



OPEN Drought, grazing, and nitrogen input influence nutrient supply and soil faunal activity in a semi-arid savannah grassland

Lawrence Munjonji¹✉, Kai Behn³, Mokoka Vincent^{3,4}, Kingsley Kwabena Ayisi², Uffe Nielsen⁵ & Anja Linstädter^{3,6}

Dryland grasslands cover approximately 16% of Earth's land surface and support the livelihoods of people worldwide. However, the mechanisms driving their nutrient dynamics under changing environmental conditions remain poorly understood. This study, conducted in a dry savanna ecosystem in South Africa, investigated how grassland management interacted with drought and nitrogen addition in their effects on soil faunal activity and plant-available macro- and micronutrients. Extreme drought did not significantly affect soil invertebrates' feeding activity in the top 8 cm, likely due to consistently dry conditions during the experimental period. In contrast, moderate grazing stimulated soil fauna feeding activity in the topsoil. Both nitrogen addition and grazing increased faunal activity, particularly at 7–8 cm depth. Drought conditions were associated with higher concentrations of manganese, zinc, and sulphur, while ambient rainfall conditions resulted in higher total nitrogen, magnesium, iron, and copper. Nitrogen addition enhanced mineral nitrogen availability and led to a fivefold increase in iron, and manganese, and doubling of copper. These findings suggest that moderate grazing management improves soil health in savanna grasslands, even under challenging climatic conditions.

Keywords Semi-arid grassland, Nutrient supply, Micronutrients, Macronutrients, Soil fauna

Grasslands cover approximately 30% of the Earth's land surface, making them the largest terrestrial biome¹. They store an estimated 10–30% of the world's soil organic carbon, serving as an important global carbon reservoir². Grasslands also support the livelihoods of more than two billion people worldwide³ provide habitat for a rich diversity of flora and fauna, including many endemic and threatened species⁴ and play a critical role in global food production by sustaining the majority of the world's grazing livestock.

Managed grasslands dominate the marginal bioclimatic and edaphic regions of drylands, which are defined by an aridity index (AI; mean annual precipitation divided by mean annual potential evapotranspiration) of less than 0.65⁵. Here, grasslands and savanna grasslands represent the most widespread land cover type, occupying ca. 40% of dryland areas⁶ which corresponds to 16% of Earth's terrestrial surface. Despite their relatively low primary productivity⁷ dryland grasslands contribute substantially to rural livelihoods, with livestock rearing being the primary land-use type⁸. They also sequester substantial amounts of carbon in their soils due to slow decomposition rates under limited water availability^{9,10}. While water is a key limiting factor for plant growth¹¹ nutrient availability – particularly nitrogen – is widely considered another main determinant of aboveground net primary production (ANPP) in dryland grasslands¹². However, increasing evidence suggests that grassland productivity is co-limited by other nutrients, such as phosphorus^{13,14}. Craine, et al.¹⁵ argue that several nutrients can simultaneously limit production, and others have shown that nutrient supply not only constrains grassland productivity but also affects plant species composition and diversity^{16,17}. Assessing nutrient supply is therefore fundamental to understanding both the functioning and the structure of grassland ecosystems.

¹Department of Soil Science, Stellenbosch University, Stellenbosch, South Africa. ²Risk and Vulnerability Science Centre, University of Limpopo, Polokwane, South Africa. ³Institute of Crop Science and Resource Conservation, University of Bonn, Bonn, Germany. ⁴Department of Geography, Geoinformatics, and Meteorology, Centre for Environmental Studies, University of Pretoria, Pretoria, South Africa. ⁵Hawkesbury Institute for the Environment, Western Sydney University, Penrith, NSW, Australia. ⁶Institute of Biochemistry and Biology, University of Potsdam, Potsdam, Germany. ✉email: Munjonji@sun.ac.za

In this context, external nutrient inputs may have important effects on the nutrient supply of grassland ecosystems, with consequences for ecosystem functions and services. Here, airborne nitrogen deposition, which results primarily from nitrogen emissions into the atmosphere, is of major importance¹⁸. These emissions originate largely from agricultural activities such as livestock farming and fertilizer application, as well as from fossil fuel combustion¹⁹. Once in the atmosphere, reactive nitrogen compounds can be transported over long distances before being deposited onto ecosystems. Climate change may further influence nitrogen deposition patterns by altering precipitation regimes, atmospheric circulation, and chemical reaction rates, potentially increasing the spatial extent and variability of nitrogen inputs to terrestrial ecosystems²⁰. The improved soil N availability may feed back to the soil environment²¹ and to soil fauna communities²².

Global climate change is projected to increase the frequency and intensity of drought events, particularly in dryland regions, with far-reaching consequences for ecosystem functioning and the provision of key ecosystem services^{6,23}. Drought can disrupt fundamental ecological processes such as nutrient cycling and organic matter decomposition²⁴ both of which are closely linked to soil fauna activity and sensitive to changes in soil moisture availability^{25,26}.

In addition to drought, livestock grazing significantly influences soil properties, fertility, and faunal communities. Herbivores contribute to nutrient inputs by depositing urine and dung, thereby affecting soil carbon and nitrogen pools and enhancing nutrient availability²⁷. Conversely, trampling by herbivores can lead to soil compaction, reducing infiltration rates and negatively impacting soil fauna habitats²⁸. Grazing management practices can thus modify soil properties, underscoring the complex interplay between biotic and abiotic factors in shaping soil ecosystem dynamics.

Despite the ecological and economic importance of dryland grasslands, the mechanisms underlying nutrient dynamics and soil fauna communities under changing environmental conditions remain poorly understood. Little is known about how grazing management interacts with global change drivers such as altered precipitation regimes and nitrogen deposition. While some studies have investigated these factors individually or in limited combinations^{29–31} few have addressed their joint effects with grazing. This has left substantial gaps regarding their combined and potentially interactive effects on biogeochemical processes and soil biological functioning under field conditions.

