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

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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 responses are merely understood. In a replicated mesocosm experiment we compared evapotranspiration (ET) and biomass productivity of two differently drought-adapted alpine grassland 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 to 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.

INTRODUCTION

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 of rainfall events 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 it 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 main interest, because functional 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, indirect mechanisms define this relationship. The abundance 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

84 al., 2004). In turn, immediate vegetation responses to fluctuations in precipitation
85 patterns and the strength of interaction with productivity functions will strongly
86 depend on the functional composition of the community and ecosystem considered.
87 Therefore, intrinsic characteristics of vegetation will impose another layer of
88 complexity for defining the interactive feedbacks in the relationship between water
89 budget and productivity.

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

102   Numerous studies were performed to reveal the responses of temperate
103 grasslands to climatic changes and droughts (Poorter et al. 2012, Reichstein et al.
104 2013). While investigations on responses of above- and belowground carbon fluxes
105 targeted Alpine systems (Bahn et al. 2009, Hasibeder et al. 2015, Ingrisch et al.
106 2017), only few studies addressed components of the ecosystem water budget (De
107 Boeck et al., 2016). While the Alps did not often experience droughts during the past
108 (van der Schrier et al., 2007), the region has undergone exceptionally fast climatic
109 changes during the late 19th through early 21st century (Auer et al., 2007; Beniston,
110 2005; Böhm et al., 2001; Ciccarelli et al., 2008; Rebetez and Reinhard, 2008). Water
111 availability, especially in the light of future climatic changes in European Alps in the
112 next 100 years (IPCC, 2007), is already seen as a limited and valuable resource with
113 the potential of socio-economical conflicts. Therefore, the importance of agricultural
114 management with a potentially higher water demand as a consequence of sprinkling
115 becomes evident. Considering the fundamental role Alpine systems have to water
116 accumulation and freshwater supply for large parts of Europe (Messerli et al., 2004;
117 Viviroli et al., 2003) it seems surprising that the responses of ecosystems in the Alps

118 to changes in precipitation have not drawn more scientific attention. However, while
119 projections suggest only moderate variations of yearly average rainfall in the Alps,
120 significant alterations within the temporal occurrence of rainfall events with a
121 decrease in summer precipitation and increases from winter through spring are
122 implied (Beniston, 2012; Beniston et al., 2007). The decrease of water supply during
123 warmer summer months will potentially increase the frequency and intensity of
124 drought events in the near and longer future in Alpine ecosystems (Gobiet et al.,
125 2014).

126 For unravelling ecosystem water fluxes at the soil-plant-atmosphere interface,
127 the lysimeter methodology provides the precise and realistic means. They also allow
128 to decompose the driving sub-processes: evapotranspiration (ET), precipitation (P)
129 and drainage below the rooting zone (Peters et al., 2014). Even quantifying
130 interception would be possible by comparing the increase of lysimeter weight and
131 soil water content during precipitation. This was however not a focus of this
132 experiment as interception is estimated to account for less than 10% of rainfall
133 during the growing season based on Wohlfahrt et al. (2006). By avoiding systematic
134 errors prone to traditional measurement systems, the determination of the net water
135 balance is highly accurate and robust (Schrader et al., 2013). If embedded into a
136 surrounding ecosystem, automated lysimeter units, which do not need access to
137 perform manual weighing, measure water fluxes with a minimum of disturbance to
138 the natural boundary layer and microclimatic conditions. Such implementations of
139 autonomous weighable high precision lysimeters provide unprecedented realism to
140 the description of ecosystem water balances, especially when filling of the lysimeters
141 was performed to maintain natural soil layering and the connectivity of pores, while
142 keeping potential impacts on the vegetation community low. Over the recent years,
143 several of these units have been established over Europe, e.g. a network of 126
144 lysimeters at 12 sites has been established to monitor climate change induced
145 alterations in hydrological cycling within the TERENO project in Germany (Bogena et
146 al., 2006; Zacharias et al., 2011). However, the large dimensions (1m diameter/
147 volume) and the corresponding economic efforts for their establishment did mostly
148 eliminate the possibility for replicated manipulative experiments employing fully
149 integrated lysimeters.

150 In a common garden experiment we used a network of automated small scale
151 lysimeters to emerge community specific differences in the temporal dynamics of soil

152 water depletion and evapotranspiration. Two different Alpine grassland communities
153 were subjected to contrasting levels of water availability. Sheltered from natural
154 precipitation, soil water content was manipulated by applying two distinct irrigation
155 regimes: one providing water in regular intervals and another exposing the
156 corresponding experimental units to extended periods of drought. Changing
157 atmospheric demand of water vapour driven by the natural variability of air
158 temperature and humidity coupled to the manipulated water availability in the soil
159 allowed to investigate and reveal vegetation specific conductance properties and
160 water utilisation patterns. For this study we hypothesize that the vegetation adapted
161 to local, humid conditions and characterized by high biomass and a water spending
162 strategy will keep transpiration rates high while soil water availability is decreasing
163 until a sudden decline near wilting point. As a consequence it will also continue to
164 produce biomass until the break point. In contrary, the water saving strategy of the
165 drought-adapted vegetation will lead to a continuous decrease of transpiration and
166 biomass production with decreasing soil water availability.

