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RESEARCH ARTICLE

Drought and warming enhance the risk of nitrogen losses in intensively managed grasslands

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Abstract

Background and aims Climate change is expected to intensify drought and heatwaves, with major consequences for nutrient cycling in grasslands. Plant-soil-microbe interactions regulate nitrogen (N) dynamics, yet their responses to simultaneous warming and drought remain unclear, especially across plant species and land management histories.

Methods We conducted a factorial warming and drought manipulation on six temperate grassland species belonging to three functional groups (grasses, forbs, legumes) grown in soils from intensively (Int) and extensively (Ext) managed grasslands. We quantified N content and biomass production across soil, microbes, roots, and shoots. We inferred fungi:bacteria by microbial C:N, not by direct soil community determination.

Results Under control and warming conditions, Int soils supported up to 50% higher plant biomass than Ext soils, but this advantage disappeared under drought, reducing plant biomass by ~ 40%. Warming consistently reduced microbial biomass by up to 30% in both soil types. In contrast, drought decreased microbial biomass in Int soils but increased it by ~ 20% in Ext soils, likely reflecting their more drought-resistant fungal communities. These changes altered N flows: extractable soil N was up to three times higher in Int soils under warming and drought, indicating greater vulnerability to N losses, whereas Ext soils maintained low extractable soil N except under combined stress.

Conclusions Intensive management boosts plant biomass under mild and warm conditions but increases susceptibility to N loss during climate extremes. Extensive management supports more stable biomass and N cycling. Integrating microbial dynamics and land-use history is essential for

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predicting grassland resilience and improving N cycling models under global change.

Keywords Grasslands · Nitrogen cycle · Nitrogen losses · Management strategies · Soil microbes · Plant biomass · Microbial biomass

Introduction

Nitrogen (N) is an essential nutrient for plant life, and its limitation diminishes plant growth, yield, and agricultural production (FAO 2006; Elser et al. 2007). Over the past decades, synthetic N-based fertilizers have become a cornerstone of agricultural productivity (grasslands representing 70% of the agricultural area, White et al. 2000), with global application rising from 12 Tg of N y^{-1} in the 1960 s to 110 Tg of N y^{-1} nowadays (IFA 2016; Battye et al. 2017). However, the vegetation typically absorbs only a fraction of the applied N, leading to widespread overfertilization (Zhang et al. 2015; Schils et al. 2022). When N applications exceed the soil and biotic uptake capacity, excess N can be reemitted to the atmosphere (either in N_2O or N_2 form) or leached into aquatic systems (mainly as nitrate, NO_3^-) (Du and de Vries 2025). Such losses have far-reaching environmental impacts, including enhanced greenhouse gas emissions and eutrophication of water bodies (Fowler et al. 2013; Battye et al. 2017).

Plant N uptake, and the balance between plant and microbial N retention and loss, is strongly influenced by water availability, temperature, and soil biological communities (Gruber and Galloway, 2008; Bender et al. 2023). At a global scale, higher air temperature and precipitation generally stimulate biomass production (Lin et al. 2010; Wu et al. 2011), and therefore plant N demand and uptake (Vallicrosa et al. 2025). Yet, by 2100, global mean surface temperature is projected to rise by 2.6–4.8 °C (IPCC 2014), alongside more frequent, severe, and prolonged droughts (Samaniego et al. 2018). These climatic shifts are expected to reduce plant N uptake and increase the risk of N losses, with drought alone projected to raise annual economic damages in Europe from €9 billion today to €65 billion by 2100 (Naumann et al. 2021). Consequently, global warming paired with periodic drought could additionally limit the plant's capacity to absorb and use N (Mariotte et al. 2020).

The soil microbial community (i.e., bacteria and fungi) plays a central role in the N cycle and provides a significant buffer for nutrient and water dynamics (Singh et al. 2020; Trivedi et al. 2021). Thus, soil microbes are often seen as potential mitigators of drought impacts and nutrient imbalances. Indeed, the soil microbial community is responsible for fixing, transforming, and accumulating N in ecosystems (Xu et al. 2013; Bardgett and van der Putten 2014; Crowther et al. 2019), either as free-living organisms or through symbiosis with plants. However, microbes are also N consumers that often experience N limitation (Cui et al. 2025), promoting competition with plants and generating both positive and negative feedback (Wardle et al. 2004; Trivedi et al. 2022). In turn, soil N availability can modify microbial biomass and community composition and abundances, for example, by increasing nitrifying and denitrifying bacteria and archaea (Zheng et al. 2023; Rasmussen et al. 2024) and decreasing the fungal community biomass and activity (Ceulemans et al. 2019; Yu and Dijkstra 2020).

Warming generally stimulates microbial activity in the short term (Fuchslueger et al. 2019), thereby increasing N mineralization and soil N availability (Dawes et al. 2017). Still, the effects of warming on microbial biomass are ambiguous, with some studies reporting decreases (Gao and Yan 2019; Marañon-Jiménez et al. 2019), while others show limited responses under soil warming (Schindlbacher et al. 2011). These contrasting results have been attributed to differences in warming intensity (Xu and Yuan 2017). Drought, on the other hand, consistently reduces microbial activity and biomass (Liu et al. 2023; Qu et al. 2023), thereby decreasing N immobilization and promoting soil N availability. In conclusion, both plants and microbes are sensitive to drought, lowering their N uptake and increasing extractable soil N (Finger-Higgens et al. 2024), whereas the effects of warming are tightly linked to water availability and intensity.

