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Community specific hydraulic conductance potential of soil water decomposed for two Alpine grasslands by small-scale lysimetry

Georg Frenck[ab], Georg Leitinger[ab], Nikolaus Obojes[a], Magdalena Hofmann[b], Christian Newesely[b], Mario Deutschmann[b], Ulrike Tappeiner[ab] & Erich Tasser[a*]

[a] Institute for Alpine Environment, EURAC research, Viale Druso 1, 39100 Bozen/Bolzano, ITA

[b] Institute of Ecology, University of Innsbruck, Sternwartestrasse 15, 6020 Innsbruck, AUT

Correspondence to: Erich Tasser (erich.tasser@eurac.edu)

Abstract: For Central Europe in addition to rising temperatures an increasing variability of precipitation is predicted. This will increase the probability of drought periods in the Alps, where water supply has been sufficient in most areas so far. For Alpine grasslands, community specific imprints on drought response are merely understood. In a replicated mesocosm experiment we compared evapotranspiration and biomass productivity of two differently drought-adapted vegetation communities during two artificial drought periods divided by extreme precipitation events using high precision small lysimeters. The drought adapted vegetation type showed a high potential to utilize even scarce water resources combined with a low potential to translate atmospheric deficits into higher water conductance with biomass production staying below those measured for the non-drought-adapted type. The non-drought-adapted type, in contrast, showed high water conductance potential with strongly increasing ET rates when environmental conditions became less constraining. With high rates even at dry conditions, this community appears not to be optimized to save water and might experience drought effects earlier and probably stronger. In summary, the vegetation's reaction two co-varying gradients of potential evapotranspiration and soil water content revealed a clear difference of vegetation development and between water-saving and water-spending strategies regarding evapotranspiration.

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Comprehensive alterations in the climate system of the earth are projected for the future decades. Due to increased greenhouse gas concentrations in the atmosphere, the global average temperature is predicted to rise. These changes in the energy budget of the atmosphere are suggested to propagate alterations in atmospheric circulation and modify precipitation patterns worldwide (IPCC, 2013; Knapp et al., 2008; Solomon et al., 2009). Such variations can result in changes of the spatial distribution of precipitation and thereby affect average values of rainfall locally. However, concurrent changes in the temporal occurrence are predicted to increase the variability of rainfall with longer intervals in between and more extreme events. This will lead to stronger variability in soil water availability and longer droughts (IPCC, 2013, 2012).

The water balance in terrestrial ecosystems is dominantly controlled by plant processes. It is suggested that up to 80% of the terrestrial water loss to the atmosphere is mediated through plant transpiration(Jasechko et al., 2013). Consequently, it is assumed that plants will experience drought stress more frequently, which may constrain primary productivity as the latter is substantially controlled by the supply of water (Knapp et al., 2008). These direct effects of limited water provision to the system will be accompanied by increased water demand in a warmer world, leading to more negative water balances, which will accentuate drought effects on vegetation processes (Heimann and Reichstein, 2008). ~~However,~~ structure and functionality of the ecosystems - defining rates of evapotranspiration - are also subject to local climatic conditions. Hence, a direct feedback mechanism is established, which might amplify or dampen the global and local consequences of climatic change on ecosystems (Heimann and Reichstein, 2008).

Defining productivity-precipitation relationships of ecosystems is of focused interest, because structural changes in soil-plant-atmosphere interface, which control water fluxes into the atmosphere will inherently be affected by the manifestation of that relationship. However, beyond the direct implications of limited water availability on biomass production and growth, the composition of individual plant species in the community and resulting functional structure of that community will adjust, optimising water use according to different life-history strategies by competitive interactions (Peñuelas et al., 2004). In turn, immediate vegetation responses to fluctuations in precipitation patterns and the strength of interaction with productivity functions will strongly depend on the functional composition of the community and ecosystem considered. Therefore, intrinsic characteristics of vegetation will impose another layer of complexity for defining the interactive feedbacks in the relationship between water budget and productivity.

The impact of shifting precipitation regimes can be predicted only inaccurately if the crucial components of the ecosystem water budget - soils, plants and the atmosphere - are evaluated separately and isolated. Due to the complex interactions and processes at different spatio-temporal scales the response of ecosystems to shifts in the water regime are preferably examined in an integrative manner on the system level (Silva, 2015). Manipulative experiments are a well suited option for investigating the effects imposed by changes in precipitation frequency and intensity below and above the natural range on the ecosystem level (Estiarte et al., 2016). Since we currently lack knowledge needed to validate the projections for consequences of future changes in rainfall regimes, insights from such integrative investigations are highly valuable for providing important benchmarks of model based assessments (Estiarte et al., 2016).

Numerous studies were performed to reveal the response of temperate grasslands to climatic changes and extremes, while only few investigations targeted Alpine systems (De Boeck et al., 2016). While the Alps did not often experience droughts during the past (van der Schrier et al., 2007), the region has undergone exceptionally fast climatic changes during the late 19th through early 21st century (Auer et al., 2007; Beniston, 2005; Böhm et al., 2001; Ciccarelli et al., 2008; Rebetez and Reinhard, 2008). Considering the fundamental role Alpine systems have to water accumulation and freshwater supply for large parts of Europe (Messerli et al., 2004; Viviroli et al., 2003) it seems surprising that the responses of ecosystems in the Alps to changes in precipitation have not drawn more scientific attention. However, while projections suggest only moderate variations of yearly average rainfall in the Alps, significant alterations within the temporal occurrence of rainfall events with a decrease in summer precipitation and increases from winter through spring are implied (Beniston, 2012; Beniston et al., 2007). The decrease of water supply during warmer summer months will potentially increase the frequency and intensity of drought events in the near and longer future in Alpine ecosystems (Gobiet et al., 2014).

For unravelling ecosystem water fluxes at the soil-plant-atmosphere interface, the lysimeter methodology provides the precise and realistic means by allowing to decompose the driving sub-processes: evapotranspiration (ET), precipitation (P) and drainage below the rooting zone (Peters et al., 2014). By avoiding systematic errors prone to traditional measurement systems, the determination of the net water balance is highly accurate and robust (Schrader et al., 2013). If embedded into a surrounding ecosystem, automated lysimeter units, which do not need access to perform manual weighing, measure water fluxes with a minimum of disturbance to the natural boundary layer and microclimatic conditions. Such implementations of autonomous weighable high precision lysimeters provide unprecedented realism to the description of ecosystem water balances, especially when filling of the lysimeters was performed to maintain natural soil layering and the connectivity of pores, while keeping potential impacts on the vegetation community low. Over the recent years, several of these units have been established over Europe, e.g. a network of 126 lysimeters at 12 sites has been established to monitor climate chance induced alterations in hydrological cycling within the TERENO project in Germany (Bogena et al., 2006; Zacharias et al., 2011). However, the large dimensions (1m diameter/ volume) and the corresponding economic efforts for their establishment did mostly eliminate the possibility for replicated manipulative experiments employing fully integrated lysimeters.

In a common garden experiment we used a network of automated small scale lysimeters to emerge community specific differences in the temporal dynamics of soil water depletion and evapotranspiration. Two different Alpine grassland communities were subjected to contrasting levels of water availability. Sheltered from natural precipitation, soil water content was manipulated by applying two distinct irrigation regimes: one providing water in regular intervals and another exposing the corresponding experimental units to extended periods of drought. The natural variability in the atmospheric demand of water vapour coupled to the manipulated water availability in the soil allowed to investigate and reveal vegetation specific conductance properties and water utilisation patterns. For this study we hypothesize that the vegetation adapted to local, humid conditions and characterized by high biomass and a water spending strategy will keep transpiration rates high while soil water availability is decreasing until a sudden decline near wilting point. As a consequence it will also continue to

produce biomass until the break point. In contrary, the water saving strategy of the drought-adapted vegetation will lead to a continuous decrease of transpiration and biomass production with decreasing soil water availability.

