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Na Wang and Longlong Xia contributed equally to this work.

Climate Change Can Accelerate Depletion of Montane Grassland C Stocks

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Key Points:

- Climate change can accelerate depletion of montane grassland C stocks
- Under warmer conditions gross primary production and ecosystem respiration (Reco) increase, but Reco with a higher temperature sensitivity
- Adaptation of grassland cutting and manure management regimes can likely reduce ecosystem carbon losses

Supporting Information:

Supporting Information may be found in the online version of this article.

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Abstract Climate warming and management will likely affect carbon (C) fluxes of montane grassland ecosystems. In this study, we assessed the effect of simultaneous warming (+2°C) and decreased precipitation (−25%) on carbon exchange of montane grasslands in S-Germany by translocating large intact plant-soil cores from a high altitude to a low altitude site. Cores received two common grassland management regimes: intensive (4–5 cuts and slurry application) and extensive (1–2 cuts and slurry application). Diurnal patterns of net ecosystem exchange (NEE) and total ecosystem respiration (Reco) were measured over 1.5 years in 2–3 weeks intervals during the snow free period. Additional data on environmental controls, that is, photosynthetic active radiation, grass height and soil moisture and temperature, were used to develop empirical models to estimate daily and annual fluxes of gross primary production (GPP) and Reco. Considering the 2 years period (2014 and 2015), we found that, under warmer and slightly drier conditions, both GPP and Reco significantly ($p < 0.01$) increased (up to 20%) but with a higher temperature sensitivity of Reco, particularly in intensive managed grassland. The higher temperature sensitivity of Reco reduced the NEE by 0.7 t C ha^{−1} yr^{−1} for both extensive and intensive management, respectively. Considering additional carbon inputs via slurry and exports via harvest (i.e., annual net ecosystem carbon budget), our results showed that managed grasslands are already a source of C under current climate conditions (1.7–1.8 t ha^{−1} yr^{−1}) which significantly ($p < 0.05$) increased under climate warming (2.3–2.9 t ha^{−1} yr^{−1}).

1. Introduction

Grasslands cover ~30% of the Earth's land surface. The corresponding soils are rich in organic carbon (C) and store about 10%–30% of total global terrestrial C stocks (Booker et al., 2013; Scurlock & Hall, 1998). Previous studies have demonstrated that the various C pools in grassland ecosystems are sensitive to climate and management changes, especially for grasslands located in montane areas, where temperature usually limits decomposition of soil organic C (SOC) and plant biomass production (Crowther et al., 2016). A recent meta-analysis conducted by Wang et al. (2019) showed that experimental warming significantly stimulated grassland C fluxes, increasing gross primary production (GPP) by 3.3%, ecosystem respiration (Reco) by 3.7%, and net ecosystem exchange (NEE, imbalance between Reco and GPP) by 8.0%, though the responses varied by grassland biomes.

Experimental warming can directly regulate the net C balance of terrestrial ecosystems by affecting plant photosynthesis and respiration and soil C decomposition (Shaver et al., 2000). Warming can also indirectly affect ecosystem C balance by extending the length of the growing season and changing plant phenology (Dunne et al., 2012; Price & Waser, 1998), increasing soil nitrogen (N) mineralization and availability (Melillo et al., 2002; Rustad et al., 2001; Wang et al., 2016), reducing soil water content (Wan et al., 2002), and shifting species composition and community structure (Harte & Shaw, 1995; Saleska et al., 2002). However, few studies have explored the effects of warming on GPP, Reco, and the balance of ecosystem C gains and losses in climate vulnerable montane grassland ecosystems (Kiese et al., 2018), but with inconsistent results. For example, a warming experiment conducted in a meadow grassland in Tibet revealed that an increase of GPP but not Reco led to a large increase of NEE, that is, of the ecosystem C sink (Chen et al., 2017). In contrast, a plant-soil translocation experiment along an elevation gradient in northern Arizona showed that warming generally stimulated both GPP and Reco, but had variable effects on NEE (Wu et al., 2011). These

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partly contradicting results highlight the need to reveal the underlying mechanisms driving on variation in the response of ecosystem C fluxes and C balance to warming in these and other sites.

Changes in precipitation can further impact ecosystem C fluxes by affecting soil moisture and plant-available water as well as the abundance and activity of soil microbes (Welzin et al., 2003). Increased precipitation and soil moisture were reported to increase both photosynthesis and decomposition (Liu et al., 2009; Risch & Frank, 2007), while plant and soil microbial activities can decrease under drought. For instance, increased precipitation significantly stimulated GPP, Reco, and NEE in a semi-arid steppe in Inner Mongolia, China (Niu et al., 2008) as well as for the driest grasslands along an elevation gradient in northern Arizona, USA, while in the latter study decreased precipitation showed no effects (Wu et al., 2011). Thus, interactive effects between changes in precipitation and warming are very common, with complex effects on ecosystem C processes and budgets (Yue et al., 2017). For example, decreased precipitation can strengthen warming-associated drying (Samaniego et al., 2018), which would make the response of ecosystem C fluxes to increased temperature more complex and difficult to predict (Lu et al., 2013). However, there is an evidence from past syntheses suggesting that interactions tend to be ameliorating or dampening rather than amplifying (Dieleman et al., 2012; Leuzinger et al., 2011).

Agricultural management practices could make the responses of ecosystem C fluxes to multiple climate change forces even more complex. Ecosystem C fluxes are closely linked to vegetation dynamics, which highly depend on seasonality and management practices such as cutting or fertilizer applications (Schmitt et al., 2010). For instance, cutting can substantially interfere grassland C cycling by (a) altering microclimate and the availability of light, water, and various nutrients; (b) by changing photosynthetic activity and stimulating compensatory growth (Anten & Ackerly, 2001); and (c) by changing Reco through altering C allocation patterns between roots and shoots (Schmitt et al., 2013). In addition, manure application can stimulate ecosystem C fluxes by increasing the N availability for both plant growth and microbial activity, while at the same time also increasing ecosystem C stocks (Eichorst et al., 2016). However, to the best of our knowledge, no study so far has explored the role of agricultural management intensity like the difference in cutting and fertilization frequency on ecosystem C fluxes and C balance under climate warming in montane grassland ecosystems. This significant knowledge gap has impeded an in depth understanding of montane grassland carbon fluxes and budgets and the role of grassland management practices under climate change.

