

Drought- and heat-induced shifts in vegetation composition impact biomass production and water use of alpine grasslands



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ABSTRACT

Future climate change scenarios predict more frequent and intense droughts for Alpine grasslands, primarily driven by altered precipitation regimes and increased evapotranspiration. The grassland community is expected to adjust to decreasing soil moisture and increasing potential evapotranspiration, optimising water use according to the individual strategies and competitive interactions between the present species. Here, we show the reaction of an intensive Alpine grassland to drought and heat at community and plant functional group levels by using small high-precision lysimeters, as well as how the community adapts by a shift from legumes to grasses after a severe drought. Drought and heating experiments revealed a decrease in evapotranspiration as well as in biomass production only at the highest drought intensity (i.e. soil water potential reaching the permanent wilting point). At plant functional group level, an upscaling from leaf porometer measurements revealed a similar decrease of transpiration for legumes and grasses, but differences between them in the rewetting phase. Legumes were strongly affected by drought and showed a low regrowth during the recovery, while grasses enhanced transpiration and even exceeded biomass productivity of the moist treatment. This imbalance between functional groups caused a shift from legumes to grasses in the grassland community. We conclude that drought-induced community re-assembly of Alpine grasslands enhances water use efficiency.

1. Introduction

Alpine grasslands provide multiple ecosystem services, e.g. forage production, provision of clean drinking water, prevention of water scarcity and maintenance or increase of soil fertility (Schirpke et al., 2017; Tasser et al. (2019)). These numerous benefits may be affected by climate change. Projected changes in the Alpine region are subject to considerable uncertainties because it is located in a transition zone of a shifting pattern of increasing precipitation in the North of Europe and decreasing precipitation in the South (Gobiet et al., 2014). Nevertheless, most projections indicate more frequent and intense drought stress for vegetation, primarily driven by altered precipitation regimes and increased potential evapotranspiration (ET) related to higher temperatures, more radiation and the resulting increase in water demand (Briffa et al., 2009). The short- and long-term effects of altered water fluxes (i.e. increased potential ET and water demand) within the soil-plant-atmosphere interface as well as functional and species

diversity have impacts on important ecosystem functions, such as biomass productivity (Frenck et al., 2018; Kardol et al., 2010), soil fertility (Dybziński et al., 2008) and carbon storage (Hungate et al., 2017).

Real Evapotranspiration and thus the water balance of grassland areas are not only influenced by climatic conditions and soil hydraulics, but also by biotic factors such as aboveground biomass, leaf area (Frenck et al., 2018; Obojes et al., 2015), species composition of the community and the interactions between them (Van den Berge et al., 2014). Under limited water availability, a plant can control water losses by stomatal conductance, which varies among plant species and also depends on water availability and carbon dioxide concentration in the atmosphere (Silva, 2015). The regulation of plant transpiration (T) by plant physiology, environmental conditions and stomatal sensitivity (Zhao et al., 2016) can improve the water use efficiency (WUE) of the individual, which is used to describe the trade-off between water loss by ET and biomass production. The regulation of T prevents the damage of the water conducting pathway and regulates photosynthetic rates

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affecting plant function and growth (Addington et al., 2004; Maherali et al., 2003; Wullschlegel et al., 2002; Zhao et al., 2016). In most Alpine grasslands, where water availability has, so far, not been limited, indigenous plants usually show a low WUE following a water-spending strategy (Brilli et al., 2011), which means that they use water exploitatively and hardly reduce T with decreasing water availability until the permanent wilting point (PWP) is reached. At this point, moisture conditions severely restrict the absorption of water by the plant. Contrastingly, plants following a water-saving strategy show a strict regulation of the stomata with decreasing water availability (Frenck et al., 2018). The difference between water spenders and water savers shows clear implications for competition and coexistence, reflecting the general distinction between conservative and exploitative strategies, respectively (Martinez-Vilalta and Garcia-Forner, 2017). Thereby, the composition of plant species in a vegetation community and the resulting functional structure has a strong effect on the community responses to stress conditions. Plant functional groups typically present in Alpine grassland communities may react differently. Forbs usually act conservatively, and their performance under drought is enhanced by a deep rooting system (Stampfli et al., 2018). Legumes tend to an exploitative strategy and are resistant to drought until near the PWP (Brilli et al., 2011; Hofer et al., 2017). On the other hand, grasses are generally extremely drought-resistant, as they dominate some of the driest ecosystems on Earth, e.g. savannahs. In addition, they show some competitive strategies, i.e. fast nitrogen acquisition and fast regrowth (Mackie et al., 2019; Stampfli et al., 2018). According to the individual strategies and by competitive interactions between the present species, the community adjusts to changing conditions, optimizing water use (Kardol et al., 2010; Peñuelas et al., 2004). After a drought event, the grassland community adjusts to enhance the recovery, which is expected to be fast in terms of biomass production (Hoover et al., 2014; Mackie et al., 2019), even at the cost of biodiversity (Stampfli et al., 2018).

In this study, we examine the effects of climate change on an intensive Alpine grassland typically used as hay meadow. We specifically hypothesise that:

- 1 Under drought conditions, ET of the intensive Alpine grassland in drought conditions keeps being close to ET in moist conditions until reaching matric potential close to the PWP; after that point, biomass productivity decreases significantly.
- 2 The reaction to increasing temperatures and persistent drought periods differs among functional groups, being less pronounced in grasses than in legumes.
- 3 After a dry and hot period, grassland aboveground biomass recovers fast by a shift in vegetation composition and increases in WUE.

By the simulation of severe drought situations (i.e. sheltering with no irrigation and heating), we assess the changes generated in ET in the intensive Alpine grassland, which is expected to follow a water-spending strategy. Therefore, it will provide a cooling feedback on climate warming by enhancing T through the stomata opening. The stomata interplay between leaf gas-exchange and maintaining favourable metabolic conditions (i.e. water status and temperature) (Reynolds-Henne et al., 2010), which may have negative consequences for biomass productivity in case of unfavourable conditions (Brilli et al., 2011). To understand the processes behind the community reaction to drought, we also examine the biomass productivity and T at functional group level (i.e. grasses and legumes) by an upscaling from stomatal conductance measurements referring to Wohlfahrt et al. (2010). After the drought treatment, a rewetting period allows to assess the recovery of the Alpine grassland in terms of regrowth and WUE, as well as the responsible mechanisms at functional group level.

2. Methodology

2.1. Experimental field site

The field site was established in the long-term socio-ecological research (LTSER) site 'Stubai Valley' (LTSER platform 'Tyrolean Alps') close to Neustift im Stubaital (Austria). The garden experiment was located at the valley floor at 972 m a.s.l. (WGS84: 47.115833 N, 11.320556 E) in a meadow used for hay production. Investigations were carried out during the growing season (May to October) in the year 2016.