To address these knowledge gaps, this study aims to investigate how grazing, extreme drought, and nitrogen addition influence nutrient supply and soil fauna feeding activity in dryland grasslands. We hypothesise that (1) both moderate grazing and extreme drought reduce plant nutrient supply; (2) extreme drought decreases soil fauna feeding activity, whereas moderate grazing enhances it; and (3) nitrogen addition increases both plant nutrient supply and soil fauna feeding activity, which is expected to move to deeper soil layers below 5 mm.

In this study, we employed Plant root simulators (PRS) probes to assess nutrient supply rates. PRS probes are ion-exchange membranes encased in plastic supports that functionally mimic plant roots by adsorbing available nutrients from the soil solution over a specified burial period. This method provides a dynamic, in situ measurement of nutrient availability, effectively integrating the effects of soil moisture, temperature, and microbial activity on nutrient fluxes. Previous research has demonstrated that PRS probes correlate well with traditional soil analyses and accurately reflect plant nutrient uptake^{32,33}. Additionally, we evaluated the feeding activity of soil invertebrates using bait lamina strips. By integrating PRS probes and bait lamina assessments, our study aimed to elucidate the complex interactions between grazing management, drought stress, nutrient supply, and soil biological activity in grassland ecosystems.

Results
Soil fauna feeding activity

We tested for the combined effects of grazing with two global change drivers (either severe drought or nitrogen addition) on the feeding activity of soil invertebrates across different soils depths (Table 1). Feeding activity was assessed in 0.5 mm intervals to a depth of 8 cm. Grazing had significant positive effects on soil faunal

(A) Drought model				(B) Nitrogen model			
Factor	z-value	p-value	Sign	Factor	z-value	p-value	Sign
Grazing	2.080	0.038	**	Grazing	2.325	0.020	**
Drought	0.467	0.640		Nitrogen	-0.041	0.968	
Depth	1.722	0.085	*	Depth	1.800	0.072	*
Grazing x Drought	-0.889	0.374		Grazing x Nitrogen	-0.721	0.471	
Drought x Depth	0.416	0.678		Nitrogen x Depth	-0.129	0.897	
Grazing x Depth	-2.131	0.033	**	Grazing x Depth	-2.1958	0.028	**
Grazing x Drought x Depth	-0.343	0.731		Grazing x Nitrogen x Depth	2.965	0.003	**

Table 1. Combined effects of grazing with drought or nitrogen addition on soil fauna feeding activity across different soil depths. Shown are the results of a cumulative link mixed model (clmm) for (A) a “drought model”, with severe “drought” (drought vs. ambient rainfall), “grazing” (grazed vs. rested)), “depth” (soil depth; 0–8 cm) and all possible interactions, and (B) a “nitrogen model”, with drought replaced by nitrogen addition effects. Both models have effective degrees of freedom of 10. Significance levels (Sign) are shown with ** for $p < 0.05$ and * for $p < 0.1$, and respective p-values are given in bold.

feeding activity in both the drought and nitrogen model compared to ungrazed conditions. Grazing also had significant interactive effects with soil depth in both drought and nitrogen models, and the three-way interaction was significant in the nitrogen model (Table 1B), highlighting the importance of aboveground feeding activities (grazing) for belowground activities. Unexpectedly, severe drought never exerted significant effects, neither alone nor in any interaction (Table 1A). In many soil depth classes, it was visually observed that there was higher invertebrate activity in grazed plots (G+) that received additional nitrogen (N+; see Fig. 1). A high feeding activity (more than 75% of partly or fully consumed bait substrate) was particularly observed in deeper soil layers (depth intervals of 7.0 to 8.0 cm), but also at 4 cm depth. Interestingly, nitrogen application under ungrazed conditions (N + G-) tended to negatively impact soil fauna feeding activity.

Soil nutrient supply

As was to be expected, the application of nitrogen in the form of urea hugely improved the availability of total mineral nitrogen (total N) and its components ammonium (NH_4^+) and nitrate (NO_3^- ; see Table 2). On average, total N experienced a fivefold increase, while the availability of NH_4^+ was increased 30-fold. Interestingly, the availability of the micronutrients iron (Fe) and manganese (Mn) also increased by more than five times, while copper (Cu) increased two-fold. Median values for iron increased from 3.71 (mad = 2.25) $\mu\text{g}/10\text{cm}^2$ to 22.26 (8.82) $\mu\text{g}/10\text{cm}^2$ while manganese increased from 7.68 (6.77) to 83.06 (54.13) $\mu\text{g}/10\text{cm}^2$. In the nitrogen model, nitrogen addition influenced total N, NO_3^- , NH_4^+ , Ca, Fe, Mn and Cu while grazing only had an effect on K and S. In the same model the interaction between grazing and nitrogen had no effect on the supply of all the nutrients analysed. However, total mineral N, NO_3^- and NH_4^+ were higher in plots that were fertilized compared to plots that were not fertilized (regardless of the grazing treatment) (Fig. 2). A similar trend was also observed for Mn, Fe and Zn.

Grazing – in combination with extreme drought – affected several plant-available macro- and micronutrients, specifically the supply of total N, NO_3^- , magnesium (Mg), zinc (Zn), iron (Fe), Mn, Cu and sulphur (S) (Table 2). Total N, Mg, Fe and Cu were all significantly higher under ambient conditions compared to extreme drought. Calcium and Mg were 33% lower under extreme drought compared to ambient rainfall. The impact of drought on NO_3^- , Mn, Zn and sulphur differed from the trend shown by total N, Ca and Mg as they were higher in the

