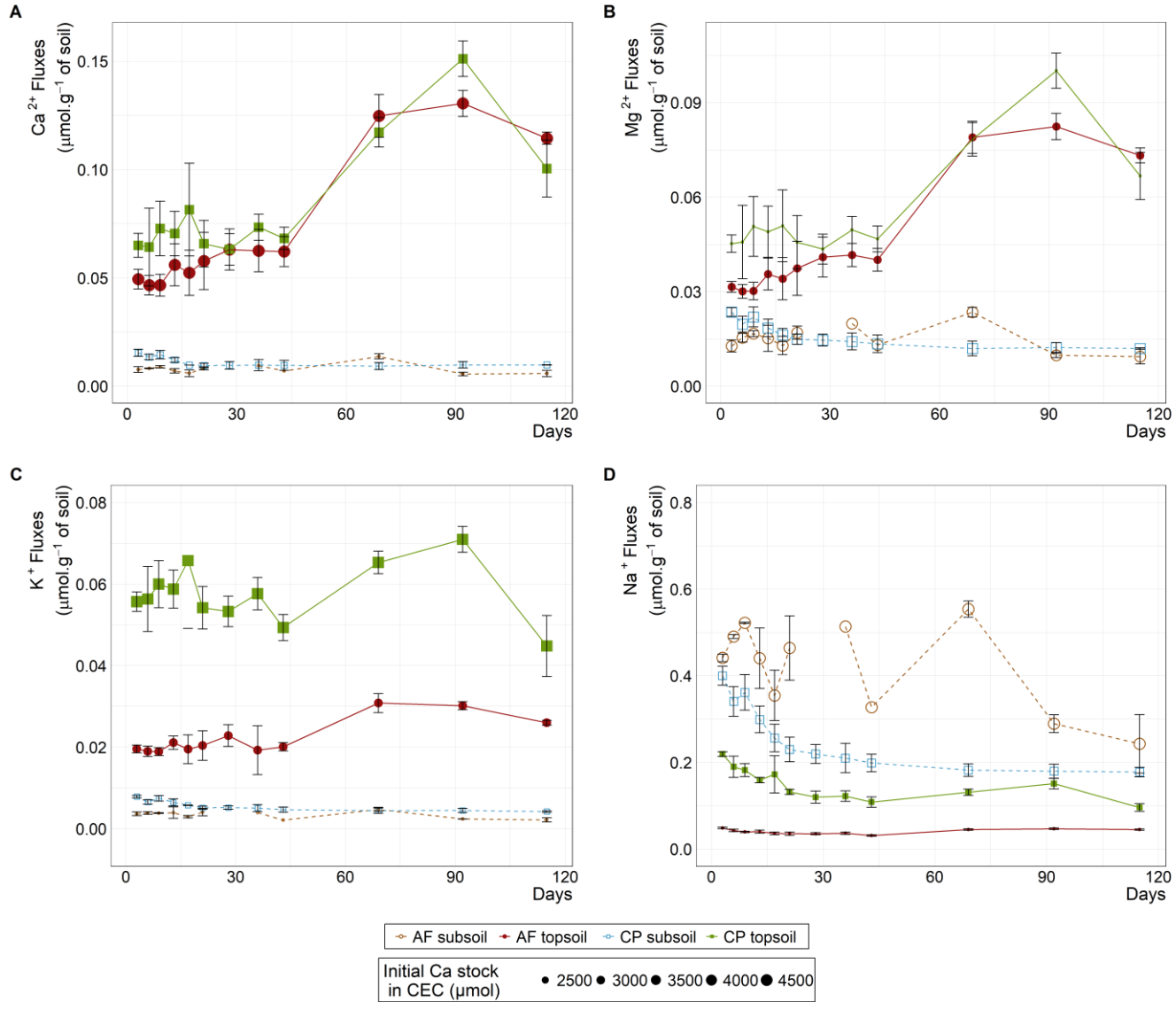

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Figure 7: Calcium (A), magnesium (B), potassium (C) sodium (D) fluxes measured in the leachates (µmol.g^{-1} of soil) from 3 to 115 days of incubation in soils without any roots added. Fluxes were directly measured in the leachates at each time step. The size of points is related to the relative stock of a given cation on the CEC. Error bars represent the triplicate variability, except for AF subsoil which was only duplicated.

430 For a given soil, the dynamics of Ca and Mg instantaneous fluxes were identical. Both elements were released in the same proportions throughout incubation, thus maintaining for each soil a constant Ca/Mg ratio (Fig. 7 (A) and (B)). However, this ratio ranging between 0.5 and 1.5 was always lower than that of the exchangeable phase (Table 3). This confirmed the systematic preferential retention of Ca, which was approximately twice that of Mg. While the instantaneous Ca and Mg fluxes from the subsoil remained constant and very low during the whole incubation, those in topsoils doubled from 43 days. This

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result is consistent with the classical lyotropic series view or Hofmeister effect for base cation exchange selectivity, based on the valence and the hydration radius of the cations (Liu et al., 2013) and means that its leaching remains limited. Comparison of this dynamic with that of anions reveals that leached Ca and Mg compensated for the release of nitrates and sulfates, whose fluxes increased significantly in the second half of incubation (Fig.4 (A) and (B), Fig.7 (A) and (B)). This charge compensation was almost stoichiometric, with 0.5 $\mu eq^{+}.g^{-1}$ for cations and 0.44 $\mu eq^{-}.g^{-1}$ for anions at the peak around 90 days. This last incubation phase also corresponded to the phase in which Na stocks in the CEC were the lowest for the two soils that initially had the lowest Na content in the CEC at the beginning of incubation.

As the least abundant cations leached, potassium did not compensate for specific anions in solution. It rather behaved intermediately between Na and Ca-Mg, depending on the Na content in the CEC (Fig.7 (C)). In subsoils with high Na content in the CEC, K was preferentially immobilized like Ca and Mg on the solid phase throughout the incubation. Conversely, AF topsoil, which had the lowest Na content in the CEC, saw K desorbing with a dynamic similar to Na, i.e., strong during the first 30 days of incubation and weaker thereafter. Interestingly, the K leaching from CP topsoil experienced two opposite dynamics compared to Na. The experiment was of sufficient duration to observe a change in the solid-phase affinity between K and Na. Given that the adsorption affinity for a cation depends on the amount adsorbed and the equilibrium concentration in the solution (Jalali et al., 2020), there is a tipping point at 30 days, beyond which Na is sufficiently depleted from the exchangeable fraction for K to be released into the solution in proportions similar to those of AF topsoil (Fig.8 (C)).