Measurements of C fluxes in grassland warming manipulation experiments are mainly based on dark (Reco) and transparent (NEE) chamber methods. Such measurements are commonly conducted on a rather low frequency, that is, mostly monthly and simply linearly interpolated to annual fluxes (Jiang et al., 2012; Niu et al., 2013; Wu et al., 2011; Xu et al., 2016). This approach likely underrepresents substantial variation in temperature, soil moisture, and photosynthetic active radiation (PAR), that all affect GPP and Reco, and can lead to large uncertainties in estimation of annual ecosystem C fluxes. Measurement informed modeling approaches estimating C fluxes in higher time resolution (Hoffmann et al., 2015) could better incorporate variations in these environmental drivers, but this approach has been rarely used in warming manipulation experiments (Wang et al., 2019).

In this study, we conducted a large plant-soil mesocosm (surface area 1 m², depth 1.4 m) translocation experiment in a montane grassland ecosystem, along an elevation gradient in the pre-alpine Ammer catchment, Southern Germany. The aims of this study were (a) to evaluate the single and interactive effects of rising temperature combined with slightly altered precipitation and agricultural management intensity on ecosystem C fluxes (GPP, Reco, and NEE) and net ecosystem carbon budget (NECB); (b) to establish empirical models to predict GPP, Reco, and NEE from continuous time series of environmental drivers; and (c) to use these models to assess annual C fluxes and C balance (NEE, NECB) response to treatments. This is of uppermost importance since intensifying grassland management as consequence of improved growth conditions (Schlingmann et al., 2020) with climate change is a likely scenario in pre-alpine regions.

2. Material and Methods

2.1. Field Sites and Experimental Setup

The CO₂ flux measurements were carried out at two grassland sites differing in elevation, and thus, climatic conditions; that is, Fendt (DE-Fen: 47.83°N, 11.06°E, 595 m a.s.l.), and Graswang (DE-Gwg: 47.57°N, 11.03°E,

Table 1
Mean Physical and Chemical Soil Characteristics

| Depths (cm) | Clay (%) | Silt (%) | Sand (%) | Organic C (g/100 g) | Total N (g/100 g) | C/N | pH | Bulk density (g/cm ³) |
|-------------|-------------------------|------------|------------|---------------------|-------------------|------------|-----------|-----------------------------------|
| 0–10 | 51.7 ± 2.5 ^a | 39.3 ± 0.9 | 9.0 ± 1.8 | 6.4 ± 0.6 | 0.7 ± 0.1 | 8.8 ± 0.1 | 6.4 ± 0.2 | 0.8 ± 0.0 |
| 10–30 | 51.0 ± 2.5 | 39.3 ± 0.7 | 9.3 ± 2.0 | 1.9 ± 0.1 | 0.2 ± 0.0 | 8.9 ± 0.2 | 6.8 ± 0.2 | 1.2 ± 0.0 |
| 30–50 | 50.7 ± 2.0 | 42.4 ± 0.9 | 6.1 ± 1.6 | 1.0 ± 0.1 | 0.1 ± 0.0 | 9.7 ± 0.4 | 6.9 ± 0.2 | 1.3 ± 0.0 |
| 50–120 | 43.3 ± 1.7 | 37.4 ± 0.8 | 19.3 ± 2.2 | 0.7 ± 0.2 | 0.1 ± 0.0 | 10.5 ± 0.3 | 7.2 ± 0.2 | 1.0 ± 0.1 |

^aMean ± SD, $n = 12$.

864 m a.s.l.) located in the TERENO pre-alpine observatory in southern Germany (Kiese et al., 2018). The mean annual (2011–2018) precipitation (MAP) at Fendt and Graswang is 961 and 1,284 mm, respectively, and mean annual temperatures (MATs) are 9.2°C and 7.1°C.

In 2011, a total of 12 large intact grassland soil monoliths (area 1 m², depth 1.4 m) were excavated from three replicated fields, representing grassland soil and management conditions at the Graswang elevation level of about 900 m.a.s.l., and transferred into closed-bottom stainless steel cylinders, that function as lysimeters. Six of these lysimeters (two from each of the three fields) remained in Graswang as controls (termed E860m), while the other six were translocated to Fendt (E860_600m), that is, a site with ~2°C higher mean temperatures, and ~25% lower mean annual rainfall. Hydrology within the lysimeters was controlled by actively adjusting the lower boundary condition (i.e., formation of seepage) to match soil moisture conditions as observed in the same depth at an adjacent grassland site. This was done based on reference water tension measurements ($N = 3$) at the same depth (140 cm) in the undisturbed soil close to the lysimeter facility. For further details see Kiese et al. (2018). At each site, half of the lysimeters ($n = 3$) received either intensive (4–5 manure applications and cutting events during the growing season) or extensive (1–2 manure applications and cutting events during the growing season) management, following local farmer's practices in the study region, as detailed below.

2.2. Soil and Plant Characteristics

The soil at the Graswang site is classified as fluvic calceric Cambisol. The top 10 cm of soil has a high (51.7 ± 2.5%) clay content, pH of 6.4, and bulk density of 0.8 g/cm³. The soil is rich in organic C (6.4%) and total N (0.7%). For further soil characteristics see Table 1.

The grassland vegetation consists of grasses and herbs with minor amounts of clover (<10%) (*Trifolium repens*). The communities are dominated by *Festuca pratensis*, *Poa pratensis*, *Prunella vulgaris*, *Plantago lanceolata*, *Knautia arvensis*, and *Pimpinella major*.