Plant functional group identity may further shape these responses. In temperate grasslands, grasses (Poaceae) typically dominate biomass and soil carbon sequestration due to their extensive root systems and high productivity (Chandregowda et al. 2023). Forbs enhance functional diversity and contribute to nutrient cycling through varied root exudates and faster

litter decomposition (Pokorny et al. 2004). Finally, legumes (Fabaceae) enhance N availability via symbiotic fixation (Ren et al. 2024). Grasses, forbs, and legumes can also form mycorrhizal associations, which boost their productivity (dos Santos Lucas et al. 2022; Soozandehfar et al. 2023; Gorgia and Tsikou 2025). Previous studies suggest that warming may favour forb growth, while legumes and grasses remain stable, whereas drought generally reduces productivity across groups (Arnone et al. 2011; Beierkuhnlein et al. 2011; A et al. 2024), regardless of the soil N status (Eze et al. 2018). Still, how these functional differences mediate plant–microbe–soil interactions under combined warming and drought remains unclear.

Land management practices are another key driver of grassland N cycling (Schils et al. 2022; Richter et al. 2024). Intensive practices such as tillage and fertilization can modify the soil physicochemical properties, reducing its water retention (Bescansa et al. 2006; Smucker et al. 2006) and altering the soil microbial community composition (Fuchslueger et al. 2014; Su et al. 2023). For example, fungal communities are more sensitive to tillage disturbances than bacteria due to the destruction of their hyphae network (Hendrix et al. 1986; Plassart et al. 2008; Helgason et al. 2009), leading to lower fungi:bacteria ratios and more bacteria-dominated soils in intensive management (Sünnemann et al. 2021). These bacteria-dominated soils are typically N-rich, as readily decomposable N incentivizes rapid bacterial N uptake and subsequent microbial biomass increase (Zhao and Neher 2014). Overall, such changes in the microbial community composition affect both C and N cycles, with intensively managed soils having less efficient N-cycling (de Vries et al. 2012; Balmford et al. 2018; Fuchslueger et al. 2019). Yet, few studies have directly tested how management history shapes coupled plant–microbe responses to warming and drought.

In this study, we aim to i) disentangle the impacts of chronic warming and extreme drought on the plant, soil, and microbial N stocks in intensively (Int) and extensively (Ext) managed grasslands across different plant functional groups (grasses, legumes and forbs); and ii) determine how the potential positive or negative feedback between plants and microbes N stocks vary for among plant functional group. We hypothesize that:

i) Extreme drought will have a stronger impact than chronic warming on both plant and microbial N stocks, leaving more unabsorbed N in the soil, with warming further exacerbating drought impacts.
ii) More productive systems (i.e., intensively managed grasslands) will be more susceptible to drought and warming than less productive ones (i.e., extensively managed) due to their higher soil N and bacterial dominance.
iii) Grasses will be the most productive functional group and therefore more susceptible to drought, while warming will stimulate legume growth in extensive soils, promoting N fixation through root symbioses.

This research will provide a holistic assessment of climate change impacts on the N cycle in temperate grasslands, informing future management practices and water eutrophication risk assessment.

Methodology

Experimental design

On February 12th-13th, we collected soil from the first 40 cm (soil B horizon, where roots can normally reach) on one intensively (Int) and one extensively (Ext) managed experimental grasslands at Agroscope (Posieux, Switzerland) (46.77 N, 7.10 E, 660 m.a.s.l.). These grasslands were managed this way for about 50 years for the extensively managed and 15 years for the intensively managed, allowing us to sample soil communities that naturally developed under these prolonged management histories. The soil was dug with shovels, and the vegetation (above and belowground) was removed by hand. Both grasslands (distant by less than 500 m) have similar parental material (moraine), soil type (cambisol), and are developed under the same climate (MAT of 9.1 °C and MAP of 1023 mm, averaged 1991–2020, MeteoSwiss), but with significant differences in management practices. The intensively managed grassland is tilled every four to five years, seeded with forage mixtures, harvested four to five times per year, and fertilized with liquid manure at the beginning of the growing season after each forage harvest and before winter, corresponding to 130 kg N per hectare per

Table 1 Initial soil physicochemical properties

	Intensive	Extensive
pH	6.89	6.72
CEC*	15.43	19.22
SOM* (%)	2.7	3.7
Clay (%)	14.9	14.1
Sand (%)	54.5	57.7
Silt %	29.0	26.2
VWC*	12.58 ± 1.73	11.92 ± 1.73
Bulk density (g/cm3)	1.1 ± 0.13	0.93 ± 0.05
DOC* (mg/kg)	92.52 ± 6.62	67.60 ± 6.5
TN* (mg/kg)	18.91 ± 4.81	14.48 ± 4.40
MB* C (mg/kg)	231.28 ± 30.00	155.08 ± 52.18
MB* N (mg/kg)	49.02 ± 6.29	33.45 ± 10.49
MB* C:N	4.73	4.62

*CEC** Cation Exchange capacity, *SOM** Soil organic matter, *VWC** Volumetric Water Content, *DOC** Dissolved organic carbon, *TN** Total nitrogen, *MB** Microbial

year. In contrast, the extensively managed grassland has not been tilled for at least 50 years; it is harvested twice a year in early July and September or occasionally once a year in early July and then grazed once by dairy cows. As a result, the soil physicochemical properties differ, with higher soil carbon (C) and nitrogen (N) levels in the soils from intensively managed grasslands (Table 1).

Standard deviation included in measures specifically sampled for this study. Sample size = 4. Measures without error values have been obtained from Agroscope's internal data.

The soils collected from the two sites were homogenized and sieved using a 2 mm mesh to remove rocks and plant biomass and then filled into 240 5 L pots (20 cm depth, 18 cm diameter, 120 pots per soil type). The pots were placed in laterally opened polytunnels (semi-cylindrical structures made of metal frames covered with transparent plastics, used to create controlled environments) under environmental temperature with artificial watering to facilitate soil subsidence.

