ENVIRONMENTAL RESEARCH LETTERS

PURPOSE-LED PUBLISHING™

Celebrating the 20th anniversary of Environmental Research Letters

ACCEPTED MANUSCRIPT • OPEN ACCESS

Management intensity mediates yield responses to rising temperatures in montane grasslands

To cite this article before publication: Anne Schucknecht *et al* 2026 *Environ. Res. Lett.* in press https://doi.org/10.1088/1748-9326/ae87b3

Management intensity mediates yield responses to rising temperatures in montane grasslands

Anne Schucknecht[1,2,*], Katrin Schneider[1,3,*], Rainer Gasche[1], Cornelia Baessler[4], Michael Dannenmann[1], Ralf Kiese[1]

[1] Institute of Meteorology and Climate Research – Atmospheric Environmental Research (IMK-IFU), Karlsruhe Institute of Technology (KIT), Garmisch-Partenkirchen, D-82467, Germany
[2] Earth Observation Applications Team, OHB System AG, Wessling, D-82234, Germany
[3] Stiftung Kunst und Natur gGmbH, Bad Heilbrunn, D-83670, Germany
[4] Department of Community Ecology, Helmholtz Centre for Environmental Research (UFZ), Halle, D-06120, Germany

* These authors contributed equally to this work.

Correspondence to: Ralf Kiese (ralf.kiese@kit.edu)

Abstract. Understanding responses of temperate grasslands to combined climate and land use changes is needed to secure yields as well as to mitigate future climate change. This study aims to analyse the long-term effects of climate change and grassland management on the water balance, yield, nitrogen uptake and species composition of montane grasslands in S-Germany. We used a space-for-time approach with large intact grassland monoliths (1 m², 1.5 m deep) translocated along an elevation and thus climatic gradient to simulate climate change. The monoliths were operated with four treatments formed by full-factorial combination of climate (current and approx. +2°C warming) and management (high and low frequency of cutting and cattle slurry fertilization events). Measurements of various climate, water balance, and vegetation variables were analysed over a nine-year period (2012–2020). The effect of management on yield was notably higher than the effect of climate change. In general, high management intensity led to higher annual yields (mean dry matter of control site: 1020 +/- 160 g m^{-2}, climate change site: 1075 +/- 200 g m^{-2}), than low management intensity (control: 784 +/-66 g m^{-2}, climate change: 786 +/- 98 g m^{-2}). Climate change conditions increased grassland yields only under high management intensity and during the first 5 years of the experiment (2012-2016), mainly due to higher yields at the first cut. Reduced nitrogen availability, in conjunction with water limitations, emerged as a key constraint on grassland productivity under climate change conditions, explaining the decline in climate change–induced yield responses toward the end of the experiment. The pronounced inter-annual differences and trends illustrated the importance of long-term field experiments. Understanding the drivers of biomass production and forage quality is crucial not only for a better understanding of ecosystem functioning but also for improving grassland management, for instance by adjusting cutting and fertilization practices to future climate conditions.

Key words: Grassland, yield, climate change, management, plant nitrogen content, species abundance

1 Introduction

Grassland ecosystems provide key services including carbon storage, biodiversity conservation, erosion control, water retention, and livestock forage production (Bengtsson et al., 2019; Zhao et al., 2020). In Europe, permanent grasslands cover

over one-third of agricultural land and are particularly important in montane and alpine regions where cropping is limited (Smit et al., 2008; Neuwirth and Hofer, 2013). However, climate change, land-use change, and increasing management intensity threaten these systems and make future service delivery uncertain (Lee et al., 2010; Schirpke et al., 2017). In recent decades, the area of permanent grassland has decreased while simultaneously, grassland management intensity has increased (White et al., 2012; Schils et al., 2022). Alpine regions are especially affected due to rapid warming, occurring at roughly twice the global average (Auer et al., 2007), with further acceleration expected (Smiatek et al., 2016). These combined pressures highlight the need to better understand grassland responses to climate and management change to support food security and climate mitigation (Bernath-Plaisted et al., 2025).

In a recent meta-analysis Wang et al. (2019) show that productivity of cold and temperate grassland biomes is expected to increase with increasing temperatures and associated extension of the growing season as far as water availability is not limiting (Petersen et al., 2021, Forstner et al., 2022). Elevated spring temperatures and earlier snowmelt extend the growing season, making spring temperature and summer water supply key drivers of annual yield variability (Niedrist et al., 2016). In this context, ~800mm annual precipitation is considered a minimum for optimal grassland growth (Neuwirth and Hofer, 2013) which is in line with findings of this study (Table S2). However, climate change is projected to shift precipitation toward drier summers, increasing drought risk in central Europe (Hari et al., 2020) and reducing productivity (Hoeppner and Dukes, 2012). Extreme events already demonstrate these impacts, with grassland productivity reductions of about 30% during the 2003 heatwave and drought (Ciais et al., 2005) and similarly low yields in the drought year 2018 as confirmed in this study (Buras et al., 2020; Reinermann et al., 2019).

Warming can also increase grassland productivity by enhancing soil nitrogen mineralization and availability (Rustad et al., 2001; Wang et al., 2016; Schlingmann et al., 2020). However, this effect may be temporary, as longer-term responses can be constrained by nutrient limitation (Sebastià, 2007). In addition, climate and management-driven changes in environmental conditions can alter species composition, leading to long-term ecosystem responses that differ from short-term effects (Saleska et al., 2002; Liu et al., 2018). In montane and alpine grasslands, rising temperatures are likely to favour fast adapting and fast growing graminoids which outcompete e.g. herbs thereby increasing biomass production (Berauer et al., 2019; Verrall et al., 2021; Forstner et al., 2022).

In addition, grassland yields are strongly influenced by management, with fertilization generally increasing productivity (Shi et al., 2024; Schils et al., 2022) and intermediate mowing frequencies often producing the highest biomass (Kondoh, 2001; Oelmann et al., 2015). Because grassland productivity underpins livestock outputs, climate and weather also affect farm income. However, unlike crop yields, grassland yields are rarely directly measured, leaving limited information on their spatial and temporal variability (Smit et al., 2008; Neuwirth and Hofer, 2013) and long-term observations or regional yield statistics including impacts of weather extremes as consequence of climate change are mostly missing. Consequently, identifying predictive variables and applying modelling approaches such as field and remote sensing data driven machine learning approaches are becoming increasingly important (Reinermann et al., 2019).

Manipulative field experiments are key to understanding warming effects on grassland productivity and species composition (Rustad, 2008), typically using open-top chambers or infrared heating, while translocation experiments are less common (Wang et al., 2019). Method strengths and limitations are discussed by Shaver et al. (2000), Dunne et al. (2004), and Aronson and McNulty (2009), with translocation approaches argued to better capture realistic warming effects, including above- and belowground processes, diurnal variability, and growing-season extension (Niedrist et al., 2016). However, most grassland translocation studies remain short-term (≤3 years) and based on small soil cores with limited area and depth (Wang et al., 2019).

The aim of this study was to analyse the long-term effects of climate change and grassland management on the water balance, yield, nitrogen uptake and species composition of montane grasslands, while accounting for trends and inter-annual variability. We established four different treatments characterized by different combinations of climate (current and approx. +2°C warming) and management (high and low frequency of cutting and cattle slurry fertilization events). For this, we used a space-for-time approach with large intact grassland monoliths (1m², 1.5m deep) translocated along an elevation and thus climatic gradient and present long-term results from 9 years (2012-2020) of measurements.

2 Material and methods

2.1 Study area and measuring setup

This study used data from the TERENO Pre-Alpine observatory in southern Bavaria (Kiese et al., 2018), analysing long-term measurements (2012–2020) from large monoliths (1 m², 1.5 m deep) and meteorological stations at two sites: Graswang (864m a.s.l.) and Fendt (595m a.s.l.) with mean annual temperature (MAT) of 6.8°C and 8.9°C and mean annual precipitation (MAP) of 1297mm and 962mm, respectively (Figure 1). Thus, the sites differ in climate, with Fendt being 2.1°C warmer and 335 mm drier on average. These gradients were used in a space-for-time approach, where undisturbed soil cores were translocated between sites in 2011 to simulate climate change. Six monoliths at Graswang served as controls (CTRL), while six moved to Fendt represented climate change (CC) treatments (Kiese et al., 2018). After setting up the experiment in 2011, at each site, monoliths were managed in low (3 cuts, 1–2 slurry applications per year) and high (4–5 cuts, 4–5 slurry applications) intensities with a mean N load of 42±10kg N ha^{-1} per application event following farmers` practice (Kiese et al., 2018), resulting in four treatments (CTRL_ext, CTRL_int, CC_ext, CC_int) with three replicates. Soils are fluvic calceric Cambisols, with the top 10 cm characterized by high clay (51.7±2.5%), organic C (6.4%) and total N (0.7%) contents, pH of 6.4 and a bulk density of 0.8g cm^{-3} (Kiese et al., 2018).