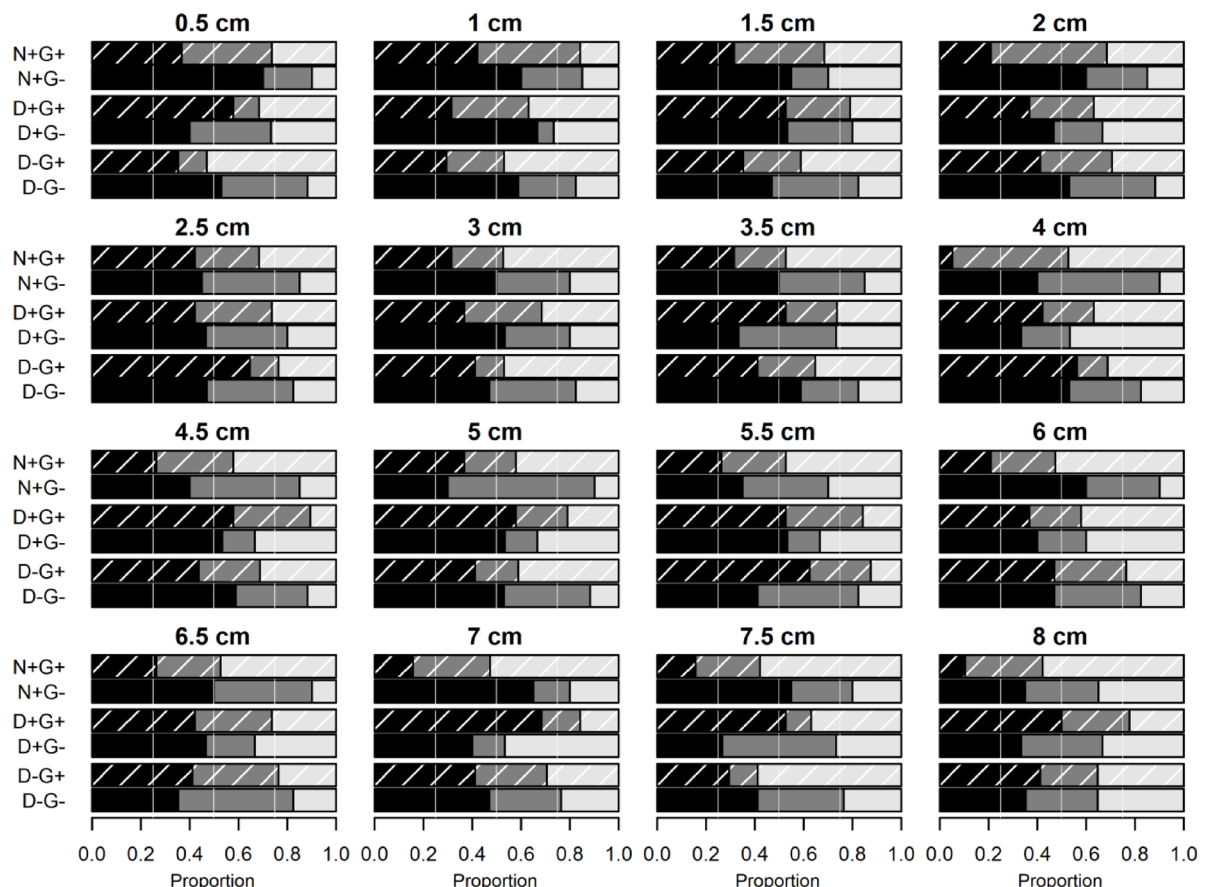


Fig. 1. Feeding activity of soil fauna – quantified as the proportion of bait portions in bait lamina strips that was not consumed (black), partly consumed (dark grey) or fully consumed (light grey) – across the six treatment combinations and across all depth classes. Shown are combinations of nitrogen addition (yes: N+, no: N-), grazing (yes: G+, rested: G- and severe drought (yes: D+, ambient rainfall: D-) across 0.5 mm soil depth intervals.

	(A) Drought model						(B) Nitrogen model					
Response	Factor	Num DF	Den DF	F	p	Sign	Factor	Num DF	Den DF	F	p	Sign
Total N	D	1	9	15.645	0.003	**	N	1	9	61.064	<0.001	**
Total N	G	1	9	7.237	0.025	**	G	1	9	1.088	0.324	
Total N	DxG	1	9	9.379	0.014	**	NxG	1	9	1.459	0.258	
NO ₃	D	1	9	14.82	0.004	**	N	1	9	59.325	<0.001	**
NO ₃	G	1	9	6.667	0.03	**	G	1	9	1.422	0.264	
NO ₃	DxG	1	9	8.48	0.017	**	NxG	1	9	1.824	0.210	
NH ₄	D	1	9	3.027	0.116		N	1	12	23.255	0.001	**
NH ₄	G	1	9	2.251	0.168		G	1	12	0.035	0.854	
NH ₄	DxG	1	9	3.791	0.083	*	NxG	1	12	0.004	0.950	
Ca	D	1	9	4.119	0.073	*	N	1	9	6.444	0.032	**
Ca	G	1	9	0.449	0.52		G	1	9	0.367	0.560	
Ca	DxG	1	9	3.459	0.096	*	NxG	1	9	3.394	0.099	*
Mg	D	1	9	11.062	0.009	**	N	1	9	0.316	0.588	
Mg	G	1	9	0.508	0.494		G	1	9	1.227	0.297	n
Mg	DxG	1	9	4.629	0.06	*	NxG	1	9	0.053	0.823	
K	D	1	9	0.024	0.88		N	1	9	0.133	0.723	
K	G	1	9	1.551	0.244		G	1	9	6.944	0.027	**
K	DxG	1	9	16.053	0.003	**	NxG	1	9	1.512	0.250	
P	D	1	9	2.766	0.131		N	1	9	2.409	0.155	
P	G	1	9	5.576	0.043	**	G	1	9	11.061	0.009	**
P	DxG	1	9	2.766	0.131		NxG	1	9	1.040	0.334	
Fe	D	1	12	9.214	0.01	**	N	1	12	48.443	<0.001	**
Fe	G	1	12	3.946	0.07	*	G	1	12	0.367	0.556	
Fe	DxG	1	12	17.062	0.001	**	NxG	1	12	1.255	0.284	
Mn	D	1	9	20.111	0.002	**	N	1	12	100.573	<0.001	**
Mn	G	1	9	3.204	0.107		G	1	12	0.045	0.836	
Mn	DxG	1	9	4.005	0.076	*	NxG	1	12	1.542	0.238	
Cu	D	1	9	0.990	0.346		N	1	12	22.719	<0.001	**
Cu	G	1	9	0.000	1		G	1	12	1.067	0.322	
Cu	DxG	1	9	6.918	0.027	**	NxG	1	12	0.717	0.414	
Zn	D	1	12	7.561	0.018	**	N	1	12	7.457	0.018	**
Zn	G	1	12	7.008	0.021	**	G	1	12	1.529	0.240	
Zn	DxG	1	12	0.049	0.828		NxG	1	12	0.480	0.502	
B	D	1	12	0.284	0.604		N	1	12	0.026	0.875	
B	G	1	12	1.596	0.23		G	1	12	0.166	0.691	
B	DxG	1	12	1.835	0.2		NxG	1	12	0.232	0.639	
S	D	1	12	16.129	0.002	**	N	1	12	2.299	0.155	
S	G	1	12	0.008	0.931		G	1	12	6.395	0.026	**
S	DxG	1	12	4.559	0.054	*	NxG	1	12	0.913	0.358	

