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REGULAR PAPER

Effects of an extended drought period on physiological properties of grassland species in the field

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Abstract A very high percentage (around 70%) of the agronomic area in Switzerland is covered by grasslands at various altitudes where environmental conditions, management, community structure and productivity vary widely. As heat waves and drought are predicted to increase in future climate, survival of plant species in grasslands is a major issue of concern in Central Europe. The effect of summer drought on representative grasslands in Switzerland was studied through drought experiments (using rain-out shelters avoiding natural precipitation) to understand the response of predominant species to changed climatic conditions. The physiological performance (gas exchange, leaf water potential) of selected species was investigated at three locations in Switzerland. The predawn leaf water potential of all species was lower (more negative) under the dryer conditions at the three sites. Net photosynthesis and stomatal conductance of forb and legume species did not show major changes under drought, while grass species showed large decreases at the lowland site. These differences between forb-legume and grass species were not observed at the pre-alpine and alpine site. The apparent drought tolerance of the forb-legume species seems to be due—at least partially—to increased water use efficiency under drought conditions.

Keywords Drought · Grassland · Leaf water status · Photosynthesis · Stomatal conductance

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Introduction

Human activities strongly affect the Earth's climate (Kerr 2001). The evidence for human effects on climate will continue through the next decades and is expected to result in a substantially warmer planet with altered weather patterns (Houghton 1995). Many global circulation models predict that temperate areas will become warmer and drier worldwide (Cao and Woodward 1998) with more extreme events such as severe heat waves and droughts (Easterling et al. 2000; Meehl et al. 2000), especially in Europe (Schär et al. 2004). Such an increase in variability would strongly increase the occurrence of heat waves and drought (Meehl and Tebaldi 2004). It was previously demonstrated that this increase in temperature variability is clearly related to the feedbacks between the land surface and the atmosphere (Seneviratne et al. 2006). Therefore, it is crucial to better understand the role of the interactions between land surface and atmosphere. Considerable efforts aim at understanding the effects of human-induced environmental changes and climate changes in particular, on forest ecosystems. However, most of this research is focused on moderate drought and heat, with rather little effort being targeted on extreme events (severe heat waves and drought) during which plants are exposed to severe or even lethal stress levels. Such severe heat waves may strongly affect the distribution of plant species, the composition of plant communities and ecosystem functioning. Indeed, a few recent studies showed that severe regional heat waves could affect species survival (Solomon and Kirilenko 1997; Stampfli and Zeiter 2004) and terrestrial carbon cycling (Ciais et al. 2005), even though climate warming is usually expected to enhance plant growth and to increase carbon sequestration in temperate forests. Concerning the projection for Switzerland, summer precipitation in 2070 (May–August) is predicted to be 20% lower compared to 1990 (Frei et al. 2006). Such changes in rainfall impact ecosystem functioning (e.g. nutrient cycling, productivity and water use). Most of the studies at present have focused on arid and semi-arid ecosystems (Karatassiou et al. 2009) and little is known for temperate ecosystems. Around 70% of the agronomic area in Switzerland is covered by grassland. Thus it is important to study the impact of drought on such ecosystems.

According to the literature, annual plant species present in grassland ecosystems are in general stress avoiders. Such species are able to reduce activity during extreme stress and to become dormant (Osmond et al. 1987). Recent studies also indicated a shift from drought avoidance to drought tolerance during drought stress (Chaves et al. 2003). Several mechanisms are involved in drought tolerance and imply structural and physiological adjustments that do not happen independently (Zavalla 2004). Characteristics of the root system (diameter, root length and number of root tips) differ significantly between grassland species and nutrients as well as drought have been shown to affect root growth and distribution (Day et al. 2003; Zaller 2007). Previous studies showed that some grassland species are able to produce deep root systems to increase soil water uptake (Grieu et al. 2001), causing a competitive advantage over other species under drought. The capacity of plants to recover from damage caused by severe drought stress is another relevant aspect in terms of competitive growth and survival for various species (Flexas et al. 2006), but such investigations were often focused on tree and shrub species (Kirschbaum 1988; Cai et al. 2005; Gallé and Feller 2007).

The effects on grasslands of predicted changes in rainfall pattern during the next decades (until 2100) are the focus of this investigation. A considerable decrease in summer precipitation must be expected (Schär et al. 2004). In order to understand the response of predominant species to extended drought periods, the effects of an artificial drought (withholding water) on representative grassland species in Switzerland were investigated at three representative altitudes (400, 1,000 and 2,000 m a.s.l.) where species composition, soil properties and climatic conditions vary in a wide range. The aim of the work reported here was to identify the performance of abundant grassland species during an extended summer drought in the field (as predicted by climate models for the end of this century) under actual management conditions. Pre-dawn and midday leaf water potential as well as leaf gas exchange properties were analysed throughout the stress and the subsequent recovery phase. Soil water potential and soil compaction were taken into account to identify effects at various soil depths. The goal of this study was to answer the following questions: (1) What are the relative susceptibilities of various species during the stress phase? (2) Which mechanisms are involved in affecting the performance of grassland species under drought stress? (3) How do various species perform during a subsequent recovery phase?

Materials and methods

Sites

The three sites used in this study differed in altitudes and management. Details concerning duration of the growing season, rainfall patterns, soil characteristics and management as well as drought effect on overall above-ground biomass production at the three sites were reported by Gilgen and Buchman (2009). Below, only a brief summary of site conditions is given.

Chamau (47°12′37″N, 8°24′38″E) is located in the Swiss lowlands (Hünenberg, ZG) at around 400 m a.s.l. The soil type was characterized as a cambisol by Roth (2006). The site was used for grass silage since 1998 but was changed into a temporary maize crop in 2001. Since 2002, it is used as meadow. Mean annual temperature between 1961 and 1990 at Buchs-Aarau (closest meteorological station that had data available) was 8.8°C and mean May–July temperature for the same period was 15.3°C. Yearly precipitation sum between 1961 and 1990 at Cham (closest meteorological station that had data available) was 1,171 mm, precipitation sum for May to July was 419 mm (Begert et al. 2003). A seed mixture containing *Trifolium repens* L. (white clover), *Lolium perenne* L. (perennial ryegrass), and *Poa pratensis* L. (smooth meadow-grass) was used to re-sow the grassland every year. At this location, the management of the grassland consisted of six cuts (with manual weed eater) per year and after each one of them slurry was added as fertilizer. However, during our experiment, plots were not fertilized and over-seeding was only done in early March 2007.

Früebüel (47°06′57″N, 8°32′16″E) is located in the Swiss pre-Alps (Walchwil, ZG) at around 1,000 m a.s.l. The soil type was described as a gleysol by Roth (2006). Mean annual temperature between 1972 and 1989 at Früebüel was 6.5°C, mean May–July temperature for the same period was 12.2°C. Yearly precipitation sum between 1972 and 1989 at Zugerberg was 1,688 mm, precipitation sum for May–July was 597 mm (Meteoswiss). This site was not reseeded each year and no manure was added. There were only two cuts per year, one in the middle of the growing season, July, and one in October.