We selected six common plant species and used their recommended varieties for Swiss grasslands (Suter et al. 2023): two grasses (*Lolium perenne* L. var. Artesia and *Festuca arundinacea* Schreb var. Otaria), two forbs (*Plantago lanceolata* L. var. Ceres Tonic and *Prunella vulgaris* L., ecotype of Eastern Swiss Plateau), and two legumes (*Trifolium repens* L. var. Apis and *Lotus corniculatus* L. var. Lotar), containing a species with high and a species with low drought-resistance in each group. *L. perenne, P. vulgaris* and *T. repense* were considered as low resistant to drought and *F. arundinaceae, P. lanceolata* and *L. corniculatus* as high resistant to drought. *L. perenne* is included in 80% of recommended forage mixtures in Switzerland, *F. arundinacea* in 20% of mixtures and *T. repens* in 60% of mixtures. The seeds were obtained from UFA Samen (Winterthur, Switzerland). On February 26th (two weeks after moving the pots into the polytunnels), three seeds of a single species were planted directly in each pot to maximize germination success and survival. Around March 17th, the seeds started to germinate, and after another two weeks, the surplus seedlings were carefully removed by hand, leaving only one healthy individual of the targeted species per pot with minimal disturbance of the system.

In April, pots were divided into two pre-treatments in separate polytunnels: control (ambient air temperature) and warming ($n = 10$ replicates per species, soil type, and pre-treatment). The polytunnels were equipped with automatic opening systems to control the air temperature indirectly. The heating treatment was controlled by setting the wall opening at 5 ºC above the control group. An artificial irrigation system combined with a systematically monitoring of the soil moisture maintained the soil water content at 60–70% of the respective maximum water holding capacity for all pots. This resulted in a total of 240 pots (2 soil types × 2 per-treatments × 6 species × 10 replicates). The plots were shuffled periodically to avoid placement effects.

After two months, on June 20th, the aboveground biomass was cut 5 cm above the ground to mimic common forage harvest practices and stimulate regrowth (Mosimann 2001). The cut material was weighed, dried at 65ºC for 72 h, and stored for further analysis. After cutting, each pre-treatment was further divided into a drought and control group, creating four treatments in total to determine how prior acclimation to warming affects responses during subsequent extreme droughts. The chronic warming treatment at + 5ºC was maintained, but the watering regime was reduced to 30–35% of the soil's water retention capacity. This reduction was conducted in half of the pots in the pre- treatments, resulting in a factorial design with control (C), warming (W),

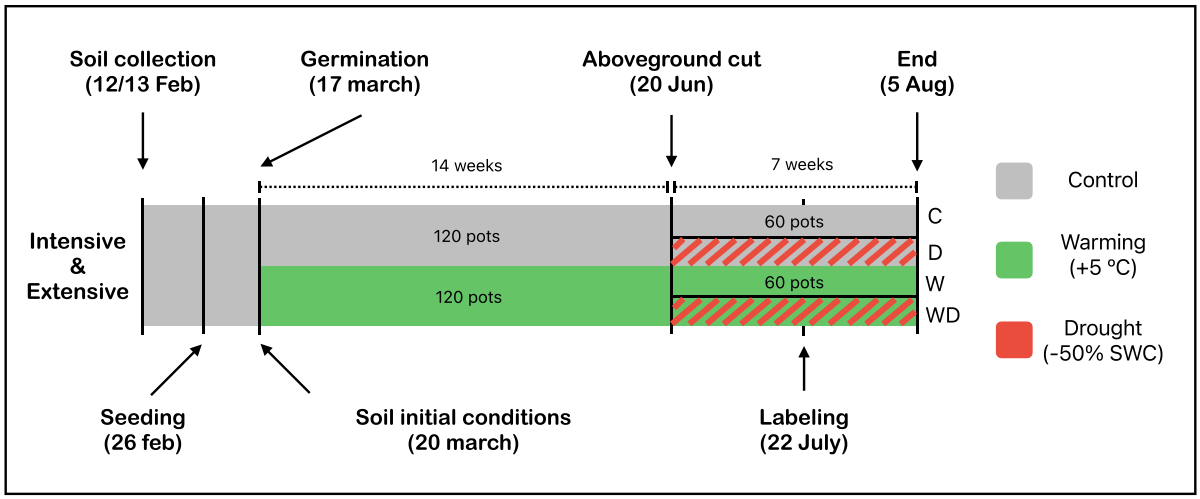


Fig. 1 Schematic representation of the experimental design. In total, 240 pots were filled with soil coming from intensively and extensively managed grasslands, where seeds from six temperate grassland species were planted. The pots were separated into control and warming (+5ºC) during the first growing period, before an aboveground cut. After the cut, two water regimes emerge from each group, reducing the water availability to 30–35% water retention capacity, obtaining a full factorial design. SWC = Soil water content. C = Control, D = Drought, W = Warming, WD = Warming + drought

drought (D), and warming + drought (WD) conditions ($n = 5$ plants per species, treatments, and soil type). When some plants started reaching their advanced flowering stage (i.e., starting seed formation, prior to plant senescence), on August 5th (after about 1.5 months of the aboveground cut), we terminated the experiment (Fig. 1).

Carbon and nitrogen content in the above and belowground plant biomass

At the end of the experiment (August 5th), the total plant biomass was destructively harvested in each pot and separated into aboveground and belowground fractions. Roots were carefully washed to remove the soil. All biomass samples were dried at 65 °C for at least 72 h before weighing. To obtain the total biomass production, we combined the aboveground and belowground dry biomass per individual (g). To obtain the biomass partitioning (unitless), we divided the aboveground dry biomass by the belowground one per individual.

After determining the total weight, the dried aboveground and belowground material was ground with a ball mill (Retsch, model MM400, Retsch GmbH) and weighed in tin capsules for further analyses. Total C and N concentrations (%) were determined by gas chromatography using an elemental analyzer interfaced with an isotope ratio mass spectrometer (PDZ Europa ANCA-GSL and PDZ Europa 20–20; Sercon Ltd.) at the Stable Isotope Facility of UC Davis (CA, USA). To calculate the plant N uptake (total N taken up by the plant since germination) (mg N/plant), we multiplied the aboveground and belowground N concentration by their respective total biomass, and summed up the two values for each plant.

