Response of water fluxes and biomass production to climate change in permanent grassland soil ecosystems

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Abstract

Effects of climate change on the ecosystem productivity and water fluxes have been studied in various types of experiment. However, it is still largely unknown whether and how the experimental approach itself affects the results of such studies. We employed two contrasting experimental approaches using high precision weighable monolithically lysimeters over a period of four years to identify and compare the responses of water fluxes and aboveground biomass to climate change in permanent grassland. The first, manipulative approach is based on controlled increases of atmospheric CO_2 concentration and surface temperature. The second, observational approach uses data from a space-for-time substitution along a gradient of climatic conditions. The Budyko framework was used to identify if the soil ecosystem is energy-limited or water-limited.

Elevated temperature reduced the amount of non-rainfall water particularly during the growing season in both approaches. In energy-limited grassland ecosystems, elevated temperature increased the actual evapotranspiration and decreased aboveground biomass. As a consequence, elevated temperature led to decreasing seepage rates in energy-limited systems. Under water-limited conditions in dry periods, elevated temperature aggravated water stress and thus resulted in reduced actual evapotranspiration. The already small seepage rates of the drier soils remained almost unaffected under these conditions compared to soils under wetter conditions. Elevated atmospheric CO_2 reduced both actual evapotranspiration and aboveground biomass in the manipulative experiment and therefore led to a clear increase and change in seasonality of seepage. As expected, the aboveground biomass productivity and ecosystem efficiency indicators of the water-limited ecosystems were negatively correlated with an increase in aridity, while the trend was unclear for the energy-limited ecosystems.

In both experimental approaches, the responses of soil water fluxes and biomass production mainly depend on the ecosystems' status with respect to energy or water limitation. To thoroughly understand the ecosystem response to climate change and be able to identify tipping points, experiments need to embrace sufficiently extreme boundary conditions as well as explore responses to individual and multiple drivers such as temperature, CO_2 concentration and precipitation including non-rainfall water. In this regard, manipulative and observational climate change experiments complement one another and thus should be combined in the investigation of climate change effects on grassland.

1 Introduction

Current and future climate change is expected to alter air temperature, CO_2 concentration in the atmosphere as well as precipitation (P; Abbott et al., 2019; IPCC, 2018). Changes in these conditions will alter hydrological processes and affect the soil water availability, which is of critical importance for the agricultural sector in terms of plant development and food production (Thornton et al., 2014). Grassland represents one of the Earth's main biomes (Blair et al., 2014). Managed grassland areas are important for carrying capacity of livestock as well as for herbage and hay production for forage. Moreover, these areas are also important for several other ecosystem services beside food production like water supply and flow regulation, erosion control, climate mitigation, pollination, carbon storage as well as cultural services (Bengtsson et al., 2019). However, services are strongly dependent on weather and climate conditions and thus potentially highly vulnerable to climate change (Gobiet et al., 2014). Since the late 19th century, air temperatures in the Alpine region have risen about twice as much as the global or Northern Hemispheric average (Auer et al., 2007). These strongly changing climatic conditions, in particular the expected increase in frequency and magnitude of extreme events such as droughts and heavy rainfalls, potentially have adverse effects on the soil water balance and biomass production of grasslands, especially in mountainous regions. Depending on the regional climate change and its local impacts, altered P regimes and higher temperatures potentially will increase actual evapotranspiration (ET_a) and thus negatively affect the local ecosystem services related to water (Schirpke et al., 2017; Rahmati et al., 2020). In addition, a shift in the temperature regime will prolong the growing season, which might change the vegetation composition, water use efficiency (WUE) of grasslands, enable a more intensified use of grassland sites (more frequent mowing) and increase the biomass production (Eitzinger et al., 2009; Tello-García et al., 2020). But this might largely depend on the hydrological status of the ecosystem, which can be characterized by the Budyko framework as energy-limited or water-limited (Budyko and Miller, 1974). For regions that are currently disadvantaged because of the climatic and topographic conditions, it may be expected that in the future aboveground biomass (AGB) production will increase due to higher temperatures (Eitzinger et al., 2009). However, the combined effect of higher temperatures, causing increased ET_a and the expected decrease in summer P also suggests more frequent and more severe occurrences of droughts (e.g. 2018 European drought; Peters et al., 2020), which may lead to a lower water availability in the soil and thus adversely affect the AGB production of grassland as well as the quantity and quality of the drainage water (Herndl et al., 2019).

To contribute to the assessment of climate change impacts on mountain grassland, there is the general need to understand the individual and combined effects of changes in temperature and P with and without elevated atmospheric CO_2 concentrations on the water balance components (including non-rainfall water NRW; i.e. dew and fog) and the connected biomass production of mountain grasslands. The use of high precision weighable lysimeter allows quantifying the water balance components of ecosystems and determining their productivity, such as shown, for instance, by Groh et al. (2020). It may be expected that even for northern humid ecosystems the formation of NRW temporarily gains importance in the water budget during droughts (Groh et al., 2018) and that under such extreme conditions, heat and/or water stress can cause a decrease in the AGB production of grasslands (Fu et al., 2006). To explore how ecosystems will respond to changes in environmental conditions, key hydroclimatical and ecohydrological indicators such as the precipitation use efficiency (PUE; Wang et al., 2019), the WUE (Hatfield and Dold, 2019; Groh et al., 2020), and the runoff coefficient (Chen et al., 2007) have been proposed to assess the impact of changing climatic conditions on the ecosystems.

To identify the response of water fluxes and AGB production to climate change in permanent grassland soil ecosystems two major approaches have been proposed. Either manipulative experiments (using multifactorial drivers) or observational experiments on environmental gradients can serve to explore the relationship between changing climate factors and ecosystem responses (Hanson and Walker, 2020; Song et al., 2019; Kreyling and Beier, 2013; Knapp et al., 2018). According to Yuan et al. (2017), the main difference between these approaches is the issue of association versus causality. Observational approaches can identify a relationship between a set of randomly selected variables of a system under natural conditions, while manipulative approaches are more likely to identify and confirm the underlying mechanism based on measuring responses of the system by controlling certain variables. It is often assumed that manipulative or observational climate change experiments lead to similar results in the assessment of climate change impacts on e.g. the components of the water balance. However, a recent meta-analysis on climate change experiments showed that the impacts of climate change on the nutrient cycle differed among the tested approaches (Yuan et al., 2017). Knapp et al. (2018) compared the response of different grassland ecosystems on climate change from manipulative and observational climate change experiments. In particular, they found that both approaches achieved similar functional relationship between growing season precipitation (GSP) and AGB, when the GSP was within the range of historical observations. The predictions outside the range of historic events, however, led to non-linear relations in the AGB response to changes in GSP (Knapp et al., 2018). This clearly demonstrates the need to impose relatively extreme changes in the boundary conditions (e.g. P reduction) in climate change experiments in order to observe the non-linear response of the soil ecosystem (i.e. AGB) to changes in the climate regime (Knapp et al., 2018). We therefore hypothesize that the response of the grassland ecosystems on changing climatic conditions will differ among the two approaches, in particular, if the soil ecosystem changes from an energy-limited to a water-limited hydrological status.

The objective of the present study was to test this hypothesis by comparing the impact of climatic factors on (i) the water balance and (ii) the AGB production within and between the manipulative and observational approaches, and (iii) to identify the impact of altered climatic conditions on the functional relationships between water balance components, AGB, and hydroclimatical and ecohydrological indicators. Data are provided from two distinct climate change experiments, namely "Lysi-T-FACE" (Climate Impact Research on Grassland; Herndl et al., 2010; Herndl et al., 2011) and TERENO-SOILCan (TERrestrial ENnvironmental Observatories; Pütz et al., 2016). The Lysi-T-FACE experiment is denoted here as manipulative approach and the TERENO-SOILCan as observational approach. In both experiments, high precision weighing lysimeters were used to quantify the water balance components and the AGB of grassland ecosystem in mountainous regions.

2 Materials and Methods

2.1 Manipulative and observational approaches

The climate change experiment Lysi-T-FACE is an experimental concept that has been designed to enable warming grassland plots using an infrared heating system (Kimball et al., 2008), and enriching the CO_2 content of the air using a Mini-FACE system (T-FACE; Miglietta et al., 2001). This experimental set-up was implemented at an alpine grassland site in 2010 and 2011 (Herndl, 2011). The overall experimental design at this site is based on a surface response approach (Piepho et al., 2017) and includes factor combinations of two elevated temperatures and two elevated CO_2 concentrations at 24 grassland plots under open-field conditions. The Lysi-T-FACE approach at weighable lysimeters (Fank and Unold, 2007) is implemented at six of these plots. The proper functioning of the T-FACE performance has been repeatedly tested and is fully operated since May 2014 at the experimental site.

The observational approach for quantifying climate change impacts in the soil-plant system is implemented in the TERENO-SOILCan lysimeter network since 2010 / 2011 (Pütz et al., 2016; Pütz et al., 2018). Intact soil monoliths were transferred within and between TERENO observatories to expose them, apart from the observations at their original site, to other climatic conditions (space-for-time substitution; see details in Pütz et al., 2016; Groh et al., 2020). The concept of the space-for-time substitution means that soils were translocated in space instead of waiting at the same location for changes in climatic conditions in time. The change of the climate regime by the transfer of the lysimeters were abrupt, which implies that we are not able to detect gradual changes of the grassland ecosystem over time as suggested in standard space-for-time approach, but can account for unsuspected effects from the past (Groh et al., 2020).

2.2 Lysimeter set up

The study was conducted at three test sites (Table 1). The Lysi-T-FACE test site is located at the Agricultural Research Centre Raumberg-Gumpenstein (GS) in Austria. The experimental site is located at an altitude of 707 m a.s.l. within the Enns valley of the Austrian Alps. The mean air temperature at the site is 7.2 °C, mean annual P is 1000 mm; and the soil is a Cambisol. Thus, the site may be considered as representative of permanent grassland in the Alps (Schaumberger, 2011). The grasses *Arrenatherum elatius* and *Festuca pratensis* and the leguminous species *Lotus corniculatus* and *Trifolium pratense* dominate the grassland established at the Lysi-T-FACE site. The grassland was mowed three times per year (see supplement Table S 1), each followed by mineral fertilization (Herndl et al., 2010), and the average length of the growing season over the observation period from 2015 to 2018 was 197 days (more details on the method see chapter 2.3 and Table S 2).