167 **MATERIAL & METHODS**

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168 *Characteristics of the experimental field site and lysimeter installation*

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

173 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 Cambisol (A-Bv-Go)			Cambisol (Ah-Bv-C)		
soil classification	loamy sand to sandy silt			loam to sandy loam		
soil physical parameters in different soil depth						
	0.05 m	0.15 m	0.25 m	0.05 m	0.15 m	0.25 m
soil texture (%)						
sand	31	31	34	25	34	40
silt	58	63	61	43	45	43
clay	11	6	6	32	21	17
soil organic matter content (%)	3.6	1.3	0.7	7.4	3.9	2.3
plant available water (vol%)	32	39	39	34	33	27
phytosociological classification	Poo trivialis - Alopecuretum pratensis (Regel 1925)			Ranunculo bulbosi-Arrhenatherum (Ellmauer)		
species inventory (responsible for 90% of total	*Achillea millefolium, Carum carvi, Pimpinella major, Poa trivialis,*			*Achillea millefolium, Anthoxanthum odoratum, Anthriscus sylvestris,*		

plant cover in the lysimeter)	*Ranunculus acris, Rumex acetosa, Taraxacum officinale, Trifolium pratense*	*Carum carvi, Festuca rubra, Leontodon hispidus, Lotus corniculatus, Poa trivialis, Primula veris, Taraxacum officinale, Trifolium montanum, Trifolium pratense, Veronica officinalis*
abundance of functional groups (%, mean ± s.d.)	graminoids forbs legumes 14.2 ± 5.5 67.8 ± 10.2 14.1 ± 9.0	graminoids forbs legumes 49.2 ± 25.1 28.3 ± 20.1 18.8 ± 17.9

174

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 and 0.3 m depth 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. With 90 % of root biomass distributed above 0.2 m in both investigated vegetation types, a lysimeter depth of 0.3 m was assumed to be sufficient. 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

200 the centre of every experimental plot within a two by two squared grid of 1.2m edge
201 length with their relative position to each other assigned randomly.

202   The two monoliths in every plot were excavated from different types of
203 vegetation, one containing a mesocosm of the meadow surrounding the
204 experimental field site (S, Table 1), and another one which was excavated and
205 transplanted from a meadow in Matsch/Mazia with contrasting environmental and
206 biotic properties to those of the study site (M, Table 1). The Stubai grassland is
207 classified as Poo trivialis - Alopecuretum pratensis with a community of low
208 complexity: abundant Poaceae accompanied by some herb species (Wohlfahrt et al.,
209 2008). The meadow is actively managed, cut two to three times each year and
210 fertilized with cow manure in spring and autumn (approximately 0.35 kg dry matter
211 per m², Table 1). The local climate is dominated by high total precipitation values,
212 especially in the summer. The vegetation of second origin (Matsch/Mazia) is
213 characterised by the traditional, more extensive use of the corresponding system.
214 The Matsch Valley has a dry inneralpine climate with a mean precipitation of 527 mm
215 per year and a mean temperature of 6.6 °C (Hydrographical Department of the
216 Autonomous Province of Bozen-South Tyrol). The vegetation is a dry hay meadow
217 (Ranunculo bulbosi - Arrhenatherum, Ellmauer) on loam to sandy loam. The site is
218 fertilized with cow dung and cut two times each year. The excavation location of the
219 replicate lysimeters was optimized according to the presence of representative and
220 joint species in the respective vegetation patches. After installing the local and
221 transplanted lysimeter mesocosms during early summer 2014 into the experimental
222 plots, the vegetation surrounding the lysimeters was allowed to recover from
223 disturbances of necessary soil works required to wire the fully automated measuring
224 system until spring 2015. This extensive recovery period of more than 8 months
225 including the winter season and the initial growth phase until the first harvest in the
226 actual measuring year should provide a sufficient acclimatisation and regeneration of
227 both vegetation and soil in the lysimeters and prevent a bias between vegetation
228 types.

229   At the field site, all experimental plots and the vegetation in the lysimeters was
230 managed (cut, fertilized) concurrently to land-use scheme of the surrounding
231 meadow. The experimental period started in the last third of June 2015 during the re-
232 growth interval after the first cut at the beginning of June. With beginning of the

233 experiment on June 10th 2015 rain shelters were closed using a UV permeable
234 transparent polythene film (Lumisol Clear AF, 88% - 92% light transmittance). Air
235 temperature (on average 0.26 K higher in the shelter) and humidity (+0.11 %) were
236 hardly affected by the shelters while radiation was reduced by 25% and wind speed
237 by 50% even though shelters were left open on the sides facing the main wind
238 direction and closed down to just 0.5 m above the soil level on the lateral sides to
239 minimize shielding of the wind. Concurrently with closing of the rain shelters (10/06)
240 precipitation was provided from the irrigation sprinklers mimicking average rain fall
241 amounts and intensities for the 30 year period between 1970 through 2000.Over a
242 period of 52 days (20/06-10/08) the plots of the experiment were subjected to control
243 watering within the two different irrigation schemes (Fig. 1), one providing water on a
244 regular basis (REG) and one with extended drought periods (D). However, due to
245 technical problems the watering scheme stayed below the intended amounts for
246 approximately the first half of the experimental period making manual compensation
247 occasionally necessary (starting on 15/07). Automated irrigation was programed to
248 occur around mid-night in order to avoid immediate transpiration from the surface
249 and allow the provided water to penetrate into the soil compartment. Manual
250 adjustments and checks on the precipitation simulator were usually performed during
251 day-time. The lysimeter mesocosms in the treatments with regular watering (REG)
252 received approx. 117 kg_{H2O} per m², those in the treatments with extended drought
253 periods an average of 65 kg_{H2O} per m² throughout the duration of the experiment and
254 according to the scheme presented in Fig. 1.