Alp Weissenstein (46°34′60″N, 9°47′26″E) is located in the Swiss Alps (Pass d'Alvra, Bergün, GR) at around 2,000 m a.s.l. This site covers the alpine altitudinal belt of the traditional Swiss Alpine agricultural system. As described in Hiller et al. (2008), the soil type is defined as slightly humous to humous sandy loam and the climatology is comparable to dry climate because of the surrounding topography.

Artificial drought

The drought experiment was started in late spring 2005 at Chamau and Früebüel and in July 2006 at Alp Weissenstein. Five to seven tunnel-shaped rain shelters (3 × 3.5 m in base area and around 2.1 m high) covered by a transparent plastic foil were installed at the three sites to exclude rainfall in summer and to simulate an artificial drought. The photosynthetically active radiation is only about 10% lower under such shelters, while the air temperature remains essentially unchanged compared to control conditions (Kahmen et al. 2005). To avoid the effect of any natural precipitation on the vegetation in the drought plots, the area below the rain shelter used for the measurement was reduced to 2 × 1 m. Next to each drought plot, a control plot that was exposed to natural precipitation was established. The combination of a control and a shelter plot was treated as a block to account for environmental gradients. Precipitation that collected on the plastic foil was evacuated from each drought plot using plastic tubes. The same plots were used again in 2006 and 2007. The timing and duration of the rainfall exclusion was determined using climate projections (Schär pers. comm.; Frei et al. 2006). According to these projections (scenarios for future climate based on climate change models) it was decided that rainfall should be excluded to simulate an extreme summer drought at these sites. Such a reduction in summer precipitation is expected until 2100. The result suggested rainfall exclusion for 8–10 weeks for the period of May to July at Chamau and Früebüel and a rainfall exclusion for 5–8 weeks starting in June at Alp Weissenstein. The drought experiment started at the beginning of June 2006 at Chamau and Früebüel whereas in 2007 it started in May.

The stress and recovery phases for each site are graphically shown in Fig. 1. In 2006, the rain shelters were installed on May 31 at Chamau and Früebüel (day 151) and on July 6 at Alp Weissenstein (day 187). The plastic foils were removed on August 17 (day 229) at Chamau and Früebüel (78 days) and on August 24 (day 236) at Alp Weissenstein (49 days). In 2007, the rain shelters were installed on May 2 at Chamau (day 122), on May 7 at Früebüel (day 127) and on June 20 (day 171) at Alp Weissenstein. The plastic foils were removed on July 10 (day 191) at Chamau (69 days), on July 20 (day 201) at Früebüel (74 days) and on August 23 (day 235) at Alp Weissenstein (64 days).

Four abundant species were selected at each site for the physiological measurements in 2006 and 2007 (Table 1). Unfortunately, not all species were present at the three sites. Some of them were tested only during 1 year due to the absence of the species or to the small size of the plants making the measurements impossible. For each species, the youngest fully expanded leaf of one plant per plot was analysed in situ for leaf water status and gas exchange.

Soil water potential and soil compaction

In 2007, soil water potential was measured at the three sites with a soil water sensor (Watermark sensor, Irrometer Company, Riverside CA, USA) during the artificial drought and the recovery phase. The sensors were placed at two different depths in the soil (15 and 30 cm) in both control and drought plots. At the same time, soil compaction was measured at Chamau and Früebüel in the control and drought plots using a soil compaction meter (Field Scout SC-900, Spectrum Technologies, Plainfield, IL, USA). Due to technical problems, soil compaction was only assessed at the beginning of the experiment at Alp Weissenstein but the data are not presented here.

Leaf water status and leaf gas exchange

Pre-dawn leaf water potential (Ψ_p) was measured in the early morning before sunrise (between 4 and 5 a.m.) and leaf water potential midday (Ψ_m) was measured between 11 a.m. and 1 p.m. on sunny days. Ψ_p and Ψ_m were determined using a Scholander pressure chamber (SKPM, Skye Instruments Ltd, Powys, UK).

Leaf gas exchange measurements were performed between 11 a.m. and 1 p.m. on sunny days. Photosynthetic gas exchange measurements were recorded in situ in saturating light condition (between 1,800 and 2,000 μmol photons m^{-2} s^{-1}) on fully sun-exposed leaves using an open infrared gas analyzer (IRGA) system (CIRAS-1, PP-Systems, Hitchin, UK). The CIRAS-1 was factory calibrated before each season. The net rate of CO_2 uptake per unit leaf area (A_n) and the stomatal conductance for water vapour (g_s) were assessed. External CO_2 was provided using a CO_2 cartridge plugged into the CIRAS-1 to adjust and maintain constant the CO_2 concentration during the measurement at 380 ± 5 ppm. Temperature inside the leaf cuvette (always in the range of 20°–25°C for Chamau and Früebüel and in the range of 15°–20°C for Alp Weissenstein) and the relative humidity were always close to the ambient air conditions. For the grass species, the area of the leaves was not covering the entire cuvette. Therefore, the real leaf area was calculated in order to determine the real value of A_n and g_s.

Table 1 Species selected at the three experimental sites

Group species	Chamau	Früebüel	Alp Weissenstein
Grasses	*Phleum pratense* L.	*Phleum Pratense* L.	*Phleum alpinum* L.
	Lolium multiflorum Lam.	*Alopecurus pratensis* L.	*Alopecurus pratensis* L.
Legume	*Trifolium repens* L.	*Trifolium repens L.*	
Forbs	*Rumex obtusifolius* L.	*Rumex obtusifolius* L.	*Rumex alpinum* L.

Abundant species were considered for the physiological analyses (different for the three sites)

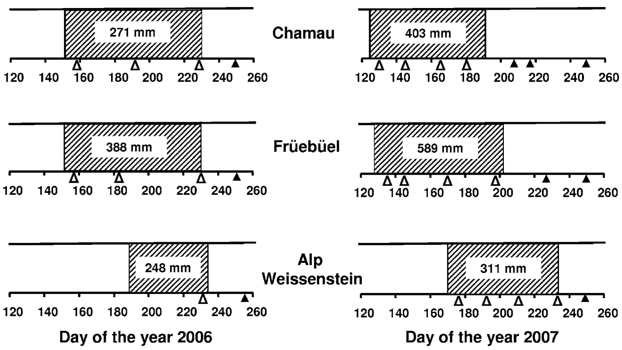

Fig. 1 Drought periods (*hatched area*) and dates for the analyses of plant performance at the three sites in 2006 and 2007. The growth period started first in the lowland (*Chamau*) and pre-alpine site (*Früebüel*) and later at the alpine site (*Alp Weissenstein*). Precipitation excluded during the experimental drought for each site is shown in the *hatched area*. Dates for analyses in the field during the stress phase (*open arrows*) and during the recovery phase (*closed arrows*) are indicated

Statistical analysis

For all physiological parameters (Ψ_p and Ψ_m, A_n and g_s), a split-plot analysis was performed taking five blocks (subplot control + subplot drought) as replicates. Since this did not show any block effect during the experiment at the three sites (data not shown), a separate analysis of variance (ANOVA) was performed to test for the difference between control and drought conditions for each species. All statistical analyses were performed using SAS procedure GLM-SNK (Student–Newman–Keuls) (SAS Version 8.1, SAS Institute, Cary NC, USA).