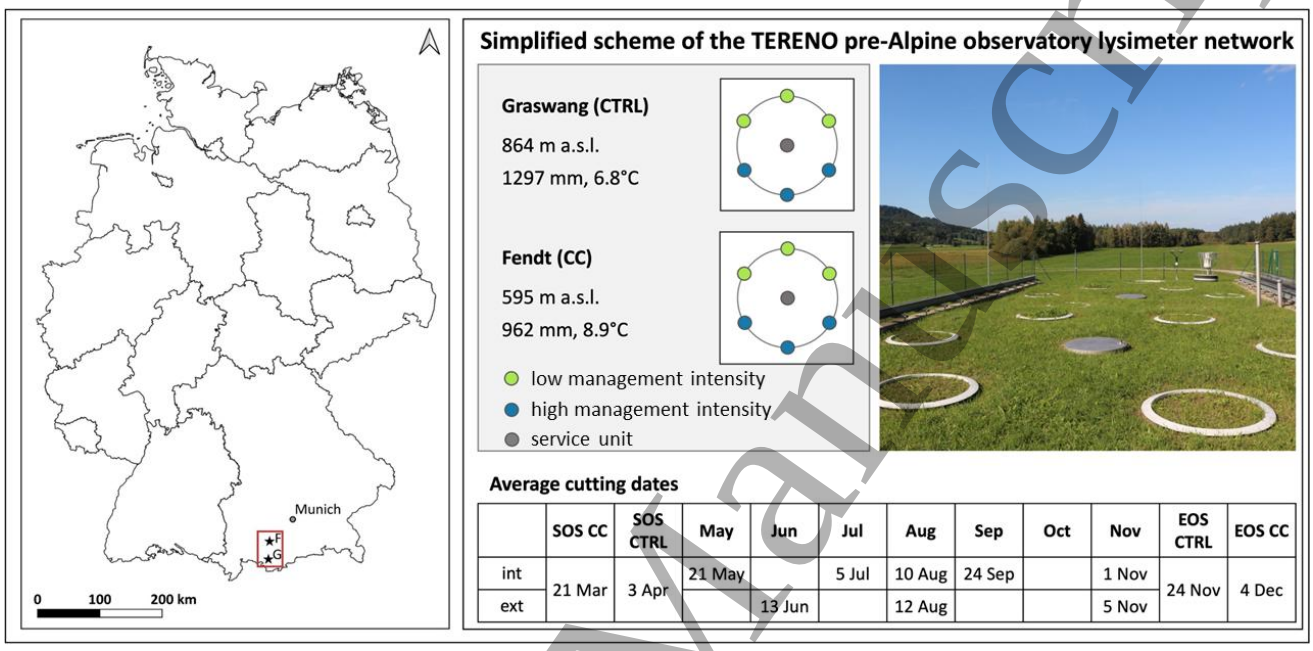


Figure 1. Location, photo and simplified scheme of the monolith lysimeter network and treatments, as well as climate characteristics including average start of season (SOS) and end of season (EOS) of the Graswang (CTRL) and Fendt (CC) sites.

2.2 Vegetation analysis

At each harvest, vegetation from the full 1 m² monolith area was cut at ~4cm above ground. Dry matter biomass (DM) was determined after drying at 60 °C to constant weight. A subsample (5–10g) was ground using a ball mill (MM400 or MM301, Retsch GmbH) and analysed for N concentration with an elemental analyser (Flash 1112 EA, Thermo Scientific, Waltham, Massachusetts, USA). In total, >400 DM and N concentration measurements were obtained across treatments, cuts, and years. Species composition was assessed annually between 31 May and 30 September using a frequency grid method (Pütz et al., 2016), with each monolith area divided into 64 (8 × 8) 10cm × 10cm quadrats. Species richness and frequency were recorded per quadrat, and data were aggregated into plant functional types (PFT: legumes, herbs, graminoids) to calculate species numbers and total occurrences per PFT. Note that differences in sampling dates among years may have introduced some uncertainty into the species richness and frequency data.

2.3 Water balance and climate data

For water balance measurements, each monolith lysimeter was equipped with three balances (load cells Model 3510, Tedea Huntleigh) recording weight changes at 1-minute time intervals. As the lysimeters are closed at the bottom, soil hydrology is controlled by actively adjusting the lower boundary condition according to reference water tension measurements (three replicated measurements) at the same depth (1.4m) in the undisturbed soil near the lysimeter site. Drainage water (DR) was collected at 1.4m depth in weighable tanks. Actual evapotranspiration (ETa) and drainage water (DR) was derived from monolith and drainage tank weight changes (Kiese et al., 2018) and processed using AWAT software for noise filtering and error correction (Peters et al., 2014, 2017). Soil moisture (CS610, Campbell Scientific) and soil temperature (SIS and TH4, METER Group) were measured at 0.1, 0.3, and 0.5m depths. Air temperature (T_{air}) (HMP45, Vaisala), precipitation (P) (pluviometer, Ott Hydromet) and photosynthetic photon flux density (PFD) (SKP215 Quantum Sensor, Campbell Scientific) were measured at a weather station nearby (<500 m) the lysimeter sites. All variables were aggregated from sub-daily to daily (sums for P, ET_a, DR; means for T_{air}, PFD, soil moisture, and temperature) and then to annual, growing season, and cutting periods. The growing season was defined using ETCCDI criteria (http://etccdi.pacificclimate.org/list_27_indices.shtml), with start (SOS) and end (EOS) of growing season and determined from 10 cm soil temperature thresholds (≥5°C for 6 consecutive days; <5 °C after July 1).

For growing seasons and the full year, we calculated the evapotranspiration ratio (ER) according to Liu et al., (2020).

$$ER = \frac{ET_a}{P}, \quad (1)$$

with ER close to 1 or > 1 indicating dry conditions likely associated with plant water stress.

2.4 Data analysis, statistics and random forest modelling

For data analyses and graph generation we used GNU R, version 3.6.1 and 4.1.0 (R Core Team, 2021) utilizing several packages (see S1). Data analysis was conducted at two temporal scales: (i) growing season (GS), where dry matter (DM) yield (sum of all cuts) and environmental variables (including plant N content) were aggregated and (ii) cutting period (CP), where cut-specific DM and N data were analyzed together with environmental conditions from the start of the season to the first cut, or between cuts. Data were tested for normality (Shapiro–Wilk test) and variance homogeneity (Bartlett test). Depending on distribution, differences between treatments were assessed using parametric or non-parametric tests: t-test or Wilcoxon rank-sum test for two-group comparisons, and one-way ANOVA or Kruskal–Wallis test for multiple groups, followed by pairwise t-tests or Wilcoxon tests for post-hoc comparisons. All analyses used dependent (repeated-measures) designs, with Holm correction for multiple testing, and significance was set at $p<0.05$.

Random Forest (RF) regression models were used to assess whether environmental and factor (e.g. management, site) variables could predict GS- and CP-specific DM yields and plant N content. RF was used as it can handle non-linear relationships, performs robustly with small sample size, and generally works well with default hyperparameters settings (Breiman, 2001; Probst et al., 2019). Models were evaluated using 6-fold cross-validation with 10 iterations using stratified sampling.

Performance was assessed by cross-validated coefficient of determination (R^2_{cval}), root mean square error ($RMSE_{cval}$), relative RMSE ($RRMSE_{cval}$; RMSE normalized by the observed data range), and bias ($Bias_{cval}$). As each fold yields unequal model performance and variable importance, we normalized the importance metric of each predictor of a certain fold with its corresponding R^2 before averaging over all folds, resulting in the mean variable importance. Normalized variable importance was analyzed to quantify predictor contributions. Further details on the method are provided in Supplement S2 and an overview of the tested models in Table S1.

3 Results

3.1 Climatic conditions during the study period

Between 2012 and 2020, the control (CTRL) and climate change (CC) sites differed significantly in precipitation, air temperature, evapotranspiration (ETa), and drainage (DR) at annual and growing season (GS) scales (Table S2). Mean annual precipitation was higher at the CTRL site (1297 mm; GS: 1044 mm) than at the CC site (962mm; GS: 797mm), while mean annual and GS temperatures were 2.1 °C (8.9 vs. 6.8°C) and 0.9°C (12.0 vs. 11.1 °C) higher at the CC site, respectively. DR was substantially greater at the CTRL site (686 mm yr^{-1}; GS: 445 mm) than at the CC site (298 mm yr^{-1}; GS: 173 mm), whereas ETa was higher at the CC site (717mm yr^{-1}; GS: 655mm) compared to the CTRL site (582mm yr^{-1}; GS: 548mm). Consequently, evapotranspiration ratios (ER) were consistently higher at the CC site (annual: 0.75; GS: 0.82) than at the CTRL site (annual: 0.46; GS: 0.54). The drought year 2018 (Schuldt et al., 2020) showed the lowest GS ER at both sites, despite GS precipitation at the CC site not being exceptionally low. Solar radiation was slightly higher at the CC site, both during GS and annually.

3.2 Effects of climate change and management on grassland biomass

3.2.1 Annual DM yield

Annual DM yield (2012–2020) varied substantially across years (701–1476 g m^{-2}) with greater variability under high than low management intensity and CC than CRTL treatments. Mean annual DM was significantly higher under high (CTRL: 1020 g m^{-2}; CC: 1075 g m^{-2}) than low management intensity (CTRL: 784 g m^{-2}; CC: 786 g m^{-2}) ($p < 0.01$), while no overall differences occurred between CTRL and CC treatments for either high or low management intensity (Figure 2a, Table S3). Excluding the drought year 2018 - the only year in which CC_int yields were lower than CTRL_int -, however, revealed significantly higher yields under CC than CTRL conditions under high management intensity ($p < 0.01$), whereas low management intensity remained unaffected (Figure 3a). Overall, CC-induced increases in DM under high management intensity were stronger before 2017, whereas responses under low management intensity were more variable with higher variation until 2016 (Figure 3a).

