

This item is the archived peer-reviewed author-version of:

Simulated heat waves affected alpine grassland only in combination with drought

Reference:

de Boeck Hans, Bassin Seraina, Verlinden Maya, Zeiter Michaela, Hiltbrunner Erika.- Simulated heat waves affected alpine grassland only in combination with drought

New phytologist - ISSN 0028-646X - (2015), p. -11

DOI: <http://dx.doi.org/doi:10.1111/nph.13601>

Handle: <http://hdl.handle.net/10067/1273290151162165141>

Simulated heat waves affected alpine grassland only in combination with drought

Running head: climate extremes in alpine grasslands

Hans J De Boeck^{*1}, Seraina Bassin², Maya Verlinden¹, Michaela Zeiter^{3,4}, Erika
Hiltbrunner⁵

¹*Research Group of Plant and Vegetation Ecology, Department of Biology, Universiteit
Antwerpen (Campus Drie Eiken), Universiteitsplein 1, B-2610 Wilrijk, Belgium*

²*Agroscope, Climate/Air Pollution Group, Reckenholzstrasse 191, CH-8046 Zurich, Switzerland*

³*School of Agricultural, Forest and Food Sciences, Bern University of Applied Sciences,
Länggasse 85, CH-3052 Zollikofen, Switzerland*

⁴*Institute of Plant Sciences, University of Bern, Altenbergrain 21, CH-3013 Bern, Switzerland*

⁵*Institute of Botany, Department of Environmental Sciences, University of Basel,
Schönbeinstrasse 6, CH-4056 Basel, Switzerland*

Word count: 6111 (introduction: 738, materials and methods: 2155, results: 1488,
discussion: 1668, acknowledgements: 62)

Word count abstract: 201

Number of references: 61

Number of tables: 3 (+6 as supplementary information)

Number of figures: 5

*Corresponding author. Tel.: +32-3-265-22-82; fax: +32-3-265-22-71

E-mail address: hans.deboeck@uantwerp.be

Universiteitsplein 1, Building B, B.0.24

B-2610 Wilrijk, Belgium

Keywords: biomass, climate extreme, event, gradient, mountain, stress,
transplantation, warming

1 **Abstract**

2 1. The Alpine region is warming fast, and concurrently, the frequency and intensity of
3 climate extremes are increasing. It is currently unclear whether alpine ecosystems
4 are sensitive or resistant to such extremes.

5 2. We subjected Swiss alpine grassland communities to heat waves with varying
6 intensity by transplanting monoliths to four different elevations (2440-660 m a.s.l.)
7 for 17 days. Half of these were regularly irrigated while the other half were deprived
8 of irrigation to additionally induce a drought at each site.

9 3. Heat waves had no significant impacts on fluorescence (F_v/F_m , a stress indicator),
10 senescence and aboveground productivity if irrigation was provided. However, when
11 heat waves coincided with drought, plants showed clear signs of stress, resulting in
12 vegetation browning and reduced phytomass production. This likely resulted from
13 direct drought effects, but also, as measurements of stomatal conductance and
14 canopy temperatures suggest, from increased high-temperature stress as water
15 scarcity decreased heat mitigation through transpiration.

16 4. The immediate responses to heat waves (with or without droughts) recorded in
17 these alpine grasslands were similar to those observed in the more extensively
18 studied grasslands from temperate climates. Responses following climate extremes
19 may differ in alpine environments, however, because the short growing season likely
20 constrains recovery.

21

22

23

24

25

26

27

28 **1. Introduction**

29

30 The number of experimental climate extreme studies performed on temperate
31 grassland systems has been growing rapidly the past years (Grime *et al.*, 2008;
32 Bloor & Bardgett, 2012; Vogel *et al.*, 2012). The same is not true for experiments
33 investigating extreme events in alpine grasslands, although these systems are
34 exposed to the observed rise in climate extremes as well (Rebetez, 2004). Moreover,
35 the increase in temperatures has been higher in the Alpine region than the global
36 average (Ceppi *et al.*, 2012). In lowland grasslands, studies have demonstrated that
37 the effect of heat waves, i.e. relatively short events with temperatures well above
38 the average, tends to be limited as long as water is available to the plants (De Boeck
39 *et al.*, 2011). Impacts of drought on ecosystem functioning have been shown to be
40 variable, depending on the phenological stage (Dreesen *et al.*, 2012), the species
41 numbers and identities involved (Kreyling *et al.*, 2008) and the interaction with other
42 factors such as temperature (Hoepfner & Dukes, 2012; Xu *et al.*, 2014) and
43 atmospheric CO₂ concentrations (Larsen *et al.*, 2011). Generally though, drought
44 seems to incite more negative responses on ecosystem structure and function than
45 heat.

46 Information on responses of grasslands in colder biomes to specific climate extremes
47 such as exceptional warmth or drought is sketchy. In polar regions, heat has been
48 documented to reduce cold limitation in some cases (Marchand *et al.*, 2005) although
49 we assume that this effect may not match the situation in alpine systems at lower
50 latitudes. These systems, like those in the arctic, are short-statured and therefore
51 have a high aerodynamic boundary resistance (Körner, 2003), but benefit from
52 higher radiation in summer. This causes alpine grassland to become significantly
53 warmer than one would assume from weather station data (Scherrer & Körner,
54 2010; Neuner & Buchner, 2012), and basic metabolic processes such as

55 photosynthesis are therefore similar to those in low elevation plants (Körner &
56 Diemer, 1987). On the other hand, higher Q₁₀ values for respiration reported for
57 alpine vegetation could imply a higher sensitivity to increased temperatures
58 (Larigauderie & Körner, 1995). Whether a period of exceptionally warm weather
59 would significantly affect alpine grasslands, is therefore an open question. In one of
60 the few studies that considered the impact of a heat wave on alpine communities,
61 satellite image analysis by Jolly *et al.* (2005) suggested that the 2003 European heat
62 and drought increased photosynthetic activity in the alpine zone. On the other hand,
63 Abeli *et al.* (2012) observed decreased flowering in their alpine grasslands during
64 that same climate anomaly, while vegetative growth was stable, although it is
65 unknown whether the reported phenological response was triggered by higher
66 temperatures or by drier conditions.

67 The Alpine region has not been regularly exposed to drought (Van der Schrier *et al.*,
68 2007), but increases in frequency and intensity are predicted for the near and long-
69 term future (Gobiet *et al.*, 2014). Responses of ecosystems in the alpine zone to
70 drought, like those to heat, have barely been documented. One study which focused
71 on alpine grassland in Switzerland found that primary production was reduced
72 already at moderate drought levels (Schmid *et al.*, 2011). Other drought studies
73 have been mainly constrained to lower elevations and have suggested both negative
74 (Gilgen & Buchmann, 2009, aboveground biomass) and little or no responses to
75 drought (Brilli *et al.*, 2011, carbon and water fluxes). Using a species distribution
76 model fed by fine-scale data, Engler *et al.* (2011) stressed the importance of
77 precipitation in alpine systems compared to rising temperatures. As drought and heat
78 are naturally coupled through atmospheric feedbacks (De Boeck & Verbeeck, 2011),
79 we specifically include their interaction here.

80 Here, we tested the impact of a heat wave as a single factor event and in conjunction
81 with a period of drought on alpine grasslands in Switzerland. To be able to detect

82 non-linear or threshold responses we used a gradient approach (Kreyling *et al.*,
83 2014), with three levels of heat wave intensity plus the unwarmed (reference)
84 situation, all crossed with drought. We hypothesize that (i) negative effects of heat
85 on plant growth and functioning would likely only occur at the hot end of the
86 gradient, where the probability is highest that temperature tolerance limits in tissues
87 are exceeded and respiration is increased; (ii) drought would result in increased
88 stress and reduced productivity; (iii) negative effects would be most apparent when
89 heat and drought co-occur, as warming speeds up drought and drought increases the
90 possibility of heat stress.

91

92

93 **2. Materials and methods**

94

95 **2.1. Location and set-up**

96 We transplanted swards of alpine grassland including its main rooting horizons
97 (monoliths) along an elevation gradient as a means of warming, a method that
98 circumvents some of the technical and logistic issues that render applying large
99 warming events difficult *in situ*. The ALPFOR research station, situated at 2440 m
100 near the Furka pass in the Swiss central Alps (46°34'N 8°25'E), has a gradient of
101 approximately 2000 meters in elevation in its surroundings which made it possible to
102 create significant temperature differences. We selected three lower-elevation sites
103 located at the West side of the pass, namely Oberwald (1390 m a.s.l., 46°32'N
104 8°21'E), Bister (1040 m a.s.l., 46°21'N 8°04'E) and Visp (660 m a.s.l., 46°17'N
105 7°53'E), creating a 1770 m vertical gradient. Using an elevation gradient also results
106 in a CO₂ gradient, as partial pressures of gases in the atmosphere decrease with
107 altitude. The pressure difference between the highest and lowest sites would have
108 been around 20% (Körner, 2003). However, any direct CO₂ 'fertilisation' effect would

109 be expected to be small as alpine systems have been shown not to be carbon limited
110 (Körner *et al.*, 1997; Inauen *et al.*, 2012).