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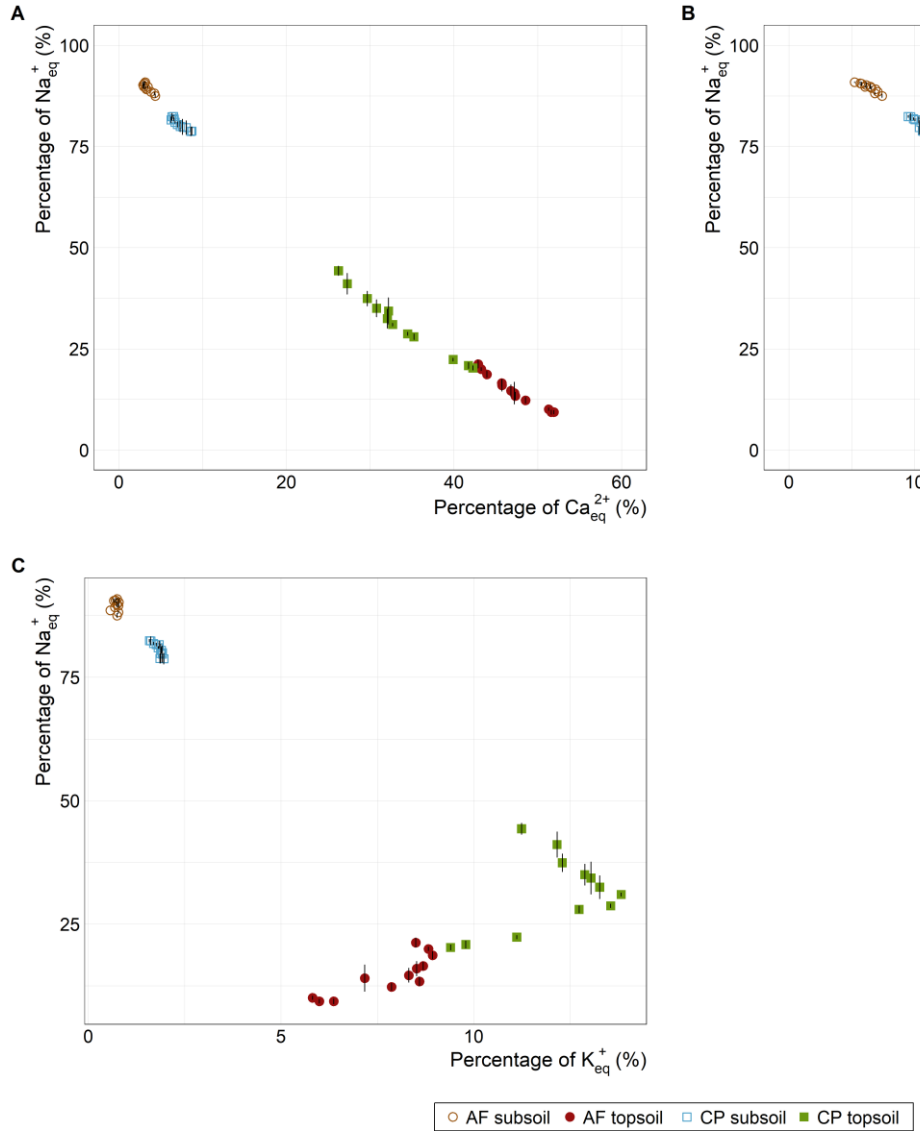

Figure 8: Proportions of Na^+ in leachates at each step of the incubation between 3 and 115 days of incubation for the four soils analyzed (AF topsoils, AF subsoils, CP topsoils, CP subsoils) without any roots added, against the proportion of (A) Ca^{2+}, (B) Mg^{2+} and (C) K^+ in these same leachates. Error bars represent the triplicate variability, except for AF subsoil which was only duplicated.

In summary, mineralization of OM by microbial activity in soil can affect the chemical composition of pore solutions. The anions and protons released by this activity are counterbalanced by exchangeable cations from the CEC, whose relative proportions are strongly influenced by the Na content in the CEC. Na content in the CEC inhibits the leaching of other cations when significant, or moderates it. It enhances the retention of Ca and Mg in the exchangeable phase, and favors that of K.

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3.2 Soils with roots

3.2.1 Respiration dynamics and carbon fluxes

The C mineralisation from the roots was calculated by the difference between the C-CO_2 emitted from soils with roots and soils without roots. It ranged from 8.2 ± 2.0 % in AF subsoil, to about 20% in both AF topsoil and CP subsoil and to 33.8 ± 11 % in CP topsoil (Fig.9 (A)). This high degree of variability in the decomposition of the same root material was somewhat unexpected, as it is usually believed that the early stages of decomposition in fresh material are primarily related to its chemical and intrinsic properties (Trinsoutrot et al., 2000; Abiven et al., 2005; Hicks Pries et al., 2017). In this study, we hypothesize that quality aspects are secondary as compared to local environmental parameters like microbiomes or nutrient availability (Schmidt et al., 2011; Wang et al., 2023). Surprisingly, roots decomposed less in the soils that originally contained teak roots. This observation goes against the home-field advantage concept (Fanin et al., 2021; Liang et al., 2024), which considers that microbes that are used to decompose one type of OM decompose it faster. The additional carbon losses observed in CP topsoils could be due to the legacy effect on priming. Indeed, as the decomposition of the root itself cannot be distinguished from its associated priming with this experimental design, the extra CO_2 emissions could be related to the decomposition of the native SOM. Schiedung et al. (2023) recently showed that the priming effect was mostly controlled by the legacy of organic inputs, i.e. the higher and more frequent the organic inputs, the lower is the priming. As microbes in CP topsoils were not used to receive teak roots derived compounds, the supposed priming effect here occurred stronger than it could in AF.