For this experiment, six plots of 3.5 x 3.5 m, defined by half-cylindrical metal frames, were established. In each corner of the plot, an irrigation sprinkler was set up. The irrigation system, described by Newesely et al. (2015), simulated local average precipitation amounts and intensities during periods of experimental manipulation of water provision. To avoid immediate transpiration from the surface and to allow the water to penetrate into the soil, automated irrigation was programmed to occur around midnight. Because of the uneven distribution of precipitation by the sprinklers and to ensure an equal irrigation within the plots, manual adjustments were made during day-time. During the experiment, the plots were closed using a UV-permeable transparent polythene film (Lumisil Clear AF, 88–92% light transmittance). The shelters reached a height of approx. 2.5 m and were closed to just 0.5 m above the soil level, but open on the sides facing the main wind direction, allowing the establishment of natural boundary conditions. A heating treatment to the plant canopies was realised using ceramic infrared heat plates with a maximum power of 600 W, placed 1 m above the individual lysimeters. Thereby, the canopy surface temperature was increased by 2 K compared to the moist plots. The respective canopy surface temperatures were measured using infrared radiometer sensors (SI-111, 22° half-angle field of view, response time 0.6 s, Apogee Instruments Inc.). Based on these measurements, the ceramic infrared heat plates were controlled automatically using a Campbell CR1000 datalogger and the Campbell 4-channel analogue output module (SDM-AO4A). Controlled by the SDM-AO4A, the heating plates were activated by a phase angle dimmer to maintain the constant 2 K temperature difference. By cautiously changing the heating energy, this difference was maintained without significant hysteresis. For a more theoretical and technical background, please refer to Kimball (2015). A microclimate station was installed in each plot, measuring air temperature and relative air humidity (height: 1 m; U23-002 HOB0® External Temperature/Relative Humidity Data Logger, Onset Computer Corporation, USA) as well as wind speed (height: 1 m; DAVIS® Standard Anemometer 7911, Davis Instruments, USA).

2.2. Lysimeter setup and measurements

In each plot, one small-scale lysimeter (Smart-Field-Lysimeter, UMS/Meter Group Munich, Germany) with a depth and diameter of 0.3 m was installed, totalling six lysimeters. Each lysimeter was filled with a horticultural standard soil, composed of 90% of silicate-carbonate mineral content and 10% compost, sterilised by soil steaming and planted with a commercial seed mixture used for intensively cultivated hay meadows (Schwarzenberger, 2018). The chosen seed mixture is typically used in some areas of the valley bottoms in the central Alps and was composed of *Achillea millefolium* agg., *Agrostis capillaris*, *Anthriscus sylvestris*, *Dactylis glomerata*, *Festuca pratensis*, *Festuca rubra*, *Poa trivialis*, *Taraxacum officinalis*, *Trifolium pratense* and *Trifolium repens*. The grass species *Dactylis glomerata*, *Poa trivialis* and *Festuca pratensis* and the legume species *Trifolium pratense* and *Trifolium repens* were selected to assess stomatal conductance and transpiration, as they (a) represented more than the 89% of the total vegetation coverage in the lysimeter, (b) were present almost over the entire vegetation period, (c) provided sufficient leaf size for measurement (0.5–2 cm) and (d) represented the two functional groups present in the vegetation (i.e.

grasses and legumes). Each week, stomatal conductance of these species was measured on the lower leaf side with a DECAGON SC-1 Leaf Porometer (Decagon Devices, 2016). Each measurement was replicated three times per functional group and lysimeter. Individuals were completely exposed to the sun during measurements. The above-ground biomass of the vegetation was assessed for each plant functional group after each cut. Three cuts were made at a height of 3 cm; the harvested biomass was separated into functional groups and leaves, stems and reproductive organs, dried at 80 °C and weighed.

To continuously measure evapotranspiration (ET), the weight was recorded each minute via an electronic weighing platform (PL-50, UMS/Meter Group Munich, Germany, accuracy of ± 7 g) located under each lysimeter. The bottoms of the lysimeters were closed with a tension-controlled hydraulic boundary connected to a bi-directional pumping system, which acted like a groundwater supplier and adjusted the water content by transferring water either from the drainage container into the lysimeter or vice versa. The adjustment was done according to a reference matric potential measured with a tensiometer at the same depth in the natural unaffected soil column of the respective experimental plots. The water container weight was also recorded each minute by an electronic weighing platform (PL-10, UMS/Meter Group Munich, Germany, accuracy of ± 1.7 g). Simultaneously, changes in soil water content (SWC) (Decagon, EC-5 Soil Moisture Sensor, accuracy of $\pm 4\%$) and matric potential (Decagon, MPS-2, accuracy of $\pm 25\%$) were monitored at a soil depth of 0.15 m for 10 min intervals. Data were stored in data loggers (Data logger DT85; dataTaker) and automatically transferred to a data server every 24 h.

2.3. Experimental scheduling

Three cuts were made concurrently to the land-use scheme of the surrounding meadow (14.06.2016, 01.08.2016 and 03.10.2016) at all lysimeters. Over a period of 140 days (17.05.2016 to 03.10.2016), the plots were subjected to different treatments: i) three lysimeters were watered on a regular basis (moist), mimicking by irrigation and groundwater supply rainfall amounts and intensities for the 30-year period between 1970 and 2000 in the Stubai Valley and ii) other three lysimeters suffered extended drought periods and an increase in the plant surface temperature by 2 K compared to the moist plots (drought).

The drought experiment was divided into four phases (Fig. 1a): 1) Pre-treatment (17.05.2016 - 30.06.2016) with regular watering and

groundwater supply, 2) Drought period 1 (30.06.2016 - 08.08.2016) with three lysimeters experiencing drought conditions, where on 30.06.2016, shelters were built to avoid natural precipitation and on 05.07.2017, the groundwater supply was switched off; 3) Rewetting (09.08.2016 - 04.09.2016) with regular watering and groundwater supply and 4) Drought period 2 (05.09.2016 - 04.10.2016) with irrigation and groundwater supply both being switched off simultaneously. IR-heating was applied in both drought periods. Lysimeters under the moist treatment received a total irrigation amount of approximately 466 mm over the entire experiment, while those under drought treatment received 250 mm (Fig. 1b).

2.4. Data processing

To accurately separate the water fluxes (i.e. precipitation and ET) at the interface between the soil-vegetation system and the atmosphere, weight differences of the lysimeter and the water reservoir were summarised. In order to separate real weight changes from noise, the AWAT (Adaptive Window Adaptive Threshold) filter (Peters et al., 2017, 2014; Peters et al., 2016) was applied. This was necessary because the sensitive weighing elements are susceptible to environmental noise or interferences. Some remaining outliers have been manually removed. After that procedure, any increase in total weight could be attributed to irrigation and any decrease to ET. Subsequently, daily totals were calculated for both mass differentials. The reference evapotranspiration (ET_0) was calculated following the FAO Penman-Monteith equation (Allen et al., 1998) to verify that other climate parameters (i.e. wind velocity or relative humidity) do not interfere on the treatment.

The integrated WUE of the vegetation in the lysimeters was calculated after each cut by dividing the total increase of dry biomass by the accumulated ET in the lysimeter during each experimental period, according to Kirkham (2005b). As biomass was always cut to the same height, total biomass increase was assumed to be the harvested biomass. This calculation allows us to compare the water flows of all the lysimeters, independent of the differences in biomass development.