111 The grassland at the reference alpine site is extensively grazed by sheep and
112 characterised by relatively deeply weathered soils of partly podzolized alpine brown
113 earth on siliceous bedrock (Inauen *et al.*, 2013). Two slopes (± 150 m apart) with
114 similar orientation (S-E) and vegetation were selected in the immediate vicinity of
115 the research station. On each slope, 24 monoliths were excavated during the first
116 week of July 2013 in a zone of approximately 4 x 10 m and adjusted with a knife to
117 tightly fit into buckets of 27.5 cm diameter and 21 cm depth, perforated at the
118 bottom. An anti-rooting mat prevented roots from growing outside of the buckets
119 while still allowing drainage. Monoliths were selected on the basis of the joint
120 presence of five common alpine species: the graminoids *Nardus stricta* and *Carex*
121 *curvula*, which together made up half or more of the vegetation according to cover
122 estimates (not shown), and *Homogyne alpina*, *Potentilla aurea* and *Geum*
123 *montanum*, which were never dominant. Other species present in many of the
124 monoliths were *Trifolium alpinum* (the only nitrogen fixing species recorded), *Poa*
125 *alpina* and *Anthoxanthum alpinum*. After excavation, monoliths were grouped based
126 on similarity of cover and then randomly allocated to treatments with equal
127 representation from each of the two excavation zones. We subsequently clipped
128 senesced shoots (but not any living tissues) to avoid erroneous attribution of leaf
129 mortality. This also means that the clipped phytomass (see later) was for the most
130 part produced during the experimental year.

131 On July 15, i.e. three to four weeks after snowmelt, monoliths were translocated to
132 the three lower sites (12 monoliths remained at the origin site Furka) and placed into
133 27.5 cm wide, 30 cm deep outer buckets that were dug 20 cm into the soil.
134 Monoliths were placed together in two groups of six on all four sites, always on a flat
135 terrain that was unshaded by trees or buildings. A 1 x 1.5 m roof made of

136 transparent PVC (4 mm thick, 90% visible light transmission) was placed 40 cm
137 above each group of six buckets (plant height was only a few centimetres). One
138 group ($n = 6$) was watered during the treatment period, the other ($n = 6$) was not.
139 Irrigation was equivalent to a rate of 80 mm month⁻¹ (an average value for July in
140 Ulrichen, 1350 m a.s.l., located between the highest and the lowest sites in our
141 gradient) and applied in four events during the 17-day treatment period (45 mm in
142 total). On August 1, all buckets were transported back to the reference site (Furka),
143 placed in a common garden and watered (copiously in drought-exposed monoliths,
144 and resupplying subsequent seepage water from the outer buckets). The monoliths
145 were finally reinstalled into the soil on their original locations on August 19.

146

147 **2.2. Measurements**

148 2.2.1. Micro-climate

149 Measurements of air temperature (T_{air}), relative humidity (RH) and photosynthetic
150 photon flux density (PPFD) were recorded every minute at each of the four sites,
151 underneath the shelters. Sensors (all Hobo Data Loggers, Onset Computer
152 Corporation, Bourne, MA, USA) were placed at 40 cm height, and the T_{air} -RH-sensor
153 was shielded from the sun by a thin wooden panel. Additional meteorological
154 measurements were made by an automatic weather station at the Furka site
155 (equipped with standard sensors) that contributes to the network of the Swiss
156 Federal Office of Meteorology and Climatology (MeteoSwiss). We also received data
157 from the official weather stations located in Ulrichen (4 km from the Oberwald site)
158 and Visp, operated by MeteoSwiss. Wind speed underneath the shelters and outside
159 (at the same height) was checked on several occasions with a pocket wind meter
160 (Kestrel 3000, Nielsen Kellerman, PA, USA) at each site to quantify wind reduction by
161 the shelter. Soil temperatures (T_{soil}) at 5 cm depth inside the buckets were recorded
162 once at each site in all monoliths (HANNA Instruments, RI, USA).

163

164 2.2.2. Leaf-level responses

165 As the number of measurements was too high to be able to collect readings at all
166 sites on the same day, we opted to pair sites: Furka-Oberwald and Bister-Visp. We
167 made physiological measurements (fluorescence and stomatal conductance, see
168 further) twice per day: before noon as well as in the afternoon at each of the paired
169 sites. This strategy was used because plant functioning (e.g. stomatal responses) is
170 likely to differ during the day, especially when stress starts affecting the plants. We
171 repeated the procedure each time at the other two paired sites the following day.
172 The statistical analyses take into account that measurements were not collected on
173 the same days at each site by focusing on the trends in time instead. After the
174 monoliths had been brought back to the alpine site and placed in a common garden,
175 measurements were made on two more days (August 3 and 10, i.e. day 19 and 26)
176 to monitor legacy effects immediately after the climate extreme. The weather during
177 the 17-day treatment period was generally stable with sunny and dry conditions on
178 ten out of twelve measurement days.

179 Leaf measurements were made on a subset of three of the five species that were
180 present in every community, namely those forbs with the largest leaves (completely
181 filling the leaf chambers): *H. alpina*, *P. aurea* and *G. montanum*. Measurements were
182 made on randomly chosen leaves (in randomly chosen monoliths) of three plants per
183 species per measurement period, located more than 2-3 cm from the bucket rim to
184 minimise edge effects. This means that six measurements per species and per
185 measurement day (three before noon and three in the afternoon) were carried out in
186 each treatment at each site. Stomatal conductance was recorded with a Decagon SC-
187 1 porometer (Decagon Devices, WA, USA), a device that allows for fast
188 measurements (30 seconds per reading) with minimal disturbance of the leaf
189 boundary layer. Chlorophyll fluorescence was used as a stress indicator by

190 determining F_v/F_m , a ratio that is usually around 0.8 under non-stressed conditions
191 across many plant species and ecotypes (Bjorkman & Demmig, 1987). Lower values
192 indicate deactivation of photosystem II as incoming radiation can no longer be
193 optimally accepted and transferred by open reaction centres and needs to be
194 dissipated through fluorescence. Measurements were made with a Plant Efficiency
195 Analyser (Hansatech Ltd., King's Lynn, England) after 30 minutes of dark adaptation
196 to allow the reaction centres to fully discharge. Realised effects, i.e. those observed
197 under light-adapted conditions, sometimes differ from potential effects measured
198 after dark adaptation, so that our measurements may over- or underestimate the
199 amount of actual stress to an extent. Nevertheless, using dark adapted leaves
200 reduces unwanted effects of fluctuating light conditions between measurements and
201 measurement days, and provides a good compromise between comparability and
202 stress detection (Maxwell & Johnson, 2000).

203

204 2.2.3. Ecosystem and community level responses

205 Because leaf measurements such as the ones mentioned above can be misleading
206 with regards to whole plant functioning (cf. Kull, 2002 on the upscaling of
207 photosynthesis) and because they only consider some of the species present, we also
208 took a number of community scale measurements. Evapotranspiration (ET) was
209 estimated by lysimetry, based on weighing (0.1 g precision) always the same four
210 monoliths per treatment per site (Mettler-Toledo Inc., Greifensee, Switzerland).
211 Because a transportable (battery-operated) scale became available only after 5 days,
212 only monoliths at Furka could be weighed on the first day of the treatment (Precisa
213 IBK 2400D scale, Obrecht, Switzerland). On two days (day 10 and 11), monoliths
214 were weighed before sunrise and after sunset at the Furka and Oberwald sites
215 simultaneously to assess daily evapotranspiration rates more precisely.

216 The percentage of green cover (between 0 and 100%), used as an indicator of leaf
217 growth, expansion and senescence, was visually estimated on each measurement
218 day for every monolith by the same observer and without looking at previously
219 recorded data to avoid bias. Canopy temperatures were recorded at each site on two
220 occasions with an infrared high resolution camera (TH9260, NEC Avio Ltd., Japan)
221 under sunny conditions. One image of each block of six monoliths (after removing
222 the shelter) was made from a 45° angle facing away from the sun. Emissivity was
223 set at 0.97. Data were processed by manually selecting desired areas (those of the
224 canopy inside the buckets) to derive average canopy temperatures per monolith
225 using irMotion software (Atus GmbH, Germany), i.e. 6 average values per treatment.
226 Aboveground plant biomass was collected on August 13. Standing plant matter
227 (phytomass) was clipped at approximately 2 cm height, separated per functional
228 group (graminoids, herbs and nitrogen fixers) and into living (green; biomass) and
229 dead phytomass (brown; necromass), dried at 70°C for two days and then weighed.