At both sites, air temperature (HMP45, Vaisala), and PAR (SKP215, Skye Instruments) were continuously measured at a nearby (<500 m distance from lysimeter station) climate station. Soil temperature (SIS, METTER Group) and soil moisture (time domain reflectometer CS610, Campbell Scientific) were continuously recorded at 10 cm soil depth within each lysimeter. In addition, soil moisture (0–5 cm; ThetaProbe type ML2x), soil temperature (5 cm; GTH 601 Digital thermometer), and the height of grassland vegetation were measured manually at the time of each CO₂ flux measurement.

2.3. CO₂ Flux Measurements

At both sites, the C flux measurements were carried out over 17 months from August 2014 to December 2015 every 2–3 weeks. On each measurement date, C flux measurements were taken over about 5 min period every 2 hr between 08:00 to 17:00 under prevailing light and temperature conditions. In the growing season 2015, these regular measurements were expanded by monthly measurements covering the period from sunrise (~06:00) to sunset (~20:00) under clear sky conditions.

NEE was measured with a transparent chamber (1 m² area, 0.7 m height) fully covering the lysimeter surface, attached to an infrared gas analyzer (IRGA: Licor-840A, Lincoln, NE, USA). The transparent chamber was built of Plexiglas with a transparency for PAR of 90%. Homogenous ventilation of chamber air was achieved by a fan mounted inside the chamber at the top. To limit temperature increases during chamber closure, cooler packs were mounted at the chamber (north direction). After the measurement of NEE, the chamber was removed, vented for several minutes, and then put back on the lysimeter, and covered with an opaque plastic sheet to allow for measurements of Reco.

Negative NEE values represent net ecosystem C uptake, and positive values represent net ecosystem C release. Concentrations of CO₂ within the chamber, as well as PAR (PQS 1 PAR Quantum sensor) and air temperature (PT100 temperature sensor) in and outside the chamber were recorded in 10-s-time intervals with a HOBO weather station data logger (Onset Computer, Bourne, MA, USA). Flux rates of NEE and Reco were calculated based on the linear increase of chamber headspace CO₂ concentration over 2 min and corrected by air temperature and pressure (Chojnicki et al., 2010). While Reco and NEE were directly measured, sub-daily GPP was calculated from Reco minus NEE. Sub-daily GPP fluxes were aggregated to daily GPP, however for daily NEE and Reco we considered also nighttime Reco. Nighttime Reco was estimated in 2-hr increments by linear interpolation of the last Reco measurement of the day (sunset situation) and the first measurement of the next day (sunrise situation) accounting for linear decrease of temperature during night time. Daily Reco was then calculated from the sum of the fluxes of day and nighttime Reco.

It should be noted that due to the Kok-effect, light enhanced dark respiration and post illumination bursts opaque chamber-based measurements of respiration are likely differing from real light conditions (Atkin et al., 2000; Heskell et al., 2013; Wohlfahrt et al., 2005). Modeled day-time NEE is not affected by this uncertainty since any over-/underestimation of Reco will be compensated by an over-/underestimation of GPP. However, using respiration values generated during the day will likely lead to overestimation of night time respiration and thus an underestimation of the C storage of the system. Considering interpolated night time respiration data for Reco model developments and short chamber closure times applied in this study are likely reducing this uncertainty.

2.4. Empirical Models for Annual Fluxes of GPP and Reco

For assessing annual grassland C fluxes based on higher temporal resolution, we developed empirical models for GPP and Reco using all individual flux measurements by considering the main environmental drivers, that is, PAR and grass height for GPP and soil moisture and temperature for Reco which greatly affect these ecosystem C fluxes. Grass height was introduced into the empirical GPP model (Ruimy et al., 1995):

$$GPP = \frac{\alpha \times PAR \times Height \times GPP_{max}}{\alpha \times PAR \times Height + GPP_{max}} \quad (1)$$

where GPP is the gross primary production (μmol/m²/s), PAR is the measured photon flux density of the PAR (μmol/m²/s), height is the grass height (cm), α is the initial slope of the regression curve, and GPP_{max} is the limit of production rate when PAR (in μmol/m²/s) approaches to light saturation conditions.

Reco is primarily driven by temperature using an exponential function (Lloyd & Taylor, 1994) with an additional effect of soil moisture following the empirical model introduced by Reichstein et al. (2003):

$$Reco = R_{10} \times \exp \left[(B * W_{-10} + C) \times \left(\frac{1}{T_{ref} - T_0} - \frac{1}{T_i - T_0} \right) \right] \quad (2)$$

where Reco is ecosystem respiration (μmol/m²/s), R₁₀ is respiration rate (μmol/m²/s) at the reference temperature of 10°C, W₋₁₀ is the measured volumetric soil moisture at 10 cm depth, and B and C are the parameters of the linear function. T_{ref} is reference temperature of 10°C (283.15 K), T₀ is the starting temperature constant (227.13 K), and T_i is the mean temperature (K).

We constructed empirical models to estimate GPP and Reco for each lysimeter for 2014 and 2015, by fitting the parameters α and GPP_{max} from Equation 1 and parameters R₁₀, B, and C from Equation 2 for four different model groups, that is, intensive, extensive management at control and climate change conditions (Table S1 in Supporting Information S1). Models were developed for growing and nongrowing season with

Reco models using soil temperature (5 cm) for nongrowing season and air temperature for growing season. Model performance measures are shown in Figures S1 and S2 in Supporting Information S1.

Based on continuous data on air and soil temperature (5 cm), soil moisture (10 cm soil depth), PAR, as well as grass height, Reco, and GPP were modeled for the entire measurement period at 30-min time intervals and aggregated to daily values. Daily NEE was derived from daily fluxes of Reco subtracted from daily GPP and annual values of all C fluxes were calculated from the cumulative daily simulated values.