255

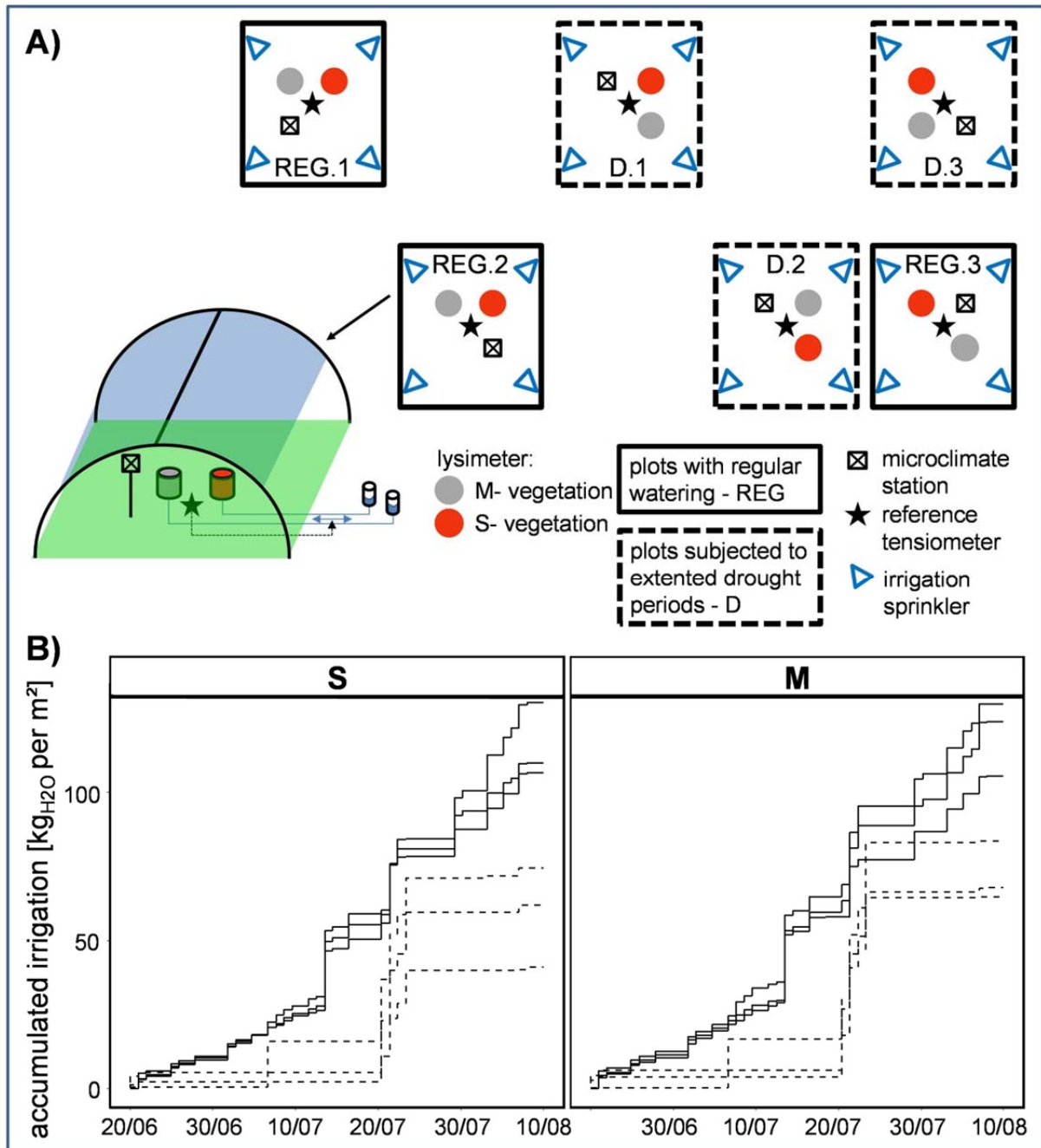



Fig 1: A) Schematic overview of the experimental design and plot setup; B) Manipulation of water availability for individual lysimeters of the two vegetation types (Stubai (S) & Matsch/Mazia (M)) by contrasting irrigation schemes - one providing water on a regular basis (REG, solid lines), one with extended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

Automated measurements

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

272   For each of the lysimeter, weight data were recorded every minute, data
273   received from matric potential, soil temperature and water content sensors (each in
274   0.05, 0.15 and 0.25 m depth) in ten minutes intervals. The hydraulic boundary at the
275   bottom of each lysimeter was connected to a reservoir of drainage water with the
276   corresponding container also being placed on a balance. A bi-directional pumping
277   system allowed the adjustment of the water content at the lower boundary of the
278   lysimeter by transferring water either from the drainage container into the lysimeter
279   or the contrary direction. This implementation allowed to adjust the water levels at
280   bottom of the lysimeter according to a reference matric potential measured at the
281   same depth in the natural unaffected soil column of the respective experimental
282   plots.

283

284   *Manual measurements of biomass development*

285   Variability of water flux from vegetation canopies to the atmosphere has two
286   components: a) the variation in standing biomass and b) the water vapour release
287   activity per unit biomass. Therefore, decomposing and addressing these two factors
288   independently is advisable, especially when functionally different communities with
289   differing biomasses are being compared. However, non-destructive biomass
290   estimation of complex stands in the field can be challenging with respect to desired
291   accuracy. In order to generate robust estimates different methodologies were
292   combined in the current experiment. Measurements of maximum and average
293   canopy height (Machado et al., 2002) were supplemented with a pin point procedure
294   (Jonasson, 1988) and measurements of projected area (Lati et al., 2013) for biomass
295   estimation in the lysimeters. For measuring pin contacts a thin metal rod was
296   lowered through a plate placed above down to the lysimeter. Pin measurements

297   were replicated in seven (out of 21) randomly assigned positions for each lysimeter

298   and point in time. Pin contacts were referenced within three height classes (0-20, 20-

299   40, 40+ cm above the ground) and by functional group identity of the plants. For the

300   determination of projected area of the lysimeter canopies the methodology proposed

301   by Tackenberg (2007) was adapted. Digital images of the lysimeter stands in front of

302   a white half-cylindrical background were scaled according to a size standard in each

303   picture, converted to a black-white colour scheme, before black pixels were

304   enumerated. On average, biomass of the lysimeters was estimated for every third

305   day through the period of the experiment. The different methods for non-destructive

306   biomass estimation were calibrated against weighted biomass at the harvests prior

307   and subsequent to the experiment (10/06 and 10/08). Based on these calibrations

308   the biomass development in the lysimeters was predicted throughout the

309   experimental period.

310

311   *Data processing and statistics*

312   To calculate the water mass fluxes at the soil-vegetation-atmosphere interface

313   of the upper lysimeter boundary, weight differentials of the drainage reservoir and

314   the lysimeters were summarized and subsequently cleared for spikes and signals of

315   implausible strength (Schrader et al., 2013). The latter was necessary because the

316   sensitive weighing elements are susceptible to environmental noise or accidental

317   interference by other experimental proceedings (e.g. biomass estimation), while

318   providing a high accuracy and temporal resolution. The combined weight signal was

319   separated into irrigation induced weight gain of the lysimeter units and weight loss

320   caused by evapotranspiration from the upper lysimeter boundary. Subsequently,

321   daily totals were calculated for both mass differentials.