At GS six lysimeters were installed; one lysimeter was operated under ambient conditions (C0T0), two under a constant warming of 3 °C of grassland (C0T2) relative to the ambient surface temperature, two under a constant elevated CO_2 concentration (300 ppm) relative to the ambient atmospheric CO_2 concentration (C2T0), and one with a combination of elevated temperature and elevated CO_2 (C2T2). The used abbreviations C and T within the treatments stand for CO_2 and temperature and the numbers 0 for ambient and 2 for specific level of the elevated conditions. A nearby weather station was used to obtain meteorological observations of reference P (tipping-bucket method; Young), air temperature, air humidity, solar radiation, net radiation, and wind speed at a height of 2 m above ground. Data from the weather station was used to calculate grass-reference evapotranspiration (ET_0) according to Penman-Monteith (Allen et al., 2006).

The two other test sites are part of the TERENO-SOILCan lysimeter network, located in the Northwest of Germany, in Rollesbroich (RO) and Selhausen (SE). Both sites have a humid temperate climate with an average annual air temperature of 8 °C and 10 °C and an average annual P of 1150 mm and 720 mm for Rollesbroich and Selhausen, respectively. The plant community consists mainly of *Lolium perenne* and *Trifolium repens*. The grassland lysimeters at both sites were subject to management (cutting and fertilizer) according to the local agricultural management of the surrounding field at Rollesbroich. This includes three to four cuts per growing season (supplement Table S1) and three to four times application of liquid manure or mineral fertilizer per year (Pütz et al., 2016). Mean length of the growing season over the observation period was 208 and 243 days in RO and SE, respectively.

At RO (C0CL0, CL stands for climate) six lysimeters were installed to quantify soil water budget and AGB under ambient conditions (RO: C0CL0). At SE (C0CL2) three lysimeter were installed to quantify soil water fluxes and AGB under altered climatic conditions (SE: C0CL2, less precipitation, higher ET_0). A weather station (WXT510, Vaisala Oyj) was installed at both sites logging the same meteorological parameters as at GS. The reference P was measured with a weighing rain gauge (OTT Pluvio², OTT HydroMet GmbH) and a net radiation sensor (LP Net07, Delta OHM S.r.L.) was installed above one lysimeter at each site. In addition, vegetation height observations were obtained for calculating ET_0 with Penman-Monteith model (Allen et al., 2006).

Table 1: Overview of the three test sites with their different approaches at the location Gumpenstein (GS), Rollesbroich (RO), and Selhausen (SE). The experiments at GS comprise treatments that have ambient (C0T0), elevated air temperature (T) (C0T2), elevated concentration of CO_2 (C2T0), and combined elevated concentration of CO_2 and T (C2T2) conditions. In the observational space-for-time substitution

approach, site RO represents ambient atmospheric demand for evapotranspiration and ambient precipitation (C0CL0). The site SE represents elevated atmospheric demand for evapotranspiration and reduce amount of precipitation (C0CL2).

Site	Project	Approach	Treatment	Symbol
Gumpenstein (GS): 707 m.a.s.l	Lysi-T-FACE	Manipulative: Lysi-T-FACE	ambient +3.0 °C +300 ppm CO_2 +300 ppm CO_2 ; +3.0°C	C0T0 C0T2 C2T0 C2T2
Rollesbroich (RO): 511 m.a.s.l	TERENO-SOILCan	Observational: Space-for-time	Original	C0CL0
Selhausen (SE): 104 m.a.s.l	TERENO-SOILCan	Observational: Space-for-time	Translocated	C0CL2

2.3 Quantifying water balance components

Weighable high precision lysimeter systems provide measurements of the components of the soil water balance equation, P, NRW, ET_a, and the vertical net flux above the lysimeter bottom (NetQ). The NetQ component comprises water flow out (Q; seepage) and into the lysimeter at the bottom; note the latter represent upward flow by capillary rise. The change in soil water storage (ΔS), which affects water availability in the soil ecosystem, was calculated as:

$$\Delta S = P + NRW - ET_a - NetQ \qquad (1)$$

The water balance components P, NRW and ET_a were obtained at each site from the highly resolved (1-minute) and precise (resolution: 0.01 mm) lysimeter observations over a period of four consecutive years (2015-01-01 until 2018-12-31). NetQ was obtained at the same time interval from a weighable water tank (resolution: 0.001 mm).

Lysimeter mass changes are prone to external disturbances like management operations or wind. Thus, lysimeter data of mass changes have been processed by pre- and post-processing routine to avoid that external errors and noise affect the determination and separation of water fluxes across the land surface (P, NRW and ET_a). The procedure included in a first step a visual data quality check of the one-minute lysimeter data. In a second step, the Adaptive Window Adaptive Threshold filter (Peters et al., 2017) was applied, which has been shown to allow the quantification of small water fluxes like dew, water vapour adsorption or nighttime ET_a (Groh et al., 2019; Kohfahl et al., 2019). Water fluxes across the land surface and bottom boundary were aggregated to 10-min time intervals for detailed analysis of P, especially the identification of NRW (Groh et al., 2018), and ET_a. Gaps in the time series of measured P and ET_a were filled with observations from parallel lysimeter observations. In case of missing parallel lysimeter observations, gaps in the hourly time series were filled using linear regression between observed water fluxes and external observations or calculations (i.e. rain gauge and ET_0). Finally, all water balance components were aggregated on a daily time scale and were averaged over the number of available repetitions for each treatment. At GS the water balance components for the treatment C2T0 in 2017 and 2018 were taken only from one lysimeter due to technical problems.

The component NRW, which includes fog, dew and hoar frost formation, was determined by lysimeter mass increases between sunset and sunrise, when the corresponding rain gauge from the meteorological station did not detect P during the corresponding 10 minute time step (Groh et al., 2018). The treatment of the Lysi-T-FACE plots at GS, i.e. free air carbon enrichment and infrared heating together, was active only during the growing season when plant growth occurs. In winter periods, CO_2 enrichment was out of operation. The CO_2 enrichment was also deactivated when the soil temperature at a depth of 10 cm was below 3 °C; a condition as used in the set-up at GS to define the non-growing season. However, in this work, the non-growing season was defined in a different way as described next for comparing the manipulative approach with the observational approach. In contrast to the CO_2 enrichment, the heating was not generally out of operation in winter periods, but only turned off if the snow cover was higher than 10 cm. Thus, comparison of the two treatments, free air carbon enrichment and infrared heating, was possible only in the growing season. Hence the water balance components of the different soils at the specific sites under the original and climate change conditions were compared separately for the growing season and non-growing season.

The mean error representing the average deviation between the daily values obtained under changed conditions and those of the ambient reference was calculated using the R software (R-Core-Team, 2016) and the function *me* of the package hydroGOF (Zambrano-Bigiarini, 2017):

$$Mean\ error = \frac{1}{N}\sum_{i=1}^{N}\left(Obs_{Ti} - Obs_{refi}\right) \tag{2}$$

where n is the number of samples and Obs_{Ti} and Obs_{refi} are the daily value on the corresponding water balance term from the treatment (subscript Ti) and reference (subscript refi). The AGB production of the grassland ecosystem were analysed solely for the growing season. A thermal based definition of the growing season and non-growing season proposed by Ernst and Loeper (1976) was employed in this study to identify the beginning and ending of the growing season /non-growing season at the corresponding site. In this approach the beginning of the growing season can be obtained by adding up all positive average daily air temperatures from January 1st and considering specific weight factors for each month. The daily means of air temperatures were multiplied by weighting factors of 0.5 (January), 0.75 (February), and 1 (March) and summed up. The beginning of the growing season in spring was defined as the day when the cumulative temperature sum exceeded a threshold of 200° C. The same approach was used to obtain the end of the growing season, yet starting the temperature sums backward from December 31, with weighting factors of 0.5 and 0.75 for December and November, respectively.

2.4 Budyko plot

The Budyko framework (Budyko and Miller, 1974) was used to obtain information about the hydrological status of the corresponding soil ecosystem. The Budyko plot characterizes how the aridity index ($AI = ET_0/P$) controls the fraction of P into evapotranspiration (evaporative index $EI = ET_a/P$) and runoff (Berghuijs et al., 2020). In case of values of $AI < 1$ the system can be described as a demand (i.e. energy-limited) and in case of of $AI > 1$ as supply (i.e. water) limited. Please note that instead of considering P alone in the Budyko framework, we have also used NRW inputs here.

2.5 Hydroclimatological and ecohydrological indicators

The dry matter AGB was gravimetrically determined with a precision balance (Gumpenstein: EA 6DCE-I, Sartorius; Selhausen and Rollesbroich: EMS 6K0.1, KERN). At GS AGB were dried at 55°C for 48 hours, at RO and SE at60°C for 24 hours. The AGB from the different cuts were summed over the growing season to annual values and averaged over the replicated treatments (see Table 1).

The crop WUE, defined here as the amount of dry AGB produced per unit of water used by a plant (Tello-García et al., 2020), was estimated as:

$$WUE = \frac{AGB}{ET_a} \tag{3}$$

where AGB represent the dry matter biomass production (g m^{-2}) and ET_a the actual evapotranspiration (mm) during the growing season of the corresponding year and treatment. The annual PUE (g m^{-2} mm^{-1}), which are defined as the ratio of AGB and mean annual P (Zhou et al., 2020) and NRW was calculated as:

$$PUE = \frac{AGB}{P+NRW} \tag{4}$$

The PUE is a key indicator that explains the response of the ecosystem productivity to P (Wang et al., 2019) and NRW. Hence, PUE is used here to explore how the relationship between water balance and the crop components in the carbon cycle reacts to changes in the environmental conditions (Zhou et al., 2020).

