

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

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31 **ABSTRACT**

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

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

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

76 Defining productivity-precipitation relationships of ecosystems is of main
77 interest, because functional changes in soil-plant-atmosphere interface, which
78 control water fluxes into the atmosphere, will inherently be affected by the
79 manifestation of that relationship. However, beyond the direct implications of limited
80 water availability on biomass production and growth, indirect mechanisms define this
81 relationship. The abundance of individual plant species in the community and
82 resulting functional structure of that community will adjust, optimising water use
83 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, Ingrisich 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**

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)	<i>Achillea millefolium</i> , <i>Carum carvi</i> , <i>Pimpinella major</i> , <i>Poa trivialis</i> ,			<i>Achillea millefolium</i> , <i>Anthoxanthum odoratum</i> , <i>Anthriscus sylvestris</i> ,		

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

174

175 For this experiment six plots of 3.5 \times 3.5 m were established. Traversing the
176 corresponding area, each plot was defined by installing half-cylindrical metal frames.
177 In the centre of each plot these frames providing the base for the rain sheltering
178 reached a height of approx. 2.5 m. In each corner at the outer plot margin four
179 irrigation sprinklers pointing towards the centre of the plot were set up. The irrigation
180 system described in detail by (Newesely et al., 2015) was used to simulate
181 precipitation during periods of experimental manipulation of water provision to the
182 system.

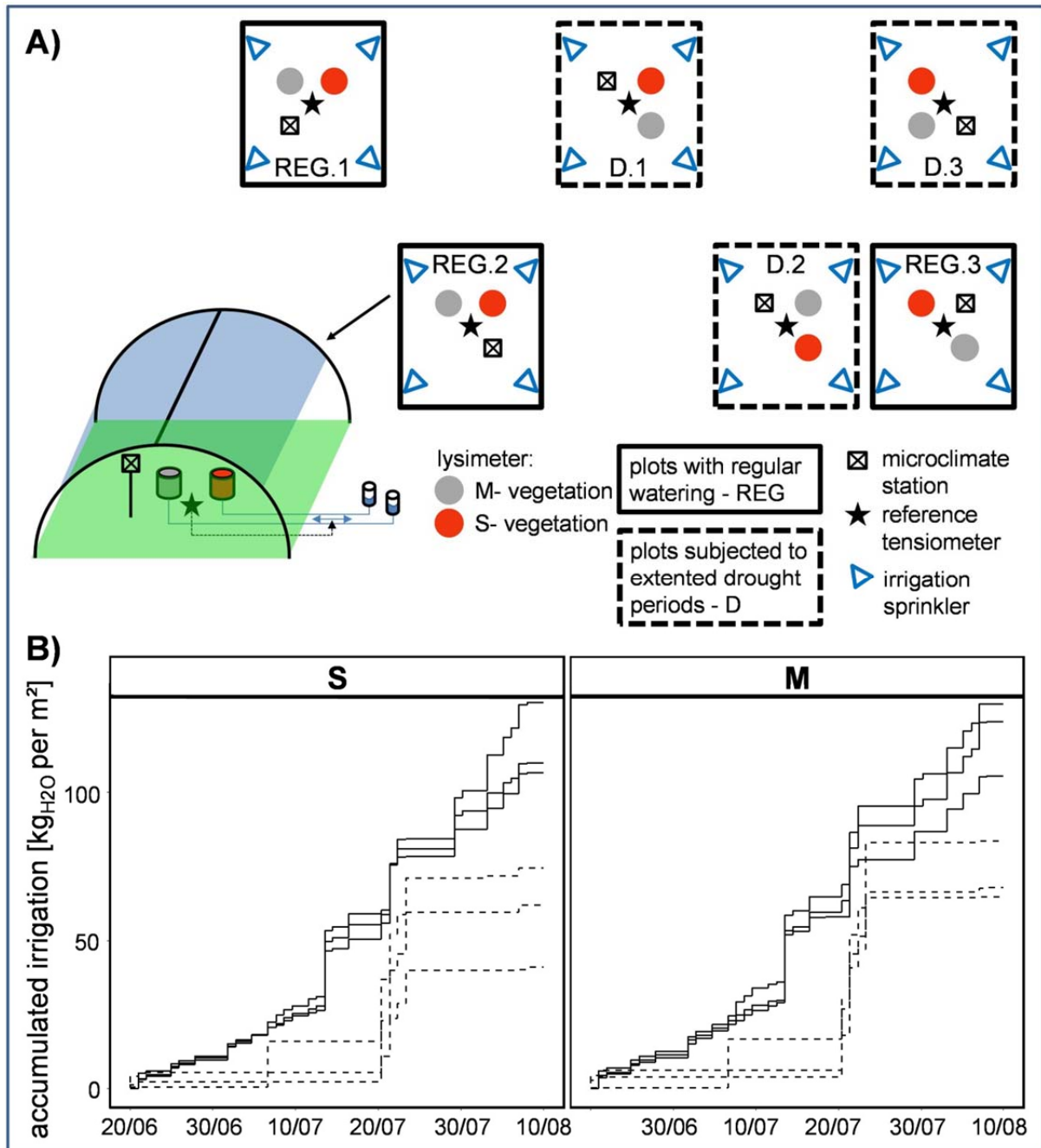
183 In the centre of each plot two small-scale lysimeters with 0.3 m diameter and
184 0.3 m depth were installed in collaboration with, and supervised by the employees of
185 the manufacturer (Smart-Field-Lysimeter, UMS/Meter Group Munich, Germany).
186 Every lysimeter was filled with a soil-vegetation monolith by cutting the hollow
187 cylindrical lysimeter blank into an undisturbed patch of the corresponding ecosystem.
188 This compression free procedure allowed to remain the original and unaffected
189 stratification of the soil and to conserve the natural composition of pore spaces within
190 the monolith. The filled lysimeter blanks were subsequently excavated and cut
191 horizontally at a depth of 0.3m. With 90 % of root biomass distributed above 0.2 m in
192 both investigated vegetation types, a lysimeter depth of 0.3 m was assumed to be
193 sufficient. The bottom of the lysimeter was closed with a tension controlled hydraulic
194 boundary connected to a bi-directional pumping system to regulate water flow into
195 and out of the lysimeter. After inserting soil moisture, temperature (EC-5 Small Soil
196 Moisture Sensor, Decagon Devices, USA) and matrix potential probes (MPS-2,
197 Decagon Devices, USA) at 0.05, 0.15 and 0.25m depth into the lysimeter monolith,
198 each system was placed on a weighing platform (accuracy of 0.005 kg, PL-50,
199 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 programmed 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