322   A soil-specific calibration of the soil moisture and the MPS-2 sensors is a

323   necessary prerequisite to achieve its highest degree of absolute accuracy in soil

324   water content (SWC) measurements. A substrate moisture retention curve (pF vs.

325   volumetric water content) and the hydraulic conductivity as a function of pF (log10 of

326   the matric potential) were determined for both types of soil-vegetation monoliths (M,

327   S). The soil hydraulic parameters were determined in the laboratory, using the

328   method of (Schindler, 1980) with the HYPROP system (UMS/Meter Group Munich,

329   Germany). Using the soil specific moisture retention curve, absolute SWC was

330   corrected based on soil matrix potential data. To summarize the time course of water

331   availability in the soil of each lysimeter unit, the average values of SWC of both

332   layers between 0.05 - 0.15m and 0.15 – 0.25m were integrated and summarized on

333   a daily basis.

334   The evaporative demand of the atmosphere is expressed by the reference crop

335   evapotranspiration (ET_0). It represents the evapotranspiration from a standardized

336   vegetated surface and was calculated in this study after the FAO Penman-Monteith

337   standard method (Allen et al., 1998). ET_0 integrates the most important atmospheric

338   components (solar radiation, temperature, VPD and wind velocity) defining the

339   atmospheric water demand. Daily averages were used as a summed up explanatory

340   parameter to capture the atmospheric draw of water vapour from the lysimeter

341   vegetation for further analysis.

342   Non-destructive estimates for the standing biomass in the lysimeters were

343   calibrated at the harvests before and after the experimental period. Nine different

344   regression models were generated for the different estimation techniques individually

345   and in combinations. Based on the prediction of these models biomass was

346   estimated for every measurement (total of 16) during the experiment. The biomass

347   development in the different lysimeters followed a non-linear trajectory. To generate

348   a consensus time-course describing the growth progression in every lysimeter, a

349   general additive mixed model smoother was fitted for each unit (gamm-function in

350   the mgcv-package, R Development Core Team, 2015) with the different prediction

351   methodologies defining random (observer) - effects. The flexibility of the time course

352   defined with these smoothers was constrained by allowing a maximum of five knots

353   for these smoothers. Granting an approximate average of three measurement points

354   per knot (16 to 5) successive sampling points were capable to change the trend of

355   biomass progression while implausible fluctuation were prevented. Based on these

356   models, standing biomass was predicted on a dry weight basis for every lysimeter

357   entity and each day of the experiment.

358   For the evaluation of evapotranspiration responses mixed effects models were

359   fitted using the *nlme*-package (Pinheiro et al., 2017). All these models included the

360   identity of the different vegetation types (categorical) in full factorial combination with

361   additional covariates defining the fixed part of the model as detailed below. To reveal

362   the drivers of variation in daily ET rates and separate the effects of variation in

363 biomass (DW –dry weight) and evapotranspiration rates per unit biomass (ET/DW)
364 among the different monoliths, a log-log-scaling method was applied on the formula
365 ET = ET/DW × DW based on the methodology provided by (Renton and Poorter,
366 2011). This procedure allows decomposing the importance of different factors of
367 sources in the variation of a synergistically (multiplicative) defined trait and is not
368 meant to establish a statistical relationship between independent parameters. For
369 summarizing the time courses of SWC and ET_0 the day of the experiment and the
370 two irrigation schemes were considered as additional categorical variates. For
371 modelling the response surface of ET along the two dimensions of ET_0 and SWC,
372 the latter two and all possible interactions with vegetation type were defined as
373 continuous covariates for the fixed part of the model. However, all models included a
374 random intercept for the experimental plot in which the data were collected. Nested
375 within the random effect for the plot, the lysimeter identity was included as another
376 random effect to fully represent the dependence structure in the hierarchical design
377 of the experiment. Where they were found to significantly improve the model fit,
378 lysimeter specific response to continuous covariates in the fixed part were included
379 as random slopes (see Table 2). Further, to account for autocorrelative errors
380 according to the time-series origin of the data, a continuous autocorrelation structure
381 (corCAR1 in *nlme*-package) was defined by the day of the experiment. All statistical
382 analysis presented here were performed using the R statistical programming
383 language (R Development Core Team, 2015).