2.1 Characteristics of the experimental field site and lysimeter installation

The study site of the experiment was established during early summer 2014 in the LTER-Austria site 'Stubai' (valley bottom meadow) Neustift im Stubaital ~~(A)~~. The site for the garden-experiment was located on the valley floor at 972 m a.s.l. (WGS84: N47.115833, E11.320556) in a meadow used for hay production.

Table 1 Summary of site conditions and vegetation properties

site	Stubai (S) – study site location	Matsch/Mazia (M) – transplant origin
municipality	Neustift im Stubaital, Wipptal/Austria	Mals/Malles, Vinschgau/Italy
elevation/ altitude (m a.s.l.)	970	1570
longitude/ latitude	47°07'05''N 11°19'17''E	46°41'19''N 10°34'42''E
average temperature (°C)	6.5	6.6
average precipitation (mm)	1097.0	526.7
growing season length (no of days with average temperature of at least 5 °C)	224	190
land-use	hay meadow/ 3cuts per yr/ fertilized with cow dung	hay meadow/ 2cuts per yr/ fertilized with cow dung
soil type	gleyed Camisol (A-Bv-Go)	Camisol (Ah-Bv-C)
classification	loamy sand to sandy silt	loam to sandy loam
phytosociological classification	Poo trivialis - Alopecuretum pratensis (Regel 1925)	Ranunculo bulbosi-Arrhenatherum (Ellmauer)
species inventory (responsible for 90% of total plant cover in the lysimeter)	*Achillea millefolium, Carum carvi, Pimpinella major, Poa trivialis, Ranunculus acris, Rumex acetosa, Taraxacum officinale, Trifolium pratense*	*Achillea millefolium, Anthoxanthum odoratum, Anthriscus sylvestris, Carum carvi, Festuca rubra, Leontodon hispidus, Lotus corniculatus, Poa trivialis, Primula veris, Taraxacum officinale, Trifolium montanum, Trifolium pratense, Veronica officinalis*

For this experiment six plots of 3.5 × 3.5 m were established. Traversing the corresponding area, each plot was defined by installing half-cylindrical metal frames. In the centre of each plot these frames providing the base for the rain sheltering reached a height of approx. 2.5 m. In each corner at the outer plot margin four irrigation sprinklers pointing

towards the centre of the plot were set up. The irrigation system described in detail by (Newesely et al., 2015) was used to simulate precipitation during periods of experimental manipulation of water provision to the system.

In the centre of each plot two small-scale lysimeters with 0.3 m diameter were installed in collaboration with, and supervised by the employees of the manufacturer (Smart-Field-Lysimeter, UMS/Meter Group Munich, Germany). Every lysimeter was filled with a soil-vegetation monolith by cutting the hollow cylindrical lysimeter blank into an undisturbed patch of the corresponding ecosystem. This compression free procedure allowed to remain the original and unaffected stratification of the soil and to conserve the natural composition of pore spaces within the monolith. The filled lysimeter blanks were subsequently excavated and cut horizontally at a depth of 0.3m. The bottom of the lysimeter was closed with a tension controlled hydraulic boundary connected to a bi-directional pumping system to regulate water flow into and out of the lysimeter. After inserting soil moisture, temperature (EC-5 Small Soil Moisture Sensor, Decagon Devices, USA) and matrix potential probes (MPS-2, Decagon Devices, USA) at 0.05, 0.15 and 0.25m depth into the lysimeter monolith, each system was placed on a weighing platform (accuracy of 0.005 kg, PL-50, UMS/Meter Group Munich, Germany). Two of these lysimeter units were installed in the centre of every experimental plot within a two by two quadratic grid of 1.2m edge length with their relative position to each other assigned randomly.

The two monoliths in every plot were excavated from different types of vegetation, one containing a mesocosm of the meadow surrounding the experimental field site (S, Table 1), and another one which was excavated and transplanted from Matsch/Mazia with contrasting environmental and biotic properties to those of the study site (M, Table 1). The Stubai grassland is classified as Poo trivialis - Alopecuretum pratensis with a community of low complexity: abundant Poaceae accompanied by some herb species (Wohlfahrt et al., 2008). The meadow is actively managed, cut two to three times each year and fertilized with cow manure in spring and autumn (approximately 0.35 kg dry matter per m², Table 1). The local climate is dominated by high total precipitation values, especially in the summer. The vegetation of second origin (Matsch/Mazia) is characterised by the traditional, more extensive use of the corresponding system. The Matsch Valley has a dry inneralpine climate with a mean precipitation of 527 mm per year and a mean temperature of 6.6 °C (Hydrographical Department of the Autonomous Province of Bozen-South Tyrol). The vegetation is a dry hay meadow (Ranunculo bulbosi - Arrhenatherum, Ellmauer) on loam to sandy loam. The site is fertilized with cow dung and cut two times each year. The excavation location of the replicate lysimeters was optimized according to the presence of representative and joint species in the respective vegetation patches. After installing the local and transplanted lysimeter mesocosms during early summer 2014 into the experimental plots, the vegetation surrounding the lysimeters could recover from disturbances of necessary soil works required to wire the fully automated measuring system until spring 2015.

At the field site, all experimental plots and the vegetation in the lysimeters was managed (cut, fertilized) concurrently to land-use scheme of the surrounding meadow. The experimental period started in the last third of June 2015 during the re-growth interval after the first cut at the beginning of June. With beginning of the experiment rain shelters were closed using a UV permeable transparent polythene film (Lumisol Clear AF, 88% - 92% light transmittance). In order to avoid shielding of

the wind and to allow the establishment of natural boundary conditions, shelters were left open on the sides facing the main wind direction and closed down to just 0.5 m above the soil level on the lateral sides. Over a period of 52 days the plots of the experiment were subjected to control watering within the two different irrigation schemes (Fig. 1). Concurrently with closing of the rain shelters precipitation was provided from the irrigation sprinklers mimicking average rain fall amounts and intensities for the 30 year period between 1970 through 2000 in the treatment with regular watering. However, due to a mistake by the technician responsible for setting up the automated irrigation protocol the watering scheme stayed below the intended amounts for approximately the first half of the experimental period making manual compensation occasionally necessary. Automated irrigation was programed to occur around mid-night in order to avoid immediate transpiration from the surface and allow the provided water to penetrate into the soil compartment. Manual adjustments and checks on the precipitation simulator were usually performed during day-time. The lysimeter mesocosms in the treatments with regular watering (REG) received approx. 117 kg$H2O$ per m², those in the treatments with extended drought periods an average of 65 kg$_{H2O}$ per m² throughout the duration of the experiment and according to the scheme presented in Fig. 1.

