



Impacts of drought stress on water relations and carbon assimilation in grassland species at different altitudes



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ABSTRACT

Grassland is an important ecosystem type which is not only used agriculturally, but also covers sites which cannot be used for other purposes, e.g. in very steep locations or above timberlines. Prolonged summer droughts in the mid-term future, as are predicted for Central Europe, are expected to have a major impact on such ecosystems. To address this topic, rainfall exclusion via shelters was performed on three grassland sites at different altitudes (393, 982 and 1978 m above sea level) in Switzerland. Diurnal drought treatment effects were studied at each study site on a completely sunny day towards the end of an 8–10 week shelter period. Ecophysiological parameters including gas exchange (A_n , g_s and intrinsic WUE) and chlorophyll a fluorescence (F_v/F_m , Φ_{PSII} and NPQ) were considered for several species. The lowland and the Alpine field site were more strongly affected by soil drought than the pre-Alpine site. At all sites, grasses showed different patterns of reductions in stomatal conductance under soil drought compared to legumes and forbs. In addition, grasses were significantly more affected by reductions in assimilation rates at all sites. Time courses of reductions in assimilation rates relative to controls differed between species at the Alpine site, as some species showed reduced assimilation rates at this site in the early morning. Thus, similar rainfall exclusion treatments can trigger different reactions in various species at different sites, which might not become obvious during mere midday measurements. Overall, results suggest strong impacts of prolonged summer drought on grassland net photosynthesis especially at the Alpine site and, within sites, for grasses

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1. Introduction

Anthropogenic climate change is relevant world-wide and these changes are intensively studied by climate modelers. Prolonged summer droughts and a higher number of heat waves have been projected for Southern and Central Europe, including Switzerland, by climate models (Fischer and Schär, 2010; Frei et al., 2006; IPCC, 2007; Schär et al., 2004). Results suggest a different rainfall pattern in the mid-term future, with less rainfall during summer months but a comparable annual precipitation. Both reduced summer precipitation and heat waves lead to an increased drought risk. Consequences may be expected in terms of yield (Boyer, 1982) and species composition (Levine et al., 2010; Morecroft et al., 2004), leading to economic and ecological implications. Furthermore, altered rainfall patterns themselves can reduce assimilation rates and stomatal conductance during the growth period (Fay et al.,

2002). Therefore, drought impacts on vegetation and lately on temperate grassland have been of great interest (Beierkuhnlein et al., 2011; Gilgen et al., 2010; Gilgen and Buchmann, 2009; Jentsch et al., 2011; Signarbieux and Feller, 2012, 2011).

Drought impacts on plants differ with endogenous factors (e.g. stomatal size and density, root structures or plant height) and with environmental conditions (e.g. air and soil temperature, air humidity and photosynthetically active radiation (PAR)). Thus, diurnal patterns of plant performance under drought are of importance. Specifically, some trees show an enhanced midday depression of the assimilation rate and of stomatal conductance under drought (Epron et al., 1992; Haldimann et al., 2008; Lüttge and Hertel, 2009). In grassland, on the other hand, assimilation rate and stomatal conductance have been found to parallel PAR. Reachable maximum values were reported to be reduced during a drought period, but highest assimilation rates were still observed at midday (Valentini et al., 1995). Thus, midday values might not give all necessary information to clarify species behavior under drought, since drought effects are not similarly related to PAR for all species. Only higher time resolution data of assimilation rates and water loss under drier conditions in the field will contribute to the understanding of

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short- and long-term species behavior and overall effects on biomass. Furthermore, diurnal measurements are of interest for modelers, when no continuous data is available. This has been stated in a study that found PAR, temperature and soil moisture to be of importance for diurnal and seasonal variation of CO₂ fluxes in a grassland (Risch and Frank, 2010). Thus, diurnal courses deliver insights into species performances under drought stress as a daily integral. They allow additional conclusions on top of the knowledge about midday performances (Signarbieux and Feller, 2012, 2011).

Diurnal variations in gas exchange due to drought can be either physical, as stress increases diffusional limitation, or biochemical, namely when changes in the photosynthetic apparatus occur (Centritto et al., 2003). Whereas effects of a less severe drought event mostly include physical limitations (Flexas and Medrano, 2002) or rapid alterations in gene expression (Bohnert and Sheveleva, 1998; Chaves et al., 2003, 2002), irreversible changes in the biochemical apparatus appear only during more severe stress (Flexas and Medrano, 2002; Loreto and Centritto, 2008). These can include chronic photoinhibition (Osmond and Grace, 1995) or metabolic changes (Lawlor, 2002; Lawlor and Cornic, 2002), which both lead to constantly reduced assimilation rates that cannot be rapidly overcome by eliminating diffusional limitations. Chronic photoinhibition is best detected via chlorophyll fluorescence (Krause and Weis, 1991; Maxwell and Johnson, 2000). At daytimes when physical limitations might be small or absent due to rather favorable environmental conditions, photoinhibitory effects could still be seen via decreased assimilation rates. Thus, the integral over the whole day is relevant for the overall performance of species under given environmental conditions and diurnal variations allow a more comprehensive analysis of drought effects. Considering the findings mentioned above, the investigations reported here were based on the hypothesis that time courses of drought effects differ between species as well as between field sites. Thus the relative contribution of individual species to the overall grassland net photosynthesis was supposed to change throughout the day. If so, then time courses should be considered for an overall estimation of drought effects in grasslands. This field study will thus allow a more detailed insight into grassland performance under reduced summer precipitation as it must be expected in the course of climate change.