RESULTS

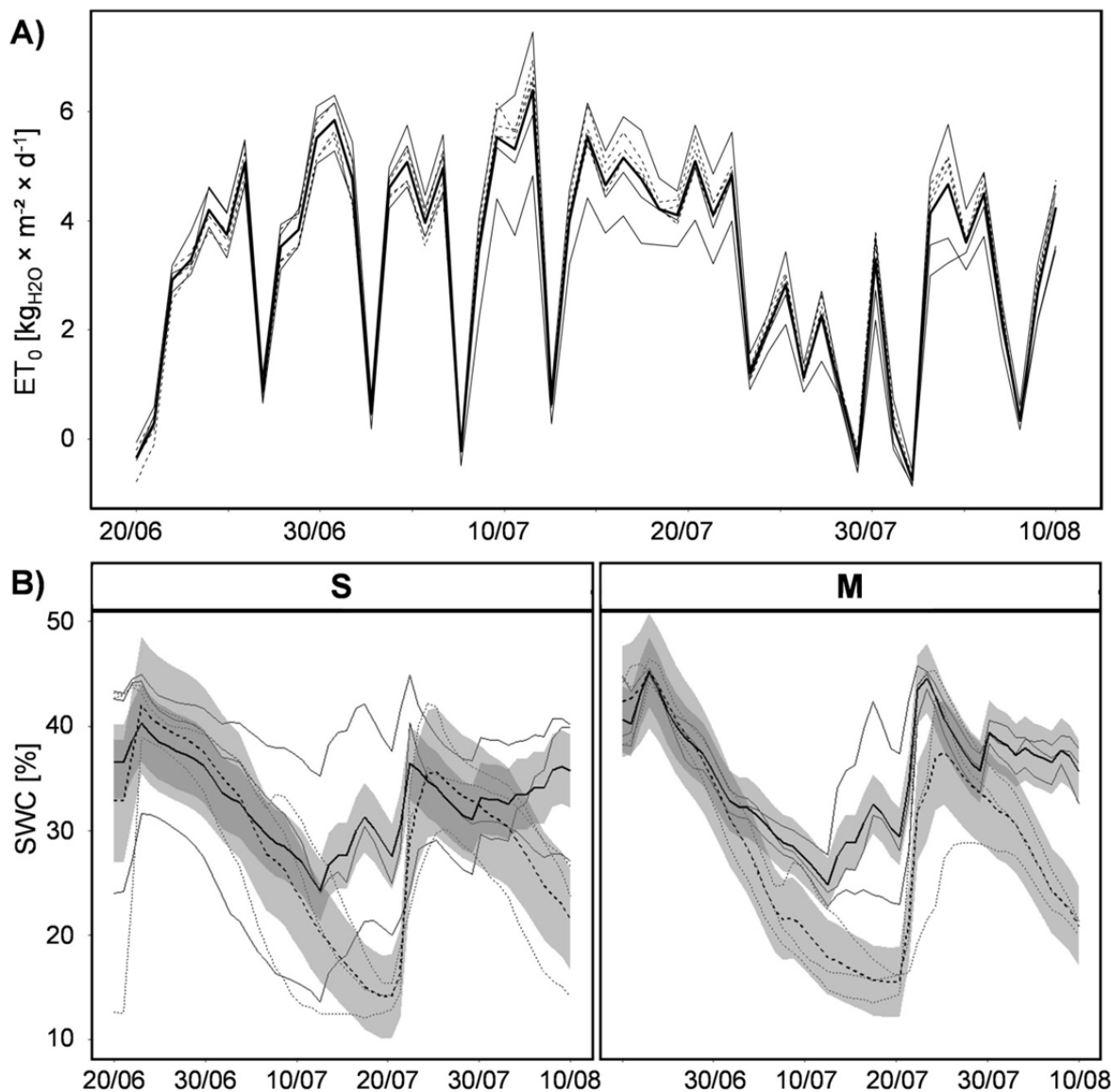



Fig 2: Atmospheric demand (ET_0) and soil water content (SWC) as drivers of ET, A) dynamics of daily average ET_0 over the course of the experiment (bold line: all plot average, thin lines: individual plots); B) dynamics of daily average SWC for two vegetation types (S & M, see Table 1) in contrasting irrigation schemes (REG - solid lines, D - dashed lines; bold lines: treatment average; shaded area: standard deviation, thin lines: individual plots); S: Stubai, M: Matsch/Mazia.

393 The average air temperature during the course of the experiment was 17.5 °C (±

394 3.1°C – standard deviation). Among the different plots no systematic variation of

395 temperature, relative humidity and solar radiation was measured by the microclimate

396 stations underneath the shelters. Summarizing the different atmospheric

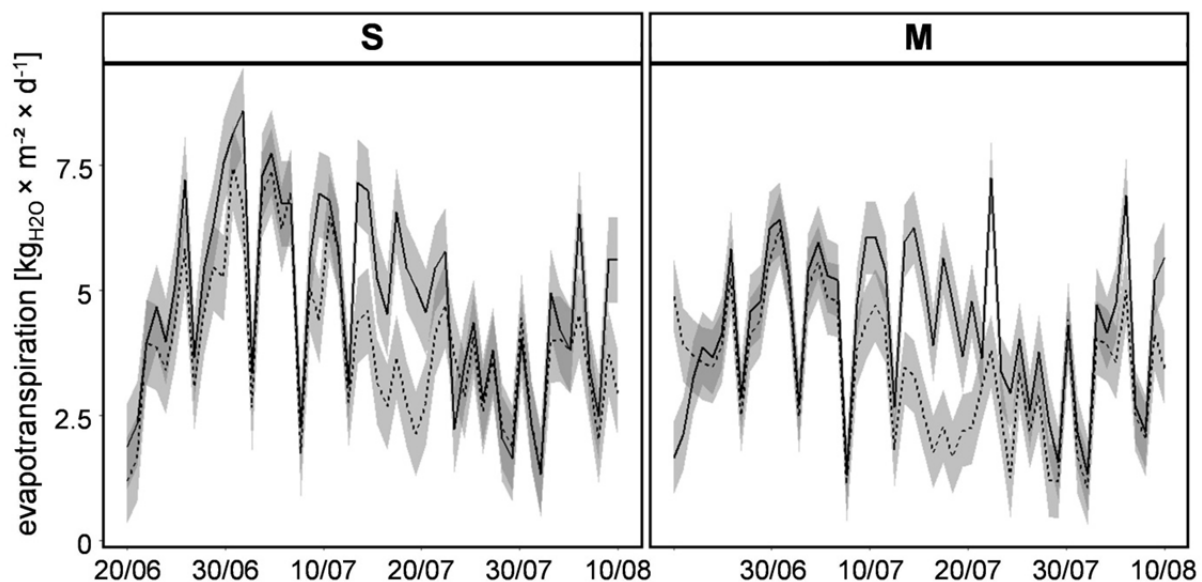
397 components defining rates of ET, ET_0 was calculated. During the duration of

398 experiment the average daily ET_0 was 3.26 kg_{H2O} m^{-2} d^{-1} (± 1.95 SD) with a minimum

399 at 0.75 and a maximum of 6.4 kg_{H2O} m^{-2} d^{-1}. However, since ET_0 is subject to short-

400 term natural variation of the underlying environmental parameters, fluctuations

401 between consecutive days were found to be very pronounced and no temporal trend

402 was revealed over the period of the experiment (Fig. 2).