2.5. Gap Filling of Data

Daily vegetation height was derived from linear interpolation of weekly/bi-weekly measured data. Continuous soil temperature data in 5 cm was generated by correlating climate station air temperature data with soil temperature data manually recorded at 5 cm during CO₂ measurements, which resulted overall very good agreement between measured and correlated values ($m = 0.99$, $r^2 = 0.99$, RMSE = 1.1). For air temperature, PAR and soil moisture interpolation was used to fill gaps that were less than 2 hr. For larger gaps of PAR, the data from a nearby grassland site (i.e., Rottenbuch, ~10 km; Kiese et al., 2018) were used. For larger gaps (several days) of soil moisture, gap filling was achieved by correlations of data between lysimeters of the same treatment. Overall, less than 7.4% of data needed to be gap-filled.

2.6. Biomass Inventories, Manure Management, and NECB

For both intensive and extensive treatments, aboveground biomass was manually cut at 5 cm above ground. After cutting, cattle slurry was applied to each lysimeter (4–5 and 1–2 times per growing season at intensive and extensive lysimeters, respectively). Harvested biomass was weighed before (fresh weight) and after drying at 60°C for 48 hr (dry weight), ground and sent to be analyzed for C (Lab Dr. Janssen GmbH, Giller-sheim, Germany).

Aboveground net primary production (ANPP) was calculated from respective biomass and C concentration data. Manure samples were analyzed for C contents at a commercial lab of Raiffeisen (Ormont, Germany). With an application volume of 1.8 m³ ha⁻¹, 1.68 and 1.76 t C ha⁻¹ yr⁻¹ manure C was added into intensive lysimeters and 0.21 and 0.47 t C ha⁻¹ yr⁻¹ into extensive lysimeters in 2014 and 2015, respectively.

As quantifying SOC storage changes over the investigation period of only 2 years is challenging and due to spatial variability associated with high uncertainty, we used the NECB approach for estimating full grass-land C balances. NECB can be calculated by the following equation (Smith et al., 2010):

$$\text{NECB} = \text{NEE} - \text{Manure C} + \text{Harvest removal C} \quad (3)$$

where NEE is the net ecosystem exchange while Manure C and Harvest removal represent C input and export via manure application and grass cutting, respectively. Note, as for NEE and NECB, positive values represent a net C loss from the ecosystem. Since DOC losses are only a marginal component (<50 kg C ha⁻¹) of the grassland C balances (Fu et al., 2019), we did not include them into the calculation scheme of NECB.

2.7. Statistical Analyses

Independent-samples *T* tests were used to assess the differences of seasonal GPP, Reco, and NEE derived from the measurements (Figure 2). To check the interactive effects between climate change and manage-ments on C fluxes, two-way repeated measures ANOVA analysis was used for GPP, Reco, and NEE based on cumulative fluxes data from growing season and nongrowing season ($N = 6$) via IBM SPSS Statistics 21.0 (IBM, Inc., USA). For ANPP and NECB, a normal two-way ANOVA was used based on annual data ($N = 3$) (Table 3). Empirical models for GPP and Reco were developed via R (version 3.3.3; R Core Team, 2017).

3. Results

3.1. Weather Conditions

During the observation period (2014–2015), the MAT was 7.5 and 7.0°C at the control (Graswang) site, which was 1.9 and 2.3°C lower than that at the translocated site (Fendt; from now on referenced as the

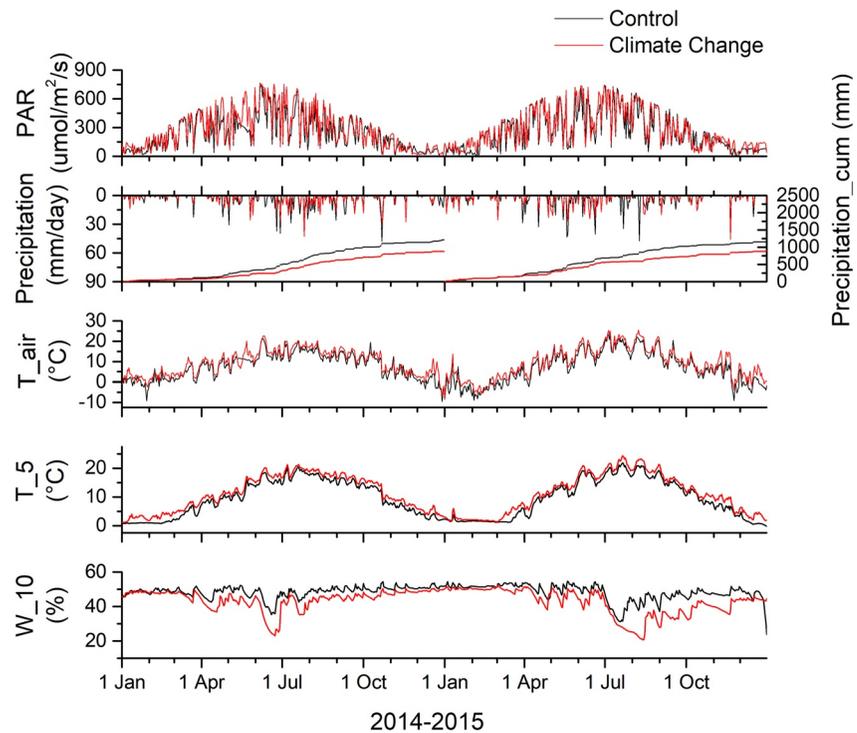


Figure 1. Daily mean photosynthetically active radiation (PAR), daily (precipitation) and cumulative precipitation (precipitation_cum), mean daily air temperature (T_{air}), mean daily soil temperature at 5 cm (T₅), and mean daily soil moisture at 10 cm (W₁₀) at the control (black line) and climate change (red line) sites. Note T₅ and W₁₀ represent lysimeters under intensive management.

climate change site). The MAP at the control site was 1,216 and 1,154 mm and thus 30.4% and 38.3% higher than at the climate change site (Table S2 in Supporting Information S1). The control site also received an average PAR of 251.6 $\mu\text{mol}/\text{m}^2/\text{s}$, which was 13.0% less than average PAR at the climate change site (284.3 $\mu\text{mol}/\text{m}^2/\text{s}$) (Figure 1). The mean (2011–2018) growing season precipitation is 866 and 663 mm at the control and the climate change site, respectively. Growing season precipitation was in the range of long term means except for the climate change site in 2015 with comparable dry (growing season precipitation of 548 mm, -17%) conditions. Mean growing season temperature was 12.1 and 13.9°C in 2014 and 12.9 and 14.8°C at the control and at the climate change site, respectively (Table S2 in Supporting Information S1).

