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Response of temperate grasslands at different altitudes to simulated summer drought differed but scaled with annual precipitation

A. K. Gilgen and N. Buchmann

Institute of Plant Sciences, ETH Zurich, Zurich, Switzerland

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Correspondence to: A. K. Gilgen (anna.gilgen@ipw.agrl.ethz.ch)

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Abstract

Water is an important resource for plant life. Since climate scenarios for Switzerland predict an average reduction of 20% in summer precipitation until 2070, understanding ecosystem responses to water shortage, e.g. in terms of plant productivity, is of major concern. Thus, we tested the effects of simulated summer drought on three managed grasslands along an altitudinal gradient in Switzerland from 2005 to 2007, representing typical management intensities at the respective altitude. We assessed the effects of drought on above- and below-ground productivity, stand structure (LAI and vegetation height) and resource use (carbon and water). Drought responses of community above-ground productivity differed among the three sites but scaled positively with total annual precipitation at the sites ($R^2=0.85$). Annual community above-ground biomass productivity was significantly reduced by summer drought at the alpine site receiving the least amount of annual precipitation, while no significant decrease (rather an increase) was observed at the pre-alpine site receiving highest precipitation amounts in all three years. At the lowland site (intermediate precipitation sums), biomass productivity significantly decreased in response to drought only in the third year, after showing increased abundance of a drought tolerant weed species in the second year. No significant change in below-ground biomass productivity was observed at any of the sites in response to simulated summer drought. However, community carbon isotope ratios increased under drought conditions, indicating an increase in water use efficiency. We conclude that there is no general drought response of Swiss grasslands, but that sites with lower annual precipitation seem to be more vulnerable to summer drought than sites with higher annual precipitation, and thus site-specific adaptation measures will be needed especially in regions with low annual precipitation.

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1 Introduction

Water availability is probably the strongest limitation to plant productivity globally, even in temperate or boreal regions (Lambers et al., 1998). Since annual above-ground productivity of vegetation strongly depends on mean annual precipitation (for grassland: Puelo et al., 1999; Knapp and Smith, 2001), water stress for plants can arise from low precipitation inputs, high rates of water loss due to high atmospheric vapour pressure deficit (VPD) or from drying soil, all mechanisms ultimately reducing plant productivity. Such effects might become more pronounced since water stress is predicted to increase in the future in certain regions due to climate change, e.g. in Central Europe, for which decreasing summer precipitation is expected (Christensen et al., 2007). Projections for Switzerland indicate that by 2070 the mean decrease of summer precipitation (June through August) might be around 20% compared to 1990 with a maximum decrease of 40% (Frei et al., 2006). Thus, we expect ecosystem processes, from microbial activities to plant performance, to be strongly affected, at the same time, the response to drought of terrestrial ecosystems might vary dependent on vegetation composition and local environmental conditions.

While research on drought effects on grassland species has often been carried out under controlled conditions (e.g. Arp et al., 1998; Karsten and MacAdam, 2001), research at the ecosystem level in the field used two approaches: (1) naturally occurring droughts and their impact on the long-term field trials (Weaver et al., 1935; Gibbens and Beck, 1988; Bollinger et al., 1991; Stampfli and Zeiter, 2004) and (2) field experiments manipulating rainfall amounts. Such manipulation studies have been carried out in arid or semi-arid regions where drought is occurring frequently (e.g. Sternberg et al., 1999; Greco and Cavagnaro, 2003; Köchy and Wilson, 2004; English et al., 2005; Schwinning et al., 2005; Heisler-White et al., 2008; Sherry et al., 2008) but also in temperate grasslands where drought is not a severe problem today (e.g. Grime et al., 2000; Morecroft et al., 2004; Kahmen et al., 2005; Mikkelsen et al., 2008). In most of these manipulation studies, productivity of common grassland species was greatly re-

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duced, carbon (C) allocation to below-ground parts increased and deep rooted species were more drought resistant, supporting studies carried out with single species under controlled conditions. However, detailed information on the drought response of grasslands along an altitudinal gradient is not available.

This study therefore aimed to assess the responses to extreme summer drought of three temperate grasslands at different altitudes in Switzerland. We excluded precipitation with transparent rain shelters and focussed on the following questions: (1) how does community above-ground biomass productivity of these three grasslands respond to drought? (2) Does vegetation structure (i.e. LAI and vegetation height) react in accordance with biomass productivity? (3) Is community below-ground biomass productivity affected by drought as well? (4) Do different plant functional types respond differently to drought? (5) How is resource use of grassland species affected by drought? We hypothesised that (1) drought decreases community above-ground productivity because water is one of the key resources for plant growth, (2) vegetation structure reacts similarly as community above-ground biomass, (3) root biomass productivity increases with drought because of increased foraging for water, (4) different plant functional types differ in their response to summer drought due to their different rooting patterns, and (5) drought increases the efficiency of plant water use.

2 Material and methods

2.1 Experimental sites and setup

The study was conducted at three different temperate grassland sites across Switzerland, representing Swiss grassland systems at the respective altitudes (Table 1). During the three years of the experiment, no fertiliser was applied to the plots and no grazing was allowed on the plots. In autumn 2006, the weed species *Rumex obtusifolius* L. had to be removed manually from the experimental plots at Chamau due to Swiss regulations (Gilgen et al., 2009), overseeding took place in early March 2007 to

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re-establish a closed vegetation cover.

The experiment was established end of June 2005 at the two lower sites, Chamau and Frübüel, and in July 2006 at the alpine site, Alp Weissenstein, and was continued until 2007, thus during three and two growing seasons, respectively. Using five portable rain shelters which were installed at each site we excluded rainfall in spring/summer to simulate a pronounced drought. In 2006, two additional rain shelters and control plots were installed at Chamau and one each at Frübüel. The tunnel-shaped rain shelters with an area of 3×3.5 m were about 2.1 m high at the highest point. During the entire drought treatment period, the steel frames were covered with transparent plastic foils (200 μm; Gewächshausfolie UV 5, folitec Agrarfolien-Vertriebs GmbH, Westerbürg, Germany). Based on regional climate model projections (e.g. Frei et al., 2006), we determined that reducing May to August precipitation by 45% compared to today would simulate an extreme summer drought in the future. A period of 8 to 10 weeks beginning in May at Chamau and Frübüel and 6 to 8 weeks at Alp Weissenstein was required to achieve this target reduction. Due to the very variable weather conditions, the amounts of precipitation excluded varied over the three years of treatment but relative amounts at the three sites were comparable within years (Table 2). We established a core area of 1×2 m in the middle of the rain shelters to exclude any direct rain input into plots. All rainfall removed by the shelters was lead away from the respective plots. Control plots located next to the sheltered plots received natural rainfall amounts. The same plots were used throughout the three years of the experiment.

2.2 Micrometeorological measurements

Microclimatic variables were continuously monitored close to the centre of two drought and control plots per site, starting in autumn 2005 at Frübüel, spring 2006 at Chamau and summer 2006 at Alp Weissenstein. Soil temperature (Precision IC Temperature Transducer AD592AN, Analog Devices, Norwood, MA, USA), soil moisture at three soil depth (5, 15 and 30 cm) using 20 cm long ECH₂O probes (EC-20, Decagon Devices, Inc., Pullman, WA, USA) and soil heat flux (HFP01, Hukseflux Thermal Sensors B.V.,

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Delft, Netherlands) close to the soil surface were recorded. We also monitored air temperature at 60 and 160 cm (using the same sensors as for soil temperature but with ventilation) and photosynthetically active radiation (PAR LITE, Kipp & Zonen B.V., Delft, Netherlands). The air temperature sensors were disconnected in winter and spring 2006/07 due to technical modifications in the same setup. After mid-October 2007, the air temperature sensors were not ventilated any more to save battery lifetime. Measurements were made every 10 s while ten minute averages were logged with a CR10X data logger (Campbell Scientific Inc., Logan, UT, USA).

To validate volumetric soil moisture measurements, we took few additional measurements of gravimetric soil water content in 2007. We therefore sampled 15 cm deep soil cores from the centre of the plots and divided them into three 5 cm pieces. Samples were stored in tightly sealed plastic bags and fresh weight was distinguished immediately after returning from the field. The soil cores were dried to weight constancy at 100°C (some days) and dry weight was measured afterwards. Gravimetric soil water content was then calculated as the difference of the dry and the fresh weight (weight of the water) divided by the dry weight (weight of the soil).