We analysed the variables of transpiration (T) using a multiple linear regressions based on six observations (i.e. lysimeters) with T as the dependent variable and senescence (i.e. number of days since last cut) and treatment - which was split into moist and drought - as independent variables. A set of ANOVAs were done to analyse the differences between lysimeters subjected to moist and drought treatment.

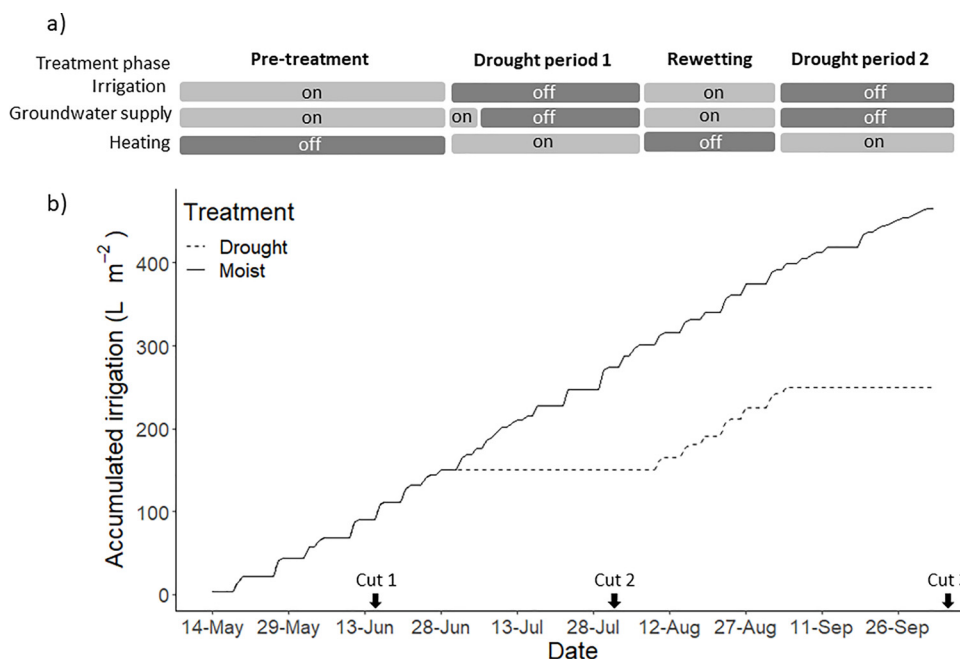


Fig. 1. Details of the different treatments: a) Schedule of the drought treatment throughout the experimental period, including the activation or inactivation of the irrigation, groundwater supply and heating systems. b) Mean accumulated precipitation (mm) along the experiment in lysimeters under drought and moist treatments. Arrows indicate the three cuts made during the experiment.

All statistical analysis presented here were performed using the R statistical programming language (R Development Core Team, 2015).

2.5. Porometer-based upscaling

Transpiration of the plant canopy of a determined functional group (T_{FG} , mm h⁻¹) was estimated by upscaling leaf-level stomatal conductance to canopy-level transpiration, using a slightly modified equation provided by Wohlfahrt et al. (2010):

$$T_{FG} = 3600 * Mw * LAI_{(FG)} * g_{l(FG)} * \frac{C_{vs(FG)} - C_{va(FG)}}{P}, \quad (1)$$

where Mw is the molecular mass of water (0.018 kg mol⁻¹), LAI (m² leaf area m⁻² ground area) is the Leaf Area Index, g_l is the leaf conductance to water vapor (g_l , mol m⁻² s⁻¹), C_{vs} (mol mol⁻¹) and C_{va} (mol mol⁻¹) are the water vapor concentration inside and outside the leaf epidermis, respectively, and P (kPa) is the atmospheric pressure, measured by the microclimate station in each plot. The index FG refers to the functional group that was measured. The parameters C_{vs} and C_{va} were calculated according to Campbell and Norman (1998):

$$C_{vs(FG)} = h_{r,leaf} * \frac{e_{s,leaf}}{P} \quad (2)$$

$$C_{va(FG)} = h_{r,air} * \frac{e_{s,air}}{P} \quad (3)$$

where $h_{r,air}$ (%) is the relative humidity in the air measured by the microclimate station and $h_{r,leaf}$ (%) the relative humidity at the leaf surface, which is always assumed as 100% of the saturated water vapor pressure. The factors $e_{s,leaf}$ (kPa) and $e_{s,air}$ (kPa) are the saturated water vapor pressure at the leaf and in the air, respectively; $e_{s,leaf}$ was calculated as a function of leaf surface temperature (T_{surf} , °C) and $e_{s,air}$ as a function of air temperature, according to Campbell and Norman (1998) and Zotarelli et al. (2015). The parameter T_{surf} was measured by infrared radiometer sensors in the drought plots during the drought periods. During the remainder phases and in the moist plots, T_{surf} was calculated from the air temperature, based on an empirical relationship.

The LAI (m² m⁻²) was calculated as follows:

$$LAI_{(FG)} = \frac{m_{FG,d} * SLA_{FG}}{A_{Lys}} \quad (4)$$

where A_{Lys} is the area of the lysimeter and SLA_{FG} (m² kg⁻¹) is the Specific Leaf Area of the functional group. The SLA values, obtained from Fontana et al. (2017), were 26.36 m² kg⁻¹ for grasses and 22.99 m² kg⁻¹ for legumes. The leaf's phytomass of the functional group per lysimeter at the measurement day (d) was represented by $m_{FG,d}$ (kg m⁻²) and determined with the help of the following regression:

$$m_{FG,d(cuts2,3)} = \left(\frac{m_{FG,c}}{\sum T_c} * \sum T_d \right) + \left(\frac{m_{FG,c} * 14}{86} \right), \quad (5)$$

where $m_{FG,c}$ (kg m⁻²) is the dry weight of the leaf phytomass of the functional group at the lysimeter area at the time of cutting (c); $\sum T_c$ (°C) is the temperature summed up until day c and $\sum T_d$ (°C) is the temperature summed up until day d. The first term calculates the biomass grown since the last cut; the second one adds the biomass which we assume to be in the lowest 3 cm of height. The cuts were always made at a height of 3 cm, and the 3-cm vegetation represents approximately 14% of the total vegetation, except for the period before the first cut, when the biomass was derived from the seed. Therefore, we used the following regression:

$$m_{FG,d(cut1)} = \left(\frac{m_{FG,c}}{\sum T_c} * \sum T_d \right) * \left(\frac{100}{86} \right) \quad (6)$$

The leaf conductance to water vapor (g_l , mol m⁻² s⁻¹) was calculated according to the following equation (Wohlfahrt et al., 2010),

assuming that the stomata are distributed only on the lower leaf side:

$$g_{l(FG)} = \frac{g_{FG} * g_b}{(g_{FG} + g_b)} \quad (7)$$

where g_{FG} (mol m⁻² s⁻¹) is the stomatal conductance of the selected functional group, measured with the SC-1 Leaf Porometer. The forced convection g_b (mol m⁻² s⁻¹) is calculated according to Campbell and Norman (1998) and Wohlfahrt et al. (2010):

$$g_b = 0.147 * \sqrt{\frac{u}{d}} \quad (8)$$

It is a function of the mean horizontal wind velocity (u , m s⁻¹) and the leaf width (d , m), depending on the functional group that we analysed and assumed to be 0.01 m for legumes and 0.005 m for grasses (Grime et al., 2007; Lauber et al., 2018). Wind speed at plant level was calculated, based on an empirical correlation between the measured wind speed at a height of 1 m and wind speed in the midst of plant cover. A validation of the porometer-based upscaling was made by using linear regression analyses based on 78 observations with ET as the dependent variable and the calculated T as independent variable. It is shown in Supplement Fig. S1.