3.2. Seasonal Patterns of Measured C Fluxes

Generally, GPP, and Reco showed similar temporal patterns among different treatments during the experimental observation period (Figure 2). GPP and Reco were usually low at the beginning of the growing season and then increased steadily following the increase in temperature, and reached the seasonal peak in May (GPP) and July (Reco). Thereafter, the fluxes gradually decreased until the end of the year (2015). In contrast, temporal development of NEE across the four treatments were less pronounced, but negative values indicating a C sink were most observed in spring and autumn.

Climate change resulted in significantly lower GPP in June and August regardless of management intensity in 2015 and higher GPP in the early (April) and late growing season (September to October) in both years. For intensive management, climate change enhanced Reco during the whole observation period, except for August. This pattern was the same for extensive management, however with generally lower differences of Reco between the climate change treatment and the control. During May to October climate change clearly increased net C losses (more positive values of NEE) compared to the control and this effect was more evident under intensive than extensive management. Considering all data repeated measures two-way ANOVA

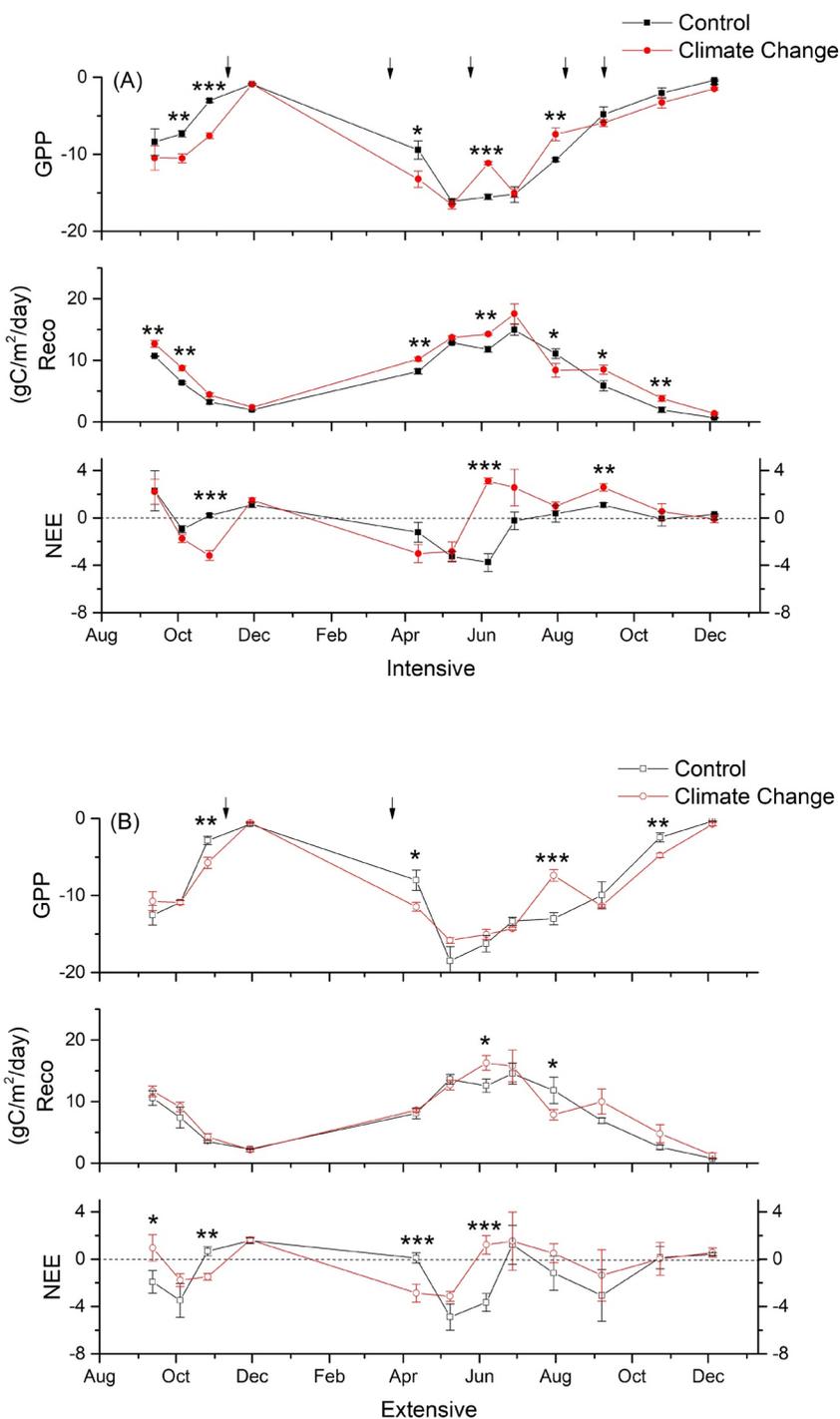


Figure 2. Mean daily gross primary production (GPP), ecosystem respiration (Reco), and net ecosystem exchange (NEE) (\pm SD) from September 2014 to December 2015 under control (black) and climate change (red) conditions at intensive (a) and extensive (b) lysimeters as calculated from subdaily measurements. Arrows represent manure application events. * $0.01 < P < 0.05$, ** $0.001 < P < 0.01$, *** $P < 0.001$.