Table 2. Key results of a type III-ANOVA using satterthwait's method applied to a linear mixed-effect model assessing the effect of drought (D) and grazing (G) ((A) Drought-Model), and nitrogen (N) and grazing (G) ((B) Nitrogen-Model) application on anion/cation- uptake simulated with PRS-probes in an experiment in South Africa in 2020. NumDF stands for numerator degrees of freedom, DenDF for denominator degrees of freedom (Satterthwaite method). Significance levels (Sign) are shown with ** for $p < 0.05$, and * for $p < 0.1$. Respective p-values are given in bold.

drought plots compared to under ambient conditions. Grazing increased total N and NO₃⁻ in soil but decreased the supply of bioavailable phosphorus by 29%. No grazing effect was observed for the other nutrients. Ungrazed plots supplied 0.55 (0.05) µg P/10cm² over 23 weeks compared to 0.39 (0.08) µg P/10cm² over the same period in grazed plots. In the drought model, the interaction of drought and grazing influenced the nutrient supply of total N, NO₃⁻, K, Fe and Cu (Fig. 3). The bioavailability of several nutrients, including total N, NO₃⁻ and Fe, were significantly higher in plots that were subjected to drought and grazing. The trend was common for many other nutrients though not statistically significant.

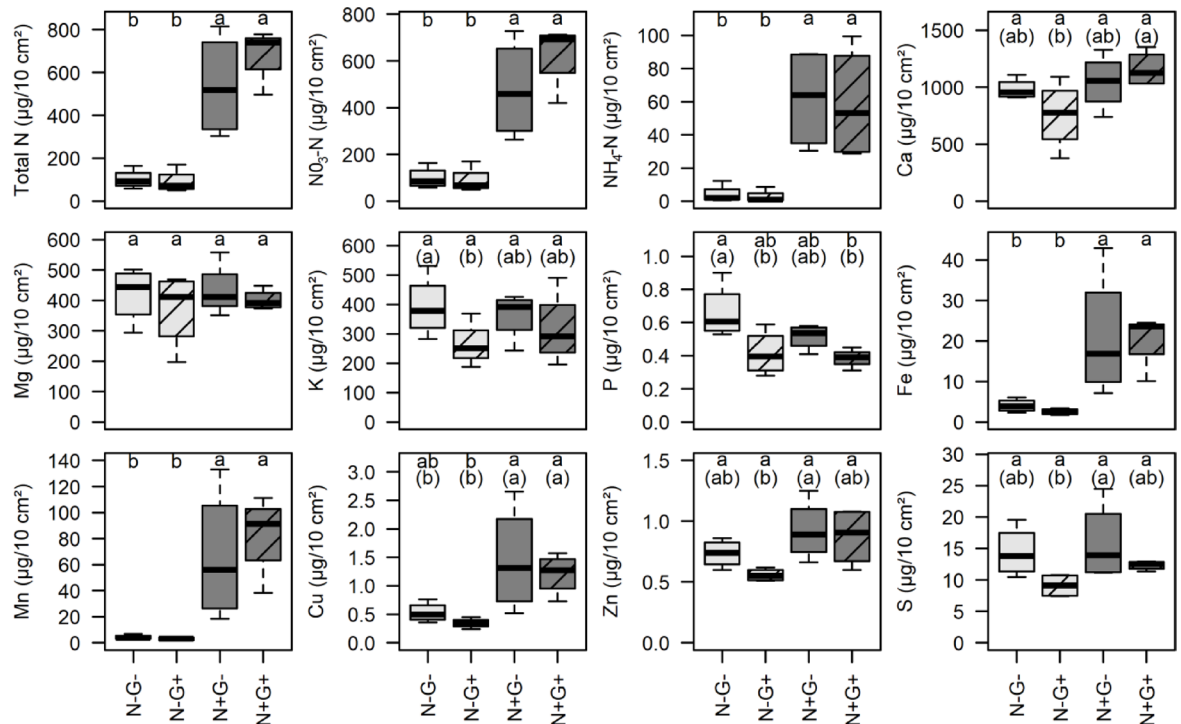


Fig. 2. Combined effects of nitrogen application (yes: N+, no: N-) and grazing (yes: G+, no: G-) on the uptake of macro- and micronutrients by resin membranes simulating plant roots. The nutrients: nitrates ($\text{NO}_3\text{-N}$), ammonium ($\text{NH}_4\text{-N}$), calcium (Ca), magnesium (Mg), potassium (K), phosphorus (P), iron (Fe), manganese (Mn), copper (Cu), zinc (Zn), and sulphur (S). All units are in $\mu\text{g}/10\text{cm}^2/160$ days. Different letters indicate significant differences at $p < 0.05$. If applicable, letters in brackets refer to an alternative threshold level of $p < 0.1$.