Results

Soil water potential and soil compaction

During the experiment, from day 122 to day 276 in 2007, values of soil water potential in control conditions at the three sites and the two depths (15 cm and 30 cm) averaged within the range of −1 to −30 kPa (Table 2). Soil water potential showed a net decrease under drought conditions at Chamau dropping to −184 and −156 kPa at the end of the drought at 15 and 30 cm depths, respectively. At Früebüel, values reached −189 and −173 kPa at 15 and 30 cm depths, respectively, at the end of the drought period. At Alp Weissenstein, soil water potential in the drought plots at 15 cm depth reached values below the detection limit of the sensor (−199 kPa) at the end of the drought treatment. Alp Weissenstein showed the lowest values for soil water potential. The recovery phase was characterized by a rapid increase of soil water potential reaching values close to the control conditions at all three locations.

At the lowland site (Chamau), soil compaction profiles were assessed during the artificial drought (day 122–day 191). As expected, no significant differences between control and drought plots were observed on day 122 (Fig. 2), but the values were quite high in all plots. These high values can be explained by the rather dry soil since there were no major rainfalls before day 122. The maximum compaction (3 MPa) was found at 10 cm depth. Control plots recovered as a consequence of rainfalls throughout the season, while values remained high under drought conditions. The maximum soil compaction was later detected at deeper soil layers under drought conditions with 12.5 cm on day 165 and 20 cm on day 191. During the recovery phase (day 191–day 232), control soil profiles remained relatively stable, while the previously high values in drought stressed plots declined and finally reached the same levels as the controls (day 232). Soil compaction was also measured at Früebüel, but no major differences in the soil profiles were detected between control and drought plots (data not shown).

Swiss lowland (Chamau 2006–2007)

Leaf water potential predawn (Ψ_p) and midday (Ψ_m), CO_2 assimilation at midday (A_n) and stomatal conductance at midday (g_s) were recorded for the gramineae species, *Phleum pratense*, at Chamau in 2006 (Fig. 3a, c, e, g) and 2007 (Fig. 3b, d, f, h). In 2006, Ψ_p of control plants remained above −0.45 MPa throughout the experiment, whereas in stressed plants values reached a minimum of −0.78 MPa at the end of the drought experiment (day 227). This was significantly lower than Ψ_p of control plants at

Table 2 Effect of the artificial drought period and the recovery phase (r) on the soil water potential at the three sites in 2007

	Soil water potential (kPa)			
	Control		Drought	
Depth (cm):	15	30	15	30
Day of the year				
Chamau				
130	−9	−6	−15	−11
143	−12	−16	−149	−96
165	−15	−15	−185	−140
180	−7	−1	−184	−156
208 r	−11	−2	−20	−1
218 r	−18	−15	−26	−20
248 r	−16	−12	−18	−15
Früebüel				
138	−4	−3	−6	−12
144	−14	−2	−62	−56
170	−3	−1	−166	−132
198	−4	−2	−189	−173
226 r	−14	−1	−16	0
249 r	−7	−3	−6	0
Alp Weissenstein				
178	−5		−7	
193	−7		−60	
212	−30		−138	
235	−11		<−199	
249 r	−20		−26	
276 r	−10		−11	

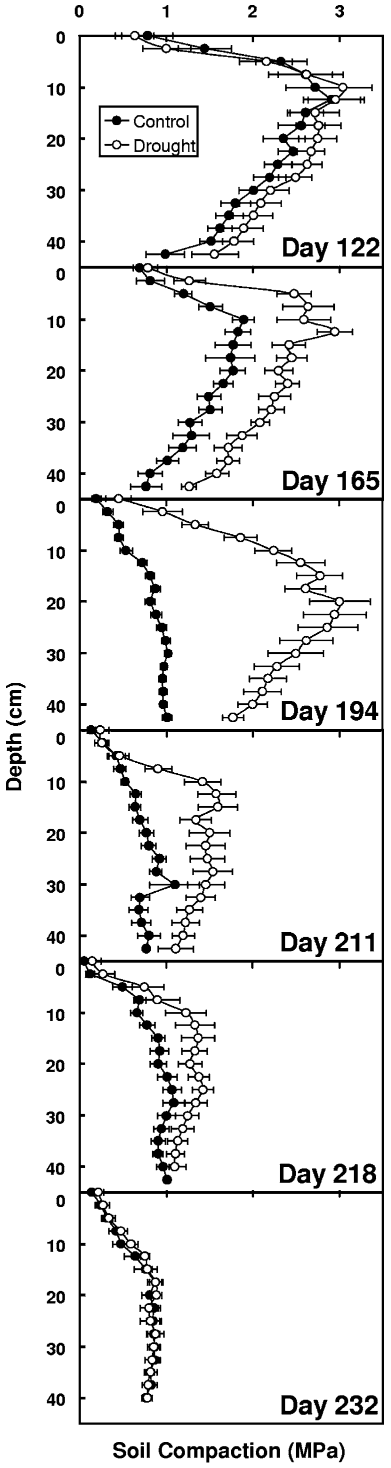

Fig. 2 Changes in soil compaction at Chamau in 2007 during the artificial drought and the recovery phase. Drought treatment started on May 2 (day 122 of the year) until July 10 (day 191 of the year). The recovery phase started on July 10. Means and standard errors are given (*n* = 4)

that date (−0.22 MPa, Fig 3a). Ψ_p had completely recovered after 20 days (day 248). In 2007, Ψ_p was also significantly lower in drought stressed plants (−0.31 MPa) than in control plants (−0.10 MPa) at the end of the artificial drought (day 180, Fig. 3b). Ψ_p had completely recovered after 17 days (day 208). Ψ_m did not show any significant differences between control and stressed plants in 2006 (Fig. 3c). The only significant difference for Ψ_m was found in 2007 (day 165). The values were not significantly different between control and drought plots at the end of the drought treatment (day 180) and during the recovery phase (Fig. 3d).

A_n was stable in control plants during the experiment in 2006 with values around 16.5 μmol CO_2 m^{-2} s^{-1} (Fig. 3e). A_n was 31% lower in stressed plants than in control plants at the end of the drought period (day 180). A_n had fully recovered after 20 days (day 248). The artificial drought in 2007 was also characterized by a gradual decline of A_n in stressed plants and showed a significant decrease (32% lower in stressed than in control plants) at the end of the drought treatment (day 180) (Fig. 3f). A_n had completely recovered after 17 days (day 208). In stressed plants, g_s decreased in parallel with A_n in both years during the artificial drought (Fig 3g, h). g_s was 31 and 40% lower