2.3 Above-ground productivity

Above-ground biomass was harvested at the cutting dates of the surrounding farm, i.e. six times per year at Chamau (three times in 2005), two times per year at Frübüel (once in 2005) and once at the end of the growing season (end of September) at Alp Weissenstein. Biomass was collected using 20×50 cm frames that were randomly placed on the plots in 2005 and installed at fixed locations starting spring 2006. Cutting height of the vegetation was approximately 7 cm above the soil according to the common management practice on the farms. Two samples per plot were taken and then pooled for the analyses (representing 0.2 m²). Biomass was stored in plastic bags at 4°C for a maximum of one week until it could be separated into species (plant functional types for Alp Weissenstein) and dried at 60°C until weight constancy. Dry matter was then determined for each species sample, and the sum of all sam-

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ples from the same plots was used as an estimate for total community above-ground biomass productivity. Each species was assigned a plant functional type (grass, forb (i.e. non-leguminous forb) or legume). The dead biomass was considered an own plant functional type and was never separated by species (i.e. biomass of the other three functional types was alive by definition). It was however included in total community above-ground productivity estimates.

2.4 LAI and vegetation height

During the growing seasons 2006 and 2007 (2007 for Alp Weissenstein only), leaf area index (LAI) was measured approximately 7 cm above soil (cutting height) using an LAI-2000 Plant Canopy Analyzer (LI-COR Biosciences, Lincoln, NE, USA). Five measurements distributed over the plot were averaged to represent the plot LAI. A 270° view cap was used to reduce plots size required for measurements, i.e. only 90° of the sensor view were used for measurements. Vegetation height was estimated at the same dates as LAI using a stick and a falling styrofoam plate (0.5×0.5 m, 1 cm thick). Two to four measurements were averaged for each plot.

2.5 Root biomass productivity

Root biomass productivity at the community level over the complete growing season was determined at Chamau and Frübüel in 2007 and over nearly two growing seasons (2006 and 2007) at Alp Weissenstein using ingrowth cores (4.4 cm diameter, 30 cm length). Cores were positioned in an angle of approximately 45°. All ingrowth cores were filled with root-free, sieved (2 mm) soil from the corresponding site. Ingrowth cores were installed from 13 March 2007 to 5 December 2007 at Chamau (267 days), from 15 December 2006 to 5 December 2007 at Frübüel (355 days), and from 14 July 2006 to 25 September 2007 at Alp Weissenstein (438 days). One ingrowth core per plot was buried at Alp Weissenstein while two cores per plot were used at the two other sites. After removal from the soil, cores were stored at 4°C until further analysis.

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The ingrown roots were washed from the soil cores in the laboratory, roots were dried to weight constancy at 60°C and the dry weight was determined. Where two ingrowth cores had been installed and recovered, root biomass of two cores was pooled to calculate root productivity of the plot. In some cases, part of the soil was lost when taking out the ingrowth cores. Therefore, the actual length of the soil core was used to calculate the amount of roots per unit soil depth. As the ingrowth cores remained in the field for different time periods at the three sites, the root weight was divided by the number of days that roots had been allowed to grow into the cores and then multiplied by 365 to represent the root mass per m² and year.

2.6 Carbon isotope measurements

To determine carbon isotope ratios ($\delta^{13}\text{C}$), the most abundant species were sampled at Chamau (*Agrostis stolonifera* L., *Alopecurus pratensis* L., *Dactylis glomerata* L., *Lolium multiflorum* LAM., *Phleum pratense* L. AGG., *Poa pratensis* L. AGG., *Poa trivialis* L. S.L., *Rumex obtusifolius* L., and *Trifolium repens* L.) and Frübüel (*Agrostis capillaris* L., *A. stolonifera*, *A. pratensis*, *Anthoxanthum odoratum* L., *P. pratense*, *P. pratensis*, *P. trivialis*, *Rumex acetosa* L., *R. obtusifolius*, and *T. repens*), while the four plant functional types were analysed at Alp Weissenstein. Biomass was ground to a fine powder and analysed using a Flash EA 1112 Series elemental analyzer (Thermo Italy, former CE Instruments, Rhodano, Italy) coupled to a Finnigan MAT Delta^{plus}XP isotope ratio mass spectrometer (Finnigan MAT, Bremen, Germany) via a 6-port valve (Brooks et al., 2003), a ConFlo III (Werner et al., 1999) and an additional Nafion-trap backed by a conventional Mg(ClO₄)₂-trap followed by a 4-port valve (Werner, 2003) between reduction tube and GC column. Post-run off-line calculations (blank, offset and possibly drift corrections) were performed to assign the final δ -values on the V-PDB and AIR-N₂ scales according to Werner and Brand (2001). The long-time precision for the lab's quality control standard tyrosine (~2.5 years) was 0.05‰ for $\delta^{13}\text{C}$. For statistical analyses, isotope data were weighted by biomass to calculate a community and functional group mean for each plot.

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2.7 Statistics

Due to the rather small number of replicates (five to seven), all biomass, vegetation height and $\delta^{13}\text{C}$ data were included in the statistical analyses. LAI values were excluded only if the standard error of the five measurements per plot was higher than a third of the mean LAI of the plot or if MTA (mean tilt angle) was below 30% (criteria used for 2007 since this information was not available for 2006).

Statistical analyses were performed using R 2.5.0 (R Development Core Team, 2007). Community above-ground and functional type biomass, LAI, vegetation height and isotope signatures were generally all analysed with the same ANOVA model. In a first step, the datasets were analysed (all sites over all years), using an ANOVA model considering site, harvest date, treatment (control vs. drought treatment) and all interactions, including the triple interaction. In a second step, datasets were analysed for each year separately using the same model. In a third step, the dataset was analysed for each site separately and finally for each harvest date separately. The model structure remained the same but the terms site and then also harvest date were removed. Root biomass data were analysed using an ANOVA model testing site, treatment and their interaction.

3 Results

3.1 Micrometeorological measurements

Annual precipitation sums were quite similar in 2005 (1170 mm and 1481 mm at Chamau and Frübüel, respectively) and 2006 (1136 mm, 1649 mm and 867 mm at Chamau, Frübüel and Alp Weissenstein, respectively), but around 100 mm higher at all three sites in 2007 (1232 mm, 1765 mm and 969 mm at Chamau, Frübüel and Alp Weissenstein, respectively, Zeeman et al., 2009 adjusted with data from nearby MeeteoSwiss stations). While in 2006, July was naturally dry, spring 2007 started with very

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low precipitation but was followed by a rather wet summer 2007 (Fig. 1a).

No impact of the rain shelters was seen on average daily air temperatures at 160 cm height which were quite similar for all drought and control plots (shown for Chamau; Fig. 1b): at Chamau, the average difference between drought and control plots was -0.03°C , at Frübüel 0.2°C and at Alp Weissenstein 0.1°C . The plastic foils reduced daily PAR sums by 20% at Chamau and Frübüel and by 26% at Alp Weissenstein (Fig. 1c). The effect of the shelters on soil temperature was also small: in general, there was an increase of less than 1°C (but a decrease of 0.3°C at Alp Weissenstein) in soil temperature under the shelters compared to unsheltered periods (Fig. 1d). However, the rain shelters had the desired effect on soil moisture. Maximum reduction of soil moisture was around 83% at Chamau, with soil moisture being reduced by 20 to 60% during the drought treatment. Additional measurements of gravimetric soil water content showed a similar pattern as the continuous measurements (Fig. 1e). At Frübüel, the effect of the shelters on soil moisture was smaller than at Chamau because the site was generally much wetter: soil moisture was reduced on average by 30% at 30 cm soil depth during the drought treatment. At Alp Weissenstein, no data from continuous measurements were available due to technical problems, but gravimetric soil water contents at the end of the drought treatment showed a significant reduction of soil moisture in 0–5 cm depth on drought compared to control plots (absolute reduction of 41%, $P < 0.001$).

3.2 Above-ground productivity

Across all sites and all three years of the experiment, total community above-ground productivity was driven by site and harvest date ($P < 0.001$) as well as drought treatment ($P = 0.04$), with significant site \times treatment interactions ($P = 0.006$), indicating differing grassland drought responses at the three sites. Including year in the analysis did not change significance levels and was thus omitted. Analysing these treatment effects on total above-ground productivities (i.e. dead and alive biomass at time of harvest) in more detail revealed that the three sites differed drastically (Table 3). At Chamau, total

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annual community above-ground productivities were similar in 2005 and 2006 for both treatments, and tended to be lower on drought than on control plots in 2007. We did not find a treatment effect at Frübüel in any of the three years, while total annual community above-ground productivity at Alp Weissenstein was significantly lower on drought than on control plots in both years. However, the total above-ground productivities at Chamau were strongly influenced by one weed species, *Rumex obtusifolius*, which gained competitive advantage over all other species in 2006 (Gilgen et al., 2009). We therefore excluded *Rumex* biomass at Chamau from all further above-ground productivity analyses. As a result, the overall drought effect across all sites and all three years became clearer ($P=0.003$).