3. Results

Since absolute values of in-situ soil moisture measurements are often questionably, we analysed only the differences between the soil water content (SWC) at a certain time and the initial water content. In the pre-treatment period, the differences were similar, meaning that the water loss or gain was similar for both treatments (Fig. 2a). After starting the first drought period, the water contents decreased drastically for the drought treatment (until -4.2% ± 0.8), whereas they increased for the wet treatment (until 10.4% ± 1.2). During the first drought period, the two contrasting irrigation regimes led to different SWC dynamics within the respective lysimeters. The positive peak at the beginning of the first drought period can be explained by the bi-directional pumping system being turned off 5 days later, meaning that some water was pumped into the system from the bottom within this time. The differing SWC dynamics became particularly evident approximately 20 days after the beginning of the treatment, when the SWC decreased significantly in drought lysimeters until close to the PWP, usually considered at a pF of 4.2 (Fig. 2b), while the SWC increased in moist lysimeters. Soil water content remains stable at the end of the drought treatment, when the SWC at 0.15 m was approximately -4%. We must interpret this data with precaution, because possible inaccuracy of the measurement devices at extremely low SWC may affect these readings. Despite the increase of SWC in lysimeters of the drought treatment during the rewetting phase by up to 7.0% (± 2.8) when compared to the initial value, the soil water contents of the two irrigation treatments remained significantly different (ANOVA, $p < 0001$). During the second drought period, the SWC differences between the contrasting treatments were also significant (ANOVA, $p < 0001$), although lysimeters under drought treatment did not reach the PWP.

The rates of daily ET varied strongly throughout the experimental period (Fig. 2b), and the ET values were similar during the Pre-treatment phase. A divergence between irrigation treatments was not evident until 17 days after the start of the Drought period 1, when the SWC had already decreased by 3.1% (± 0.4) and it was near the PWP (Fig. 2b). During the Rewetting and Drought period 2, the ET rates of moist lysimeters were slightly higher, but not significantly different, than lysimeters under drought treatment. The accumulated ET within the different phases of the experiment revealed differences between treatments only during Drought period 1 (ANOVA, $p = 0.05$), where moist lysimeters showed an accumulated ET of 255 mm (± 30.7) and the drought lysimeter had an accumulated ET of 152 mm (± 7.6). On the other hand, the accumulated ET₀ shows no differences between

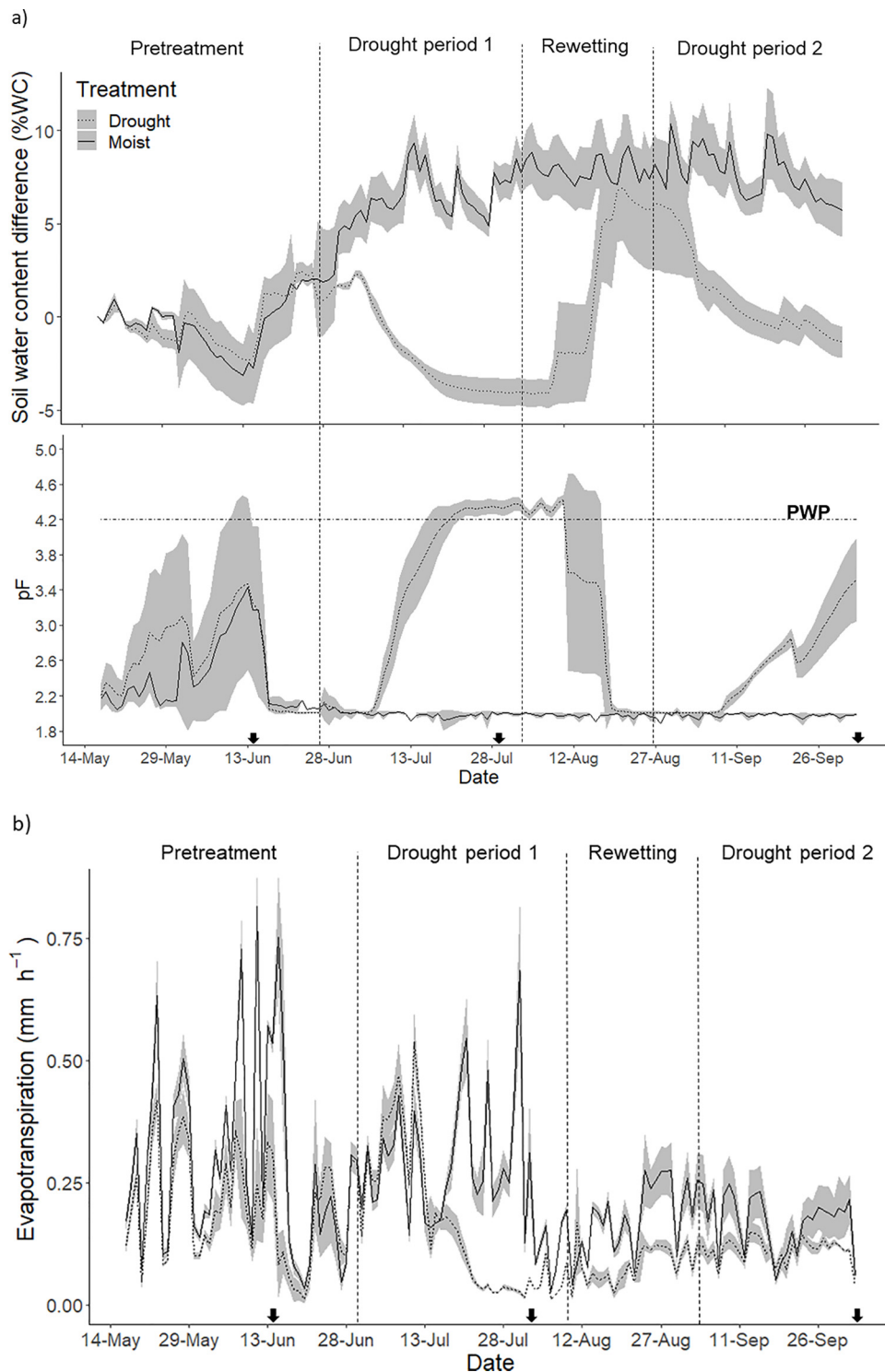


Fig. 2. Dynamics of (a) difference of average daily mean soil water content (% water content) at 0.15 m compared to the beginning of the experiment (17.05.2016) and pF at 0.15 m, $pF = \log_{10}(-\Psi)$, where Ψ (cm) is the matric potential. The permanent wilting point (PWP) is indicated with a line at a pF of 4.2 cm. Dynamics of (b) daily average ET (mm h^{-1}) in moist and drought treatments throughout the experimental period. The shaded area represents the standard error (SE). Arrows indicate the three cuts made during the experiment. The difference of daily SWC and the daily ET of each lysimeter are available in the Supplement Fig. S2 and S3 respectively.

moist and drought treatment. Moist plots had an accumulated ET_0 of $118 \text{ mm} (\pm 10.1)$ and drought plots showed an accumulated ET_0 of $113 \text{ mm} (\pm 18.8)$.