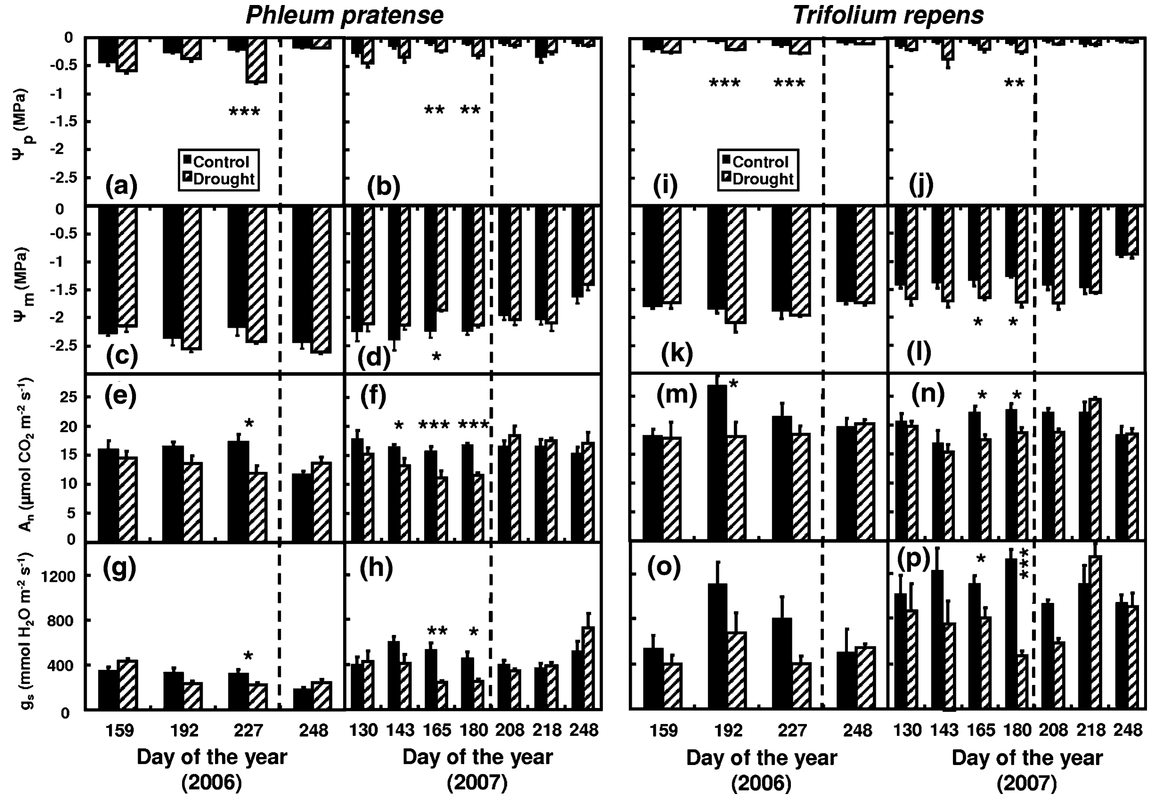

Fig. 3 Effect of drought on pre-dawn leaf water potential (Ψ_p), leaf water potential at midday (Ψ_m), CO_2 assimilation rate at midday (A_n) and stomatal conductance at midday (g_s) of *Phleum pratense* and *Trifolium repens* at Chamau during the growing seasons 2006 and 2007. The *broken line* indicates the beginning of the recovery phase (day 229 in 2006, day 191 in 2007). Means and standard errors ($n = 4$–5) are given. Significant differences are indicated by * for $0.05 \geq P > 0.01$, ** for $0.01 \geq P > 0.001$ and *** for $P \leq 0.001$

in stressed than in control plants in 2006 (day 227) and in 2007 (day 180), respectively. The recovery was complete after 20 days in 2006 (day 248) and after 17 days in 2007 (day 208).

In the legume species, *Trifolium repens*, Ψ_p in control conditions ranged between −0.1 and −0.2 MPa in 2006 and between −0.1 and −0.15 MPa in 2007 (Fig. 3i, j). Ψ_p was significantly lower for stressed plants in 2006 (day 227) and in 2007 (day 180) at the end of the artificial drought. Values of Ψ_p for stressed plants were quickly restored to values of control plants during the recovery phase. Ψ_m of control and stressed plants remained unchanged over the artificial drought in 2006 (Fig. 3k). In 2007, the effect of drought was more pronounced on Ψ_m (day 165 and 180, Fig. 3l). Ψ_m was restored after 17 days of recovery (day 208).

In 2006, A_n was not significantly affected by the treatment at the end of the artificial drought (day 227). The only significant difference was found on day 192 with a lower A_n for the water stressed plants compared to control plants (Fig. 3m). After 20 days of recovery, A_n of control and stressed plants was similar. In 2007, A_n was significantly affected by drought on day 165 and day 180 (Fig. 3n). A_n was 18% lower in stressed than in control plants at the end of the artificial drought (day 180). The recovery was complete after 27 days (day 218). In 2007, g_s was 65% lower in stressed than in control plants at the end of the drought treatment (day 180, Fig. 3p). As for A_n, the recovery phase was progressive and similar values between control and drought plants were reached after 27 days (day 218).

Swiss pre-alps (Früebüel 2006–2007)

In control plants of the gramineae species *Phleum pratense*, Ψ_p ranged between −0.34 and −0.25 MPa in 2006 and between −0.36 and −0.1 MPa in 2007 (Fig. 4a, b). The treatment difference in Ψ_p was highly significant at the end of the drought period in 2006 (day 229) and in 2007 (day 198). These differences were restored after 22 days in 2006 (day 251) and after 25 days in 2007 (day 226). Ψ_m did not show major differences between control and stressed plants in both years (Fig. 4c, d).

A_n of control plants was quite stable at values around 18.4 µmol CO_2 m^{-2} s^{-1} during the artificial drought in 2006 (Fig. 4e). Stressed plants showed a slow decrease during that period and at the end of the drought period (day 229) A_n was 31% lower in stressed plants than in