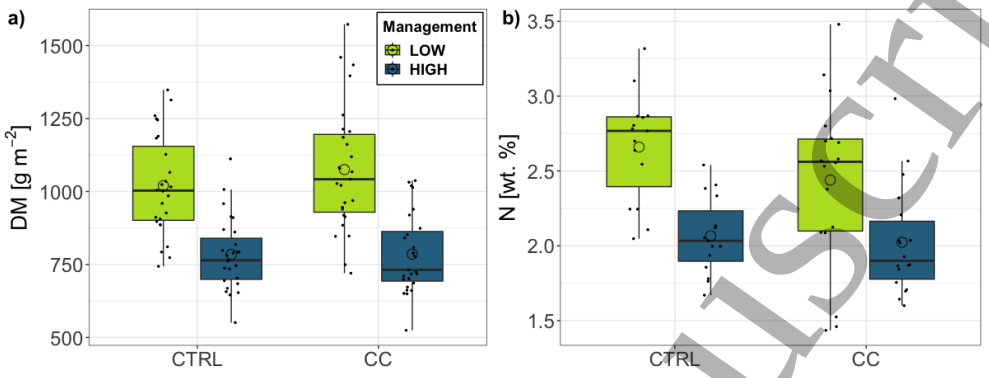


Figure 2. a) Annual DM yields and b) mean plant N content for 2012-2020 across different treatments. Black circles represent treatment means.

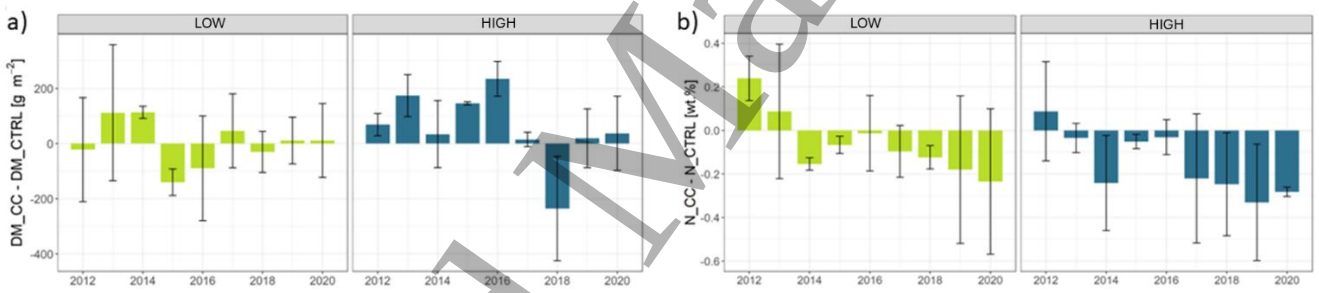


Figure 3. (a) Annual differences in dry matter (DM) yield between climate change (CC) and control (CTRL) treatments under low (LOW) and high (HIGH) management intensity. (b) Annual differences in plant N content between CC and CTRL under low and high management intensity.

3.2.2 Cutting period (CP) specific DM yield

Monoliths with low management intensity showed significant differences in DM yield among cuts, with the first cut contributing most (CTRL: 400g m^{-2}; CC: 393g m^{-2}; ~50% of annual yield) followed by sharp declines in later cuts (Figure 4a). Mean DM differences between CTRL and CC were small and not significant, while CP-level variability was high (CV: 42–120%), exceeding annual variability (8.5%-18.6%), and peaking at the first cut.

Under high management intensity, DM yield declined with successive cuts. Differences among cuts were generally significant ($p<0.01$) within both CTRL and CC, except between selected middle cuts. The first cut yielded the most, particularly under CC (378g m^{-2}), and was significantly higher than CTRL (302g m^{-2}), where the first two cuts did not differ significantly (Figure 4b). The first cut contributed 35% (CC) and 30% (CTRL) of annual yield. Variability at CP level (44–162% CV) was much higher than under low management intensity and again much higher than annual variability, with the greatest variation in the first cut.

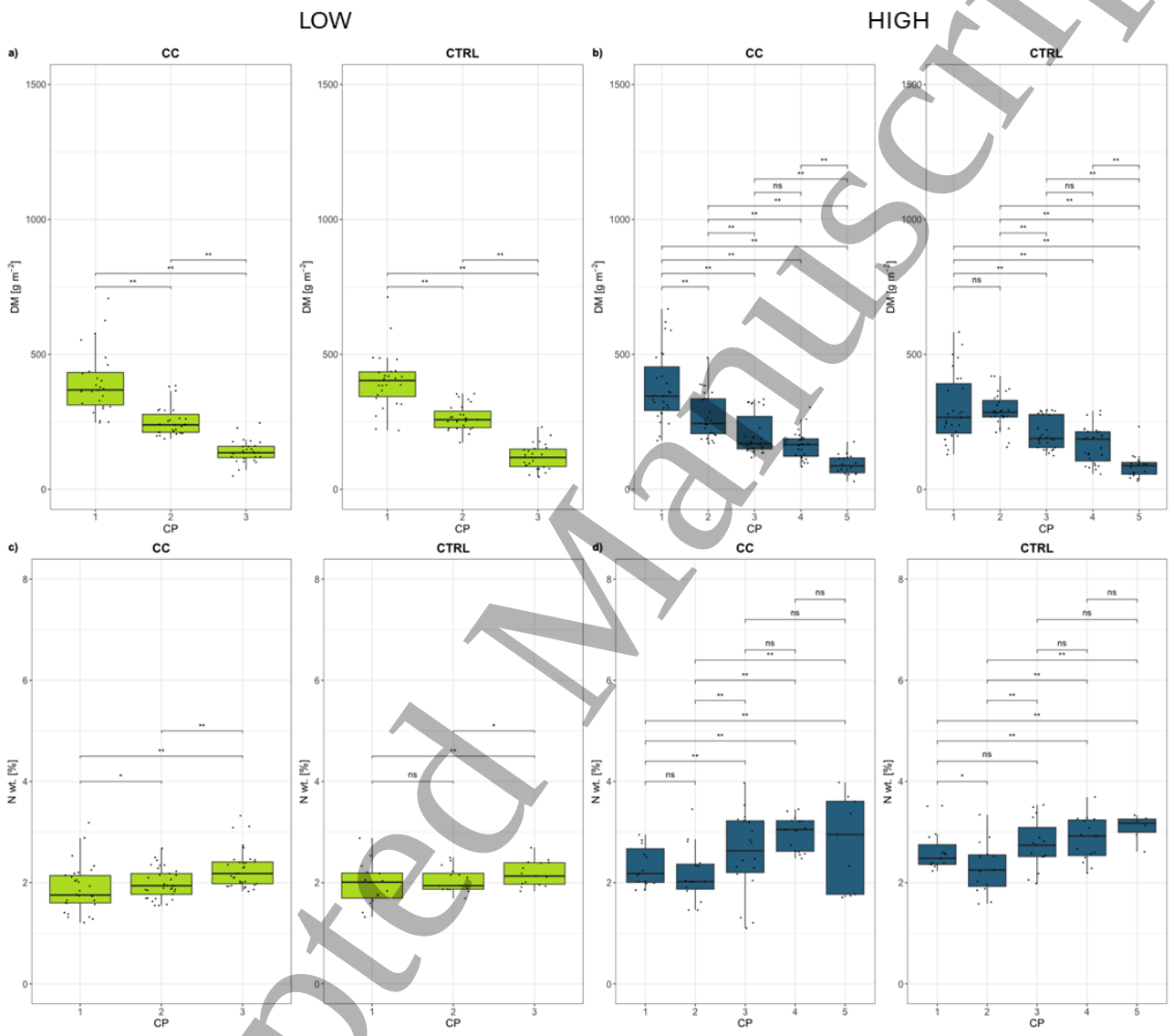


Figure 4. Cutting-period (CP)-specific dry matter (DM) yields. a) for low management intensity (LOW); b) for high management intensity (HIGH). CP-specific plant N content. c) for low management intensity (LOW); d) for high management intensity (HIGH) for 2012-2020. The p-value of the pairwise comparison is represented by ns: $p > 0.05$, *: $p \leq 0.05$ and **: $p \leq 0.01$.