Carbon and nitrogen content in soils and microbes

The remaining soil was homogenized and sieved through a 2 mm mesh for further analysis. We acknowledge that the microbial community tightly attached to the radicular system was most likely taken away with the roots and not considered as part of the soil microbial community. The samples were stored in sealed plastic bags to maintain humidity and kept at ambient temperature. All the soil samples were processed within three days after collection. To extract and measure the total soil and microbial C and N content (mg/pot), we used the fumigation-extraction method according to Vance et al. 1987. Briefly, aliquots of each soil sample were divided into two groups: non-fumigated and fumigated with chloroform (24 h, which releases C and N from the

microbial structures). From both fumigated and non-fumigated samples, extractable organic C and total extractable N were extracted from both soil subsamples using 0.5 M K_2SO_4 and measured with a TOC/TN analyser (TOC-V, Shimadzu, Tokyo, Japan). Microbial C and N were calculated as the differences between fumigated and non-fumigated soil extracts, and no correction factor was applied. Microbial C was used as a proxy of microbial biomass across the study (Vance et al. 1987).

Soil nitrate concentrations

To determine the potential leachability of the extractable soil N, we determined the concentration of nitrate (NO_3^-) in non-fumigated soil solution extracted with K_2SO_4. We used a reduction-to-nitrite technique with a Reduction-diazotisation reagent (Miranda et al. 2001). We then performed a spectrophotometric determination of nitrate in soil extracts by using a 96-well plate reader. The measurements were compared to calibration curves to determine the final NO_3^- values.

Data processing and statistical analysis

To determine the impact of the climatic treatments (C, D, W, WD) and soil type (Ext and Int) on plant biomass production, microbial biomass, plant N stocks, microbial N stocks, microbial CN ratios, aboveground vs. belowground biomass partitioning, extractable soil N, and soil nitrate, we fit analysis of variance models (ANOVA) following the structure "variable ~ Treatment*Soil type". Each plant individual was used as a replicate (5 replicates per soil type, treatment, and species). We used this approach for the entire dataset and for subsets by plant group (grasses, legumes, and forbs). We then calculated the Tukey Honest Significant Differences with a confidence level of 0.95. We plotted the results using ggplot2 (Wickham 2016) and multcompView (Graves et al. 2024).

To complement the visual representation, we also computed linear mixed models using lme4 (Bates et al. 2015) and lmerTest (Kuznetsova et al. 2017), following the structure "variable ~ Treatment*Soil type + (1|Species)". We also tested the correlation between plant N uptake and extractable soil N stocks following the structure "lmer(plant_n_stocks ~ soil_n_stocks + Treatment*Soil + (1|Species))".

To test the effect of the drought tolerance group, we used the model structure "variable ~ Treatment*Soil type + Treatment*Drought tolerance group + (1|Species)". Adding the species as a random factor did not significantly change the results in any analysis.

To study the correlation between plant N stocks and microbial ones by plant functional group, we divided the microbial N stocks by the plant N stocks and log-transformed the variable for normality purposes. This way, values above 0 would imply higher N in the microbial community, and values below 0 would imply higher N in plants. We analysed the microbial:plant proportion following the same procedure as before.

Results

Plant and microbial biomass responses to warming and drought

At the first cut, plants growing in intensively managed (Int) soils produced 70% more aboveground biomass than those in extensively managed (Ext) ones ($p = 0.0003$). Warming promoted the aboveground biomass even further in Int soils, nearly doubling production compared to Ext soils ($p = 0.0007$) (Table S1).

By the end of the experiment, plants in Int soils remained 43% more productive than those growing on Ext soils, but only under control (C) and warming (W) conditions (Fig. 2a, Table S2). Under drought (D) or combined warming and drought (WD), biomass production no longer differed between soil types. The combined stresses (WD) decreased biomass by 59% compared to the control, leading to the lowest productivity overall (Fig. 2a, Table S2).

Treatment effects also varied between soil types. In Ext soils, total plant biomass did not differ significantly among treatments. In contrast, in Int soils, plants were more productive under C and W than under D and WD (Fig. 2a). In addition, there were no significant differences in total plant or microbial biomass among drought-tolerance groups for any treatment ($p = 0.82$ and $p = 0.65$) (Table S2).

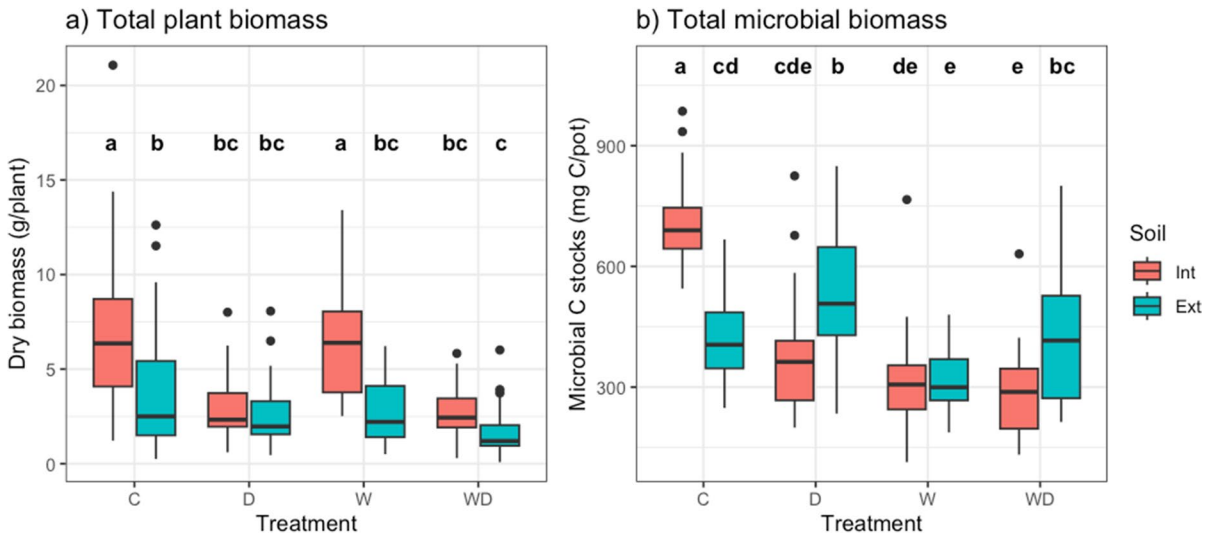


Fig. 2 Boxplots describing dry plant productivity (**a**) and microbial biomass (**b**) in intensively (Int) and extensively (Ext) managed soils. Different letters disclose significant differences among treatments and soil types (p-value < 0.05)