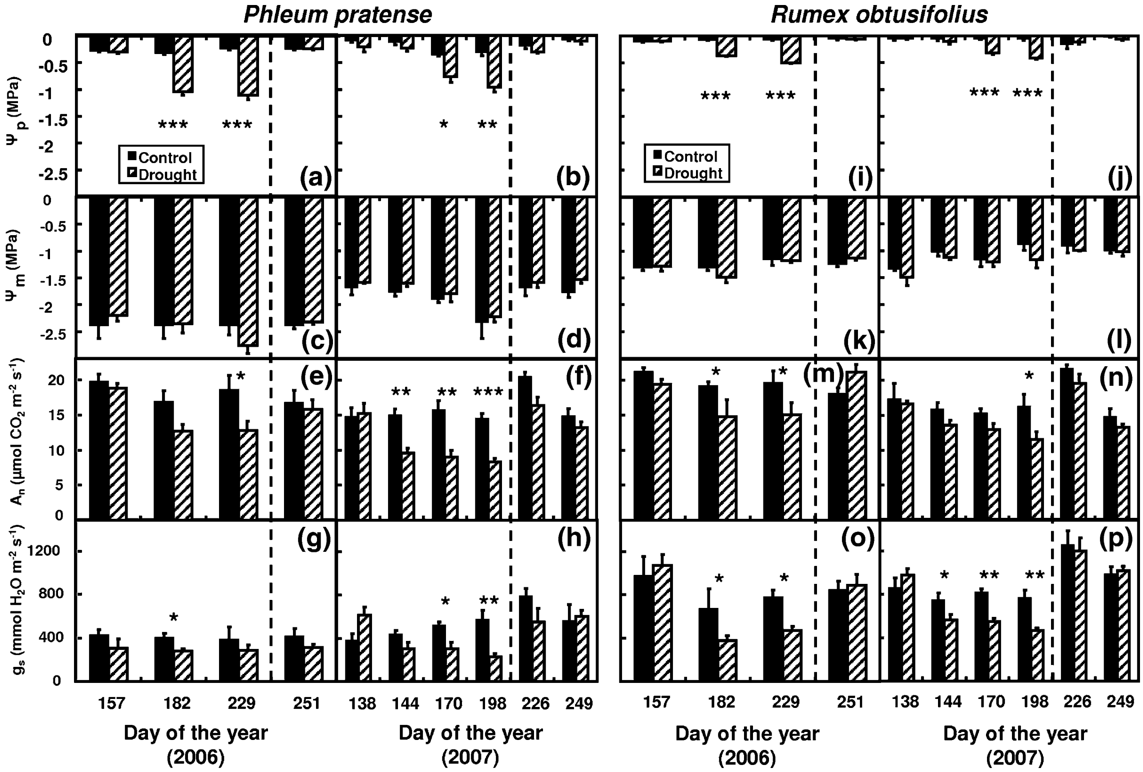

Fig. 4 Effect of drought on pre-dawn leaf water potential (Ψ_p), leaf water potential at midday (Ψ_m), CO_2 assimilation rate at midday (A_n) and stomatal conductance at midday (g_s) of *Phleum pratense* and *Rumex obtusifolius* at Früebüel during the growing seasons 2006 and 2007. The *broken line* indicates the beginning of the recovery phase (day 229 in 2006, day 201 in 2007). Means and standard errors ($n = 4$–5) are given. Significant differences are indicated by * for $0.05 \geq P > 0.01$, ** for $0.01 \geq P > 0.001$ and *** for $P \leq 0.001$

controls. Stressed plants had recovered after 22 days (day 251). A_n in stressed plants was 43% lower than controls in 2007 (Fig. 4f) and was restored during the recovery phase. The only significant difference between g_s of control and stressed plants in 2006 was found on day 182 with a lower value under drought conditions (Fig. 4g). In 2007, g_s decreased similar to A_n and was 60% lower in drought conditions than in controls (Fig. 4h). The recovery was complete after 48 days (day 249).

The forb species *Rumex obtusifolius* showed Ψ_p of control plants between −0.1 and −0.06 MPa in 2006 and 2007 (Fig. 4i, j). Ψ_p was significantly lower in drought stressed than in control plants at the end of the drought period in 2006 (day 229) and in 2007 (day 198). In both years, Ψ_p had fully recovered after 22 (day 251) and 25 days (day 226), respectively. The values of Ψ_m ranged between −0.9 and −1.5 MPa in 2006 and 2007 during the experiment and did not show significant differences between control and drought conditions (Fig. 4k, l).

A_n was significantly reduced by drought in both years. Values were 23 and 29% lower in stressed than in controls plants in 2006 (day 229) and 2007 (day 198), respectively (Fig. 4m, n). In parallel with the decline of A_n, g_s of drought plants decreased continuously in both years and was significantly different from control values at the end of the drought period (Fig. 4o, p). Stressed plants were respectively 40 and 39% lower than controls on days 229 and 198. g_s had recovered after 22 days in 2006 (day 251) and after 25 days in 2007 (day 226).

Swiss alps (Alp Weissenstein 2007)

At Alp Weissenstein, Ψ_p of the gramineae species *Alopecurus pratensis* and the forb species *Rumex alpinus* were considerably affected by drought on day 212 and day 235 (Fig. 5a, b). Stressed plants showed lower Ψ_p than controls at the end of the treatment (day 235). Ψ_m of the gramineae species ranged between −2.3 and −1.5 MPa, whereas the forb species ranged between −1.5 and −0.8 MPa during the experiment (Fig 5c, d). Both species showed a decrease of A_n under drought. The gramineae species was 32% lower in stressed than in control plants (Fig. 5e), while the forb was 42% lower in stressed plants than in controls (Fig. 5f). The decrease in A_n was paralleled by a gradual decline in g_s under drought for both species and g_s was significantly affected by drought on day 235 (Fig. 5g, h). g_s was still significantly lower in stressed plants than in

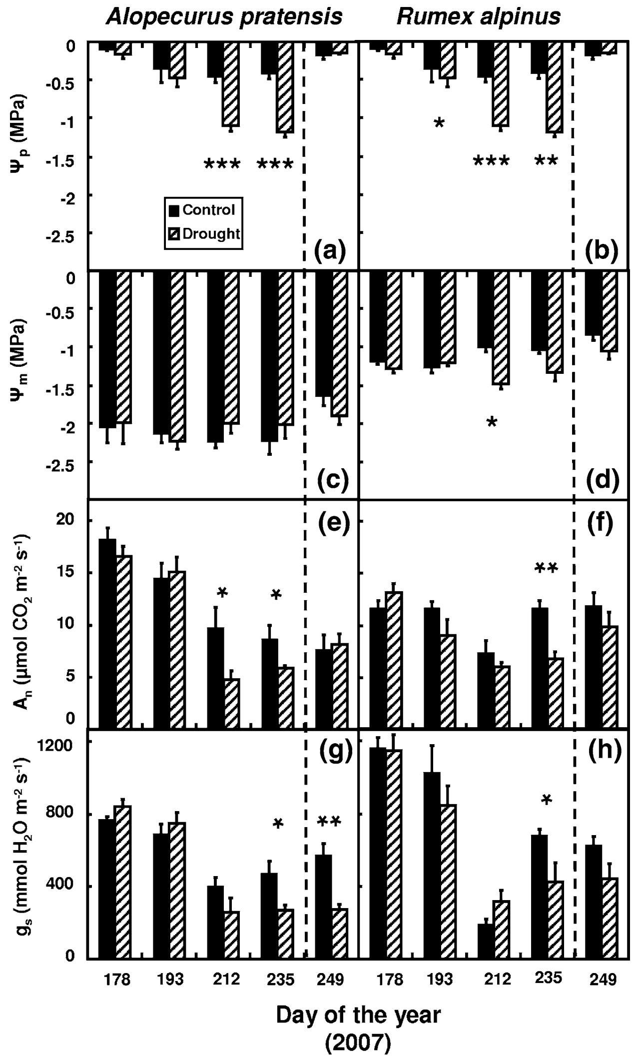

Fig. 5 Effect of drought on pre-dawn leaf water potential (Ψ_p), leaf water potential at midday (Ψ_m), CO_2 assimilation rate at midday (A_n) and stomatal conductance at midday (g_s) of *Alopecurus pratensis* and *Rumex alpinus* at Alp Weissenstein during the growing season 2007. The *broken line* indicates the beginning of the recovery phase (day 235). Means and standard errors ($n = 4$–5) are given. Significant differences are indicated by * for $0.05 \geq P > 0.01$, ** for $0.01 \geq P > 0.001$ and *** for $P \leq 0.001$

controls for *Alopecurus pratensis* but not for *Rumex alpinus* after 14 days of recovery (day 249).

