Burning poop: chemical composition and carbon dynamics of large herbivore dung burned in African savanna fires

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ABSTRACT

Background. Fire and herbivores are essential to savanna ecosystems, consuming vegetation and recycling nutrients. Fire volatilises some elements and makes others readily available through ash, while herbivores redistribute nutrients via dung (excrement, faeces). **Aims.** We investigate, for the first time, fire's role in consuming dung and affecting nutrient cycling. **Methods.** We examined the chemical characteristics of wild large herbivore dung (buffalo, elephant, giraffe, wildebeest, zebra) burned during African savanna fires (Kruger National Park, South Africa) and estimated carbon and nutrients losses from dung burning. **Key results.** Smouldering combustion of dung led to high carbon loss to the atmosphere (C: 41% and 4.1% in unburned and burned dung) and high enrichment of nutrients (e.g. Ca, P) and metals (e.g. Cu, Fe, Zn) in the burned residue. Flaming combustion of grass resulted in lower carbon loss (C: 43% and 23% in vegetation and ash), leaving more carbon in the ash and lower relative enrichment of other nutrients and metals. **Conclusions.** Burned dung forms nutrient hotspots with physicochemical characteristics distinct from vegetation ash. **Implications.** Taking dung from wild or domestic herbivores into account in fuel inventories can improve estimations of fire-related carbon emissions and provide better understanding of fire impacts on nutrients cycling.

Keywords: Africa, biogeochemical cycles, carbon emissions, droppings, dung, grass fires, herbivores, manure, nutrient cycling, pellets, savannas, smouldering.

Background

Fire is a crucial ecological driver in savannas. The high fire frequency characteristic of these ecosystems regulates the balance between grass and trees coverage (Van Langevelde *et al.* 2003). Fire also acts as a key recycling agent, contributing to nutrient cycling and mobilising nutrients in various ways (Pausas and Bond 2020). Fire accelerates the mineralisation of organic matter, releasing and increasing the bioavailability of most nutrients that are part of the burned material. Although some nutrients previously stored in the organic matter can be transported over long distances as particulates and gases via smoke, other fire-affected nutrients remain on site in the resultant ash (i.e. 'the particulate residue remaining or deposited on the ground, from the burning of wildland fuels and consisting of mineral materials and charred organic components'; Bodí *et al.* 2014, p. 104). Within the ash, certain elements become readily available for plants and animals. This is particularly relevant in savanna environments where soils are usually highly deficient in a range of nutrients like nitrogen (N), phosphorus (P) or calcium (Ca) (Augustine *et al.* 2003; Pellegrini 2016).

Along with fire, the presence of large mammalian herbivores also plays a vital role shaping the savanna ecosystems (Karp *et al.* 2024). These herbivores, found in high densities in many African savannas, regulate plant communities by consuming vegetation and contribute to nutrient cycling and redistribution by eating biomass and dispersing nutrients across the landscape through dung (Augustine and Frank 2001; Veldhuis *et al.* 2018). The concentration of nutrients in the dung can enrich soils and influence seed germination and plant growth, as

well as plant community and diversity (Sitters and Olde Venterink 2021*a*; Guevara-Torres and Facelli 2023). After dung deposition, decomposers like dung beetles and other macrodetritivores contribute to the mineralisation and spatial distribution of dung nutrients across the landscape. Estimates suggest that within 4 days of dung deposition, approximately a quarter of the dung's dry weight is redistributed by these organisms (Freymann *et al.* 2008; Veldhuis *et al.* 2018).

Several studies (Table 1) have assessed the chemical characteristics of herbivore dung from different regions and ecosystems (e.g. African savannas, Australian grasslands, Dutch nature reserves) but have focused their analyses mostly on carbon (C), N and P concentrations in a limited number of mammals such as elephant (e.g. Dougall 1963; Anderson and Coe 1974; Masunga *et al.* 2006; Stanbrook 2018; Sandhage-Hofmann *et al.* 2021), zebra, giraffe (e.g. Le Roux *et al.* 2020; Sitters and Olde Venterink 2021*a*), kangaroo, sheep, cattle, deer and rabbit (e.g. Holter 2016; Valdés-Correcher *et al.* 2019; Guevara-Torres and Facelli 2023). A small number of studies have also analysed other nutrients like Ca, Mg, Na and metals like Fe, Cu, Mn, Zn and Al (e.g. Masunga *et al.* 2006; Guevara-Torres and Facelli 2023). Herbivore dung is a well-known fuel source used for centuries by humans in cooking or heating (Miller 1984). Given the substantial presence of large herbivores across African savanna landscapes, these features also make dung a potentially important, but to date mostly unquantified, additional fuel component for landscape fires.

The intrinsic high fire recurrence in savannas results in the frequent modification of dung by burning. Observations during savanna fires suggest that dung undergoes a different burning process compared with the fine vegetation fuels that are predominant in savanna fires. Whereas fine fuels, such as grass or litter, tend to burn mostly by rapid flaming combustion, dung burns mostly via slow smouldering combustion, which often continues long after the flaming front has passed (Scholes *et al.* 1996; Wooster *et al.* 2011). The longer burning duration of smouldering combustion potentially allows a more complete volatilisation of organic compounds, and therefore, of C. Additionally, Wooster *et al.* (2011) noted that burning of animal dung in South African savannas could substantially alter fire emissions, with the chemical composition of the smoke plume changing compared with when only vegetation fuels were burned.

In recent decades, our understanding of the chemical composition of ash from the burning of wildland fuels (i.e. wildland fire ash) has gained traction and its role in redistributing C and other nutrients and metals across the landscape is now more widely recognised (Bodí *et al.* 2014; Sánchez-García *et al.* 2023; Girona-García *et al.* 2024). However, to our knowledge, the chemical characteristics of the burned dung have not been examined in detail to date. This study aims to determine the chemical composition of ash derived from burned large herbivore dung and its role in the C dynamics of African savanna fires. This should allow

more accurate estimations of the overall C released during savanna fires given that they are the dominant source of global CO_2 emissions from vegetation fires (~50%) owing to their high frequency and the large annual area burned (van Wees *et al.* 2022).

The objectives of this study are: (i) to examine the chemical characteristics of burned dung from large African savanna herbivores; and (ii) to quantify C losses from the combustion of herbivore dung and its role in the C fluxes of African savanna fires. Kruger National Park (KNP) is uniquely placed to be the focus of this study as it hosts one of the longest burning experiments on the planet, the Experimental Burn Plots (EBPs) trial, which has been running since 1954 with the aim of studying the effects of different fire regimes on South African savanna landscapes (Biggs *et al.* 2003). To the authors' knowledge, dung loads have not been previously quantified in KNP. The third objective of this study is, therefore, (iii) to quantify herbivore dung loads and their contribution to the overall fuel loads during African savanna fires.