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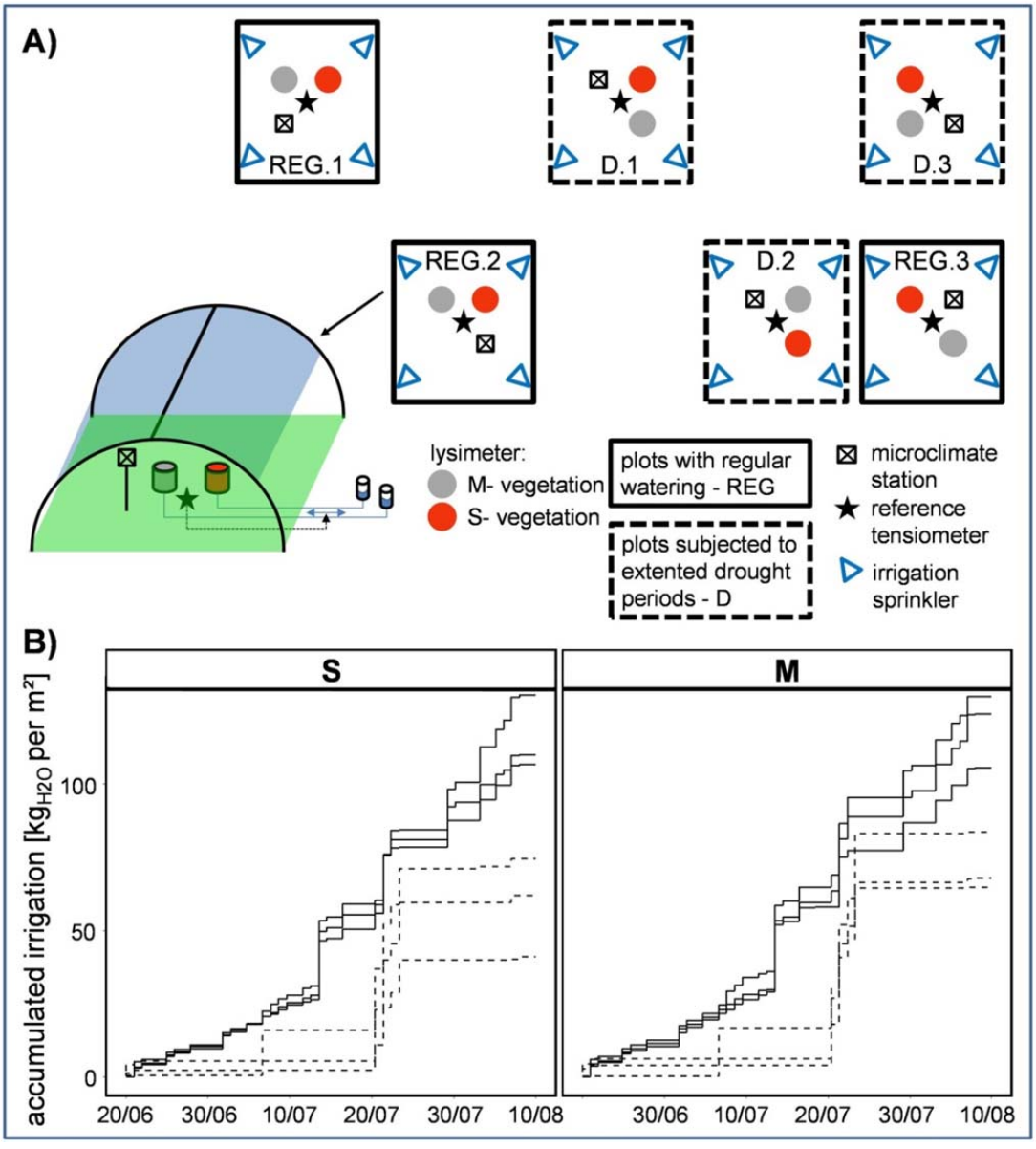

148

149 **Fig 1: A) Schematic overview of the experimental design and plot setup; B) Manipulation of water availability for individual**
150 **lysimeters of the two vegetation types (Stubai (S) & Matsch/Mazia (M)) by contrasting irrigation schemes - one providing water on**
151 **a regular basis (REG, solid lines), one with extended drought periods (D, dashed lines)**

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153 **2.2 Automated measurements**

154 In the centre of each of the six plots a microclimate station measuring air temperature and relative humidity (height:
155 1m; U23-002 HOBO® External Temperature/Relative Humidity Data Logger, Onset Computer Corporation, USA), solar
156 radiation (height: 1m; S-LIB-M003, Solar Radiation Sensor, Onset Computer Corporation, USA), wind speed (height: 1 m;
157 DAVIS® Standard Anemometer 7911, Davis Instruments, USA) and soil water content 0.05 and 0.2m below the ground (S-
158 SMA-M005, Soil Moisture Smart Sensor – 0.2 m ECH2O® probes, Decagon, USA) was installed. The corresponding
159 measurements were logged for every ten minutes interval (HOBO Microstation® Data Logger; Onset Computer Corporation,
160 USA).

161 For each of the lysimeter, weight data were recorded every minute, data received from matric potential, soil
162 temperature and water content sensors (each in 0.05, 0.15 and 0.25 m depth) in ten minutes intervals. The hydraulic
163 boundary at the bottom of each lysimeter was connected to a reservoir of drainage water with the corresponding container
164 also being placed on a balance. A bi-directional pumping system allowed the adjustment of the water content at the lower
165 boundary of the lysimeter by transferring water either from the drainage container into the lysimeter or the contrary
166 direction. This implementation allowed to adjust the water levels at bottom of the lysimeter according to a reference matric
167 potential measured at the same depth in the natural unaffected soil column of the respective experimental plots.
168

169 **2.3 Manual measurements of biomass development**

170 Since variation in total water flux from vegetation canopies to the atmosphere is a product of the variation in standing
171 biomass and the water vapour release per unit biomass decomposing and addressing these two factors is advisable, especially
172 in replicated experiments or when communities with different biomass progression rates are being compared over longer
173 periods. However, non-destructive biomass estimation of complex stands in the field can be challenging with respect to
174 desired accuracy. In order to generate robust estimates different methodologies were combined ~~in current experiment~~.
175 Measurements of maximum and average canopy height (Machado et al., 2002) were supplemented with a pin point
176 procedure (Jonasson, 1988) and measurements of projected area (Lati et al., 2013) for the estimation of biomass present in
177 the lysimeters. For measuring pin contacts a thin metal rod was lowered through a plate placed above down to the lysimeter.
178 Pin measurements were replicated in seven (out of 21) randomly assigned positions for each lysimeter and point in time. Pin
179 contacts were referenced within three height classes (0-20, 20-40, 40+ cm above the ground) and by functional group
180 identity of the plants. For the determination of projected area of the lysimeter canopies the methodology proposed by
181 Tackenberg (2007) was adapted. Digital images of the lysimeter stands in front of a white half-cylindrical background were
182 scaled according to a size standard in each picture, converted to a black-white colour scheme, before black pixels were
183 enumerated. On average, biomass of the lysimeters was estimated for every third day through the period of the experiment.
184 The different methods for non-destructive biomass estimation were calibrated against weighted biomass at the harvests prior

and subsequent to the experiment. Based on these calibrations the biomass development in the lysimeters was predicted throughout the experimental period.

2.4 Data processing and statistics

To calculate the water mass fluxes at the soil-vegetation-atmosphere interface of the upper lysimeter boundary, weight differentials of the drainage reservoir and the lysimeters were summarized and subsequently cleared for spikes and signals of implausible strength (Schrader et al., 2013). The latter was necessary because the sensitive weighing elements are susceptible to environmental noise or accidental interference by other experimental proceedings (e.g. biomass estimation), while providing a high accuracy and temporal resolution. The combined weight signal was separated into irrigation induced weight gain of the lysimeter units and weight loss caused by evapotranspiration from the upper lysimeter boundary based on the recorded activity times of the precipitation simulator. Subsequently, daily totals were calculated for both mass differentials.