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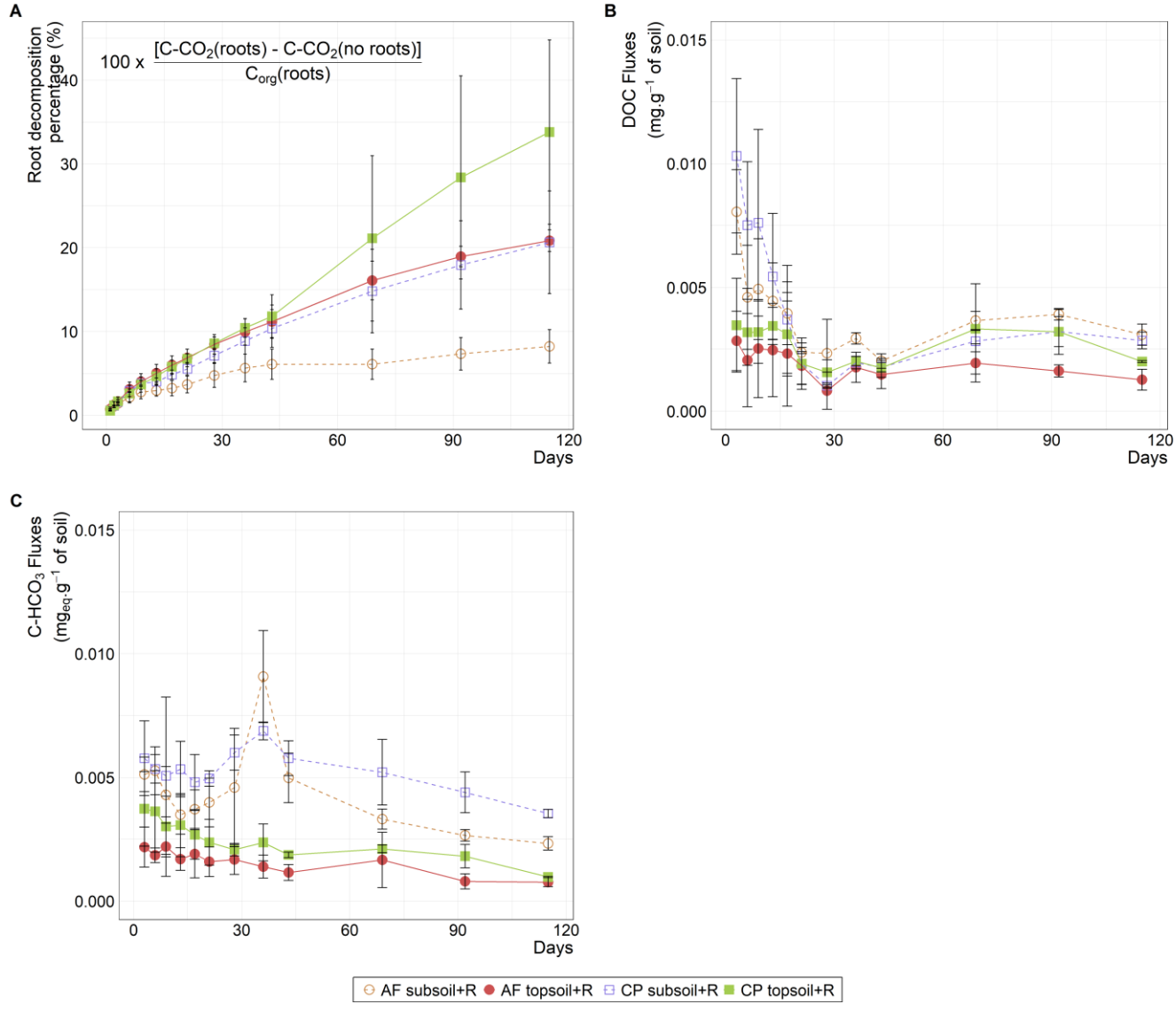

Figure 9: Total cumulative carbon emissions from CO2 (mg.g^{-1} of soil) from 0 to 115 days of incubation (A) and DOC (B) and theoretical C-HCO_3^- (C) fluxes in the leachates (mg eq-.g^{-1} of soil) from 3 to 115 days of incubation in soils with roots added. DOC fluxes were directly measured in the leachates at each time step. C-HCO_3^- fluxes were estimated based on the difference between the cations and anions sums at each time step. Error bars represent the triplicate variability.

As for soil without roots, DOC instantaneous fluxes varied with depth but not with land use. In topsoils with roots, it accounted for 1% of the C-CO_2 fluxes and 0.2-0.4% of the C_{org} (without taking into account the added C_{org} stocks of the roots), while in subsoils with roots it accounted for 4% of the C-CO_2 ones. In terms of fluxes in topsoils, the addition of roots did not have any impact on DOC fluxes for both sites. However, in the subsoils, adding roots into the system resulted in a net positive flux of DOC (Fig.9 (B)). This flux was weak but constant during the whole incubation period and in the end the total cumulative DOC fluxes were of 4.5E-2 mg.g^{-1} of soil for AF and of 5.0E-2 mg.g^{-1} of soil for CP. The higher fluxes during the first 15 days may

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be associated with some remaining OM washed from the root surfaces. This net flux of DOC occurred in the same range for both sites, which was surprising considering that root decomposition was almost three times higher in CP than in AF subsoils (Fig.9 (A)).

C-HCO_3^- instantaneous fluxes estimated from default alkalinity were similar to those of soils without roots, except for CP subsoil for which they were almost 2 times higher. These higher C-HCO_3^- fluxes in CP subsoil with roots added compared to soil without roots started from 28 days and then decreased until the end of the incubation. At 115 days they were still significantly higher than the C-HCO_3^- fluxes from CP subsoil without roots. In AF subsoils with roots the same tendencies as CP were observed. However, variability in both AF subsoils with and without roots was much higher and did not allow to identify significant changes due to the addition of roots (Fig.9 (C)). Total default C-HCO_3^- extracted corresponded to 1% of the C-CO_2 emissions in topsoils with roots, to 4-5% in subsoils with roots and accounted for 10-13% of the C_{inorg} in CP and AF topsoils and for 48-63% of both subsoils (Table S3).

3.2.2 Initial and final soil elemental stocks

After 115 days of incubation, the rise in C_{org} content in soils in which roots were added, was around +2 $g.kg^{-1}$ for both AF and CP topsoils, and was +0.8 $g.kg^{-1}$ and +1.5 $g.kg^{-1}$ for CP subsoil and AF subsoil respectively, while C_{inorg} content remained steadily close to the detection limit. As for soils without roots, the variations in the measured N_{tot} stocks before and after the experiment were small and fell within the detection limit of the analyser for both top- and sub-soils (Table 2).