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

261

262 *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,

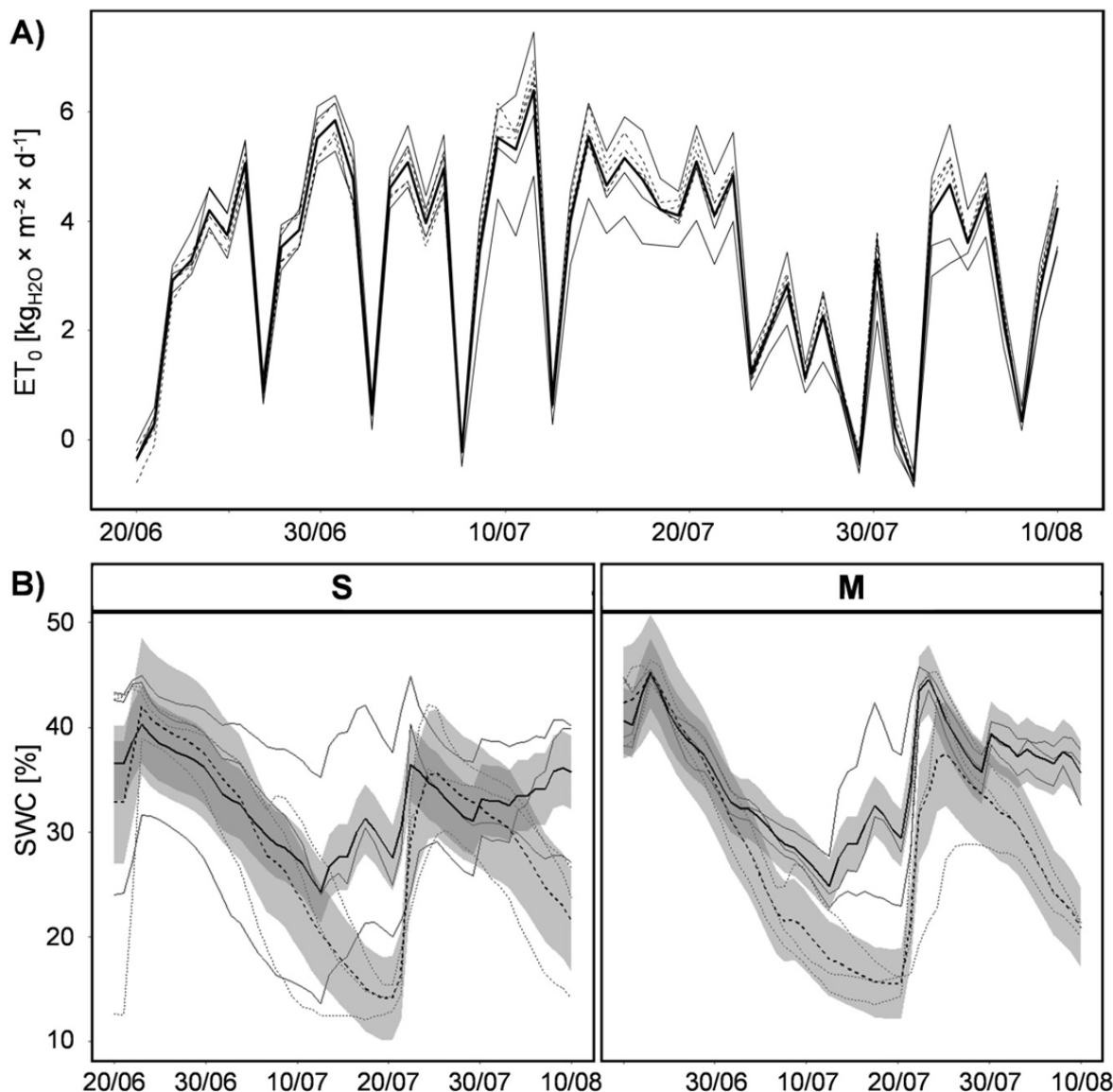
329 Germany). Using the soil specific moisture retention curve, absolute SWC was
330 corrected based on soil matrix potential data. To summarize the time course of water
331 availability in the soil of each lysimeter unit, the average values of SWC of both
332 layers between 0.05 - 0.15m and 0.15 – 0.25m 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.