3.3 Effects of climate change and management on plant nitrogen content

3.3.1 Mean annual plant nitrogen content

Monoliths with high management intensity had significantly higher plant N contents (~0.5wt%) than monoliths with low management intensity (CTRL: 2.52 vs. 1.93wt%; CC: 2.37 vs. 1.87wt%; Figure 2b). Climate change (CC) had a smaller but

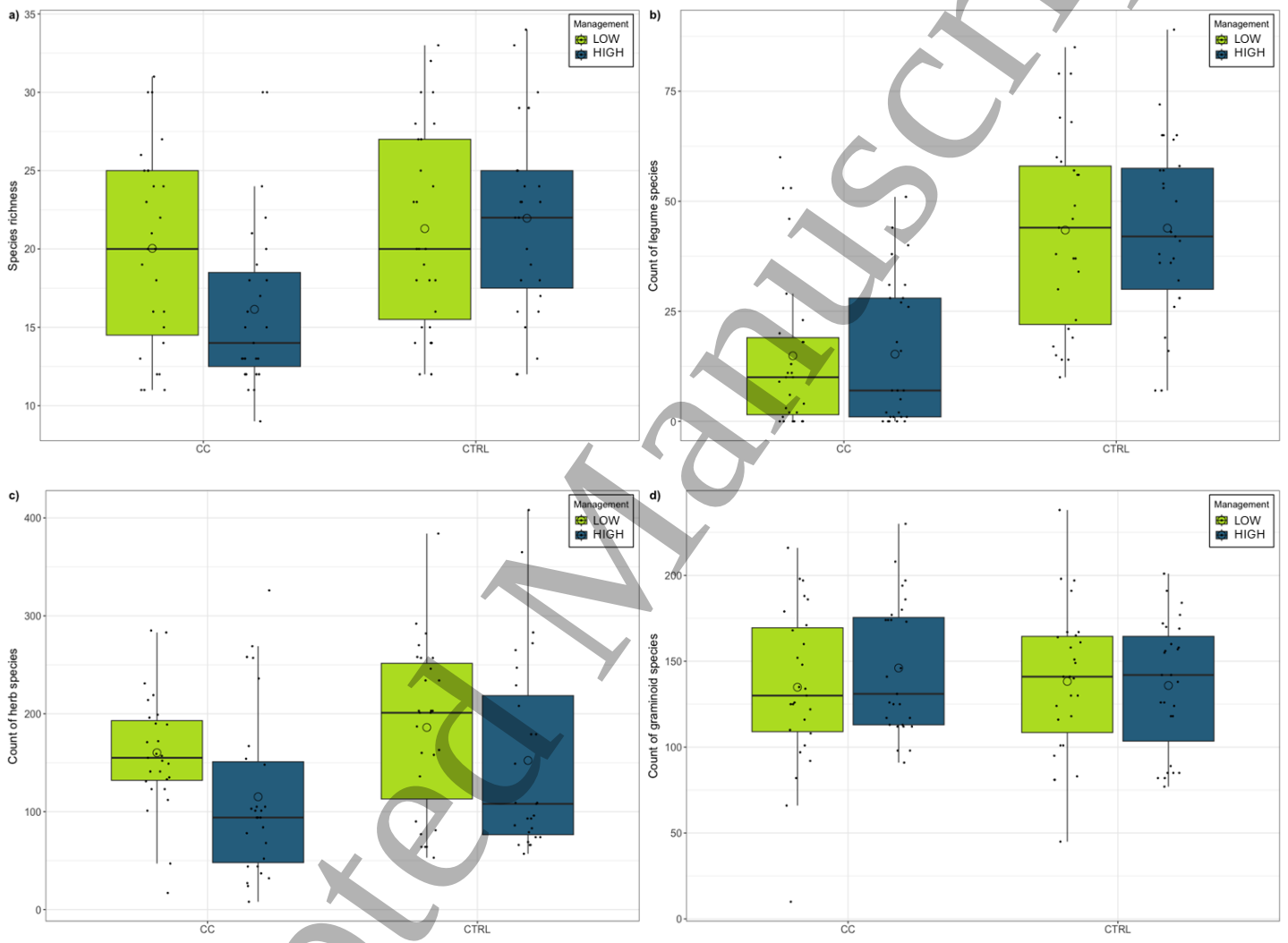
significant effect, reducing N content by ~0.1 wt.%. Differences between CC and CTRL and between management intensities were analyzed over time. CC increased plant N content during the first two years but led to lower N content thereafter (Figure 3b), with regression analysis showing a significant ($p<0.01$) temporal divergence between CC and CTRL for both management types. No temporal trend was found for management intensity differences (Table S4). Annual N content varied more under CC (CV: 15.8–17.5%) than CTRL conditions (CV: 11.9–12.1%).

3.3.2 Cutting period (CP) specific plant N content

Under low management intensity, N content significantly ($p<0.05$) increased from the first to the third cut in both CTRL and CC treatments (CTRL: 1.84–2.06wt%; CC: 1.63–2.17wt%; Figure 4c). Under high management intensity, temporal variation was smaller, with significantly ($p<0.05$) lower N contents in the first and second cuts (CTRL: 2.16–2.42wt%; CC: 1.97–2.08wt%) and highest values in cuts three to five (CTRL: 2.65–2.75wt%; CC: 2.53–2.76wt%; Figure 4d). CTRL and CC showed similar trends across cuts. However, CC significantly ($p<0.05$) reduced plant N content under low management intensity for the first cut, while under high management intensity significant ($p<0.05$) reductions occurred in the first three cuts (Figure 4d).

3.4 Species and plant functional type (PFT) analysis

Species richness varied strongly over time across treatments. Mean richness in CTRL_LOW, CTRL_HIGH, and CC_LOW ranged from 20.0–22.0 species and did not differ significantly, whereas CC_HIGH had significantly ($p<0.01$) lower richness (16.1 species; Figure 5a). CC_HIGH also showed the lowest numbers of legume and herb species (Figure 5b, c), while the number of graminoid species did not differ among treatments (Figure 5d). Independent of management, the number of legume species was significantly lower under CC than CTRL, and low management intensity supported more herb species than high management intensity, with significant ($p<0.05$) differences within CTRL and CC treatments.



220 **Figure 5. a) Species richness (number of plant species), b) Count of legume species, c) Count of herb species, d) Count of graminoid species for 2012-2020 across different treatments. White dots- Black circles indicate treatment means.**

3.4 Relation of DM with environmental variables

3.4.1 Correlation of annual DM yield with average growing season environmental variables

Annual DM yield was positively correlated with ETa (R=0.5–0.6) and growing-season PFD (R=0.36–0.56) across all treatments. DM yield also correlated positively with growing-season precipitation under high management intensity (CTRL_HIGH: R=0.33; CC_HIGH: R=0.24), but not under low management intensity. No strong or consistent correlations were found with air or soil temperature, soil moisture, drainage, or evaporation rate.

3.4.2 RF models for estimating annual DM yield

The RF model including all predictors (GS_full) explained 61% of annual DM yield variance with an RRMSEcval of 13.9% (Table S1, Figure 6), but overestimated low and underestimated high DM values. Management, year, and plant N content were the most important predictors, whereas climatic and hydrological variables had low importance (<10%). Increasing the number of samples by including less predictors (GS_reduced) only slightly improved model performance (Table S1). A model using only commonly available environmental variables (GS_environmental) explained just 12% of DM yield variance (Table S1). The cut-specific DM yield model with all predictors (CP_all) explained 70% of variance ($RRMSE_{cval}$=10.4%; Table S1), with highest importance for year, PFD, and cut number, while management and N content were less important than in the GS model. The reduced predictor model (CP_reduced) performed better (R^2_{cval}=0.79; $RRMSE_{cval}$ = 8.3%), and the environmental-only model (CP_environmental) achieved comparable performance, explaining ~71% of variance, mainly driven by PFD and soil temperature (st10) (Table S1, Figure S1).

3.4.4 RF models for estimating plant nitrogen content

The RF model with all predictors (GS_full) explained 74% of the variance in mean annual plant N content ($RRMSE_{cval}$ = 12.6%), with year, treatment and management as the most important predictors (Table S1, Figure 6). The GS_reduced model performed similarly, whereas the CP_environmental model explained only 15% of the variance. Despite a much larger sample size, the cut-specific model (CP_full) performed similarly (R^2_{cval}=0.71; $RRMSE_{cval}$=10.3%) than the GS_full model, with year, ETa, and days since last cut as key predictors. The CP_reduced model showed comparable performance (R^2_{cval}=0.71) while the CP_environmental model using only satellite data explained only 59% of the variance (Table S1).