The aridity index (-) and the ratio of seepage (Q) to P and NRW (-) were determined by equations (5) and (6):

$$AI = \frac{ET_0}{P+NRW} \tag{5}$$

$$QP = \frac{Q}{P+NRW} \tag{6}$$

The QP ratio is a dimensionless indicator that describes the portion of P and NRW that becomes seepage and eventually will contribute to groundwater recharge. Here, we used QP ratio as indicator to assess how changing climatic conditions affect the hydrological functioning of the soil ecosystem. It should be noted that for QP, AI, and PUE normally only P is used, as quantitative information on NRW are often not available. Linear correlations between AGB, ET_a, ET_0, WUE, GSP, PUE, and AI were generated by the use of the package *lm* (R-Core-Team, 2016) to determine the responses of the corresponding variable/indicator under changing climate and the reference conditions of the manipulative or observational approach. The significance level ($p < 0.05$) was used to indicate if the relationship between the variables are statistically significant.

3 Results

3.1 Impact on the water balance components

3.1.1 Precipitation and non-rainfall water

The average annual P for the manipulative climate change approach at GS ranged from 1088 to 1131 mm a^{-1} across the observation period (2015 – 2018; Table 2; more details in Table S 3). The values of P were generally larger during growing (average range: 691 to 724 mm) than non-growing seasons (average range: 396 to 408 mm; Table 2). The average annual NRW ranged between 52 and 76 mm (Table 2; more details in Table S 4), which corresponds to 4.8 to 6.7 % of P (Table S 5). In contrast to P, NRW was on average larger during the non-growing season (34 to 48 mm) than during the growing seasons (20 to 28 mm). The treatments at GS showed differences in P and NRW, despite no active direct control on these variables. The lysimeters solely enriched with CO_2 (C2T0: 1131 mm) achieved on average similar annual P amounts over the observation period than the reference lysimeter (C0T0: 1125 mm). In contrast, the annual P amounts of the temperature-increased treatment (C0T2: 1096 mm) and the combined CO_2-enriched and temperature-increased treatment (C2T2: 1088 mm) were on average smaller than the reference observation (C0T0). A similar tendency on daily P between the treatments and the ambient measurement was observed for the non-growing (Fig. 1 A) and growing season (Fig. 1 B), with negative mean error values for treatments C0T2 and C2T2 and positive values for C2T0. Most pronounced differences between treatments with an elevated temperature and reference were detected during the growing season and the mean error of daily P ranged between -0.12 to -0.14 mm d^{-1} (Fig. 1 B).

Table 2: Average values of the soil water balance components: precipitation (P), non-rainfall water (NRW), actual evapotranspiration (ET_a), net water flux across the lysimeter bottom (NetQ), and change of the soil water storage (ΔS). The values were averaged across the non-growing seasons, growing seasons and annual values for the period 2015 - 2018, from replicated lysimeter measurements at each test site: Gumpenstein (GS) with C2T0 (CO_2: +300 ppm; two lysimeter), C0T2 (temperature: +3°C, two lysimeter), C0T0 (ambient, one lysimeter), C2T2 (CO_2: +300ppm, and temperature: +3°C, one lysimeter), Rollesbroich (RO) with C0CL0 (original, six lysimeter) and Selhausen (SE) with C0CL2 (translocated, three lysimeter).

Component	Season	Gumpenstein				Rollesbroich	Selhausen
		C2T0	C0T2	C0T0	C2T2	C0CL0	C0CL2
		mm					

P	non-growing	407.6	400.8	405.8	396.2	516.0	212.6
	growing	723.7	695.3	718.9	691.4	503.8	401.7
	annual	1131.3	1096.1	1124.7	1087.6	1019.8	614.3
NRW	non-growing	48.1	36.7	39.9	33.5	30.9	21.6
	growing	28.2	19.5	24.7	18.8	24.8	22.8
	annual	76.3	56.2	64.6	52.3	55.7	44.4
ET_a	non-growing	114.9	133.7	109.6	125.0	87.3	88.7
	growing	541.6	696.8	620.2	645.0	552.0	596.1
	annual	656.5	830.5	729.8	770.0	639.3	684.8
NetQ	non-growing	351.5	272.3	326.0	285.3	429.4	30.0
	growing	201.4	54.5	122.1	61.9	28.3	-58.2
	annual	552.9	326.8	448.1	347.2	457.7	-28.2
ΔS	non-growing	-10.7	31.5	10.1	19.4	30.2	115.5
	growing	8.9	-36.5	1.3	3.3	-51.7	-113.4
	annual	-1.8	-5.0	11.4	22.7	-21.5	2.1

All treatments had a visible impact on the formation of dew in comparison to the ambient conditions (C0T0; Table 2). Observations reveal that an increase in canopy surface temperature (C0T2 or C2T2) goes along with a decreasing formation of NRW with negative mean error values during both periods (Fig. 1 E and F). The change in temperature and CO_2 concentration reduced the annual NRW on average for C0T2 by 13 % and for C2T2 by 19 % in comparison to the ambient variant C0T0. Results for C2T2 indicate that the elevated surface temperature is the dominating factor in dew formation. This treatment generally achieved the lowest relative contribution of NRW at the annual scale and the largest negative mean error values. Our results reveal that an elevated CO_2 concentration also seems to influence the formation of NRW, as NRW increases by 18 % for treatment C2T0 compared to the reference C0T0. Seasonal and annual values of P and NRW amounts were generally significantly lower for 2018 compared to the other three years (Table S 3 and S 4). However, the relative contribution of NRW to P is similar to the previous years.

The annual P at the observational site RO was in general lower in the growing seasons (average range: 388 to 569 mm) than during the non-growing seasons (average range: 484 to 581 mm4). Similar to GS, the lysimeters from RO in SE obtained higher values of P in growing seasons (average: 402 mm) than in non-growing seasons (average: 213 mm). The transfer of lysimeter brought the soil ecosystem from a region with high (RO) to a region with low P (SE). As compared to RO, the average annual P at SE is lower by 406 mm (i.e., a decline of 40 %) and there is a shift in the seasonal P distribution, with higher P during the growing season. According to the Budyko framework, the change in P and the higher ET_0 in SE lead to a shift from an energy-limited (RO) to a water-limited regime (SE) with values for AI larger than one (Fig. 2). The latter one is important, as the soil ecosystems at the two sites are characterized by different soil water dynamics at the beginning of the growing season. Daily P values in C0CL2 on average were 1.57 and 0.76 mm per day smaller during the non-growing and growing season, compared to C0CL0 (mean error, Fig. 1 C and D). The annual average NRW was 20 % larger for C0CL0 (55.7 mm) than for C0CL2 (44.4 mm, Table S 4). However, the amount of water from NRW relative to P was higher for

C0CL2 (7.2 %) than for C0CL0 (5.5 %, Table S 5). The seasonal distribution of NRW at RO and SE shows, similar to GS, larger values of NRW during non-growing seasons. The mean daily deviation of NRW between RO and SE was similar during the non-growing and growing season (-0.03 mm). Larger differences were found during winter, when snow covered the grassland at RO (i.e. no measurements on P and NRW possible) whereas in SE NRW inputs could be determined (Fig. 1 G). The lowest annual P values of the observation period 2015-2018 were observed in the drought year 2018 with 872 mm at RO and 485 mm at SE (Table S 3). Similarly, also relatively small NRW values were observed at both sites in 2018 (RO: 45 mm; SE: 38 mm). Despite the lower NRW inputs in 2018, the amount of water from NRW relative to P was 7.9 % at SE, which is the highest value during the observation period. Again, this demonstrates the importance of NRW inputs in dry years when rainfall is low.