Final CEC in topsoils were identical to initial ones and to those without roots. Final CEC in subsoils with added roots increased to levels identical to those without roots (AF: +6 $cmol+.kg^{-1}$ / CP: +4 $cmol+.kg^{-1}$) (Table 3). Only the K content in the CEC increased significantly in all soils during the incubation with roots, as compared to soils without roots. This increase corresponded, in topsoils, to the content present in the added roots, i.e. 2 $\mu eq.g^{-1}$ of soil, and to half of it in subsoils (Table 3 and Table 4). This indicates that all K contained in the roots would have been mobilized during the incubation period, regardless of the final degree of root decomposition in these soils, and that the released K was subsequently transferred to the exchangeable fraction without significant leaching (Fig.2 (B)). This interpretation is consistent with the high mobility of K in plants, which is linked to its physiological roles and weak complexation with plant tissues (review in Hawkesford et al., 2012). Its rapid leaching during the decomposition of tree leaves, including those of tropical trees, is also well documented (e.g. O'Connell and Sankaran, 1997; Rogers, 2022).

3.2.3 Leached N, S and P fluxes

N-NO_3^- instantaneous fluxes leached from topsoils with roots, 0.2-0.3 $\mu mol.g^{-1}$ of soil, were 6 to 8 times lower than those from root-free soils (Table S1), indicating the organisation of mineral N by microbes during the mineralization of roots. Fig.10 (A) shows a classical dynamic of mineral N when organic input has a high C to N ratio, with a first phase of immobilisation of the nitrogen, then a release of nitrate and ammonium as the microbial biomass decays (Mary et al., 1993). Leaching fluxes from subsoils were one order of magnitude lower than in topsoils (Fig.10 (A)). The nitrogen potentially released by root

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mineralization in subsoils was therefore retained in its entirety throughout the incubation. Thus, none of the N-NO_3^- outgoing fluxes for each soil were correlated with the final decomposition rate of roots (R2=0.28).

S-SO_4^{2-} instantaneous fluxes of the two topsoils with roots were similar, but 3–4 times lower than those from the same soils without roots (Table S1, Fig.10 (B)). As for nitrogen, sulfur that may be produced by root decomposition or mobilized from topsoil stocks was also effectively retained in the soil. However, on the contrary to N-NO_3^-, S-SO_4^{2-} outgoing fluxes were correlated, for each soil, with the final decomposition rate of roots (R2=0.89), so the effect of soil nature or land use on P-PO_4^{3-} fluxes was indirect. In subsoils, the leachate fluxes were close to 0, and thus similar to those extracted without roots (Fig.10 (B)). Here again, the sulfur potentially produced by root decomposition was retained in the soil. Since only the excess S-SO_4^{2-} not used for cellular synthesis would be leached from the soil (Wilhelm Scherer, 2009), the immobilization observed here may indicate that soil microbial biomass not only persisted but also increased as a result of root decomposition in the topsoil.

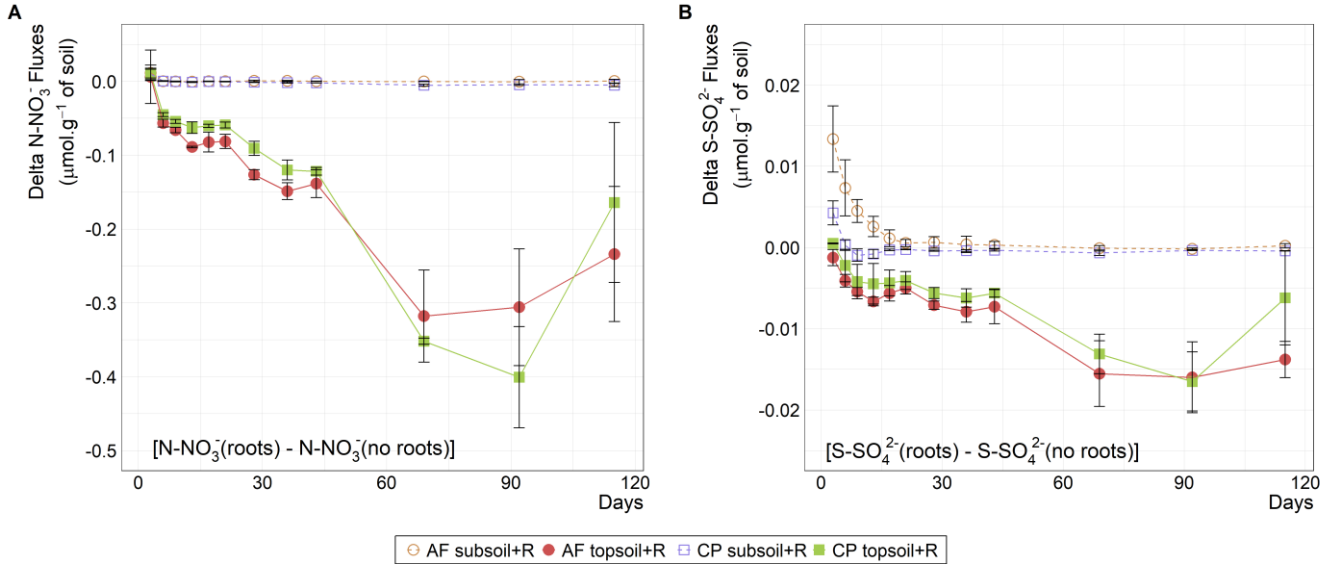

Figure 10: Nitrogen from NO_3^- (A) and Sulfur from SO_4^{2-} (B) production (>0) or immobilization (<0) derived from root decomposition (µmol.g^{-1} of soil) in comparison to the cumulative root decomposition percentage from 3 to 115 days of incubation. It was calculated by subtracting the S-SO_4^{2-} concentrations measured in the leachates of soils without roots to the ones of soils with roots. Error bars represent the triplicate variability.