When analysing the three years separately (Table 4), site and harvest date explained most of the variation in productivity in 2005, while the overall treatment effect was marginally significant in 2006 ($P=0.06$) and significant in 2007 ($P=0.01$). There were significant site \times treatment interactions in 2006 and 2007, indicating differences in the drought responses at the different sites. The factor harvest date was highly significant for all sites, indicating quite different regrowth patterns among the three sites during the growing season. The drought treatment showed no effects on above-ground productivities at Frübüel ($P=0.5$), but highly significant effects at Chamau ($P=0.001$) and Alp Weissenstein ($P<0.001$). The date \times treatment interaction term was never significant, indicating that the direction of the drought response of the respective grasslands did not change over time. Also focussing on single harvests revealed no treatment effects at Frübüel and in the two first years at Chamau (except for the fifth harvest in 2006), while total community above-ground productivities were significantly reduced by the treatment at Chamau in the third year (first, third and fourth harvest) and clearly at Alp Weissenstein.

Focussing on plant community composition by analysing the drought responses of the four plant functional types (PFT) separately (Table 4) revealed only slight differences of annual above-ground productivities between treatments. Overall, productivities differed among sites (with highest annual sums at Chamau and lowest sums at

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Alp Weissenstein, $P < 0.001$), except for forbs that were not significantly affected by site. The drought treatment decreased grass and forb above-ground biomass productivities ($P = 0.08$ and $P = 0.06$, respectively). A significant site \times treatment interaction for grasses pointed towards differing biomass responses at the different sites (in contrast to the other sites, grass biomass responded positively to drought at Frübüel). When analysing the years separately, site was the only factor influencing annual above-ground biomass productivities in most cases. The treatment significantly affected the amount of dead biomass in 2006 ($P = 0.05$) and grass biomass in 2007 ($P = 0.03$). Annual above-ground productivities of forbs and legumes were not affected by the drought treatment in any of the three years. When focussing on the differences within years by analysing the harvest biomass (Table 4), it became clear that grasses resembled the drought response of total above-ground community productivity best (independent of *Rumex*). Overall, grass productivity differed among the three sites and grass regrowth changed during the growing season (site and harvest date effects: $P < 0.001$). The drought treatment was clearly decreasing grass regrowth above-ground ($P = 0.001$), but this response differed among sites (drought strongly decreased grass productivities at Chamau and Alp Weissenstein but no effect was observed at Frübüel; site \times treatment interactions: $P < 0.001$). Similar patterns for total and grass above-ground productivity were also found when analysing the years separately (except site effect in 2005). Also forb productivity differed among sites and regrowth changed during the season (site and harvest date effects: $P < 0.001$) with differing effects of the harvest dates at the different sites (site \times harvest date interaction: $P < 0.001$). During the course of the experiment, forb productivity differed among sites (Chamau $>$ Frübüel $>$ Alp Weissenstein; site effect: $P < 0.001$), but remained relatively stable during the years (harvest date effect: $P > 0.05$, except 2006). Furthermore, legumes were generally positively affected by the drought treatment (overall: $P = 0.005$), which was mainly driven by their response in 2007. In contrast, the amount of dead biomass differed significantly across sites and harvest dates, but was not affected by the drought treatment (only significant in 2006).

At Alp Weissenstein, annual grass and legume productivities were significantly re-

duced by the drought treatment (with differing responses in legumes in the two years; harvest date \times treatment interaction: $P < 0.001$) but no effect on forbs and dead biomass was seen. Also the amount of dead biomass was differently affected by the treatment in the two years, showing an increase in 2006 and a decrease in 2007 (year \times treatment interaction: $P = 0.03$). Biomass of all PFT differed between years at Frübüel ($P \ll 0.05$) and only legume productivity was slightly reduced by the drought treatment ($P = 0.07$) while all other PFT did not respond to drought. At Chamau, grasses and dead biomass responded differently in the three years ($P < 0.001$) and were significantly affected by the treatment. No change in forb and legume productivities was found.

3.3 LAI and vegetation height

LAI measurements during 2006 and 2007 (Fig. 3) represented above-ground biomass regrowth patterns in higher temporal resolution than total community above-ground productivity and varied significantly during the growing seasons ($P < 0.001$). Similar to productivity measurements, we did not find significant differences in LAI between drought and control plots at Chamau in 2006 (except very early in the season), probably confounded by *Rumex* abundance. In contrast, the drought response of LAI in 2007 was stronger than that of above-ground productivity, with much lower LAI values for drought than for control plots ($P < 0.001$). At Frübüel, LAI was negatively affected by drought in both years ($P < 0.001$) although there was no such effect on total above-ground biomass. At Alp Weissenstein, the LAI values were lower on drought compared to control plots ($P = 0.02$), but despite the large decrease in biomass under drought conditions this trend was not significant at the different measurement dates. No relationship of LAI before the cut with harvested community above-ground biomass was found at any of the three sites ($R^2 \leq 0.1$, $P > 0.2$ but $P < 0.001$ for Chamau).

Vegetation height (data not shown) developed similar to LAI but was not as strongly affected by the drought treatment as LAI (except for Alp Weissenstein where vegetation height was significantly lower on drought compared to control plots). Vegetation height before the cuts was not related to total community above-ground biomass at Chamau

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and Alp Weissenstein, in contrast to Frübüel ($R^2=0.4$, $P<0.001$).

3.4 Root biomass

Root biomass productivity differed significantly among sites ($P=0.01$), with productivities being almost twice as high at Alp Weissenstein compared to Frübüel and Chamau (Fig. 4). However, below-ground productivity was not affected by the drought treatment ($P=0.9$). In addition, the site \times treatment interaction term was not significant ($P=0.9$), indicating that the response of below-ground productivity to drought was similar across all three sites.

3.5 Carbon isotope measurements

Bulk above-ground carbon isotope ratios ($\delta^{13}\text{C}$) ranged between -31.3‰ and -26.7‰ for the grassland communities (Fig. 5), with significant differences among sites ($P<0.001$). $\delta^{13}\text{C}$ values were highest for Alp Weissenstein and varied over the course of the growing season ($P<0.001$). In addition, we found significant effects of the drought treatment on $\delta^{13}\text{C}$ at all sites ($P<0.001$). While the drought increased $\delta^{13}\text{C}$ in 2005 and 2007, there was only a delayed response in 2006 at Chamau (date \times treatment interaction: $P<0.001$; Fig. 5a–c). This was controlled by the drought response of grasses that contributed most to community biomass. Legumes on the other hand did not react to drought in 2005 and 2007 but instead significantly decreased their $\delta^{13}\text{C}$ values in 2006 (data not shown). At Frübüel, the drought response of community $\delta^{13}\text{C}$ varied throughout the experiment but a non-significant harvest date \times treatment interaction indicated no change in the direction of the drought effect (Fig. 5d–f). Grasses were the only functional group displaying an overall positive drought response but forbs also showed slightly increasing $\delta^{13}\text{C}$ values in response to drought in 2007. The drought response of community $\delta^{13}\text{C}$ at Alp Weissenstein was mainly driven by a very strong positive drought effect in the first year (significant date and date \times treatment interaction effects; Fig. 5g–h), dominated by grasses that showed

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highest increases in $\delta^{13}\text{C}$ in response to drought as well as by the positive drought effect on $\delta^{13}\text{C}$ of forbs in 2006. Interestingly, $\delta^{13}\text{C}$ values of legumes were not significantly affected by drought, although legume biomass had been reduced significantly.

On the single species level, no clear patterns could be detected. Grass species showed clear drought responses but no species differed strikingly from the others. An outstanding drought response was observed in *R. obtusifolius* at Chamau (excluded from all analyses, for detailed results see Gilgen et al., 2009).