A soil-specific calibration of the soil moisture and the MPS-2 sensors ~~sensor~~ is a necessary prerequisite ~~for a sensor~~ to achieve its highest degree of absolute accuracy in soil water content (SWC) measurements. A substrate moisture retention curve (pF vs. volumetric water content) and the hydraulic conductivity as a function of pF (log10 of the matric potential) were determined for both types of soil-vegetation monoliths (M, S). The soil hydraulic parameters were determined in the laboratory, using the method of (Schindler, 1980) with the HYPROP system (UMS/Meter Group Munich, Germany). Using the soil specific moisture retention curve, absolute SWC was corrected based on soil matrix potential data. To summarize the time course of water availability in the soil of each lysimeter unit, the average values of SWC of both layers between 0.05 - 0.15m and 0.15 – 0.25m were integrated and summarized on a daily basis.

The evaporative demand of the atmosphere is expressed by the reference crop evapotranspiration (ET_0). It represents the evapotranspiration from a standardized vegetated surface and was calculated in this study after the FAO Penman-Monteith standard method (Allen et al., 1998). ET_0 integrates the most important atmospheric components (solar radiation, temperature, VPD and wind velocity) defining the atmospheric water demand. Daily averages were used as a summed up explanatory parameter to capture the atmospheric draw of water vapour from the lysimeter vegetation for further analysis.

Non-destructive estimates for the standing biomass in the lysimeters were calibrated at the harvests before and after the experimental period. Nine different regression models were generated for the different estimation techniques individually and in combinations (appendix 1). Based on the prediction of these models biomass was estimated for every measurement (total of 16) during the experiment. Generating a consensus time-course for the biomass development in every lysimeter a general additive mixed model smoother was fitted for each unit (gamm-function in the mgcv-package, R Development Core Team, 2015) with the different prediction methodologies defining random (observer) - effects. In order to generate a more conservative pattern, the flexibility of the time course defined with these smoothers was constrained by allowing a maximum

of five knots for these smoothers. Based on these models, standing biomass was predicted on a dry weight basis for ~~every~~ lysimeter ~~entity~~ and ~~each~~ day of the experiment.

All statistical analysis presented here were performed using the R statistical programming language(R Development Core Team, 2015). For the evaluation of evapotranspiration ~~responses~~ mixed effects models were fitted using the *nlme*-package. These models included the identity of the different vegetation types (categorical) in full factorial combination with additional covariates defining the fixed part of the model. To reveal the drivers of variation in daily ET rates and separate the effects of variability in biomass (DW –dry weight) and evapotranspiration rates per unit biomass (ET/DW) among the different monoliths a log-log-scaling method was applied on the formula ET = ET/DW × DW based on the methodology provided by (Renton and Poorter, 2011). For summarizing the time courses of SWC and ET_0 the day of the experiment and the two irrigation schemes were considered as additional categorical variates. For modelling the response surface of ET along the two dimensions of ET_0 and SWC, the latter and all possible interactions with vegetation type were defined as continuous covariates for the fixed part of the model. However, all models included a random intercept for the experimental plot in which the data were collected. Nested within the random effect for the plot, the lysimeter identity was included as another random effect to fully represent the dependence structure in the hierarchical design of the experiment. ~~Were~~ they were found to significantly improve the model fit, lysimeter specific response to continuous covariates in the fixed part were included as random slopes. Further, to account for autocorrelative errors according to the time-series origin of the data, a continuous autocorrelation structure (corCAR1 in *nlme*-package) was defined by the day of the experiment.

The drivers of ET: The average air temperature during the course of the experiment was 17.5 °C (± 3.1°C – standard deviation). Among the different plots no systematic variation of temperature, relative humidity and solar radiation was measured by the microclimate stations underneath the shelters. ~~S~~ummarizing the different atmospheric components defining rates of ET, ET0 was calculated. During the duration of experiment the average daily ET0 was 3.26 kgH2O m-2 d-1 (± 1.95 SD) with a minimum at 0.75 and a maximum of 6.4 kgH2O m-2 d-1. However, since ET0 is subject to short-term natural variation of the underlying environmental parameters, fluctuations between consecutive days were found to be very pronounced and no temporal trend was revealed over the period of the experiment (Fig. 2).

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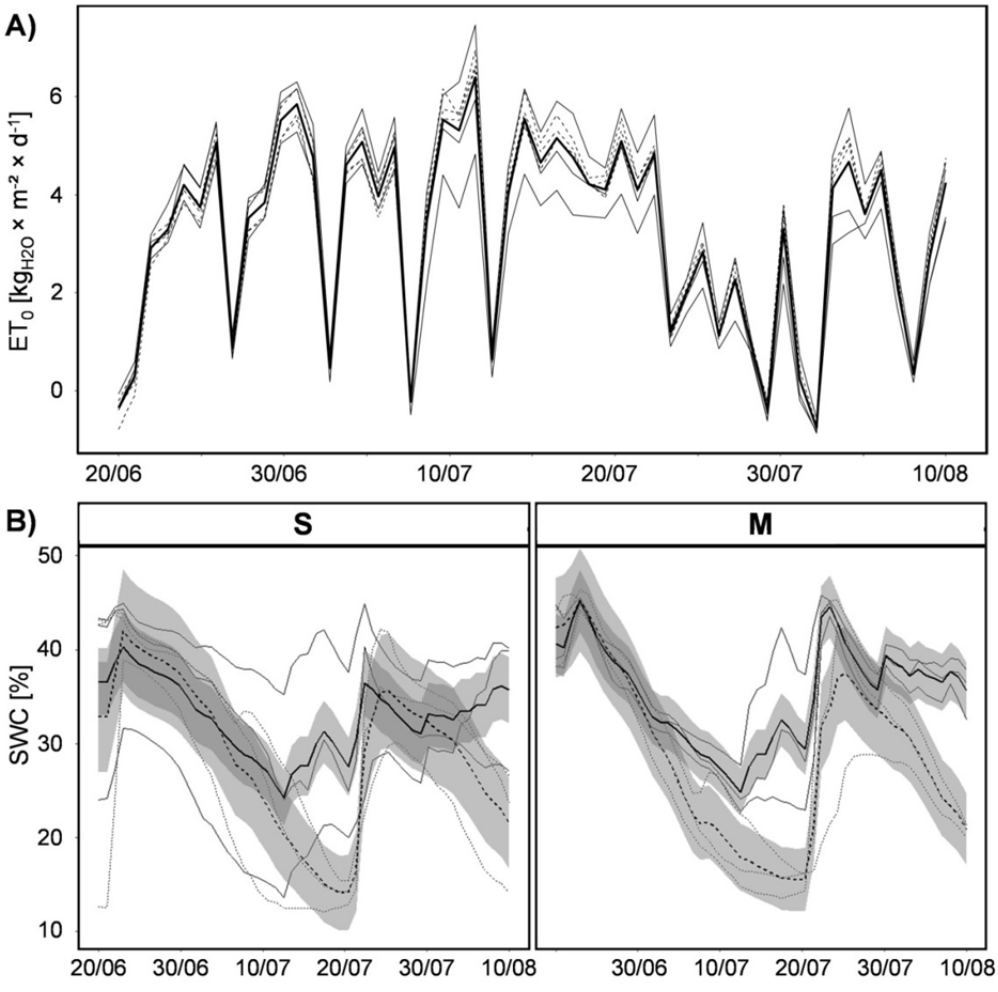