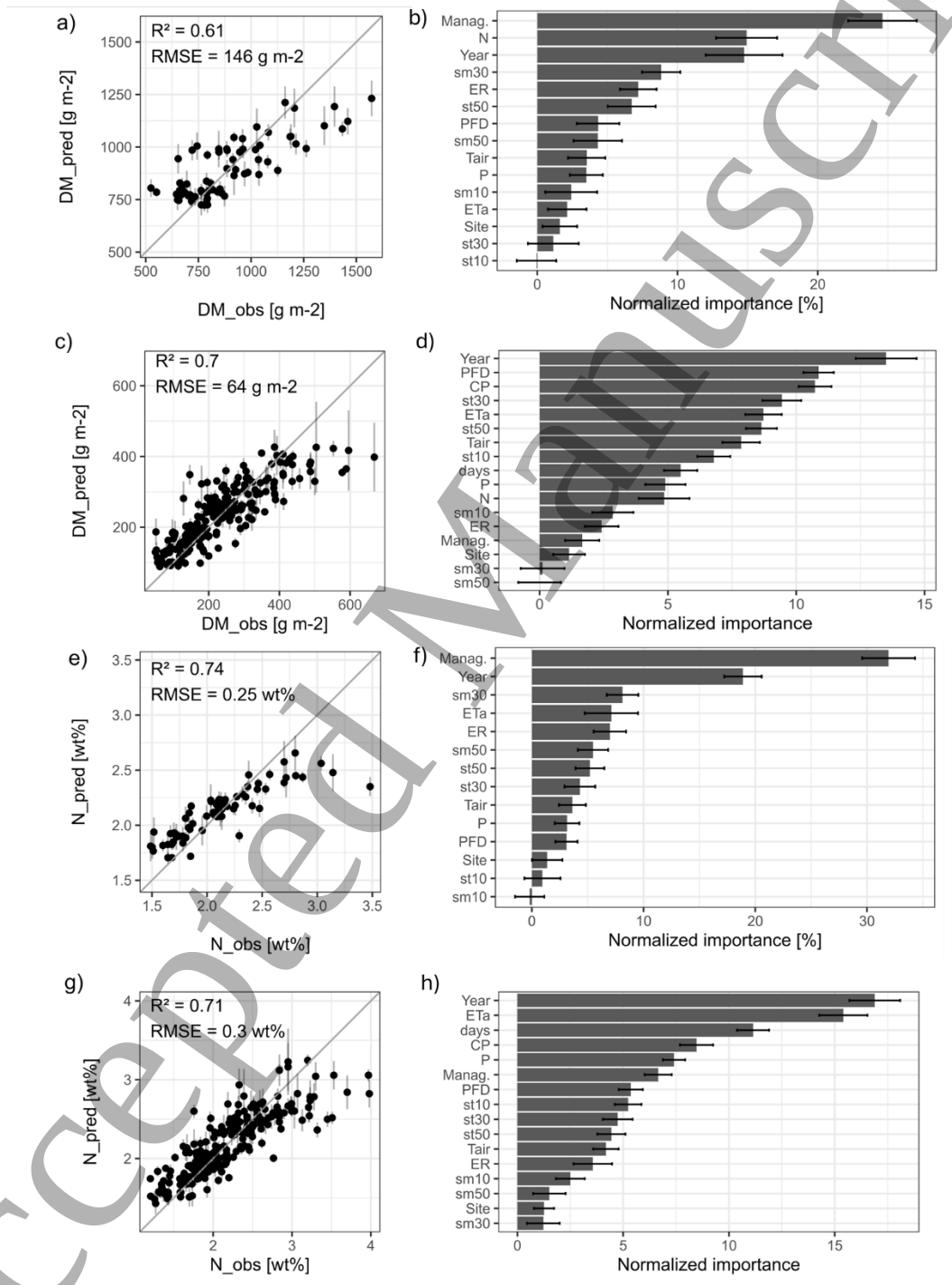


Figure 6. Scatter plots of observed vs. predicted a) annual and c) cut specific DM yields, e) annual and g) CP-specific plant N content. Normalized variable importance for RF models using all predictors (GS_full, CP_full). For b) annual and d) CP-specific DM yields and f) annual and h) CP-specific plant N content. Line in a), c), e), g) is a visual aid for predictions matching observations.

4 Discussion

4.1 Interactive effects of climate change and management intensity on grassland yields

While climate and land management intensity are expected to jointly influence ecosystem functions, their interaction has rarely been demonstrated in long-term experimental studies (Oliver & Morecroft, 2014). Using a space-for-time approach, we examined how climate and management influence grassland water budgets, yields, plant nitrogen concentrations, and species composition. Unlike most grassland warming studies, which last ≤3 years (Wang et al., 2019), this experiment spanned 9 years (2012–2020) and combined management (high vs. low cutting and fertilization) with climate change and control treatments. Climate change shifted the grassland water balance from seepage-water dominated (ER = 0.46) to evapotranspiration-dominated (ER = 0.75). However, except for the drought year 2018, grasslands remained more energy- than water-limited. This agrees with studies from similar climates (Forstner et al., 2021, 2022; Wieser et al., 2018), which found little drought stress in Alpine grasslands even in dry years. Water availability therefore generally did not limit evapotranspiration or plant growth, although temporary drought stress occurred in 2018.

Besides water and energy, nutrient availability can strongly limit grassland productivity, reflected in yield differences between management regimes. In our study, mean annual yields at the control site were 784±66 and 1020±160g m^{-2} yr^{-1} under low and high management intensity, respectively, placing them among the upper range of values reported for comparable grassland systems (Ammann et al., 2007; Hoekstra et al., 2010; Nüsse et al., 2018; Grigulis & Lavorel, 2020; Sieve et al., 2021; Wang et al., 2021). In our long-term study, N addition rates were more than doubled under high management intensity, while yields increased by less than 25%. This modest response likely reflects the low contribution of recent fertilizer N to plant nutrition in SOM-rich grassland soils, where only ~10% of plant N uptake derives from fertilizer (Schlingmann et al., 2020; Zistl-Schlingmann et al., 2020; Schreiber et al., 2022; Dannenmann et al., 2025). In montane grasslands, plant nutrition therefore largely depends on soil organic nitrogen (SON) mineralization (Han et al., 2025), implying that fertilizer primarily serves to replenish SON pools rather than directly supply plant-available N. With high soil organic carbon (SOC) and total nitrogen (TN) concentrations of 6.4% and 0.7% in the 0–10cm layer (Kiese et al., 2018), it was demonstrated earlier that gross N mineralization rates exceed plant N demand, particularly under climate change conditions (Wang et al., 2016). Accordingly, as long as these SOM stocks are maintained, yield gains under intensified management are likely driven more by increased cutting frequency and longer growing seasons under warming than by higher N fertilization rates. Consistent with this, our results show that climate change increased grassland yields only under high management intensity (Fig. 2a, 3a).

Similar warming-induced growth stimulation has been reported for C- and N-rich grasslands in cool, moist climates (Sebastià et al., 2008; Niedrist et al., 2016; Berauer et al., 2019; Forstner et al., 2022). A global meta-analysis (Wang et al., 2019) likewise showed that warming increases yields most in cold systems, less in temperate systems, and can reduce them in semi-arid grasslands, highlighting that warming benefits temperature-limited rather than water-limited ecosystems. In such systems, warming both enhances growth and extends the growing season, consistent with observed shifts of up to 14 days earlier first cuts in the study region (Petersen et al., 2021).

Our results highlight the strong importance of the first cut for yield increases under climate change, with most gains under high management intensity and only minor contributions from the fifth cut, while other cuts and all low management yields showed no climate effect (Figure 4). In contrast, the extreme drought year 2018 caused strong yield reductions across all cuts under climate change due to low spring and summer soil moisture. In other dry years (e.g. 2015), post-drought regrowth partially compensated for losses, consistent with Chen et al. (2020). The variable contribution of individual cuts and climatic conditions also helps explain the weak relationship between seasonal climate and annual yields, as shown previously by Neuwirth and Hofer (2013) and confirmed here: annual yields in RF models were better explained by integrative factors such as year, treatment, and management than by climatic variables alone (Figure 6b, d). No yield reductions occurred under low management intensity in 2018, consistent with evidence that grasslands under low management intensity are more drought-resistant (Korell et al., 2024). This also explains why differences between high and low management yields were much smaller under drought than under normal conditions (Figure 3b). Overall, this suggests, that lower cutting frequencies, which also support biodiversity, may become increasingly relevant under continued climate change. Greater drought resistance is further reflected in lower interannual yield variability (CV) under low management intensity (Table S3). At the cooler, wetter control site, high management yields remained relatively high in 2018, supporting the view that in temperature-limited grasslands, soil moisture is the key factor modulating warming effects on productivity (Sieve et al., 2021; Forstner et al., 2022).

Beyond water limitation, our results indicate that nitrogen availability is also a key control on grassland productivity under climate change. The strongest yield increases occurred early in the translocation experiment (until 2016 under high and 2014 under low management intensity), but these effects declined over time (Figure 3a). Previous work on the same soils reported strongly negative N (and C, Wang et al., 2021) budgets (-86 ± 29kg N ha^{-1} yr^{-1} under low and -47 ± 18kg N ha^{-1} yr^{-1} under high management intensity), driven by biomass export and fertiliser-related gaseous losses, with climate change further increasing N deficits via higher plant N uptake particularly under high management intensity (Zistl-Schlingmann et al., 2020). Given the strong dependence of plant N supply on SON mineralization and SOM content (Booth et al., 2005; Schlingmann et al., 2020), initial yield increases under warming likely reflect stimulated mineralization (Wang et al., 2016, 2019), whereas their decline over time may result from progressive SOM depletion and reduced N mineralization capacity (Garcia-Franco et al., 2024, Han et al., 2025). This is most evident under climate change conditions, where changing yield differences between high and low management treatments coincide with lower mean plant N content and a decline of plant N content over time in the climate change treatment relative to the control (Figure 2b, 3b). These results highlight the importance of long-term experiments and show that climate-driven yield gains can only be sustained if fertiliser inputs are adjusted accordingly (Lee et al., 2013; Petersen et al., 2021). Alternatively, or in addition to increasing N fertilizer rates improved N management, such as slurry injection instead of broadcast application, can reduce SON depletion and associated environmental N losses (Schreiber et al., 2022; Floßmann et al., 2025).