230

231 **2.3. Statistics**

232 All statistical analyses were performed with the R statistical package (version 2.12.1;
233 R Development Core Team 2010). Two different measures were used as explanatory
234 variables: VPD and T_{air} . In both cases we used the average daytime values across the
235 whole study period (Table 1). Separate models were fitted for each of these variables
236 because the two are correlated ($r = 0.95$). We consider VPD as the most relevant
237 explanatory variable, as it combines temperature and humidity, two important
238 parameters in assessing heat and drought effects (De Boeck *et al.*, 2011).

239 For the data that were collected during the course of the experiment
240 (evapotranspiration, stomatal conductance, fluorescence and green cover), we fitted
241 and evaluated linear mixed models with Gaussian error distributions, using the
242 function 'lmer' (lme4 package; Bates *et al.*, 2010). All response variables except ET

243 were transformed (square root, arcsin or logarithmic) to achieve normal distribution
244 of the residuals. The models included irrigation treatment (irrigation vs. no irrigation)
245 as a categorical fixed factor, the average daytime VPD or T_{air} across the study period
246 and time (measuring day) as continuous fixed factors, as well as all interactions.
247 Random effects were fitted for site, monolith nested within site and census
248 (categorical, 1-5 measurements performed on 2 consecutive days). Models
249 explaining physiological measurements (fluorescence and stomatal conductance)
250 further included random effects for species and session (before noon vs. afternoon
251 measurements, nested within census). Full models were simplified by removing non-
252 significant parameters to obtain minimum adequate models. The significance of fixed
253 factors was assessed by posteriori likelihood ratio tests. Using autocorrelation
254 function plots we checked for autocorrelation in the residuals of the final models, at
255 various time lags, but did not observe any significant temporal autocorrelation.
256 The analyses for data recorded repeatedly in time during the extreme event were
257 done in three steps: (i) an overall analysis, (ii) a separate analysis for the irrigated
258 and non-irrigated treatments in case of a significant drought x time interaction in
259 step 1 (this was always the case), with time, VPD or T_{air} and their interaction as fixed
260 factors, and (iii) in case of a significant time x VPD or T_{air} interaction in step 2, a
261 further analysis of the last time step (day 16 or 17) to study cumulative effects was
262 carried out with only VPD or T_{air} as a fixed factor. Phytomass data were tested using
263 ANOVA for each functional group and for biomass and necromass separately, with
264 VPD or T_{air} as a continuous fixed factor, irrigation treatment as a categorical fixed
265 factor, and monolith (nested within site) as a random factor.
266 Separate analyses were performed to look for changes after the end of the imposed
267 extreme event (recovery or continuing damage). We calculated the difference
268 between the measurement at the end of the treatments (day 16 or 17) and the last
269 measurement day in this legacy phase. For fluorescence and green cover this was on

270 day 26, for stomatal conductance on day 19 as humid conditions prevented stable
271 calibration on day 26. Differences in stomatal conductance and fluorescence were
272 analysed using linear mixed models, with irrigation and heat as fixed factors, and
273 site, species and session as random factors (see above). The difference in green
274 cover was analysed using ANOVA (see above).

275

276

277 **3. Results**

278

279 **3.1. Micro-climate**

280 Averages of T_{air} , RH, calculated vapour pressure deficits (VPD, based on one-minute
281 readings of T_{air} and RH) and PPFD measured underneath the shelters and in nearby
282 meteorological stations are given in Table 1 and Table S1. Daytime temperatures
283 were more than 10 °C higher and VPD was more than doubled at the warmest and
284 driest site (Bister) compared to the reference site (Furka). In comparison, the 2003
285 heat wave during the first 15 days of August at the nearby Gütsch meteorological
286 station (2287 m a.s.l.) increased mean T_{air} by 6.7 °C compared to the average from
287 1954 to 2012 for the same period (15.2 °C versus 8.5 °C). Surprisingly, the site at
288 the lowest elevation (Visp) was not the hottest or most water-demanding location.
289 One explanation is that the Visp site was located just inside a side valley, sheltering
290 it from prevailing East and West oriented winds. The result is that average air
291 temperature differed only little between the two lowest sites, while evaporative
292 forcing (VPD), which combines air temperature and humidity, differed clearly
293 between all sites (Table 1). The soil temperature readings (at 5 cm depth) suggest
294 that non-irrigated monoliths were 2-3 °C warmer than irrigated monoliths during
295 daytime at the lower elevations, and were less than 1 °C warmer at the reference
296 site, where drying was least pronounced (Table S2).

297 Wind speed measurements underneath and outside the shelters suggest only minor
298 differences (Table S3), which implies that effects of sheltering on canopy
299 temperatures would have been small (cf. De Boeck *et al.*, 2012). Other warming
300 effects by the shelters (e.g. by disrupting convection, i.e. trapping heat) also seemed
301 limited. We compared the 24 hours before shelters were installed in Visp with the 24
302 hours after (both days with clear skies), which were very similar regarding average
303 air temperature (0.35 °C difference) and radiation (1% difference) according to the
304 Meteoswiss weather station. Air temperatures measured at our site at 40 cm height
305 did not differ (<0.1 °C) between these two 24h periods, indicating that shelter-
306 induced increases in T_{air} were likely lower than 0.5 °C. By comparing PPFD readings
307 just before and after shelters were removed at the end of the experiment, we found
308 that PPFD reduction was around 12% at all sites. Differences in PPFD between sites,
309 affected by topography influencing sunrise and sunset times, were limited to 7% at
310 maximum (Table 1), with the warmest site also being the brightest.

311

312 **3.2. Leaf-level responses**

313 Data of F_v/F_m reveal that this ratio in general (i.e. across the treatment period)
314 differed significantly between the irrigated and non-irrigated monoliths, with lower
315 values – indicating increased stress – observed in the latter (Fig. 1). We also
316 uncovered a significant interaction between VPD (site) and irrigation treatment,
317 which, when analysing both irrigation treatments separately, was found to result
318 from the fact that F_v/F_m values were similar in irrigated monoliths across all sites (no
319 VPD effect) while there was a significant VPD effect in non-irrigated monoliths (Fig. 1
320 and Table S4). The VPD × time interaction was significant in non-irrigated monoliths,
321 and further analysis from data of the last treatment day (day 17) revealed a
322 significant influence of VPD on the F_v/F_m ratio (Table S4), reflecting stress levels that
323 increased more in some sites than others during the course of the experiment (Fig.

324 1). In general, the analysis shows that higher VPD only led to measureable
325 differences in plant stress if plants were not irrigated (Fig. 1). The same patterns
326 were observed with temperature as an explanatory variable (Table S5).
327 Regarding stomatal conductance, we found significantly lower values in the non-
328 irrigated than in the irrigated communities (Fig. 2), but like for fluorescence the
329 effect differed with site (VPD \times drought interaction, Table S4). Considering each
330 irrigation treatment separately, we observed a similar response of g_s over time for all
331 sites when no water was added (significant time effect, but no significant VPD or VPD
332 \times time effects, Fig. 2, Table S4). This trend differed between sites when monoliths
333 were watered (VPD \times time effect). The lower values at Bister, the hottest and driest
334 of all sites, towards the end of the treatment period may have triggered this VPD \times
335 time interaction. Like for fluorescence, statistical analysis of g_s using temperature
336 instead of VPD as the explanatory variable yielded the same results (Table S5). No
337 change in g_s or F_v/F_m was found immediately after the end of the climate extreme,
338 suggesting that recovery was largely absent.

339

340 **3.3. Ecosystem and community level responses**

341 Across the period where monolith weight could be determined at all sites (day 6-17),
342 ET was more than twice as high in irrigated than in non-irrigated monoliths (3.87 vs.
343 1.73 mm day⁻¹, Fig. 3). When considering each irrigation treatment separately, ET
344 significantly decreased with time at all sites for the drought-exposed monoliths, as
345 indicated by the significant time effect but absence of significant VPD or VPD \times time
346 effects (Table S4). In the irrigated communities neither time nor VPD was significant.
347 The analyses using temperature as the explanatory variable revealed similar results,
348 with the exception that the overall analysis revealed a significant time \times VPD \times
349 drought interaction, caused by a significant positive relationship between
350 temperature and ET at the last treatment day in the irrigated monoliths only (Table

351 S5). The more detailed assessment of ET during two consecutive days and one night
352 (Table 2), measured simultaneously at the Furka and the Oberwald site, confirmed
353 the significantly lower evapotranspiration in non-irrigated monoliths compared to
354 irrigated monoliths ($p < 0.001$).