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242 **Fig 2: Atmospheric demand (ET0) and soil water content (SWC) as drivers of ET, A) dynamics of daily average ET0 over the**
243 **course of the experiment (bold line: all plot average, thin lines: individual plots); B) dynamics of daily average SWC for two**
244 **vegetation types (S & M, see Table 1) in contrasting irrigation schemes (REG - solid lines, D - dashed lines; bold lines: treatment**
245 **average; shaded area: standard deviation, thin lines: individual plots); S: Stubai, M: Matsch/Mazia.**

246

247 During the time of the experiment the two contrasting irrigation schemes led to distinct SWC dynamics within the respective
248 mesocosms (Fig. 2). Since SWC in all lysimeters was high at the beginning of the experiment the value initially decreased in
249 all plots irrespective of treatment indicating that the water irrigated on plots with regular irrigation did not fully compensate
250 the loss of water by ET of the corresponding communities. The first clear effects of differential irrigation became only
251 apparent in the lysimeters with the M-type of vegetation after applying approximately two weeks of drought. Variation in
252 SWC of lysimeters belonging to the S-type of vegetation was rather strong and it took those units longer to manifest distinct
253 effects of the different watering schemes. After approximately one month, SWC in both vegetation types revealed clear

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effects of the contrasting irrigation strategies. At that time, SWC of both treatments was restored to similar values observed during the initial stages of the experimental period in order to avoid distress in the drier mesocosms. Rates of daily ET from the lysimeters were varying very strongly through the period of the experiment and did not reveal a general temporal trend (Fig. 3). The average evapotranspirative water loss for the lysimeter unit during the duration of the experiment was 4.9 kgH20 m-2 d-1. Subject to the atmospheric water vapour pressure deficit the recorded fluxes were characterised by a similar unsteadiness as the variability of the underlying environmental parameters would suggest. No consistent differences in daily water flux from the lysimeter mesocosms to the atmosphere could be detected according to the identity of the community. Also the contrasting irrigation regimes did not impose a overall difference in the rates of ET within the experimental period. However, during periods of strong divergence of SWC among the two irrigation treatments, daily ET was lower for entities subjected to experimental drought.

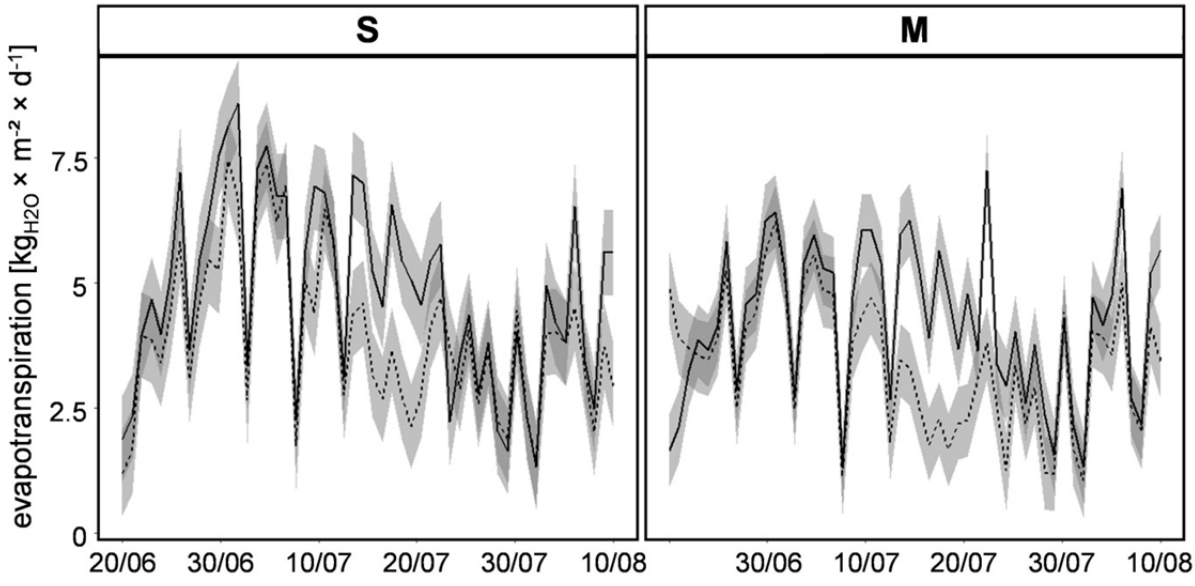

Fig 3: Dynamics of daily average ET over the course of the experiment for two different vegetation types (S & M, Table 1) subjected to contrasting irrigation regimes (REG - solid lines, D - dashed lines; shaded area – standard deviation); S: Stubai, M: Matsch/Mazia.

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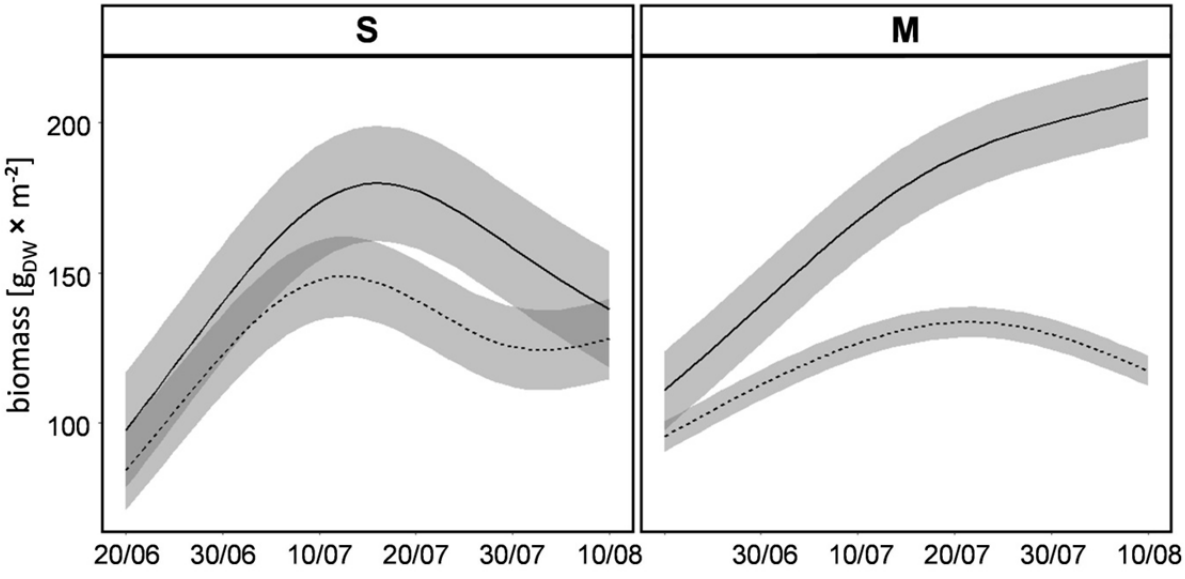

Fig 4: Trajectories of biomass development for the two vegetation types (S: Stubai, M: Matsch/Mazia, Table 1) subjected to contrasting irrigation regimes (REG - solid lines, D - dashed lines; shaded area – standard deviation) throughout the duration of the experiment

The prediction of biomass development combined from the different non-invasive estimation methods suggested distinct growth trajectories for the two vegetation types in interaction with the two irrigation regimes. The mesocosms with communities belonging to the local S-type revealed larger biomass differentials during early stages of the experiment irrespective of the applied irrigation regime. However, with increasing duration of the experiment, growth dynamics started diverging in treatments with contrasting water provision, with biomass differences peaking at the mid-time of the experimental period. After that peak, the prediction of dry weight suggested a decline in standing biomass for both water regimes in the S-communities. Towards the end of the experiment, biomasses of communities in the different water treatments converged to similar values. A different pattern of biomass development was detected for the transplanted mesocosms (M). From the beginning of the experiment growth processes of the different irrigation treatments yielded distinct trajectories. In the treatment experiencing regular water provision the biomass gain per unit time was stronger than in the mesocosms being subjected to irregular watering. That pattern was consistent throughout the experiment, with a strictly monotonic increase of standing biomass in the M communities of well-watered plots. In contrast, the vegetation of the M-type in the plots with restricted watering growth started stagnating during the second half of the experimental period. Unlike the S-type, at the end of the investigation period, biomasses in the M-type communities were clearly distinct according to the different watering regimes, with the standing mass in the regularly watered plots approximating double the amount compared to the treatment with restricted water provision.