Table 3 summarizes the effects of the artificial drought on all species studied for the experiments in 2006 and 2007. Ψ_p of all species was strongly affected by drought in both years, whereas Ψ_m was only significantly lower in stressed plants than in controls for *Trifolium repens* in 2006 and 2007. At the lowland site Chamau, A_n decreased in the gramineae species by about 30% in the stressed plants compared to controls in both years, while g_s declined by 40%. In 2006 the forb *Rumex obtusifolius* and the legume *Trifolium repens* did not show major differences in A_n and g_s between control and drought conditions. A_n of *Trifolium repens* was only slightly affected in 2007 but the decline by 65% of g_s in stressed plants was much higher than for the gramineae species. At the pre-Alp site Früebüel, A_n decreased in a similar manner for all species under drought conditions, though the effect was not significant for *Trifolium repens* in 2006. The decline in g_s for stressed plants was again higher for *Trifolium repens* and *Rumex obtusifolius* compared to the two gramineae species. In 2007, decreases in A_n and g_s were not markedly different between species. At the alpine site Alp Weissenstein, A_n of the gramineae *Phleum alpinum* was more reduced by drought in 2006 than the forb *Rumex alpinus* but the reduction in g_s did not really differ between the two species. In 2007, the gramineae and the forb were affected in the same manner regarding A_n and g_s.

Discussion

The individual species were investigated in long-term grasslands in the field under existing species composition and management conditions. The drought experiment in 2006 and 2007 revealed different physiological responses of the various species. First of all, these artificial drought periods resulted in limited water availability for all plants considered, as indicated by the decline of the pre-dawn leaf water potentials (Ψ_p, Table 3). At the lowland site Chamau, the plant water status decreased for all species under drought. The response of the forb *Rumex obtusifolius* and of the legume *Trifolium repens* differed from those of grasses (*Phleum pratense* and *Lolium multiflorum*). A_n and g_s decreased in parallel in the grass species whereas *R. obtusifolius* and *T. repens* did not show significant differences. These results demonstrate the regulatory function of stomata in minimizing water loss under reduced water supply by decreasing g_s. The reduced g_s might be also important in maintaining hydraulic conductance in the plant and for the avoidance of embolism (Aranda et al. 2005). It has been shown previously that *R. obtusifolius* can grow quite fast under drought (Pino et al. 1995). The tap root system of this species can reach deep soil layers down to 2.5 meters (Kutschera et al. 1992). Therefore this species may access water from deeper soil layers which is not available to other plant species with smaller root systems like grasses, under drought (Zaller 2007). Results from the physiological analyses reported here were consistent with previously published findings indicating that *R. obtusifolius* was able to increase its above-ground biomass production under drought conditions in 2006, as a consequence of a competitive advantage of this species over the others (Gilgen et al. 2010). In 2006, the higher leaf water potentials (Ψ_p and Ψ_m) of *R. obtusifolius* compared to the

Table 3 Summary of effects of artificial drought after 6–10 weeks of treatment on all species selected for the experiments in 2006 and 2007

	Ψ_p (MPa)			Ψ_m (MPa)			A_n (μmol CO_2 m^{-2} s^{-1})			g_s (mmol H_2O m^{-2} s^{-1})		
	Control	Drought	$\Delta\Psi_p$	Control	Drought	$\Delta\Psi_m$	Control	Drought	ΔA_n (%)	Control	Drought	Δg_s (%)
Chamau 2006												
Phleum pratense	−0.22 ± 0.01	−0.78 ± 0.03	−0.56***	−2.17 ± 0.14	−2.42 ± 0.03	−0.25	17.2 ± 1.3	11.9 ± 1.3	−31*	325.0 ± 30.8	224.0 ± 17.3	−32*
Lolium multiflorum	−0.21 ± 0.03	−0.70 ± 0.05	−0.49***	−1.94 ± 0.08	−2.20 ± 0.10	−0.26	18.8 ± 0.9	12.6 ± 0.6	−33***	372.6 ± 33.6	216.2 ± 38.3	−42*
Trifolium repens	−0.13 ± 0.02	−0.26 ± 0.01	−0.13***	−1.88 ± 0.14	−1.96 ± 0.03	−0.08	21.5 ± 2.3	18.5 ± 1.4	−14	799.4 ± 195.0	402.0 ± 71.4	−50
Rumex obtusifolius	−0.07 ± 0.01	−0.25 ± 0.01	−0.18***	−1.44 ± 0.06	−1.52 ± 0.08	−0.08	19.8 ± 1.0	18.8 ± 1.4	−5	797.0 ± 119.5	514.6 ± 53.6	−35
Chamau 2007												
Phleum pratense	−0.11 ± 0.01	−0.31 ± 0.04	−0.20***	−2.24 ± 0.07	−2.13 ± 0.05	0.11	16.8 ± 0.4	11.6 ± 0.5	−31***	453.4 ± 56.2	249.4 ± 26.0	−45*
Lolium multiflorum	−0.16 ± 0.03	−0.31 ± 0.04	−0.15*	−1.90 ± 0.08	−1.94 ± 0.14	−0.04	19.3 ± 1.0	12.8 ± 1.3	−34**	390.9 ± 32.6	238.0 ± 45.0	−39*
Trifolium repens	−0.09 ± 0.01	−0.24 ± 0.04	−0.15**	−1.27 ± 0.02	−1.73 ± 0.09	−0.46*	22.7 ± 1.0	18.6 ± 0.9	−18*	1,325.8 ± 84.8	469.2 ± 42.0	−65***
Früebüel 2006												
Phleum pratense	−0.25 ± 0.02	−1.11 ± 0.08	−0.86***	−2.39 ± 0.18	−2.76 ± 0.14	−0.37	18.6 ± 3.0	12.8 ± 1.3	−31*	384.1 ± 114.4	284.5 ± 50.7	−26
Alopecurus pratensis	−0.22 ± 0.05	−1.24 ± 0.03	−1.02***	−2.42 ± 0.14	−2.80 ± 0.13	−0.38	15.9 ± 1.4	12.8 ± 0.4	−19*	370.8 ± 63.2	275.8 ± 26.7	−26*
Trifolium repens	−0.11 ± 0.01	−0.62 ± 0.04	−0.51***	−1.50 ± 0.05	−1.93 ± 0.11	−0.43*	19.1 ± 3.0	14.3 ± 1.1	−25	941.0 ± 279.8	357.8 ± 70.3	−62*
Rumex obtusifolius	−0.07 ± 0.01	−0.50 ± 0.02	−0.43***	−1.16 ± 0.12	−1.17 ± 0.04	−0.01	19.6 ± 1.7	15.1 ± 1.7	−23*	780.0 ± 63.3	470.3 ± 34.1	−40*
Früebüel 2007												
Phleum pratense	−0.11 ± 0.01	−0.31 ± 0.04	−0.20**	−2.34 ± 0.29	−2.23 ± 0.10	0.11	14.5 ± 0.7	8.3 ± 0.5	−43***	575.8 ± 81.3	230.0 ± 31.0	−60**
Alopecurus pratensis	−0.74 ± 0.09	−1.60 ± 0.04	−0.86***	−2.34 ± 0.25	−2.09 ± 0.27	0.25	12.2 ± 1.1	7.7 ± 1.0	−37*	542.9 ± 50.9	259.8 ± 26.5	−52**
Rumex obtusifolius	−0.06 ± 0.02	−0.41 ± 0.03	−0.35***	−0.88 ± 0.11	−1.17 ± 0.14	−0.29	16.3 ± 1.7	11.5 ± 1.2	−29*	768.0 ± 69.8	467.8 ± 21.3	−39**
Alp Weissenstein 2006												
Phleum alpinum	−0.19 ± 0.03	−0.72 ± 0.09	−0.53***	−2.02 ± 0.07	−2.05 ± 0.08	−0.03	11.8 ± 0.6	6.9 ± 1.2	−42**	482.9 ± 34.3	258.4 ± 32.9	−46**
Rumex alpinus	−0.08 ± 0.01	−0.57 ± 0.04	−0.49***	−1.46 ± 0.08	−1.50 ± 0.07	−0.04	10.4 ± 0.5	7.7 ± 0.5	−26**	541.4 ± 45.9	270.6 ± 39.7	−50**
Alp Weissenstein 2007												
Alopecurus pratensis	−0.40 ± 0.07	−1.19 ± 0.07	−0.79***	−2.24 ± 0.17	−2.01 ± 0.19	0.23	8.6 ± 1.4	5.9 ± 0.3	−32*	471.9 ± 66.2	266.7 ± 30.9	−43*
Rumex alpinus	−0.10 ± 0.03	−0.68 ± 0.16	−0.58*	−1.05 ± 0.05	−1.33 ± 0.12	−0.28	11.6 ± 0.7	6.8 ± 0.6	−42**	679.5 ± 33.5	423.3 ± 108.1	−38*