355 The analysis of percentages of green cover broadly confirms visual trends in Fig. 4.
356 The amount of green cover was significantly lower in the monoliths where irrigation
357 was withheld compared to the irrigated monoliths, while the time \times irrigation
358 treatment interaction suggests different impacts of the irrigation treatments on
359 greenness trends (Table S4; Fig. 4). The response over time seen in irrigated
360 communities was not related to VPD. Raw data suggests a peak in green cover
361 around 1 August in irrigated monoliths (Fig. 4), which corresponds to the normal
362 peak biomass date in these alpine grasslands. Such a peak could not be identified
363 when drought was applied, even at the Furka site, which seems to indicate that
364 drought suppressed normal plant development even under normal temperatures.
365 Specifically, green cover in non-irrigated monoliths varied in time across sites
366 (significant VPD \times time interaction), with differences between sites growing bigger
367 during the treatment period (significant VPD effect at last measurement day, Table
368 S4). No significant differences between values recorded at the last day of the climate
369 extreme and 9-10 days later were found. Statistical analysis using temperature
370 instead of VPD as the explanatory variable showed the same results (Table S5).

371 The importance of drought for community development was confirmed by the
372 analyses of aboveground phytomass. In general, phytomass was reduced by 34 to
373 49% and biomass by 40 to 76% due to drought and any of its indirect effects (Fig. 5,
374 Table S6). Significant effects of drought on biomass production were found for both
375 graminoids and non-nitrogen fixing herbs, while there was a trend towards lower
376 production for nitrogen-fixing (*Trifolium*) species ($p = 0.06$), whose contribution to
377 the overall biomass was marginal (Fig. 5). In irrigated monoliths, no biomass

378 differences between sites were discernible for any of the three functional groups
379 (Table S6). The same was found when non-irrigated monoliths were analysed
380 separately, with the exception of the nitrogen fixing species (VPD: $p < 0.05$). The
381 amount of necromass (pooled across functional groups because of the small
382 quantities) was significantly higher in non-irrigated communities than in irrigated
383 communities, with some differences between sites (VPD effect) but only a trend ($p =$
384 0.07) of a VPD \times irrigation treatment interaction (Table S6). The same patterns were
385 found when temperature was used as explanatory variable (Table S6).

386 Canopy temperatures were recorded via infrared imaging on two occasions at each
387 site: at day 10 or 11 of the treatment, and at day 16 or 17 (Table 3). Drought led to
388 a clear temperature increase when comparing irrigated and non-irrigated monoliths,
389 which likely stems from the lower values of stomatal conductance observed (Fig. 2).
390 The increase was already high at the lower elevation sites at day 10/11 (+7.5 to 9.2
391 $^{\circ}\text{C}$), while at that time it was still below 5 $^{\circ}\text{C}$ at the Furka site, increasing towards
392 the end of the treatment (+9.1 $^{\circ}\text{C}$). Together with leaf fluorescence and greening
393 data (Fig. 1 and 4), this suggests that drought stress developed more slowly at the
394 highest (coolest and most humid) site. In irrigated systems, canopy temperatures
395 were above air temperatures at all sites as well (a consequence of the high
396 irradiation), but this relative difference (around 6-8 $^{\circ}\text{C}$ at the three lower sites)
397 seemed substantially more pronounced at Furka, the highest and coolest site (12-14
398 $^{\circ}\text{C}$). This means that inter-site differences in tissue temperatures were likely smaller
399 than would be expected from air temperatures under non-drought conditions.

400

401

402 **4. Discussion**

403 Intuitively, one would expect that exposing plant communities that usually grow
404 under midday air temperatures of 10-15 $^{\circ}\text{C}$ to temperatures that occasionally

405 reached 35 °C would cause them harm. However, our data showed that, as long as
406 the soil did not dry out, direct effects of temperature increases on fluorescence (a
407 stress indicator), canopy greenness and aboveground production were insignificant.
408 None of our measurements indicated gradual changes with increasing temperature,
409 which suggests that short-term warming without concomitant drought affects these
410 alpine grasslands via thresholds (which were not exceeded here) rather than
411 progressively. It is important to note that differences between canopy and air
412 temperatures were more pronounced at the highest site (12-14 °C) than at the
413 lowest three sites (6-8 °C), meaning that canopy temperatures differed less between
414 the highest and lowest sites than air temperatures (cf. Cernusca & Seeber, 1981).
415 Higher heat dissipation through evapotranspiration at all the lower sites, triggered by
416 substantially higher atmospheric water demand compared to the reference site may
417 be the reason (cf. Van den Bergh *et al.*, 2013). Such a mitigating effect on tissue
418 temperatures has been demonstrated for temperate systems (De Boeck *et al.*,
419 2011), but depends on the availability of soil water reserves.

420 This also highlights the notion that air temperatures can be misleading (Körner,
421 2003; Scherrer & Körner, 2010; De Boeck *et al.*, 2012) and that actual tissue
422 temperatures should be used to judge whether excessive heat occurs in plants.
423 Tissue temperatures also explain why the imposed heat wave did not alleviate any
424 growth limitation by cool temperatures. The abovementioned large differences
425 between canopy and air temperatures at the highest site (Furka) led plant tissues to
426 be warmed above 25 °C and even above 30 °C during daytime. The possibility of a
427 heat wave mitigating any low-temperature related growth restrictions, as observed
428 by Marchand *et al.* (2005) in tundra ecosystems and suggested in the warming study
429 by Cavieres & Sierra-Almeida (2012) in the Andes, therefore seems unlikely here and
430 was not supported by any changes in aboveground dry matter production. Also,
431 unlike in Marchand *et al.* (2005), fluorescence measurements after the imposed heat

432 wave did not reveal any increase in stress resulting from the return to cooler
433 conditions.

434 Alpine grasslands thus seem stable in the face of heat waves varying in intensity, but
435 this no longer proved true when heat coincided with drought. In that case,
436 aboveground production decreased and the proportion of necromass to biomass
437 increased, with two measurements directly related to stress, fluorescence and
438 greenness of the vegetation, changing linearly with VPD (Fig. 1 and 4), suggesting
439 that drought effects get progressively worse when the air gets warmer and drier.
440 This is likely caused by both direct and indirect effects of drought. Direct effects were
441 demonstrated by drought impacts being significant also without warming, at the
442 reference site. The fact that a heat wave, regardless of intensity, had little directly
443 measureable effects on plant functioning as a single factor, whereas drought did, is
444 similar to findings for lowland grassland species (De Boeck *et al.*, 2011; Poirier *et al.*,
445 2012; Hoover *et al.*, 2014). Earlier studies on drought in alpine systems were not
446 conclusive, with for example, Wieser *et al.* (2008) suggesting that even during dry
447 years the importance of water stress in grassland ecosystems in the Austrian Alps
448 was limited, whereas others did observe negative single factor drought effects
449 (Gilgen & Buchmann, 2009; Schmidt *et al.*, 2011). Common direct effects include
450 lower photosynthesis, growth reduction as meristems become less active, decreased
451 leaf expansion, and tissue and plant mortality. Reductions in photosynthesis can
452 occur either through direct limitation of CO₂ through closure of stomates (Cornic,
453 2000; Chaves *et al.*, 2002) or by metabolic constraints (Flexas *et al.*, 2008), with the
454 second process likely more important when drought stress is intense. Yet,
455 photosynthesis as such was probably not a key factor in propagating negative
456 drought effects due to the low sensitivity to carbon of these alpine systems (Körner,
457 1997; Inauen *et al.*, 2012). Growth reduction, earlier senescence and tissue
458 mortality was evident from greenness and aboveground phytomass data.

459 The observation that drought impacts became progressively stronger with higher
460 temperatures and atmospheric water demand, likely relates to more than merely an
461 increase in drought stress. One important indirect effect of intense drought is a
462 higher probability of high-temperature stress as heat mitigation through transpiration
463 fails when water reserves are depleted (De Boeck *et al.*, 2011). Also in the current
464 study, drought increased the likelihood of tissue temperatures reaching damaging
465 levels (cf. Neuner & Buchner, 2012; Hasanuzzaman *et al.*, 2013). Indeed, above 40-
466 45 °C surface temperatures were almost exclusively recorded in the non-irrigated
467 communities. Photosystems are thought to be fairly heat-sensitive (Larcher, 2003),
468 and the functioning of photosystem II decreased as the drought progressed and
469 associated tissue temperatures increased. This loss of function could not be
470 attributed specifically to direct drought effects or indirect ones such as overheating,
471 however, as fluorescence is a universal stress indicator. Another potential indirect
472 effect of drought is nutrient limitation as nutrients become immobilised in the dry soil
473 (e.g. Joslin *et al.*, 2000). The role of nutrient starvation in the current experiment
474 may not have been substantial, however. The period in which nutrient transport may
475 have been severely obstructed was likely limited, as data of stomatal conductance
476 (Fig. 2) and evapotranspiration data (Fig. 3) demonstrate that water was still being
477 cycled at significant rates at least until half of the 17-day treatment period.

