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Can permanent grassland soils with elevated organic carbon buffer negative effects of more persistent precipitation regimes on forage grass performance?

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Abstract

Agricultural practices enhancing soil organic carbon (SOC) show potential to buffer negative effects of climate change on forage grass performance. We tested this by subjecting five forage grass varieties differing in fodder quality and drought/flooding resistance to increased persistence in summer precipitation regimes (PR) across sandy and sandy-loam soils from either permanent (high SOC) or temporary grasslands (low SOC) in adjacent parcels. Over the course of two consecutive summers, monoculture mesocosms were subjected to rainy/dry weather alternation either every 3 days or every 30 days, whilst keeping total precipitation equal. Increased PR persistence induced species-specific drought damage and productivity declines. Soils from permanent grasslands with elevated SOC buffered plant quality, but buffering effects of SOC on drought damage, nutrient availability and yield differed between texture classes. In the more persistent PR, *Festuca arundinacea* FERMINA was the most productive species but had the lowest quality under both ample water supply and mild soil drought, while under the most intense soil droughts, *Festulolium* FESTILO maintained the highest yields. The hybrid *Lolium x boucheanum* kunth. MELCOMBI had intermediate productivity and both *Lolium perenne* varieties showed the lowest yields under soil drought, but the highest forage quality (especially the tetraploid variety MELFORCE). Performance varied with plant maturity stage and across seasons/years and was driven by altered water and nutrient availability and related nitrogen nutrition among species during drought and upon rewetting. Moreover, while permanent grassland soils showed the most consistent positive effects on plant performance, their available water capacity also declined under increased PR persistence. We conclude that permanent grassland soils with historically elevated SOC likely buffer negative effects of increasing summer weather persistence on forage grass performance, but may also be more sensitive to degradation under climate change.

1. Introduction

Climate change is threatening grassland ecosystem service provisioning (e.g., hay production, carbon storage) by rapidly altering rainfall patterns, atmospheric temperatures and dryness (De Boeck *et al.*, 2010; Allan *et al.*, 2020) and the related soil water and nutrient regimes within these generally shallow-rooted ecosystems (Poirier *et al.*, 2012; Klaus *et al.*, 2020; Van Sundert *et al.*, 2020; Van Sundert *et al.*, 2021; Reynaert *et al.*, 2022). For instance, hotter and more intense droughts cause declines in tiller survival, productivity and quality (Poirier *et al.*, 2012; Fariaszewska *et al.*, 2020), whilst simultaneously inducing more pronounced transient pulses of microbial activity and nutrient availability upon rewetting (Borken & Matzner, 2009; Van Sundert *et al.*, 2020) as well as increasing the risk of nutrient leaching and undesired eutrophication elsewhere (Loecke *et al.*, 2017; Klaus *et al.*, 2020). As such, altered rainfall variability may not only impact plants directly through altering soil water dynamics, but also indirectly by altering nutrient cycling, potentially benefiting species which can rapidly extract available resources during transient periods of abundance (Hofer *et al.*, 2017; Reynaert *et al.*, 2021; Van Sundert *et al.*, 2021).

Much research has focused on how more intense weather with longer, more extreme droughts and more concentrated rainfall may affect managed grassland ecosystem functioning (Knapp *et al.*, 2008; Grant *et al.*, 2014; Hofer *et al.*, 2017; Meisser *et al.*, 2019; Fariaszewska *et al.*, 2020; Van Sundert *et al.*, 2020; Van Sundert *et al.*, 2021) but less is known about the effects of recently observed increases in summer weather persistence in the mid-latitudes, i.e., the lengthening of both dry and wet spells compared to historic averages (Zolina *et al.*, 2013; Pfleiderer *et al.*, 2019; Felton *et al.*, 2021; Reynaert *et al.*, 2021; Reynaert *et al.*, 2022; Reynaert *et al.*, 2023a). The few experimental studies performed on unfertilized systems (Reynaert *et al.*, 2021; Reynaert *et al.*, 2022; Li *et al.*, 2023a; Reynaert *et al.*, 2023b) generally indicate negative species-specific effects on productivity (up to – 50 %; see Li *et al.* (2023a)) related to differences in plant metabolism under drought (Zi *et al.*, 2023a), and both positive and negative effects on forage quality (Reynaert *et al.*, 2023b; Zi *et al.*, 2023b). However, plant growth is disturbed more regularly and temporary changes in nutrient availability are more pronounced in fertilized grasslands under cutting management (Fariaszewska *et al.*, 2020), which could amplify adverse effects on plant performance due to a lack of built-up reserves (Reynaert *et al.*, 2022) and reduced drought resistance (Van Sundert *et al.*, 2021).

Changing climate regimes guide the selection of forage grass varieties which guarantee future sustainable ecosystem provisioning in oceanic Europe (Dumont *et al.*, 2015; Lüscher *et al.*, 2022). Common forage species respond differently to altered water availability (Volaire *et al.*, 2009; Bahrani *et al.*, 2010; Poirier *et al.*, 2012; Dumont *et al.*, 2015; Fariaszewska *et al.*, 2020; Lüscher *et al.*, 2022). Whereas *Lolium perenne* variants are highly productive and of high quality under ample water supply, *Festuca arundinacea* variants are anisohydric and show reduced plant quality but comparably higher productivity under drought and/or during recovery because of a more developed rooting system, greater nutrient-use efficiency and the ability to lower their water potential more, though with considerable variation between cultivars (Durand *et al.*, 1997; Van Eekeren *et al.*, 2010; Cougnon *et al.*, 2017; Fariaszewska *et al.*, 2017; Becker *et al.*, 2020; Fariaszewska *et al.*, 2020). The use of polyploid species (Bothe *et al.*, 2018) or hybrids such as the increasingly common *Festulolium* variants aims at providing more stable yields by combining the positive traits of both species (Durand *et al.*, 1997; Fariaszewska *et al.*, 2017) and some also show improved flooding resistance (Macleod *et al.*, 2013). In addition, given the adverse environmental impacts of intensive fertilizer use (Stoate *et al.*, 2009) and the increased risk of N leaching after drought (Klaus *et al.*, 2020), species with high N yield are increasingly selected since they generally decrease N leaching from the system (Moir *et al.*, 2013). *Festuca arundinacea* shows overall greater N yield compared to *Lolium perenne (*Cougnon *et al.,* 2014)*,* indicating higher efficiency of converting available nutrients into biomass but the mechanisms behind this are not fully understood (Moir *et al.*, 2013; Cougnon *et al.*, 2017). Repeated dry-wet cycles affect plant-available soil N and thus plant quality and nitrogen status (Borken & Matzner, 2009; Grant *et al.*, 2014; Hofer *et al.*, 2017; Meisser *et al.*, 2019), complicating how increasing weather persistence could affect N yield, plant quality and leaching.

Soil texture and land-use history determine forage grass and soil responses to drought and flooding (Dodd & Lauenroth, 1997; Alaoui *et al.*, 2018; Nguyen *et al.*, 2019; Klaus *et al.*, 2020; Van Sundert *et al.*, 2020; Chang *et al.*, 2021; Patel *et al.*, 2021; Radujković *et al.*, 2021; Van Sundert *et al.*, 2021). In particular, practices that increase soil organic carbon (SOC) such as permanent grassland management (Crème *et al.*, 2020; Guillaume *et al.*, 2021) have been associated with increased crop yields (D'Hose *et al.*, 2014; Schjønning *et al.*, 2018; Buttler *et al.*, 2019; Oldfield *et al.*, 2019; Sun *et al.*, 2020), greater potential to buffer climate change impacts by improving soil water availability during drought (Hudson, 1994; Minasny & McBratney, 2018) and reduced nutrient leaching during periods of intense rainfall (Kanthle *et al.*, 2016; Xu *et al.*, 2016; Ahmed *et al.*, 2019).

We investigated whether previous permanent grassland management enhancing SOC could ameliorate the response of forage grass varieties to experimentally imposed increased weather persistence with longer dry and wet spells. Differences in the persistence of precipitation regimes were imposed by subjecting monoculture mesocosms to either repeated 3-day (historically normal) or 30-day (extreme) wet/dry cycles whilst keeping total precipitation equal. We tested this across five recently developed forage grass varieties differing in drought resistance and forage quality and across both sandy and sandy-loam soils originating from either permanent (high SOC) or temporary (low SOC) grasslands in adjacent parcels. Our main goals were to (1) evaluate how the quality and aboveground productivity of distinct cultivars is affected by increased weather persistence across different soil texture classes and historical grassland management scenarios and (2) identify underlying drivers in terms of soil water and nutrient dynamics, and their relationships with plant quality and productivity.

Since previous studies in unfertilized grasslands indicate that increasing summer weather persistence generally affects plants by limiting water availability (Reynaert *et al.*, 2021; Reynaert *et al.*, 2023b), we hypothesized (i) that plant growth would be more constrained under longer dry and wet spells, accentuating differences between soils and species. Furthermore, regarding the five forage grass varieties we expected (ii) a gradient of more to less drought resistance (and lower to higher quality) from *Festuca arundinacea* FERMINA to *Festulolium* FESTILO to *Lolium x boucheanum* kunth. MELCOMBI to *Lolium perenne* (tetraploid) MELFORCE to *Lolium perenne* (diploid) MELSPRING, respectively. Finally, we expected (iii) soils from permanent grasslands with a high SOC content to be able to maintain plant productivity and quality better under extreme precipitation regimes with more pronounced effects on sandy soils, due to the positive effects of finer particles and elevated SOC on soil water and nutrient availability.

2. Material and methods

2.1. Field site and experimental setup

An open-air field experiment was set up during spring 2021 at the Drie Eiken Campus in Wilrijk, Belgium (51°09’41” N, 04°24’9” E). A total of 200 mesocosms (30 cm diameter, 50 cm depth) were equally distributed across five plots and filled with sandy or sandy-loam soil from neighboring parcels differing in organic C content generated by differences in grassland management (Table 1). Mesocosm pots were filled halfway with top soil (0-25 cm) and halfway with deeper soil (25-50 cm) from parcels in Zele, Belgium (51°04'25" N, 04°00'49" E; sandy soil) and Melle, Belgium (50°59'02" N 03°47'01" E; sandy-loam soil), after which all soils were equally compacted.