Research design and methods

Study sites

This study was performed in KNP, located in northeastern South Africa, covering an area of nearly 2 million ha. KNP is a dry savanna biome with hot semi-arid climate with humid and hot summer days. The rainy season here lasts from September to May. The EBPs trial in KNP comprise a total of 16 strings of 12–14 plots each, covering four major savanna landscapes (Fig. 1*a*). The EBPs are burned periodically with recurrences that vary between 1 and 6 years, and at different times of the year (late summer, autumn, late winter, following first spring rains and mid-summer; Biggs *et al.* 2003).

Four EBPs were selected for this study covering a range of savanna types and the two main geological substrates in KNP (sandy granitic and clayey basaltic; Table 2). Two plots were in the Pretoriuskop area (PB1, PB3), and two others in the Mopani (MB1) and Satara (SB3) areas. The selected plots represent two of the most common fire frequencies in these savannas, i.e. annually burned (PB1 and MB1), and triennially burned (PB3 and SB3). The experimental fires took place in August 2018, in the middle of the dry season, coinciding with the peak fire season in KNP.

Experimental fire monitoring and sampling

The set-up for the experimental burns has been described in a previous publication (Sánchez-García *et al.* 2021) and it is therefore only summarised here. At each study site, a 30 × 30 m plot was set up within the selected EBPs before the experimental fires, except for Mopani where a 20 × 20 m plot had to be selected to ensure sufficient fuel continuity. At each plot, we selected three parallel transects (T1–T3, 30 m long, 15 m apart for PB1, PB3 and SB3, and 20 m long, 10 m apart

Table 1. Chemical composition of unburned dung reported in the literature expressed as proportion of dry weight.

Location	Animal	pH	C (%)	N (%)	P (mg kg⁻¹ dung)	K	Ca	Mg	Na	Fe	Cu	Mn	Zn	Al	C:N	C:P	N:P	Publication
Nature reserves in The Netherlands and Belgium	European bison		44.5	1.13	2130	–	–	–	–	–	–	–	–	–	39.8	224	5.67	Valdés-Correcher et al. (2019)
	Cow		48	1.06	1670	–	–	–	–	–	–	–	–	–	45.7	317	7	
	Horse		47.3	1.07	1290	–	–	–	–	–	–	–	–	–	44.2	376	8.46	
	Fallow deer		43.2	1.97	2760	–	–	–	–	–	–	–	–	–	22.5	187	8.65	
	Rabbit		43.8	1.66	1010	–	–	–	–	–	–	–	–	–	26.4	462	17.4	
African savanna (Kenya)	Zebra		–	–	–	–	–	–	–	–	–	–	–	–	–	–	3.5	Sitters and Olde Venterink (2021a)
	Giraffe		–	–	–	–	–	–	–	–	–	–	–	–	–	–	6.4	
Sub-Saharan savanna	Elephant		39	–	–	–	–	–	–	–	–	–	–	–	–	–	–	Sandhage-Hofmann et al. (2021)
Aberdare NP (Kenya)	Elephant		36.75	1.76	–	–	–	–	–	–	–	–	–	–	20.9	–	–	Stanbrook (2018)
Tsavo NP (Kenya)	Elephant			1.28	–	–	–	–	–	–	–	–	–	–	–	–	–	Dougall (1963)
Tsavo NP (Kenya)	Elephant		49.82	1.39	3900	–	–	–	–	–	–	–	–	–	36	–	–	Anderson and Coe (1974)
Chobe NP (Botswana)	Elephant		39.3	1.62	2800	16,600	10,200	2300	300	670	10.9	367	38.3	473.7	24	–	–	Masunga et al. (2006)
Global	Cattle	7.3	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	Holter (2016)
	Sheep	8.3	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	
	Various ruminants	–	–	2.51 (1.5–5.7)	–	–	–	–	–	–	–	–	–	–	21	–	–	
	Various non-ruminants	–	–	1.88 (0.8–4.9)	–	–	–	–	–	–	–	–	–	–	–	–	–	
Organic farms, wildlife parks, private stocks in Germany	Various	–	–	–	–	–	–	–	–	–	–	–	–	–	26.8	–	–	Frank et al. (2017)
Grassland (South Australia)	Kangaroo	–	–	1.79	4200	7000	16,900	4400	1500	–	–	–	–	–	–	–	–	Guevara-Torres and Facelli (2023)
	Sheep	–	–	2.98	9500	11,000	25,100	8600	3500	–	–	–	–	–	–	–	–	
Tropical forest in Mudamulai National Park (India)	Elephant	–	40.8	1.1	–	–	–	–	–	–	–	–	–	–	–	–	–	Chaudhary et al. (2020)
	Gaur	–	38.9	1.6	–	–	–	–	–	–	–	–	–	–	–	–	–	
South African protected savanna	Various herbivores (grazers, browsers, mixed feeders)	–	–	1.7–2.1	2800–6060	–	–	–	–	–	–	–	–	–	–	–	2.9–6.3	Le Roux et al. (2020)
Overall ranges (minimum and maximum values)			36.8–49.8	1.06–2.9	1010–9500	7000–16,600	10,200–25,100	2300–8600	300–3500						20.9–45.7	187–462	3.5–17.4	