4 Discussion

4.1 Above-ground productivity

Drought typically reduces above-ground biomass productivity in grasslands (Hopkins, 1978; Bollinger et al., 1991; Kahmen et al., 2005). In contrast to these findings and rather unexpected, no consistent decrease in total community above-ground biomass under drought was observed in our experiment for all sites in all years. As environmental and management characteristics differed considerably among the three sites (i.e. site explained most of the differences in community above-ground biomass productivity) and with time (i.e. significant effect of the harvest date), the sites seemed to react rather site- and year-specific. However, when probing for general relationships, we found a strong relationship of average above-ground biomass response with annual precipitation ($R^2=0.85$, $P<0.001$; Fig. 6). Sites with lower annual precipitation thus seem to be more vulnerable to summer drought than sites with higher annual precipitation. Moreover, if annual precipitation is very high (above 1500–2000 mm), drought can even generate a beneficial effect on annual above-ground biomass productivity. No such relationship was found between above-ground biomass response and the fraction of annual precipitation excluded by the shelters ($R^2<0.001$, $P=0.89$) nor with growing degree days ($R^2<0.001$, $P=0.5$), clearly indicating that long-term annual precipitation rather than temperature controlled the drought response of these grasslands. A de-

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pendence of biomass production on soil moisture at drier sites but not at wetter sites was found for shrublands (Penuelas et al., 2007).

Grasses contributed most to community biomass (generally more than 50%, except for Chamau in 2006), thus reflecting the response of the community well or rather shaping the response of the community. Although grasses are generally deep rooted (Bessler et al., 2009), their resistance to drought seemed to be rather small. Also Grime et al. (2000) had found that perennial grasses were particularly vulnerable to climate change in a limestone grassland. On the other hand, we found only slight effects of drought on forbs or legumes (except for *R. obtusifolius* at Chamau in 2006, Gilgen et al., 2009). Although *Trifolium repens*, the most abundant legumes species at our sites, has been shown to be drought sensitive (Foulds, 1978; Stevenson and Laidlaw, 1985), in our study, the fraction of *T. repens* of total biomass was not significantly affected by drought (except at Alp Weissenstein in 2006). Furthermore, the amount of dead biomass was slightly increased under drought, with the strongest effect again at the driest site, Alp Weissenstein, in 2006. This increase in dead biomass on drought plots was probably caused by earlier senescence as has been reported in other studies as well (Voltaire, 2002; Monti et al., 2007).

Although other factors than water can also limit plant productivity, such as N (Harpole et al., 2007), we can fairly assume that the three grasslands studied here were not limited throughout the experiment. The two lower sites are regularly fertilised with manure, according to Swiss regulations. At Chamau, this high fertilisation was even shown to control the C cycle more than climate (Zeeman et al., 2009). Also at the alpine site we can assume no N limitation since biomass productivity was even higher in the second year than in the first year of the experiment.

4.2 Below-ground productivity

But also below-ground productivity can react: plants are able to sense the water available in soils and when the soil dries out, they produce abscisic acid (ABA) which was shown to maintain or increase root growth while shoot growth is inhibited (Saab et al.,

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1990; Davies and Zhang, 1991; Tardieu et al., 1992). Indeed, increased root growth under drought was often found in other studies (Jupp and Newman, 1987; Field et al., 1992; Kalapos et al., 1996; van den Boogaard et al., 1996; Kahmen et al., 2005). However, in our study, no change in below-ground biomass productivity was observed at any of the three sites. One reason could be that roots of different grass species reacted differently to drought (Molyneux and Davies, 1983; Bessler et al., 2009) and could thus compensate each other to hold community root biomass constant. Another explanation could be timing. Since our ingrowth cores remained in the field for a whole season or longer and not only during the drought treatment, the untreated conditions during most of the season might have dampened any drought effect. Still, on an annual basis, constant below-ground compared to decreasing above-ground productivity resulted in a higher root/shoot ratio of total plant biomass, thus indicating an increased allocation of resources to root growth.

4.3 Carbon isotope measurements

According to theory, $\delta^{13}\text{C}$ of plants can be used as an estimate for water use efficiency (WUE) because the ^{13}C signature depends on the ratio of intercellular to ambient CO_2 concentrations (c_i/c_a , Farquhar et al., 1982) and an increase in $\delta^{13}\text{C}$ is thus coupled to a decrease in c_i/c_a , which can either be caused by higher photosynthetic fixation or decreasing stomatal conductance (Farquhar et al., 1989). Although this simplified view has recently been discussed rather critically (Seibt et al., 2008), our data still met the predictions made based on those earlier assumptions, i.e. an increase in $\delta^{13}\text{C}$ under drier condition due to decreased stomatal conductance (Signarbieux and Feller, 2009). Community $\delta^{13}\text{C}$ was more positive on drought plots than on control plots at all sites in all years, although also other physiological processes than just photosynthesis, e.g. cell elongation and protein synthesis, might affect growth even more strongly than photosynthesis (Lambers et al., 1998). Nevertheless, community $\delta^{13}\text{C}$ was mainly controlled by grass $\delta^{13}\text{C}$ values that were also higher on drought plots than on control plots while forb and legume $\delta^{13}\text{C}$ values were unaffected by drought indicating no

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change in WUE efficiency in these two plant functional types.

4.4 Perspectives

Extrapolating results of the present study to the future might be difficult, since not only the amount of summer precipitation is changing under climate change but also of winter precipitation as well as timing and variability of rainfall, both important for grassland productivity (Nippert et al., 2006; Heisler-White et al., 2008). Future winters are predicted to be wetter than today in Central Europe (Frei et al., 2006). Higher winter precipitation will therefore probably recharge water reservoirs regularly, thereby buffering any summer drought effects. In addition, it has been shown that winter precipitation had no effect on biomass productivity, which was rather controlled by summer precipitation of the previous and the current year (Morecroft et al., 2004). This indicates that even if community above-ground biomass productivity recovered quickly after the removal of the rain shelters in our experiment, a long-term effect could still have been preserved.

Under future climate change drier summers will also be accompanied by higher atmospheric CO₂ concentrations. These have been shown to lead to water savings due to a reduced stomatal opening (Campbell et al., 1997; Volk et al., 2000). However, the relatively strong reductions of biomass productivity at Alp Weissenstein and at Chamau in 2007 will probably not be offset by the typically small water saving effects under increasing CO₂ as observed in Swiss forest (Leuzinger et al., 2005) and grassland sites (Volk et al., 2000).

In conclusion, results from this study indicate that there is no uniform grassland response to drought in Switzerland. Different grassland types as well as different plant functional types differed in their response to drought. However, the drought response scaled with total annual precipitation, thus sites with high annual precipitation seem to be better buffered against disturbance by summer drought than sites with low annual precipitation. If this is also true in other parts of Europe remains to be tested, but it already now emphasises the strong needs for adaptation measures in the drier parts of Switzerland.

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References

- Arp, W. J., Van Mierlo, J. E. M., Berendse, F., and Snijders, W.: Interactions between elevated CO₂ concentration, nitrogen and water: effects on growth and water use of six perennial plant species, *Plant Cell Environ.*, 21, 1–11, 1998.
- Bessler, H., Temperton, V. M., Roscher, C., Buchmann, N., Schmid, B., Schulze, E. D., Weisser, W. W., and Engels, C.: Above-ground overyielding in experimental grassland mixtures is associated with reduced biomass partitioning to below-ground organs, *Ecology*, in press, 2009.
- Bollinger, E. K., Harper, S. J., and Barrett, G. W.: Effects of seasonal drought on old field plant communities, *Am. Midl. Nat.*, 125, 114–125, 1991.
- Brooks, P. D., Geilmann, H., Werner, R. A., and Brand, W. A.: Improved precision of coupled $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ measurements from single samples using an elemental analyser/isotope ratio mass spectrometer combination with a post-column 6-port valve and selective CO₂ trapping; improved halide robustness of the combustion reactor using CeO₂, *Rapid Commun. Mass Sp.*, 17, 1924–1926, 2003.
- Campbell, B. D., Smith, D. M. S., and McKeon, G. M.: Elevated CO₂ and water supply interactions in grasslands: A pastures and rangelands management perspective, *Glob. Change Biol.*, 3, 177–187, 1997.
- Christensen, J. H., Hewitson, B., Busuioc, A., Chen, A., Gao, X., Held, I., Jones, R., Kolli, R. K., Kwon, W.-T., Laprise, R., Magaña Rueda, V., Mearns, L., Menéndez, C. G., Räisänen, J., Rinke, A., Sarr, A., and Whetton, P.: Regional Climate Projections, in: *Climate Change*

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2007: the Physical Science Basis. Contribution of Working Group I to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change edited by: Solomon, S., Qin, D., Manning, M., Chen, Z., Marquis, M., Averyt, K. B., Tignor, M., and Miller, H. L., Cambridge University Press, Cambridge, UK, 847–940, 2007.