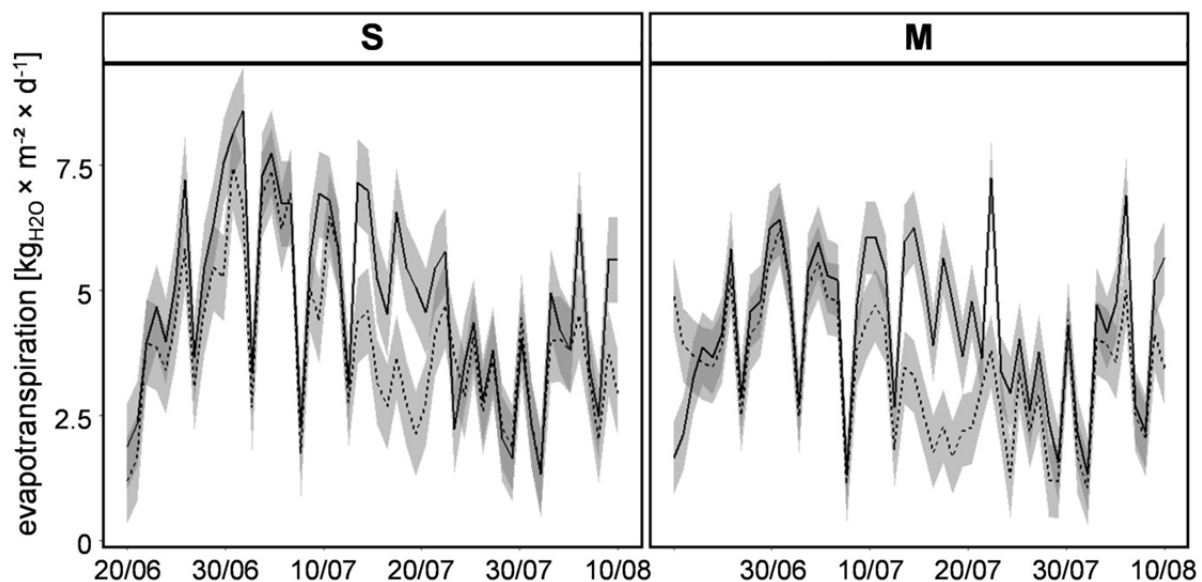
358 For the evaluation of evapotranspiration responses mixed effects models were
359 fitted using the *nlme*-package (Pinheiro et al., 2017). All these models included the
360 identity of the different vegetation types (categorical) in full factorial combination with
361 additional covariates defining 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 $ET = ET/DW \times DW$ 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).



385
 386 Fig 2: Atmospheric demand (ET₀) and soil water content (SWC) as drivers of ET, A)
 387 dynamics of daily average ET₀ over the course of the experiment (bold line: all plot
 388 average, thin lines: individual plots); B) dynamics of daily average SWC for two
 389 vegetation types (S & M, see Table 1) in contrasting irrigation schemes (REG - solid
 390 lines, D - dashed lines; bold lines: treatment average; shaded area: standard
 391 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).