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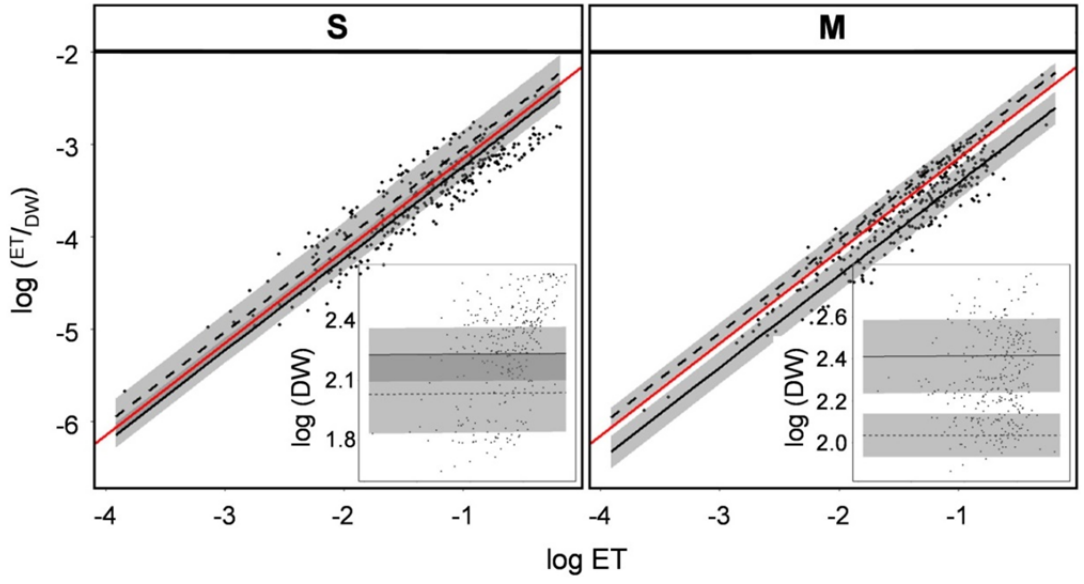

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291 **Fig 5: Log-log scaling for the two factors defining variability of ET: ET rates per unit dry weight (ET/DW) and standing biomass**
292 **(=dry weight, DW) for the two different vegetation types (S & M, Table 1) subjected to contrasting irrigation regimes (REG - solid**
293 **lines, D - dashed lines; shaded area – standard deviation), red line indicates a reference function with the slope of 1.**

294

295 Variability of ET is subject to variation in evapotranspiration rates per unit biomass (ET/DW) and the variation in the
296 standing biomass. Hence, when comparing rates of ET differentiating both underlying components will provide deeper
297 insights on how the vegetation interface of different communities mediates the water flux from the soil. A strong positive
298 correlation of total daily ET and ET/DW was found (Fig 5). The log-log-scaling of ET/DW with ET revealed a slope of
299 0.998 arguing that variation in ET rates measured during the course of this experiment is almost exclusively defined by the
300 variation in ET rates per unit biomass (100% = 1). This relationship was independent of vegetation type and irrigation
301 scheme. The effect of biomass variation on the variance of total rates of ET however did have a very small and insignificant
302 effect. For the local communities (S) the more biomass to be found in the lysimeter mesocosms the bigger was the total daily
303 water flux to the atmosphere, while the transplanted communities revealed a different pattern. For M-type communities the
304 amount of biomass in the lysimeters had no strong effect on the rates of total ET.

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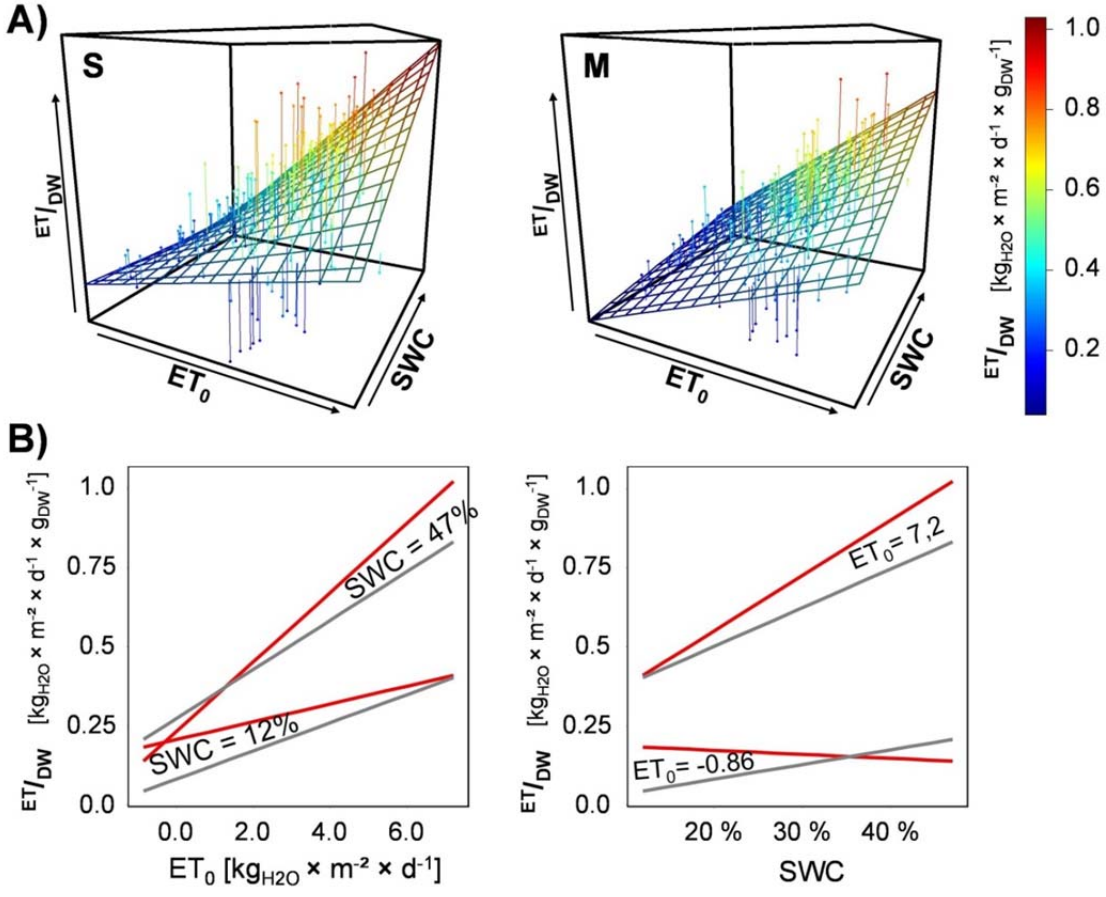