Discussion

While the individual effects of global change drivers such as altered precipitation and nitrogen deposition are increasingly understood, their interactions with grassland management in dryland ecosystems remain poorly resolved^{24,34}. Our findings contribute to narrowing this gap by examining how grazing influences nutrient dynamics and soil faunal activity jointly with extreme drought or nitrogen addition.

A key finding was the lack of a significant effect of drought on the feeding activity of soil fauna – a proxy for their contribution to decomposition processes³⁵. This result was unexpected, as previous studies have consistently reported drought-induced reductions in soil biological activity (e.g.^{36–39}). Moreover, a previous study from the same experimental site as this study²⁴ reported higher soil carbon stocks and lower soil CO_2 emission rates under drought, which further supports the idea of a reduced decomposition activity under dry conditions. One possible explanation of our findings lies in the fact that the second half of the 2018/19 growing season (January to May) received only 35 mm of rainfall and thus more than 80% less than the long-term mean during these months, suggesting that baseline soil moisture was already low even in ambient treatments. Consequently, differences in water availability between drought and control plots may have been too small to elicit contrasting soil faunal responses. Similar underestimations of drought effects have been reported elsewhere⁴⁰.

It is also possible that the drought led to a spatial redistribution of soil invertebrates rather than a reduction in their activity per se. Drier conditions in the topsoil often cause certain invertebrate groups to migrate to deeper soil layers^{41,42} with ants and termites being particularly dominant in southern Africa's semi-arid grasslands⁴³. In this context, we hypothesised that, under drought, soil fauna would shift their feeding activity to layers below the top 5 cm of the soil, the region for which Hamel, et al.⁴⁴ and Filzek, et al.⁴⁵ reported the highest activity, because moisture conditions are usually more favourable. Although the results are not conclusive, our findings (Fig. 1) indicate a slight increase in feeding activity at lower soil layers (7–8 cm) compared to the upper most layers. The limited response to drought may be explained by the minimal differences in soil moisture between treatments and the restricted depth of bait lamina insertion (max. 8 cm). It remains possible that greater feeding activity occurred below this depth, but this could not be captured with our method.

In contrast, the combination of nitrogen addition and grazing (N + G+) resulted in increased feeding activity throughout the topsoil. This likely reflects enhanced nutrient inputs: Urea provides inorganic nitrogen, while livestock contribute additional substrates for soil fauna in the form of urine and dung²⁷. Urine is rich in nitrogen (in the form of urea), and dung provides organic carbon¹⁰ both of which stimulate microbial and invertebrate activity⁴⁶. Moreover, livestock trampling helps incorporate surface litter into the soil^{47,48} making it more accessible to decomposers⁴⁹. We found this effect to appear strongest in the upper 0–5 cm, with particularly

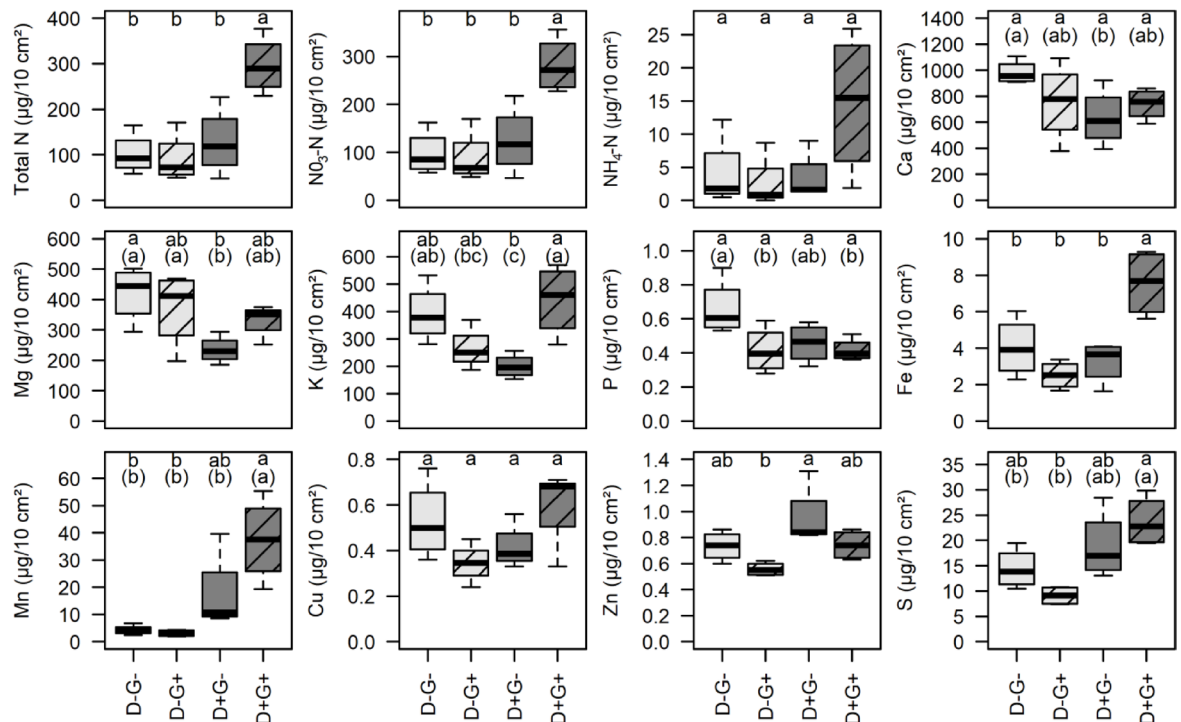


Fig. 3. Combined effects of drought (yes: D+; no: D-) with grazing (yes: G+; no: G-) on plant-available cations and anions (measured as their uptake by resin membranes simulating plant roots). The nutrients: nitrates ($\text{NO}_3\text{-N}$), ammonium ($\text{NH}_4\text{-N}$), calcium (Ca), magnesium (Mg), potassium (K), phosphorus (P), iron (Fe), manganese (Mn), copper (Cu), zinc (Zn), and sulphur (S). All units are in $\mu\text{g}/10\text{ cm}^2/160$ days. Different letters indicate a significant difference at $p < 0.05$. If applicable, letters in brackets refer to an alternative threshold level of $p < 0.1$.

elevated activity between 1 and 2 cm. In addition, grazing in subtropical grasslands may enhance belowground carbon allocation to roots⁵⁰ providing further energy sources for soil biota.