As for N-NO_3^- and S-SO_4^{2-}, P-PO_4^{3-} instantaneous fluxes leached from soils with roots varied with depth but not with land use. However, on the contrary to N-NO_3^- , the P-PO_4^{3-} fluxes were correlated with the final decomposition rate of roots (R2=0.76), so the effect of soil nature or land use on P-PO_4^{3-} fluxes was indirect. Subsoil fluxes were four times higher when roots were added than without (Table S1). From a dynamic perspective, all the instantaneous fluxes extracted from soils with roots followed a similar pattern (although with varying intensities), showing a steady increase during the first 40–50 days, followed by a continuous decline (topsoils) or a decline followed by stagnation (subsoils) until the end of the incubation (Fig.11). The

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fact that leaching dynamics were similar across all soils with roots during the first 40–50 days suggested that the released P-PO_4^{3-} originated from the roots rather than the soil. This correlation also indicates that P-PO_4^{3-} may not be significantly immobilized by the soil during this phase of incubation (Fig.11). The mobility and mineralization of phosphorus during root decomposition is known (e.g. Scheffer and Aerts, 2000). However, significant sorption and/or adsorption onto soil particles would have been expected as P-PO_4^{3-} , in particular phytate, can be adsorbed onto soil particles within minutes (Garcia-Lopez et al. 2024). But it was shown that phytate sorption can be coupled with the release of inorganic P to the solution, due to competition between the two forms (Berg and Joern, 2006; Garcia-Lopez et al. 2024). Another possible explanation is that phosphorus was mineralized as the root decomposed without diffusing into the soil, and that it is the addition of MQ water prior to extraction that leached directly this phosphorus, with nearly no interaction with the soil. One argument in favor of this hypothesis is that the instantaneous flux of P extracted beyond 50 days decreased significantly for both soils with roots and soils without roots when the sampling interval shifted from one week to one month. If this hypothesis was confirmed, it would mean that the flux of extractable phosphorus from an incubation with soil is primarily governed by the sampling interval of the solutions and is therefore protocol dependent. In the natural environment, where the percolation rates of pore solutions are generally slow—taking a few months to a few years to travel the first meters in this type of soil (Riotte et al., 2014)—phosphate ions would likely be adsorbed in the vicinity of decomposing roots. Despite this potential analytical limitation, a comparison of the total P-PO_4^{3-} fluxes extracted from the four soils indicated that, at equivalent rates of root decomposition, phosphorus was retained twice (CP subsoil) to four (AF and CP topsoils) times more in AF subsoil than in the other soils (Fig. S3).

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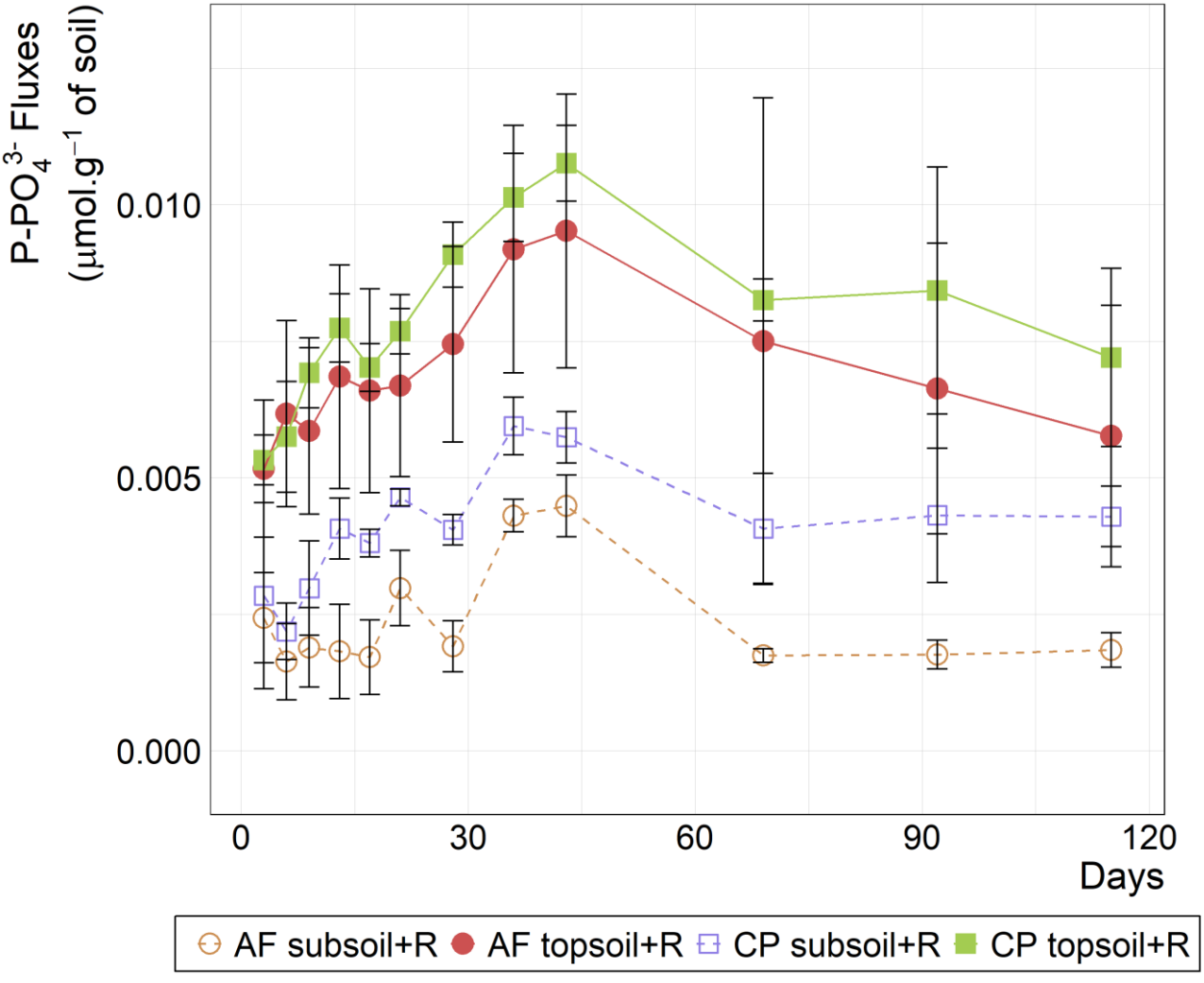

Figure 11: Phosphorus fluxes from PO_4^{3-} measured in the leachates (µmol.g^{-1} of soil) from 3 to 115 days of incubation in soils with roots added. Fluxes were directly measured in the leachates at each time step. Error bars represent the triplicate variability.