478 The interplay between heat and drought also led to different responses between
479 functional groups. At Oberwald, the graminoid proportion of total aboveground
480 biomass in droughted vs. irrigated monoliths was 74% vs. 52%, at Bister 89% vs.
481 60% and at Visp 65% vs. 55%. This suggests that the broadleaved species present
482 in our systems suffered more than graminoids from the combination of drought and
483 heat. Their anatomy (broader leaves with an approximate horizontal orientation)
484 could have caused excess heat stress because they capture more midday radiation
485 and dissipate the heat more slowly than graminoids (which have narrow leaves with

486 a more vertical orientation, such as *Nardus stricta* and *Carex curvula*). Resistance did
487 not differ for single-factor droughts (i.e. at the reference site), with graminoids
488 making up 54% and 55% of (living) aboveground biomass in non-irrigated and
489 irrigated monoliths, respectively. This contrasts with findings of a drought study by
490 Gilgen & Buchmann (2009) at a subalpine grassland site, who observed that grasses
491 suffered most from drought.

492 Our data consistently indicate that heat wave impacts in alpine grasslands, much like
493 in temperate grasslands, are likely to be limited unless coinciding with drought. The
494 importance of changes in moisture compared to those in air temperature also in an
495 alpine environment had been hinted upon by Fu *et al.* (2013), who found that
496 warming effects on the aboveground productivity on the Northern Tibetan Plateau
497 depended largely on soil drying. The importance of soil moisture in systems with a
498 short growing season has furthermore been stressed by Le Roux *et al.* (2013), who
499 observed that fine-scale variation in soil moisture was strongly related to species
500 occurrence patterns. Low elevation studies show that on longer time scales, a single
501 drought event (with associated high temperatures) can be the instigator of long-
502 lasting vegetation change (Kreyling *et al.*, 2011). In a long-term observation study,
503 Stampfli & Zeiter (2004) found that relative cover of the major growth forms present
504 in their study area, graminoids and forbs, changed more in the period following
505 extreme drought than at other times. Changes in recruitment may be key as gaps
506 opened by mortality after the extreme event generate opportunities for colonization
507 (cf. Vittoz *et al.*, 2009), especially if propagule rain is changed in response to a
508 climate extreme, as was observed by Ertl (2013) in alpine areas. Recruitment by
509 seed currently plays a minor role in the system studied, since most species grow
510 clonally and some have been shown to be thousands of years old (De Witte *et al.*,
511 2012). Like for drought, legacy effects of short but intense warm episodes may be
512 relevant, even if the alpine systems in our study seemed to be very resistant in the

513 short term. Processes that could be affected are altered allocation to storage organs
514 (affecting next year's growth) or to a lesser extent effects on recruitment from seed
515 (cf. Liu *et al.*, 2012). Moreover, ongoing increases in mean temperatures can affect
516 growing season length (Jolly *et al.*, 2005), plant-animal interactions (Liu *et al.*, 2011;
517 Wu *et al.*, 2011) and other factors that change the competitive balance between
518 species. The timing of warm spells could also be an important factor in alpine
519 environments (Volk *et al.*, 2014).

520 Like observations made by Scherrer & Körner (2010), our findings suggest that
521 future research into temperature effects in cold biomes should take into account that
522 air and tissue temperatures may deviate substantially, and that the latter parameter
523 is of most significance when trying to determine whether plants may be directly
524 affected by heat or low temperature. Some of the drought levels we exposed the
525 grasslands to are probably very extreme as soil drying would have been accelerated
526 by decoupling the systems from full soil conditions. However, experiments that
527 extend beyond common ranges of environmental conditions can be highly
528 informative (Kayler *et al.* 2015), and here, our observations clearly suggest that high
529 temperatures have much more potential for immediate, significant effects on plant
530 functioning in alpine grasslands when water is limiting. As we noted, this is similar to
531 earlier observations in temperate grasslands. In contrast to such grasslands,
532 however, where resilience is an important ecosystem trait (Brilli *et al.*, 2011;
533 Dreesen *et al.*, 2014), short-term regrowth in systems where the growing season
534 only lasts two to three months and where life strategy is centred on persistence
535 rather than vigour, is inherently constrained, as was confirmed by our observations.
536 A more complete assessment of the sensitivity of alpine systems to climate change
537 will require future studies to take into account both direct impacts and longer term
538 legacy effects of increasingly intense climatic extremes.

539

540

541 **Acknowledgements**

542 H.J. De Boeck was supported by the Fund for Scientific Research – Flanders. We
543 thank the scientists and staff at Alpine Research and Education Station Furka
544 (ALPFOR) for practical help, the community of Obergoms, the Zeiter family and
545 Landwirtschaftszentrum Visp for providing locations for our study, Christian Körner
546 for comments on earlier versions of the manuscript, and the referees for their
547 suggestions.

548

549

550

551

552 **References**

553

554 **Abeli T, Rossi G, Gentili R, Gandini M, Mondoni A, Cristofanelli P. 2012.** Effect
555 of the extreme summer heat waves on isolated populations of two orophitic plants in
556 the north Apennines (Italy). *Nordic Journal of Botany* **30**: 109-115.

557

558 **Bates D, Maechler M, Bolker B. 2010.** lme4: linear mixed-effects models using
559 Eigen and S4 classes. <http://www.r-project.org/web/packages/lme4/index.html>. Last accessed on
560 20 April 2014.

561

562 **Bjorkman O, Demmig B. 1987.** Photon yield of O₂ evolution and chlorophyll
563 fluorescence characteristics at 77 K among vascular plants of diverse origins. *Planta*
564 **170**: 489-504.

565

566 **Bloor JMG, Bardgett RD. 2012.** Stability of above-ground and below-ground
567 processes to extreme drought in model grassland ecosystems: Interactions with
568 plant species diversity and soil nitrogen availability. *Perspectives in Plant Ecology,*
569 *Evolution and Systematics* **14**: 193–204.

570

571 **Brilli F, Hörtnagl L, Hammerle A, Haslwanter A, Hansel A, Loreto F,**
572 **Wohlfahrt G. 2011.** Leaf and ecosystem response to soil water availability in
573 mountain grasslands. *Agricultural and Forest Meteorology* **151**: 1731-1740.

574

575 **Cavieres LA, Sierra-Almeida A. 2012.** Facilitative interactions do not wane with
576 warming at high elevations in the Andes. *Oecologia* **170**: 575-584.

577

578 **Ceppi P, Scherrer SC, Fischer AM, Appenzeller C. 2012.** Revisiting Swiss
579 temperature trends 1959–2008. *International Journal of Climatology* **32**: 203-213

580

581 **Cernusca A, Seeber MC. 1981.** Canopy structure, microclimate and the energy
582 budget in different alpine plant communities. In: Grace J, Ford ED, Jarvis PG, eds.
583 *Plants and their atmospheric environment*. Oxford, UK: Blackwell, 75-81.

584

585 **Chaves MM, Pereira JS, Maroco J, Rodrigues ML, Ricardo CP, Osório ML,**
586 **Carvalho I, Faria T, Pinheiro C. 2002.** How plants cope with water stress in the
587 field. Photosynthesis and growth. *Annals of Botany* **89**: 907–916.

588

589 **Cornic G. 2000.** Drought stress inhibits photosynthesis by decreasing stomatal
590 aperture – not by affecting ATP synthesis. *Trends in Plant Science* **5**: 187–188.

591

592 **De Boeck HJ, Dreesen FE, Janssens IA, Nijs I. 2011.** Whole-system responses
593 of experimental plant communities to climate extremes imposed in different seasons,
594 *New Phytologist* **189**: 806-817.
595

596 **De Boeck HJ, Verbeeck H. 2011.** Drought-associated changes in climate and their
597 relevance for ecosystem experiments and models. *Biogeosciences* **8**: 1121-1130.
598

599 **De Boeck HJ, De Groot T, Nijs I. 2012.** Leaf temperatures in glasshouses and
600 open-top chambers. *New Phytologist* **194**: 1155-1164.
601

602 **De Witte LC, Armbruster GF, Gielly L, Taberlet P, Stocklin J. 2012.** AFLP
603 markers reveal high clonal diversity and extreme longevity in four key arctic-alpine
604 species. *Molecular Ecology* **21**: 1081-1097.
605

606 **Dreesen FE, De Boeck HJ, Janssens IA, Ivan Nijs. 2012.** Summer heat and
607 drought extremes trigger unexpected changes in productivity of a temperate
608 annual/biannual plant community. *Environmental and Experimental Botany* **79**: 21-
609 30.
610

611 **Dreesen FE, De Boeck HJ, Janssens IA, Ivan Nijs. 2014.** Do successive climate
612 extremes weaken the resistance of plant communities? An experimental study using
613 plant assemblages. *Biogeosciences* **11**: 109-121.
614

615 **Engler R, Randin CF, Thuiller W, Dullinger S, Zimmermann NE, Araujo MB,**
616 **Pearman PB, Le Lay G, Piedallu C, Albert CH et al. 2011.** 21st century climate
617 change threatens mountain flora unequally across Europe. *Global Change Biology*
618 **17**: 2330-2341.