$\Delta\Psi_p$ and $\Delta\Psi_m$ represent the differences between drought and control values in MPa at the end of the drought period, while ΔA_n and Δg_s are expressed in % of the control values. The significant differences are indicated by * for $0.05 \geq P > 0.01$, ** for $0.01 \geq P > 0.001$ and *** for $P \leq 0.001$

Ψ_p pre-dawn leaf water potential, Ψ_m midday leaf water potential, A_n CO_2 assimilation rate at midday, g_s stomatal conductance at midday grass species support this hypothesis. *T. repens* is well known to be sensitive and less tolerant to drought than several other perennial species when grown in pasture mixture due to its shallow, less extensive root system and earlier leaf senescence (Whitehead 1983; Thomas 1984; Guobin and Kemp 1992; Brink and Pederson 1998). However, the capacity of *T. repens* to reach water from deeper soil reserves than co-occurring some other species has also been reported (Johns and Lazenby 1973; Guckert et al. 1993), especially when grown together with *Lolium perenne* (Grieu et al. 2001). As *R. obtusifolius*, *T. repens* showed higher (less negative) Ψ_p and Ψ_m than the grass species under drought, most likely by reaching and extracting water from deeper soil layers. Besides that, the two dicotyledonous species showed similar A_n under drought and control conditions but lower g_s under drought which results in a higher intrinsic water use efficiency ($WUE = A_n/g_s$). This adjustment of the intrinsic water use efficiency under drought may represent an adaptive mechanism for these two species to prevent drought stress. The fact that *T. repens* was affected by drought at Chamau in 2007 and not in 2006 could be explained by the more severe drought (271 mm rain excluded in 2006 as compared to 403 mm in 2007). A_n and g_s of the two species recovered within 20 days indicating that no irreversible damages were caused by this drought.

Values found for soil water potential are consistent with those reported by another drought experiment in the field (Saidi et al. 2008). Previous studies have also shown that drought can increase soil compaction and reduces the water uptake ability of deep roots (Zegada-Lizarazu and Iijima 2005; Iijima et al. 2007) and also enhance root competition for existing soil water (Zegada-Lizarazu et al. 2006). As the availability of water in soil becomes a key factor limiting growth and survival of plants (Liste and White 2008), the deeper root system of *T. repens and R. obtusifolius* as compared to grasses may represent a competitive advantage to access soil water.

The observed differences concerning the drought effects in Chamau between the two dicotyledonous species *R. obtusifolius* and *T. repens* on one hand and the grasses on the other hand were not detected at the pre-Alps site Früebüel. At this site, *T. repens* did not show major differences in A_n under drought but g_s was considerably reduced. In this case, the control of g_s and thus of the water loss seems to be the major mechanism of drought tolerance for *T. repens*. The apparent drought tolerance of this species was probably related to improved intrinsic water use efficiency (Skinner 2008).

At the alpine site Alp Weissenstein both grass species (*Phleum alpinum* and *Alopecurus pratensis*) and the forb species *Rumex alpinus* showed a similar reduction in A_n and g_s under drought and suggest a stomatal down-regulation of photosynthesis. Soil compaction data at Alp Weissenstein revealed a strongly compacted soil below 15 cm depth (data not shown). Thus, a possible explanation that the species reacted in a same manner to drought could be the absence of deep root competition for water due to this excessively hard soil in the rooting zone.

In summary, the future reduction of summer precipitation, as predicted by climate models, would highly likely affect the performance (photosynthesis and water-using) of grassland species in Central Europe. Despite the fact that an increase in water use efficiency may partially compensate the reduced water availability, the negative effects of drought stress on photosynthetic performance of key species must be expected. This study indicates that the response of grassland species to reduced precipitation must be addressed in a site-specific manner, since other environmental factors (e.g. soil properties, ambient temperature) may interfere with water availability.

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References

Aranda I, Gil L, Pardos JA (2005) Seasonal changes in apparent hydraulic conductance and their implications for water use of European beech (*Fagus sylvatica* L.) and sessile oak *Quercus petraea* (Matt.) Liebl in South Europe. Plant Ecol 179:155–167

Begert M, Seiz G, Schlegel T, Musa M, Baudraz G, Moesch M (2003) Homogenisierung von Klimamessreihen der Schweiz und Bestimmung der Normwerte 1961–1990: Schlussbericht des Projekts NORM90. Veroff. MeteoSchweiz 67:1–170

Brink GE, Pederson GA (1998) White clover response to a water-application gradient. Crop Sci 38:771–775

Cai ZQ, Chen YJ, Guo YH, Cao KF (2005) Responses of two field-grown coffee species to drought and re-hydration. Photosynthetica 43:187–193

Cao MK, Woodward FI (1998) Net primary and ecosystem production and carbon stocks of terrestrial ecosystems and their responses to climate change. Glob Change Biol 4:185–198

Chaves MM, Maroco JP, Pereira JS (2003) Understanding plant responses to drought—from genes to the whole plant. Funct Plant Biol 30:239–264

Ciais P, Reichstein M, Viovy N, Granier A, Ogee J, Allard V, Aubinet M, Buchmann N, Bernhofer C, Carrara A, Chevallier F, De Noblet N, Friend AD, Friedlingstein P, Grunwald T, Heinesch B, Keronen P, Knohl A, Krinner G, Loustau D, Manca G, Matteucci G, Miglietta F, Ourcival JM, Papale D, Pilegaard K, Rambal S, Seufert G, Soussana JF, Sanz MJ, Schulze ED, Vesala T, Valentini R (2005) Europe-wide reduction in primary productivity caused by the heat and drought in 2003. Nature 437:529–533