Fig 6 A) 3D plots: response surface of ET per unit DW (ET/DW) along the two-dimensional variation of ET0 and SWC for the two different vegetation types (S: Stubai, M: Matsch/Mazia, Table 1); B) projections of ET/DW response along ET0 and SWC at maximum/minimum value of the particular other (red: S-communities, grey: M-communities)

After revealing ET/DW as the most important driver in defining variation in the rates of total ET from the lysimeter mesocosms, the effect of combined variation in ET_0 and SWC on rates of ET per unit biomass was modelled in dependence of the vegetation type (ET/DW = f(ET_0×SWC×vegetation type)). The average daily sums of ET_0 ranged from -0.75 to a maximum of 6.4 kg_{H2O} m^{-2} d^{-1}, while the averaged SWC realized during the duration of the experiment covered a range from approximately 12-47% (Fig. 5). Both, ET_0 and SWC had a highly significant and positive effect on achieved rates of ET/DW (Fig. 6, Table 2). However, as implied by a significant synergistic interaction of ET_0 and SWC, rates of ET/DW increased stronger if SWC and ET_0 increased concurrently than the individual gradients of either would imply (Fig 6.). With increasing ET_0 the response of EVT/DW was stronger the higher SWC was. However, there was a significant difference how both vegetation types responded within the landscape of environmental drivers defining ET/DW (Table 2). The local (S) vegetation had higher rates of ET/DW - when both ET_0 and SWC were low - than the transplanted vegetation type (M), suggesting a higher base rate of ET/DW. On the low end of investigated SWC the M-vegetation had a stronger response to

ET_0 than the local S-vegetation. Despite that stronger response of the transplanted vegetation (M) along the ET_0 gradient at low SWC, the maximum rates of ET/DW converted to similar values due to the higher base flux at low ET_0/ low SWC in the S-vegetation. In turn, under conditions of high soil water availability the ET_0-response of the S-type was much more pronounced than in the M-type. A similar pattern was found comparing the SWC-response of both vegetation types for the range of different ET_0 values realized during the experiment. At low ET_0 the M-type vegetation responded stronger to variations in SWC, while there was almost no response in the S-type. However, at high ET_0 the response of the S-type to increasing SWC was again much more pronounced than in lysimeters with the M-type. Because of the higher rates of ET/DW at low ET_0/SWC and the overall increased response potential of the S-type vegetation, the ET/DW values achieved in the M-communities stayed below those found in the local vegetation for almost the entire range of combinations between ET_0 and SWC investigated in this experiment.

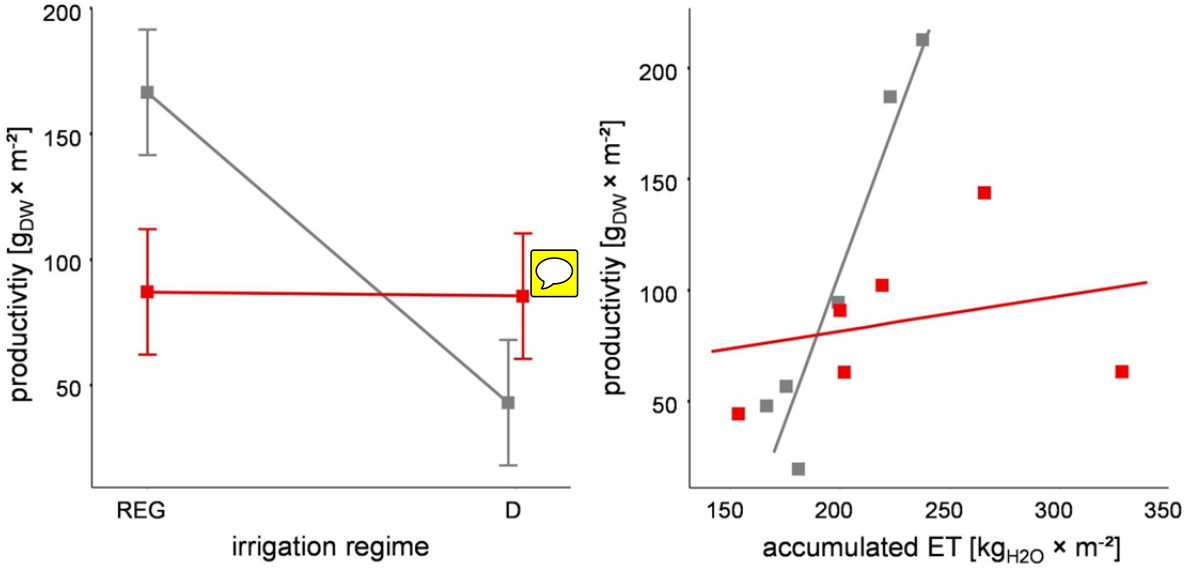

Fig 7: Productivity of two vegetation types (± standard error, Stubai - red & Matsch/Mazia - grey; Table 1) subjected to contrasting irrigation schemes (Fig 1), right panel: dry matter productivity of two vegetation types (see above) as function of accumulated evapotranspiration over the experimental duration

Comparing the productivity of the two vegetation types among the two irrigation treatments revealed a contrasting response for the DW productivity (Fig. 7, left panel). For the local S-Type the biomass gain over the experimental period did not show a strong dependence on the applied watering regime. The productivity of the S-type stayed well below from what would be expected for the vegetation outside the experimental site in both treatments. For the M-communities, however, productivity was on average more than two fold higher in the plots experiencing regular water provision compared to those exposed to extended periods of drought.

Integrated over the entire experimental period, the biomass productivity per unit water was significantly higher for the transplanted mesocosms M (Fig 7, right panel). The data suggested a productivity increase of 2.6g_{DW} per kg of water for the

M vegetation. In contrast, for the S-type mesocosms the average increase of productivity per 1kg of evapotranspiration was approximately only 0.16g. This pattern suggests that biomass generation in the M-type vegetation is significantly more dependent on water availability, while the differences in the slope imply lower efficiency of water use with respect to dry weight accumulation in the S mesocosms.

It is intuitive to understand, that ET_0 and SWC impose independent and interacting effects on water fluxes from the soil to the atmosphere with one of either constraining the total rates of ecosystem ET (Kim and Verma, 1991; Perez et al., 2006). Beyond the effects of these abiotic drivers, the measurements of the present experiment reveal a community specific signal in the definition of ecosystem water exchange. The community specific configuration of the soil-plant-atmosphere interface is instinctively acknowledged if distinct vegetation types are compared. Water fluxes from the system will to some degree always scale with productivity and total biomass of the vegetation (Zeppel et al., 2014and references therein). This context will drive variation in ET of contrasting biomes together with environmental parameters affecting the availability of water and the atmospheric deficit.