Soil invertebrates play a key role in organic matter decomposition and nutrient mineralisation⁵¹ making their activity essential for plant nutrient supply^{52,53}. Beyond faunal activity, our study also investigated how the treatments affected nutrient availability. We found that drought significantly reduced the supply of calcium (Ca) and magnesium (Mg) while increasing sulphur (S) availability. The latter aligns with findings from Sardans, et al.⁵⁴ who also found increased soil sulphur due to drought. The reduced availability of Ca and Mg reflects their lower solubility or diffusivity in dry soils compared to other nutrients⁵⁵.

Nitrogen addition increased not only ammonium and nitrate availability but also stimulated the availability of several micronutrients, particularly iron (Fe), manganese (Mn) and copper (Cu). The supply of Fe and Mn increased fivefold, while Cu supply doubled. These results are consistent with the findings of Rutkowska, et al.⁵⁶ and Li, et al.⁵⁷ who also reported enhanced micronutrient availability following nitrogen addition. Ammonium-based fertilizers tend to acidify the soil through nitrification⁵⁸ and since micronutrient mobility increases under lower pH, this may explain the observed increase.

Our results suggest that even a modest nitrogen addition ($3.3\text{ g N}/\text{m}^2$) can enhance the availability of essential nutrients in semi-arid grasslands, potentially leading to a higher primary productivity. Cattle grazing can also add nitrogen to the system through uneven but locally high deposition of urine and dung⁵⁹ with faecal nitrogen from cattle averaging approx. 0.8 g N per 100 g of dry matter consumed, while nitrogen concentrations in urine range from 1 to 20 g/L ⁶⁰. This phenomenon is well-known from semi-arid grasslands, in particular from the biospheres around artificial water points^{61,62}. Although not statistically significant, grazed plots in our study showed slightly higher mineral and total nitrogen levels, in line with these processes.

Conclusion

This study found that exposure to extreme drought did not significantly affect soil faunal activity. However, the very low ambient rainfall during the experimental period may have masked potential treatment effects by creating uniformly dry conditions across all plots. In contrast, the combination of livestock grazing and nitrogen addition enhanced soil faunal activity in the topsoil, likely due to increased nutrient inputs and improved litter incorporation. Furthermore, nitrogen addition in the form of ammonium not only increased the availability of inorganic nitrogen but also stimulated the supply of key micronutrients, including iron, manganese, and copper. These findings suggest that moderate nutrient inputs and grazing can support belowground processes in semi-arid grasslands, even under challenging climatic conditions.

Methodology

Study site

The study was conducted at the University of Limpopo's Syferkuil experimental farm, Limpopo Province, South Africa (Fig. 4). The climate is classified as arid steppe hot climate⁶³ which receives annual average rainfall ranging from 400 to 600 mm⁶⁴. Average minimum and maximum temperatures are 4–20 °C in winter and 17–27 °C in summer.

Only 32 mm of rain fall was received from March to August 2020, the period in which the experiment was carried out. Daily temperature, rainfall and other weather data were recorded from an automatic weather station installed at the experimental farm. The maximum temperature, minimum temperature and rainfall recorded in the year 2020 are shown in (Fig. 5).

The soils are mainly shallow (30–50 cm), reddish-brown loamy sand soils, underlain by soft plinthic B horizon and classified as Plinthisols^{65,66}. The vegetation has been described as an open thorn bush savanna belonging to the Pietersburg Plateau False Grassveld type (Acocks, 1994). The herbaceous layer is dominated by perennial C4 grasses such as *Themeda triandra* Forssk., *Digitaria eriantha* Steud., *Schmidtia pappophoroides* Steud. ex J.A.Schmidt and *Eragrostis* spp., while the woody component is dominated by *Vachellia tortilis* (Forssk.) Galasso & Banfi (Low and Rebelo, 1998).

The experimental site is part of a rotational camp system that is moderately grazed at a stocking density of 0.11 LSU ha⁻¹ where a Large Stock Unit (LSU) is equivalent to a mature cow with a bodyweight of 450 kg (Meissner, 1983). Grazing periods did not exceed 30 days, with intermittent recovery of not less than six weeks during the growing season (eight weeks during the dry season, respectively). The rotational management was established six years prior to the set-up of the experiment, resulting in good rangeland condition at the onset of treatments.

Experimental design

We conducted our experiment within the large field experiment 'DroughtAct', which combines a severe drought treatment with a resting treatment. A full factorial experimental design was applied, with crossed drought treatments (two levels: severe drought D+, or ambient rainfall D-); grazing treatments (two levels: moderate grazing G+ or resting, G-) and nitrogen addition (two levels: nitrogen added N+ or not added N-) replicated over four blocks. The resulting 24 plots (10 × 10 m) were separated by corridors with a width of 5 m. Cattle grazing on G- plots was excluded with the aid of permanent wire fences. On D+ plots, rainfall was reduced