The ranges are provided in brackets (i.e. minimum and maximum) where more than one value is given for a given study and animal. NP, National Park
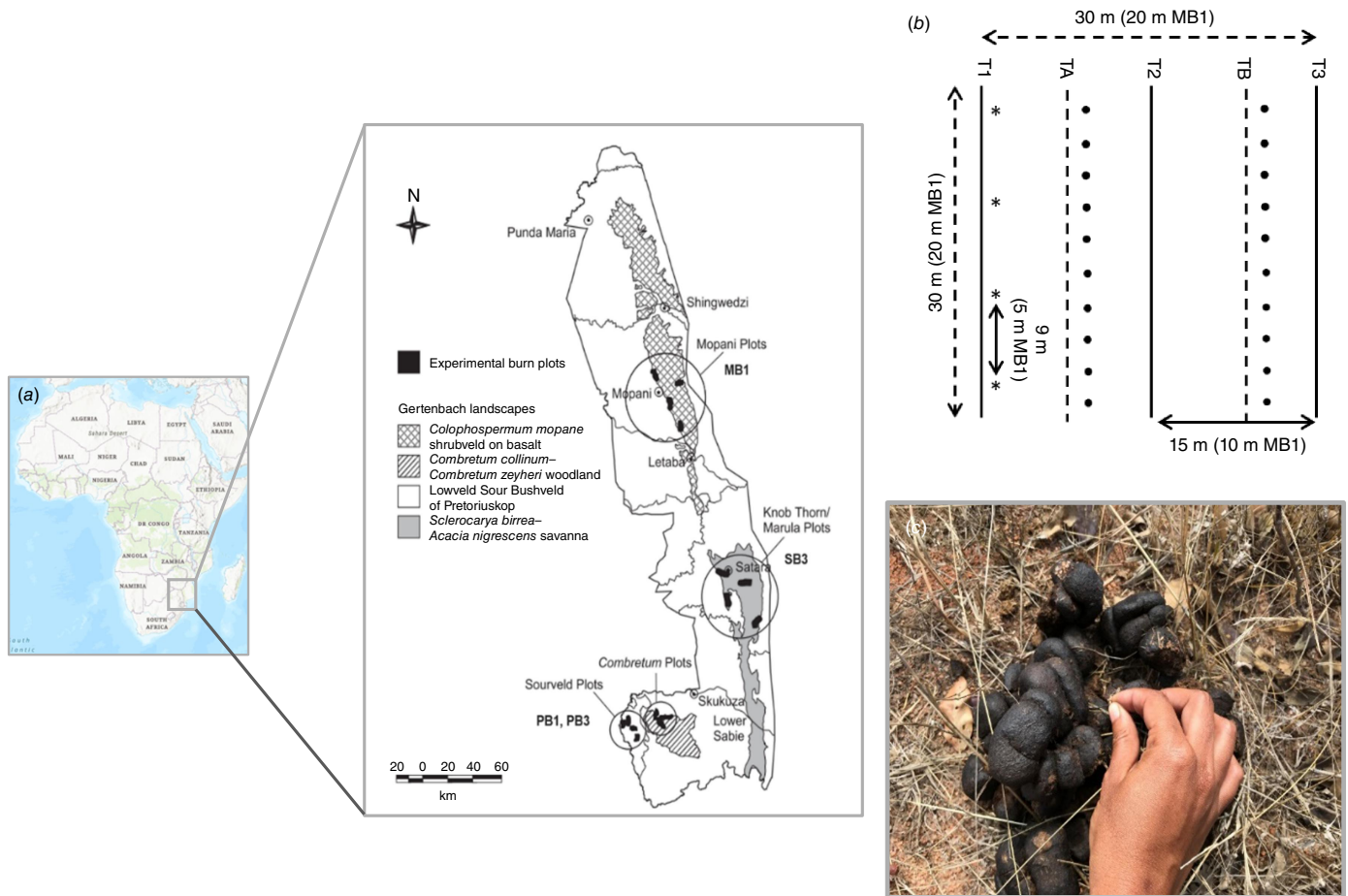
Fig. 1. (*a*) Location of the Kruger National Park (KNP) in South Africa (left) and location of the Experimental Burn Plots (EBPs) in the park (right). The circles indicate the location of the four EBPs used in this study. (*b*) Experimental plot diagram for PB1, PB3, SB3 plots (dimensions for the MB1 plot in brackets). Solid lines represent the experimental transects (T1–T3) and dotted lines represent control transects (TA and TB). Dots along the control transects represent the location of destructive grass sampling. Asterisks along the experimental transects represent the locations of the thermocouples and the ash samples. (*c*) Thermocouple being installed in zebra dung (at PB1) before the experimental fire.

for MB1) for fire monitoring and post-fire ash sampling. We also selected two control transects of the same length each situated parallel and 7.5 m apart from T1, T2 and T3 for PB1, PB3 and SB3, and 5 m apart for MB1 (Fig. 1*b*) for quantifying vegetation loads before fire (Fig. 1*b*). To quantify vegetation fuel loads, the grass was sampled in the two control transects using 50 × 50 cm sampling squares (10 sampling points per transect, one every 3 m; Fig. 1*b*). Owing to the absence of leaves and shrubs at the time of the fires, fuel loads from vegetation were restricted to the fine fuels only, specifically grass. Along each transect, we inserted *K*-type thermocouples and dataloggers (Lascar, Easylog) to monitor temperatures during the burns. These were installed in the soil surface (~1 cm depth) and within the grass (~50 cm above ground) at 9 m intervals in PB1, PB3 and SB3, and at 5 m intervals in MB1 (Fig. 1*b, c*).

Quantification and sampling of unburned (pre-fire) and burned dung were carried out, respectively, within a few hours before and after the fires. Before the fires, all dung from large herbivores (i.e. buffalo, elephant, giraffe, wildebeest

and zebra) within the plots was identified, mapped and weighed. We also collected comparable unburned dung of similar freshness from adjacent areas for chemical and moisture content analyses ($n = 11$). For temperature monitoring, thermocouples were inserted in some *in situ* dung samples across the plots from different species ($n = 9$ for PB1 and PB3, and $n = 6$ for MB1 and SB3; Fig. 1*c*).

The fire characteristics at each plot are given in Table 3. A few hours after each fire, all dung within the respective plots was collected and weighed once it had stopped smouldering. We differentiated between burned dung and any dung that remained partially or fully unburned after the fires. On the same day as the experimental burns, we also collected the vegetation ash layer present on the soil surface using a 20 × 20 cm frame at the exact locations where thermocouples were placed in the soil ($n = 12$) (as described in Sánchez-García *et al.* 2021). All samples were air-dried to constant weight and stored in sealed containers in dry conditions in the laboratory.

Table 2. Description of the KNP experimental burned plots selected for this study.

Plot	Area	Location (lat., long.)	Geology, soils	Dominant vegetation		Mean annual rainfall (mm)	Fire regime
				Tree	**Grass**		
PB1	Pretoriuskop	25°08′24″S; 31°12′26″E	Sandy granitic	*Terminalia sericea, Dichrostachys cinerea*	*Hyperthelia dissoluta, Themeda triandra, Setaria sphacelata*	705	Burnt annually
PB3	Pretoriuskop	25°08′06″S; 31°12′24″E	Sandy granitic	*Terminalia sericea, Dichrostachys cinerea*	*Hyperthelia dissoluta, Themeda triandra, Setaria sphacelata*	705	Burnt triannually
MB1	Mopani	23°33′48″S; 31°27′24″E	Clayey basaltic	*Colophospermum mopane*	*Bothriochloa radicans*	451	Burnt annually
SB3	Satara	24°23′58″S; 31°44′12″E	Clayey basaltic	*Acacia nigrescens, Sclerocarya birrea*	*Themeda triandra, Urochloa mosambicensis, Bothriochloa radicans*	507	Burnt triannually

Table 3. Moisture in the dung before the experimental fires, experimental fire characteristics including atmospheric conditions (wind speed, air temperature (Air T) and relative humidity (RH)), maximum temperature range (T_{max}) registered during the fires just below the soil surface, in grass and in dung, and details of fire impacts on vegetation.