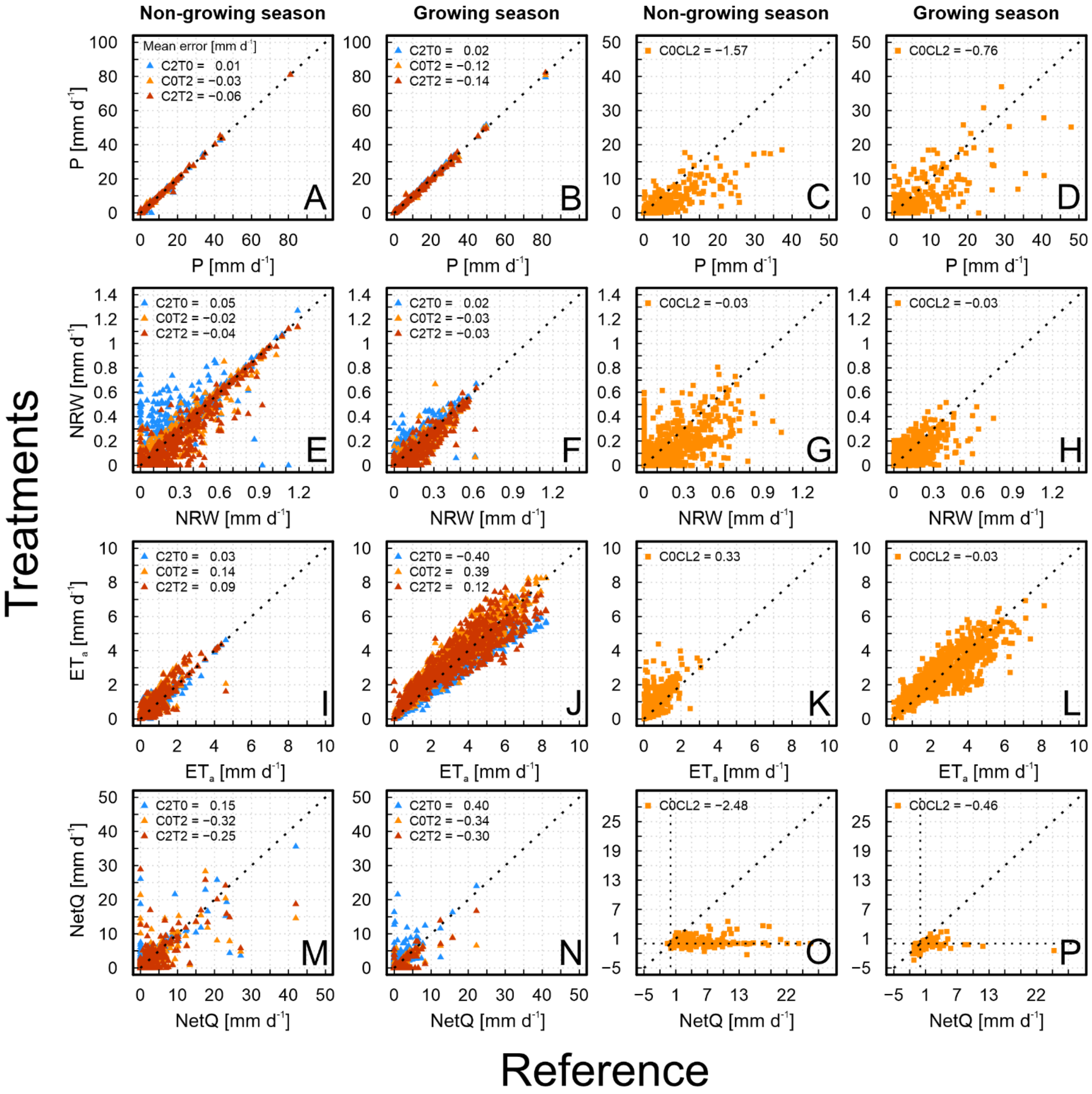

Figure 1: Comparison of all soil water balance components for all treatments, or sites of the two approaches (Lysi-T-FACE: C2T0, C0T2, C2T2: TERENO-SOILCan: C0CL2) to ambient reference of the two approaches (Lysi-T-FACE: C0T0; TERENO-SOILCan: C0CL0). Subplot A, B, C and D show the daily precipitation (P) of the treatments against the reference observation for the non-growing and growing season (2015 to 2018) for the manipulative (A and B) and the observational experiment (C and D). The same is shown for the non-rainfall water (NRW) in subplot E, F, G, and H, for the actual evapotranspiration (ET_a) in I, J, K, and L, as well as for net water flux across the lysimeter bottom (NetQ) in M, N, O and P. Average daily values were obtained from replicate lysimeter of the same treatment or site. The mean error (mm d^{-1}) was calculated to express the average deviation between the daily values obtained under changed conditions and those of the ambient reference.

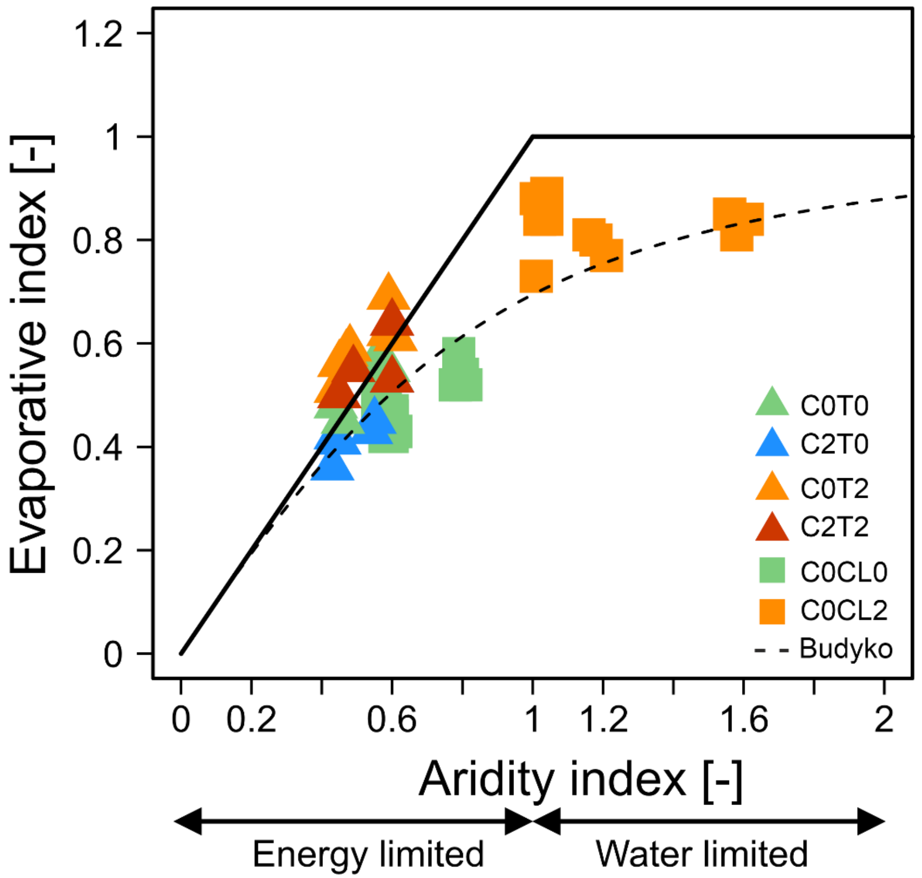

Figure 2: Budyko plots for the two approaches (Lysi-T-FACE: C2T0, C0T2, C2T2: TERENO-SOILCan: C0CL2) to ambient reference of the two approaches (Lysi-T-FACE: C0T0; TERENO-SOILCan: C0CL0) during 2015-2018. The aridity index and evaporative index are the ratios of the cumulated yearly grass reference evapotranspiration and actual evapotranspiration to the incoming atmospheric water (i.e. precipitation and non-rainfall water). The dotted curve shows the Budyko curve (ω = 2.6).

3.1.2 Evapotranspiration

The average annual ET_a for the manipulative approach at GS ranged between 657 and 831 mm among the different treatments and reference during the observation period (Table 2, more details in Table S 6). The average difference between the treatments in the non-growing season were relatively small (max. 24 mm per period) in comparison to the growing season (max. 155 mm per period; Table 2; Table S 6). During time periods with an active control on CO_2 and surface temperature, treatments largely differed from the reference observations. Compared to the reference, the average daily ET_a of the treatment with CO_2 enrichment (C2T0) decreased by 0.40 mm, whereas that of the treatment with an elevated surface temperature (C0T2) increased by 0.39 mm (Fig. 1 J). Our results for the combined treatment C2T2, in general (despite 2018), showed larger daily ET_a values in comparison to the reference, but the average deviation was only 0.12 mm. In the growing season of the exceptionally dry and warm year 2018, the ET_a response to treatment changed as compared to the previous years. For C2T0, the growing season ET_a in 2018 showed an increase by 42 mm compared to average values from previous years (2015 to 2017). Despite the observed increase relative to previous years, C2T0 still showed the lowest ET_a rates of the treatments in 2018. For C0T2 and C2T2, ET_a in 2018 was lower than the average of the previous years (46 and 80 mm, respectively). This decline suggests that ET_a at the heated plots was temporarily limited by the low soil water availability resulting from a decrease in soil water storage in 2018. In contrast, ET_a of the reference C0T0 did not differ in the growing season 2018 from the average ET_a values of the previous years 2015 to 2017. This demonstrates that the ET_a at the reference plot was not limited by water (Fig.2). The annual average ET_a of the observational approach was lower at RO (639 mm) than at SE (685 mm; Table 2). The length of the growing season increased on average by 36 days over the observation period due to the translocation from RO (C0CL0) to SE (C0CL2). Compared with the reference C0CL0, the average daily ET_a of C0CL2 was lower by 0.03 mm in the growing season and larger by 0.33 mm in the non-growing season (Fig. 1 K-L). Interestingly, during the 2018 European drought-affected growing season, average daily ET_a responded with an increase of 4% for C0CL0, while it decreased for C0CL2 by 18% in 2018 compared to the previous years.

3.1.3 Seepage and soil water storage

The water flux across the lysimeter bottom (NetQ) of C2T0 was larger than that of the reference C0T0 at GS (Figs. 1 M and 1 N). As expected, this difference is most pronounced during the growing seasons when the physiological effect of CO_2 enrichment reduces ET_a (Table S 7). Elevated CO_2 (i.e., C2T0) thus appears to affect the observed seasonality of seepage through the reduction of ET_a in the growing season. In contrast, the seepage of the treatments C0T2 and C2T2 was lower than that of C0T0 both in the growing and the non-growing periods (see values in Table S 7 and the negative mean errors in Fig. 1 M and N). Thus, water savings due to elevated CO_2 resulted in a significant increase of seepage (23 % compared to the reference), whereas higher temperature reduced seepage (for C0T2 27 % and for C2T2 23 % compared to the reference). Likewise, different effects of the treatments are apparent in the changes of the soil water storage (ΔS) during the growing season (Table S 8). C0T2 showed a depletion of the soil water storage in the growing seasons of all years, whereas the other treatments tend to positive values of ΔS in the growing season. An exception is the drought year 2018, where an increase of soil water storage during the growing season was observed only at C2T0. Also, the combined treatment C2T2 shows less depletion of the soil water storage than the reference in the growing season of 2018. This suggests that the aforementioned water savings due to CO_2 enrichment are particularly effective under drought conditions.

Impacts of the European drought in 2018 were also clearly visible in the measured NetQ during the growing season, which were nearly zero at all treatments (Table S 7). Compared to the averages of the previous years, the seepage in the growing season 2018 decreased between 95 to 98 %. This suggests that the seepage and thus groundwater recharge at such alpine grassland sites was considerably affected by the 2018 drought. Interestingly, the water saving effect of CO_2, which was found to mitigate the depletion of the soil water storage under drought (Table S 8), was not evident in the seepage rates observed in 2018 (Table S 7).

The NetQ from the observational approach showed extreme differences between the seasonal values over the observation period. Largest difference in NetQ between C0CL0 and C0CL2 were observed especially during the non-growing season (mean error of -2.48 mm; Fig, 1 O). In comparison to the reference C0CL0, NetQ of C0CL2 on average changed by -106 %. This demonstrates that for the water-limited site at SE the rewetting in the non-growing season is not sufficient to contribute to NetQ and hence water from P and NRW are mainly used to refill the depleted soil water storage. This is confirmed by the increase of soil water storage during the non-growing season, which on average is much larger at SE (116 mm) compared to RO (30 mm). Values of NetQ during the growing season were always negative for C0CL2, which indicates an upward directed flow from deeper soil or groundwater (Table S 7). However, the upward direct water fluxes did not compensate losses of water by ET_a and thus on average resulted in a clear depletion of the soil water storage at RO (-52 mm) and SE (-113 mm; Table S 8) in the growing season.