Microbial biomass also differed among soil types in C, D, and WD (Table S1) even though microbial CN remained generally higher in Ext (Figure S1). In Int soils, microbial biomass was highest under C conditions, and similarly low under D, W, and WD. In Ext soils, microbial biomass was highest under D and WD (Fig. 2b). Warming reduced microbial biomass in both soils, leading to similar values under W (Fig. 2b). The combination of warming and drought did not further reduce microbial biomass compared to W in Int soils and was similar to D in Ext soils. These results suggest important opposite drought responses between plants and microbes and contrasting patterns between soil management practices.

Across plant functional groups, biomass responses were generally consistent, except for legumes, which were more productive under W than in C, but only in Int soils (Figure S2). The aboveground-to-belowground biomass ratio remained stable across treatments and soil types, averaging around 1.5 (Figure S3). Microbial biomass patterns were also consistent across plant groups, with mild exceptions in grasses, where Ext soils showed higher microbial biomass than Int soils under D, W, and WD (Figure S4).

Plant and microbial N stocks responses to warming and drought

Soil type significantly influenced plant N stocks across all three plant functional groups (Table S3). Generally, plants growing in Int soils showed higher plant N stocks under C and W treatments, while D and WD reduced these differences, equalizing N stocks between soil types. The N concentration in the plant tissues remained relatively stable across treatments (Figure S4). As a result, plant N stock patterns followed a similar pattern to that of plant biomass production. An exception was observed for grasses, which showed higher plant N stocks in Ext under C conditions (Fig. 3abc). Interestingly, grasses growing on Ext soils accumulated more N despite lower soil N availability, whereas Int soils – initially richer in N – supported plants with lower tissue N concentrations in both shoots and roots (Fig. 3abc, Figure S5).

Under control conditions, microbial N stocks were about 200% higher in Int soils than in Ext soils across all plant functional groups. However, these differences disappeared under stress treatments, as microbial N stocks became similar between soil types (Fig. 3def). The lowest microbial N stocks were observed under W across all plant functional groups (Table S3).

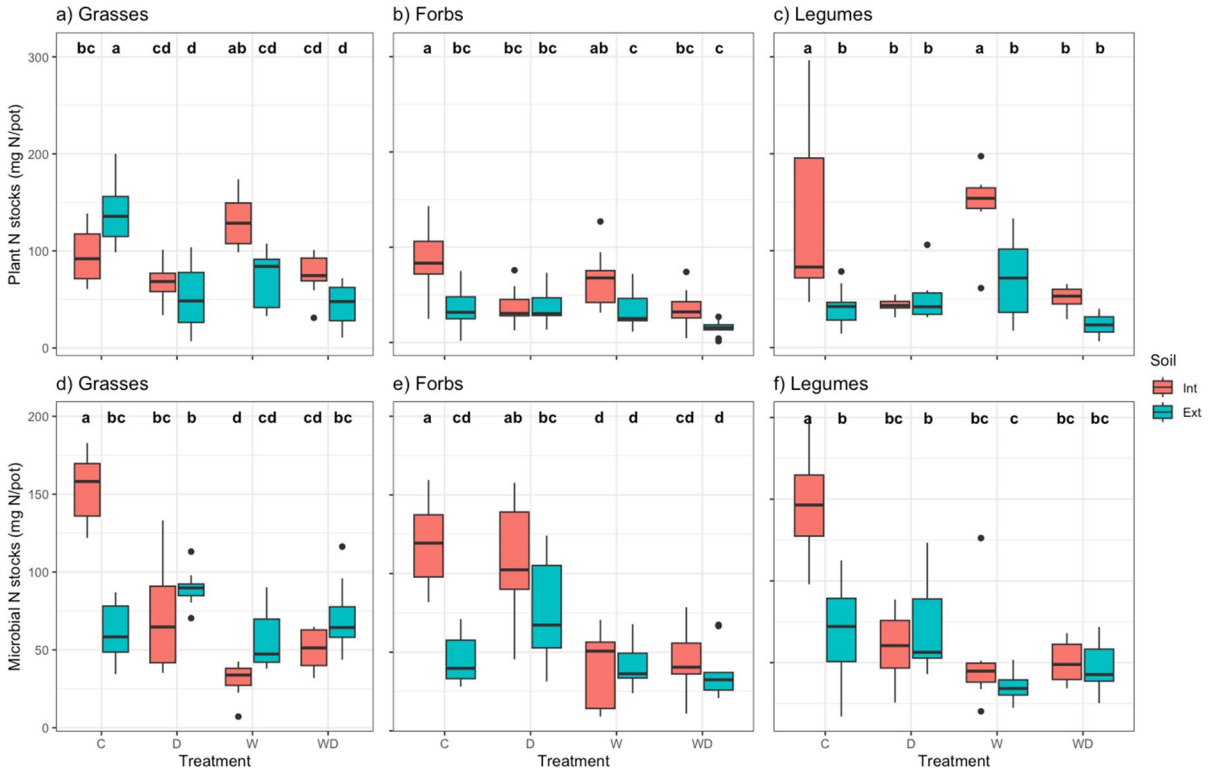


Fig. 3 Boxplots describing dry plant nitrogen (N) stocks and microbial N stocks in both intensively (Int) and extensively (Ext) managed soils in grasses, forbs, and legumes mesocosms. Different letters disclose significant differences among treatments and soil types (p-value < 0.05)