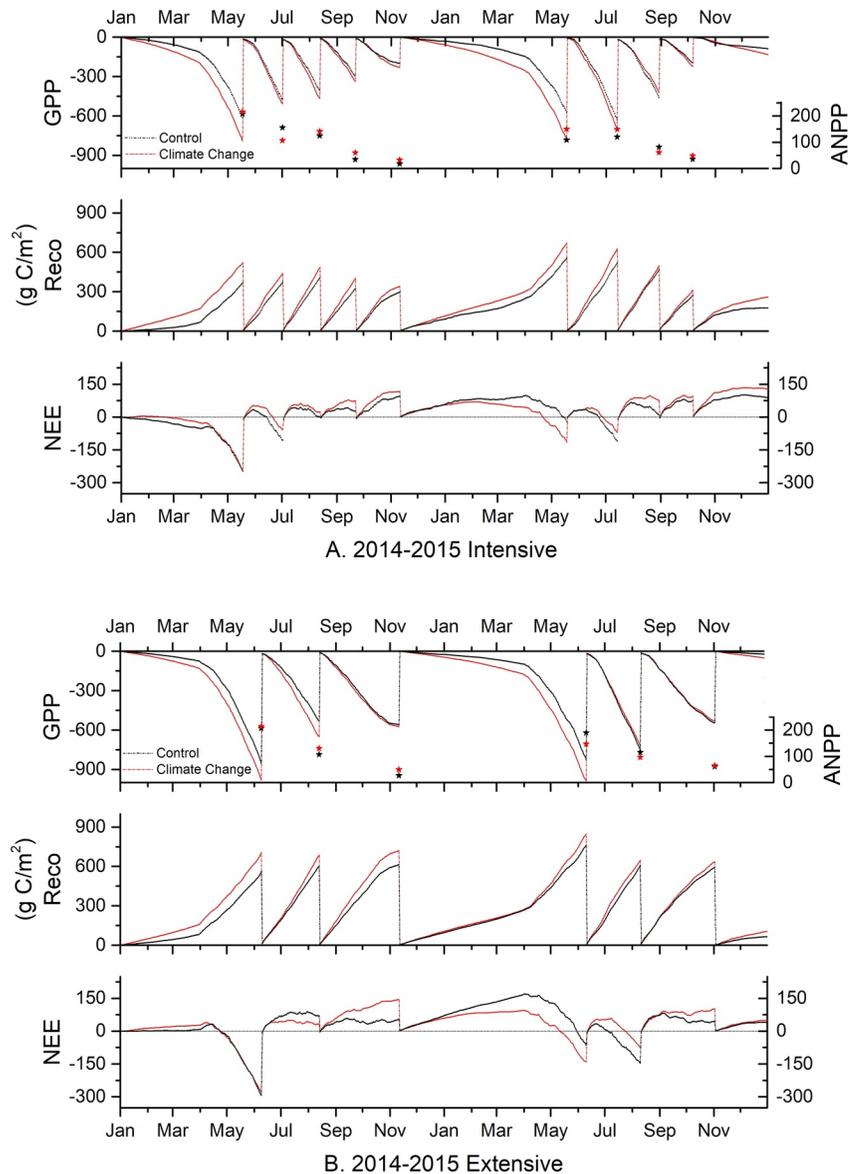


Figure 3. Cumulative (per cutting event) gross primary production (GPP), ecosystem respiration (Reco), and net ecosystem exchange (NEE) in 2014 and 2015 based on modeling under control (black) and climate change (red) treatments at intensive (a) and extensive (b) lysimeters. Stars represent measured above-ground net primary production (ANPP) at each cutting event.

revealed that only for Reco a significant ($p < 0.05$) control of climate while management and interactions did not significantly impact grassland C fluxes.

3.3. Empirical Model Based Temporal Dynamics and Annual Budgets of Grassland C Fluxes

Irrespective of the treatment, cumulative GPP and ANPP were highest at the first cutting event and decreased thereafter, while Reco showed less differences across cutting events with a trend of highest cumulative fluxes for the second and third cutting event (Figure 3). Due to the different temporal patterns of GPP and Reco, cumulative NEE was most negative at first and second cutting events, while both intensive and extensive grassland lysimeters turned from a C sink into a C source at later cutting events. Climate change stimulated Reco throughout the year for both intensive and extensive treatments, while this effect was less obvious for GPP and NEE.

Table 2
Annual (2014, 2015) Mean \pm SD Fluxes of Gross Primary Production (GPP), Ecosystem Respiration (Reco), Net Ecosystem Exchange (NEE), Aboveground Net Primary Production (ANPP), and Net Ecosystem Carbon Budget (NECB) in the Montane Grassland Ecosystem Under Different Climatic and Management Conditions