3.2.4 Leached cations

The total fluxes of Na and K extracted from topsoils with roots were equivalent (AF) or 20% lower (CP) than those from soils without roots, while those of Ca and Mg were 40 to 50% lower (Table S2). In contrast, the fluxes extracted from subsoils with roots were significantly higher than those from subsoils without roots, ranging from +13-46% for Na in AF and CP subsoils respectively, to +100–150% for Ca and Mg and +200% for K (Table S2), although the fluxes for K were still very low in

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comparison with other cations. Despite the increase of K, Ca, and Mg fluxes from subsoils, these remained well below the amounts supplied by the roots. For K at least, this limited flux was consistent with its transfer on the CEC (see section 3.2.2.). This may not be the case for Ca and Mg which play a structural role in organic compounds or may be accumulated in inorganic forms, as Mg can be accumulated in vacuoles (Sarraf et al., 2026 and references therein) and Ca as oxalate in parenchyma, phloem and cambium (Baptista et al., 2013). In any case, the possible transfer of Ca and Mg from the root to the CEC during root degradation could not have been detected by analyzing CEC stocks, since the inputs from the roots were too small to have a significant impact on the stocks present in the CEC.

In the same way as for root-free soils, the nature and intensity of cation fluxes extracted from soils with roots were influenced both by the anions produced during the mineralization of soil and root OM and by the distribution of cations within the exchange sites of each soil. The proportions of cations extracted from soils with roots were quite similar to those from soils without roots. Na still accounted for 31 to 89% of the molar flux of extracted cations and therefore remained dominant (Fig. 3). The inhibitory effect due to the high proportion of Na in the CEC on Ca and Mg leaching (subsoils) was less clear than for soils without roots, as indicated by the general increase in leached fluxes from subsoils (Table S2 and Fig. 12). As with phosphate, this difference in behavior could be partly due to the decision not to grind the roots and to facilitate the extraction of pore water by adding ultrapure water to the soil surface. A small portion of the cations released during root degradation could have been leached out during extraction without having reached equilibrium with the soil's CEC. This hypothesis would explain both the flux of Na extracted from subsoils—which was greater with roots than without—and those of Ca and Mg (Table S2). While the degradation of the entire root reflected field conditions, the same may not be true for the rapid leaching of pore solutions, particularly in subsoil. Under our experimental conditions—and here again, as with phosphate—the mobility of the cation, although limited, is probably still overestimated.

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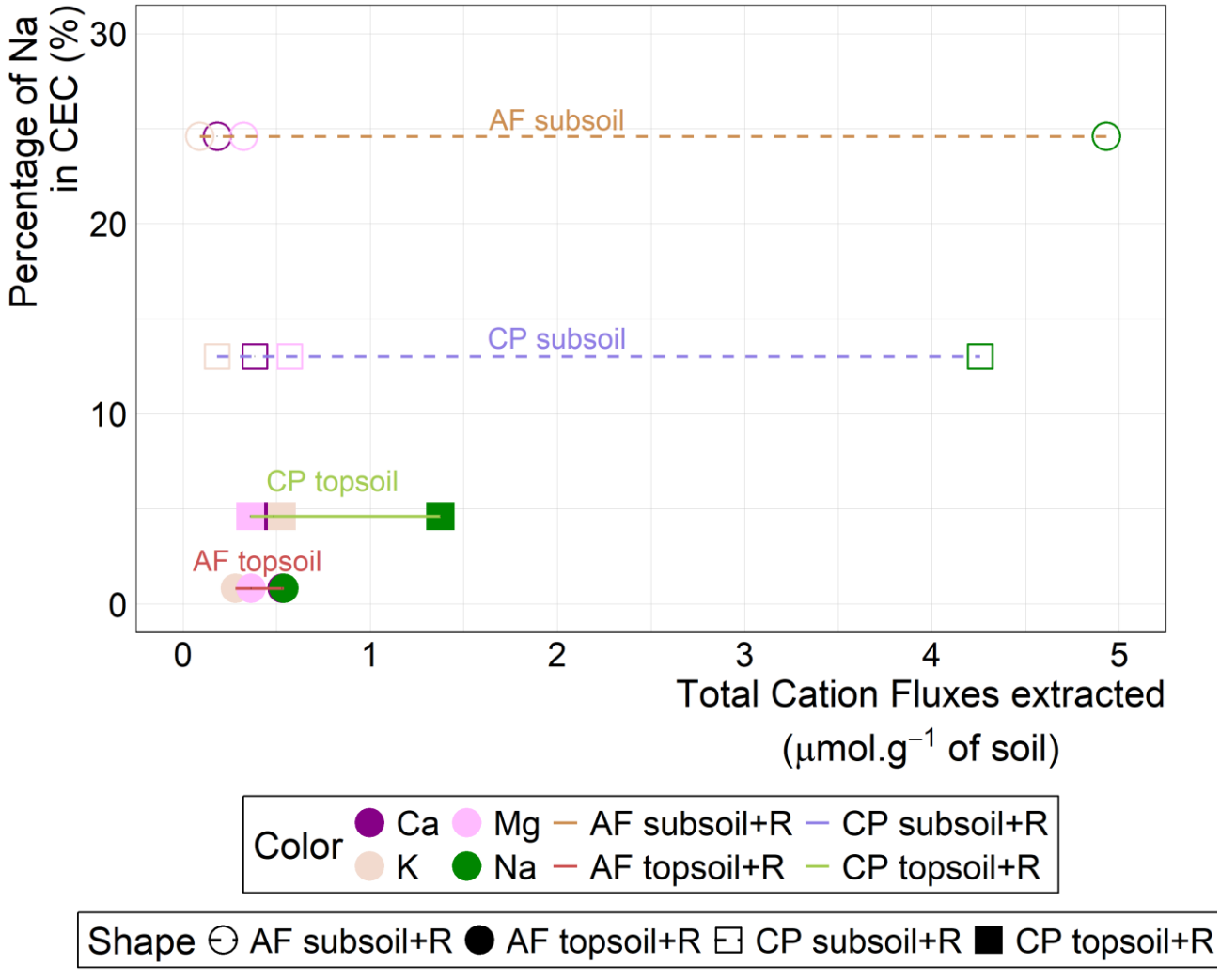

Figure 12: Total cumulative cations fluxes (Ca^{2+}, Mg^{2+}, Na^{+}, K^{+}) extracted from 3 to 115 days of incubation in soils with roots added, versus the content of the same cations in the CEC (µmol.g^{-1} of soil). Plain (topsoils) or dotted (subsoils) lines join the cations from the same soil. Error bars represent the triplicate variability.