The weighted biomass showed also differences between moist and drought treatments. During the early season (cut 1) most of the biomass was yielded in all the lysimeters ($1685 \text{ g}_{\text{DW}} \text{ m}^{-2} \pm 80.2$ in moist lysimeters and $1246 \text{ g}_{\text{DW}} \text{ m}^{-2} \pm 218.5$ in drought lysimeters), followed by a decrease in biomass throughout the vegetation season (Table 1). Differences between treatments were evident in cut 2, where the mean biomass was $363 \text{ g}_{\text{DW}} \text{ m}^{-2} (\pm 21.1)$ in drought lysimeters and $846 \text{ g}_{\text{DW}} \text{ m}^{-2} (\pm 90.3)$ in moist lysimeters (ANOVA, $p = 0.013$). Contrastingly,

Table 1

Share of the total biomass (%) at each cut throughout the experimental period, total biomass after the experimental period (g m^{-2}) and standard error ($\pm \text{SE}$) in the lysimeters subjected to moist and drought treatments.

Treatment	Share of the total biomass (%)			Total biomass (g m^{-2})
	Cut 1	Cut 2	Cut 3	
Moist	56.3 (± 3.2)	28.2 (± 3.0)	15.5 (± 2.0)	3000 (± 49.6)
Drought	64.0 (± 5.5)	19.5 (± 1.9)	16.5 (± 3.6)	1906 (± 185.7)

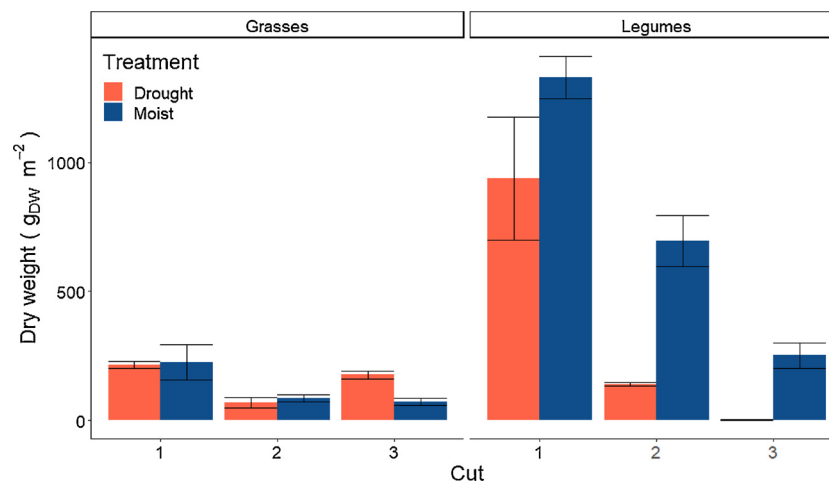


Fig. 3. Average of dry weight biomass ($\text{g}_{\text{DW}} \text{m}^{-2}$) and standard error of each functional group, weighted after each cut for vegetation subjected to different treatments: drought (red) and moist (blue).

in cut 3, dry weight was not significantly different in both treatments ($469 \text{ g}_{\text{DW}} \text{m}^{-2} \pm 67.7$ in moist lysimeters and $296 \text{ g}_{\text{DW}} \text{m}^{-2} \pm 41.5$ in drought lysimeters), and the share of the total biomass obtained was similar.

Analysis of the functional groups present in the lysimeters revealed differences in biomass productivity. Legumes showed a general decrease in biomass over time (ANOVA, $p < 0.001$). After cut 1, they represented $79.1\% (\pm 5.2)$ of the total biomass in moist lysimeters and $71.8\% (\pm 7.0)$ in drought lysimeters (Fig. 3). The share of legume biomass decreased after cuts 2 and 3 (ANOVA, $p < 0.001$ in both cuts), and the biomass was different between moist and drought treatments in cut 2 (ANOVA, $p < 0.01$) and in cut 3 (ANOVA, $p = 0.015$), where legumes in drought lysimeters were negligible (Fig. 3). Nevertheless, grass biomass was similar in cut 1 and 2 and differed in cut 3 (ANOVA, $p = 0.017$), where weighted grass dry biomass and the percentage of grass biomass in the drought treatment ($176 \text{ g}_{\text{DW}} \text{m}^{-2} \pm 16.9$ and $60.8\% \pm 4.4$) were higher than in the moist treatment ($71.5 \text{ g}_{\text{DW}} \text{m}^{-2} \pm 13.5$ and $15.1\% \pm 1.1$).

Along with a functional group shift, coverage changed at species level (Table 2). Moist and drought treatment lysimeters showed similar shares of species at cut 1, during the pretreatment, when the dominance of *Trifolium pratense* was evident. *Trifolium pratense* coverage decreased slightly at cut 2 after Drought period 1 (80.3%) and further decreased at cut 3 (13.5%). *Trifolium repens* coverage also decreased after Drought period 1, although in all periods and treatments, its abundance was low. In contrast to legumes, the most abundant grass species *Dactylis glomerata* increased its coverage in the drought treatment, approximately 64% from cut 1 to cut 3. The less abundant grass species (*Poa trivialis*, *Festuca rubra* and *Festuca pratensis*) decreased under drought conditions, with a total coverage below 5%. Under moist conditions *Trifolium pratense* abundance decreased by only 14.0% from cut 1 to cut 3, while *Dactylis glomerata* abundance increased by 7.0%.

Table 2

Coverage (%) (\pm SE) of the most abundant species present in the lysimeters subjected to moist and drought treatment, assessed after each of the three cuts made during the experiment. Species represented in the table represented more than 95% of the total coverage, other species are considered negligible.