Table 1. Soil characteristics at the start of the experiment.

Soil texture	**Grassland management**	**Depth**	**OC**	**pH**	**N_{tot}**	**K**	**Mg**	**Ca**	**P**
Sand	Permanent	0-25 cm	1.83	5.9	0.17	7	27	104	19
		25-50 cm	0.16	5.4	0.02	4	13	69	4
	Temporary	0-25 cm	1.48	5.7	0.13	20	19	108	50
		25-50 cm	0.21	5.8	0.02	14	19.	99	28
Sandy loam	Permanent	0-25 cm	1.39	4.8	0.14	10	18	61	31
		25-50 cm	0.38	4.8	0.04	6	15.	42	9

Temporary	0-25 cm	0.87	6.0	0.09	27	16	81	23
	25-50 cm	0.33	5.5	0.04	10	10	54	10

Organic carbon (OC) and total nitrogen (N_{tot}) content are expressed in % dry matter (DM). K, Mg, Ca and P concentrations are expressed in mg 100 g^{-1} DM.

Five distinct cultivars of commonly used C3 forage species were selected to create a gradient in trade-offs between drought/flooding resistance and plant quality. From generally more to less drought resistant (and generally less to more quality; Fariaszewska *et al.* (2020)) these included *Festuca arundinacea* FERMINA, *Festulolium* FESTILO, *Lolium x boucheanum* kunth. MELCOMBI - referred to as *Lolium hybridum* from here-on -, *Lolium perenne* (tetraploid) MELFORCE and *Lolium perenne* (diploid) MELSPRING. Seeds were sown in seedling containers under greenhouses late February and regularly watered over the course of the following two months to promote germination and seedling development. At the end of April, 37 healthy seedlings per species were transplanted into each of 40 mesocosms in a predetermined grid, ensuring equal planting densities (interspace of 4.5 cm). Two replicate mesocosms of every unique combination of soil type and species were assigned to each of the five plots, and their locations were randomized to account for potential edge effects. Seedlings that did not survive transplanting were replaced until the end of May. Manual weeding was done throughout the experiment. All mesocosms received equal amounts of water until mid-July 2021, to maintain the soils close to field capacity before the start of the experiment (Elst *et al.*, 2017; Reynaert *et al.*, 2021).

From 14/07/21 until 10/11/21 (DOY 165 – DOY 314; 120 days total in 2021), half of the mesocosms were subjected to a historically close to normal precipitation regime (PR) (sequences of 3 days wet / dry) and the other half to an extreme PR with highly persistent weather (sequences of 30 days wet/dry) (Reynaert *et al.*, 2021). These regimes were simulated accurately utilizing automated dripper irrigation below plot-level screens that close automatically upon rain-detection to block-out ambient precipitation (Reynaert *et al.*, 2021). Water volumes applied were equal in total between treatments (60 days wet and 60 days dry) and per irrigation event (6.87 L m^{-2} which is 1.5 times the daily Belgian average to compensate for artificially increased evapotranspiration in the mesocosms; Reynaert *et al.* (2021)). This resulted in a full factorial design containing a total of five replicates (1 per plot) per unique factor combination of the two soil textures, two SOC levels, two PR treatments and five species (Fig. 1).

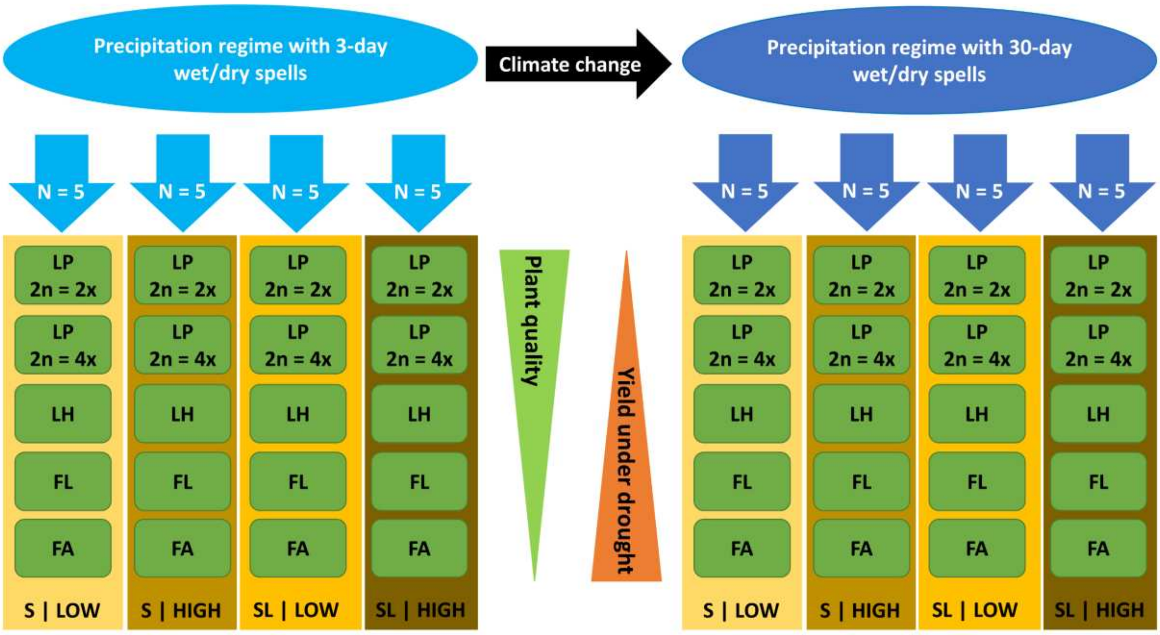

Figure 1. Schematic of the experimental setup including all treatments, with a total of 200 mesocosms. *Lolium perenne, Lolium hybridum, Festulolium* and *Festuca arundinacea* are abbreviated by LP, LH, FL and FA, respectively. Diploid, tetraploid, sandy soil, sandy-loam soil and soil organic carbon level are abbreviated by 2n = 2x, 2n = 4x, S, SL, LOW and HIGH, respectively. The plant quality and yield under drought trends show hypothesized differences based on previous studies (Fariaszewska *et al.*, 2017; Fariaszewska *et al.*, 2020).

Since our experiment focused on simulation of increasing summer weather persistence, mesocosms were subjected to ambient precipitation over winter. From 02/03/22 – 27/10/22 (DOY 61 - DOY 300; 240 days total in 2022), all mesocosms were again subjected to their respective PR treatment. Fertilization was equal for all mesocosms and occurred in line with common agricultural practices (Table S1), resulting in the application of 153 g N ha^{-1}, 38 kg P ha^{-1} and 165 kg K ha^{-1} in the installation year (2021) and 302 g N ha^{-1}, 38 kg P ha^{-1} and 325 kg K ha^{-1} in the first production year (2022). (Table S2). A dissolved fertilizer was used and to mimic realistic grassland management, fertilization was fractionated and applied after every cut (except the last per year) when the soil was wet (Table S2).

2.2. Measurements and calculations

Across the full experimental period, soil water content averaged over 30 cm depth and soil surface temperatures were logged automatically every half-hour utilizing CS650-DS Reflectometers (Campbell® Scientific INC.) in a total of 40 mesocosms (1 per unique full-factorial treatment combination). Photosynthetically active radiation (PAR) was measured every 10 min in the vicinity of the plots, utilizing a SKP215 Quantum Sensor (Campbell® Scientific INC., Logan, Utah, USA). Hourly values of air temperature (T) and relative humidity (RH) were collected at 1.5 m height from a nearby weather station in Woensdrecht, The Netherlands (50°56’34’’ N, 5°34’44’’ E). Utilizing these values, we calculated average daily vapor pressure deficit (VPD) during sunshine hours. We also collected green cover estimates from all mesocosms by visually estimating the fraction of plant cover that was green to the closest 5% on a weekly basis starting from the first harvest every year and with a break in winter.

Aboveground biomass was harvested four times in 2021 and five times in 2022 in all mesocosms by clipping all standing biomass above 4.5 cm (Table S2). Biomass was then air-dried, stored in paper bags and oven dried for > 72 h, followed by immediately weighing to the closest 0.01 g. For two cuts in 2022 (June and August – to capture variation across summer), we also determined crude protein content (CPC), *in vitro* organic matter digestibility (IVOMD) and nitrogen (N) content of the harvested plant material. Samples were first ground (mesh size = 1 mm) and then scanned for near infrared reflectance spectroscopy (NIRS) spectra utilizing a Foss NIRSystems 5000 (FOSS NIRSystems, Silver Springs, MD, USA) and the ISIscan 2.85.1 software (Infrasoft international, Port Matilda, PA, USA). The NIRS equations for CPC and IVOMD were based on chemical calibration of 40 of the most spectrally distant samples, following the Kjeldahl method and Tilley and Terry (1963), respectively (Cougnon *et al.*, 2014). Per sample, N content was then estimated as % CPC / 6.25 (Jones, 1931).

Based on plant N content and biomass estimations we then calculated the nitrogen nutrition index (NNI) for June and August of 2022 to assess the nitrogen limitation following Lemaire *et al.* (1997) as $NNI = N_{measured} / N_{critical}$. Here, $N_{measured}$ is the N concentration (%) in the aboveground biomass and $N_{critical}$ the critical N concentration needed in the grass for unlimited growth in case of unlimited other resources (i.e., light, water, etc.) depending on dry matter yield (DMY). For C_3 grasses $N_{critical} = 4.8 \times DMY\ (\text{in t ha}^{-1})^{-0.32}$. When DMY < 1, we considered $N_{critical}$ to be 4.8 %, assuming absence of competition among individuals with low aboveground productivity (Poirier *et al.*, 2012).