Under current legislation, only more efficient fertilisation or moderate increases in mineral N inputs are feasible to sustain productivity under warming, as higher organic fertilisation rates conflict with the German Fertiliser Ordinance (170 kg N ha^{-1} yr^{-1} limit). Reported substantial N deficits therefore suggest that both improved application techniques and slightly higher

inputs are needed to maintain productivity and fodder quality in high-SOM grasslands. In the pre-Alpine region, this appears compatible with water protection due to strong nitrate retention in SOC-rich soils (Fu et al., 2017; Dannenmann et al., 2025). Furthermore, N_2O emissions are relatively low in SOC-rich grassland soils developed on carbonatic parent material (Schlingmann et al., 2020; Schreiber et al., 2022), as pH values around 6–7 enhance N_2O reductase activity and promote complete denitrification to N_2 (Chen et al., 2015; Zistl-Schlingmann et al., 2019).

Beyond changes in climatic and biogeochemical conditions, shifts in grassland species composition driven by management intensity and climate change can also strongly influence productivity. Korell et al. (2024) showed that higher plant diversity at lower-intensity management can stabilize productivity under drought. Our grasslands independent of management intensity were comparable species-rich (>15 species, Figure 5a), which likely contributed to yield stability across control and climate change treatments (Fig. 2a). Consistent with other translocation studies (Niedrist et al., 2016; De Boeck et al., 2016; Tello-García et al., 2020), the reduction in species richness under intensive climate change was mainly due to drought induced declines in legumes and herbs (Fig. 5b, c), but had little effect on yields given their low abundance (<5%). Yield stability was likely maintained by compensatory responses of graminoids, which benefit from warmer, drier conditions and are particularly competitive in spring when cool soils favour grass growth. In temperate grasslands, graminoids generally possess shallower and more flexible root systems than herbs and legumes. Although these traits increase their sensitivity to drought, they also confer greater physiological and growth plasticity, enabling rapid responses to changing environmental conditions (Liu et al., 2018; Bardgett et al., 2014; Kubert et al., 2019).

4.2 Prediction of drivers of biomass production

Understanding drivers of biomass production and forage quality is important both for ecosystem insight and for improving grassland management and yield prediction. Beyond process-based models, machine learning approaches combined with remote sensing are increasingly used for this purpose. Here, the best random forest (RF) model using environmental and management variables achieved good performance for GS dry matter (R^2_{cval}=0.64; $RRMSE_{cval}$=12.4%), comparable to process-based models applied to similar grassland systems (Petersen et al., 2021). However, model performance was mainly driven by nitrogen content and factorial variables (year, management), while environmental predictors played a smaller role. Cutting-period models likely also due to increased number of samples performed even better (up to R^2_{cval}=0.79; $RRMSE_{cval}$=8.3%), with factorial variables (i.e., year and cutting period) remaining very important, but with increased relevance of environmental drivers such as PFD and soil temperature.

A reduced model for CP-specific DM using only satellite-retrievable environmental variables still achieved strong performance (R^2cv=0.71), comparable to a Sentinel-2-based regression approach (R^2=0.68; Reinermann et al., 2025) derived from field measurements, while the performance was lowest for plant N content (Table S1). Together, these results suggest that different modelling approaches serve complementary purposes: the RF models presented here are well suited for identifying drivers of dry matter production, process-based models for scenario analyses, and remote-sensing approaches for yield prediction with minimal in situ data requirements.

5 Conclusion

This long-term monolith experiment demonstrates that both climate change and management intensity strongly influence the functioning of montane grasslands, particularly in terms of water balance, productivity, and nutrient dynamics. While warming shifted the grasslands from energy toward an more water limited system, still management intensity had a greater overall effect on yield than simulated climate change conditions. Although yields under high management intensity were consistently higher than under low management intensity, the difference was small, as the key process supporting plant growth was the mineralization of soil nitrogen from organic-rich soils rather than direct fertilization. Climate warming enhanced productivity only temporarily and primarily under high management intensity. Over time, negative nitrogen balances involving high plant nitrogen export led to reduced soil nitrogen availability. This constrained the positive growth effects of climate warming and reduced plant nitrogen content, thereby diminishing fodder quality. These findings highlight the need for adaptive management strategies in montane grasslands, such as higher or more efficient fertilization. Slurry injection, rather than broadcast application, can reduce or prevent SON mining and thereby enhance plant growth while mitigating environmental N losses and their adverse effects on water, air, soil, and biodiversity. This is crucial because the German Fertiliser Ordinance restricts organic inputs to 170 kg N ha^{-1} yr^{-1} across a farm's utilized area, allowing only efficiency improvements or added mineral fertilization to sustain grassland productivity and resilience under climate warming. Maintaining grassland productivity in systems of high management intensity may also facilitate extensification strategies, thereby supporting other ecosystem services such as wildlife conservation and biodiversity at the regional scale. Overall, our findings highlight the complex and time-dependent interactions between climate and management and underscore the necessity of long-term experiments to capture delayed ecosystem responses. The main limitation of our study relates to the mismatch between the experimental scale (1 m^2 lysimeters) and the field scale of grassland ecosystems. Future satellite-based remote sensing offers strong potential to bridge this gap by linking long-term experimental results with repeated, spatially extensive field observations of grassland yields, plant nitrogen content, and species traits at the regional scale (Dashpurev et al., 2025).

Acknowledegments

The species inventories were conducted yearly between 31 May and 30 September by the Helmholtz Centre for Environmental Research (UFZ) in Leipzig, Department of Community Ecology. We thank Jens Stolle, Sandra Richter, Katharina Amann, Kathrin Fuchs, and Jana Zeppan, for contributions to the processing and analysis of species data. Furthermore, we thank Bumsuk Seo for the support with the RF modelling and our KIT colleagues, especially Marcus Schlingmann for the support and help with monolith sampling.

Funding

The infrastructure of the TERENO pre-Alpine Observatory was initially funded by the Helmholtz Association (HGF) and the German Federal Ministry of Education and Research (BMBF). This study was conducted within the SUSALPS project

(https://www.susalps.de/). The work was supported by the German Federal Ministry of Education and Research (grant numbers 031B0027A, 031B0516A). The article processing charges for this open-access publication were covered by the Karlsruhe Institute of Technology (KIT).

CRediT authorship contribution statement

Anne Schucknecht: Writing – review & editing, Writing – original draft, Methodology, Formal analysis, Data curation. **Katrin Schneider**: Writing – review & editing, Writing – original draft, Formal analysis, Data curation. **Rainer Gasche**: Writing – review & editing, Investigation, Data curation. **Cornelia Baessler**: Writing – review & editing, Data Curation, Funding Acquisition. **Michael Dannenmann**: Writing – review & editing, Supervision, Funding acquisition, Conceptualization. **Ralf Kiese:** Writing – review & editing, Writing – original draft, Supervision, Funding acquisition, Conceptualization.

Generative AI statement

The author(s) declare that no Generative AI was used in the creation of this manuscript.

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.

References

Ammann, C., Flechard, C. R., Leifeld, J., Neftel, A., & Fuhrer, J. (2007). The carbon budget of newly established temperate grassland depends on management intensity. Agriculture, Ecosystems & Environment, 121, 5–20.

Aronson, E. L., & McNulty, S. G. (2009). Appropriate experimental ecosystem warming methods by ecosystem, objective, and practicality. Agricultural and Forest Meteorology, 149, 1791–1799.

Auer, I., Reinhard, B., Jurkovic, A., Lipa, W., Orlik, A., Potzmann, R., … Nieplova, E. (2007). HISTALP – historical instrumental climatological surface time series of the Greater Alpine Region. International Journal of Climatology, 17–46. https://doi.org/10.1002/joc.1377

Bardgett, R. D., Mommer, L., & De Vries, F. T. (2014). Going underground: root traits as drivers of ecosystem processes. Trends in Ecology & Evolution, 29, 692–699.

Bengtsson, J., Bullock, J. M., Egoh, B., Everson, C., Everson, T., O'Connor, T., … Lindborg, R. (2019). Grasslands – more important for ecosystem services than you might think. Ecosphere, 10, e02582. https://doi.org/10.1002/ecs2.2582

Berauer, B. J., Wilfahrt, P. A., Arfin-Khan, M. A. S., Eibes, P., von Heßberg, A., Ingrisch, J., … Jentsch, A. (2019). Low resistance of montane and alpine grasslands to abrupt changes in temperature and precipitation regimes. Arctic, Antarctic, and Alpine Research, 51, 215–231.

Bernath-Plaisted, J. S., Handler, S. D., Ahlering, M., Brandt, L. A., Maresh Nelson, S. B., Niemuth, N. D., … Zuckerberg, B. (2025). A climate adaptation menu for North American grasslands. Conservation Science and Practice, 7(4), e70017. https://doi.org/10.1111/csp2.70017

Booth, M. S., Stark, J. M., & Rastetter, E. (2005). Controls on nitrogen cycling in terrestrial ecosystems: A synthetic analysis of literature data. Ecological Monographs, 75, 139–157.