Species	Moist			Drought		
	Cut 1	Cut 2	Cut 3	Cut 1	Cut 2	Cut 3
<i>Dactylis glomerata</i>	2.3 (± 1.1)	2.7 (± 1.0)	9.3 (± 2.4)	5.7 (± 1.9)	6.7 (± 1.7)	70.0 (± 3.3)
<i>Festuca pratensis</i>	1.0 (± 0.5)	1.2 (± 0.8)	1.5 (± 1.1)	1.3 (± 0.7)	0.7 (± 0.3)	0.5 (± 0.4)
<i>Festuca rubra</i>	1.7 (± 0.6)	1.3 (± 0.3)	3.0 (± 0.0)	1.5 (± 0.4)	1.3 (± 0.3)	5.0 (± 0.0)
<i>Poa trivialis</i>	0.5 (± 0.2)	0.5 (± 0.4)	3.7 (± 2.6)	1.0 (± 0.5)	1.3 (± 0.7)	0.0 (± 0.0)
<i>Trifolium pratense</i>	90.3 (± 1.4)	89.7 (± 1.1)	76.3 (± 0.7)	85.7 (± 3.1)	80.3 (± 2.6)	13.5 (± 8.1)
<i>Trifolium repens</i>	3.3 (± 0.7)	3.3 (± 0.7)	5.0 (± 2.1)	8.3 (± 1.4)	7.7 (± 1.1)	5.0 (± 0.0)

Table 3

Results (regression coefficients, β) of multiple linear regressions to predict the transpiration of grasses and legumes at the different phases of the experiment, based on the number of days since the last cut (Senescence) and the effect of the drought treatment. Significant correlations are shown in bold (* $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$).

Treatment phases	Grass T		Legume T	
	Senescence	Treatment	Senescence	Treatment
Pre-treatment	-0.001	0.160	0.002 *	-0.259
Drought period 1	-0.003	-0.178 *	0.007	-0.699 ***
Rewetting	-0.012	0.161 *	-0.002	-0.219 ***
Drought period 2	0.002	-0.037	0.002	-0.429 *

Comparison between lysimeters under moist and drought conditions within each functional group suggested differences not only in biomass, but also in T rates (Table 3, Fig. 4). Grass T differed between treatments during Drought period 1 (lm, $p = 0.036$, $R^2 = 0.137$), where drought and heat had a negative effect on T. The T of grasses also differed during Rewetting (lm, $p = 0.014$, $R^2 = 0.261$), although in this case, lysimeters which have had suffered a drought treatment showed higher T values. Nevertheless, in both cases, the coefficient of determination (R^2) was low. In Drought period 2, grass T did not differ between treatments. On the other hand, drought showed negative effects on legume T during Drought period 1 (lm, $p < 0.001$, $R^2 = 0.522$), Rewetting (lm, $p < 0.001$, $R^2 = 0.527$) and Drought period 2 (lm, $p = 0.015$, $R^2 = 0.486$). Legume T in Rewetting and Drought period 2 was low (near 0) because of an actual lower T of the plant or because the low presence of legumes leaves (Fig. 3) difficult the measurement of the stomatal conductance. The number of days since the last cut represents the senescence of the vegetation and is only significant for

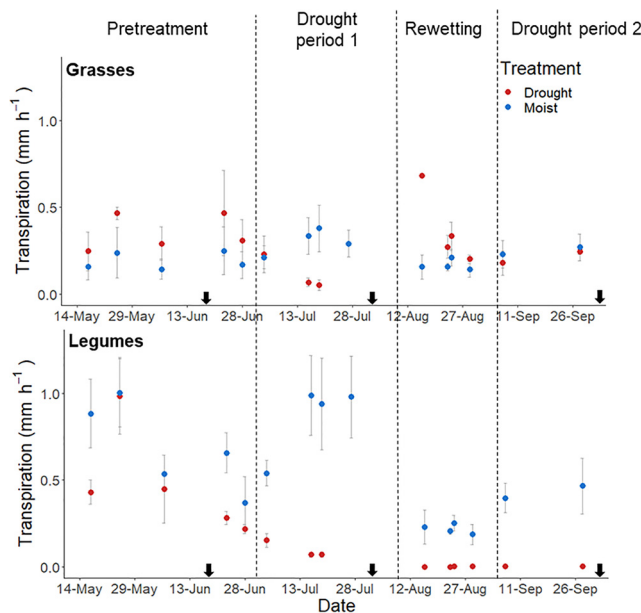


Fig. 4. Changes in the average transpiration (mm h^{-1}) (\pm SE) of grasses and legumes throughout the experimental period. Arrows indicate the three cuts made during the experiment.

legume T during the Pre-treatment, when a cut was made in the middle of the phase and the aging of the plants affects T positively.

To assess the performance of the vegetation after the drought periods and to compare it to the other phases of the experiment, the WUE ($\text{g}_{\text{DW}} \text{kg}_{\text{H}_2\text{O}}^{-1}$) was calculated after every cut as the dry weight of plant material produced (Fig. 4) per unit of water used (ET). The WUE levels for the lysimeters in both treatments were similar at cut 1 (Fig. 5) and decreased over time in all lysimeters. Biomass productivity per unit water usage at cut 2, after Drought period 1, was lower in drought ($1.4 \text{ g}_{\text{DW}} \text{kg}_{\text{H}_2\text{O}}^{-1} \pm 0.3$) than in moist lysimeters ($2.7 \text{ g}_{\text{DW}} \text{kg}_{\text{H}_2\text{O}}^{-1} \pm 0.1$; ANOVA, $p = 0.017$). After Rewetting and Drought period 2, the WUE in drought lysimeters increased slightly at cut 3 ($1.8 \text{ g}_{\text{DW}} \text{kg}_{\text{H}_2\text{O}}^{-1} \pm 0.1$), with similar values when compared to the moist lysimeters.

4. Discussion

4.1. Alpine grassland responses to drought

As expected, the intensive Alpine grassland followed a water-spending strategy and therefore hardly reduced ET with decreasing

water availability until close to the PWP. During the first drought period, pF was close to PWP, total biomass productivity was also negatively affected by drought and heating, and the share of biomass productivity throughout the vegetation period was altered, decreasing the yield after the first drought. During Drought period 2, there were no differences in ET between treatments, despite the reduction in SWC, but the PWP was not reached. At the third cut, all lysimeters had the same share of biomass for both treatments. As Naudts et al. (2011) noted, a severe drought event during the growing season does not alter the overall response of plant productivity after a period of recovery. Walter et al. (2011) highlight the ability of grasses to be more resistant to recurrent droughts; however, in this study, it is difficult to determine if the higher resistance is more related to the recurrence or to the lighter intensity of the Drought period 2. Although both drought and heating were implemented, we attribute the measured effects mainly to drought or a combination of drought and heating, since ET_0 was similar in both treatments, and temperature - which is a variable in the FAO Penman-Monteith equation - does not seem to have a high impact. Accordingly, De Boeck et al. (2016) concluded that plants suffered clear stress only when heat waves were combined with drought, and suggested that it may be a direct effect of drought as well as of a combination of a high-temperature stress and decreased water to mitigate it. Another aspect that must be considered in this study is the effect of the heterogeneity of the treatment between the small lysimeters caused by uneven irrigation - which we tried to solve by manual adjustments - or by the uneven IR radiation of the lysimeters. Heterogeneity can also be caused by a different development of the canopy structure, although slight differences in coverage between lysimeters are only visible for *Dactylis glomerata*.