To investigate effects of soil texture, organic carbon content, PR treatment and species on nutrient supply rates in the rooting zone upon rewetting after drought in the 30-day PR, we installed eight Plant root simulator (PRS®) probes (Western Ag Innovations, Saskatoon, Canada) at 3-9 cm depth in each of 40 mesocosms (2 cation and 2 anion pairs per unique treatment combination) in 2022 between 30/06 and 5/7 (DOY 181-186; following harvesting). After five days, probes were collected, cleaned with distilled water and returned to the manufacturer for lab analysis of total N, $NO3^-$, P, K, Ca, Mg, Fe, B, Al, Zn and Mn contents.

Finally, after the last biomass harvest, we collected a total of 20 soil cores in the 5-10 cm soil layer to determine top soil bulk density (BD) and the water retention curves of the four respective soils. To capture variation induced by the various treatments, we collected 5 cores per unique soil type (texture x SOC), 4 cores per species and 10 cores per PR. We then calculated separate mean values of FC and PWP per unique soil texture x grassland management combination (Table 2), which were further utilized to determine the plant available water per soil type and to calculate a soil drought index.

Table 2. Soil hydrological properties per soil texture class at the end of the experiment.

			Average volumetric moisture content (cm³ / cm³)				
Soil texture	**Grassland management**	**Bulk density (g / cm³)**	**pF 4.2 (PWP)**	**pF 2.7**	**pF 2.0 (FC)**	**pF 0**	**AWC (FC - PWP)**
Sand	Permanent	1.098 ± 0.032^{a}	0.042 ± 0.001^{a}	0.160 ± $0.011^{a,b}$	0.264 ± 0.012^{a}	0.526 ± 0.009^{a}	0.222 ± 0.011^{a}
	Temporary	1.152 ± 0.008^{a}	0.039 ± 0.001^{a}	0.150 ± $0.016^{a,b}$	0.258 ± 0.016^{a}	0.488 ± $0.014^{a,b}$	0.219 ± $0.015^{a,b}$
Sandy loam	Permanent	1.206 ± 0.029^{b}	0.038 ± 0.001^{a}	0.170 ± 0.019^{b}	0.302 ± 0.010^{b}	0.470 ± 0.003^{b}	0.264 ± 0.008^{b}
	Temporary	1.196 ± 0.020^{b}	0.035 ± 0.001^{a}	0.141 ± 0.009^{a}	0.266 ± 0.009^{a}	0.478 ± 0.007^{b}	0.231 ± 0.009^{a}

Average soil hydrological properties (± 1 SE) per unique soil texture class x grassland management combination (n=5) taken from the 5-10 cm soil layer at the end of the experiment. Permanent wilting point, field capacity and plant available water (difference between PWP and FC) are abbreviated as PWP, FC and AWC, respectively. ^{a,b}Different letters indicate significant differences ($P < 0.05$) of Tukey tests comparing treatments.

The drought index utilized was drought intensity (I_s)(Vicca *et al.*, 2012), which integrates both the duration and extent to which daily average SWC declines below a critical soil water threshold (at relative extractible water < 0.4). First, total extractable water (TEW) was calculated over the 30 cm sensor depth:

$$TEW_{max}\ (\%) = SWC_{FC}\ (\%) - SWC_{PWP}\ (\%)$$

$$TEW_{day}\ (\%) = SWC_{day}\ (\%) - SWC_{PWP}\ (\%)$$

We then determined relative extractible water (REW) as $REW_{day} = TEW_{day} / TEW_{max}$, finally resulting in I_s at daily and over a period basis:

$$I_{s,\,day} = 0.4 - REW_{day} \text{ if } REW_{day} < 0.4 \text{ and } I_{s,\,day} = 0 \text{ if } REW_{day} > 0.4$$

$I_{s,\text{ period}} = \sum I_{s,\text{ first day of period}} + \ldots + I_{s,\text{ last day of period}}$

We calculated this index for each mesocosm with SWC sensor (n = 40) both per harvest and per year to assess how precipitation regime, soil texture, grassland management and species identity determined ecological soil drought extremity over the course of the two year experiment.

2.3. Statistical analysis

All statistics were performed in R (version 4.0.4). We assumed significance of effects for *P*-values < 0.05. Where possible, we always started from a full model including all hypothesized interactions and selected final models by removing insignificant higher-order interactions based on F-test model comparison. Model assumptions were verified utilizing residual plots and tests. Post-hoc Tukey tests were applied to further explore 2-by-2 differences utilizing the package emmeans (Lenth *et al.*, 2018). Where necessary because of residual heteroscedasticity, we log transformed variables and/or allowed variance to vary with factor levels, utilizing the *varIdent()* or *dispformula()* functions in nlme *(Pinheiro et al., 2017)* and glmmTMB (Magnusson *et al.*, 2017), respectively.

To asses general drivers and indicators of plant stress, we first performed ANOVA on two generalized linear mixed models (GLMMs) (family = gaussian, link = identity) testing for the effects of soil texture, year, grassland management, species identity, PR and their interactions on average soil moisture and drought intensity. These models included mesocosm nested in plot as random intercept. Next, we conducted ANOVA on a GLMM (family = beta, link = logit) including green cover as response variable, with soil texture, DOY, grassland management, species identity, PR and their interactions as fixed effects and mesocosm nested in plot as random intercept. Cover proportions were transformed in order to avoid extreme values of 0 and 1 which is necessary for beta regression (Damgaard & Irvine, 2019; Clavel *et al.*, 2021). To further asses plant responses, we then used ANOVA to test for the effects of soil texture, grassland management, species identity, PR and their interactions on aboveground productivity (both cumulative per year, and per harvest) and plant quality (IVOMD, CPC and N-content; per harvest) in five GLMMs (family = gaussian, link = identity), again including mesocosm nested in plot as random intercept.

Underlying mechanisms for the observed patterns related to soil water availability were then explored by performing ANOVA on a GLMM (family = gaussian, link = identity) including bulk density as response variable, with soil texture, PR and grassland management and their interactions as fixed effects and species identity as random intercept (due to limited observations, species samples were not taken representatively across all treatment levels). Next, we constructed a GLMM (family = gaussian, link = identity) with moisture content as response variable and pF value, soil texture, grassland management, PR and their interactions as fixed effects and mesocosm nested in species identity as random intercept (due to limited observations, species samples were not taken representatively across all treatment levels). To unravel the role of soil nutrient dynamics, we also performed ANOVA on 11 GLMMs (family = gaussian, link = identity) for each of the measured nutrient supply rates during rewetting in July of 2022 (total N, $NO3^-$, P, K, Ca, Mg, Fe, B, Al, Zn and Mn), always including PR, species, soil texture and grassland management as well as their two-way interactions as fixed effects, and mesocosm as random intercept. To asses effects on the nutrient status of the plants, we performed ANOVA to test for the effects of soil texture, grassland management, species identity, PR and their interactions on NNI (family = gaussian, link = identity), again with mesocosm nested in plot as random intercept. Finally, we constructed a set of five models (family = gaussian, link = identity) testing the interactive effects of water (drought intensity) and nutrient (NNI) limitation on plant biomass and quality across species and harvests, and integrated these findings in nonmetric multidimensional scaling (NMDS) ordination on observations from mesocosms with soil water sensors (N = 40) in June (early 30-day PR drought) and August (post 30-day PR rewetting) of 2022.

3. Results

3.1. Patterns in weather, soil water availability and plant green cover

Ambient weather conditions contrasted between the two years of the experiment, with a relatively cold and humid summer in 2021 followed by a hot and dry summer in 2022, as indicated by differences in air temperature, vapor pressure deficit and soil surface temperatures (Fig. S1 & S2).

Soil moisture trajectories generally reflected these weather differences, with more extreme declines in available soil water in 30-day PR and during 2022 (Fig. 2). As expected, the 30-day PR generally reduced the available water in the soil on average (-8 % compared to the 3-day PR), resulting in higher drought intensity across both years ($P < 0.001$; Fig. 2; Fig. S4; Table S3). Soils from permanent grasslands contained on average more water compared to temporary grasslands, but only in 2021 (+2.3 %; $P = 0.004$; Table S3). In contrast, differences in soil water availability induced by PR and between species were more pronounced in 2022 ($P < 0.001$; Table S3) and within the 30-day PR among species ($P = 0.007$; Table S3), with *Festuca* experiencing more extreme soil moisture declines compared to all other species, *Lolium hybridum* more compared to *Festulolium* and *Lolium perenne* MELSPRING, and *Lolium perenne* MELFORCE more compared to *Lolium perenne* MELSPRING (Fig. S3; Table S3).