619

620 **Ertl S. 2013.** Positive effects of an extremely hot summer on propagule rain in
621 upper alpine to subnival habitats of the Central Eastern Alps. *Plant Ecology &*
622 *Diversity* **6**: 467-474.

623

624 **Flexas J, Ribas-Carbó M, Diaz-Espejo A, Galmés J, Medrano H. 2008.**
625 Mesophyll conductance to CO₂: current knowledge and future prospects. *Plant Cell*
626 *and Environment* **31**: 602–621.

627

628 **Fu G, Zhang X, Zhang Y, Shi P, Li Y, Zhou Y, Yang P, Shen Z. 2013.**
629 Experimental warming does not enhance gross primary production and above-ground
630 biomass in the alpine meadow of Tibet. *Journal of Applied Remote Sensing* **7**:
631 073505.

632

633 **Gobiet A, Kotlarski S, Beniston M, Heinrich G, Rajczak J, Stoffel M. 2014.** 21st
634 century climate change in the European Alps - a review. *Science of The Total*
635 *Environment* **493**: 1138-1151.

636

637 **Gilgen AK, Buchmann N. 2009.** Response of temperate grasslands at different
638 altitudes to simulated summer drought differed but scaled with annual precipitation.
639 *Biogeosciences* **6**: 2525–2539.

640

641 **Grime JP, Fridley JD, Askew AP, Thompson K, Stevens CJ, Bennett CR. 2008.**
642 Long-term resistance to simulated climate change in an infertile grassland.
643 *Proceedings of the National Academy of Sciences USA* **105**: 10028-10032.

644

645 **Hasanuzzaman M, Nahar K, Alam MM, Roychowdhury R, Fujita M. 2013.**
646 Physiological, Biochemical, and Molecular Mechanisms of Heat Stress Tolerance in
647 Plants. *International Journal of Molecular Sciences* **15**: 9643-9684.
648

649 **Hoeppner SS, Dukes JS. 2012.** Interactive responses of old-field plant growth and
650 composition to warming and precipitation. *Global Change Biology* **18**: 1754-1768.
651

652 **Hoover DL, Knapp AK, Smith MD. 2014.** Resistance and resilience of a grassland
653 ecosystem to climate extremes. *Ecology* **95**: 2646-2656.
654

655 **Inauen N, Körner C, Hiltbrunner E. 2012.** No growth stimulation by CO₂
656 enrichment in alpine glacier forefield plants. *Global Change Biology* **18**: 985-999.
657

658 **Inauen N, Körner C, Hiltbrunner E. 2013.** Hydrological consequences of declining
659 land use and elevated CO₂ in alpine grassland. *Journal of Ecology* **101**: 86-96.
660

661 **Jolly WM, Dobbertin M, Zimmermann NE, Reichstein M. 2005.** Divergent
662 vegetation growth responses to the 2003 heat wave in the Swiss Alps. *Geophysical*
663 *Research Letters* **32**: L18409, doi:10.1029/2005GL023252.
664

665 **Joslin JD, Wolfe MH, Hanson PJ. 2000.** Effects of altered water regimes on forest
666 root systems. *New Phytologist* **147**: 117-129.
667

668 **Kayler ZE, De Boeck HJ, Fatichi S, Grünzweig JM, Merbold L, Beier C,**
669 **McDowell N, Dukes JS. 2015.** Experiments to confront the environmental
670 extremes of climate change. *Frontiers in Ecology and the Environment* **13**: 219-225.
671

672 **Körner C, Diemer M, Schächli B, Niklaus P, Arnone J. 1997.** The responses of
673 alpine grassland to four seasons of CO₂-enrichment: a synthesis. *Acta Oecologica*
674 **18**: 165-175.

675

676 **Körner C. 2003.** *Alpine plant life, 2nd edition*. Heidelberg, Germany: Springer.

677

678 **Körner C, Diemer M. 1987.** In situ photosynthetic responses to light, temperature
679 and carbon dioxide in herbaceous plants from low and high altitude. *Functional*
680 *Ecology* **1**: 179-194.

681

682 **Kreyling J, Wenigmann M, Beierkuhnlein C, Jentsch A. 2008.** Effects of
683 extreme weather events on plant productivity and tissue die-back are modified by
684 community composition. *Ecosystems* **11**: 752-763.

685

686 **Kreyling J, Jentsch A, Beierkuhnlein C. 2011.** Stochastic trajectories of
687 succession initiated by extreme climatic events. *Ecology Letters* **14**: 758-764.

688

689 **Kreyling J, Jentsch A, Beier C. 2014.** Beyond realism in climate change
690 experiments: gradient approaches identify thresholds and tipping points. *Ecology*
691 *Letters* **17**: 125-e1.

692

693 **Kull O. 2002.** Acclimation of photosynthesis in canopies: models and limitations.
694 *Oecologia* **133**: 267-279.

695

696 **Larcher W. 2003.** *Physiological plant ecology, 4th edition*. Berlin, Germany:
697 Springer-Verlag.

698

699 **Larigauderie A, Körner C. 1995.** Acclimation of leaf dark respiration to
700 temperature in alpine and lowland plant species. *Annals of Botany* **76**: 245–252.
701

702 **Larsen KS, Andresen LC, Beier C, Jonasson S, Albert KR, Ambus P, Andersen**
703 **KS, Arndal MF, Carter MS, Christensen S et al. 2011.** Reduced N cycling in
704 response to elevated CO₂ warming and drought in a Danish heathland: Synthesizing
705 results of the CLIMAITE project after two years of treatments. *Global Change Biology*
706 **17**: 1884-1899.
707

708 **Le Roux PC, Aalto J, Luoto M. 2013.** Soil moisture's underestimated role in
709 climate change impact modelling in low-energy systems. *Global Change Biology* **19**:
710 2965–2975.
711

712 **Liu Y, Reich PB, Li G, Sun SC. 2011.** Shifting phenology and abundance under
713 experimental warming alters trophic relationships and plant reproductive capacity.
714 *Ecology* **92**: 1201–1207.
715

716 **Liu Y, Mu J, Niklas KJ, Li G, Sun S. 2012.** Global warming reduces plant
717 reproductive output for temperate multi-inflorescence species on the Tibetan
718 plateau. *New Phytologist* **195**: 427-36.
719

720 **Marchand FL, Mertens S, Kockelbergh F, Beyens L, Nijs I. 2005.** Performance
721 of High Arctic tundra plants improved during but deteriorated after exposure to a
722 simulated extreme temperature event. *Global Change Biology* **11**: 2078-2089.
723

724 **Maxwell K, Johnson GN. 2000.** Chlorophyll Fluorescence: a practical guide.
725 *Journal of Experimental Botany* **51**: 659-668.

726

727 **Neuner G, Buchner, O. 2012.** Dynamics of tissue heat tolerance and
728 thermotolerance of PS II in alpine plants. In: Lütz C, Ed. *Plants in alpine regions: cell*
729 *Physiology of adaptation and survival strategies*. Vienna, Austria: Springer-Verlag,
730 61-74.

731

732 **Poirier M, Durand JL, Volaire F. 2012.** Persistence and production of perennial
733 grasses under water deficits and extreme temperatures: importance of intraspecific
734 vs. interspecific variability. *Global Change Biology* **18**: 3632–3646.

735

736 **R Development Core Team. 2010.** *R: A language and environment for statistical*
737 *computing*. Vienna, Austria: R Foundation for Statistical Computing.

738

739 **Rebetez M. 2004.** Summer 2003 maximum and minimum daily temperatures over
740 a 3300 m altitudinal range in the Alps. *Climate Research* **27**: 45-50.

741

742 **Scherrer D, Körner C. 2010.** Infra-red thermometry of alpine landscapes
743 challenges climatic warming projections. *Global Change Biology* **16**: 2602-2613.