Extractable soil N and nitrate stocks responses to warming and drought

Extractable total N stocks in the soil were lowest under control conditions, with no differences between the two soil types (Table S4), and negatively correlating with plant N uptake (−0.15x, $p = 0.001$; Table S5). In Int soils, both D and W increased extractable soil N by approx. 100% and 137%, respectively, compared to the control. In contrast, extractable soil N in Ext soils remained stable under C, D, and W and increased only under WD (Fig. 4a). Responses also varied among plant functional groups. For grasses, extractable soil N showed similar trends across both soil types (Fig. 4d, Table S3). However, forbs and legumes displayed strong contrasts between soils, especially under W and D, where Int soils had significantly higher extractable N than Ext soils (Fig. 4ef, Table S3).

Soil nitrate stocks responded similarly to total extractable N, showing parallel treatment and soil-type effects (Fig. 4b, Table S4). On average, nitrate accounted for about 49% of the total extractable soil N, with only minor but significant differences between soils and treatments (Fig. 4c, Table S6).

Plant—microbial nitrogen ratios

In general, the plant-to-microbial N ratio was similar between soil types under both C and D conditions, remaining slightly above 0, which indicates that more N was retained in microbes than in plants (Fig. 5a, Table S7). An exception was observed for grasses, where Int soils stored more N in the microbial compartment, while in Ext, most of the N was held in plants (Fig. 5b). Under W and WD, the pattern shifted: plants accumulated more N than microbes overall, yet the microbial community in Ext soils retains more N than that in Int soils (Fig. 5, Table S7).

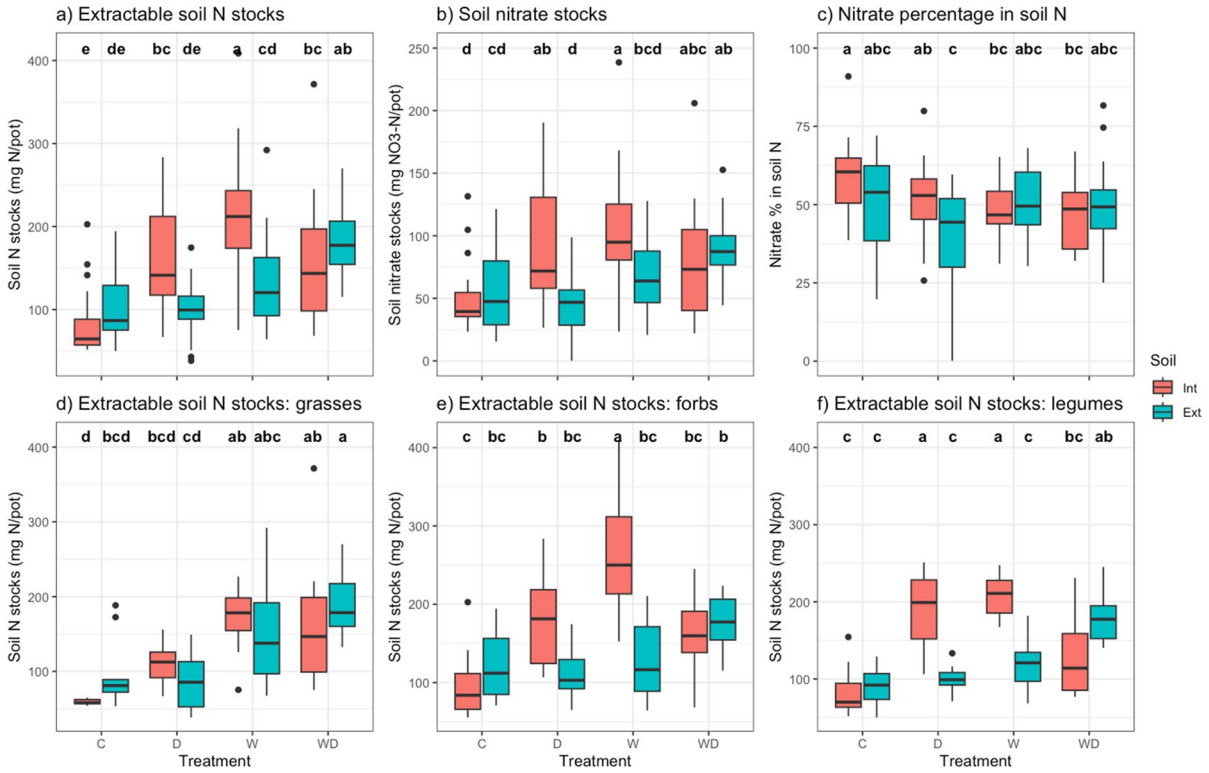


Fig. 4 Boxplots describing extractable soil nitrogen (N) (**a**), soil nitrate stocks (**b**), and nitrate percentage in total soil N (**c**) in both intensively (Int) and extensively (Ext) soils. Plots show general values (a,b,c) and values of extractable soil N by plant group (d,e,f). Different letters disclose significant differences among treatments and soils (p-value < 0.05)

Discussion

Our study demonstrates that plant and microbial communities respond differently to extreme drought and chronic warming, and that these responses are strongly shaped by land-use history management and plant functional group. Aligning with our hypothesis, drought consistently decreased plant biomass and plant N stocks, while warming primarily reduced microbial biomass and microbial N stocks. Intensively managed soils (Int) supported higher productivity under control and warming, but this advantage disappeared under drought. The decrease in plant N uptake due to drought leads to greater accumulation of extractable soil N and soil nitrate. In contrast, extensively managed soils (Ext) maintained more stable plant and microbial biomass and N cycling across treatments, except under combined warming and drought. Plant–microbe N relationships were positively correlated in forbs and legumes but negatively correlated in grasses, suggesting contrasting strategies of nutrient acquisition and competition.