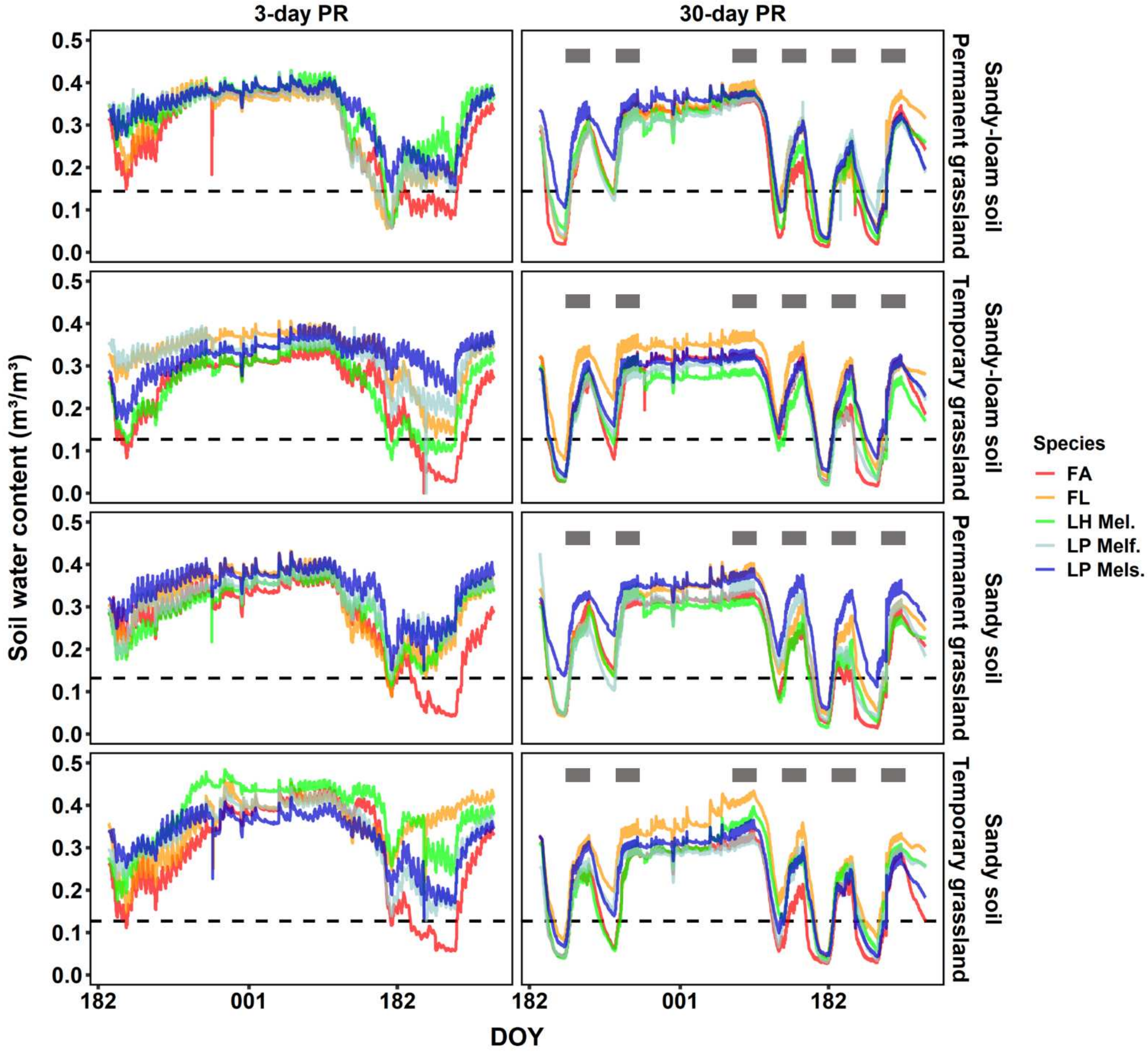

Figure 2. Effects of precipitation regime (PR) on temporal trajectories of soil water content per species, texture class (sandy vs sandy-loam), grassland management level (permanent vs temporary grassland). Grey boxes highlight the wet periods of the 30-day regimes and the dashed line indicates where 40 % of water at FC is still available in the soil. Species names including *Festuca arundinacea*, *Festulolium*, *Lolium hybridum*, *Lolium perenne* MELFORCE (tetraploid) and *Lolium perenne* MELSPRING (diploid) are abbreviated as FA, FL, LH Mel., LP Melf. and LP Mels., respectively. Day of the year is abbreviated as DOY.

Plant green cover trajectories generally confirmed these trends. Plants subjected to the 30-day PR were on average 20 % less green compared to those growing under the 3-day PR. Differences between PR were most pronounced under hotter and drier weather conditions and towards the end of the growing season (Fig. 2; $P < 0.001$; Table S4). Plants growing on soils from permanent grasslands were on average greener across 2021, but this effect disappeared and even reversed by September and October of 2022 (Fig. 2; $P < 0.001$; Table S4). This grassland management effect differed between soil textures, with mostly positive effects of permanent grassland history in sandy-loam soils, but neutral or negative effects in sandy soils (Fig. 2; $P = 0.022$; Table S4). On average, plants were also greener (+ 7 %) when growing on sandy-loam soils and these effects were most pronounced in the summer of 2022 (Fig. 2; $P < 0.001$; Table S4).

Differences among species were greatest in the recovery phase following harvesting, and during hot and dry atmospheric conditions in the 30-day PR vs during cold and humid weather in the 3-day PR (Fig. 2; $P < 0.001$; Table S4). In line with our expectations, *Festuca* was on average greener compared to *Festulolium*, *Lolium hybridum*, and *Lolium perenne* MELFORCE (Fig. 3; $P = 0.001$; Table S4; Fig. S4). However, rather unexpected, both *Lolium perenne* cultivars were on average greener than *Festulolium,* and, *Lolium perenne* MELSPRING was on average greener compared to *Lolium hybridum* and *Lolium perenne* MELFORCE (Fig. 3; $P = 0.001$; Table S4; Fig. S4). Rapid changes in plant greenness suggested that *Festuca* had the most plastic response (i.e. recovery ability) to the treatments under the imposed cutting management, bouncing between the highest highs (e.g., July 2022) and the lowest lows (e.g., August 2022) out of any species (Fig. 3; $P < 0.001$; Table S4).

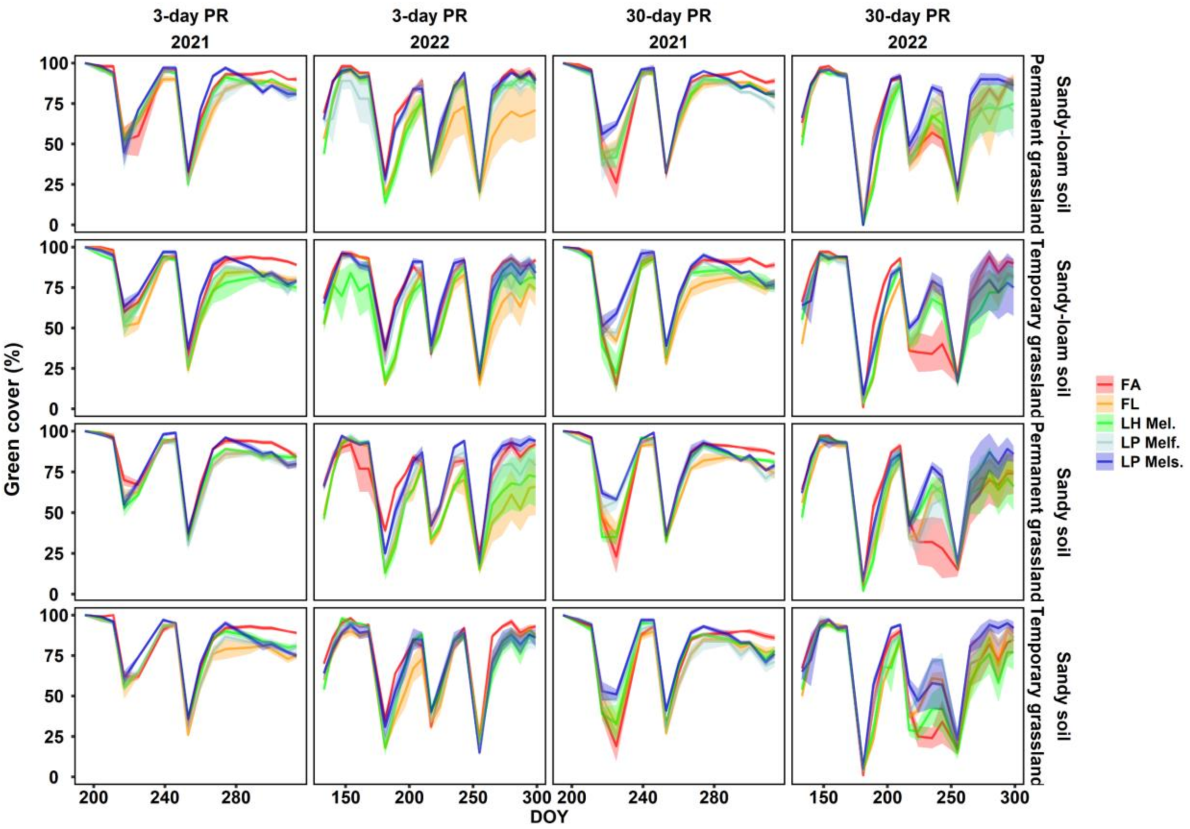

Figure 3. Effects of precipitation regime (PR) on temporal trajectories of green cover per species, texture class (sandy vs sandy-loam) and grassland management level (permanent vs temporary grassland). The shaded area indicates +/- 1 SE on the mean. Species names including *Festuca arundinacea*, *Festulolium*, *Lolium hybridum*, *Lolium perenne* MELFORCE (tetraploid) and *Lolium perenne* MELSPRING (diploid) are abbreviated as FA, FL, LH Mel., LP Melf. and LP Mels., respectively. Day of the year is abbreviated as DOY. The sharp current dips in the curves indicate biomass harvesting.

3.2. Patterns in dry matter yield and forage quality

Subjection to the 30-day PR reduced cumulative aboveground productivity by 4 % in 2021 and by 14% in 2022 on average compared to 3-day PR ($P < 0.001$; Table S5; Fig. 4) without differentially affecting species. Only within the 3-day PR ,growing on soils from permanent grasslands generally improved cumulative productivity (+ 5 %).($P = 0.014$; Table S5; Fig. 4). The influence of grassland management on cumulative productivity contrasted between texture classes and years, with permanent grassland enhancing productivity compared to temporary grassland on sandy-loam soils (by 23 %, only in 2022), but the opposite trend on sandy soils across both years (- 12 % in 2021 and - 6 % in 2022) (*P* = 0.001; Table S5; Fig. 4). *Festuca* outperformed all other species on average in 2021 (+ 24 %) but this effect disappeared in the following year. In 2022, *Festulolium* performed on average slightly better compared to *Lolium perenne* MELFORCE (+ 6 %) and *Lolium perenne* MELSPRING (+ 8 %) (*P* < 0.001; Table S5; Fig. 4). These differences in cumulative species performance were generally more pronounced in sandy-loam soils compared to sandy soils (species × texture interaction; *P* = 0.002; Table S5; Fig. 4). Across both years, *Lolium perenne* MELSPRING overall had the lowest cumulative productivity (*P* < 0.001; Table S5; Fig. 4).