During the drought in 2018, RO showed, similar to GS, a significant decrease in NetQ. However, the impact on NetQ at SE (-20 mm) was low compared to observations from the previous years (-31 mm). This was mainly related to large amounts of P during the autumn and winter months of 2017, which caused a much faster refill of the soil water storage (Table S 8) in comparison to other years and consequently a higher seepage that compensated the larger upward directed water flux at the site during the drought in 2018.

3.2 Hydroclimatological and ecohydrological indicators

3.2.1 Aboveground biomass and water use efficiency

At GS, annual AGB was largest in 2016 with an average value of 845.2 g m^{-2}. The lowest AGB production was obtained in 2015 with an average amount of 709.7 g m^{-2}. For the years 2017 and 2018, average AGB values of 821.1 g m^{-2} and 795.2 g m^{-2} were obtained (see Table S 9 for more details). The year-by-year fluctuations of AGB are mainly induced by varying weather conditions at GS, as the management (cutting, fertilizer) was identical during the different growing seasons (Fig. 3 A). The reference C0T0 showed on average the largest AGB (1092.5 g m^{-2}). Among the treatments, C0T2 on average had the largest annual AGB (743.3 g m^{-2}) and C2T2 (635.0 g m^{-2}) the lowest. This reveals that the combined treatment with elevated temperature and elevated CO_2 concentration (C2T2) resulted in reduced grassland productivity compared to the reference C0T0. The average annual AGB of C2T0 (700.5 g m^{-2}) was also smaller than that of the reference C0T0. In 2018, C2T0 yielded slightly higher values of AGB than C0T2, but for the other years AGB of C2T0 was lower than that of C0T2 (Fig. 3 A).

The negative effect of elevated temperature and elevated CO_2 concentration on the AGB was also seen for WUE (Fig. 3 C). The WUE of C2T2 (1.0 g m^{-3}) was on average smaller than that of C0T2, C2T0 and C0T0 (1.1, 1.3 and 1.8 g m^{-3}). For all years, the ambient WUE was much larger than the respective WUE of the treatments. This reveals a negative effect of elevated

CO_2 concentration and elevated temperature on WUE for this grassland ecosystem. Among the treatments the highest WUE was obtained for C2T0, which corresponds to the aforementioned water saving effect of elevated CO_2 (see sections 3.1.2 and 3.1.3).

For the observational approach, on average a higher grassland productivity was obtained under wetter and colder conditions (C0CL0: 794 g m^{-2}; C0CL2: 721 g m^{-2}). The year 2015 was an exception where AGB was higher at the warmer and drier site (Fig. 3 B). During this year, the larger AGB mainly resulted from the first cut in the season, where the grassland ecosystems of C0CL2 and C0CL0 achieved on average values of 556 and 316 g m^{-2} (Table S 9). For the other cuts, AGB on average was much larger under wetter and colder conditions (C0CL0), despite the longer growing season at the warmer and drier site SE (C0CL2). This was especially visible for the last cuts of the season in 2016 and 2018, when AGB was lower for C0CL2 than C0CL0. Heatwaves in 2016 and 2018 and the decrease of growing season P by 36 % in 2018 in comparison to the average values of the previous years reduced drastically the AGB of C0CL2.

The WUE at the wetter and colder climate was on average 1.53 g m^{-3} and thus clearly higher than under warm and dry conditions (1.29 g m^{-3}, Fig. 3 D). These results show that decreasing P and increasing ET_0 led to a decrease of WUE by 22 %. Average differences of WUE between both sites of the second and third cut showed values up to 0.63 g m^{-3}. For these two cuts, differences between C0CL0 and C0CL2 were largest, whereas WUE of the first cut was similar at the two sites (data not shown). This suggests that the difference of soil water availability between C0CL0 and C0CL2 increases within the growing season (large depletion of soil water storage at C0CL2), which affects plant growth. The exceptional drought in 2018 affected largely the WUE, as the value for last cut in 2018 was vanishingly small at C0CL2 (0.16 g m^{-3}) and lower by 65 % in comparison to results from C0CL0.

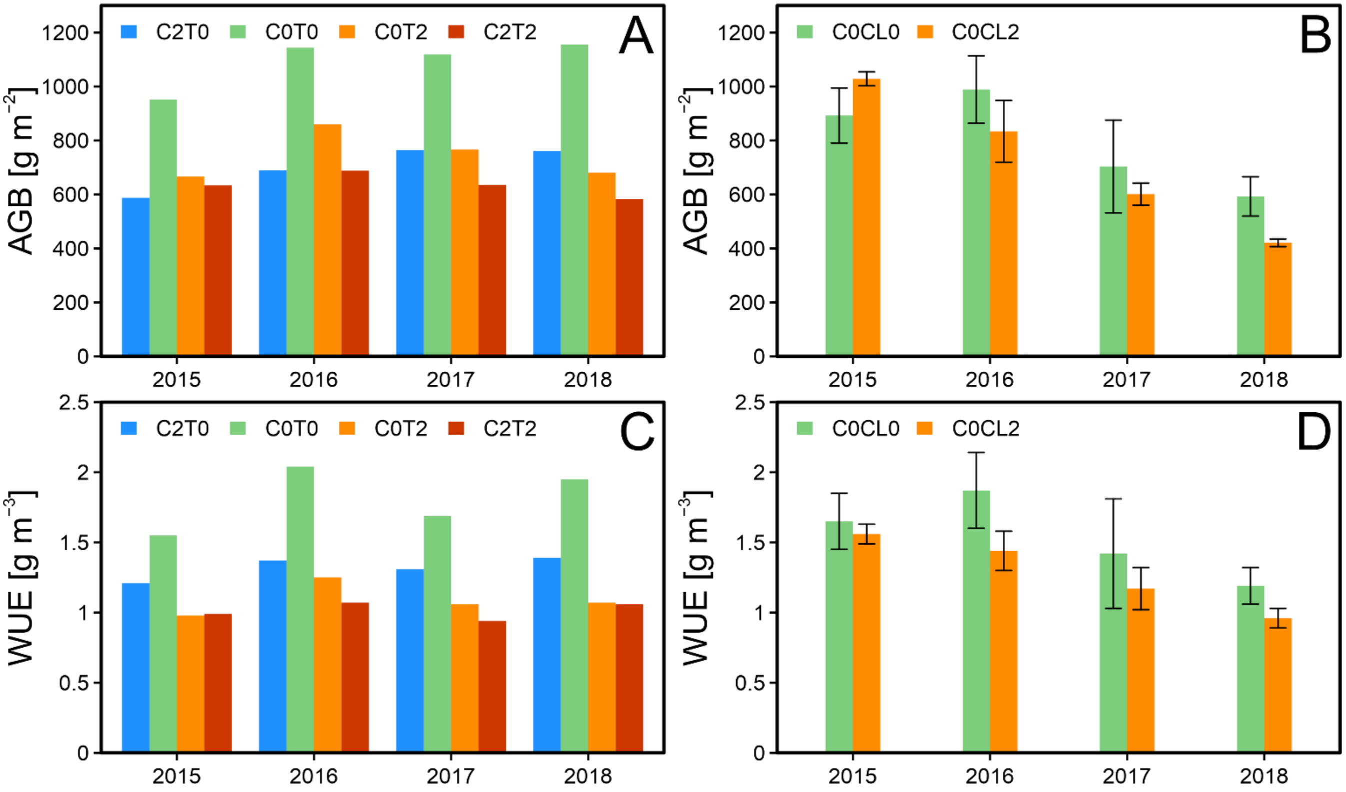

Figure 3: Dry aboveground biomass (AGB) during the observational periods 2015-2018 for the manipulative approach Lysi-T-FACE (C2T0; C0T0; C0T2; C2T2) (A) and observational approach TERENO-SOILCan (Rollesbroich C0CL0; Selhausen C0CL2) (B) as well crop water use efficiency (WUE) for the manipulative (C) and observational approach (D).

3.2.2 Precipitation use efficiency and seepage to precipitation ratio

For the manipulative approach, PUE ranged from 0.5 to 1.1 g m^{-2} mm^{-1} across the reference and the different treatments (Fig. 4 A). The highest value was obtained under ambient conditions (C0T0) in the drought year 2018. All treatments led to a decline of PUE in comparison to C0T0 (1.2 g m^{-2} mm^{-1}) and showed the same average PUE (0.61 g m^{-2} mm^{-1}). These observations suggest that all treatments had a strong effect on the PUE of the grassland ecosystem. In the drought year 2018, however, PUE of C2T0 was much larger than those of C0T2 and C2T2. This might be a result of a CO_2 fertilization effect yielding higher AGB at C2T0 as compared to the other treatments under the drought conditions of 2018.

Results from the observational approach showed different patterns under warmer and drier climate conditions. The PUE at C0CL2 was on average 45 % higher than at C0CL0. Nevertheless, Figure 4 B also shows a clear decline of PUE at C0CL2 from 2015 (1.37 g m^{-2} mm^{-1}) to 2018 (0.8 g m^{-2} mm^{-1}), which is accompanied by a decrease of P and NRW by 31 and 22 %, respectively.

The QP ratio obtained for both approaches (Fig. 4 C and D) show declines if the grassland ecosystem was exposed to warming (i.e. C0T2 and C0CL2). Elevated CO_2 increased the QP ratio; on average the values were 21 % higher than for the reference C0T0. However, the most drastic changes in the QP ratio were visible in the observational approach where QP changed on average by 81 % due to the transfer to a warmer and drier climate (Fig. 4 D). The increase of the QP ratio observed for C0CL2 in 2018 relative to the previous years is related to the large amounts of P during the autumn and winter months of 2017 (see also section 3.1.3).