744

745 **Schmid S, Hiltbrunner E, Spehn EM, Lüscher A, Scherer-Lorenzen M. 2011.**
746 Impact of experimentally induced summer drought on biomass production in alpine
747 grassland. In: Pötsch EM Krautzer B Hopkins A, eds. *Grassland Farming and Land*
748 *Management Systems in Mountainous Regions*, Proceedings of the 16th Symposium
749 of the European Grassland Federation, Gumpenstein, Austria, 214-216.

750

751 **Stampfli A, Zeiter M. 2004.** Plant regeneration directs changes in grassland
752 composition after extreme drought: a 13-year study in southern Switzerland. *Journal*
753 *of Ecology* **92**: 568–576.

754

755 **Van der Schrier G, Efthymiadis D, Briffa KR, Jones PD. 2007.** European Alpine
756 moisture variability for 1800–2003. *International Journal of Climatology* **27**: 415-
757 427.

758

759 **Van den Bergh T, Inauen N, Hiltbrunner E, Körner C. 2013.** Climate and plant
760 cover co-determine the elevational reduction in evapotranspiration in the Swiss Alps.
761 *Journal of Hydrology* **500**: 75–83.

762

763 **Vittoz P, Randin C, Dutoit A, Bonnet F, Hegg O. 2009.** Low impact of climate
764 change on subalpine grasslands in the Swiss Northern Alps. *Global Change Biology*
765 **15**: 209-220.

766

767 **Vogel A, Scherer-Lorenzen M, Weigelt A. 2012.** Grassland resistance and
768 resilience after drought depends on management intensity and species richness. *PloS*
769 *one* **7**: e36992.

770

771 **Volk M, Wolff V, Bassin S, Ammann C, Fuhrer J. 2014.** High tolerance of
772 subalpine grassland to long-term ozone exposure is independent of N input and
773 climatic drivers. *Environmental Pollution* **189**: 161-168.

774

775 **Wieser G, Albin Hammerle, Georg Wohlfahrt. 2008.** The Water Balance of
776 Grassland Ecosystems in the Austrian Alps. *Arctic, Antarctic, and Alpine Research* **40**:
777 439-445.

778

779 **Wu XJ, Duffy E, Reich PB, Sun S. 2011.** A brown-world cascade in the dung
780 decomposer food web of an alpine meadow: effects of predator interactions and
781 warming. *Ecological Monographs* **81**: 313-328.

782

783 **Xu ZZ, Shimizu H, Ito S, Yagasaki Y, Zou CJ, Zhou G, Zheng Y. 2014.** Effects of
784 elevated CO₂, warming and precipitation change on plant growth, photosynthesis
785 and peroxidation in dominant species from North China grassland. *Planta* **239**: 421-
786 435.

787 **Table S1:** Meteorological measurements collected at stations near the sites used in
788 our experiment.

789 **Table S2:** Soil temperatures recorded in each monolith at the end of the imposed
790 climate extreme.

791 **Table S3:** Wind speed measured consecutively underneath and outside of the
792 shelters.

793 **Table S4:** Parameter estimates and significances in mixed-effects models using
794 vapour pressure deficit as the explanatory variable characterising different sites.

795 **Table S5:** Parameter estimates and significances in mixed-effects models using air
796 temperature as the explanatory variable characterising different sites.

797 **Table S6:** Effects of heat, drought and their interaction on biomass and on
798 necromass.

799

800

801

802

803

804

805

806

807

808

809

810

811

812

813

814 **Table 1:** Description of the sites where monoliths were transported to during the
 815 treatment period (15/07-01/08/2013). Mean values of one-minute measurements
 816 made throughout the treatment period underneath the rainout shelters, at 40 cm
 817 height. Vapour pressure deficit (VPD) was determined from air temperature (T_{air}) and
 818 relative humidity (RH). Photosynthetic photon flux density (PPFD) is the average of
 819 measurements during daylight (± 15 hours day^{-1}).

	Site			
	Furka	Oberwald	Bister	Visp
Coordinates	46°34'N 8°25'E	46°32'N 8°21'E	46°21'N 8°04'E	46°17'N 7°53'E
Elevation (m)	2440	1390	1040	660
T_{air} (°C) 24h	11.9	16.8	21.4	20.9
T_{air} (°C) day	14.1	19.8	24.5	23.8
T_{air} (°C) night	8.1	11.8	15.9	16.0
RH (%) 24h	77	73	67	75
RH (%) day	72	64	60	68
RH (%) night	87	89	79	87
VPD (kPa) 24h	0.40	0.75	1.14	0.85
VPD (kPa) day	0.55	1.08	1.56	1.19
PPFD ($\mu\text{mol m}^{-2} \text{s}^{-1}$) day	708	681	727	675

820

821 **Table 2:** Evapotranspiration (ET) determined by weighing monoliths ($n = 6$) before
 822 and after sunrise on two consecutive days (day 10 and 11 of the treatment)
 823 simultaneously at two sites (Furka and Oberwald).

treatment	Site			
	Furka (2440 m)		Oberwald (1390 m)	
	irrigated	non-irrigated	irrigated	non-irrigated
ET (mm day^{-1}) \pm SE (day1)	3.35 \pm 0.29	2.11 \pm 0.55	3.52 \pm 0.16	1.75 \pm 0.32
ET (mm day^{-1}) \pm SE (night)	0.32 \pm 0.02	0.22 \pm 0.05	0.23 \pm 0.03	0.12 \pm 0.03
ET (mm day^{-1}) \pm SE (day2)	3.38 \pm 0.41	1.80 \pm 0.46	3.19 \pm 0.19	1.47 \pm 0.27

824

825 **Table 3:** Averages of canopy temperatures ($T_{\text{canopy}} \pm \text{SE}$) recorded with an infrared
826 camera at two different dates per site: day 11 and 16 for Furka and Oberwald, day
827 10 and 17 for Bister and Visp. Air temperature ($T_{\text{air}} \pm \text{SE}$), photosynthetic photon flux
828 density (PPFD) and vapour pressure deficit (VPD) recorded at the time (average of
829 10 one-minute readings) of T_{canopy} measurements is also given (at 40 cm height).
830 Temperatures partly reflect dried (dead) leaves and minor fractions of bare soil
831 related to stress-induced plant senescence.

	Day	Treatment	Site			
			Furka	Oberwald	Bister	Visp
T_{canopy} (°C)	10 or 11	irrigated	33.8 ± 1.4	38.3 ± 0.9	38.3 ± 0.9	40.7 ± 1.0
T_{canopy} (°C)	10 or 11	non-irrigated	38.2 ± 2.4	47.5 ± 1.4	45.8 ± 1.7	48.8 ± 2.0
T_{air} (°C)	10 or 11	both	21.5	30.5	33.6	34.0
PPFD ($\mu\text{mol m}^{-2} \text{s}^{-1}$)	10 or 11	both	1869	1445	2151	2139
VPD (kPa)	10 or 11	both	1.08	2.74	3.29	3.03
T_{canopy} (°C)	16 or 17	irrigated	32.3 ± 0.7	32.5 ± 0.6	42.7 ± 0.8	38.3 ± 1.2
T_{canopy} (°C)	16 or 17	non-irrigated	41.4 ± 1.0	43.0 ± 0.7	52.0 ± 1.0	48.2 ± 2.2
T_{air} (°C)	16 or 17	both	18.2	25.3	34.1	31.5
PPFD ($\mu\text{mol m}^{-2} \text{s}^{-1}$)	16 or 17	both	1650	1924	1877	1806
VPD (kPa)	16 or 17	both	0.82	1.93	3.24	2.43

832

833

834

835

836

837

838

839

840

841

842

843 **Fig. 1** Maximal efficiency of PSII photochemistry (ratio of F_v/F_m , a stress indicator)
844 during and after the imposed climate extremes (day 1 = July 15, end of extreme
845 indicated by dotted line) at the different sites. Measurements made on three dicot
846 species always both before and after noon and data pooled per treatment (mean \pm
847 SE, n=18). Inset graph shows F_v/F_m at the last day of the extreme, in function of
848 average daytime VPD (during the extreme) of the four sites, with the line depicting a
849 significant trend.

850

851 **Fig. 2** Ratio of stomatal conductance (g_s) during and after the imposed climate
852 extremes (day 1 = July 15, end of extreme indicated by dotted line) at the different
853 sites. Measurements made on three dicot species always both before and after noon
854 and data pooled per treatment (mean \pm SE, n=18). Inset graph shows g_s at the last
855 day of the extreme, in function of average daytime VPD (during the extreme) of the
856 four sites.

857

858 **Fig. 3:** Monolith weight (mean \pm SE, n=4) during the imposed climate extremes
859 (day 1 = July 15) at the different sites. Inset graph shows average
860 evapotranspiration (ET) from day 6-17, calculated from weights and irrigation
861 quantities, in function of average daytime VPD (during the extreme) of the four sites.