The grassland community appears not to be optimised to save water and might experience drought effects more strongly and earlier than other grassland communities with a conservative strategy (Frenck et al., 2018). The WUE of the grassland decreased by the first drought, when more water was needed to produce biomass, and it showed similar values than in the moist treatment after the rewetting and second drought. On the other hand, the WUE in the moist treatment also showed a dramatic decrease from cut 1 to cut 2. This could be explained by the increased temperatures in July (between cut 1 and 2), when leaves could enhance stomatal conductance and T to compensate the heat increment (Briffa et al., 2009), losing water and disturbing the trade-off between carbon assimilation and T. The strategy followed by the intensive Alpine grassland could also be described as anisohydric, which means a non-strict regulation of T. However, this terminology only describes the water regulation of the vegetation and excludes biomass productivity, which is included when using the terms water spenders or savers (Frenck et al., 2018; Martinez-Vilalta and Garcia-Forner, 2017). Although the results on the isohidricity (i.e. water

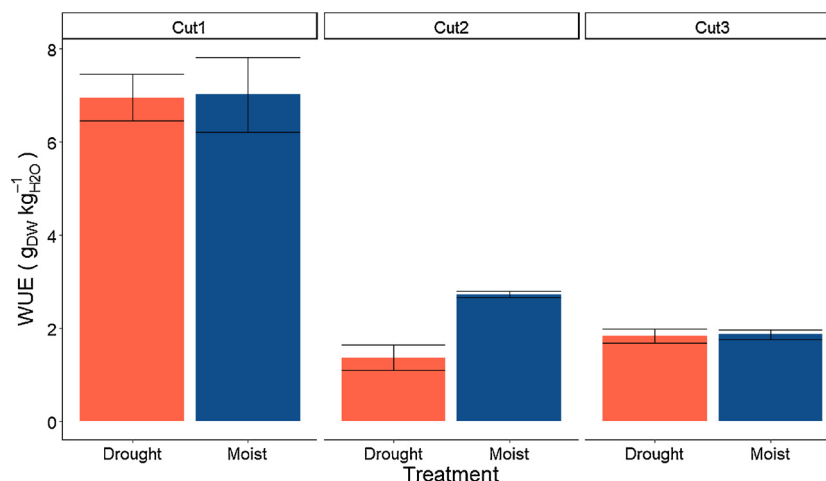


Fig. 5. Water use efficiency (WUE) ($\text{g}_{\text{DW}} \text{kg}_{\text{H}_2\text{O}}^{-1}$) at each cut for the lysimeters subjected to drought (red) or moist (blue) treatments.

regulation) and WUE seem to agree, other parameters, which were not varied in this study have a high impact on WUE, i.e. light use efficiency and soil texture (Konings and Gentine, 2017).

4.2. Drought impacts at the plant functional group level

Detailed investigations showed the processes underlying the strategy followed by the grassland community. The adaptation to increasing temperatures and persistent drought periods was specific to each functional group present in the lysimeters. Grasses seem to have a better resistance to drought and heat and reacted differently than legumes in terms of biomass productivity. During the first drought period, both legumes and grasses showed a decrease in transpiration in relation to the vegetation under the moist treatment. Measurements showed that stomatal conductance increased at the beginning of the drought treatment to compensate the heat increment in the drought plots by cooling the ambient by higher T (Briffa et al., 2009) when groundwater supply was still generous. When water was scarce, T decreased until almost zero, and either the stomata were closed to avoid losing water or there was no more available water to transpire and the leaves wilted. A difference between grasses and legumes is evident at this point. Although transpiration decreased for both functional groups, legumes produced less biomass in the drought lysimeters than in the moist lysimeters, whereas grasses maintained a similar biomass. Thus, grasses produced the similar amount of biomass with lower water resources, showing higher WUE values than legumes. In contrast to our results, in a drought experiment performed by Hofer et al. (2017) with four grassland species, legumes (*Trifolium repens* and *Trifolium pratense*) lost a lower amount of biomass and were more resistant to drought conditions than non-legumes (*Lolium perenne*, *Cichorium intybus*), as long as the water scarcity did not become extreme enough to reach the PWP. In the studied intensive grassland, water scarcity was so severe that the PWP was reached soon. The PWP is understood as the minimal matric potential at which plants are able to take up water, nevertheless grasses may resist and absorb water at lower matric potentials (Kirkham, 2005a). This higher resistance of grasses may be explained by the structure and architecture of the plant community and of each functional group. Legumes usually invest most of their energy in the stems which raise the horizontal leaves to the highest levels of the canopy. The upper leaves are fully exposed to sunlight and heat; in addition, the horizontal leaves shade the competitors (Tappeiner and Cernusca, 1996). On the other hand, the leaves of grasses are hidden on a lower level, do not receive direct sunlight at noon because of their angular orientation and are narrow; these traits reduce the level of exposure to the sun and therefore also leaf heating and transpiration (de Bello et al., 2010; Knight and Ackerly, 2003; Tappeiner and Cernusca, 1996). As Kardol et al. (2010) suggest, the responses of the subdominant community (grasses in this case) often do not reflect the climate change responses of the whole community. The dominant functional group (legumes) may respond to the direct impact of the drought treatment, whereas the subdominant group responds to altered competitive interactions with the dominant species. Thus, the response of grasses should be interpreted as a combined response to the drought treatment and the competition with the dominant legumes.

During rewetting, legumes, which were strongly affected during Drought period 1, did not recover in terms of water fluxes or biomass productivity. The low values of T may be attributed to the absence or lower representation of leaves in legumes because of a poor regrowth of the plants. In contrast, grasses recovered fast from Drought period 1. They show a fast regrowth, as suggested by Stampfli et al. (2018), and even exceeded the transpiration rates of lysimeters under moist conditions. The fast recovery of grasses indicates a good resilience as well as the absence of biochemical or photosynthetic damage (Brilli et al., 2011), contrary to legumes. The decrease in legumes could be at some point positive for the recovery of grasses, enabling them to receive more light and to have more space to grow. In addition, when rewetting

occurs after a drought period, the microbial activity in soils increases rapidly (Borken and Matzner, 2009), being an important source of C and N, which increase when fresh litter (i.e. roots, leaves) becomes available (Borken and Matzner, 2009; Hofer et al., 2017). Nitrogen availability is even higher if the necromass is from legumes. Grasses, which respond strongly to nutrient addition (Klanderud, 2005; Stampfli et al., 2018), could use the increasingly available nutrients to grow even more than the vegetation under moist conditions, showing a high resilience.

Grass T seemed to be insensitive to the Drought period 2, and biomass productivity was even strengthened. Although increased leaf heating may enhance transpiration, the usual formation of dew at this time of the year may moisten the environment and alleviate drought stress. Legumes, however, were affected even by the slighter drought (Drought period 2). The uncertainties in the T results during the second drought period could be explained by the small number of stomata measurements (only two) and by the little legume biomass present or the sensitivity of legumes to other factors, i.e. heat. Plants with wide leaves, i.e. legumes, would rather be affected by the increase in the ET due to an increase in temperature. Because of the long duration of the experiment, the phenology of the species could also have a considerable effect. Although the analysed legumes usually show a long flowering time, from May to September for *Trifolium repens* and to October for *Trifolium pratense* (Landolt et al., 2010), they may have more difficulties to regrow after a severe drought in August because of the advanced stage in the growing season. According to Landolt et al. (2010), *Dactylis glomerata* flowers only in early spring, from May to June, however, this experiment revealed a still high abundance of *Dactylis glomerata* at the end of Drought period 2 in September.