Plot	Fire date	Pre-fire dung moisture (%)	Atmospheric conditions			T_{max} (°C)			Fire impacts on vegetation
			Wind speed (m s^{-1})	**Air T (°C)**	**RH (%)**	**Soil surface**	**Grass**	**Dung**	
PB1	19/08/18	23.3–36.8	2.3	26	41	40–225	484–744	32–795	In both PB1 and PB3, the fire burned the entire experimental plot with complete combustion of fine fuels and no unburned grass left. Woody fuels were mostly unaffected and wood on the ground (down wood) and bark from standing trees and shrubs remained uncharred.
PB3	19/08/18	9.9–110	2.3	31	30	40–182	651–918	22–825	
MB1	23/08/18	1.4–2.6	2.7	31	41	40–498	452–850	153–712	In both MB1 and SB3, most (>90%) of the fine fuels on the ground were burned. In MB1, coarser woody fuels remained largely unaffected. No shrubs or trees were present in SB3.
SB3	27/08/18	6.0–6.5	1.8	21	58	40–817	68–783	41–724	

Dung and ash chemical analyses

The pH, electrical conductivity (EC) and total concentrations of major nutrients and metals were analysed in unburned ($n = 8$) and burned dung ($n = 7$), grass ($n = 12$) and vegetation ash samples ($n = 12$) using established methods. Briefly, pH and EC were analysed in water using a mass-to-water ratio of 1:20 after stirring for 5 min and waiting for 10 min (Buurman *et al.* 1996). Total C and N concentrations were determined using a Total Analyzer Leco TruSpec CHN (Leco Corp., St Joseph, MI, USA), whereas the total concentration of major nutrients and metals (Al, Ca, Co, Cr, Cu, Fe, Mg, Mn, Ni P, and Zn) was extracted in duplicate by adding 8 mL of a mixture of HNO_3/HCl (3:5, v/v) in a 120 mL Teflon bomb containing 0.5 g of previously dried and ground sample and heating the mixture in an Ethos Plus microwave lab station. The efficiency of the extraction process was evaluated by analyzing certified reference material (MESS-3 and SOIL SO3), ranging from 90.1% of chromium (Cr) to 105% for lead (Pb) (Otero *et al.* 2016). The element concentration was measured by atomic absorption in a PerkinElmer PinAAcle 500 spectrometer. Total P was measured in the same extracts by colorimetry in a Jasco V360 spectrophotometer. All equipment used was washed thoroughly with HCl (5%) for at least 48 h, and then with ultrapure water (Milli Q).

An enrichment index (Ei), representing the change in nutrient, metal and metalloid concentration in dung and grass with fire, was calculated as follows: Ei = (concentration in burned dung or grass/concentration in unburned dung or grass) – 1; where Ei > 0 indicates that elements have undergone relative enrichment compared with their concentration in the unburned dung or grass, whereas Ei < 0 indicates that a loss of the element occurred in the burned dung or grass compared with its original concentration in the unburned dung or grass.

Data analysis

The Shapiro–Wilk test was used to test for normality in the data. The non-parametric Mann–Whitney U test was used to test for statistical differences in the chemical characteristics of unburned and burned dung, and vegetation ash (accepted at $P < 0.05$). The tests were performed in R (R Core Team 2014).

Results

Dung loads and burning behaviours

Before the fires, dung loads amounted, on average, to 130 kg ha^{-1}, equivalent to 3% of the vegetation fuel loads (4225 kg ha^{-1}) but varying across the selected EBPs, from 2% (40 kg ha^{-1}) in SB3 to 6% (240 kg ha^{-1}) in MB1 (Fig. 2a). Overall, the largest dung loads were observed for elephant and zebra (80 and 32 kg ha^{-1}, respectively). However, the dung load composition varied across the plots. For instance, in PB1 and SB3, the highest dung loads were from zebra and elephant, whereas in PB3, it was zebra and buffalo. In MB1, elephant dung accounted for 72% of the total dung load (Fig. 2a).

The fires led to substantial consumption of the dung (Figs 2b and 3), with a decrease of dung loads of ~85% compared with those found before the fires (mean: 20 kg ha^{-1}) (Table 4). In most plots, some dung remained unburned (7 to 32% in PB1 and PB2, respectively; Fig. 3c), except at MB1, where nearly all the dung was consumed by the fires (Fig. 2b). Some elephant dung in MB1, however, had been used by termites and had a large soil component in it (Fig. 3d). This soil component was discounted from dung calculations, which introduces some uncertainty into the quantification of burned dung loads.

As expected, the type of combustion differed between dung and grass as indicated by the temperature profiles recorded during the fires (Fig. 4). Dung exhibited typical smouldering combustion characteristics, with lower average maximum temperatures (435°C) but longer burning durations (1780 s) compared with flaming combustion of grass (636°C and 174 s, respectively) (Fig. 4). These different fire behaviours resulted in the burned residues being also
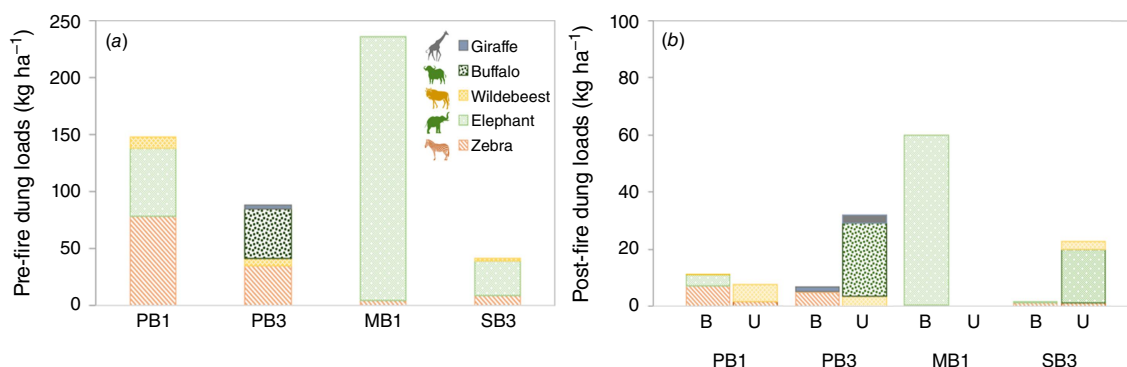

Fig. 2. (*a*) Dung loads (kg ha^{-1}) before the experimental fires, and (*b*) unburned (U) and burned residue (B) dung loads after the experimental fires categorised by species in the four experimental burn plots. Note the different scale in the vertical axes.