Contrasting drivers for plants and microbes

As hypothesized, drought emerged as the dominant stressor for plants, reducing both biomass and N uptake across all functional groups and soil types. This pattern aligns with previous reports where water limitation directly restricts photosynthesis, growth, and nutrient acquisition (e.g., Liu et al. 2023; Finger-Higgens et al. 2024). Reduced soil moisture not only limits root water uptake but also slows nutrient diffusion and mass flow, thereby restricting N availability for plant uptake. Consequently, drought conditions suppress plant productivity even when soil N pools remain high (Schimel 2018).

Warming alone had little effect on plant productivity, but when combined with drought, it exacerbated plant stress, particularly in Ext soils. This likely reflects the increased soil water loss under

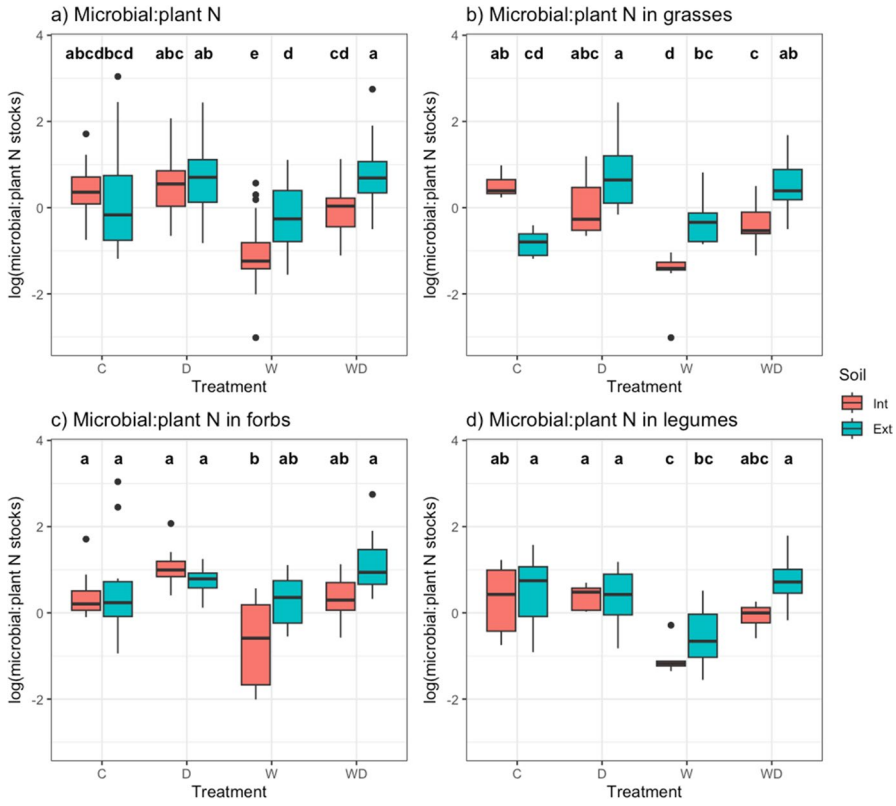


Fig. 5 Boxplots describing the microbial:plant nitrogen ratio in both intensively (Int) and extensively (Ext) soils. Plots show general values (a) and values by plant group (b,c,d). Different letters disclose significant differences among treatments and soils (p-value < 0.05)

higher temperatures, which amplifies soil water deficit (Schimel 2018). Thus, while warming alone does not directly limit growth, it can intensify the negative effects of drought on plants.

In contrast to plants, microbial communities were primarily limited by warming rather than drought. Warming decreased microbial biomass and N stocks by up to 80% in both soil types. With elevated air temperature, the microbial activity increases as well as microbial respiration, incentivizing microbial C and biomass losses (Fuchslueger et al. 2019). This decline is consistent with other studies from grasslands and forests where warming decreased soil microbial biomass over both short and long timescales (Tian et al. 2023; Marañón-Jiménez et al. 2025). However, not all studies agree—the meta-analysis performed by Li et al. (2024) reported no effect of warming on microbial biomass in grasslands, highlighting the context-dependency of microbial thermal responses.

Drought responses, on the other hand, diverged between soil types. In Int soils, drought generally reduced microbial biomass, whereas in Ext soils it increased by roughly 20%. This contrast could suggest differences in microbial community composition: bacteria are generally more abundant in Int soils and are generally more susceptible to desiccation, while fungi generally dominate Ext soils and are better adapted to water stress due to their filamentous hyphal networks and osmotic regulation capabilities (Sun et al. 2020; Doménech-Pascual et al. 2024; Canarini et al. 2024). The microbial CN values were systematically higher in Ext soil, indicating higher fungi abundance in Ext soils therefore sustaining the thesis of contrasting soil communities in both managing styles (Strickland and Rousk 2010; Mouginot et al. 2014). However, this explanation remains speculative and further studies including changes in microbial:fungi ratio in this context are desired.

Altogether, these results suggest that intensive management leads to faster, more drought-sensitive bacterial systems, whereas extensive management fosters fungal-dominated communities that buffer drought impacts. The enhanced microbial resilience in Ext soils, combined with reduced plant uptake under drought, likely frees up soil N for microbial use, leading to the observed

increase in microbial biomass. These contrasting plant–microbe responses highlight how land-use history and community composition mediate ecosystem resilience to interacting climate stressors. Nonetheless, more research accounting for microbial diversity is needed to confirm such relationships.

Functional group-specific plant–microbe interactions

Our results showed apparent differences in responses and plant–microbe N relationships among functional groups. As hypothesized, grasses were the most productive functional group, especially under control and warming conditions, while legumes and forbs showed comparably lower growing rates. Even though grasses experienced the largest productivity decrease under drought, they still maintained higher biomass than the other groups.