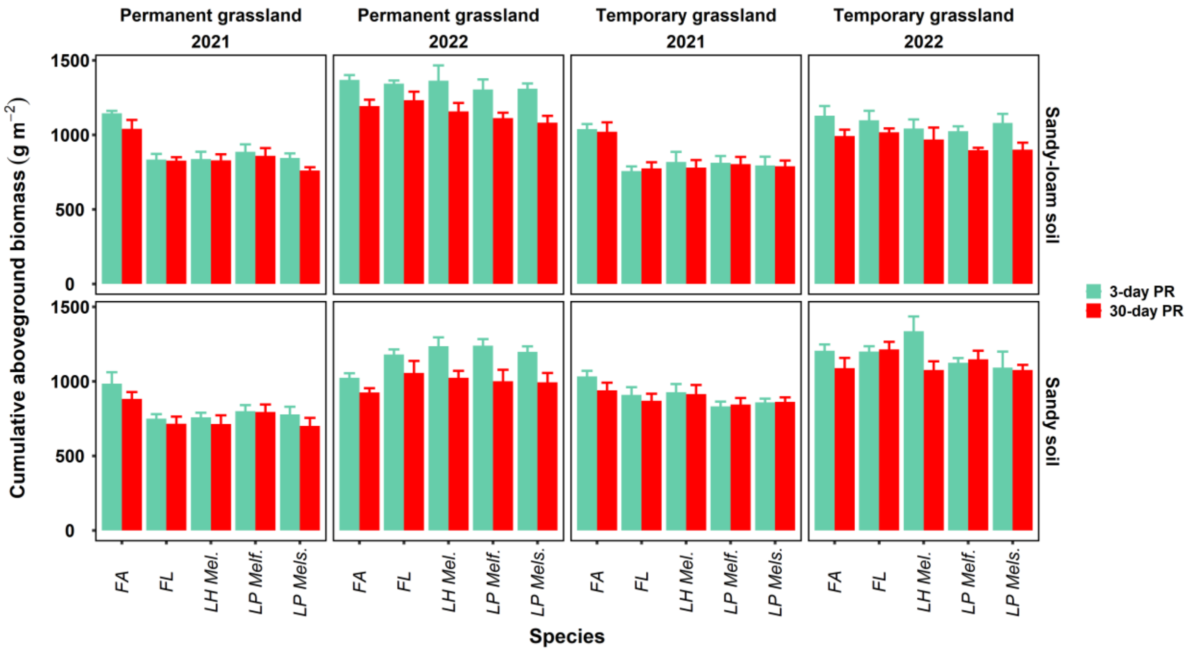

Figure 4. Effects of precipitation regime (PR) on cumulative aboveground biomass per species and year for each soil texture and grassland management level. *Festuca arundinacea*, *Festulolium*, *Lolium hybridum* MELCOMBI, *Lolium perenne* MELFORCE and *Lolium perenne* MELSPRING are abbreviated by FA, FL, LH Mel., LP Melf. and LP Mels., respectively. Error bars indicate +/- 1 SE on the mean.

When considering biomass differences on a per harvest basis, similar patterns emerged (Fig. S5). Most notably, negative effects of PR and modulating influences of grassland management, species identity and soil texture were strongest during hot and dry periods (i.e. mid-summer: DOY 150 - 250) and in 2022 (Fig. S5; $P < 0.001$; Table S5). Moreover, across 2022, grassland management did not significantly impact productivity on a per harvest basis within the sandy soils (contrasting with the cumulative response), whereas a permanent grasslands history consistently positively influenced yields for sandy-loam soils (Fig. S5; $P < 0.001$; Table S5).

The forage quality parameters in summer 2022 were influenced by PR, grassland management, soil texture, harvesting date and species identity(Fig. 5; Table S6). Under 30-day PR in August, CPC was increased for soils from permanent grasslands (+ 1.5 %; $P = 0.032$; Table S6; Fig. 5), or with a sandy-loam texture (+ 1 %; $P = 0.022$; Table S6; Fig. 5). Generally, crude protein content (CPC) was on average 8 % higher in August compared to June ($P < 0.001$; Table S6; Fig. 5). . Differences between species also contrasted between harvests, with *Festuca* having a higher CPC compared to *Festulolium* and *Lolium hybridum* in June, but a lower CPC compared to all others in August ($P < 0.001$; Table S6; Fig. 5). Furthermore, *Festulolium* and *Lolium hybridum* had lower CPC compared to *Lolium perenne* cultivars, but only in June ($P < 0.001$; Table S6; Fig. 5) and these species differences were slightly modified by soil texture ($P = 0.002$; Table S6; Fig. 5)..

Given the utilized calculation, trends in N-content were virtually the same as in CPC (Fig. 5; Table S6). However, in contrast, IVOMD was on average 0.6 % higher in 30-day PR vs 3-day PR in August ($P = 0.012$; Table S6; Fig. 5). Following the CPC trends, *Festuca* generally had higher digestibility in June but lower in August compared to others and both *Lolium perenne* cultivars were most digestible (up to 12 % higher in August compared to *Festuca*; $P = 0.003$; Table S6; Fig. 5).

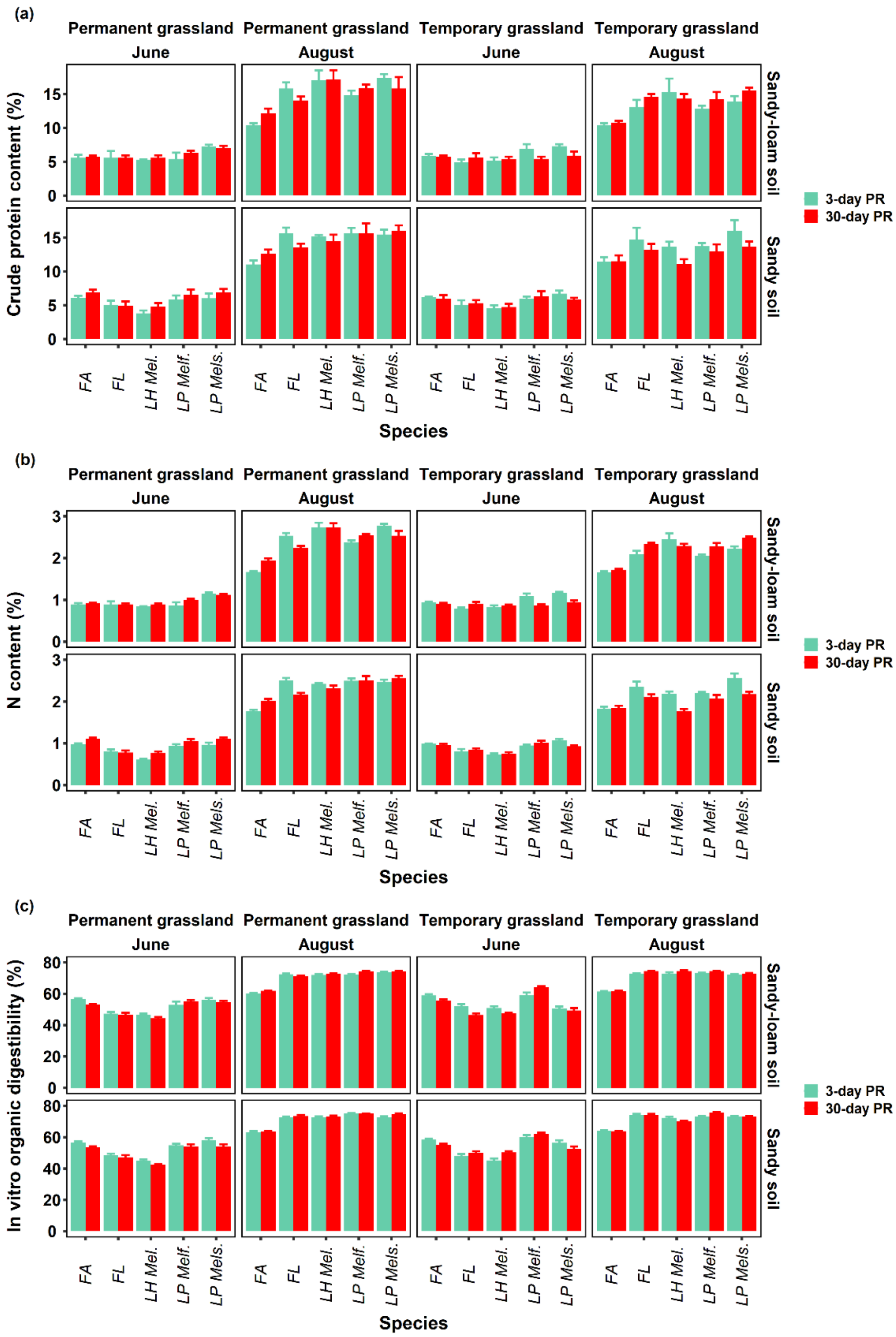

Figure 5. Effects of precipitation regime (PR) on plant quality (a: Crude protein content, b: N content, c: In vitro organic matter digestibility) in June and August of 2022 per species, texture class (sandy vs sandy-loam) and grassland management (permanent vs temporary grassland) level. The error bars indicate +/- 1 SE on the mean. Species names including *Festuca arundinacea*, *Festulolium*, *Lolium*

hybridum, *Lolium perenne* MELFORCE (tetraploid) and *Lolium perenne* MELSPRING (diploid) are abbreviated as FA, FL, LH Mel., LP Melf. And LP Mels., respectively. Day of the year is abbreviated as DOY.

3.3. Drivers of patterns in forage grass performance and quality

3.3.1. Effects of precipitation regime and grassland management on nutrient availability and soil hydrological properties

To disentangle nutrient dynamics and soil properties underlying these trends, we characterized nutrient availability during a 30-day PR rewetting event in July 2022 (see Fig. S6 for detailed soil water trajectories). Increased PR persistence generally affected nutrient supply on a species-specific basis, only increasing N and K supply for *Festuca* (+ 102% N; $P < 0.001$; Table S8; Fig. S7a) and *Lolium perenne* MELFORCE (+ 92% K; $P = 0.023$; Table S7; Fig. S7d), respectively, and doing the opposite regarding K supply for *Festulolium* (- 76% K; $P = 0.023$; Table S7; Fig. S7d). However, buffering effects of permanent grassland management on nutrient supply generally mirrored the productivity trends, with permanent grassland management overall not affecting or improving N, NO_3^- , P and Mn supply in sandy-loam soils, but neutral or opposite effects in sandy soils (Table S7; Fig. S7).