Fig. 3. Herbivore dung after the experimental fires: (*a*) elephant, (*b*) zebra, (*c*) buffalo, (*d*) elephant used by termites with substantial mineral soil component left unburned.

different, with ash from grass being darker in colour and ash from burned dung being lighter (Fig. 3*a*), which indicates the latter is the result of greater combustion completeness (Campbell *et al.* 2024).

Chemical characteristics of burned dung and nutrient enrichment

Among all the analysed nutrients in the burned dung, Ca, C, Fe, Al and Mg were found in the highest concentrations (mean: 47.2, 41.2, 27.3, 20.5 and 11.9 g kg^{-1}, respectively), whereas the lowest concentrations were observed for Cr, Ni, Cu and Co (mean: 163, 92, 56 and 23 mg kg^{-1}, respectively) (Fig. 5).

The total concentrations of all the major nutrients (C, N, Ca, Mg and P) were significantly different between unburned and burned dung (Fig. 5). C and N concentrations in the burned dung were an order of magnitude lower compared with the unburned dung (C: 41 and 4.1%, N: 1.1 and 0.3% in unburned and burned dung). Their corresponding enrichment factors were negative, at −0.9 for C and −0.7 for N. Surprisingly, the concentration of Mg also exhibited a decrease in burned dung with a mean value of 24.2 g kg^{-1} in unburned dung and 12.0 g kg^{-1} in burned dung.

In contrast, P and Ca were more than fourfold higher in burned compared with unburned dung (P: 1.7 and 9.2 g kg^{-1};

Ca: 11.7 and 47.2 g kg^{-1} in unburned and burned dung, respectively) with positive enrichment factors of 4.4 and 3.0 respectively. The analysed metal concentrations (Al, Co, Cr, Cu, Fe, Mn, Ni and Zn) were all higher in burned than in unburned dung (Fig. 5), also showing positive enrichment indexes (Table 4). pH and EC increased significantly from 7.2 and 1955 µS cm^{-1} in unburned dung to 10.4 and 10,279 µS cm^{-1} in burned dung, respectively.

When compared with vegetation ash, the C content in the burned dung was an order of magnitude lower (4.1% vs 23%; Table 4). Average Mg concentration in burned dung did not differ much from vegetation ash (9.5 g kg^{-1}); however, the enrichment indexes show Mg enrichment in vegetation ash and the opposite in burned dung (Table 4). Average Ca concentration in burned dung was similar to that observed in vegetation ash (33.7 g kg^{-1}); however, vegetation ash showed an enrichment factor twice that of burned dung. Although the concentrations of P and metals like Cu, Co, Ni, Cr and Al were significantly higher in burned dung than in vegetation ash (which is related to the proportionally larger losses of C and N in the former during burning; Fig. 5), their enrichment indexes showed varying trends. Cu, Co, Ni and Cr showed greater enrichment in burned dung than in vegetation ash, whereas the opposite was observed for P and Al (Table 4).

The elements considered in this study did not show the same pattern when comparing unburned dung samples of the different herbivore species. Owing to the limited sample size available, meaningful statistical analyses were not feasible, so a quantitative description of these variations is provided here. In unburned dung, Cu concentration, for instance, was an order of magnitude higher in elephant dung (0.012 g kg^{-1}) compared with other species (Table 4). Conversely, Ca was an order of magnitude lower in unburned zebra dung (3.8 g kg^{-1}) than in the other species, whereas Fe concentration in unburned buffalo dung was an order of magnitude lower (0.6 g kg^{-1}) than those in elephant, wildebeest and zebra dung. Elephant dung showed P and Mn concentrations an order of magnitude lower than buffalo and zebra dung (Table 4).

Carbon loads in dung and their losses during fire

Understanding how C loads differ among fuel types is key to predict C emissions associated with savanna ecosystems. In this study, C loads from vegetation fuels were two orders of magnitude higher than from herbivore dung (mean: 1842 and 53.7 kg C ha^{-1}, respectively; Table 5). For both, grass and dung, the lowest C loads were observed in SB3 (grass: 1100, dung: 16.6 kg C ha^{-1}) and the highest in MB1 (dung: 99.7, grass: 2942 kg C ha^{-1}) coinciding with the lowest and highest fuel loads in these plots.

Following the experimental fires, we observed on average a reduction of 52.9 kg C ha^{-1} in the total C dung loads relative to unburned dung (ranging from 16.5 to 97.5 kg C ha^{-1} in SB3 and MB1; Table 5), meaning that 98.5% of C was released

Table 4. Chemical characteristics of unburned and burned dung and vegetation, and post-fire enrichment indexes (Ei).

Material	Species	Loads across plots (kg ha⁻¹)	pH	EC (µS cm⁻¹)	C (%)	N	P (g kg⁻¹)	Cu	Co	Zn	Ni	Mn (mg kg⁻¹)	Cr	Ca	Mg (g kg⁻¹)	Fe	Al
Unburnt dung	Buffalo (n = 1)	0–43.9	7.4	2010	41.2	1.2	1.5	6.6	2.4	61.4	4.1	246.0	8.9	11.8	26.2	0.6	6.3
	Elephant (n = 3)	0–231.5	6.8–7.1	1558–2010	39.7–43.1	1.1–1.4	0.8–2.6	9.4–16.7	3.5–5.6	22.5–38.4	6.7–18.2	88.3–206	6.3–14.3	17.4–18.9	20.8–30.0	1.1–4.5	13.1–26.4
	Wildebeest (n = 2)	0–9.1	7.4–7.5	1882–3160	39.6–41.1	1.1–1.3	1.4–2.9	6.7–8.9	2.1–5.03	53.6–60.7	4.3–5.6	158–174	7.7–26.2	10.0–10.2	15.4–28.5	1.1	7.2–11.5
	Zebra (n = 2)	4.8–78.2	7.1–7.5	1115–1893	41.3–43.1	0.80–0.81	1.2–1.8	4.5–10.4	2.8–6.4	25.8–37.7	1.1–28.9	102–262	8.9–11.3	2.2–5.4	13.8–31.4	0.5–3.4	7.1–20.8
Burnt dung	Buffalo (n = 1)	0–1.8	9.9	15,580	5.8	0.5	12.4	33.2	11.5	270	16.7	1343.0	85.3	65.3	13.6	4.5	7.6
	Elephant (n = 3)	0–59.4	9.7–11.1	3260–15,730	2.6–4.4	0.21–0.26	5.6–7.6	41.4–81.1	15.0–41.6	135–149	34.2–325	853–1081	76.3–311	36.3–82.0	9.0–24.3	15.6–56.0	19.3–33.5
	Zebra (n = 3)	0.6–7.3	9.8–10.9	2340–14,890	4.1–4.5	0.3–0.5	6.0–15.6	34.6–76.8	12.1–31.4	126–205	13.5–101	582–1729	84.4–237	23.1–35.1	8.7–9.9	5.9–54.0	10.2–32.1
Overall Ei burnt dung	–	–	–	–	-0.9	-0.7	4.4	5.1	4.4	3.1	7.8	5.1	12.8	3.0	-0.5	13.7	0.5
Unburnt vegetation (n = 12)	–	2559–6672	–	–	39.4–46.5	0.4–1.3	0.5–1.9	3.7–7.9	6.7–9.5	13.6–27.9	1.3–7.3	34.0–161.4	3.6–11.5	1.8–13.4	0.6–2.6	0.1–1.1	0.08–0.5
Vegetation ash (n = 12)	–	384–897.4	9.6–10.8	1763–13,770	15.8–30.1	0.3–0.7	3.7–12.2	20.9–39.0	0.5–20.9	114–227	6.9–46.6	236–1687	39–84.6	15.6–48.4	6.4–17.9	4.6–8.7	3.4–12.7
Overall Ei vegetation ash	–	–	–	–	-0.5	-0.4	5.9	3.9	0.0	7.8	4.2	9.7	6.9	6.6	6.2	15.5	33.6