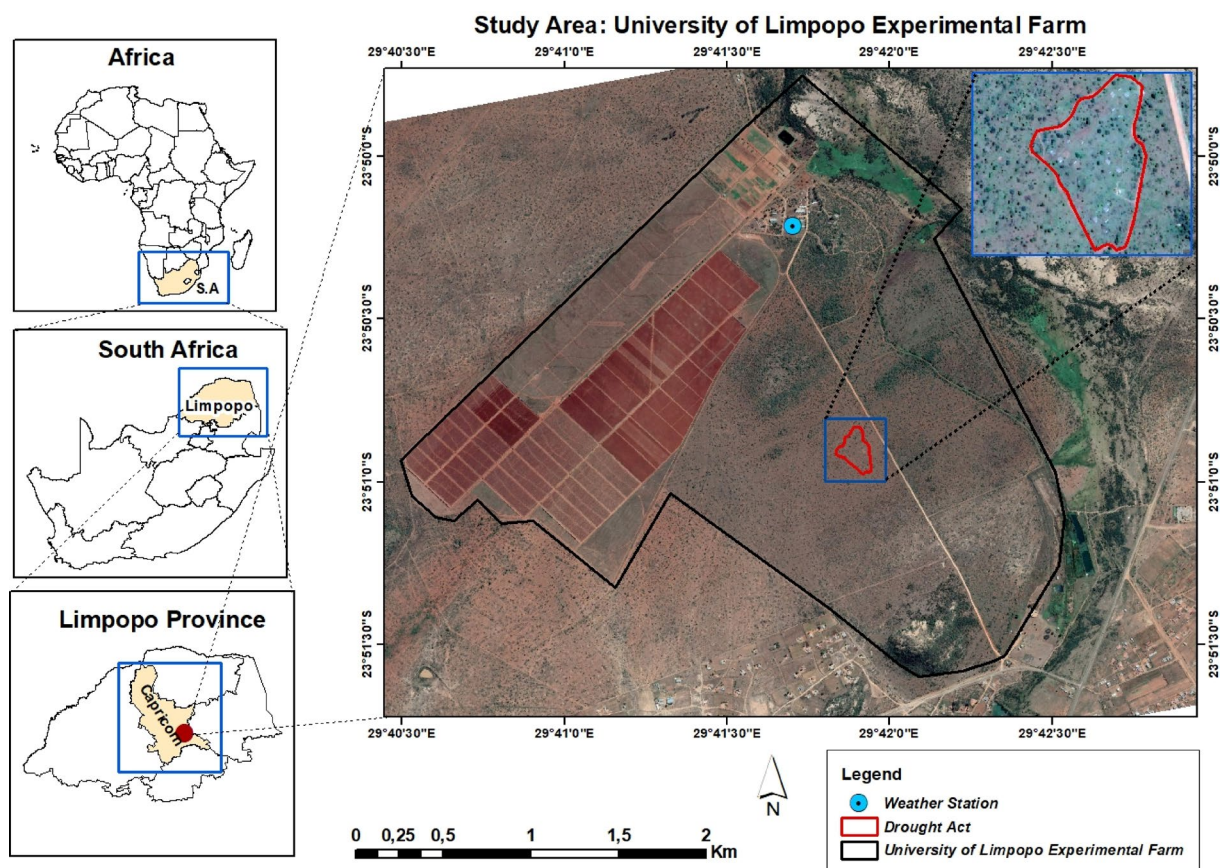


Fig. 4. Location of the DroughtAct experiment at the University of Limpopo's experimental farm in South Africa's Capricorn District of Limpopo Province (adopted from²⁴).

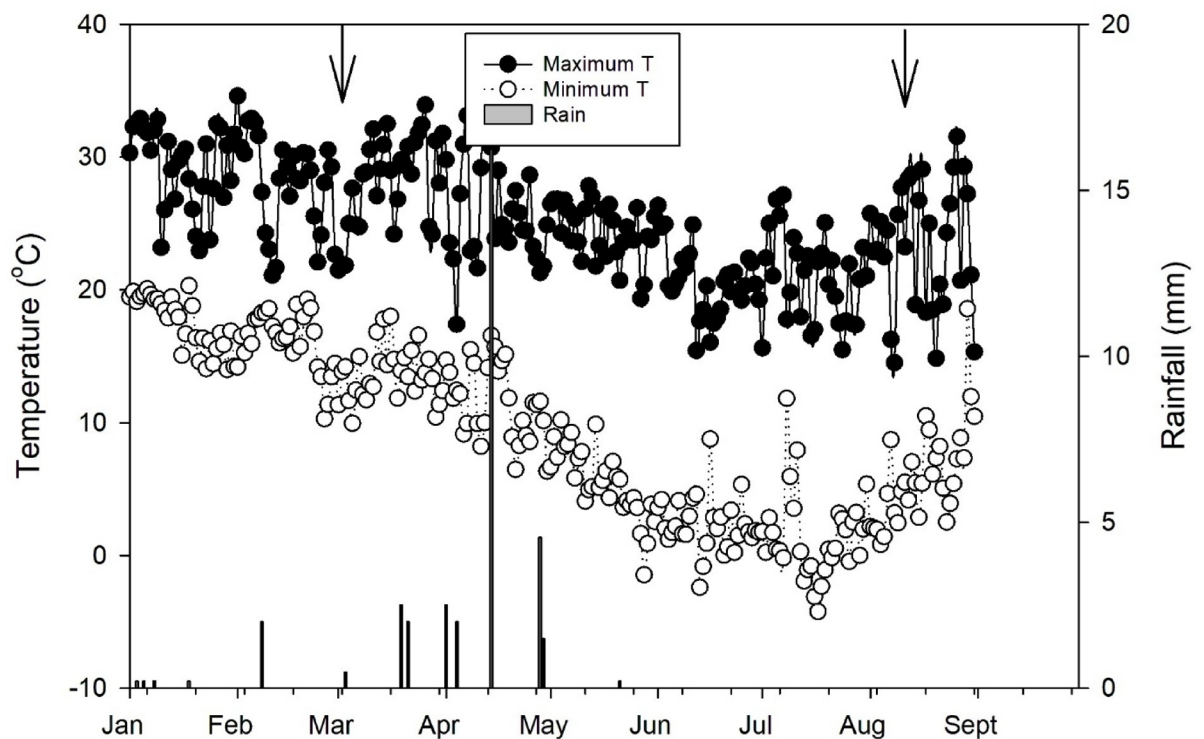


Fig. 5. Rainfall, maximum and minimum temperature recorded in the year 2020 at the weather station situated in ca. 1 km distance to the field experiment. Minimum T = minimum temperature, Maximum T = maximum temperature. The arrows pointing downwards show the onset and end of the period when the bait lamina strips and the PRS probes were buried.