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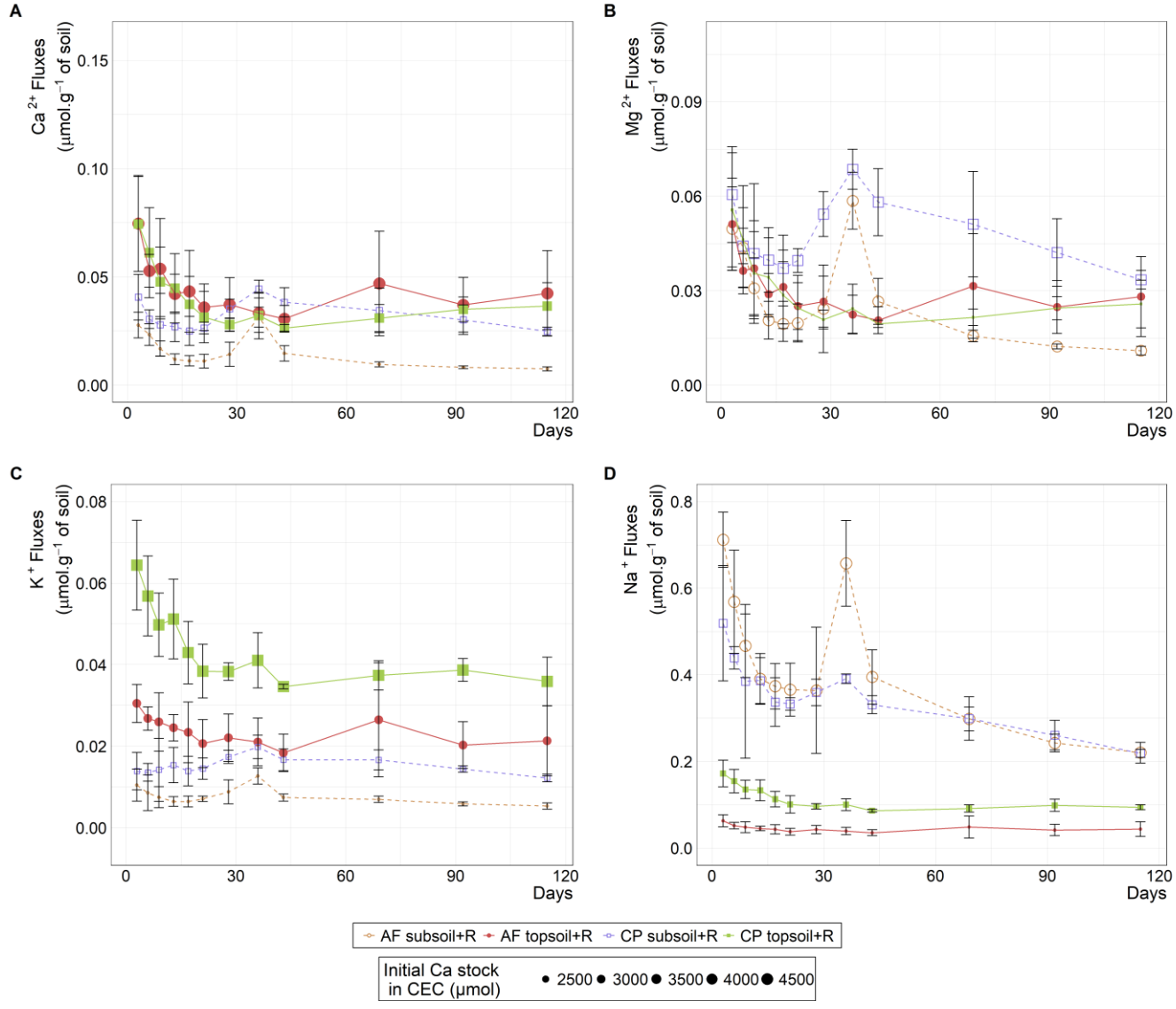

Figure 13: Calcium (A), magnesium (B), potassium (C) sodium (D) fluxes measured in the leachates (µmol.g^{-1} of soil) from 3 to 115 days of incubation in soils with roots added. Fluxes were directly measured in the leachates at each time step. The size of points is related to the relative stock of a given cation in the initial CEC. Error bars represent the triplicate variability. Error bars represent the triplicate variability.

However, in terms of dynamics, instantaneous cation fluxes (Fig. 13) exhibit profiles that differ from those observed in the absence of roots (Fig. 8). The initial instantaneous cation fluxes were similar to those in soils without roots. Except for K in CP subsoil, these fluxes decreased sharply and tended toward a narrower range by 20–30 days. Such a trend could not be explained by root decomposition, the rate of which was zero at the start of the experiment and then ranged between 5 and 8% at 30 days (Fig. 9 (A)). However, the fact that initial fluxes varied by up to an order of magnitude depending on soil type—as

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was the case for soils without roots—and that Na and K fluxes were proportional to the CEC indicate that this initial phase corresponded to the leaching of residual salts from the soil, which were buffered by the CEC. The decrease in Na was indeed balancing in intensity the one of Cl, while the decrease of other cations was compensating alkalinity and in the initial stages for topsoils, by $N\text{-}NO_3^-$ also likely residual (Table S1 and Table S2).

A very pronounced peak in Ca and Mg at 40 days was then observed in both subsoils, along with a peak in Na for AF one, as well as small peaks in CP topsoil (Fig. 13). These peaks were offset by default alkalinity in the subsoils and by $C\text{-}HCO_3^-$, $P\text{-}PO_4^{3-}$, and $S\text{-}SO_4^{2-}$ in CP topsoil (Fig. 9 (C)). With a root decomposition rate nearly identical to that at 30 days (Fig. 9 (A)), these fluxes could not be explained by a significant change in root decomposition that would have released cations. One possible explanation could be the dissolution of carbonates or the release of cations from the CEC associated with a temporary change in soil pH, resulting either from root degradation or from a change in redox conditions.