- 5 Davies, W. J. and Zhang, J. H.: Root signals and the regulation of growth and development of plants in drying soil, *Annu. Rev. Plant Phys.*, 42, 55–76, 1991.
- English, N. B., Weltzin, J. F., Fravolini, A., Thomas, L., and Williams, D. G.: The influence of soil texture and vegetation on soil moisture under rainout shelters in a semi-desert grassland, *J. Arid. Environ.*, 63, 324–343, 2005.
- 10 Farquhar, G. D., O'Leary, M. H., and Berry, J. A.: On the relationship between carbon isotope discrimination and the inter-cellular carbon-dioxide concentration in leaves, *Aust. J. Plant Physiol.*, 9, 121–137, 1982.
- Farquhar, G. D., Ehleringer, J. R., and Hubick, K. T.: Carbon isotope discrimination and photosynthesis, *Annu. Rev. Plant Phys.*, 40, 503–537, 1989.
- 15 Field, C. B., Chapin, F. S., Matson, P. A., and Mooney, H. A.: Responses of terrestrial ecosystems to the changing atmosphere – A resource-based approach, *Annu. Rev. Ecol. Syst.*, 23, 201–235, 1992.
- Foulds, W.: Response to soil moisture supply in three leguminous species. 1. Growth, reproduction and mortality, *New Phytol.*, 80, 535–545, 1978.
- 20 Frei, C., Scholl, R., Fukutome, S., Schmidli, R., and Vidale, P. L.: Future change of precipitation extremes in Europe: Intercomparison of scenarios from regional climate models, *J. Geophys. Res.-Atmos.*, 111, D06105, doi:10.1029/2005JD005965, 2006.
- Gibbins, R. P. and Beck, R. F.: Changes in grass basal area and forb densities over a 64-year period on grassland types of the Jornada Experimental Range, *J. Range Manage.*, 41, 186–192, 1988.
- 25 Gilgen, A. K., Signarbieux, C., Feller, U., and Buchmann, N.: Competitive advantage of *Rumex obtusifolius* L. might increase in intensively managed temperate grasslands under drier climate, *Agr. Ecosyst. Environ.*, in revision, 2009.
- Greco, S. A. and Cavagnaro, J. B.: Effects of drought in biomass production and allocation in three varieties of *Trichloris crinita* P. (Poaceae) a forage grass from the arid Monte region of Argentina, *Plant Ecol.*, 164, 125–135, 2003.
- 30 Grime, J. P., Brown, V. K., Thompson, K., Masters, G. J., Hillier, S. H., Clarke, I. P., Askew, A. P., Corker, D., and Kielty, J. P.: The response of two contrasting limestone grasslands to

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- simulated climate change, *Science*, 289, 762–765, 2000.
- Harpole, W. S., Potts, D. L., and Suding, K. N.: Ecosystem responses to water and nitrogen amendment in a California grassland, *Glob. Change Biol.*, 13, 2341–2348, 2007.
- Heisler-White, J. L., Knapp, A. K., and Kelly, E. F.: Increasing precipitation event size increases aboveground net primary productivity in a semi-arid grassland, *Oecologia*, 158, 129–140, 2008.
- Hopkins, B.: Effects of 1976 drought on chalk grassland in Sussex, England, *Biol. Conserv.*, 14, 1–12, 1978.
- Jupp, A. P. and Newman, E. I.: Morphological and anatomical effects of severe drought on the roots of *Lolium perenne* L., *New Phytol.*, 105, 393–402, 1987.
- Kahmen, A., Perner, J., and Buchmann, N.: Diversity-dependent productivity in semi-natural grasslands following climate perturbations, *Funct. Ecol.*, 19, 594–601, 2005.
- Kalapos, T., van den Boogaard, R., and Lambers, H.: Effect of soil drying on growth, biomass allocation and leaf gas exchange of two annual grass species, *Plant Soil*, 185, 137–149, 1996.
- Karsten, H. D. and MacAdam, J. W.: Effect of drought on growth, carbohydrates, and soil water use by perennial ryegrass, tall fescue, and white clover, *Crop Sci.*, 41, 156–166, 2001.
- Keller, P.: Vegetationskundliche Untersuchungen und Ertrag der Grünlandflächen im Gebiet der ETH-Forschungsstation Alp Weissenstein GR, Diploma Thesis, University of Zurich, Switzerland, 119 pp., 2006.
- Knapp, A. K. and Smith, M. D.: Variation among biomes in temporal dynamics of aboveground primary production, *Science*, 291, 481–484, 2001.
- Köchy, M. and Wilson, S. D.: Semiarid grassland responses to short-term variation in water availability, *Plant Ecol.*, 174, 197–203, 2004.
- Lambers, H., Chapin, F. S., and Pons, T. L.: *Plant physiological ecology*, Springer, New York, NY, USA, 1998.
- Leuzinger, S., Zotz, G., Asshoff, R., and Körner, C.: Responses of deciduous forest trees to severe drought in Central Europe, *Tree Physiol.*, 25, 641–650, 2005.
- Mikkelsen, T. N., Beier, C., Jonasson, S., Holmstrup, M., Schmidt, I. K., Ambus, P., Pilegaard, K., Michelsen, A., Albert, K., Andresen, L. C., Arndal, M. F., Bruun, N., Christensen, S., Danbaek, S., Gundersen, P., Jorgensen, P., Linden, L. G., Kongstad, J., Maraldo, K., Prieme, A., Riis-Nielsen, T., Ro-Poulsen, H., Stevnbak, K., Selsted, M. B., Sorensen, P., Larsen, K. S., Carter, M. S., Ibrom, A., Martinussen, T., Miglietta, F., and Sverdrup, H.: Experimental

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- design of multifactor climate change experiments with elevated CO₂, warming and drought: the CLIMAITE project, *Funct. Ecol.*, 22, 185–195, 2008.
- Molyneux, D. E. and Davies, W. J.: Rooting pattern and water relations of three pasture grasses growing in drying soil, *Oecologia*, 58, 220–224, 1983.
- 5 Monti, A., Barbanti, L., and Venturi, G.: Photosynthesis on individual leaves of sugar beet (*Beta vulgaris*) during the ontogeny at variable water regimes, *Ann. Appl. Biol.*, 151, 155–165, 2007.
- Morecroft, M. D., Masters, G. J., Brown, V. K., Clarke, I. P., Taylor, M. E., and Whitehouse, A. T.: Changing precipitation patterns alter plant community dynamics and succession in an ex-arable grassland, *Funct. Ecol.*, 18, 648–655, 2004.
- 10 Nippert, J. B., Knapp, A. K., and Briggs, J. M.: Intra-annual rainfall variability and grassland productivity: can the past predict the future?, *Plant Ecol.*, 184, 65–74, doi:10.1007/s11258-005-9052-9, 2006.
- Paruelo, J. M., Lauenroth, W. K., Burke, I. C., and Sala, O. E.: Grassland precipitation-use efficiency varies across a resource gradient, *Ecosystems*, 2, 64–68, 1999.
- 15 Penuelas, J., Prieto, P., Beier, C., Cesaraccio, C., de Angelis, P., de Dato, G., Emmett, B. A., Estiarte, M., Garadnai, J., Gorissen, A., Lang, E. K., Kroel-Dulay, G., Llorens, L., Pellizzaro, G., Riis-Nielsen, T., Schmidt, I. K., Sirca, C., Sowerby, A., Spano, D., and Tietema, A.: Response of plant species richness and primary productivity in shrublands along a north-south gradient in Europe to seven years of experimental warming and drought: reductions in primary productivity in the heat and drought year of 2003, *Glob. Change Biol.*, 13, 2563–2581, 2007.
- 20 R Development Core Team: R: A language and environment for statistical computing, 2.5.0 ed., R Foundation for Statistical Computing, Vienna, Austria, 2007.
- 25 Roth, K.: Bodenkartierung und GIS-basierte Kohlenstoffinventur von Graslandböden: Untersuchungen an den ETH-Forschungsstationen Chamau und Frübüel (ZG, Schweiz), Diploma Thesis, University of Zurich, Switzerland, 132 pp., 2006.
- Saab, I. N., Sharp, R. E., Pritchard, J., and Voetberg, G. S.: Increased endogenous abscisic acid maintains primary root growth and inhibits shoot growth in maize seedlings at low water potentials, *Physiol. Plant.*, 93, 1329–1336, 1990.
- 30 Schärer, M.: Kurzbericht der Fallstudie Alp Weissenstein. Nährstoffanalysen in Alpweiden Sommer 2002, Term Paper, ETH Zurich, Switzerland, 44 pp., 2003.
- Schwinning, S., Starr, B. I., and Ehleringer, J. R.: Summer and winter drought in a cold desert