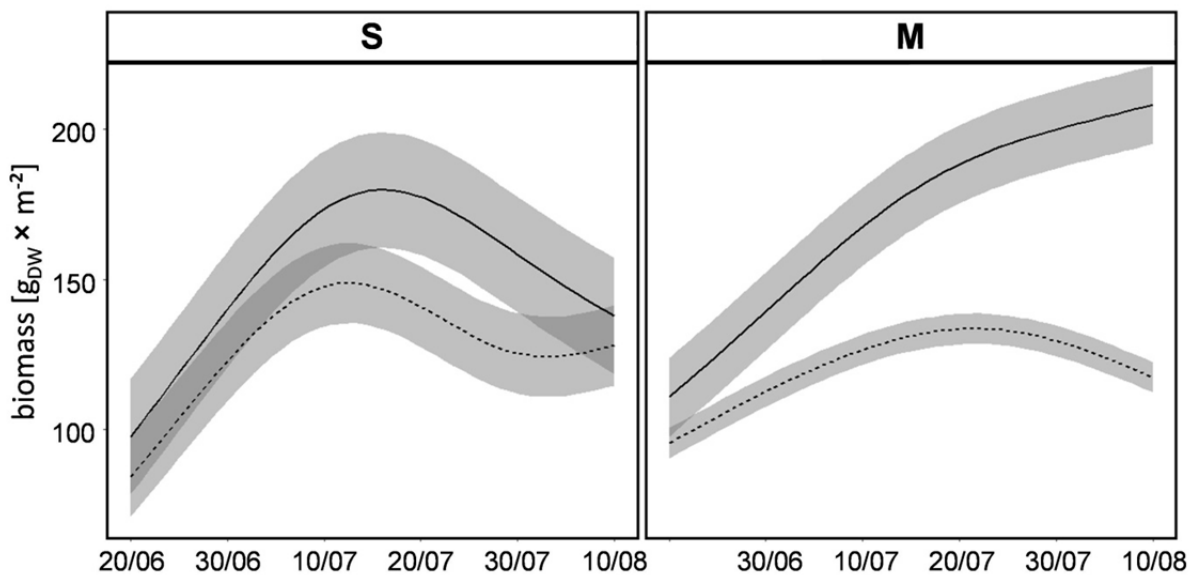


403
 404 Fig 3: Dynamics of daily average ET over the course of the experiment for two
 405 different vegetation types (S & M, Table 1) subjected to contrasting irrigation regimes
 406 (REG - solid lines, D - dashed lines; shaded area – standard deviation); S: Stubai, M:
 407 Matsch/Mazia.

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

415 apparent in the lysimeters with the M-type of vegetation only after applying
 416 approximately two weeks of drought. In the lysimeters with the S-type of vegetation
 417 the variability of SWC was far stronger, a distinct difference between watering
 418 schemes could be observed there only after the start of additional manual watering.
 419 After approximately one month, SWC in both vegetation types revealed clear effects
 420 of the contrasting irrigation strategies. At that time, SWC of both treatments was
 421 restored to similar values observed during the initial stages of the experimental
 422 period in order to avoid distress in the drier mesocosms. Rates of daily ET from the
 423 lysimeters were varying very strongly through the period of the experiment and did
 424 not reveal a general temporal trend (Fig. 3). As the canopy height and biomass of
 425 both vegetation types was clearly higher than the reference vegetation assumed for
 426 ET_0 , the average evapotranspirative water loss for the lysimeter unit during the
 427 duration of the experiment also surpassed ET_0 with $4.9 \text{ kg}_{\text{H}_2\text{O}} \text{ m}^{-2} \text{ d}^{-1}$. Subject to the
 428 atmospheric water vapour pressure deficit the recorded fluxes were characterised by
 429 a similar unsteadiness as the variability of the underlying environmental parameters
 430 would suggest. During the first third of the experiment ET of the S-type lysimeters
 431 was on average higher than the M-type, afterwards no clear difference between
 432 vegetation types could be detected.. A clear difference of ET between contrasting
 433 irrigation regimes was only found during periods of strong divergence of SWC
 434 among the two treatments (approx. 15/07 to 25/07) during the rest of the
 435 experimental period ET on the drought regime was only slightly lower than in the
 436 regular one.