Breiman, L. (2001). Random forests. Machine Learning, 45, 5–32. https://doi.org/10.1023/A:1010933404324

Buras, A., Rammig, A., & Zang, C. S. (2020). Quantifying impacts of the 2018 drought on European ecosystems in comparison to 2003. Biogeosciences, 17(6), 1655–1672. https://doi.org/10.5194/bg-17-1655-2020

Chen, Z., Wang, C., Gschwendtner, S., Willibald, G., Unteregelsbacher, S., Lu, H., … Dannenmann, M. (2015). The relationships between denitrification gene expression, dissimilatory nitrate reduction to ammonium and nitrous oxide and dinitrogen production in montane grassland soils. Soil Biology & Biochemistry, 82, 67–77.

Chen, N., Zhango, Y., Zue, J., Zhua, J., & Chena, Y. (2020). The compensation effects of post-drought regrowth on earlier drought loss across the Tibetan Plateau grasslands. Agricultural and Forest Meteorology. https://doi.org/10.1016/j.agrformet.2019.107822

Ciais, P., Reichstein, M., Viovy, N., … Valentini, R. (2005). Europe-wide reduction in primary productivity caused by the heat and drought in 2003. Nature, 437. https://doi.org/10.1038/nature03972

Dannenmann, M., Yankelzon, I., Wähling, S., Ramm, E., Schreiber, M., Ostler, U., … Scheer, C. (2025). Fates of slurry nitrogen applied to mountain grasslands: The importance of dinitrogen emissions versus plant N uptake. Biology and Fertility of Soils, 61, 455–468. https://doi.org/10.1007/s00374-024-01826-9

Dashpurev B., Piatka D.R., Krämer A., Schucknecht A., Butterbach-Bahl K., Kiese R. (2025). Potential use of multi-year UAV imagery for monitoring vegetation traits in grasslands. Ecological Indicators. https://doi.org/10.1016/j.ecolind.2025.114371

Dunne, J., Saleska, S., Fischer, M., Harte, J. (2004). Integrating experimental and gradient methods in ecological climate change research. Ecology, 85, 904–916.

Floßmann, S., Lei, K., van Grinsven, S., Ostler, U., Stange, F. C., Kögel-Knabner, I., & Dannenmann, M. (2025). Full nitrogen balances for different cattle slurry fertilization techniques in a temperate grassland. Agriculture, Ecosystems & Environment, 393, 109843. https://doi.org/10.1016/j.agee.2025.109843

Forstner, V., Groh, J., Vremec, M., Herndl, M., Vereecken, H., Gerke, H. H., … Pütz, T. (2021). Response of water fluxes and biomass production to climate change in permanent grassland soil ecosystems. Hydrology and Earth System Sciences, 25, 6087–6106. https://doi.org/10.5194/hess-25-6087-2021

Forstner, V., Vremec, M., Herndl, M., & Birk, S. (2022). Effects of dry spells on soil moisture and yield anomalies at a montane managed grassland site: A lysimeter climate experiment. Ecohydrology, 16(3), e2518. https://doi.org/10.1002/eco.2518

Fu, J., Gasche, R., Wang, N., Lu, H., Butterbach-Bahl, K., & Kiese, R. (2017). Impacts of climate and management on water balance and nitrogen leaching from montane grassland soils of S-Germany. Environmental Pollution, 229, 119–131.

Garcia-Franco, N., Wiesmeier, M., Buness, V., Berauer, B. J., Schuchard, M. A., Jentsch, A., … Dannenmann, M. (2024). Rapid loss of organic carbon and soil structure in mountainous grassland topsoils induced by simulated climate change. Geoderma, 442, 116807. https://doi.org/10.1016/j.geoderma.2024.116807

Grigulis, K., & Lavorel, S. (2020). Simple field-based surveys reveal climate-related anomalies in mountain grassland production. Ecological Indicators, 116. https://doi.org/10.1016/j.ecolind.2020.106519

Han, J., Schlingmann, M., Gasche, R., Garcia-Franco, N., Wiesmeier, M., Kiese, R., … Dannenmann, M. (2025). High importance of organic fertilizer nitrogen applied to temperate grassland for plant nitrogen uptake in the years following fertilization. Agriculture, Ecosystems & Environment, 389, 109653. https://doi.org/10.1016/j.agee.2025.109653

Hari, V., Rakovec, O., Markonis, Y., Hanel, M., & Kumar, R. (2020). Increased future occurrences of the exceptional 2018–2019 Central European drought under global warming. Scientific Reports. https://doi.org/10.1038/s41598-020-68872-9

Hoekstra, N. J., Lalor, S. T. J., Richards, K. G., O'Hea, N., Lanigan, G. J., Dyckmans, J., … Schmidt, O. (2010). Slurry 15NH4-N recovery in herbage and soil: Effects of application method and timing. Plant and Soil, 330, 357–368.

Hoeppner, S. S., & Dukes, J. S. (2012). Interactive responses of old-field plant growth and composition to warming and precipitation. Global Change Biology, 18(5), 1754–1768. https://doi.org/10.1111/j.1365-2486.2011.02626.x

Kiese, R., Fersch, B., Baessler, C., Brosy, C., Butterbach-Bahl, K., Chwala, C., … Schmid, H. P. (2018). The TERENO pre-Alpine observatory: Integrating meteorological, hydrological, and biogeochemical measurements and modeling. Vadose Zone Journal, 17, 180060. https://doi.org/10.2136/vzj2018.03.0060

Kondoh, M. (2001). Unifying the relationships of species richness to productivity and disturbance. Proceedings of the Royal Society B: Biological Sciences, 268, 269–271.

Korell, L., Andrzejak, M., Berger, S., Durka, W., Haider, S., Hensen, I., … Auge, H. (2024). Land use modulates resistance of grasslands against future climate and inter-annual climate variability in a large field experiment. Global Change Biology, 30, e17418. https://doi.org/10.1111/gcb.17418

Kubert, A., Götz, M., Kuester, E., Piayda, A., Werner, C., Rothfuss, Y., & Dubbert, M. (2019). Nitrogen loading enhances stress impact of drought on a semi-natural temperate grassland. Frontiers in Plant Science, 10, 1051.

Lee, M., Manning, P., Rist, J., Power, S. A., & Marsh, C. (2010). A global comparison of grassland biomass responses to CO2 and nitrogen enrichment. Philosophical Transactions of the Royal Society B, 365, 2047–2056. https://doi.org/10.1098/rstb.2010.0028

Lee, J. M., Clark, A. J., & Roche, J. R. (2013). Climate-change effects and adaptation options for temperate pasture-based dairy farming systems: A review. Grass and Forage Science, 68, 485–503. https://doi.org/10.1111/gfs.12039

Liu, H., Mi, Z., Lin, L., … He, J.-S. (2018). Shifting plant species composition in response to climate change stabilizes grassland primary production. PNAS, 115, 4051–4056. https://doi.org/10.1073/pnas.1700299115

Liu, Z., Cheng, L., Zhou, G., Chen, X., Lin, K., Zhang, W., … Zhou, P. (2020). Global response of evapotranspiration ratio to climate conditions and watershed characteristics in a changing environment. Journal of Geophysical Research: Atmospheres, 125. https://doi.org/10.1029/2020JD032371

Neuwirth, C., & Hofer, B. (2013). Spatial sensitivity of grassland yields to weather variations in Austria and its implications for the future. Applied Geography, 45, 332–341. https://doi.org/10.1016/j.apgeog.2013.08.010

Niedrist, G., Tasser, E., Bertoldi, G., Della Chiesa, S., Obojes, N., Egarter-Vigl, L., & Tappeiner, U. (2016). Down to future: Transplanted mountain meadows react with increasing phytomass or shifting species composition. Flora, 224, 172–182.

Nüsse, A., Linsler, D., Loges, R., Reinsch, T., Taube, F., & Ludwig, B. (2018). Effect of grassland harvesting frequency and N fertilization on stocks and dynamics of soil organic matter in the temperate climate. Archives of Agronomy and Soil Science, 64, 1925–1931.

Oelmann, Y., Vogel, A., Wegener, F., Weigelt, A., & Scherer-Lorenzen, M. (2015). Management intensity modifies plant diversity effects on N yield and mineral N in soil. Soil Science Society of America Journal, 79, 559–568. https://doi.org/10.2136/sssaj2014.05.0191

Oliver, T. H., & Morecroft, M. D. (2014). Interactions between climate change and land use change on biodiversity: Attribution problems, risks, and opportunities. WIREs Climate Change, 5, 317–335.

Peters, A., Groh, J., Schrader, F., Durner, W., Vereecken, H., & Pütz, T. (2017). Towards an unbiased filter routine to determine precipitation and evapotranspiration from high precision lysimeter measurements. Journal of Hydrology, 549, 731–740. https://doi.org/10.1016/j.jhydrol.2017.04.015

Peters, A., Nehls, T., Schonsky, H., & Wessolek, G. (2014). Separating precipitation and evapotranspiration from noise – a new filter routine for high-resolution lysimeter data. Hydrology and Earth System Sciences, 18, 1189–1198. https://doi.org/10.5194/hess-18-1189-2014

Petersen, K., Kraus, D., Calanca, P., Semenov, M. A., Butterbach-Bahl, K., & Kiese, R. (2021). Dynamic simulation of management events for assessing impacts of climate change on pre-alpine grassland productivity. European Journal of Agronomy. https://doi.org/10.1016/j.eja.2021.126306

Probst, P., Wright, M.N., & Boulesteix, A.-L. (2019) Hyperparameters and tuning strategies for random forest. WIREs Data Mining and Knowledge Discovery, 9(3), e1301. https://doi.org/10.1002/widm.1301

Pütz, T., Kiese, R., Wollschläger, U., Groh, J., Rupp, H., Zacharias, S., … Vereecken, H. (2016). TERENO-SOILCan: A lysimeter-network in Germany observing soil processes and plant diversity influenced by climate change. Environmental Earth Sciences, 75, 1242. https://doi.org/10.1007/s12665-016-6031-5

R Core Team. (2021). R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.