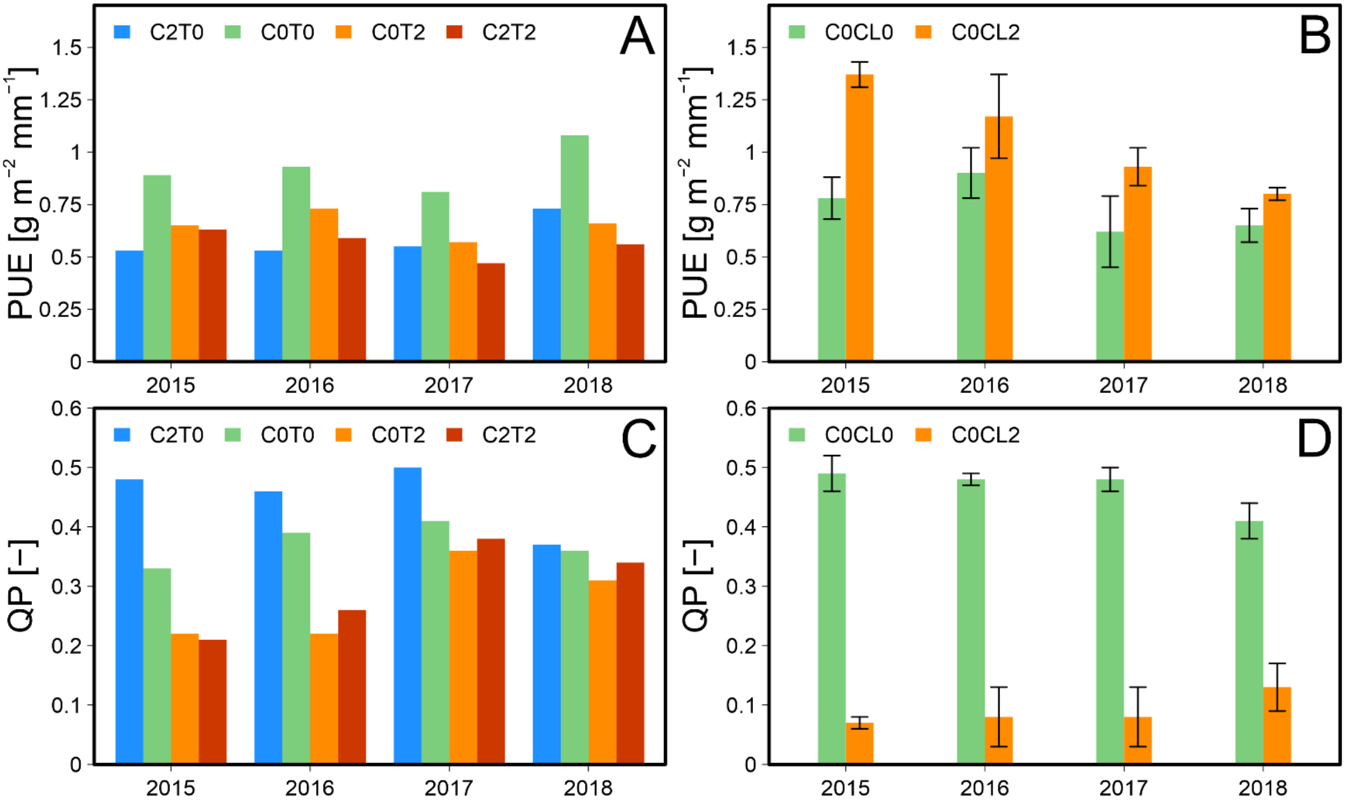

Figure 4: Precipitation use efficiency (PUE) during the observational periods 2015-2018 for the manipulative approach Lysi-T-FACE (C2T0; C0T0; C0T2; C2T2) (A) and observational approach TERENO-SOILCan (Rollesbroich C0CL0; Selhausen C0CL2) (B) as well as seepage to precipitation and NRW ratio QP (-) for the manipulative (C) and observational approach (D).

3.2.3 Relationship between hydroclimatological and ecohydrological indicators

The ecosystem productivity (i.e. AGB), in general, increased with GSP and growing season NRW (Fig. 5 A). Thus, the response of ecosystem productivity to P and NRW follows similar patterns in the manipulative and the observational approach. However, only for the observational approach the relationships were found to be significant ($p < 0.05$). ET_a in the growing season also increased with increasing GSP and growing season NRW for both approaches, but this relationship was statistically significant only for the observational approach, except for C0T2 (Fig. 5 B). ET_a showed particularly strong correlation with GSP and growing season NRW for C0CL2 from the observational approach (adjusted R^2 of 0.9). The relationship between ET_a and ET_0 during the growing season was significant and found to be negative for the observational approach, but positive for the manipulative approach (Fig. 5 C). The relationship between AGB and AI of the observational approach indicates a decrease in ecosystem productivity with increasing aridity under water- and energy-limited conditions. Yet, when the water limitation diminishes according to the Budyko framework (AI<1), the correlation between AGB and AI weakens (i.e. C0CL0) or disappears (i.e. GS, see Fig. 5 D). Thus, for the manipulative approach, no clear changes of AGB with changing AI were visible because of the relatively wet conditions (low AI). The relationships between WUE and AI are similar to those shown before for AGB and AI (Fig. 5 E). The relationships between the PUE and AI (Fig. 5 F) in the observational approach show that the PUE of the grassland ecosystem adapts to increasing water limitation. No relationships from the manipulative climate change experiment were significant, as inter-annual variability of climate conditions (wet and dry) were relatively well buffered by the soil water storage, and the hydrological status of the alpine site generally is energy-limited rather than water-limited. Nevertheless, the dependencies of AGB, WUE, and PUE on AI found in the manipulative approach appear to be similar to those at the energy-limited site (C0CL0) of the observational approach.

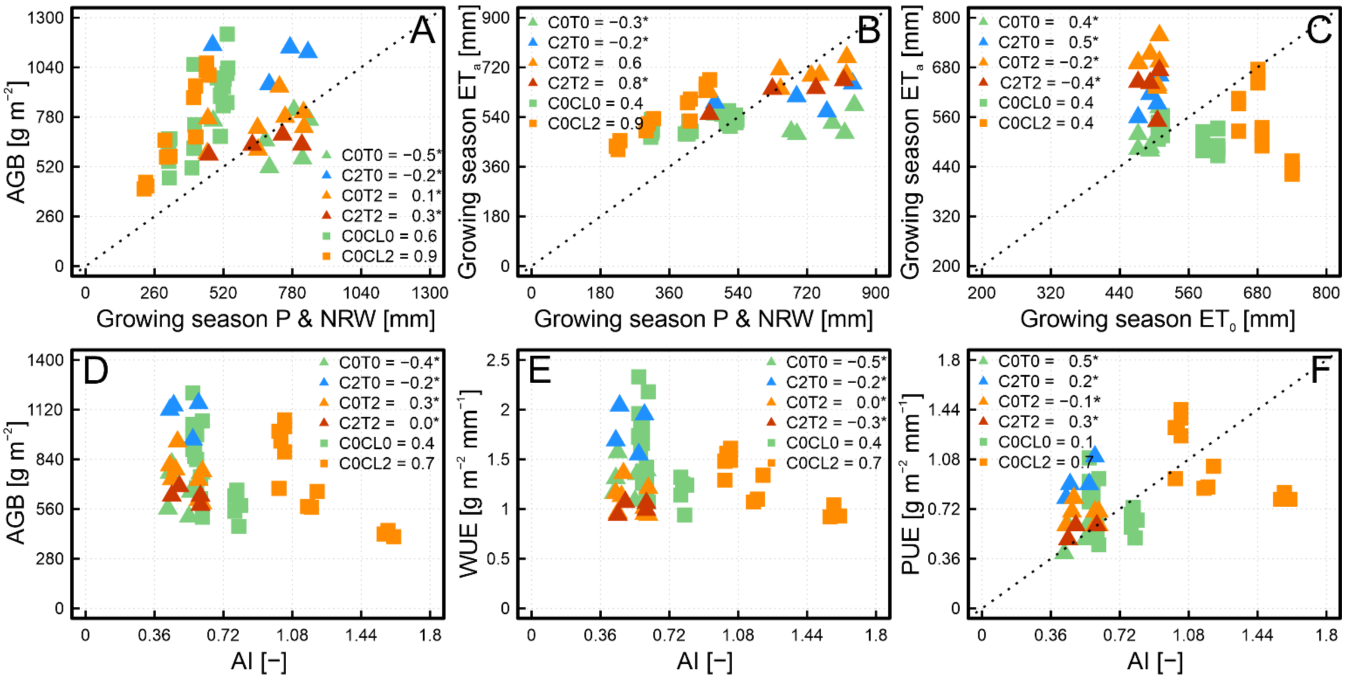

Figure 5: Scatterplots of aboveground biomass (AGB) to growing season precipitation (P) and non-rainfall water (NRW; A); growing season evapotranspiration (ET_a) to growing season P and NRW (B); growing season ET_a to growing season grass-reference evapotranspiration (ET_0; C); AGB to aridity index (AI; D); water use efficiency (WUE) to AI (E); and precipitation use efficiency (PUE) to AI (F). In each subplot variables are shown for all treatments from the manipulative (Lysi-T-FACE C2T0; C0T0; C0T2; and C2T2) and observational

climate change approaches (TERENO-SOILCan Rollesbroich C0CL0; Selhausen C0CL2) for the period 2015 to 2018. The adjusted R^2 values for each soil ecosystem are given in the legend and * means that the linear relationship was not statistically significant (p-value > 0.05).

4. Discussion

4.1 Response of water fluxes to climatic changes

The quantitative contribution of NRW to the soil water balance is of ecological relevance (e.g. by foliar water uptake Dawson and Goldsmith, 2018) and can become important for crop production, especially under water-limiting conditions. This is demonstrated by the impact of the extreme weather conditions in 2018, which were associated with a decrease in Northern European crop production (i.e. drought, heat wave; Beillouin et al., 2020). The results from both experimental approaches show that the amount of NRW formed in the non-growing season is higher than that of the growing season. This agrees well with previous findings on the seasonality of dew formation across different climate zones (Zhang et al., 2019; Groh et al., 2019; Atashi et al., 2019). The results from the treatments with elevated temperature demonstrate an impact of warming on the incoming atmospheric water, i.e. NRW and P. Under these treatments, the amount of water reaching the soil ecosystem in the growing season decreases by up to 4 % for P and by up to 24 % for NRW. The observed decrease in NRW agrees well with Feng et al. (2021), who showed that heating with an infrared heater system reduced dew formation for an alpine grassland ecosystem of the Tibetan Plateau by up to 91 %. Surprisingly not only warming but also elevated CO_2 was found to alter the amount of NRW. One possible reason for the observed increase in NRW might be related to the plants itself. It is frequently assumed that an increase in atmospheric CO_2 concentration leads to a decrease in stomatal conductivity, which increases leaf temperature (less evaporative cooling; Kirschbaum and McMillan, 2018) but simulation at the leaf level showed that leaf temperature is far more affected by leaf size or wind speed than by indirect effects of elevated atmospheric CO_2 (Konrad et al., 2021). However, effects might be more complex since a recent investigation by Habermann et al. (2019) demonstrated a clear impact of elevated atmospheric CO_2 on the leaf anatomy and physiology of the C4 forage species *Panicum maximum*. Thus, also anatomical and physiological changes of the plant leaves might be an possible explanation of higher dew amounts, because surface properties (i.e. radiative and wetting) are of crucial importance for the formation of dew and dew yield (Trosseille et al., 2021).