403

404 Fig 3: Dynamics of daily average ET over the course of the experiment for two

405 different vegetation types (S & M, Table 1) subjected to contrasting irrigation regimes

406 (REG - solid lines, D - dashed lines; shaded area – standard deviation); S: Stubai, M:

407 Matsch/Mazia.

408

409 During the time of the experiment the two contrasting irrigation schemes led to

410 distinct SWC dynamics within the respective mesocosms (Fig. 2). Since SWC in all

411 lysimeters was high at the beginning of the experiment the value initially decreased

412 in all plots irrespective of treatment indicating that the water irrigated on plots with

413 regular irrigation did not fully compensate the loss of water by ET of the

414 corresponding communities. The first clear effects of different irrigation became

apparent in the lysimeters with the M-type of vegetation only after applying approximately two weeks of drought. In the lysimeters with the S-type of vegetation the variability of SWC was far stronger, a distinct difference between watering schemes could be observed there only after the start of additional manual watering. After approximately one month, SWC in both vegetation types revealed clear 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). As the canopy height and biomass of both vegetation types was clearly higher than the reference vegetation assumed for ET_0, the average evapotranspirative water loss for the lysimeter unit during the duration of the experiment also surpassed ET_0 with 4.9 kg_{H20} 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. During the first third of the experiment ET of the S-type lysimeters was on average higher than the M-type, afterwards no clear difference between vegetation types could be detected.. A clear difference of ET between contrasting irrigation regimes was only found during periods of strong divergence of SWC among the two treatments (approx. 15/07 to 25/07) during the rest of the experimental period ET on the drought regime was only slightly lower than in the regular one.

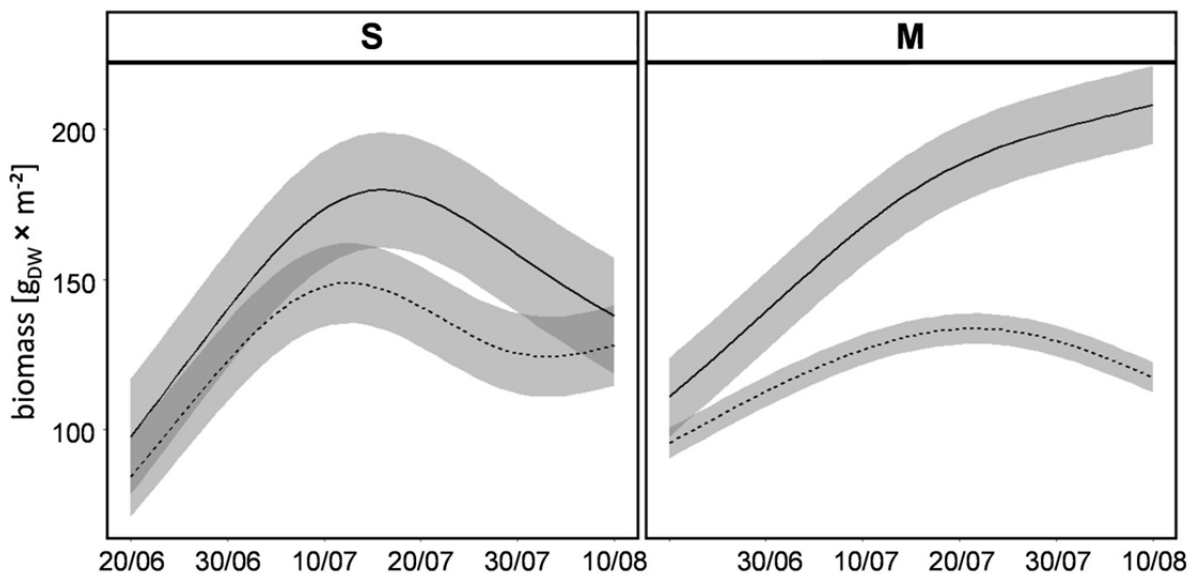



Fig 4: Predictions of biomass development for the two vegetation types (S: Stubai, M: Matsch/Mazia, Table 1) subjected to contrasting irrigation regimes (REG - solid lines, D - dashed lines; shaded area – standard deviation) throughout the duration of the experiment based on non-destructive measurements

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 increment 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. This pattern of vegetation development indicates that the early irrigation rates of the REG treatment were indeed too low and the manual compensation came too late for a regular development of the vegetation. Thus, also the S-type lysimeters subjected to the REG-treatment suffered a drought related early peak of biomass and subsequent senescence with just a short delay to the D-treatment. 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.

471

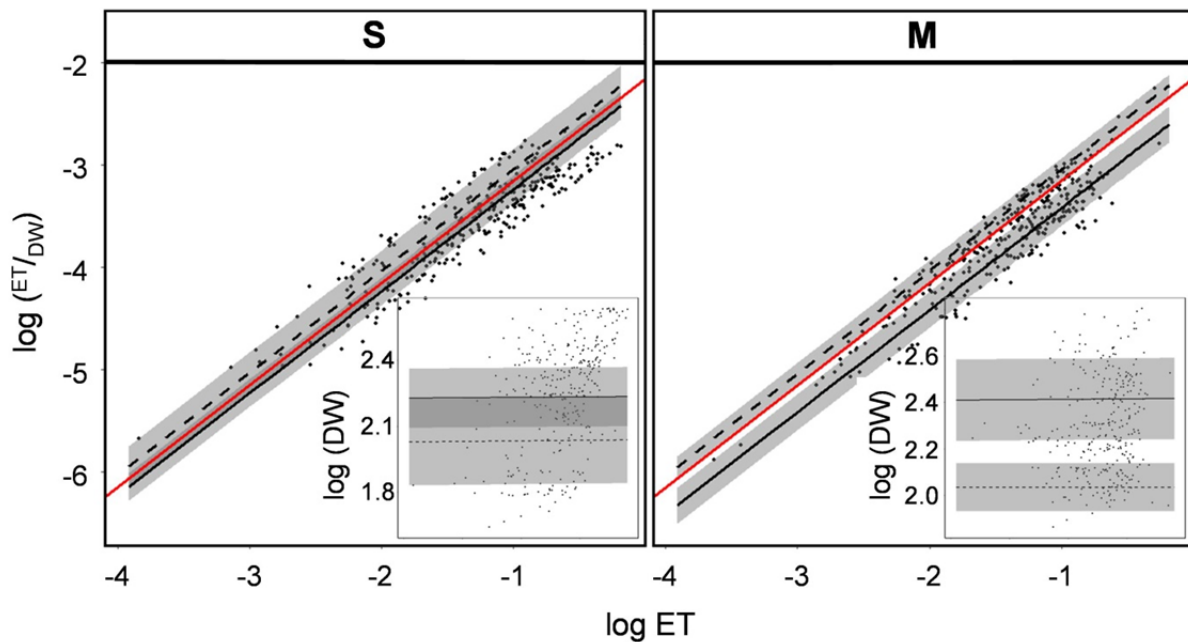



Fig 5: Log-log scaling for the two factors defining variability of ET: ET rates per unit dry weight (ET/DW) and standing biomass (=dry weight, DW) for the two different vegetation types (S & M, Table 1) subjected to contrasting irrigation regimes (REG - solid lines, D - dashed lines; shaded area – standard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