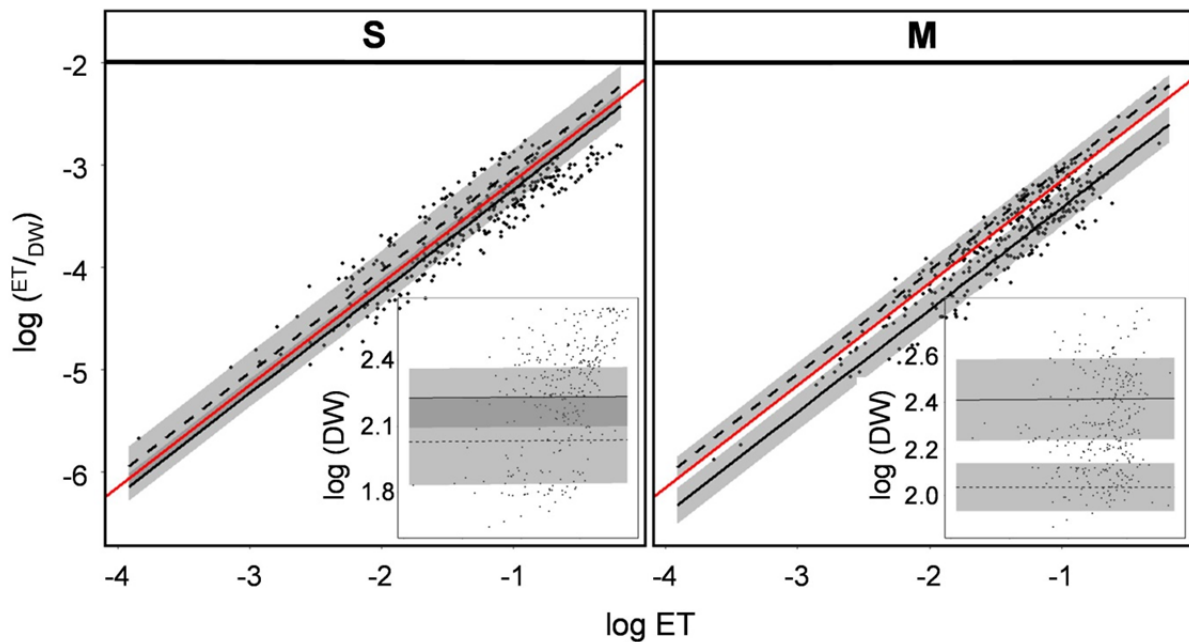


438 Fig 4: Predictions of biomass development for the two vegetation types (S: Stubai,
439 M: Matsch/Mazia, Table 1) subjected to contrasting irrigation regimes (REG - solid
440 lines, D - dashed lines; shaded area – standard deviation) throughout the duration of
441 the experiment based on non-destructive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

442

443 The prediction of biomass development combined from the different non-
444 invasive estimation methods suggested distinct growth trajectories for the two
445 vegetation types in interaction with the two irrigation regimes. The mesocosms with
446 communities belonging to the local S-type revealed larger biomass increment during
447 early stages of the experiment irrespective of the applied irrigation regime. However,
448 with increasing duration of the experiment, growth dynamics started diverging in
449 treatments with contrasting water provision, with biomass differences peaking at the
450 mid-time of the experimental period. After that peak, the prediction of dry weight
451 suggested a decline in standing biomass for both water regimes in the S-
452 communities. Towards the end of the experiment, biomasses of communities in the
453 different water treatments converged to similar values. This pattern of vegetation
454 development indicates that the early irrigation rates of the REG treatment were
455 indeed too low and the manual compensation came too late for a regular
456 development of the vegetation. Thus, also the S-type lysimeters subjected to the
457 REG-treatment suffered a drought related early peak of biomass and subsequent
458 senescence with just a short delay to the D-treatment. A different pattern of biomass
459 development was detected for the transplanted mesocosms (M). From the beginning
460 of the experiment growth processes of the different irrigation treatments yielded
461 distinct trajectories. In the treatment experiencing regular water provision the
462 biomass gain per unit time was stronger than in the mesocosms being subjected to
463 irregular watering. That pattern was consistent throughout the experiment, with a
464 strictly monotonic increase of standing biomass in the M communities of well-
465 watered plots. In contrast, the vegetation of the M-type in the plots with restricted
466 watering growth started stagnating during the second half of the experimental period.
467 Unlike the S-type, at the end of the investigation period, biomasses in the M-type
468 communities were clearly distinct according to the different watering regimes, with

469 the standing mass in the regularly watered plots approximating double the amount
470 compared to the treatment with restricted water provision.