However, this biomass dominance did not translate into higher plant N stocks. In fact, under control conditions in Int soils, grasses exhibited unexpectedly low plant N stocks, reflecting very low N concentrations in their tissues. This counterintuitive result suggests that grass productivity in Int soils may be constrained by belowground N competition, rather than by N availability alone.

When considered together with microbial data, it becomes evident that N allocation between plants and microbes differs sharply between soil types: in Int soils, most N is concentrated in the microbial community, while in Ext, it is predominantly stored in plants. This indicates that competition for N between grasses and microbes is soil-dependent. Grasses may acquire N more efficiently when competing with fungal-dominated microbial communities (typical of Ext soils), but less effectively when facing bacteria-dominated communities. These contrasting results were not found in forbs nor legumes, which maintained more balanced relationships with the microbial community. This pattern suggests a greater functional complementarity between these groups and soil microbes, possibly due to differences in root traits, exudation profiles, or symbiotic associations (Cong and Eriksen 2018; Ren et al. 2024).

Implications for nitrogen losses and grassland management

Extractable soil N dynamics revealed a key vulnerability in intensively managed systems. Under warming and drought, the extractable soil N was up to three times higher in Int soils than in Ext ones, reflecting reduced plant and/or microbial N uptake. Approximately half of the extractable N pool was in nitrate form, which substantially increases the risk of N losses through leaching during heavy rainfall or gaseous emissions following rewetting events (Fowler et al. 2013; Weitzman et al. 2022; Pietrzak and Urbaniak 2024). In contrast, Ext soils maintained consistently low extractable soil N levels under all single-stressor conditions, only rising under combined warming and drought.

These patterns suggest that while Int soils can deliver high productivity under favourable conditions, they are more vulnerable to N losses and reduced resilience under climate extremes. Conversely, Ext soils, likely due to higher water retention capacity, greater fungal abundance, and slower nutrient cycling, offer greater stability in biomass production and N retention (de Vries et al. 2006). This highlights a trade-off between productivity and resilience, suggesting that land management practices promoting diverse microbial communities and improved soil structure could mitigate N losses under future climate conditions.

Our experimental design allows us to isolate the plant-soil-microbial interactions by species and functional group, allowing us to quantify their individual and combined responses under controlled environmental conditions. However, in this research, we used pots, which confine the radicular system into a determined volume of soil. This way, our conclusions do not include potential competition and synergies among species or individuals nor potential spatial niche separations due to divergent radicular structures (i.e., deeper or wider roots) that might have occurred in a natural grassland. Moreover, we did not observe changes in the aboveground vs. belowground biomass partitioning regardless of the plant size, which suggests that differences between the pot and the grassland radicular system are unlikely. We also used a monospecific approach, isolating individuals, so differences

due to individuals' density and intra-specific interactions might occur. Therefore, field-based studies incorporating species mixtures and realistic rooting environments are essential to validate these findings and better assess how plant–microbe–soil feedback influence N cycling and resilience under climate change. Further research could benefit from a more detailed characterization of the bacteria:fungi ratio, since it would provide a more mechanistic understanding of the impacts of soil management practices in the soil N cycle.

Broader implications

Intensively managed soils are typically fertilized and tilled to maximize plant productivity and economic return, requiring substantial resource and labour investment. Nonetheless, our study shows that this productivity advantage only happens under moist and warm conditions, and disappears under drought, when compared to extensive practices. In addition, the productivity gain under warming comes at a cost of higher extractable soil N, increasing the risk of N losses and water eutrophication.

Future climate scenarios predict changes towards warmer air temperatures and reduced soil water content (IPCC 2014). In addition, the more time-condensed precipitation regimes will perpetuate longer drier periods with short torrential rains in many regions (Samaniego et al. 2018). Our results anticipated changes in the plant and microbial N use while warming and drought conditions are at play, which might advise against intensive management practices in grasslands. Drier conditions would prevent plants from growing and incorporating available N, while warming would decrease microbial N, both doubling the extractable soil N and soil nitrate. In combination with torrential rains, the N losses by leaching are expected to increase substantially. On the other hand, Ext soils remained more stable, reducing potential N losses, maintaining both biomass production and microbial biomass except on the combination of both W and D simultaneously. Overall, our findings suggest that extensive management practices offer a more sustainable strategy to maintain grassland productivity while minimizing N losses in a warmer and drier future climate.

Conclusion

In this study, we showed that intensively managed soils are more productive only under control and warming conditions, while their advantage disappears under drought. We also showed that microbes and plants respond to different dominant stressors: plant productivity is mostly reduced by drought, while microbial biomass declines with warming. As a result, drought and warming conditions can generate an accumulation of soil N that can later be leached into groundwater or surface water, as well as being reemitted to the atmosphere.

We further identified contrasting plant–microbe interactions across functional groups. Forbs and nitrogen-fixing legumes tended to show complementarity, cooperative relationships with soil microbes, while the opposite interaction was demonstrated in grasses.

These findings will help better incorporate the role of microbes in the N cycling, better understand the impacts of future conditions of warming and drought, and plan management strategies accordingly. Management strategies aimed at maximizing productivity under current conditions may inadvertently increase vulnerability to nutrient losses in future, more extreme climates. In contrast, less intensive management practices could enhance ecosystem resilience and stability, though potential trade-offs in yield will need to be carefully evaluated.

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Authors contribution Helena Vallicrosa, Pierre Mariotte and Charlotte Grossiord conceived the ideas and designed the methodology. Helena Vallicrosa performed the experiments, collected and analysed the data and wrote the initial manuscript. Frank Hagedorn provided lab and conceptual support. Lucia Fuchslueger and Nathielly Martins provided conceptual support. Ariann Milano provided field and lab support. All authors contributed critically to the drafts and gave final approval for publication.

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Data availability The data and code generated for this study is available at https://github.com/helenavallicrosa/Plant-soil-microbes-experiment

Declarations

Conflict of interests The authors declare no conflict of interest.

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