When *n* > 1, the ranges (i.e. minimum and maximum) are given. (Note: burned dung from wildebeest was not analysed.)

from dung during experimental fires. This C loss of 98.5% from dung is proportionally higher than the 91.8% released into the atmosphere from vegetation (grass) burning (average: 1690 kg C ha^{-1}).
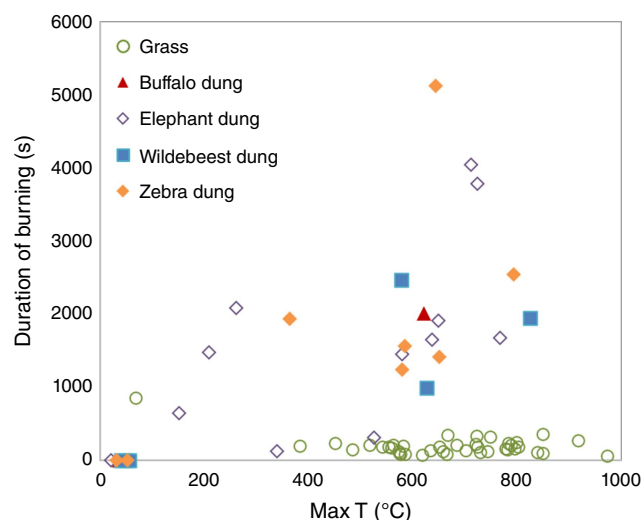

Fig. 4. Relationship between the maximum temperatures and burning durations recorded in grass (flaming combustion) and dung from different species (smouldering combustion). Note: an outlier for elephant dung with burning duration >11,000 s (T_{max}: 485°C) is not shown in the graph.

Discussion

Effect of combustion and herbivore species on dung chemical composition

Large herbivores play an important role in maintaining the ecological balance of several ecosystems (Pringle *et al.* 2023). One of the most important processes in which large herbivores are involved is nutrient flow, with dung deposition being one of the main mechanisms of nutrient influx and acceleration of nutrient cycling (Sitters *et al.* 2017; Valdés-Correcher *et al.* 2019; Sitters and Olde Venterink 2021b; Barbero-Palacios *et al.* 2023).

Dung composition has higher concentrations of nutrients than the plant material on which herbivores feed (Pastor *et al.* 1993; Hobbs 1996), and a substantial fraction of the nutrients are in soluble and therefore highly bioavailable forms (Arnuti *et al.* 2020). In addition, the effect of the fire leads to rapid mineralisation of fuel organic materials such as dung, thus increasing the bioavailability of the nutrients present in this material (Lopez *et al.* 2023).

The chemical composition of the unburned dung analysed in the present study is consistent with findings reported in previous research. However, it is important to note that the composition of the excrement varies temporally for each species, influenced by plant phenology (Verheyden *et al.* 2011). For instance, the average C and N contents of dung in the present study (41.3 and 1.1%, respectively) fall within
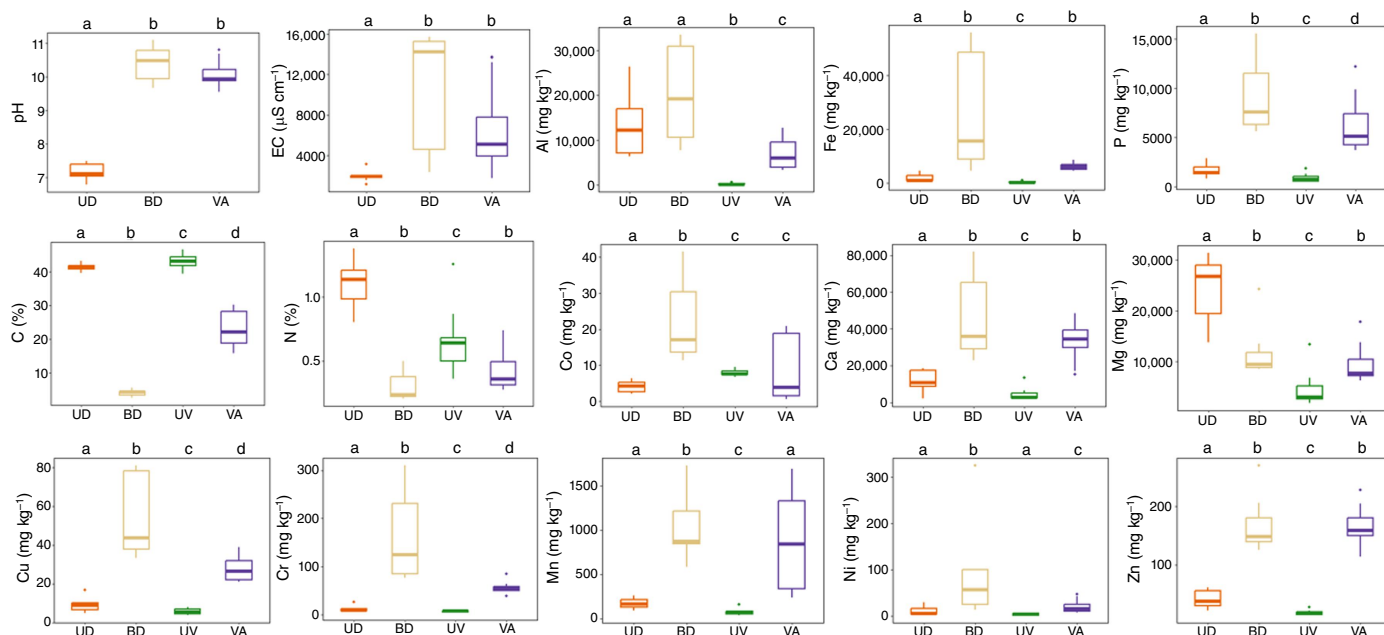