Day KJ, John EA, Hutchings MJ (2003) The effects of spatially heterogeneous nutrient supply on yield, intensity of competition and root placement patterns in *Briza media* and *Festuca ovina*. Funct Ecol 17:454–463

Easterling DR, Meehl GA, Parmesan C, Changnon SA, Karl TR, Mearns LO (2000) Climate extremes: observations, modeling, and impacts. Science 289:2068–2074

Flexas J, Bota J, Galmes J, Medrano H, Ribas-Carbo M (2006) Keeping a positive carbon balance under adverse conditions: responses of photosynthesis and respiration to water stress. Physiol Plantarum 127:343–352

Frei C, Scholl R, Fukutome S, Schmidli R, Vidale PL (2006) Future change of precipitation extremes in Europe: intercomparison of scenarios from regional climate models. J Geophys Res Atmos 111:D06105

Gallé A, Feller U (2007) Changes of photosynthetic traits in beech saplings (Fagus sylvatica) under severe drought stress and during recovery. Physiol Plant 131:412–421

Gilgen AK, Buchman N (2009) Responses of temperate grasslands at different altitudes to simulated summer drought differed but scaled with annual precipitation. Biogeosciences 6:2525–2539

Gilgen AK, Signarbieux C, Feller U, Buchmann N (2010) Competitive advantage of *Rumex obtusifolius* L. might increase in intensively managed temperate grasslands under drier climate. Agric Ecosyst Environ 135:15–23

Grieu P, Lucero DW, Ardiani R, Ehleringer JR (2001) The mean depth of soil water uptake by two temperate grassland species over time subjected to mild soil water deficit and competitive association. Plant Soil 230:197–209

Guckert A, Robin C, Grieu P, Gras F (1993) Influence du déficit hydrique sur le trèfle blanc. Fourrages 135:369–381

Guobin L, Kemp DR (1992) Water stress affects the productivity, growth components, competitiveness and water relations of *Phalaris* and white clover growing in mixed pasture. Aust J Agric Res 43:659–672

Hiller R, Zeeman MJ, Eugster W (2008) Eddy-covariance flux measurements in the complex terrain of an alpine valley in Switzerland. Bound Lay Meteorol 127:449–467

Houghton J (1995) The roles of carbon-dioxide and water-vapor in warming and cooling the Earths troposphere—comment. Spectrochim Acta A 51:1391–1392

Iijima M, Morita S, Zegada-Lizarazu W, Izumi Y (2007) No-tillage enhanced the dependence on surface irrigation water in wheat and soybean. Plant Prod Sci 10:182–188

Johns GG, Lazenby A (1973) Defoliation, leaf area index, and water use of 4 temperate pasture species under irrigated and dryland conditions. Aust J Agric Res 24:483–795

Kahmen A, Perner J, Buchmann N (2005) Diversity-dependent productivity in semi-natural grasslands following climate perturbations. Funct Ecol 19:594–601

Karatassiou M, Noitsakis B, Koukoura Z (2009) Drought adaptation ecophysiological mechanisms of two annual legumes on semi-arid Mediterranean grassland. Sci Res Essays 4:493–500

Kerr RA (2001) Climate change—it's official: humans are behind most of global warming. Science 291:566–566

Kirschbaum MUF (1988) Recovery of photosynthesis from water-stress in *Eucalyptus pauciflora*. A process in 2 stages. Plant Cell Environ 11:685–694

Kutschera L, Lichtenegger E, Sobotik M (1992) Wurzelatlas mitteleuropäischer Grünlandpflanzen. Gustav Fischer, Stuttgart

Liste HH, White JC (2008) Plant hydraulic lift of soil water—implications for crop production and land restoration. Plant Soil 313:1–17

Meehl GA, Tebaldi C (2004) More intense, more frequent, and longer lasting heat waves in the 21st century. Science 305:994–997

Meehl GA, Washington WM, Arblaster JM, Bettge TW, Strand WG (2000) Anthropogenic forcing and decadal climate variability in sensitivity experiments of twentieth- and twenty-first-century climate. J Clim 13:3728–3744

Osmond CB, Austin MP, Berry JA, Billings WD, Boyer JS, Dacey JWH, Nobel PS, Smith SD, Winner WE (1987) Stress physiology and the distribution of plants. Bioscience 37:38–48

Pino J, Haggar RJ, Sans FX, Masalles RM, Hamilton RNS (1995) Clonal growth and fragment regeneration of *Rumex obtusifolius* L. Weed Res 35:141–148

Roth K (2006) Bodenkartierung und GIS-basierte Kohlenstoffinventur von Graslandböden: Untersuchungen an den ETH-Forschungsstationen Chamau und Früebüel (ZG, Schweiz). Diploma thesis, University of Zurich, Switzerland

Saidi A, Ookawa T, Motobayashi T, Hirasawa T (2008) Effects of soil moisture conditions before heading on growth of wheat plants under drought conditions in the ripening stage: insufficient soil moisture conditions before heading render wheat plants more resistant to drought during ripening. Plant Prod Sci 11:403–414

Schär C, Vidale PL, Lüthi D, Frei C, Häberli C, Liniger MA, Appenzeller C (2004) The role of increasing temperature variability in European summer heatwaves. Nature 427:332–336

Seneviratne SI, Lüthi D, Litschi M, Schär C (2006) Land-atmosphere coupling and climate change in Europe. Nature 443:205–209

Skinner RH (2008) Yield, root growth, and soil water content in drought-stressed pasture mixtures containing chicory. Crop Sci 48:380–388

Solomon AM, Kirilenko AP (1997) Climate change and terrestrial biomass: what if trees do not migrate!. Global Ecol Biogeogr 6:139–148

Stampfli A, Zeiter M (2004) Plant regeneration directs changes in grassland composition after extreme drought: a 13-year study in southern Switzerland. J Ecol 92:568–576

Thomas H (1984) Effects of drought on growth and competitive ability of perennial ryegrass and white clover. J Appl Ecol 21:591–602

Whitehead DC (1983) The influence of frequent defoliation and of drought on nitrogen and sulfur in the roots of perennial ryegrass and white clover. Ann Bot Lond 52:931–934

Zaller JG (2007) Effect of patchy distribution of soil nutrients on root morphology and biomass allocation of selected grassland species: experimental approach. Pol J Ecol 55:731–747

Zavalla MA (2004) Integration of drought tolerance mechanisms in Mediterranean sclerophylls: a functional interpretation of leaf gas exchange simulators. Ecol Model 176:211–226

Zegada-Lizarazu W, Iijima M (2005) Deep root water uptake ability and water use efficiency of pearl millet in comparison to other millet species. Plant Prod Sci 8:454–460

Zegada-Lizarazu W, Izumi Y, Iijima M (2006) Water competition of intercropped pearl millet with cowpea under drought and soil compaction stresses. Plant Prod Sci 9:123–132