2. Materials and methods

2.1. Field sites and experimental setup

Drought effects at three different field sites at different altitudes in Switzerland were studied in detail. Site L (Chamau, low altitude, 393 m) is intensively managed grassland with up to six cuts per year. The pre-Alpine site M (Früebüel, middle altitude, 982 m) is intermediately managed with two cuts per year and the Alpine site H (Alp Weissenstein, high altitude, 1978 m) is grazed. However, at site H the experimental area was cut once at the end of the season, since grazing was not compatible with the experimental setup. Sites L and M are located within the canton of Zug, whereas site H is located in the canton Grisons. Mean annual precipitation recorded by nearby MeteoSwiss stations between 1973 and 2011 were 1111 mm for site L (station Cham), 1518 mm for site M (station Zugerberg) and 975 mm for site H (station Latsch). All three field sites differ in their soil types, which have been classified as Cambisol at site L, Gleysol at site M (Roth, 2006) and humous sandy loam at site H (Schärer, unpublished). The onset of the vegetation periods differs at the three sites and is in April, May and June, respectively. The growing seasons end either in October (sites L and M) or September (site H). The treatment was achieved through rainfall exclusion with rain shelters covering an area of

3 m × 3.5 m, which is a well-established method (Gilgen et al., 2010; Gilgen and Buchmann, 2009; Kahmen et al., 2005; Signarbieux and Feller, 2011). Transparent plastic foils (200 μm; Gewächshausfolie UV B-window, folitec, Westerbürg, Germany) with a specified light permeability of 90% were placed over permanently installed steel frames. Rain shelters were tunnel-shaped, with the open sites oriented towards the main wind direction to minimize temperature effects. The duration of exclusion aimed at achieving severe drought conditions, based on projections of reduced summer precipitation by regional climate models under the A1B scenario (IPCC, 2007). At site L, rain shelters were established in 2010, at site M rain shelters were at the same place in their seventh year and at site H the treatment was applied for the third time. Five to six treatment and control plots were installed at each field site. Control plots received natural rainfall. The core area used for measurements was 2 m long and 1 m wide in order to make sure that no incoming rainfall interfered with the analyses. Diurnal measurements took place at sunny days towards the end of the treatment in the middle of vegetation periods. At site L this was the day of the year (DOY) 179, at site M DOY 213 and at site H DOY 222. The duration of rain exclusion, the cutting frequency and the measurement days are illustrated (Fig. 1).

2.2. Soil moisture

Soil moisture was assessed at measurement days with permanently installed soil moisture sensors (Watermark Sensor, Irrrometer Inc., Riverside, CA, USA). Measurements took place in three to four randomly assigned plots at 15 cm and 30 cm depth at all sites plus at 40 cm depth at site L.

2.3. Species considered

Species were selected concerning abundance and possibilities of inter-site comparisons and included white clover (*Trifolium repens*) and two grasses at site L (*Lolium multiflorum*, *Phleum pratense*) and at site M (*Agrostis stolonifera*, *P. pratense*). At site H site red clover (*Trifolium pratense*), a grass species (*Trisetum flavescens*), and two forbs (*Rumex alpinus*, *Alchemilla vulgaris*) were taken into account. All ecophysiological measurements were performed on youngest fully expanded leaves.

2.4. Ecophysiological analyses

Predawn (Ψ_{PD}) and midday (Ψ_M) leaf water potentials were measured for three replicates per species and treatment at each field site with a Scholander pressure chamber (SKPM, Skye Instruments Ltd, Powys, UK). Measurements took place before sunrise (5–6 a.m.) and at midday (12–1 p.m.), respectively.

Net assimilation rate (A_n ; $\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$) and stomatal conductance (g_s ; $\text{mmol H}_2\text{O m}^{-2} \text{ s}^{-1}$) were measured using a portable photosynthesis measuring device (CIRAS 1, PP Systems, Hitchin, UK) connected to a broad leaf cuvette (PLC 6). Measurements were taken at 385 ppm CO₂ (supplied from a CO₂ cartridge), ambient light and ambient temperature. All measurements included three to four replicates. Intrinsic water use efficiency (WUE) represents the quotient A_n/g_s .

The chlorophyll-a-fluorescence parameters potential (F_v/F_m) and effective (Φ_{PSII}) quantum efficiency of photosystem II as well as non-photochemical quenching (NPQ) were calculated according to Maxwell and Johnson (2000). Underlying parameters were determined with the saturation pulse method using a pulse amplitude modulated fluorometer connected to a leaf clip holder (PAM-2000, Heinz Walz GmbH, Effeltrich, Germany). Measurements on three to four replicates were first done in the light and after a darkening period of 20 min the potential quantum yield was assessed on the same leaf area in

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