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- ecosystem (Colorado Plateau) part II: effects on plant carbon assimilation and growth, *J. Arid. Environ.*, 61, 61–78, 2005.
- Seibt, U., Rajabi, A., Griffiths, H., and Berry, J. A.: Carbon isotopes and water use efficiency: sense and sensitivity, *Oecologia*, 155, 441–454, 2008.
- 5 Sherry, R. A., Weng, E., Arnone III, J. A., Johnson, D. W., Schimel, D., Verburg, P. S., Wallace, L. L., and Luo, Y. Q.: Lagged effects of experimental warming and doubled precipitation on annual and seasonal aboveground biomass production in a tallgrass prairie, *Glob. Change Biol.*, 14, 2923–2936, 2008.
- Signarbieux, C. and Feller, U.: Effects of an extended drought period on physiological properties of grasslands species in Switzerland, in preparation, 2009.
- 10 Stampfli, A. and Zeiter, M.: Plant regeneration directs changes in grassland composition after extreme drought: a 13-year study in southern Switzerland, *J. Ecol.*, 92, 568–576, 2004.
- Sternberg, M., Brown, V. K., Masters, G. J., and Clarke, I. P.: Plant community dynamics in a calcareous grassland under climate change manipulations, *Plant Ecol.*, 143, 29–37, 1999.
- 15 Stevenson, C. A. and Laidlaw, A. S.: The effect of moisture stress on stolon and adventitious root development in white clover (*Trifolium repens* L.), *Plant Soil*, 85, 249–257, 1985.
- Tardieu, F., Zhang, J., Katerji, N., Bethenod, O., Palmer, S., and Davies, W. J.: Xylem ABA controls the stomatal conductance of field-grown maize subjected to soil compaction or soil drying, *Plant Cell Environ.*, 15, 193–197, 1992.
- 20 van den Boogaard, R., Veneklaas, E. J., and Lambers, H.: The association of biomass allocation with growth and water use efficiency of two *Triticum aestivum* cultivars, *Aust. J. Plant Physiol.*, 23, 751–761, 1996.
- Voltaire, F.: Drought survival, summer dormancy and dehydrin accumulation in contrasting cultivars of *Dactylis glomerata*, *Physiol. Plant.*, 116, 42–51, 2002.
- 25 Volk, M., Niklaus, P. A., and Körner, C.: Soil moisture effects determine CO₂ responses of grassland species, *Oecologia*, 125, 380–388, 2000.
- Weaver, J. E., Stoddart, L. A., and Noll, W.: Response of the prairie to the great drought of 1934, *Ecology*, 16, 612–629, 1935.
- Werner, R. A., Bruch, B. A., and Brand, W. A.: ConFlo III – An interface for high precision $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ analysis with an extended dynamic range, *Rapid Commun. Mass Sp.*, 13, 1237–1241, 1999.
- 30 Werner, R. A. and Brand, W. A.: Referencing strategies and techniques in stable isotope ratio analysis, *Rapid Commun. Mass Sp.*, 15, 501–519, 2001.

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Werner, R. A.: The online $^{18}\text{O}/^{16}\text{O}$ analysis: Development and application, *Isot. Environ. Health S.*, 39, 85–104, 2003.

Zeeman, M. J.: Environmental processes affecting the carbon dioxide budget of grasslands along an elevational gradient in Switzerland, PhD Thesis, ETH Zurich, Switzerland, 219 pp., 2008.

5

Zeeman, M. J., Hiller, R., Gilgen, A. K., Michna, P., Plüss, P., Buchmann, N., and Eugster, W.: Management, not climate, controls net CO_2 fluxes and carbon budgets of three grasslands along an elevational gradient in Switzerland, *Agr. Forest Meteorol.*, in revision, 2009.

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Table 1. Description of the three experimental grassland sites in Switzerland.

	Chamau	Früebüel	Alp Weissenstein
Political community	Hünenberg, ZG	Walchwil, ZG	Bergün, GR
Coordinates WGS84	47°12'37" N, 8°24'38" E	47°6'57" N, 8°32'16" E	46°34'60" N, 9°47'26" E
Elevation [m above sea level]	393	982	1978
Growing season length	mid-April to October	May to mid-October	mid-June to September
Soil type	cambisol ^a	gleysol ^a	humous sandy loam ^b
Annual precipitation sum [mm] ^c	1179	1632	918
Mean annual temperature [°C] ^c	9.8	7.7	2.3
Vegetation type	grass-legume mixture (<i>Trifolium repens</i> L., <i>Lolium perenne</i> L., <i>Poa pratensis</i> L.)	Deschampsio cespitosae- permanent managed pasture	Poetum alpini ^d
Number of species (approx.)	20	>30	around 20
Management			
type of usage	silage; sheep grazing in autumn	silage/hay; cattle grazing in autumn	cattle and horse grazing
intensity	intensive	intermediate	extensive
number of cuts per year	6	1–2	0
type of fertiliser	liquid manure	solid manure	none

^a according to Roth (2006);

^b according to Schärer (2003);

^c data from Zeeman (2008) adapted with data from MeteoSwiss;

^d according to Keller (2006).

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Table 2. Dates of rain exclusion and amounts of precipitation excluded at all sites during the three years of experiment. The fraction of annual precipitation is given in brackets.

	2005		2006		2007	
	Duration	Amount [mm]	Duration	Amount [mm]	Duration	Amount [mm]
Chamau	24.6.–19.9.	491 (42%)	31.5.–17.8.	271 (24%)	2.5.–10.7.	403 (33%)
Früebüel	23.6.–19.9.	763 (52%)	31.5.–17.8.	388 (24%)	7.5.–20.7.	589 (33%)
Alp Weissenstein	–	–	6.7.–24.8.	248 (29%)	20.6.–23.8.	311 (32%)

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Table 3. Effect of drought on total, alive and dead annual community above-ground biomass productivity at Chamau, Frübüel and Alp Weissenstein. Means and standard errors are given ($n=5-6$). Significantly different means ($P \leq 0.05$) are given in bold, marginally significant differences ($0.1 \geq P > 0.05$) in italics.

	Chamau			Frübüel			Alp Weissenstein		
	control	drought	<i>P</i>	control	drought	<i>P</i>	control	drought	<i>P</i>
2005 ^a									
total	477±53	425±60	0.5	248±40	260±53	0.9	–	–	–
alive	457±55	398±60	0.5	220±35	235±49	0.8	–	–	–
dead	20±4	26±5	0.3	28±6	26±4	0.7	–	–	–
2006									
total	931±174	895±185	0.9	590±77	607±69	0.9	284±9	184±26	0.007
alive	909±173	862±181	0.9	535±76	531±61	0.9	180±11	55±7	<0.001
dead	22±2	33±4	0.1	55±6	76±12	0.1	104±2	128±24	0.3
2007									
total	<i>1211±134</i>	<i>887±56</i>	0.06	616±77	676±57	0.5	487±30	338±45	0.02
alive	1160±130	820±52	0.04	416±64	477±30	4.0	191±34	119±28	0.1
dead	<i>52±6</i>	<i>67±6</i>	0.08	200±25	199±38	1.0	<i>296±23</i>	<i>218±29</i>	0.07

^a Annual biomass productivity sum based on only three (instead of six) and one (instead of two) harvests at Chamau and Frübüel, respectively.

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Table 4. Results of the ANOVA models for annual sums and harvest yields of total and plant functional type above-ground biomass (excluding *Rumex obtusifolius*). Main factors are site (Chamau, Frübüel or Alp Weissenstein), harvest date and treatment (drought vs. control). Significant *P* values ($P \leq 0.05$) are given in bold, marginally significant values ($0.1 \geq P > 0.05$) in italics; $n=5-6$.