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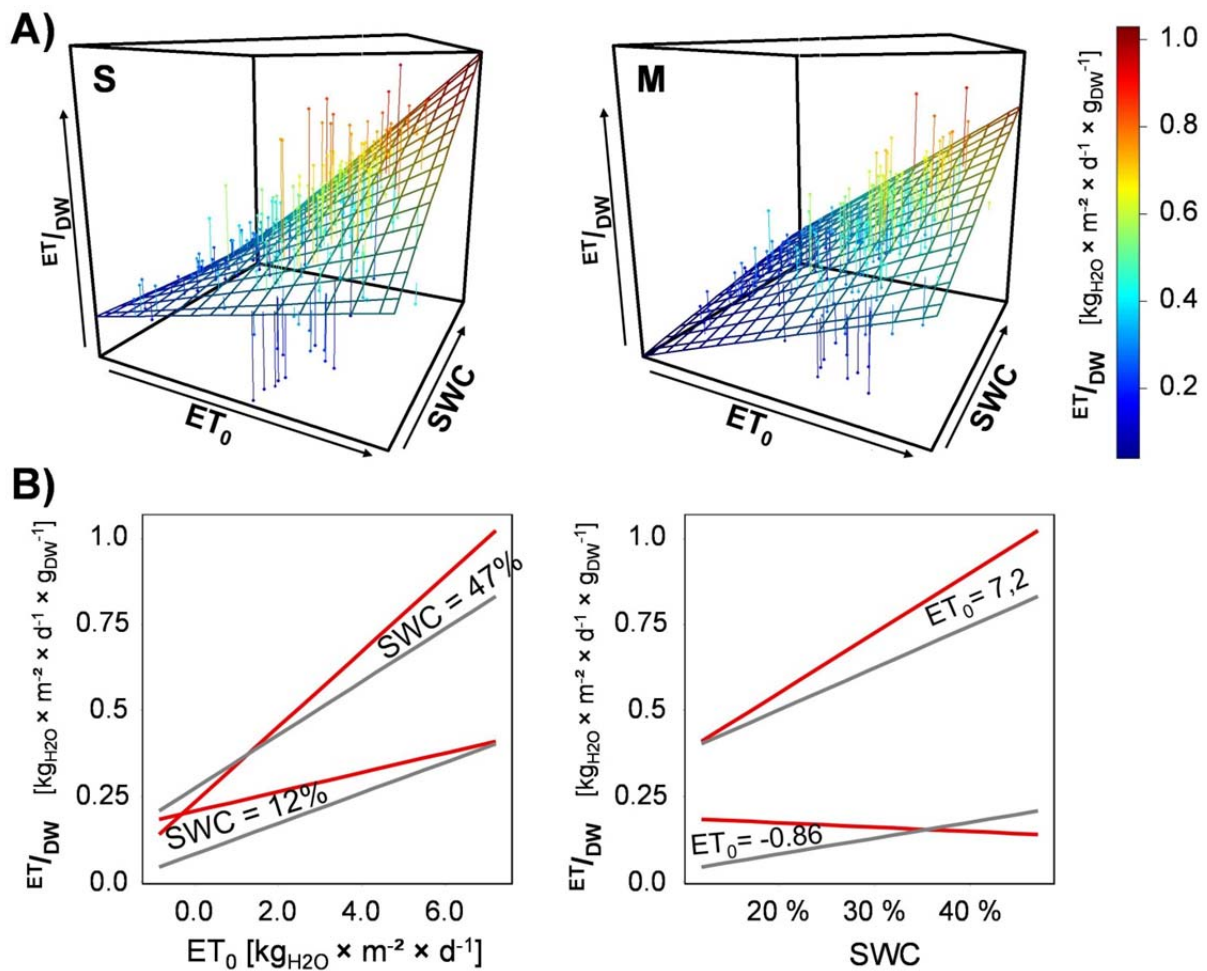
Variability of ET is subject to variation in evapotranspiration rates per unit biomass (ET/DW) and the variation in the standing biomass. Hence, when comparing rates of ET differentiating both underlying components will provide deeper insights on how the vegetation interface of different communities mediates the water flux from the soil. A strong positive 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 0.998 arguing that variation in ET rates measured during the course of this experiment is almost exclusively defined by the variation in ET rates per unit biomass (100% = 1). This relationship was independent of vegetation type and irrigation scheme.

488 However, variations of biomass did not have an effect on the variability of total ET
489 rates (Fig. 5).

491 Fig 6 A) 3D plots: response surface of ET per unit DW (ET/DW) along the two-
492 dimensional variation of ET_0 and SWC for the two different vegetation types (S:
493 Stubai, M: Matsch/Mazia, Table 1); B) projections of ET/DW response along ET_0 and
494 SWC at maximum/minimum value of the particular other (red: S-communities, grey:
495 M-communities)

496   After revealing ET/DW as the most important driver in defining variation in the
497 rates of total ET from the lysimeter mesocosms, the effect of combined variation in
498 ET_0 and SWC on rates of ET per unit biomass was modelled in dependence of the
499 vegetation type (ET/DW = f(ET_0×SWC×vegetation type)).On the entire field site, on
500 average the daily sums of ET_0 ranged from -0.75 to a maximum of 6.4 kg_{H2O} m^{-2} d^{-1},
501 while within the individual plots daily average values ranged from -0,86 to 7,2 of 6.4
502 kg_{H2O} m^{-2}. 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 ET/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.