862

863 **Fig. 4** Visual estimates of green cover (mean \pm SE, n=6) during and after the
864 imposed climate extremes (day 1 = July 15, end of extreme indicated by dotted line)
865 at the different sites. Inset graph shows green cover at the last day of the extreme,
866 in function of average daytime VPD (during the extreme) of the four sites, with the
867 line depicting a significant trend.

868

869 **Fig. 5** Aboveground phytomass of all monoliths collected on August 13 (12 days
870 after the end of the climate extreme) and separated per functional group and into
871 living (biomass) and dead (necromass). Error bars depict the standard error (6
872 monoliths per site and per irrigation treatment).

873

874

875

876

877

878

879

880

881

882

883

884

885

886

887

888

889

890

891

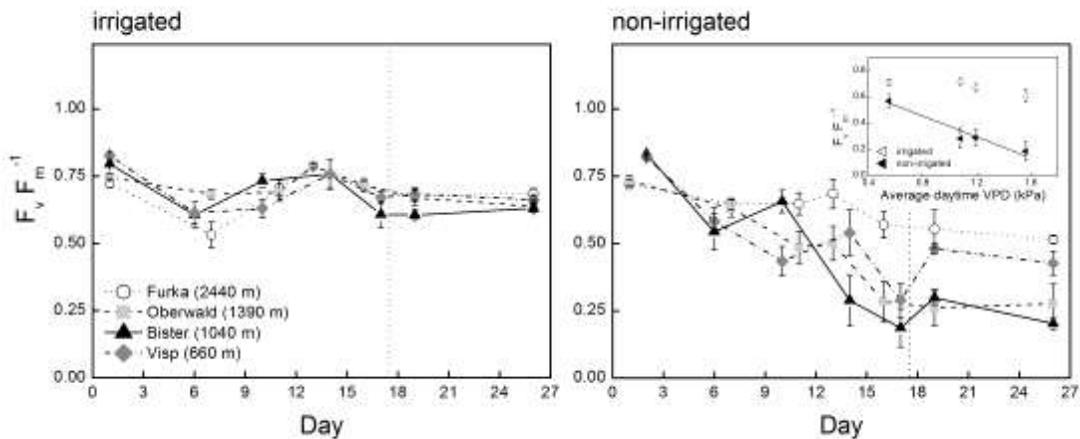
892

893

894

895

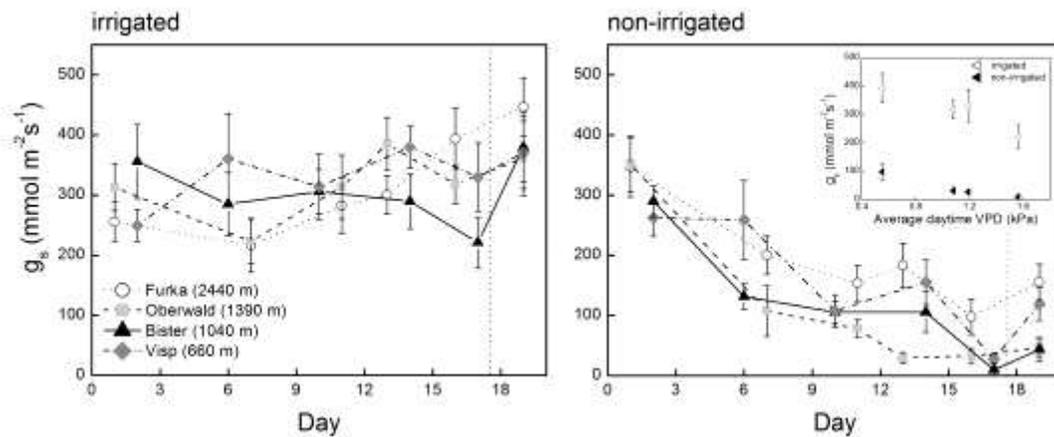
896 **Fig. 1**



897

898

899 **Fig. 2**



900

901

902

903

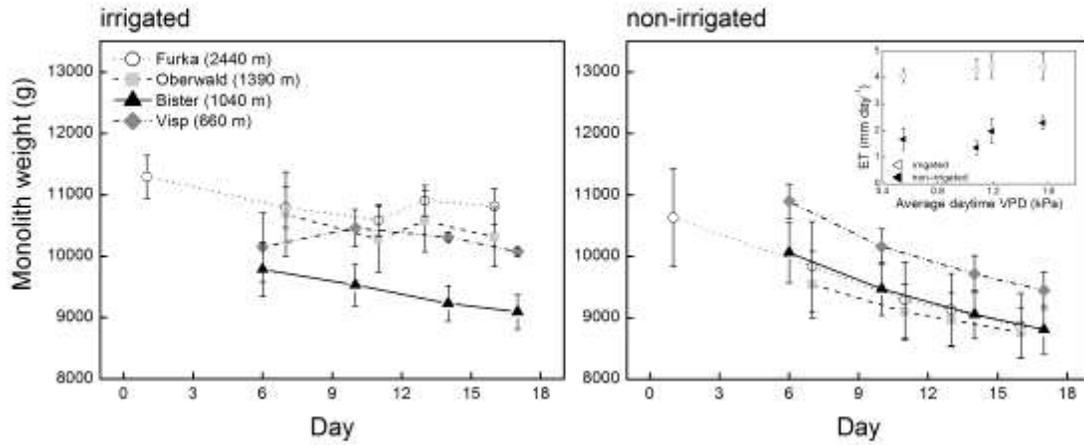
904

905

906

907

908 **Fig. 3**

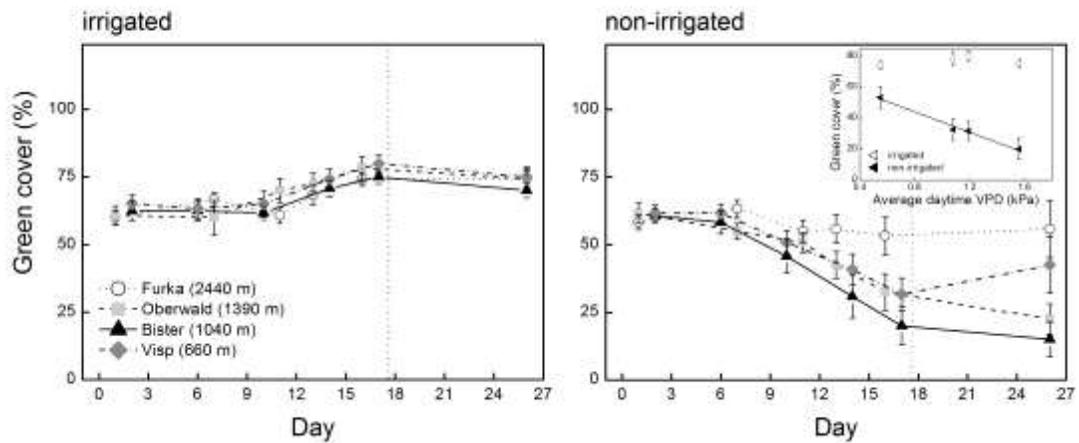


909

910

911

912 **Fig. 4**



913

914

915

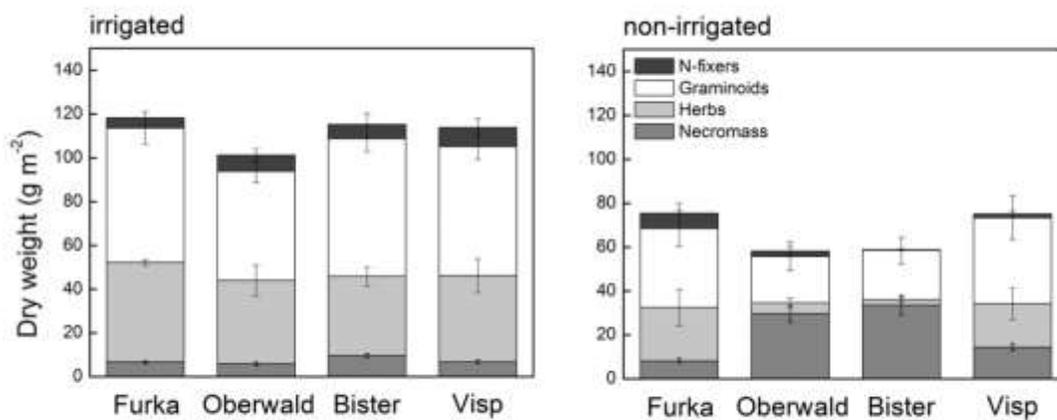
916

917

918

919

920 **Fig. 5**



921

922