The responses of the analysed functional groups throughout the experiment may be supported by the strategies and the ecology of the species present (da Silveira Pontes et al., 2015). According to Landolt et al. (2010), *Trifolium pratense* and *Dactylis glomerata* show a high preference for moderately humid soils, while *Trifolium repens*, *Poa trivialis* and *Festuca pratensis* are more variable and could also be found in moderately dry soils. In agreement, *Trifolium pratense* coverage decreased when the soil was dry enough to reach the PWP. On the other hand, *Trifolium repens*, *Poa trivialis* and *Festuca pratensis* showed a slight decrease in coverage, despite their adaptive capacities; *Dactylis glomerata* coverage increased throughout the experimental period, even after Drought period 1. Other investigations made in the laboratory by Brilli et al. (2011) showed that *Trifolium pratense* and *Dactylis glomerata*, among other species, are insensitive to progressive drought until extremely low SWC (PWP), acting like water-spending plants. In our experiment, the PWP was reached, and thus, *Trifolium pratense* abundance decreased, although *Dactylis glomerata* remained insensitive. Other studies performed in the Mediterranean region (Zhou et al., 2019) agree with our results about *Dactylis glomerata*, determining that some hybrids were able to regrow after severe drought and produce even better than the parents under rain-fed conditions in spring. Regarding the resilience of the studied legumes and according to Hofer et al. (2017), *Trifolium pratense* shows a high resilience, which does not agree with our results. The differences among different studies may stem from the different severities of the drought treatment.

4.3. Implications of a shift in vegetation composition

The different strategies followed by the studied functional groups caused a shift in vegetation composition from legumes to grasses, where the most resilient species enhanced their coverage and productivity. This shift in the dominance of functional groups was beneficial after an extreme drought event (Drought period 1), increasing the WUE of the community up to the same values than moist lysimeters, but not exceeding them. This also raises the biomass productivity near to the values at moist conditions. However, it is unclear whether this is a short-term adaptation or whether the new composition will show a high

resistance, resilience and quality of the biomass in the future. However, the shift from legumes to grasses affects other aspects of the ecosystem, such as soil nutrient availability. Legumes have a high importance in crops mixed with other species because they lower the effects of N leaching. Legumes also fix high amounts of atmospheric nitrogen, making them available to other plants, and release high-quality organic matter to the soil in terms of the C/N ratio, which facilitates nutrient solubilisation and uptake from deeper soil layers (Stagnari et al., 2017; Vogeler et al., 2019). In the absence of legumes, the addition of external nitrogen is usually necessary, although there are evidences that the nitrogen use efficiency of many plants is strongly reduced by replacing biological nitrogen fixation by legumes with external fertiliser (Adams et al., 2018). In addition, forage quality may change in accordance to a new community structure. Regarding the nutrient aspects of each functional group, grasses provide more fibre because of their high contents of lignin, cellulose and hemicellulose. On the other hand, legumes usually provide high amounts of protein (French, 2017). There are some disagreements in the literature regarding which type of grassland provides better forage, mainly because of the variability in species composition and the differences when the samples are taken. For example, *Dactylis glomerata*, as a grass, provides fibre but also increases the protein content (Aufère et al., 2003; Davies and Morgan, 1982), which could compensate for the absence of proteins from legumes after the drought period. In general, species-rich compositions improve forage quality (French, 2017; Reiné et al., 2014), especially compared to monocultures (i.e. *Phleum pratense* and *Dactylis glomerata*) of some grasses, and contain elevated levels of specific minerals associated with livestock growth and health (Ca, Mn and K) (French, 2017). Thus, we should highlight and consider that not only the amount of forage is important, but also the quality.

4.4. Implications for alpine grasslands

Alpine grassland species often follow water-spending strategies under severe drought conditions, especially in the Austrian Alps, which follow a less conservative strategy compared to the Italian and French Alps (Frenck et al., 2018; Leitinger et al., 2015). Such a lack of gradual stomatal regulation to progressive soil water reduction is likely the result of an evolutionary adaptation to an environment rarely subjected to water scarcity (Brilli et al., 2011; Hofer et al., 2017). According to Wieser et al. (2008), Austrian Alpine grasslands are currently not threatened by severe drought periods, and even when up to 90% of the precipitation are evaporated, no water stress occurs. However, in a scenario with persistent droughts (Gobiet et al., 2014) Alpine soils will reach critical SWC levels, and the grassland composition is expected to change, as predicted in this study. In addition, non-native or invasive plant species with more conservative water use strategies, more plasticity in terms of WUE (Brock and Galen, 2005) and in the interaction with other species (Klanderud, 2005) may gain advantages over the existing plant association. The shift of species in Alpine grasslands and an excessive use of water resources may have consequences not only for ecosystem services at local level, i.e. forage production and quality, biodiversity, soil fertility and water quality (Schirpke et al., 2017), but also for downstream water users (Brilli et al., 2011), which may diminish the potential for hydroelectric production and have impacts at the socio-economical level (Beniston, 2012; Schirpke et al., 2019).

Given the importance of Alpine grasslands not only at a local scale, but at different spatial levels, more studies are needed to fully understand the water fluxes and reactions of grasslands to the predictions made in the Alpine region (Gobiet et al., 2014). According to the presented results, the main share of the yield is produced at the beginning of the season, where the WUE is higher. Therefore, the loss of yield due to summer drought periods represents a slight share of the total forage production, while drought and heating events in spring may be more damaging and should be analysed in more detail. For a better understanding of the water fluxes underlying grassland productivity, further

studies should also consider the importance of the belowground biomass on productivity, water fluxes and plant adaptation. Because plants under drought stress invest their energy in root development, rather than in aboveground biomass (da Silveira Pontes et al., 2015; Knapp et al., 2008), this issue deserves further attention.

CRediT authorship contribution statement

Elena Tello-García: Conceptualization, Formal analysis, Methodology, Writing - original draft. **Lisa Huber:** Conceptualization, Formal analysis, Methodology, Writing - review & editing. **Georg Leitinger:** Conceptualization, Writing - review & editing, Resources, Supervision. **Andre Peters:** Software. **Christian Newesely:** Resources. **Marie-Eve Ringler:** Investigation, Formal analysis. **Erich Tasser:** Conceptualization, Writing - review & editing, Supervision, Project administration.

Declaration of Competing Interest

The authors declare that there are no conflicts of interest.

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Appendix A. Supplementary data

Supplementary material related to this article can be found, in the online version, at doi:<https://doi.org/10.1016/j.envexpbot.2019.103921>.

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