Reinermann, S., Boos, C., Kaim, A., Schucknecht, A., Asam, S., Gessner, U., … Kiese, R. (2025). Grassland yield estimation – potentials and limitations of remote sensing, process-based modelling and field measurements. Biogeosciences, 22, 4969–4992. https://doi.org/10.5194/bg-22-4969-2025

Reinermann, S., Gessner, U., Asam, S., & Kuenzer, C. (2019). The effect of droughts on vegetation condition in Germany: An analysis based on two decades of satellite earth observation time series and crop yield statistics. Remote Sensing, 11, 1783. https://doi.org/10.3390/rs11151783

Rustad, L. (2008). The response of terrestrial ecosystems to global climate change: Towards an integrated approach. Science of the Total Environment, 404, 222–235. https://doi.org/10.1016/j.scitotenv.2008.04.050

Rustad, L., Campbell, J., Marion, G., Norby, R., Mitchell, M., Hartley, A., … Gurevitch, J. (2001). A meta-analysis of the response of soil respiration, net nitrogen mineralization, and aboveground plant growth to experimental ecosystem warming. Oecologia, 543–562. https://doi.org/10.1007/s004420000544

Saleska, S. R., Shaw, R., Fischer, M. L., Dunne, J. A., Still, C. J., Holman, M. L., & Harte, J. (2002). Plant community composition mediates both large transient decline and predicted long-term recovery of soil carbon under climate warming. Global Biogeochemical Cycles, 16(4), 1055. https://doi.org/10.1029/2001GB001573

Sebastià, M. T. (2007). Plant guilds drive biomass response to global warming and water availability in subalpine grassland. Journal of Applied Ecology, 44, 158–167. https://doi.org/10.1111/j.1365-2664.2006.01232.x

Sebastià, M.-T., Kirwan, L., & Connolly, J. (2008). Strong shifts in plant diversity and vegetation composition in grassland shortly after climatic change. Journal of Vegetation Science, 19, 299–306.

Schils, R. L. M., Bufe, C., Rhymer, C. M., … Price, P. N. (2022). Permanent grasslands in Europe: Land use change and intensification decrease their multifunctionality. Agriculture, Ecosystems & Environment, 330, 107891.

Schirpke, U., Kohler, M., Leitinger, G., Fontana, V., Tasser, E., & Tappeiner, U. (2017). Future impacts of changing land-use and climate on ecosystem services of mountain grassland and their resilience. Ecosystem Services, 26, 79–94. https://doi.org/10.1016/j.ecoser.2017.06.008

Schlingmann, M., Tobler, U., Berauer, B., Garcia-Franco, N., Wilfahrt, P., Wiesmeier, M., … Dannenmann, M. (2020). Intensive slurry management and climate change promote nitrogen mining from organic matter-rich montane grassland soils. Plant and Soil. https://doi.org/10.1007/s11104-020-04697-9

Schreiber, M., Bazaios, E., Strobel, B., Wolf, B., Ostler, U., Gasche, R., … Dannenmann, M. (2022). Impacts of slurry acidification and injection on fertilizer nitrogen fates in grassland. Nutrient Cycling in Agroecosystems. https://doi.org/10.1007/s10705-022-10239-9

Schuchardt, M. A., Berauer, B. J., von Heßberg, A., Wilfahrt, P., & Jentsch, A. (2021). Drought effects on montane grasslands nullify benefits of advanced flowering phenology due to warming. Ecosphere, 12(7), e03661. https://doi.org/10.1002/ecs2.3661

Schucknecht, A., Seo, B., Krämer, A., Asam, S., Atzberger, C., & Kiese, R. (2022). Estimating dry biomass and plant nitrogen concentration in pre-Alpine grasslands with low-cost UAS-borne multispectral data – a comparison of sensors, algorithms, and predictor sets. Biogeosciences, 19, 2699–2727. https://doi.org/10.5194/bg-19-2699-2022

Schuldt, B., Buras, A., Arend, M., Vitasse, Y., Beierkuhnlein, C., Damm, A., … Kahmen, A. (2020). A first assessment of the impact of the extreme 2018 summer drought on Central European forests. Basic and Applied Ecology, 45, 86–103. https://doi.org/10.1016/j.baae.2020.04.003

Schwieder, M., Buddeberg, M., Kowalski, K., Pfoch, K., Bartsch, J., Bach, H., & Hostert, P. (2020). Estimating grassland parameters from Sentinel-2: A model comparison study. PFG – Journal of Photogrammetry, Remote Sensing and Geoinformation Science, 88, 379–390. https://doi.org/10.1007/s41064-020-00120-1

Shaver, G. R., Canadell, J., Chapin, F. S., Gurevitch, J., Harte, J., Henry, G., … Sala, O. E. (2000). Global warming and terrestrial ecosystems: A conceptual framework for analysis ecosystem responses to global warming will be complex and varied. Bioscience, 50, 871–882. https://doi.org/10.1641/0006-3568(2000)050[0871:GWATEA]2.0.CO;2

Shi, T.-S., Collins, S. L., Yu, K., Peñuelas, J., Sardans, J., Li, H., & Ye, J.-S. (2024). A global meta-analysis on the effects of organic and inorganic fertilization on grasslands and croplands. Nature Communications, 15, 341. https://doi.org/10.1038/s41467-024-47829-w

Sieve, F., Isselstein, J., & Kayser, M. (2021). Short-term changes of the δ15N natural abundance of aboveground biomass and topsoil in temperate grassland – Effects of prolonged summer drought. Ecological Indicators. https://doi.org/10.1016/j.ecolind.2021.108359

Smiatek, G., Kunstmann, H., & Senatore, A. (2016). EURO-CORDEX regional climate model analysis for the Greater Alpine Region: Performance and expected future change. Journal of Geophysical Research: Atmospheres, 121, 7710–7728. https://doi.org/10.1002/2015JD024727

Smit, H. J., Metzger, M. J., & Ewert, F. (2008). Spatial distribution of grassland productivity and land use in Europe. Agricultural Systems, 98, 208–219.

Tello-Garcia, E., Huber, L., Leitinger, G., Peters, A., Newesely, C., Ringler, M.-E., & Tasser, E. (2020). Drought- and heat-induced shifts in vegetation composition impact biomass production and water use of alpine grasslands. Environmental and Experimental Botany. https://doi.org/10.1016/j.envexpbot.2019.103921

Verrall, B., Green, K., & Pickering, C. M. (2021). Dynamics in plant diversity and composition on Australian alpine summits over time. Biodiversity and Conservation, 30, 1855–1880. https://doi.org/10.1007/s10531-021-02171-1

Wang, C., Chen, Z., Unteregelsbacher, S., Lu, H., Gschwendtner, S., Gasche, R., … et al. (2016). Climate change amplifies gross nitrogen turnover in montane grasslands of Central Europe in both summer and winter seasons. Global Change Biology, 22, 2963–2978. https://doi.org/10.1111/gcb.13353

Wang, N., Quesada, B., Xia, L., Butterbach-Bahl, K., Goodale, C. L., & Kiese, R. (2019). Effects of climate warming on carbon fluxes in grasslands – a global meta-analysis. Global Change Biology, 25, 1839–1851. https://doi.org/10.1111/gcb.14603

Wang, N., Xia, L., Goodale, C. L., Butterbach-Bahl, K., & Kiese, R. (2021). Climate change can accelerate depletion of montane grassland C stocks. Global Biogeochemical Cycles. https://doi.org/10.1029/2020GB006792

White, S. R., Carlyle, C. N., Fraser, L. H., & Cahill, J. F. (2012). Climate change experiments in temperate grasslands: Synthesis and future directions. Biology Letters, 8, 484–487. https://doi.org/10.1098/rsbl.2011.0956

Wieser, G., Hammerle, A., & Wohlfahrt, G. (2018). The water balance of grassland ecosystems in the Austrian Alps. Arctic, Antarctic, and Alpine Research, 40(2), 439–445.

Zhao, Y., Liu, Z., Wu, J. (2020). Grassland ecosystem services: a systematic review of research advances and future directions. Landscape Ecology, 35, 793–814 https://doi.org/10.1007/s10980-020-00980-3

Zistl-Schlingmann, M, Feng, J., Kiese, R., Stephan, R., Zuazo, P., Willibald, G., … & Dannenmann (2019). Dinitrogen emissions: an overlooked key component of the N balance of montane grasslands. Biogeochemistry, 143, 15-30 https://doi.org/10.1007/s10533-019-00547-8

Zistl-Schlingmann, M., Kengdo, S. K., Kiese, R., & Dannenmann, M. (2020). Management intensity controls nitrogen-use-efficiency and flows in grasslands – A N-15 tracing experiment. Agronomy, 10. https://doi.org/10.3390/agronomy10040606