| C fluxes t C ha ⁻¹ yr ⁻¹ | Management | 2014 | | 2015 | | 2014–2015 average | |
|--|------------|-----------------|-----------------|-----------------|-----------------|-------------------|-----------------|
| | | Control | Climate change | Control | Climate change | Control | Climate change |
| GPP | IM | -19.6 \pm 0.3 | -23.1 \pm 0.6 | -18.4 \pm 0.1 | -21.3 \pm 0.2 | -19.0 \pm 0.7 | -22.2 \pm 1.1 |
| | EM | -19.7 \pm 0.9 | -22.5 \pm 0.9 | -21.2 \pm 0.7 | -22.5 \pm 0.8 | -20.4 \pm 1.1 | -22.5 \pm 0.8 |
| Reco | IM | 17.9 \pm 0.08 | 22.2 \pm 0.3 | 18.3 \pm 0.03 | 21.7 \pm 0.5 | 18.1 \pm 0.2 | 21.9 \pm 0.5 |
| | EM | 18.6 \pm 0.2 | 22.1 \pm 0.5 | 19.2 \pm 0.08 | 21.2 \pm 0.6 | 18.9 \pm 0.3 | 21.7 \pm 0.7 |
| NEE | IM | -1.7 \pm 0.3 | -0.9 \pm 0.8 | -0.1 \pm 0.1 | 0.4 \pm 0.7 | -0.9 \pm 0.9 | -0.2 \pm 1 |
| | EM | -1.0 \pm 1.0 | -0.4 \pm 1.4 | -2.0 \pm 0.8 | -1.2 \pm 1.2 | -1.5 \pm 0.9 | -0.8 \pm 1.3 |
| ANPP | IM | 5.4 \pm 0.1 | 5.6 \pm 0.6 | 3.5 \pm 0.1 | 4.1 \pm 0.1 | 4.4 \pm 1.1 | 4.8 \pm 0.9 |
| | EM | 3.4 \pm 0.5 | 3.9 \pm 0.6 | 3.7 \pm 0.2 | 3.1 \pm 0.1 | 3.5 \pm 0.4 | 3.5 \pm 0.6 |
| Manure | IM | 1.7 \pm 0.2 | 1.7 \pm 0.2 | 1.8 \pm 0.2 | 1.8 \pm 0.2 | 1.7 \pm 0.1 | 1.7 \pm 0.1 |
| | EM | 0.2 \pm 0.03 | 0.2 \pm 0.03 | 0.5 \pm 0.07 | 0.5 \pm 0.07 | 0.3 \pm 0.1 | 0.3 \pm 0.1 |
| NECB | IM | 2.0 \pm 0.1 | 3.0 \pm 0.5 | 1.6 \pm 0.07 | 2.7 \pm 0.7 | 1.8 \pm 0.2 | 2.9 \pm 0.6 |
| | EM | 2.2 \pm 0.5 | 3.3 \pm 0.9 | 1.2 \pm 0.6 | 1.4 \pm 1.2 | 1.7 \pm 0.7 | 2.3 \pm 1.4 |

Note. For NEE and NECB, positive values represent C loss, whereas negative positive values represent C gain. EM, extensive management; IM, intensive management.

On annual scale, our results show that climate change significantly increased GPP and Reco ($p < 0.01$) while there was no influence on NEE, even though climate change tended to decrease ecosystem C sink regardless of management practices (Tables 2 and 3). Generally, grassland C fluxes were not significantly affected by management and its interaction with climate (Table 3). The 2-year averaged annual GPP was -19.0 and -20.4 t C ha⁻¹ yr⁻¹ for IM and EM of under control, which was increased by 17% and 10% under climate change, respectively. Similarly, average annual Reco significantly increased by 20.1% and 15% from 18.1 and 18.9 t C ha⁻¹ yr⁻¹ for IM and EM, respectively. Overall, grasslands were a carbon sink for both intensive (-0.9 t C ha⁻¹ yr⁻¹) and extensive (-1.5 t C ha⁻¹ yr⁻¹) management under current and climate change conditions; however the latter reduced by 0.7 t C ha⁻¹ yr⁻¹ in both management treatments (Table 2). Considering different years, drier conditions in 2015 resulted in lower GPP and ANPP in the intensive treatment which changed the grassland ecosystem from a carbon sink into a source while ANPP, GPP, and NEE remained unchanged in the extensive treatment (Table 2).

Including additional C inputs via slurry and export via harvest (i.e., ANPP), the 2-year mean annual NECB varied from 1.7 to 2.9 t C ha⁻¹ yr⁻¹ across all treatments. This indicates that the grasslands were losing carbon, regardless of management or climate conditions. While differences across management treatments were not statistically different, climate change significantly ($p < 0.05$) aggravated the negative ecosystem C balance (Tables 2 and 3).

4. Discussion

4.1. Effects of Climate Change and Management Intensity on Ecosystem C Fluxes

Our results show that across the 2-year investigation period, climate change (warming and decreased precipitation) significantly increased the ecosystem C exchange through GPP and Reco under both intensive and extensive management (Tables 2 and 3). Warming can increase soil respiration by promoting the activity of soil microbes (Zhang et al., 2015), consequently favoring soil N transformation and thus increasing the nitrogen availability for plant growth. This was demonstrated by Wang et al. (2016) which found that climate change significantly enhanced soil gross N mineralization in the same grassland soils. The NEE values from our control treatments (-0.2 to -1.5 t C ha⁻¹ yr⁻¹) compare well to the range of -0.7 to -1.0 t C

Table 3
Statistical Measures for Climate (C) and Management Effects (M) and Interaction (C × M) on Grassland C Fluxes in the Monate Grassland Ecosystems for Single Years 2014 and 2015 and for the Whole Investigation Period

| C fluxes | Factors | 2014 | 2015 | 2014–2015 |
|----------|---------|-------|-------|-----------|
| GPP | C | * | ** | ** |
| | M | ** | 0.38 | 0.86 |
| | C × M | 0.093 | 0.074 | 0.078 |
| Reco | C | ** | ** | ** |
| | M | 0.11 | 0.21 | 0.17 |
| | C × M | 0.053 | 0.061 | 0.057 |
| NEE | C | 0.16 | 0.42 | 0.27 |
| | M | 0.58 | 0.31 | 0.52 |
| | C × M | 0.57 | 0.98 | 0.77 |
| ANPP | C | 0.27 | 0.78 | 0.33 |
| | M | *** | *** | *** |
| | C × M | 0.56 | *** | 0.26 |
| NECB | C | * | 0.18 | * |
| | M | 0.41 | 0.085 | 0.47 |
| | C × M | 0.89 | 0.29 | 0.57 |

Note. ANPP, aboveground net primary production; GPP, gross primary production; NECB, net ecosystem carbon budget; NEE, net ecosystem exchange; Reco, ecosystem respiration. * $0.01 < P < 0.05$, ** $0.001 < P < 0.01$, *** $P < 0.001$.