	All years					2005					2006					2007					
	Total	Grass	Forb	Leg.	Dead	Total	Grass	Forb	Leg.	Dead	Total	Grass	Forb	Leg.	Dead	Total	Grass	Forb	Leg.	Dead	
Annual above-ground biomass sums																					
Site	<0.001	<0.001	0.2	<0.001	<0.001	0.002	<0.001	0.01	<i>0.07</i>	0.4	<0.001	<0.001	0.3	<0.001	<0.001	<0.001	<0.001	0.2	0.006	<0.001	
Treatment	0.1	<i>0.08</i>	<i>0.06</i>	0.2	1	0.7	0.7	0.3	0.2	0.7	0.1	0.2	0.1	0.99	0.05	<i>0.05</i>	0.03	0.6	0.2	0.4	
Site × Treatment	0.2	0.05	0.7	0.1	0.6	0.6	0.1	0.2	0.04	0.4	0.3	0.4	0.7	0.9	0.8	<i>0.05</i>	0.004	0.4	0.2	0.2	
Above-ground biomass per harvest																					
Site	<0.001	<0.001	<0.001	<0.001	<0.001	0.02	0.5	<0.001	0.7	<0.001	<0.001	<0.001	<0.001	0.003	<0.001	<0.001	<0.001	<0.001	0.002	<0.001	
Harvest date	<0.001	<0.001	<0.001	<i>0.05</i>	<0.001	0.01	0.004	0.9	0.5	<0.001	<0.001	<0.001	0.02	0.003	<0.001	<0.001	0.8	0.2	<i>0.05</i>		
Treatment	0.003	0.001	0.006	0.005	0.8	0.6	0.5	0.2	0.1	0.7	<i>0.06</i>	<i>0.05</i>	0.01	0.4	0.01	0.01	0.002	0.5	0.01	0.3	
Site × Harvest date	0.2	0.3	<0.001	<i>0.09</i>	<0.001	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	
Site × Treatment	0.001	<0.001	0.7	0.03	0.01	0.6	0.2	0.002	<i>0.06</i>	0.4	<i>0.06</i>	<i>0.07</i>	0.3	0.5	<i>0.1</i>	0.006	0.005	0.2	0.1	0.001	
Harvest date × Treatment	0.6	0.6	0.6	0.7	0.02	0.97	0.9	0.9	0.2	0.6	0.3	0.5	0.8	0.7	0.3	0.2	0.2	0.9	0.6	1	

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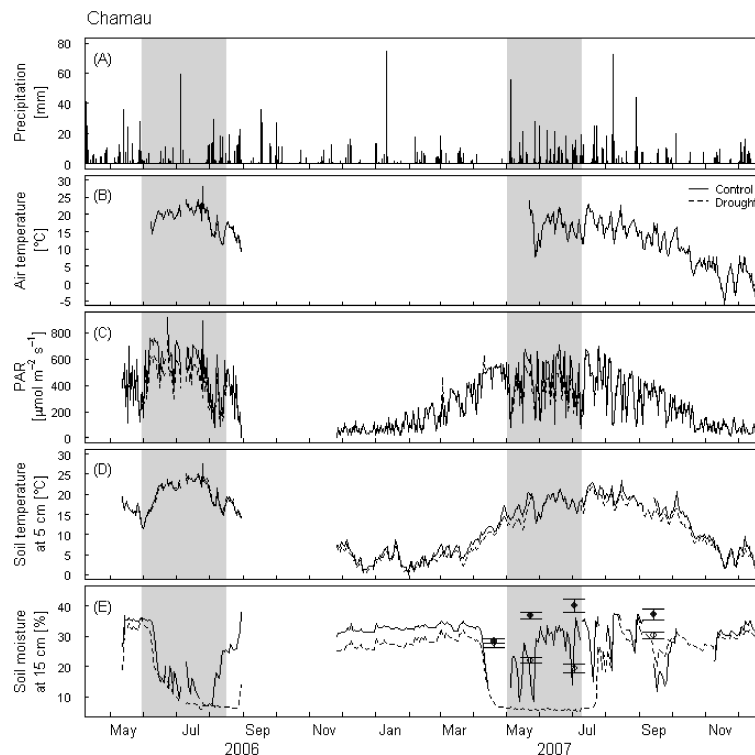


Fig. 1. Micrometeorology during the experiment at Chamau: daily precipitation sum **(A)**, daily means of air temperature at 160 cm **(B)**, photosynthetically active radiation (PAR, **C**), soil temperature at 5 cm depth **(D)**, and soil moisture at 15 cm depth **(E)**. Solid lines: control plots, dashed lines: drought plots. Measurements of gravimetric soil water content in soil cores from 10–15 cm are given as points (open symbols for drought plots). The periods of drought treatment are shaded in grey. Averages of two plots per treatment are shown.

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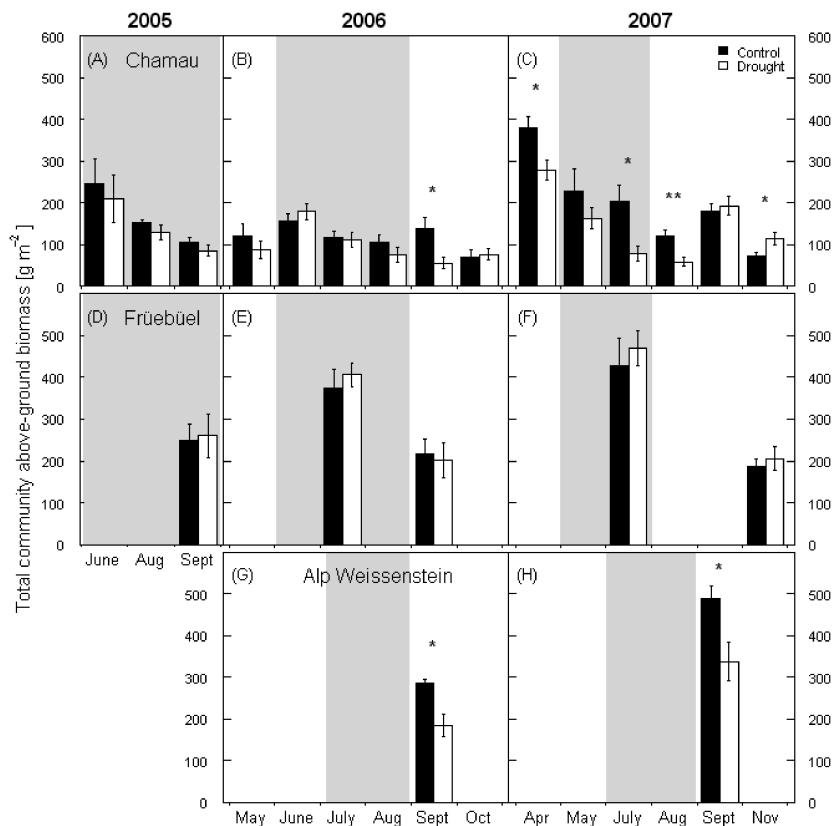


Fig. 2. Effect of summer drought on total community above-ground biomass at Chamau (excluding *R. obtusifolius* biomass, **A–C**), Frübüel (**D–F**) and Alp Weissenstein (**G–H**) during the experiment. Means and standard errors are given ($n=5-7$). Periods of drought treatment are shaded in grey. * $0.05 \geq P > 0.01$, ** $0.01 \geq P > 0.001$.

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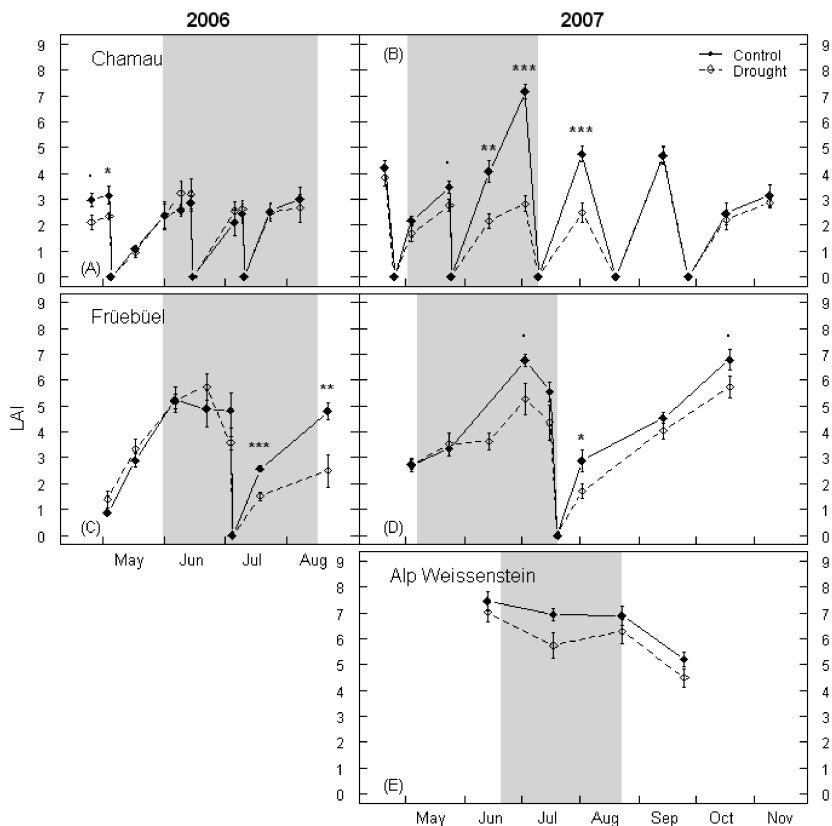


Fig. 3. Effect of summer drought on community leaf area index (LAI) at Chamau (A, B), Fruebüel (C, D) and Alp Weissenstein (E) during the experiment. Means and standard errors are given ($n=3-7$). Periods of drought treatment are shaded in grey. • $0.1 \geq P > 0.05$, * $0.05 \geq P > 0.01$, ** $0.01 \geq P > 0.001$, *** $P \leq 0.001$.