During the second half of the incubation period (the last 60 days), the leachable cation fluxes from soils with roots were more uniform than those from soils without roots, as if advanced root decomposition were buffering these fluxes. Fluxes in subsoils decreased steadily, whereas in topsoils, relative stability (Na, K) or a slight increase (Ca, Mg) was observed (Fig. 13). The fluxes of Ca and Mg in topsoils were much lower than those in soils without roots because they did not have to compensate for massive leaching of nitrate and sulfate during this phase (see section 3.1.4) (Fig. 13 (A) and (B)). This shows that the retention of anions resulting from root decomposition limits the leaching of cations compared to the same soil without roots added. In subsoils, Ca, Mg, and K were less leached than in topsoils with roots, even as root decomposition rates increased (Fig. 13 and Fig 9 (A)). Cation fluxes in subsoils appeared to primarily offset an alkalinity flux (Fig. 9 (C)). The buffering capacity of subsoils and their ability to retain nutrients such as K and Ca released by root degradation were two to four times greater for AF than for CP at an equivalent rate of root degradation (Fig. S6). This could indicate that subsoils with roots—even at low densities—are more able to retain nutrients resulting from root decomposition than soils that have never had roots or have not had them for a long time.

3.2.5 General discussion

To summarize, carbon fluxes emitted as CO_2 differed significantly according to soil depth and land use. In the absence of roots, nearly 98% of mobilized carbon was released as CO_2, indicating that dissolved carbon losses (DOC and $C\text{-}HCO_3^-$) were negligible. When roots were added, root decomposition inferred from CO_2 fluxes was greater in the topsoil of the conventional irrigated plot with only shallower annual rooting than in the topsoil of the agroforestry plot (perennial deep rooting), although a potential priming effect in the first case cannot be excluded. The excess CO_2 observed in the conventional irrigated system may therefore partly reflect decomposition of native SOM. By contrast, the agroforestry soils may reflect a legacy effect, with no clear evidence of priming, possibly because they were already adapted to recurring inputs of similar OM.

Focusing on the associated anion fluxes, even though land-use significantly impacted CO_2 emissions, only depth played a significant role. Nitrogen and sulfur showed a distinct behavior compared to phosphorus. In the absence of roots, topsoils exhibited substantial fluxes of these elements, especially after 60 days, whereas subsoils released very little, consistent with

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their low nitrogen content. With roots added, N and S fluxes remained low in both top- and subsoils, suggesting that these elements were rapidly retained during decomposition, most likely through microbial immobilization and biomass development. However, phosphorus behaved differently depending on whether roots were present. Without roots, topsoils, amended with phosphorus, showed a relatively steady and significant phosphate leaching. With roots, however, phosphorus was progressively leached during the first half of the incubation in all soils, indicating a likely root-derived source despite the relatively low decomposition rates, but then P fluxes decreased. Thus, $P\text{-}PO_4^{3-}$ phosphate release was probably influenced by the sampling interval, since longer sampling intervals were associated with lower phosphorus fluxes, suggesting that $P\text{-}PO_4^{3-}$ may have been retained by adsorption or fixation on soil minerals. Under natural conditions, where pore-water percolation is slower, retention of phosphate by soil minerals would likely dominate. Taken together, these results suggest a partial decoupling between N and S on one hand, and P on the other hand.

Finally, the anions produced by mineralization of SOM and root decay were compensated by cation release from the soil exchange complex. So here again, only a significant depth effect was recorded on the contrary to CO_2 fluxes. The relative fluxes contribution of each cation depended on its abundance in the CEC and on its affinity for exchange sites. Monovalent cations, especially Na and K, seemed preferentially leached relative to divalent cations such as Ca and Mg. Even a few percent of Na in the exchange complex of soils without added roots was sufficient to suppress the leaching of Ca, Mg, and K and to promote preferential Na export. Dynamically, Na leaching was concentrated in the first part of the incubation. During the second half of the experiment, nitrogen and sulfur release in topsoils without roots was mainly balanced by Ca and Mg, showing that pore-water stoichiometry can shift rapidly in response to changing anion fluxes. Root decomposition in the four soils produced more homogeneous Ca, Mg, and K fluxes than in soils without roots, with a small additional contribution of cations derived directly from roots. By the end of incubation, however, potassium from the roots was largely transferred to the CEC. All these results taken together point to a direct link between biological processing and nutrient retention in the soil.

These results shed new light on the dynamics of carbon stocks in these tropical soils. The dynamics of organic matter degradation are not only limited to an interaction between carbon and nitrogen, but involve multiple correlations among more than a dozen elements, each with its own dynamics. Contrary to concepts inspired by Liebig's law (or the law of the minimum), the co-limitation of decomposition by various elements may be more complex to model than previously thought.

4 Conclusion

This incubation experiment demonstrates that the mineralization of SOM and the decomposition of root inputs exert strong but element-specific effects on nutrient mobility in tropical soils, with soil depth emerging as the primary control on all measured fluxes. By contrast, land use produced comparatively limited effects on elemental dynamics, although it significantly affected CO_2 production and the intensity of root decomposition. These results indicate that deep tropical soils material are not inert reservoirs but chemically and biologically active compartments whose buffering capacity depends on their initial OM content, exchange properties, and mineral reactivity.

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Overall, this study shows that decomposition-driven nutrient mobilization is strongly filtered by soil depth and by the chemistry of the adsorption and ion exchange pools. At equivalent rates of root decomposition, subsoils retained N, S, P, K, and Ca more effectively than topsoils, and this retention was generally stronger under agroforestry than under conventional irrigated agriculture without perennial deep rooting. These findings support the view that agroforestry enhances the capacity of deep tropical soils to act as nutrient sinks and biogeochemical buffers, thereby improving internal nutrient recycling and potentially increasing the resilience of the agrosystem.

Code and data availability

Data will be provided on DataSuds after acceptance of the paper.

Supplement link

https://docs.google.com/document/d/1H77iGFwIz_dmW82p8rZ-vR9fIgSQERNoqrDqrItMVFA/edit?usp=sharing

Author contributions

J.R., S.A. and M.S. acquired the funding. J.R., P.O., H.P., J.P., C.J. L.R. conceptualized and conducted the field work. Z.F., J.R., P.O. and S.A. conceptualized the experimental work. Z.F., J.R., B.A., Z.O., H.P. and J.P. acquired the data. Z.O., Z.F., conducted the data analysis with the contribution of J.R., P.O., S.A. during data interpretation. Z.O., J.R., P.O. and S.A. wrote the manuscript with contributions of all authors. The final version of the manuscript was approved by all authors.

Competing interests

No competing interests.

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The review statement will be added by Copernicus Publications listing the handling editor as well as all contributing referees according to their status anonymous or identified.

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