$\text{ha}^{-1} \text{yr}^{-1}$ reported for a temperate mountain grassland in Austria (Wohlfahrt et al., 2008) and -0.6 – $3.4 \text{ t C ha}^{-1} \text{yr}^{-1}$ reported for grasslands in our study region (Zeeman et al., 2017), which were both measured by eddy covariance technique. Compared to the control, climate change attended to decrease the ecosystem carbon sink strength (NEE), particularly at the drier year 2015 (Tables 2 and 3). Overall, this can be explained by higher temperature but lower moisture sensitivity of Reco as compared to GPP (Wang et al., 2019), which was more evident under intensive than extensive management. Plant stress in the drier 2015 as compared to 2014 is further supported by significant yield (ANPP) reductions mainly under intensive grassland management (Table 2), indicating a higher resistance of extensively used grasslands to drought. Yield reductions (2015 vs. 2014) of 35% compare well with numbers reported for a four-cut grassland system in N-Germany (Emadodin et al., 2021). We found that GPP between intensive and extensive treatments was not statistically different but ANPP (Table 3) was significantly lower in extensive treatments. This could indicate a higher belowground C allocation under extensive management likely supporting better adaptation to drought. This finding is in line with the significantly higher root biomass reported for extensive than intensive managed paired temperate grasslands systems (de Vries et al., 2012). Overall, our results indicate that varying the timing of cutting events in relation to temporal developments of droughts could be a measure in avoiding negative effects on, or even improving yields and the net carbon uptake of grassland ecosystems. This is of uppermost importance since in the European Alps frequency and intensities of summer droughts are likely increasing in the future (Gobiet et al., 2014; Samaniego et al., 2018).

4.2. Are Montane Grasslands Net Sources for CO_2 ?

The NECB is a measure to more comprehensively estimate total ecosystem C balances since it further considers C additions and removals compared to NEE (Smith et al., 2010). While NEE showed that grassland ecosystems were a C sink, rather unexpected, NECB calculations revealed significant ecosystem C losses of 1.7 and 2.9 $\text{t C ha}^{-1} \text{yr}^{-1}$ for both control and climate change treatments, irrespective of management intensity. This is mainly due to the much higher plant C removal than C applied with slurry. The observed decrease in SOC is further supported by the negative soil N balance (-239 to $-75 \text{ kg N ha}^{-1} \text{yr}^{-1}$) reported by Zistl-Schlinmann et al. (2020) in the same soils, attributed to the substantial mineralization of soil organic matter. Calculated soil C losses based on the C/N ratio of the topsoil agree well with the observed negative NECB of this study (Table 1). Similar C losses were also reported for other non-grazing montane grasslands across Europe. For example, Wohlfahrt et al. (2008) reported a NECB of 0.2–1.1 $\text{t C ha}^{-1} \text{yr}^{-1}$ from a 5-year field experiment in a temperate mountain grassland in Austria. Ammann et al. (2007) found that a temperate grassland in Oensingen (Switzerland) under extensive management had C losses of 0.3–1.5 $\text{t C ha}^{-1} \text{yr}^{-1}$. However, these results are the opposite of findings reported for grazing grassland systems across Europe. For example, Soussana et al. (2007) reported that grazed montane grasslands in Laqueuille and Malga (France) act as net C sinks with NECB ranging between -0.5 and $-4.6 \text{ t C ha}^{-1} \text{yr}^{-1}$, irrespective of the grazing intensity. Similarly, Felber et al. (2016) found a NECB of $-0.2 \text{ t C ha}^{-1} \text{yr}^{-1}$ for grazed montane grassland in Switzerland. The main difference between grazed and cut grassland systems is likely the high differences of harvest C removal and the much lower C input via slurry application (Table 2). Poyda et al. (2021) found that a comparably low fraction (17%) of NPP was allocated to roots in a temperate grassland with intensive management, which may be a further reason for the net soil C source ($0.3 \text{ t C ha}^{-1} \text{yr}^{-1}$) of our grassland, along with the high plant C removal. In contrast, for light grazing, the direct return of animal excreta and the likely higher plant litter production due to higher standing biomass may be beneficial to maintain grassland soil C stocks (Abdalla et al., 2018). Ammann et al. (2007) reported that, under current climate conditions, the montane

grassland was changed from net C source (NECB: 0.2 to 1.13 t C ha⁻¹ yr⁻¹) into net C sink (NECB: -0.3 to -2.7 t C ha⁻¹ yr⁻¹), if the management practice was shifted from extensive to intensive management with high manure-C application. However, in our study, this effect was not evident since NECB was not statistically different between the two management treatments. Our results further demonstrate that, compared to control, climate change significantly increased (Table 3) grassland C losses of 1.1 and 0.6 t C ha⁻¹ yr⁻¹ for intensive and extensive management, respectively. Similarly, through a 4-year climate manipulation experiment in a subalpine grassland ecosystem in Switzerland, Puissant et al. (2017) found that climate warming and decreased precipitation significantly decreased the top SOC content by up to 30%. In view of the high soil C depletion particularly under climate change, the findings of this study call for adaptation of montane grassland management. Replacing one application of slurry (18–20 m³, 5%–7% dry matter content) by solid manure (10–15 t ha⁻¹; 30% dry matter content) would result in a higher C return of up to 1.5 t C ha⁻¹. Moreover, the effect of higher remaining standing biomass in autumn (unpublished data of last cut in October/November) would contribute to about 0.5 t C ha⁻¹ yr⁻¹. Considering that extensive management is currently the dominating grassland management at the elevation level of 900 m.a.s.l., our study shows that both climate change and intensive grassland management could negatively impact grassland C balances as indicated by less negative NEE and more positive NECB (Table 2).

Our study shows that climate change significantly increased GPP and Reco by 10%–20.1%, depending on management intensity, but we found no significant interaction between climate and management intensity. Due to the higher temperature sensitivity of Reco, climate change tended to decrease NEE. Based on ecosystem C balance calculations (NECB), we found that managed grasslands are already a source of C under current climate conditions, which is further aggravated by climate change. Overall, this worrying result highlights the necessity of optimizing management practices to sustain grassland soil C stocks and productivity under changing environmental conditions.

Data Availability Statement

All data of this manuscript are available from the figshare repository: https://figshare.com/articles/dataset/Data_of_publication_Wang_et_al_under_review_GBC/14566215.

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