Fig. 5. Total element content, pH and EC for the unburned (UD) and burned (DB) dung, and for unburned vegetation (UV) and vegetation ash data (VA). pH and EC data for VA were not available. Central line, bottom and top boundaries of the boxes are the median, 25th and 75th percentiles. Lines extending above and below the boxes represent maximum and minimum values. Dots are the outliers. Different letters above each boxplot (a–d) indicate significant differences between unburned and burned dung, unburned vegetation and vegetation ash, unburned dung and unburned vegetation, and burned dung and vegetation ash at *P* < 0.05.

Table 5. Pre- and post-fire C loads and C loads released with the fires.

Plot	Pre-fire C loads (kg ha^{-1})		Post-fire C loads (kg ha^{-1})		C loads released with fire (kg ha^{-1})	
	Dung	Grass	Dung	Grass	Dung	Grass
PB1	62.1	1108	0.5	95.3	61.6	1013
PB3	36.2	2218	0.4	163.8	35.8	2054
MB1	99.7	2942	2.2	256.7	97.5	2686
SB3	16.6	1100	0.1	91.7	16.5	1008
Mean ± s.d.	53.7 ± 35.9	1842 ± 902	0.8 ± 1.0	152 ± 77.4	52.9 ± 35.0	1690 ± 826

the ranges reported for various herbivore species in the literature (C: 36.8–49.8%, N: 1.1–2.9%; Table 1).

A few studies have reported chemical composition for some of the species analysed here (Dougall 1963; Anderson and Coe 1974; Masunga *et al.* 2006; Stanbrook 2018; Sandhage-Hofmann *et al.* 2021). For elephant dung, for example, the concentrations of C, N and P (C: 36.8 –49.8%, N: 1.1–1.8%, P: 2.8–3.9 g kg^{-1}; Table 1) in previous studies are in line with the values reported in this study (C: 39.7–43.1%, N: 1.1–1.4, P: 0.8–2.6 g kg^{-1}; Table 4). Only the study by Masunga *et al.* (2006) reports additional element concentrations for elephant dung, with Ca, Cu, Mn and Zn of the same order of magnitude as our average concentrations, whereas Na, Fe and Al are an order of magnitude lower than ours (Tables 1 and 4).

When comparing unburned dung with burned dung, we observed that C and N concentrations are an order of magnitude lower in the latter (Fig. 5). This substantial loss of C and N during burning is expected, as these two elements are the ones starting to be volatilised at the lowest temperatures (300–500°C; Bodí *et al.* 2014), together with water, which becomes volatilised already at much lower temperatures. Unexpectedly, our Mg results showed a decrease in concentration in burned dung. We do not have a plausible explanation for the Mg results as the geochemical behaviour of Mg is similar to that of Ca, and it is not expected to be volatilised at temperatures lower than 1100°C (Bodí *et al.* 2014), which were not reached during the burning of dung (Table 3).

A key observation from the four studied savanna fires is that the C and N losses for dung during combustion are much higher than for vegetation, associated with the different burning behaviours of these two wildland fuels. Dung mostly burned by smouldering combustion whereas the fine grass vegetation burned mostly by flaming combustion. Smouldering combustion tends to result in more complete combustion and most organic matter being volatilised (Rein 2013; Fig. 3). The greater volatilisation of organic compounds also explains the higher concentration of mineral elements, like nutrients and metals, in burned dung when compared with vegetation ash. Vegetation ash produced during these fires contained a higher proportion of pyrogenic carbonaceous materials (Bird *et al.* 2015), and thus its composition differed substantially from the ash resulting from burned dung, with

more C and N and, consequently, less enrichment of nutrients and metals. When compared with unburned dung, burned dung was also enriched in most nutrients and metals (e.g. P, Ca, Fe, Co) as shown by their positive enrichment indexes.

We also observed differences in dung combustion between species, which could be attributed to different compositions associated with digestive physiologies and feeding strategies (Demment and Van Soest 1985). For instance, wildebeest and buffalo, as grazers, eat a diet richer in fibre and cellulose, and as ruminants have more than one stomach, allowing them to digest food almost completely. In contrast, elephants, being non-ruminants and browsers, have a more varied diet than grazers, nutrient-rich and lower in fibre, producing less dense dung containing partially digested grass material, making it more flammable and easier to ignite than denser dung from species like zebra or buffalo. This is in line with our observation of elephant dung displaying more complete combustion and explains the large reduction in dung loads after fire in the MB1 plot where nearly all dung was from elephants (Fig. 2). The more complete combustion of elephant dung led to increased volatilisation of organic compounds, which resulted in the lower C, N and P concentrations than in burned dung from species like wildebeest and buffalo. The more complete combustion also resulted in the production of lighter and finer ash that was visually different from that of species such as zebra or buffalo, which maintained their shape and generated darker ash (Fig. 4). The substantially larger elephant dung loads in the northern plot from this study (MB1) than in the southern ones (PB1, PB3 and SB3) (Fig. 2a) are a result of the greater presence of elephants in relation to other species like zebra or buffalo in this area of the KNP (Abraham *et al.* 2021).

Burned dung as a nutrient hotspot

Our findings emphasise the role of fire as a recycling pathway for nutrients. Many elements essential for plant and microorganism growth (e.g. Ca, P, Fe, Co) are found in much higher concentrations in the burned dung than in the unburned material because these elements do not volatilise at the temperatures typically achieved during wildfires (Tuhý *et al.* 2021; Roshan and Biswas 2023).

After the fires, the higher pH observed in burned dung, compared both with unburned dung and vegetation ash, is

likely a result of substantial concentrations of compounds that undergo alkali reactions, such as calcium oxide or potassium oxide, generated during the more complete biomass combustion (Bodí *et al.* 2014; Sánchez-García *et al.* 2023). In acid soils, the availability of nutrients for plants and micro-organisms is often limited, whereas others such as Al can become toxic (Foth and Ellis 1997). However, this higher pH in burned dung can induce an increase in the solubility and bioavailability of certain macronutrients such as P, N, Ca, Mg and K, mainly attributed to the transformation of the organic forms fixed in the biomass into soluble inorganic forms (Sertsu and Sánchez 1978; Cade-Menun *et al.* 2000; Roshan and Biswas 2023). This same argument also applies to trace metals. Pinedo-Gonzalez *et al.* (2017) found an increase in the solubility and bioavailable forms of many trace metals (both cations and anions) after fire, which is also related to the combustion of organic matter and an increase in soil pH. Something similar may occur during the combustion of faecal material. In contrast, major metals such as Fe or Mn decrease in solubility because they are transformed into poorly soluble oxides, such as haematite or magnetite in the case of Fe (Parra *et al.* 1996; Roshan and Biswas 2023).