In terms of soil characteristics determining available water, bulk density remained unaffected by PR and grassland management but was generally higher in sandy loam soils compared to sandy soils ($P = 0.02$; Table S8; Fig. S9).. However, 30-day PR generally negatively influenced soil water retention capacity ($P < 0.001$; Table S8; Fig. 6), though the extent of this decline was determined by grassland management and only significant in permanent grasslands ($P = 0.02$; Table S8; Fig. 6). More water was retained in soils from permanent grasslands on average across both texture classes, although only when subjected to the 3-day PR ($P = 0.02$; Table S8; Fig. 6). Furthermore, soil water retention showed an interaction between grassland management and texture class ($P < 0.001$; Table S7; Fig. 6), indicating that soils originating from permanent grasslands had on average increased water retention at intermediate pF but only in the sandy-loam texture class (Fig. 5).

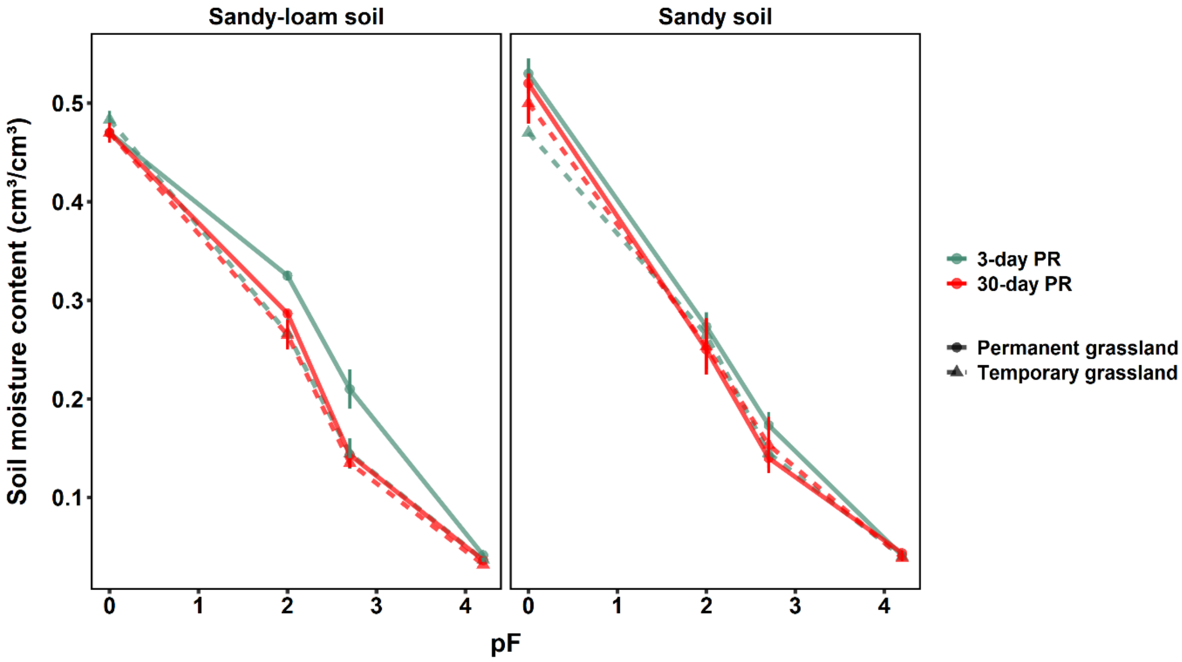

Figure 6. Effects of precipitation regime (PR) on water retention curves for the top soil layer (5- 10 cm) at the end of the experiment per soil type differing in grassland management and soil texture. The error bars indicate +/- 1 SE on the mean.

3.3.2. Effects of precipitation regime and grassland management on forage nitrogen nutrition

Since increased PR persistence may not only affect nutrient and moisture availability but also uptake, we further explored patterns in nitrogen limitation to plant growth (i.e., nitrogen nutrition index (NNI); section 3.2). These differed between June (during drought in 30-day PR) and August (after rewetting in 30-day PR) of 2022, and were affected by PR, grassland management, species identity and soil texture (Fig. 7; Table S9). In August, nitrogen nutrition was higher in 30-day PR vs 3-day PR for *Festuca* (*P* = 0.007; Table S9; Fig. 7) and in sandy-loam vs sandy soils within 30-day PR (*P* = 0.015; Table S9; Fig. 7). Soils from permanent grassland increased NNI only in sandy-loam soils (*P* = 0.001; Table S9; Fig. 7), and this effect was strongest in August (*P* < 0.001; Table S9; Fig. 7). Growing on sandy-loam soils improved nitrogen nutrition most for *Lolium hybridum* (*P* = 0.002; Table S9; Fig. 7) and differences between species were on average greater in sandy-loam soils (*P* = 0.002; Table S9; Fig. 7).

Differences in nitrogen nutrition among species were generally also more pronounced in the 3-day PR and in June (*P* = 0.007; Table S9; Fig. 7). Within the 3-day PR in June, *Festuca* and both *Lolium perenne* variants had increased nitrogen nutrition compared to *Lolium hybridum*, and *Lolium perenne* MELSPRING had increased nitrogen nutrition compared to *Festulolium* (*P* = 0.007; Table S9; Fig. 7). Under 30-day PR in June, only *Lolium hybridum* had significantly reduced nitrogen nutrition compared to both *Lolium perenne* variants (*P* = 0.007; Table S9; Fig. 7). In August, the opposite was seen, with *Festuca* having the lowest nitrogen nutrition compared to all other species within 3-day PR and reduced NNI compared to *Lolium perenne* MELSPRING in the 30-day PR (*P* = 0.007; Table S9; Fig. 7).

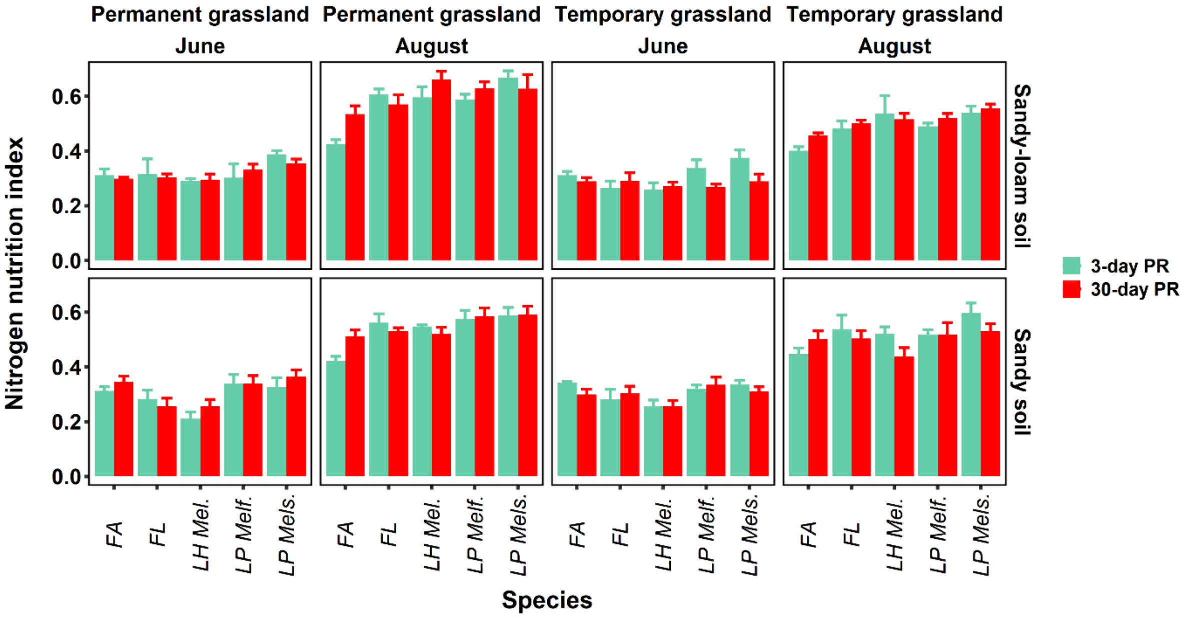

Figure 7. Effects of precipitation regime (PR) on the nitrogen nutrition index in June and August 2022 per species, texture class (sandy vs sandy-loam), grassland management (permanent vs temporary grassland) level. The error bars indicate +/- 1 SE on the mean. Species names including *Festuca arundinacea*, *Festulolium*, *Lolium hybridum*, *Lolium perenne* MELFORCE (tetraploid) and *Lolium perenne* MELSPRING (diploid) are abbreviated as FA, FL, LH Mel., LP Melf. and LP Mels., respectively. Day of the year is abbreviated as DOY.

3.3.3. Interactions between water and nutrient limitations

Both nitrogen limitation and water availability together determined aboveground productivity and forage quality. More intense PR-induced soil drought reduced cumulative biomass on average significantly in 2022 but not in 2021 (*P* < 0.001; Table S10; Fig. S10a). These effects also differed between soils and species, with the biomass of *Lolium hybridum* actually increasing with increasing drought severity in temporary grassland soils in 2021, and biomass of *Lolium perenne* MELFORCE decreasing most out of all species in permanent grassland soils in 2022 (*P* = 0.03; Table S10; Fig. S10a). On a per harvest basis, differences among species followed similar trends (*P* < 0.001; Table S10; Fig. S10b), with generally more positive effects of drought intensity on biomass production during autumn 2021 and spring 2022 (wet and cool conditions) and more negative effects during summer 2022 (dry and hot conditions). Furthermore, more productive mesocosms were generally more nitrogen limited (*P* < 0.001; Table S10; Fig. S11). The effects of drought intensity on biomass interacted with nitrogen limitation, showing a tendency for more negative effects of drought on productivity in mesocosms with low NNI, or, more positive effects of increased NNI on biomass in mesocosms under more intense drought (*P* = 0.001; Table S10; Fig. S12a).