by 66% through the use of large rainout shelters with a size of 36 m², established at the centre of the plots. The rainout shelters allowed for cattle to roam and graze under them. Because the shelters were open on all sides and had a minimum height of 2 m, they had negligible effects on the air temperature beneath them (data not shown). We also oriented the lower sides of the shelters to intercept rain from the dominant wind direction⁶⁷. To prevent interference of lateral soil water movements, we trenched around the perimeter of the rainout shelters to maximum soil depth (≤ 70 cm) and inserted an impermeable plastic sheet. Sampling was restricted to a central subplot area in each plot (4.8 m x 4.8 m) to reduce marginal effects. Grazing and drought treatments were established in October 2014, i.e., before the vegetation period 2014/15. More information on the experimental layout can be obtained in Munjonji, et al.²⁴.

In early 2019, at the onset of the fifth treatment year of DroughtAct, two nitrogen addition treatments were conducted as an add-on to the DroughtAct design. Specifically, we added nitrogen to grazed plots (N + G+) and to plots with grazing exclosure (N + G-), both under ambient rainfall conditions. In these treatments, 10 g N / m² in form of granular Urea (46% N) was applied in three single doses at a rates of 7.6 g Urea / m² equating 3.3 g N m⁻² (33 kg N ha⁻²) in the first half of the rainy season 2019/2020. The latest application was about six weeks before installing the bait lamina strips and PRS probes. Nitrogen treatments were not combined with the ongoing drought treatment.

Assessment of soil fauna feeding activity

To assess the feeding activity of edaphic fauna under field conditions, bait lamina strips were used, which are a commonly applied, standardized field method⁶⁸. Each strip had a size of 6 mm x 120 mm and contained 16 holes filled with an artificial organic bait substrate (1.5 mm in diameter) spaced at 5 mm intervals. Five replicate strips were carefully inserted vertically into the top 8 cm soil horizon, making sure that they did not break. Bait lamina strips were installed in the second half of the rain season, i.e., on 03 March 2020, and remained until well after the vegetation period (in total, 23 weeks). Upon retrieval on 23 August 2020, visual inspection was undertaken to evaluate feeding activity. For each hole, feeding activity was scored as empty (1), partly empty (0.5), or filled (0) for each of the bait-filled holes. When the hole was empty it meant that all the bait was fed on by the soil fauna and when partly empty means only a small part was consumed while filled meant that no feeding activity occurred.

After retrieval, the strips were visually inspected to evaluate feeding activity. For each hole, feeding was scored as: empty (1) if all the bait had been consumed, partly empty (0.5) if some bait remained, and filled (0) if no feeding activity was evident.

Assessment of plant nutrient supply

We used Plant Root Simulator (PRS[®]) probes (Western Ag Innovations, Saskatoon, SK, Canada) to assess plant-available nutrient supply rates in the rooting zone. Each PRS probe consists of a pair of ion exchange membranes – one for anions and one for cations – encapsulated in a plastic frame. These membranes have a high density of ion adsorption sites on their resin surface, enabling them to function as ion sinks when placed in soil, mimicking the nutrient uptake of plant roots. When placed in the soil during the growth period, they provide a seasonally integrated estimate of plant-available macro- and micronutrients, also in dryland grasslands⁶⁹. In each plot, four pairs of PRS probes were installed vertically at a depth of 10 cm. The probes remained in the soil for 23 weeks, from 3 March to 11 August 2020. After retrieval, they were gently washed with deionised water to remove any adhering soil, then packed and sent to the Western Ag Innovations laboratory for analysis (see https://www.westernag.ca/innovations/technology/analysis_units). The analyses were conducted for micro and macro nutrients.

Burial period

The bait lamina strips and PRS probes were originally intended to remain in the ground for six weeks, until the end of April 2020; however, due to COVID-19 restrictions, they could only be retrieved in August 2020. This delay is unlikely to have affected the results, as the last significant rainfall occurred at the end of May and the plant growing season had already concluded by that time.

Data processing and statistical analysis

Soil fauna feeding activity was analyzed using two separate Cumulative Link Mixed Models (clmm from R-package ordinal⁷⁰), whereby the response was a factor of three levels of feeding activity: no activity (filled holes), medium activity (partly filled holes), and high activity (empty holes) on the bait lamina strip. One model tested drought, grazing, depth and their interactions, the second nitrogen, grazing, depth and their interactions. In both models, the individual bait lamina strip was included as random effect. For the visualization, the proportion of no, medium, and high activity, was calculated for all treatments and depths separately.

The effects of drought and grazing and their interaction, as well as the effects of nitrogen and grazing and their interaction on cation/anion uptake were assessed via two separate linear mixed effect models considering the block as random factor and followed by a Type III-ANOVA with Satterthwait's method, using lmerTest package⁷¹. If needed, the response variable was log-transformed prior to analysis to meet the assumptions of ANOVA. A Tukey-HSD test was further used for a pairwise comparison of treatments. We further calculated median values and median absolute deviation (mad) for cation/anion uptake for different treatments. All statistics were done with R⁷².

Data availability

The datasets generated during and/or analysed during the current study are available from the corresponding author on reasonable request.

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Author contributions

All authors contributed to the study conception and design, led by A Linstädter and K Behn. Funding acquisition: A Linstädter and KK Ayisi; data collection: K Behn and VM Mokoka; data analysis: L Munjonji, K Behn, and UN Nielsen. The first draft of the manuscript was written by L Munjonji, and all authors commented on subsequent versions of the manuscript. All authors read and approved the final manuscript.

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Declarations

Competing interests

The authors declare no competing interests.

Additional information

Correspondence and requests for materials should be addressed to L.M.

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