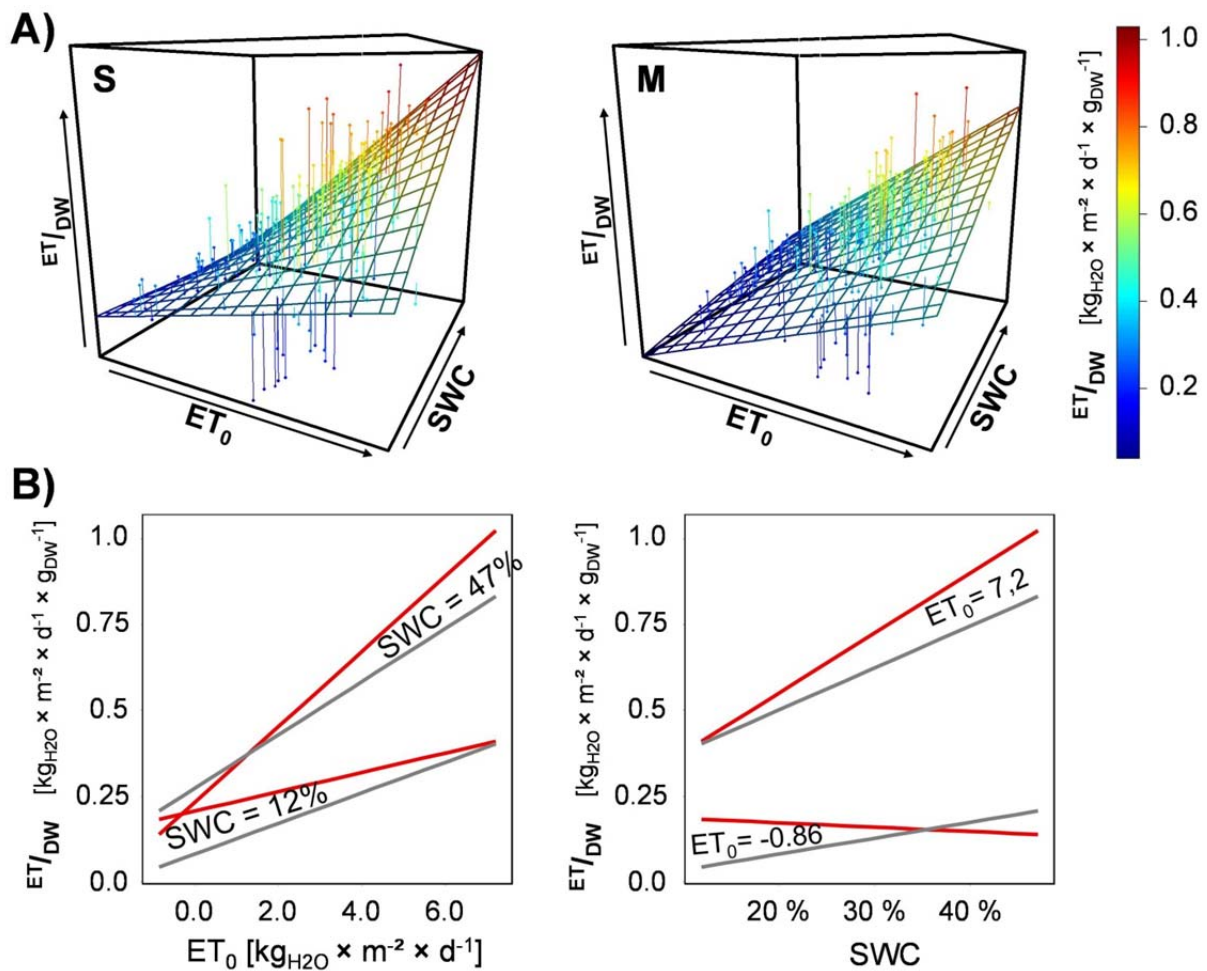
471

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

478

479 Variability of ET is subject to variation in evapotranspiration rates per unit
480 biomass (ET/DW) and the variation in the standing biomass. Hence, when
481 comparing rates of ET differentiating both underlying components will provide deeper
482 insights on how the vegetation interface of different communities mediates the water
483 flux from the soil. A strong positive correlation of total daily ET and ET/DW was
484 found (Fig 5). The log-log-scaling of ET/DW with ET revealed a slope of 0.998
485 arguing that variation in ET rates measured during the course of this experiment is
486 almost exclusively defined by the variation in ET rates per unit biomass (100% = 1).
487 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).



490

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

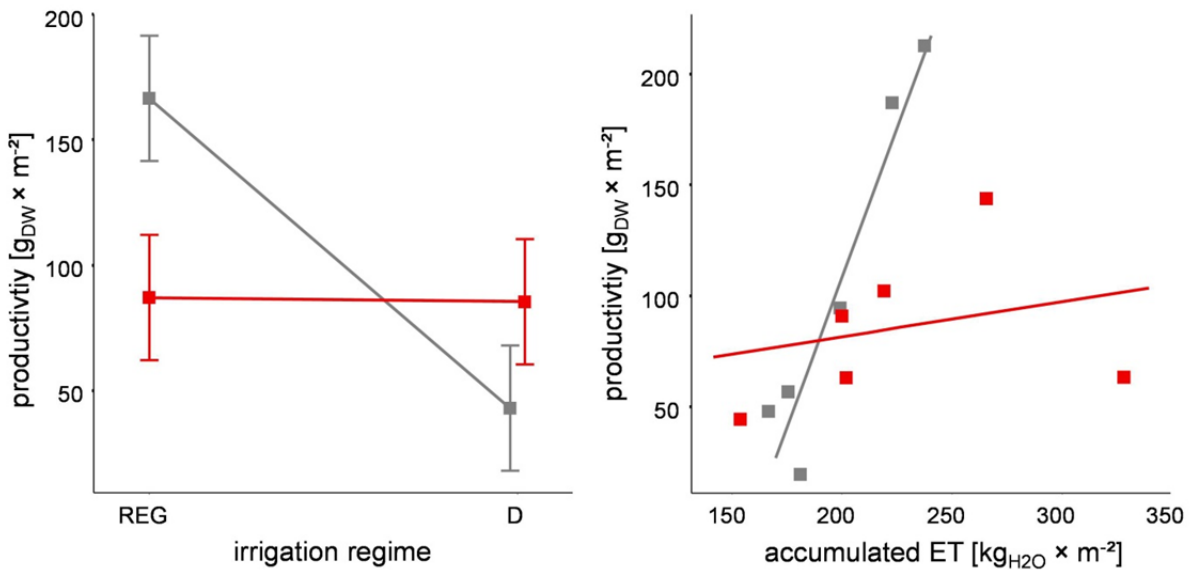
496 After revealing ET/DW as the most important driver in defining variation in the
 497 rates of total ET from the lysimeter mesocosms, the effect of combined variation in
 498 ET₀ and SWC on rates of ET per unit biomass was modelled in dependence of the
 499 vegetation type (ET/DW = f(ET₀×SWC×vegetation type)). On the entire field site, on
 500 average the daily sums of ET₀ 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