Regarding forage quality, NNI interacted with drought intensity to determine CPC, leading to a positive effect of drought intensity on CPC (strongest for *Lolium perenne* MELSPRING), but only under low nitrogen nutrition (*P* = 0.016; Table S10; Fig. S12c). IVOMD was not influenced by drought intensity (*P* = 0.9; Table S10; Fig. S12b). However, IVOMD generally related positively to NNI (*P* < 0.001; Table S10; Fig. S12b) and this effect was strongest for *Lolium perenne* MELFORCE (*P* < 0.001; Table S10; Fig. S12b).

Integrating our observations, PERMANOVA analysis revealed that across all factors, harvesting moment (R^2 = 0.73; *P* = 0.001; Table S11), followed by PR (R^2 = 0.05; *P* = 0.001; Table S11) explained most of the variance in observations, with generally higher soil drought intensity under 30-day PR, and low plant quality but high productivity and vice versa in June versus August 2022 (Fig. 8). Aboveground productivity and minimum green cover during the period preceding harvest were overall positively influenced by increased water availability but related negatively to NNI and plant quality, though more negative to IVOMD than to CPC and N content (Fig. 7). Additionally, NNI was positively related to plant quality and IVOMD declined least under reductions in soil water availability of all plant quality parameters (Fig. 8). Separations among species were also visible ($R^2 = 0.04$; $P = 0.001$; Table S11) and species identity interacted with harvesting moment ($R^2 = 0.03$; $P = 0.011$; Table S11; Fig. S13a), because *Festuca* tended to perform largely equally than other species in June, while it was the most productive under the most intense soil drought and of the least quality in August (Fig. 8; Fig. S13a). Moreover, in June, *Lolium* hybridum clearly separated from *Lolium perenne* MELSPRING, with the first being on average more productive under more intense soil drought and of less quality compared to the latter (Fig. 8; Fig. S13a). Finally, species identity also interacted with PR, indicating that *Festuca* was greener and more productive in 3-day PR but under most intense soil drought in 30-day PR (closely followed by *Lolium hybridum*) compared to other species ($R^2 = 0.02$; $P = 0.026$; Table S11; Fig. S13b).

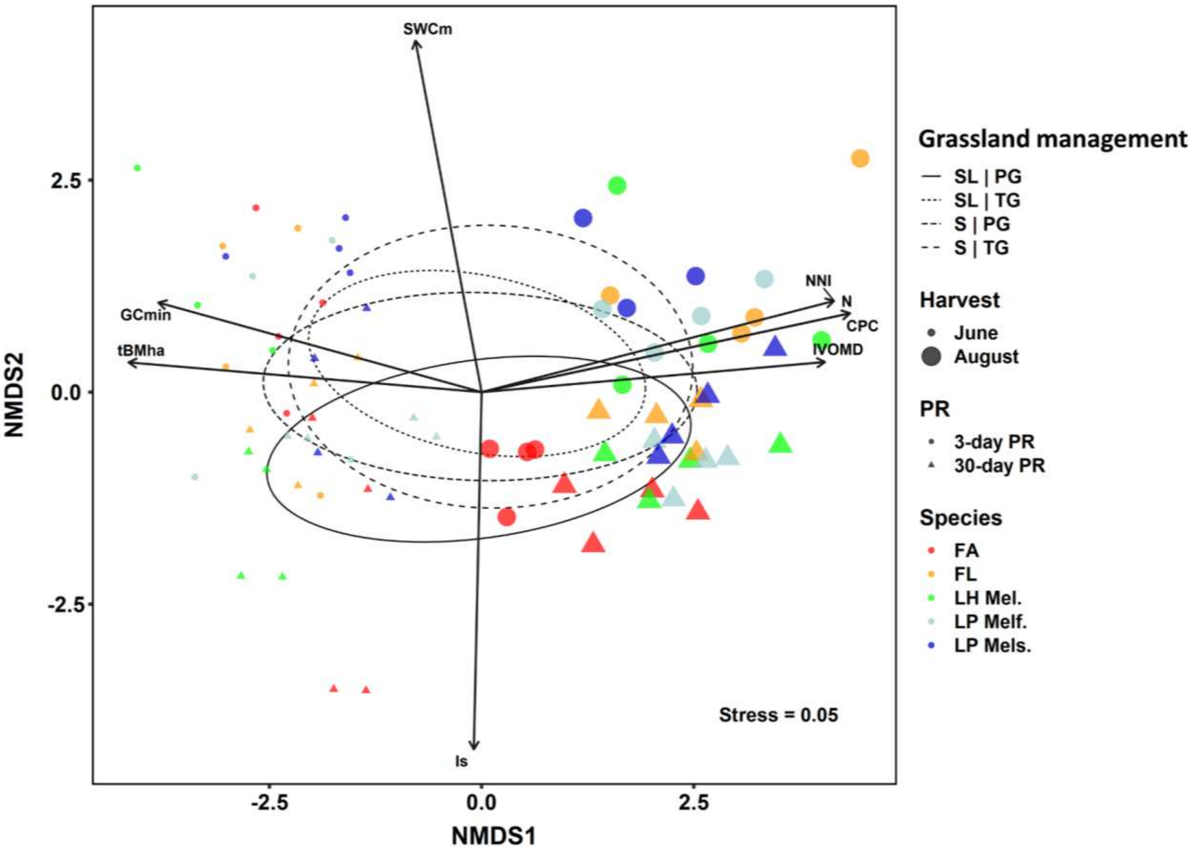

Figure 8. Nonmetric multidimensional scaling ordinations of mesocosms with soil water content sensor (N = 40) based on Euclidian dissimilarities of harvests in June (during drought) and August (post-rewetting) of 2022. Species names including *Festuca arundinacea*, *Festulolium*, *Lolium hybridum*, *Lolium perenne* MELFORCE (tetraploid) and *Lolium perenne* MELSPRING (diploid) are abbreviated as FA, FL, LH Mel., LP Melf. and LP Mels., respectively. Sandy-loam soils, sandy soils, permanent grasslands and temporary grasslands are abbreviated by SL, S, PG and TG, respectively. Based on permutation tests (n=999), significant vector fits were found for all ordination variables ($R^2 >= 0.75$; $P = 0.001$) including mean soil water content (SWCm), minimum green cover (GCmin) and drought intensity (Is) in the period preceding harvest, total aboveground biomass per ha (tBMha), N nutrition index (NNI), as well as, plant N (N), crude protein content (CPC) and in vitro organic matter digestibility (IVOMD). The estimated vectors of CPC and N content overlap.

4. Discussion

Recent observations indicate that summer weather persistence is increasing in the mid-latitudes (Zolina *et al.*, 2013; Coumou *et al.*, 2018; Pfleiderer *et al.*, 2019), with profound consequences for the ecosystem functioning of unfertilized temperate grasslands (Reynaert *et al.*, 2021; Reynaert *et al.*, 2022; Li *et al.*, 2023b; Zi *et al.*, 2023a). We explored if and how such altered weather regimes with longer dry and wet spells influence the productivity and quality of intensively managed monoculture forage grasslands across soil textures and whether management aiming at elevated SOC and choice of species or cultivars buffer those influences. In line with Grant *et al.* (2014) and Fariaszewska *et al.* (2020), our results indicate that increased persistence in precipitation regimes (PR) leads to more intense soil drought which reduces the yield of forage grass species. *Festuca arundinacea* and *Festulolium* remained the most productive species overall, and *Lolium perenne* MELSPRING (diploid) the least. Forage quality was overall neutrally or positively influenced by increased PR persistence in 30-day PR, with the highest quality found for *Lolium perenne* MELFORCE (tetraploid). Our results also revealed species-specific trade-offs between plant quality and productivity under increasing drought stress, and differences in nitrogen nutrition during 30-day PR drought and upon 30-day PR rewetting. Moreover, forage grass responses to increased weather persistence under varying levels of grassland management related SOC differed between soil textures. Although elevated SOC generally improved plant quality, its buffering effects on drought damage, productivity and nutrient availability were found consistently only in sandy-loam soils but not sandy soils.

4.1. Differences in growth strategy determine productivity and quality of forage grass under increased weather persistence

In line with our first hypothesis, subjection to precipitation regimes with longer dry and wet spells reduced productivity and greenness of all cultivars by reducing water availability (Hofer *et al.*, 2017; Meisser *et al.*, 2019; Reynaert *et al.*, 2022). As expected, either *Festuca* or *Festulolium* were the most productive species across both years under the more severe PR, confirming their overall greater productivity under more irregular water availability compared to *Lolium* variants. This was likely related to differences in root architecture, stomatal regulation and water potential adjustment under drought (Durand *et al.*, 1997; Ebrahimiyan *et al.*, 2013; Cougnon *et al.*, 2017; Fariaszewska *et al.*, 2017; Becker *et al.*, 2020; Curran *et al.*, 2020; Fariaszewska *et al.*, 2020). Within the *Lolium* varieties, *Lolium hybridum* and *Lolium perenne* MELFORCE extracted more water from the soil, leading to elevated biomass or improved plant quality during some harvests compared to *Lolium perenne* MELSPRING.