As mentioned above, both experimental approaches show that the formation of NRW declines if temperature increases. This agrees well with Tomaszkiewicz et al. (2016), who predicted a decline in dew formation for forecasted trends of increasing temperature and relative humidity under future climatic scenarios for the Mediterranean region. As opposed to the changes in absolute values of NRW, the percentage of NRW relative to P was found to be lower only under the elevated temperature of the manipulative approach, whereas this percentage increased under the warmer conditions in the observational approach. This is related to an important difference of the two approaches, namely the controlled change of individual factors in the manipulative experiment as opposed to the concurrent change of multiple drivers in the observational approach. More specifically, in the observational approach, the site with elevated temperature receives less P than the higher elevated, colder site. Thus, the relative contribution of NRW appears to be more affected by the changes in P than by the effect of warming.

A direct comparison of effects resulting from changes in P in the two experiments is difficult, because only the observational approach includes explicitly a change of P within its design. Including a change of P, especially during the growing season, is important for climate change studies, as the inter-annual variability of the ecosystem productivity (i.e. AGB) at least under water-limited conditions is strongly correlated (Knapp et al., 2018). Hence, climate change experiments that contain information on key interacting variables such as P are indispensable to provide observations that enable a more mechanistic understanding of the ecosystem response (Hanson and Walker, 2020). The manipulative experiment shows relatively low inter-annual variability of AGB (Fig. 3 A), although the observation period includes the drought of the year 2018. According to the Budyko framework, the hydrological status at the experimental site was energy-limited even in 2018 (Fig. 2). Thus, the inter-annual changes in P were not sufficiently strong to cause a shift to water-limited conditions. Assessing impacts of water stress at the site of the manipulative experiment thus requires including P as an additional treatment in the experimental design. Despite no active control on P within the manipulative approach, treatments with an increased surface temperature affected not only the formation of NRW but to some extent also the amount of P. Apparently, the effect of local warming on the relative humidity of the air within and above the canopy plays a role here. The local decrease of relative humidity might enable some ET_a during P events, thus violating the assumption of zero ET_a during rainfall, underlying the analysis of the lysimeter data. Such local effects on NRW and P in manipulative climate change experiments need further investigation, as they may lead to an under- or overestimation of ecosystem responses.

For ET_a, treatments at GS with an elevated CO_2 and increased temperature resulted in contrasting impacts due to their opposite individual effects on transpiration (Sorokin et al., 2017). Plants respond to elevated atmospheric CO_2 concentrations with a reduced stomatal opening and an increase in photosynthesis (Kruijt et al., 2008; Ainsworth and Rogers, 2007). This is expected to lead to lower ET_a and higher AGB and thus an enhanced plant WUE (Hovenden et al., 2017) compared to other treatments. Our results confirm the water saving effect of CO_2, whereas an effect on AGB was not observed.

In contrast to elevated CO_2, elevated temperatures lead to an increase in the vapour pressure deficit and thus enhanced evapotranspiration (Kirschbaum and McMillan, 2018). Kirschbaum and McMillan (2018) suggested for a range of locations from tropical to boreal forest that the transpiration-depressing effect of elevated CO_2 was stronger than the opposite effect of elevated temperatures. Lenka et al. (2020) showed that treatments with an elevated CO_2 concentration as well as combined increase of CO_2 and temperature reduced the stomatal conductance, lowered the ET_a, and consequently improved WUE of soybeans. In our experiments, ET_a of C2T2 was higher compared to reference, but clearly below values of ET_a from C0T2. This suggests that the effect of elevated CO_2 to reduce ET_a only partially compensated for the effect of elevated temperature in the combined C2T2 treatment.

Kirschbaum (2004) suggested that the effect of CO_2 on ET_a is more pronounced for C3 plants under water-limited conditions and at higher temperatures (Kirschbaum, 2004), because it enhances the WUE of the plant (Kirschbaum and McMillan, 2018).

However, its effect under non-water-limited but temperature limited growth conditions on plants is still unclear. The low ET_a of the treatment C2T0 during the dry year 2018 indicates that elevated CO_2 can mitigate effects of summer droughts on alpine grasslands, which agrees well with Inauen et al. (2013). They showed that elevated CO_2 reduced ET_a by up to 7 % across a range of different grassland types in the central Swiss Alps.

Interestingly, the ET_a response to the drought conditions in 2018 differed between the manipulative and observational approach. In the manipulative experiment, ET_a was found to be mainly energy-limited (Fig. 2) and thus increased under conditions with elevated temperatures (Fig. 1 J). In contrast, the observational approach showed a clear decrease in ET_a under conditions with elevated temperatures, as the soil ecosystem was shifted from an energy-limited to a water-limited regime (Fig. 2) due to the transfer from RO to SE (Rahmati et al., 2020). A similar reduction of ET_a across different ecosystem types was observed for sites in Europe affected by the drought in 2018 (i.e. forests, grasslands, croplands and peatlands; Graf et al., 2020). Our results revealed that the limitation of the water supply at site SE increased during the drought and the heat wave intensified the water stress (AI in 2018 ≥ 1.6) and thus significantly reduced grassland ET_a.

The above discussion shows that the manipulative experiment mainly provides insights into effects of climatic changes under energy-limited conditions, whereas the observational approach enables investigations under both energy-limited and water-limited conditions. Despite this advantage in the design of the observational approach, the influence of elevated atmospheric CO_2 on the ET_a response of the soil ecosystem is missing, which is an important aspect for assessment of future climate change impacts.

Another question was how climatic changes affected the drainage behaviour (NetQ) and water storage of the soil ecosystems. In the manipulative approach, elevated CO_2 resulted in a significant increase in NetQ, whereas elevated temperatures (C0T2 and C2T2) significantly reduced NetQ. Ultimately, this is a result of the above-described changes in grassland ET_a, which agrees well with findings from Mastrotheodoros et al. (2020) for the European Alps. Previous investigation for a grassland at the Swiss Alps showed only a slight increase of seepage under elevated atmospheric CO_2 (Inauen et al., 2013). These changes in seasonal seepage potentially affect the catchment runoff, which is important for hydropower productivity and profitability in Alpine regions (Anghileri et al., 2018).

The observational approach also showed the tendency for NetQ to decrease under elevated temperature, but in a much more pronounced way and for different reasons. At water-limited site SE, the non-growing season P is mainly used to replenish the large decrease in ΔS observed during the growing season. This partly explains the low impact of the dry year 2018 on NetQ at water-limited site SE. However, for the energy-limited ecosystem a strong decline in growing season NetQ (159 %) was observed in 2018 compared to the average 2015 to 2017, which eventually is expected to affect stream flow. Although stream flows are buffered by groundwater, reduced recharge will deplete regional water storage reserves as shown by Fennell et al. (2020) for a catchment in 2018 in Scotland. Long-lasting droughts can affect the soil water storage even in the following year, if winter P is not sufficient to fully replenish the depleted soil water storage (Riedel and Weber, 2020). The decrease of NetQ underlines that the physical and biological response to changing climatic conditions as well as the hydrological status of the ecosystem control water fluxes. Warming of land surface, reduced P, increased atmospheric concentrations of CO_2 and higher atmospheric demand for evaporation reduce seepage and thus groundwater replenishment.

4.2 Climate change impact on biomass production and ecohydrological indicators

The partially sharp decline in AGB production under changing climatic conditions observed in both experimental approaches can be attributed to very distinct reasons. The AGB decrease for the manipulative approach might be related to an increase of heat stress due to the treatments, which is either directly induced by an elevated canopy temperature or in case of elevated CO_2 indirectly, because elevated CO_2 probably reduces evaporative cooling of plants (Obermeier et al., 2018). The results are in contrast to the widely expected positive effects of increasing CO_2 on productivity of agricultural land (Amthor, 2001; Degener, 2015; Zheng et al., 2018). The positive effect of CO_2 fertilization on AGB was only visible for the treatment C2T0 under the conditions with less P and higher temperatures in the year 2018. This agrees well with previous studies (see e.g. Morgan et al., 2004; Ainsworth and Rogers, 2007). In addition, the vegetation composition might have changed between treatments and reference, as drought and heat induced shifts at the community and plant functional group level impact AGB production of alpine grasslands (Tello-García et al., 2020).

The decline of AGB under a drier and warmer climate of C0CL2 in the observational approach is closely related to the hydrological status of the soil ecosystem. The combination of lower incoming atmospheric water (i.e. P and NRW) coupled with higher evaporative demand and a longer growing season results in greater pressure on the soil water resources under water-limited than under energy-limited conditions. The AGB for C0CL2 was reduced during heatwaves in 2016 and 2018. In the summer 2018, the soil ecosystem was exposed to an increasing drought intensity and the plants turned slightly dry and brown and were visibly affected by drought stress (Rahmati et al., 2020).