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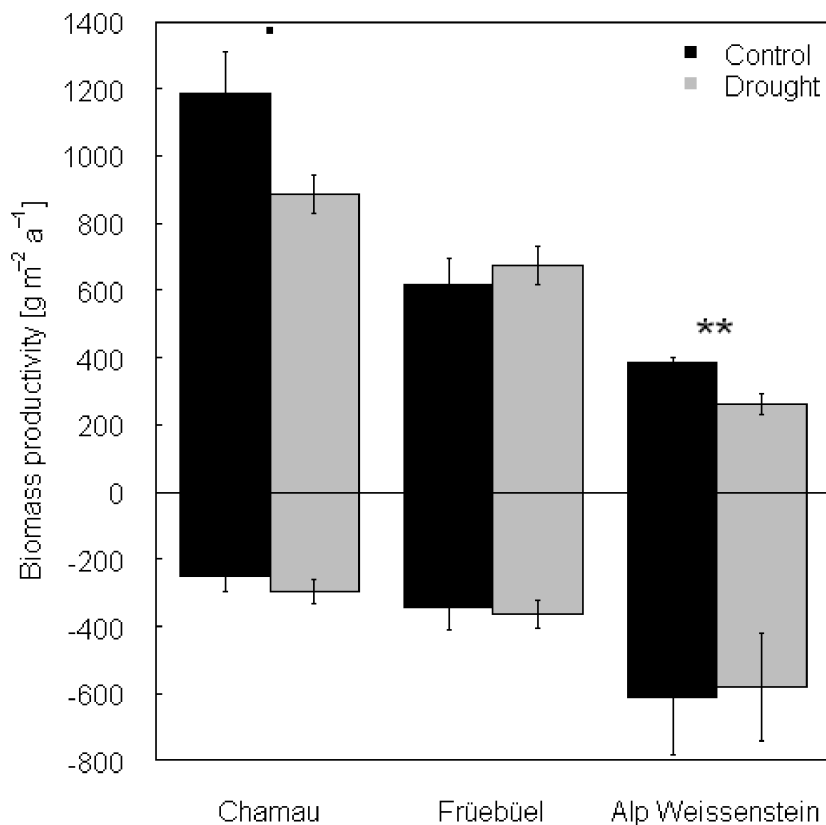


Fig. 4. Effect of summer drought on annual above- and below-ground biomass productivity at the three sites. Below-ground biomass was estimated using ingrowth cores. Means and standard errors are given ($n=3-6$). • $0.1 \geq P > 0.05$, ** $0.01 \geq P > 0.001$. No significant treatment effects on the below-ground biomass productivity were found.

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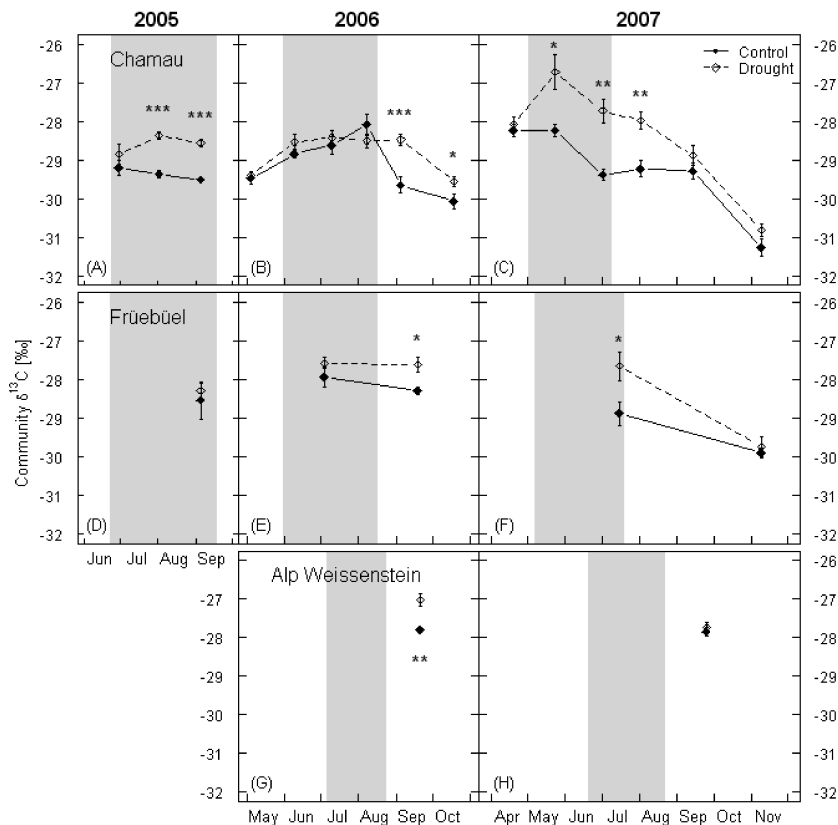


Fig. 5. Effect of summer drought on community $\delta^{13}\text{C}$ at Chamau (excluding *Rumex obtusifolius*, **A–C**), Fruebüel (**D–F**) and Alp Weissenstein (**G–H**) during the experiment. Means and standard errors are given ($n=5-7$). Periods of drought treatment are shaded in grey. * $0.05 \geq P > 0.01$, ** $0.01 \geq P > 0.001$, *** $P \leq 0.001$.

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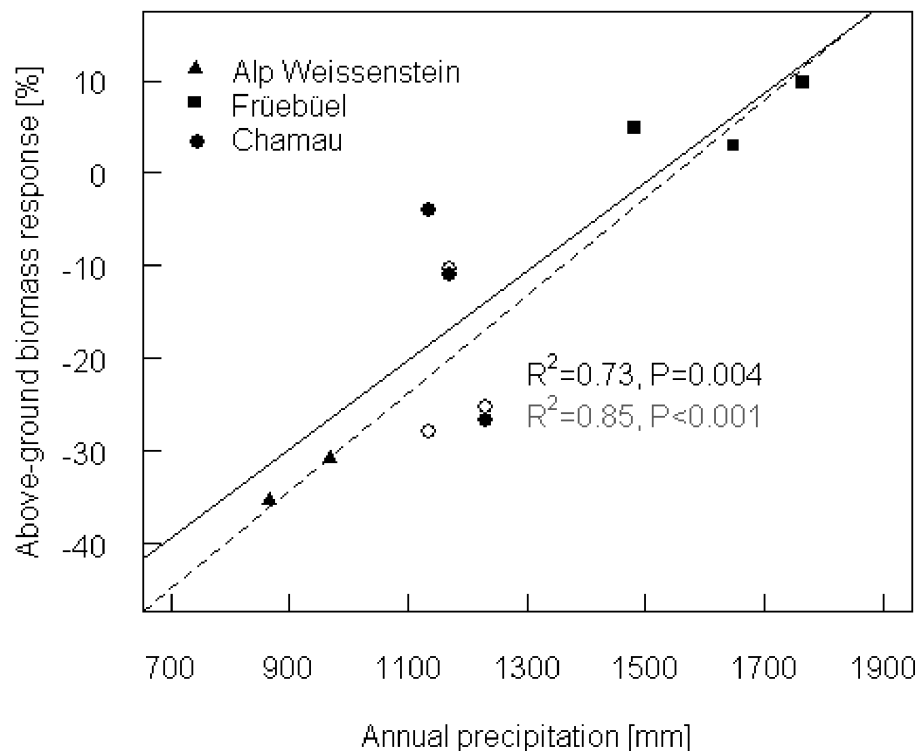


Fig. 6. Relationship of annual precipitation sums and average change in annual above-ground biomass productivities in response to the drought treatment. R^2 and P values for the regression of annual above-ground biomass excluding *Rumex obtusifolius* at Chamau are given in grey (open symbols, dashed line).

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