However, our second hypothesis was only partially confirmed. In contrast to previous experiments (Fariaszewska *et al.*, 2017; Fariaszewska *et al.*, 2020), *Festuca* outperformed other species most in the establishment year. While the improved drought resistance of *Festuca* usually shows only from the second year after establishment due to slow early sward development (Fariaszewska *et al.*, 2020), the lack of extreme ecological soil drought in any treatment in 2021 and our method of manually transplanting individuals may have allowed *Festuca* to effectively utilize its other superior resource extraction traits already in 2021 when all species still had immature rooting systems. However, rather unexpectedly, *Festuca* did not outperform others under the most intense droughts in 2022 (June and

September), whereas *Festulolium* outperformed or did equally well as *Lolium* variants in those cases. For *Festuca* this may be attributable to the mesocosm containers simulating relatively shallow soils, preventing this species to access water in deeper soil layers (Fariaszewska *et al.*, 2017), while *Festulolium* is able to extract water well in shallow layers (Durand *et al.*, 1997). Nonetheless, *Festuca* generally showed the most rapid greenness recovery after harvest or drought (excluding August 2022) and also had greater nutrient supply in the soil and higher nitrogen nutrition in 30-day PR upon rewetting. Moreover, *Festuca* generally showed the ability to reduce soil water most compared to all other species across seasons and treatments, without this necessarily negatively affecting its green cover, productivity or quality (again excluding Aug 2022). In line with previous studies, this indicates that *Festuca* generally outperforms other cultivars under ample water availability and mild drought stress (Neal *et al.*, 2009; Cougnon *et al.*, 2014; Becker *et al.*, 2020; Fariaszewska *et al.*, 2020). In addition to greater water and nutrient use efficiency, these differences may be related to its crown/root metabolism (Perlikowski *et al.*, 2020; Perlikowski *et al.*, 2023) or greater root biomass and coarser structure (Cougnon *et al.*, 2017), either improving plant performance directly by facilitating water and nutrient uptake (Cougnon *et al.*, 2014) or indirectly by increasing SOC (Hayashi *et al.*, 2023), boosting soil nutrient and water availability in the long term. However, despite the use of mesocosms limiting rooting depth (Fariaszewska *et al.*, 2017), the low water availability and reduced greenness in Aug 2022, and the comparatively low yields in June and September 2022 under 30-day PR indicate that this rapid conversion of available resources into biomass may potentially also reduce yield when prolonged extreme drought conditions are recurrent within one growing season and plants may not have enough stored reserves to properly recover (Van Eekeren *et al.*, 2010; Cougnon *et al.*, 2017). Indeed, despite a lack of direct effect of PR on NNI and thus N limitation to growth under drought in June 2022 (Hofer *et al.*, 2017; Meisser *et al.*, 2019), we found that increasing drought intensity generally reduced biomass more in cultivars with lower NNI, indicating that increased soil N availability or plant N reserves could partially buffer impacts of drought on plant productivity (Hofer *et al.*, 2017).

Contrasting with earlier studies and our expectations(Grant *et al.*, 2014; Fariaszewska *et al.*, 2017; Fariaszewska *et al.*, 2020; Reynaert *et al.*, 2023b), increased PR persistence did not affect plant quality during drought in June 2022. However, following Reynaert *et al.* (2023b), 30-day PR induced a slight increase in IVOMD (and nitrogen nutrition for *Festuca*) in August 2022 after rewetting and the following plant recovery. Nonetheless, it is important to note that declines in leaf non-structural sugars and increased leaf lignin contents with more persistent PR (Zi *et al.*, 2023b) may nullify positive effects of increased digestibility on plant quality.

Given the strong negative effect of flowering and grass maturity on plant quality (Nelson & Moser, 1994), the high stem to leaf ratio for all species during the relatively late June harvest may have precluded detection of quality differences in response to increased PR persistency among them. In line with our second hypothesis, plant quality was generally highest for both *Lolium perenne* variants (particulary *Lolium perenne* MELFORCE) across both PR in June and August of 22. However, rather surprisingly, nitrogen nutrition and plant quality (mostly digestibility) was significantly greater for *Festuca* compared to *Festulolium* and *Lolium hybridum* in June. This could be related to its generally reduced productivity due to comparatively rapid water limitation in May/June resulting in concentration of nutrients (Grant *et al.*, 2014) and/or its earlier flowering coinciding with the May harvest (7th May on average) in comparison to *Lolium* variants (26th of May on average) (Nelson & Moser, 1994; ILVO, 2022a; ILVO, 2022b).

4.2. Interactions between soil texture and grassland management modify species-specific responses to increased weather persistence

Given the contrasting responses of species to elevated SOC from permanent grasslands among texture classes, the species specific ability to withstand drought and convert more available nutrients and water from the soil into biomass likely determines whether grassland management or soil texture positively affects plant productivity and quality under increased PR persistence (D'Hose *et al.*, 2014; Buttler *et al.*, 2019). Indeed, positive effects of elevated SOC or finer texture on biomass seemed most pronounced for *Festulolium* and *Festuca*, whereas positive effects on nitrogen nutrition and plant quality showed a tendency to be strongest for the most drought sensitive species (*Lolium perenne* and *Lolium hybridum*), likely because the more drought resistant other species had already extracted available nutrients and converted them into biomass prior to harvest (Grant *et al.*, 2014).

Overall, positive effects of elevated SOC on nutrient and water availability related to grassland management (Buttler *et al.*, 2019) were more pronounced in sandy-loam soils compared to sandy soils, only partially confirming our third hypothesis and contrasting with Minasny and McBratney (2018). Whereas plant greenness, water and nutrient supply was highest in sandy-loam soils with a permanent grassland history, nutrient supply and greenness were higher in sandy soil from the temporary grassland compared to sandy-loam soil from temporary grassland and sandy soil from permanent grassland. This was possibly due to historically increased nutrient availability as indicated by higher K and P levels compared to other soils at the start of the experiment, allowing plant productivity to compensate for expected differences in plant performance related to SOC (Buttler *et al.*, 2019) or texture classes (Dodd & Lauenroth, 1997). In contrast with Mallory and Porter (2007), these trends indicate that grassland management resulting in increased nutrient availability can override positive effects of elevated SOC on plant responses to climate change (Minasny & McBratney, 2018), especially when SOC differences are not very pronounced (1.48 % in temporary grassland vs 1.83 % in permanent grassland for sandy soils) or when soils are already relatively SOC saturated (Georgiou *et al.*, 2022). Nonetheless, positive effects of temporary grassland management in sandy soils became less pronounced in 2022, whereas elevated SOC consistently positively influenced plant quality across both texture classes under increased weather persistence, highlighting its importance for improving plant functioning under altered rainfall variability.

In contrast to Van Sundert *et al.* (2020), effects of preceding soil drought intensity on nutrient supply during post-drought rewetting were only clear for N in *Festuca* across soils. Whereas K supply was increased under 30-day PR vs 3-day PR for *Lolium perenne* (cfr. Van Sundert *et al*., 2020) , the opposite was found for *Festulolium*. This may indicate that species-specific differences in belowground investment and resource extraction capacity can strongly influence the magnitude of transient nutrient pulses upon rewetting under altered rainfall variability (Borken & Matzner, 2009). Moreover, Birch effects may be generally less pronounced in highly fertilized grasslands (Van Sundert *et al.*, 2020) and diminish in strength over time under repeated dry-wet cycles, because of exhausted labile organic C pools (Birch, 1958) or gradual shifts in bacterial composition leading to adaptation (Borken & Matzner, 2009). Hence, effects of grassland management relating to SOC and historical nutrient availability may have been more important in determining nutrient supply than the imposed PR regime for all nutrients except for N and K. As expected, nutrient supply was highest in sandy-loam soils with high SOC (Borken & Matzner, 2009), but historically elevated P availability in the sandy soil from temporary grassland was likely able to override positive effects of elevated SOC or texture on nutrient supply from other soils, translating in comparatively high productivity. Interestingly, differences in Mn supply reflected general patterns in aboveground productivity related to soil texture and grassland management most accurately, largely independent of species identity or PR. This result may further highlight the importance of micronutrients in co-limiting grassland biomass production, even under high fertilization rates (Radujković *et al.*, 2021).

Finally, our study adds to growing evidence that weather regimes with longer and more extreme dry and wet spells may worsen soil quality and functioning (Borken & Matzner, 2009; Buttler *et al.*, 2019; Zhang *et al.*, 2019; Klaus *et al.*, 2020; Li *et al.*, 2023b). Despite boosting greenness, biomass and nutrient supply, sandy-loam soil from permanent grasslands with elevated SOC also showed a tendency for inducing the highest soil drought intensities (Fig. 8; Fig. S3). The main cause for this was likely the increased evapotranspiration of generally more productive plant communities with increased leaf area (Wang *et al.*, 2007), related to higher total water and nutrient availability in SOC enriched soils (Dodd & Lauenroth, 1997; D'Hose *et al.*, 2014; Buttler *et al.*, 2019). Nonetheless, soil water retention curves indicated that soils from permanent grasslands (and sandy-loam soil in particular) were most affected by increased weather persistence in terms of water holding capacity.

In contrast to what Buttler *et al.* (2019) found regarding aboveground responses, this may indicate that soils with high SOC content from permanent grasslands are more sensitive to change in precipitation regime because they have a greater potential of losing soil structure and aggregation (Lal & Shukla, 2004). Specifically, whilst such soils may improve growing forage grass yield and quality under climate change (Buttler *et al.*, 2019), they can simultaneously experience greater degradation of physical soil properties compared to soils from temporary grasslands which have little to lose in terms of structure (Lal & Shukla, 2004). Given that SOC rich soils have been associated with high fungal C (Liu *et al.*, 2023) which may improve soil aggregation and water holding capacity (Wilson *et al.*, 2009; Querejeta, 2017; Bowles *et al.*, 2018), it is also possible that a reduction of fungal diversity and abundance under increased PR persistence (Li *et al.*, 2023b) contributed to worsening soil hydrological properties (Querejeta, 2017).

5. Conclusions

Management strategies improving SOC show potential to sustainably improve forage grass performance under climate change and guarantee future ecosystem service provisioning (Buttler *et al.*, 2019). Our results indicate that forage grass varieties differing in drought strategy and quality respond differently to increasing summer weather persistence due to differences in resource extraction and resource use efficiency, and that grassland practices resulting in elevated SOC may ameliorate these responses. In particular, *Festulolium* and *Festuca* overall retained the highest productivity under drought, whereas *Lolium perenne* MELFORCE (tetraploid) had the highest quality. While soils from permanent grasslands with elevated SOC buffered plant quality across texture classes, they also showed the steepest decline in soil water retention under increased PR persistence, and the productivity of sandy soils from temporary grasslands was unexpectedly high. Therefore, future studies should also consider other grassland management factors such as (micro)nutrient availability besides SOC when assessing forage grass and soil responses to climate change. In conclusion, permanent grassland soils with historically elevated SOC likely buffer negative effects of increased summer weather persistence onforage grass performance, but may also be more sensitive to degradation under climate change.

6. Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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