In 2015, the AGB of C0CL2 was higher than that of C0CL0, which differs from the other years. This might be related to a moderate drought in 2015 (Ionita et al., 2016) combined with higher temperatures and solar radiation. For the first and most important cut in the season, C0CL0 achieved a below-average biomass, which can be explained by the exceptional dry conditions in May in this region (i.e. second driest month since 1950; Ionita et al., 2016). The soil ecosystem C0CL2 in SE, however, was less affected by this drought, as biomass production was able to develop much earlier in this season. The year 2015 had the longest growing season (250 days) in SE and the warm conditions before the drought in May and a sufficient water availability after winter led to similar AGB as in 2016. However, also here a change in plant community composition might be the reason for the altered AGB production. Observations on the species abundance from the observational approach underlines this explanation, as the plant community of the transferred soil ecosystem changed under water-limited conditions, by reducing the abundance of herbs on cost of grass species (Jarvis et al., 2021). Ecohydrological simulation of the grassland at RO and SE by Jarvis et al. (2021) for the years 2013 to 2018 suggests that the plant community adapted to the changing climate conditions in SE by developing a deeper root system, with a greater proportion of assimilates being distributed below ground, while stomatal conductance also increased significantly. These results show the importance of the interplay between environmental conditions (i.e., temperature) and the seasonal development of the plants (e.g., duration of the vegetation period), which cannot be taken into account in the treatments of the manipulative approach and thus represents a further limitation.

As expected, the different treatments also affected the WUE of the alpine grassland. Among the different treatments C2T0 achieved the highest WUE. It was also shown previously for a range of different agricultural ecosystems (Nendel et al., 2009; Roy et al., 2016) that WUE increases, as plants increase their assimilation rates and simultaneously reduce their water loss by decreasing stomatal conductance under elevated CO_2 (Lammertsma et al., 2011). A higher temperature, however, seems to increase the “non-productive” water losses, as evident from treatment C0T2 or C2T2, which led to less efficient crop water use as compared to the unheated plots (Fig. 3 C). The small difference between WUE of C0T2 and C2T2 suggests that the higher temperatures dominated the response of the grassland ecosystem under conditions with elevated temperature and atmospheric CO_2 concentration (no compensation). The largest difference in WUE between C2T2 and C0T0 was seen in 2016 and 2018. This might be related to increasing heat stress under this treatment (Obermeier et al., 2018).

Similar to the manipulative approach, the observational approach showed lower WUE under elevated temperature. De Boeck et al. (2006) also showed that warming of several grasslands in Belgium led to a decrease of biomass production and WUE. But the same study also implies that WUE of individual species was affected differently by warming, which might have led to compositional changes in the ecosystem. One reason for lower WUE under elevated temperature and/or water-limited conditions might the divergent biomass partitioning to above and below ground in grasslands. Experimental studies found that frequent soil drying and droughts enhance root growth and the production of below-ground biomass production (e.g. Hofer et al., 2017; Nosalewicz et al., 2018; Padilla et al., 2013). At least for the observational approach, simulation of crop growth and water fluxes with an eco-hydrological model reveals a deeper root growth (i.e. more below ground biomass) under drier climatic conditions at SE (Jarvis et al., 2021).

Comparing the results of WUE and AGB between both approaches suggests that the impact of drought in 2018 on the WUE and AGB under ambient conditions is much larger in the lowlands than at higher altitudes. Both approaches showed a decline in AGB and WUE under dry conditions. In addition to possible plant compositional changes, an elevated heat stress might further explain the different response to AGB and WUE within the manipulative experiment, whereby for the observational approach additional water stress due low GSP and a more depleted soil water storage was the main driver for changes in AGB and WUE.

The PUE values obtained are within the range (0.05 to 1.81 g m^{-2} mm^{-1}) reported by Le Houérou et al. (1988) and Jia et al. (2015). The observed effect of elevated temperature on PUE was different among the approaches. The water-limited soil ecosystem C0CL2 consumed nearly all incoming atmospheric water (i.e., P and NRW) for plant growth and drastically reduced drainage (average QP < 0.1), whereas at energy-limited ecosystem water was not limiting plant productivity (range QP:0.2 to 0.5). Our results further suggest that the formation of NRW should be part of PUE calculations, as under dry conditions water from dew or fog might be beneficial for plants and their biomass production. NRW can be either directly taken up by plants

(Berry et al., 2019) or indirectly improve their growth conditions (Dawson and Goldsmith, 2018) by e.g. reducing leaf temperature, increasing the albedo, and decreasing the vapour pressure deficit (Gerlein-Safdi et al., 2018).

4.3 Climate change impact on functional relationships

The observational approach demonstrates a clear pattern in functional relationships. Decreasing incoming atmospheric water during the growing season (P and NRW) significantly reduced biomass productivity of the grassland, which is consistent with other studies (Zhang et al., 2020; Hossain and Beierkuhnlein, 2018; Bernhardt-Römermann et al., 2011). Our results are in contrast to findings of Knapp et al. (2018), as the slope of the relationship between AGB and the incoming atmospheric water in the growing season was steeper in the observational compared to the manipulative approach (Fig. 5 A). The lower sensitivity of AGB to P and NRW in the manipulative approach suggests that under non-water-limited conditions other climatic variables, such as temperature, or additional factors, such as the frequency of disturbance and fertilisation, may be more important for AGB productivity (Bradford et al., 2006). This is consistent with the low inter-annual variability in growing season ET_a. Even between years with contrasting P and NRW (e.g. average reduction by 23 % from 2017 to 2018), ET_a was only slightly reduced (e.g. average reduction by 9 % from 2017 to 2018). Thus, water availability generally is not the limiting factor for ET_a at the alpine site, although water stress may occur temporarily under drought. Our results agree well with a previous study by Wieser et al. (2008), which showed for 16 sites across different altitudes (580 and 2550 m a.s.l.) that grassland ecosystems in the Austrian Alps seem not to suffer from water stress even in drier years.

The functional relationship of AGB, WUE or PUE with AI also reflect the importance of the hydrological status (i.e. water limitation) on ecosystem productivity and efficiency. These functional relationships were significantly negative under the water-limited conditions of the observational approach, i.e. increasing aridity caused decreases in these indicators. A negative significant relationship also found for the energy-limited soil ecosystem (C0CL0) is mainly related to the exceptionally dry year 2018. In other years, AGB and WUE varied considerably at the energy-limited sites both in the observational and the manipulative approach, while AI did not change (Fig. 5 D, E, and F).

The analysis of the functional relationships between hydroclimatological and ecohydrological indicators reveals that climate change experiments need to include sufficiently extreme conditions to resolve the key question: “How changes in the climate regime will affect and alter the ecosystem function in the future?” (Knapp et al., 2018). Ecosystem responses to changes in P are of crucial importance to assess future changes in the carbon and water cycle (Paschalis et al., 2020). More distinct changes in the P conditions, e.g. by using rain shelter, in the manipulative approach thus would allow to better capture the response of the ecosystem to future climate change.

5. Conclusions

A manipulative and an observational lysimeter-based approach was used to assess the climate change impacts on the water balance and productivity of a low mountain and alpine grassland ecosystem. Both approaches showed that elevated temperature increases actual evapotranspiration (ET_a) and decreases aboveground biomass (AGB) of grassland ecosystems but has the opposite effect on ET_a under drought conditions. This is most evident from results of the observational approach, but also found in the manipulative experiment during exceptionally dry periods in 2018. The incoming amount of atmospheric water (i.e. precipitation (P) and non-rainfall water (NRW)) and temporal variability of the events thus played a major role in the response of the ecosystem but responses in terms of the water balance and biomass production were partially buffered by the soil. In the manipulative approach, both elevated temperature and elevated CO_2 concentration altered P and NRW, suggesting that effects of the experimental conditions on NRW and P need to be considered to avoid an over- (elevated temperature) or underestimation (elevated CO_2) of the effects on ecosystems response, especially for sites where water limitation plays a role. Elevated temperature was the dominant factor for changes in ET_a under the non-water-limited conditions of the manipulative experiment. Elevated CO_2 concentration only partially compensated the effect of higher temperatures (increasing ET_a) within the combined treatment. However, the water-saving effect of elevated CO_2 gained importance under drought conditions.

The imposed changes in the climatic conditions resulted in a modification of the seasonal patterns of seepage and thus affects groundwater recharge in both experimental approaches. The effects of drought on drainage and soil water storage were more pronounced at sites under wetter (i.e. energy-limited) soil conditions, because here the higher demand for evapotranspiration could be satisfied at the expense of a decreasing soil water storage. Under water-limited conditions, seepage was found to depend strongly on the replenishment of the soil-water storage during the non-growing season.

Indicators such as aridity index and its relationship to ecosystem productivity (AGB) and efficiency (i.e. water and precipitation use efficiency) differed between the two approaches. It was found that distinguishing between energy-limited and water-limited conditions is important to understand the response of the ecosystem to changing climatic conditions. Water-limited ecosystems show distinct relationships between hydrological and ecological indicators. In contrast, ecological indicators may vary considerably in energy-limited systems even if hydrological indicators remain nearly constant.

The responses of soil water fluxes and biomass production strongly depend on the ecosystems’ status with respect to energy or water limitation. In the present study, only the observational approach covered both of these conditions, confirming our hypothesis about the different ecosystem response to changing climatic conditions between the approaches. Yet, only the manipulative approach included elevated CO_2. It was found that manipulative and observational approaches complement each other, but that it is important to consider both the general state of the ecosystem and the occurrence of extreme conditions in the approaches. Future studies should integrate all factors (precipitation, temperature and CO_2) from the manipulative and the observational approach in order to obtain a complete ecosystem response and better understanding of tipping points in ecosystems, which may help improving model predictions of how changes in climate regimes will affect the function of ecosystems.

Data availability

All data for the specific lysimeter and weather station (raw data) can be freely obtained from the TERENO data portal (https://teodoor.icg.kfa-juelich.de/ddp/index.jsp (last access: 9 February 2021; Kunkel et al., 2013), lysimeter station Rollesbroich and Selhausen: RO_Y_01 and SE_Y_02). The processed data to support the findings of this study can be acquired upon request from Jannis Groh. The raw data for the lysimeter and weather station can be obtained upon request from Markus Herndl.

Author contribution

MH and TP conceived the experiments at the corresponding site in Austria and Germany. JG and VF had the idea and designed the study. MH and JG provided the data for the corresponding lysimeter stations. VF and JG performed the data analysis, and reviewed and wrote the manuscript with equal contributions from all co-authors.

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Competing interests

The authors declare that they have no conflict of interests.

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