Table 2 Parameter and parameter interactions affecting the ET_0-SWC landscape of ET

Parameter	F-value	p-value
ET_0	341.31	**<0.001**
SWC	28.09	**<0.001**
vegetation type	2.81	0.154
ET_0 × SWC	37.20	**<0.001**
ET_0 × vegetation type	1.24	0.265
SWC × Vegetation type	2.74	0.098

ET$_0$ × SWC × Vegetation type	7.08	**0.008**

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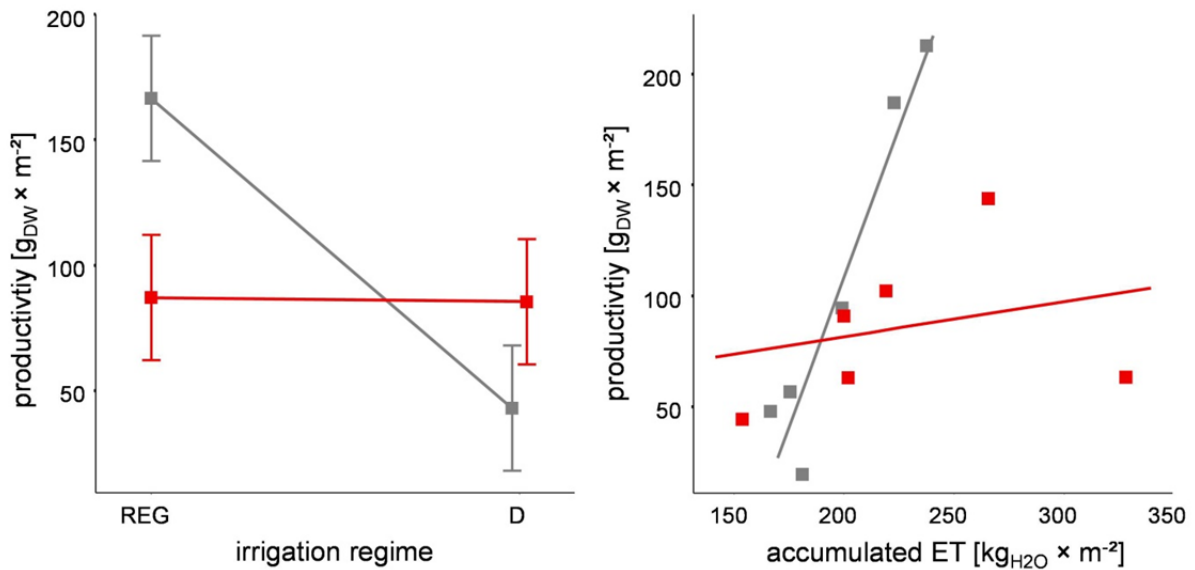
Fig 7: Productivity of two vegetation types (± standard error, Stubai - red & Matsch/Mazia - grey; Table 1) subjected to contrasting irrigation schemes (Fig 1), right panel: dry matter productivity of two vegetation types (see above) as function of accumulated evapotranspiration over the experimental 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. Due to the insufficient irrigation mentioned before 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 usage 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$_{DW}$ per kg but was strongly influenced by highly variable productivity of the two lysimeters with the

551 highest accumulated ET (Neglecting this one observation, productivity in the S-
552 vegetation was around $0.91g_{DW}$ per kg of water). This pattern suggests that biomass
553 generation in the M-type vegetation is strongly dependent on ET and therefore water
554 availability. For the S-type vegetation the early decrease of biomass in both
555 treatments and the high variability of productivity at high ET made it difficult to
556 assess an integrated trend in water use efficiency for the entire experimental period.

557

558 DISCUSSION

559   It is intuitive to understand, that ET_0 and SWC impose independent and
560 interacting effects on water fluxes from the soil to the atmosphere with one of either
561 constraining the total rates of ecosystem ET (Kim and Verma, 1991; Perez et al.,
562 2006). Beyond the effects of these abiotic drivers, the measurements of the present
563 experiment reveal a community specific signal in the definition of ecosystem water
564 exchange. The community specific configuration of the soil-plant-atmosphere
565 interface is instinctively acknowledged if distinct vegetation types are compared.
566 Water fluxes from the system will to some degree always scale with productivity and
567 total biomass of the vegetation (Zeppel et al., 2014 and references therein). This
568 relationship will drive variation in ET of contrasting biomes together with
569 environmental parameters affecting the availability and the atmospheric demand of
570 water.
571   However, results of this experiment reveal that vegetation specific differences
572 have a component, which defines ecosystem water flux beyond the impact of
573 variations in total biomass. Such differences will be important to understand and to
574 consider if communities of the same type need to be evaluated with respect to their
575 particular impact on the hydrological regulation of the ecosystem. The response of
576 water fluxes along co-operating gradients of SWC and ET_0 indicated divergence in
577 the conductance potential of the two alpine grassland communities, which were
578 independent from the biomass present. At low SWC lower values of ET/DW for the
579 M-type vegetation indicate a better ability to control water loss in dry conditions event
580 though the difference to the S-type diminishes with increasing ET_0. Conversely,
581 under conditions of high soil water availability water fluxes from the S-type
582 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, ET of the S-type increased far stronger 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 overall lower ET rates than for the S-type for most environmental scenarios included within the experimental period and a stronger control of transpiration especially at low SWC. . 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 this community 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 of soil hydrological properties event though the slightly higher amount of plant available water for the S-type might be offset by a finer texture and higher organic matter content regarding soil water storage capacity. The different pattern of SWC with an earlier distinction between REG- and D-Treatment after the first 2-3 weeks of the experiment are more likely caused by the lower ET of the M-type vegetation during this period. 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).

CONCLUSION

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. Hence, the optimization of future grassland management could play a crucial role by adapting species composition. Furthermore, understanding the specific hydraulic conductance potential of soil water for varying grassland ecosystems is a prerequisite to achieve maximum agricultural yield in a future environment. 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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