The sudden pulse in nutrient bioavailability from burned dung may benefit a range of savanna plants that thrive in this post-fire environment and thus increase spatial species heterogeneity not only of plants, but also of soil fauna and microbial communities. These results show, for the first time, the role of burned dung as a nutrient and metal hotspot, which may have a localised impact on soil physical and chemical properties distinct from that of vegetation ash. This has implications for nutrient cycling and redistribution not only for savanna ecosystems, but potentially also for any ecosystems in which herbivore dung represents a notable fuel component during vegetation fires.

Some animals may make use of this resource too. There is observational evidence of big mammals such as impala, warthogs or wildebeest licking the ground in recently burned areas and they could be doing this to obtain specific minerals, such as calcium, from ash hotpots such as the ones identified in this study (Fig. 6a, b). More research is needed into this matter. Although some studies have examined the redistribution of nutrient in unburned dung by macrodetritivores like dung beetles (e.g. Holter 2016; Veldhuis *et al.* 2018), the redistribution of nutrients from burned dung by organisms, wind, or water is also a field that deserves further

Fig. 6. Zebra (*a*) and impala (*b*) licking the ground of recently burned sites in the Kruger National Park (South Africa). (*c*) Large piece of down wood burned via smouldering combustion, also in Kruger National Park.

attention. In addition to burned dung giving a faster and more concentrated nutrient input than decomposing dung, chemical characteristics may also differ between the two. Fire alters the elemental concentration and form in which elements occur, so differences are expected between burned and decomposing dung. Moreover, the seasonal conditions under which these processes occur (fire: dry season vs dung decomposition: wet season) may play an important role as differing moisture levels can influence the decomposition of compounds with different recalcitrance (e.g. sugars vs lignin; Chaudhary *et al.* 2020). However, to our knowledge, no studies have investigated these effects.

Finally, it is also worth noting that, although our vegetation ash resulted from grass burned via flaming combustion, during the studied fires we also observed, as anecdotal evidence, a few large pieces of down wood burned via smouldering combustion producing white ash (Fig. 6c). Although smouldering of litter and wood played a minor and unquantified role in our KNP plots, the combustion of these fuels is likely to be more significant in woodier savanna environments where these fuels are more predominant. Thus, smouldering of coarse wood could also yield nutrient hotspots that should be investigated in future studies.

Implications of dung burning for the carbon dynamics of African savannas

Our observations of dung loads suggested that herbivore dung can represent on average an additional fuel mass of 129 kg ha^{-1}, equivalent to 3% of the vegetation fuel loads (average 4225 kg ha^{-1}). Our estimates are consistent with those of Wooster *et al.* (2011) also from the KNP, where dung load estimates ranged from 100 to 500 kg ha^{-1}. This indicates that dung can be an important but currently unaccounted for fuel component that should be included in fuel inventories, particularly in ecosystems with high densities of wild large herbivores, such as African savannas (Karp *et al.* 2024), or domestic grazing animals. It is, however, important to note that KNP, as a protected area, has higher densities of wild large herbivores than other African savannas, so our estimates are likely at the high end of the spectrum for these ecosystems.

In addition to wild herbivores, domesticated herbivores such as cattle are predominant in many savanna environments. We do not have data for domesticated herbivores as they are not present in Kruger, but they are widespread in other savanna environments. For example, average cattle biomass density was more than three times higher than wildlife populations (including zebra, giraffe, buffalo, gazelle) in an African savanna in northern Kenya (Hempson *et al.* 2017), and between 1.6 and 4.3 times higher than macropod populations in an Australian tropical savanna (Reid *et al.* 2020). The role of these domesticated populations should be examined in future studies investigating nutrient dynamics from burned herbivore dung. Our results show that 98.5% of the C contained in dung was volatilised into the atmosphere during

fire, highlighting the notable role of dung in the C emissions of savanna fires in relation to their overall contribution to fuel loads. Although we do not know in what form C was emitted during the burns in this study, in an experiment also in KNP, Wooster *et al.* (2011) observed that emission ratios of CO/CO_2 were up to four times higher when burning dung compared with grass. Similarly, Christian *et al.* (2007) reported larger amounts of CO and CH_4 from burning of dung than from grass in pasture fires in Brazil. Therefore, the burning of dung should be taken into consideration from a C and nutrient dynamics point of view and when quantifying gas emissions from ecosystems where dung represents a notable fraction of the fuel loads. Nevertheless, it is important to stress that our sampling areas covered overall less than 1 ha of the approximately 2 million ha spanning the KNP, making it difficult to capture differences in animal density across the park and beyond. Future research involving a larger sampling effort is needed to quantify nutrient dynamics from burned dung from a range of herbivore species and at larger spatial scales.

Conclusions

We have studied, for the first time, the chemical composition of dung from large herbivores burning during African savanna fires and quantified its contribution to total fuel loads. Our findings improve the understanding of the role of herbivore dung and savanna fire in regulating the nutrient landscape. Burned dung was enriched in nutrients (e.g. Ca and P) compared with unburned dung and vegetation ash, except for Mg, which was unexpectedly lower in burned dung. Overall, burned dung represents a nutrient hotspot with physicochemical characteristics distinct from vegetation ash, potentially affecting localised plant and soil properties. This has implications for nutrient cycling and redistribution not only for savanna ecosystems, but potentially also for any ecosystems in which herbivore dung represents a notable fuel component during vegetation fires.

Unburned dung loads represented an additional 3% of the vegetation fuel loads with the release of C from dung being equivalent to 6% of the total C released from burning of vegetation. Our results, though limited to the study area, emphasise the significance of dung in African savanna fire dynamics and emissions, highlighting the importance of dung as a contributor to overall C released from African savanna fires, especially in areas of density of large herbivores. Additionally, owing to the different combustion processes in dung (smouldering) and the main fuel source in this ecosystem, grass (flaming), burning dung may have implications for the localised emission of more harmful gasses (CO, CH_4) compared with burning grasses (CO_2). Overall, these findings suggest that in ecosystems where dung makes up a substantial amount of fuel loads, such as African savannas, incorporating dung in fuel inventories and C dynamics assessments could improve the accuracy of these predictions.

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