However, results of this experiment reveal that vegetation specific differences have a component, which defines ecosystem water flux beyond the impact of variations in total biomass. Such differences will be important to understand and to consider if communities of the same type need to be evaluated with respect to their particular impact on the hydrological regulation of the ecosystem. The response of water fluxes along co-operating gradients of SWC and ET_0 indicated divergence in the conductance potential of the two alpine grassland communities, which were independent from the biomass present. At low SWC the response of the M-type to increasing ET_0 was much stronger than for the S-type arguing for a higher efficiency to mobilise limited water resources from the soil column. Conversely, under conditions of high soil water availability water fluxes from the S-type responded much stronger to increases of ET_0 suggesting a higher overall conductance potential. Similar implications were revealed along the gradient of soil water availability. SWC variations had almost no effect on the S-type communities when the atmospheric draw was small, while the M-type mesocosm still mediated fluxes to the atmosphere. Under high ET_0 however, the divergence in the response of ET between S & M-communities to varying SWC suggests that, from starting at similar rates, the S-type became much more efficient to conduct water to the atmosphere the less soil water became limiting. These differences between the two vegetation types indicate different strategies in the water utilisation. For the M-type this strategy may be summarized by a high potential to utilize even scarce water resources, a lower potential to translate atmospheric deficits into higher water conductance with rates of ET staying below those measured for the S-type for most environmental scenarios included within the experimental period. This implies an overall conservative and water saving strategy. For the S-communities, in contrast, which show high water conductance potential with strongly increasing ET rates when environmental conditions become less constraining, an acquisitive strategy is suggested. With high rates even at base level these communities appear not to be optimized to save

water and might experience drought effects earlier and probably stronger, when water availability becomes limiting. There might be some dampening effect as soil hydrological properties indicate a higher amount of plant available water for the S-type. The permanent wilting point (pF 4.2) in the main rooting zone (averaged values for 0.05m, 0.15m, 0.25m soil depth) was at a SWC of 13% (± 8.3 SD) and 17% (± 3.1 SD) for the S-vegetation type and the M-vegetation type, respectively. Whereas field capacity (pF 2.1) was found to be at a SWC of 46% (± 4.4 SD) and 43% (± 6.8%) for the S-vegetation type and the M-vegetation type, respectively. In summary, the plant available water was found to be 33 vol% for the S-type and 26 vol% for the M-type. However, the variation at 0.05m soil depth was very low and even a slightly higher amount of plant available water was found for the M-type (S-type: 28 vol%; M-type: 29 vol%) at this soil depth. Although soil hydrological properties play a role in the community specific conductance potential of soil water to the atmosphere, differences found for the investigated two different vegetation types turned out to be not decisive in this context.

Sharing a common environment, the differences in biomass-independent conductance potential between the two Alpine grassland communities are likely to have a foundation in a contrasting physiological, functional and structural organisation of the vegetation. Functional divergence in water utilisation, evapotranspiration and other aspects of hydrological regulation of ecosystems (e.g. infiltration, surface run-off) between communities can be manifested by the frequency distribution in the values of particular traits (Díaz et al., 2013). Canopy complexity - density and size, growth form composition, composition and diversity of vascular structures, stomatal density and conductance mediate community specific differences in the evapotranspiration aboveground (de Bello et al., 2010) Belowground, the structure and depth of the individual rooting systems is an important determinant for the water utilisation potential of communities (Knapp et al., 2008). Along the variation and composition of these traits water usage and consequently also drought resistance of contrasting communities is defined. The differences in the two vegetation types suggest high exploitation potential for scarce soil water, probably facilitated by a higher priority on water exploitation in the soil in the M-mesocosms and, conversely, a stronger importance on aboveground structures mediating light capture and gas-exchange, leading to an increased response potential of ET for atmospheric triggers in the local S-communities.

The clear vegetation response to variable water availability observed in the present experiment is not common in studies targeting Alpine grasslands (de Bello et al., 2010). Based on multi-annual measurements of evapotranspiration at 16 sites in the Austrian Alps, it was suggested, that even during years with low annual precipitation Alpine grasslands do not experience water stress (Wieser et al., 2008). Gilgen and Buchmann (2009) could not conclude on a general drought response of grasslands in Switzerland, while acknowledging a site-specific impact with communities receiving less annual precipitation being more susceptible to drought stress than those at higher rainfall levels. Also arguing for a co-defined and interactive manifestation in the effects of varying water availability, a strong drought response of Alpine grassland functioning was revealed under scenarios of co-occurring heat waves (De Boeck et al., 2016). A modelling study for grassland ecosystems in the Austrian- and French Alps suggested a higher vulnerability to drought for communities with a water spending strategy targeting on water provision of the ecosystems in general (Leitinger et al., 2015). However, it seems inappropriate to synthesize a general summary on the response of Alpine grasslands to variations in water availability given

the small body of research performed. Considering the different spatio-temporal scales, the range of parameters measured, and the management and biodiversity spectrum of different grassland types in the Alps, drawing broad and universal generalisation yet becomes unrewarding. For experiments with contrasting treatments the practicalities of manipulating water availability potentially also need to be considered for the interpretation of the results.

Drought scenarios are usually generated by rain-out shelters using a UV-permeable, transparent film for roofing. If compared to unroofed controls, temperature differences and attenuation of photosynthetically active radiation reducing total productivity will have to be expected as pure artefacts of the sheltering (Vogel et al., 2013). However, even if both treatments are sheltered, differential irrigation may not immediately lead to the realisation of varying water availabilities. The beginning of the present experiment was marked by the establishment of the rain-out shelters and the omission of irrigation in the treatments with irregular watering (D). From this point, it took approximately two weeks for the SWC of both irrigation schemes to diverge significantly in M-type mesocosms, for the S-type even longer. Therefore, regular irrigation and, respectively, its omission can, counter-intuitively, only be an indicator of contrasting water availability. The establishment of drought conditions in the strict sense of a depleted soil water reservoir is realized by the interaction of pre-treatment SWC, standing biomass and atmospheric effects. Variations in vegetation water status have to be defined in context of water availability (supply) and physiology, phenology and the leaf-to-air evaporative gradient (Gilbert and Medina, 2016). The beginning of the experiment was characterized by combination of days with consistently high averages of ET_0 and high SWC in all mesocosms. This combination led to high ET and a decrease of SWC for all experimental units. Due to the parallel decline of SWC irrespective the watering regime applied, the water availability differentiation among the treatments was delayed. For such reasons, it was argued to define variations in water availability not purely on the basis of contrasting regimes of water input (i.e. irrigated vs. non-irrigated) if these are not causing systematic variations in soil moisture (Kramer, 1983). Defining water supply based on the continuous range of SWC rather than discrete irrigation treatments considers soil type specific characteristics of matric potential and hydraulic conductivity. Also practical problems with realizing discrete treatments of water availability in the field (i.e. precipitation entry to sheltered plots due to heavy winds, spatio-temporal variation in the effectiveness of automated irrigation) will be migrated by referencing ecosystem responses to gradients of water supply. Defining vegetation responses along continuous ranges of environmental factors will further yield stronger information about the response surface of the system and improves model building and testing (Beier et al., 2012).

Irrespective the variability of different water availabilities within the two irrigation regimes, mesocosms subjected to regular watering (REG) had on average a higher productivity than those with irregular and in total less irrigation. However, significant differences between the different communities were found in the response to variations in the water supply (Fig 7). Relating total productivity to the amount of evapotranspirative water release over the experimental period revealed a higher biomass gain per unit water in the M-type communities. The higher water use efficiency in the biomass production of these mesocosms together with their overall stronger water saving strategy reinforces their optimisation to scarce water supply. For the local S-communities, in contrast, the low biomass differential per unit water consumption indicates a high

potential to conduct water from the soil to the atmosphere and that productivity of this vegetation is probably not often constrained by water availability in its natural context. (Brilli et al., 2011) expect from a water spending strategy to have a cooling feedback in terms of climate warming. However, a negative feedback for water provision services (i.e. down-stream water users) has to be expected. Further decisive changes remain debatable: How will 'water spending' plant communities adapt if droughts occur more frequently and possibly with higher intensities (Bahn et al., 2014; Reichstein et al., 2013). To what extent play – at least initially - physiological and morphological changes a role or is there an immediate shift to a better adapted community?

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