503 covered a range from approximately 12-47% (Fig. 5). Both, ET_0 and SWC had a
504 highly significant and positive effect on achieved rates of ET/DW (Fig. 6, Table 2).
505 However, as implied by a significant synergistic interaction of ET_0 and SWC, rates of
506 ET/DW increased stronger if SWC and ET_0 increased concurrently than the
507 individual gradients of either would imply (Fig 6.). With increasing ET_0 the response
508 of ET/DW was stronger the higher SWC was. However, there was a significant
509 difference how both vegetation types responded within the landscape of
510 environmental drivers defining ET/DW (Table 2). The local (S) vegetation had higher
511 rates of ET/DW - when both ET_0 and SWC were low - than the transplanted
512 vegetation type (M), suggesting a higher base rate of ET/DW. On the low end of
513 investigated SWC the M-vegetation had a stronger response to ET_0 than the local S-
514 vegetation. Despite that stronger response of the transplanted vegetation (M) along
515 the ET_0 gradient at low SWC, the maximum rates of ET/DW converted to similar
516 values due to the higher base flux at low ET_0 / low SWC in the S-vegetation. In turn,
517 under conditions of high soil water availability the ET_0 -response of the S-type was
518 much more pronounced than in the M-type. A similar pattern was found comparing
519 the SWC-response of both vegetation types for the range of different ET_0 values
520 realized during the experiment. At low ET_0 the M-type vegetation responded stronger
521 to variations in SWC, while there was almost no response in the S-type. However, at
522 high ET_0 the response of the S-type to increasing SWC was again much more
523 pronounced than in lysimeters with the M-type. Because of the higher rates of
524 ET/DW at low ET_0 /SWC and the overall increased response potential of the S-type
525 vegetation, the ET/DW values achieved in the M-communities stayed below those
526 found in the local vegetation for almost the entire range of combinations between
527 ET_0 and SWC investigated in this experiment.

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

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

530



531

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

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

545 Integrated over the entire experimental period, the biomass productivity per unit
 546 water usage was significantly higher for the transplanted mesocosms M (Fig 7, right
 547 panel). The data suggested a productivity increase of 2.6g_{DW} per kg of water for the
 548 M vegetation. In contrast, for the S-type mesocosms the average increase of
 549 productivity per 1kg of evapotranspiration was approximately only 0.16g_{DW} per kg but
 550 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 ET₀ 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 ET₀ 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 ET₀. Conversely,
581 under conditions of high soil water availability water fluxes from the S-type
582 responded much stronger to increases of ET₀ suggesting a higher overall

583 conductance potential. Similar implications were revealed along the gradient of soil
584 water availability. SWC variations had almost no effect on the S-type communities
585 when the atmospheric draw was small, while the M-type mesocosm still mediated
586 fluxes to the atmosphere. Under high ET_0 however, the divergence in the response
587 of ET between S & M-communities to varying SWC suggests that, from starting at
588 similar rates, ET of the S-type increased far stronger the less soil water became
589 limiting. These differences between the two vegetation types indicate different
590 strategies in the water utilisation. For the M-type this strategy may be summarized by
591 overall lower ET rates than for the S-type for most environmental scenarios included
592 within the experimental period and a stronger control of transpiration especially at
593 low SWC. . This implies an overall conservative and water saving strategy. For the
594 S-communities, in contrast, which show high water conductance potential with
595 strongly increasing ET rates when environmental conditions become less
596 constraining, an acquisitive strategy is suggested. With high rates even at base level
597 this community appear not to be optimized to save water and might experience
598 drought effects earlier and probably stronger, when water availability becomes
599 limiting. There might be some dampening effect of soil hydrological properties event
600 though the slightly higher amount of plant available water for the S-type might be
601 offset by a finer texture and higher organic matter content regarding soil water
602 storage capacity. The different pattern of SWC with an earlier distinction between
603 REG- and D-Treatment after the first 2-3 weeks of the experiment are more likely
604 caused by the lower ET of the M-type vegetation during this period. Although soil
605 hydrological properties play a role in the community specific conductance potential of
606 soil water to the atmosphere, differences found for the investigated two different
607 vegetation types turned out to be not decisive in this context.

608 Sharing a common environment, the differences in biomass-independent
609 conductance potential between the two Alpine grassland communities are likely to
610 have a foundation in a contrasting physiological, functional and structural
611 organisation of the vegetation. Functional divergence in water utilisation,
612 evapotranspiration and other aspects of hydrological regulation of ecosystems (e.g.
613 infiltration, surface run-off) between communities can be manifested by the
614 frequency distribution in the values of particular traits (Díaz et al., 2013). Canopy
615 complexity - density and size, growth form composition, composition and diversity of
616 vascular structures, stomatal density and conductance mediate community specific

617 differences in the evapotranspiration aboveground (de Bello et al., 2010)
618 Belowground, the structure and depth of the individual rooting systems is an
619 important determinant for the water utilisation potential of communities (Knapp et al.,
620 2008). Along the variation and composition of these traits water usage and
621 consequently also drought resistance of contrasting communities is defined. The
622 differences in the two vegetation types suggest high exploitation potential for scarce
623 soil water, probably facilitated by a higher priority on water exploitation in the soil in
624 the M-mesocosms and, conversely, a stronger importance on aboveground
625 structures mediating light capture and gas-exchange, leading to an increased
626 response potential of ET for atmospheric triggers in the local S-communities.

627 The clear vegetation response to variable water availability observed in the
628 present experiment is not common in studies targeting Alpine grasslands (de Bello et
629 al., 2010). Based on multi-annual measurements of evapotranspiration at 16 sites in
630 the Austrian Alps, it was suggested, that even during years with low annual
631 precipitation Alpine grasslands do not experience water stress (Wieser et al., 2008).
632 Gilgen and Buchmann (2009) could not conclude on a general drought response of
633 grasslands in Switzerland, while acknowledging a site-specific impact with
634 communities receiving less annual precipitation being more susceptible to drought
635 stress than those at higher rainfall levels. Also arguing for a co-defined and
636 interactive manifestation in the effects of varying water availability, a strong drought
637 response of Alpine grassland functioning was revealed under scenarios of co-
638 occurring heat waves (De Boeck et al., 2016). A modelling study for grassland
639 ecosystems in the Austrian- and French Alps suggested a higher vulnerability to
640 drought for communities with a water spending strategy targeting on water provision
641 of the ecosystems in general (Leitinger et al., 2015). However, it seems
642 inappropriate to synthesize a general summary on the response of Alpine grasslands
643 to variations in water availability given the small body of research performed.
644 Considering the different spatio-temporal scales, the range of parameters measured,
645 and the management and biodiversity spectrum of different grassland types in the
646 Alps, drawing broad and universal generalisation yet becomes unrewarding. For
647 experiments with contrasting treatments the practicalities of manipulating water
648 availability potentially also need to be considered for the interpretation of the results.

649 Drought scenarios are usually generated by rain-out shelters using a UV-
650 permeable, transparent film for roofing. If compared to unroofed controls,

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

682

683 **CONCLUSION**

684 Irrespective the variability of different water availabilities within the two irrigation
685 regimes, mesocosms subjected to regular watering (REG) had on average a higher
686 productivity than those with irregular and in total less irrigation. However, significant
687 differences between the different communities were found in the response to
688 variations in the water supply (Fig 7). Relating total productivity to the amount of
689 evapotranspirative water release over the experimental period revealed a higher
690 biomass gain per unit water in the M-type communities. The higher water use
691 efficiency in the biomass production of these mesocosms together with their overall
692 stronger water saving strategy reinforces their optimisation to scarce water supply.
693 For the local S-communities, in contrast, the low biomass differential per unit water
694 consumption indicates a high potential to conduct water from the soil to the
695 atmosphere and that productivity of this vegetation is probably not often constrained
696 by water availability in its natural context. Brilli et al. (2011) expect from a water
697 spending strategy to have a cooling feedback in terms of climate warming. Hence,
698 the optimization of future grassland management could play a crucial role by
699 adapting species composition. Furthermore, understanding the specific hydraulic
700 conductance potential of soil water for varying grassland ecosystems is a
701 prerequisite to achieve maximum agricultural yield in a future environment. However,
702 a negative feedback for water provision services (i.e. down-stream water users) has
703 to be expected. Further decisive changes remain debatable: How will 'water
704 spending' plant communities adapt if droughts occur more frequently and possibly
705 with higher intensities (Bahn et al., 2014; Reichstein et al., 2013). To what extent
706 play – at least initially - physiological and morphological changes a role or is there an
707 immediate shift to a better adapted community?

708

709

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