Leaf and ecosystem response of mountain grassland gas exchange to soil water availability

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Abstract

The response of CO_2 and H_2O exchange of a mountain grassland to natural fluctuations of soil water content (SWC) was evaluated during 2001–2009. The physiological response of mountain grassland species to drought was explored in a laboratory experiment. The natural occurrence of dry periods did not lead to substantial reductions in net ecosystem gas exchange. Laboratory experiments confirmed that the investigated plant species are insensitive to soil drying until very low SWCs, which never occurred under field conditions, are reached. The investigated mountain grassland contributes to recession in stream flow during dry periods with negative consequences for down-stream water users.

Keywords: climate change, drought, photosynthesis, evapotranspiration, montane ecosystem

1 Introduction

In the greater Alpine region (GAR) a comprehensive analysis of 200 years of precipitation data (Brunetti et al. 2006) indicates a trend towards an increase in total precipitation in the northern and a highly significant decrease in the southern part. For both regions, a shift in rainfall contribution, from summer and autumn to winter and spring is observed. While regional climate change scenarios regarding the GAR are still highly uncertain (Smiatek et al. 2009), projected precipitation trends suggest further reductions in summertime precipitation (Rotach et al. 1997; Smiatek et al. 2009). Exacerbated by increasing temperatures (Calanca et al. 2006), a limited soil water supply in the GAR may strongly influence rates of carbon assimilated by plants through photosynthesis, as well as the flux of evapotranspired water (Lawlor & Cornic 2002; Loreto & Centritto 2004).

Likely due to the considerable hydrologic surplus of the Alps, also referred to as the "Water towers of Europe" (Viviroli et al. 2007), several field studies (e.g. Hammerle et al. 2008; Schmitt et al. 2010; Wohlfahrt et al. 2008) confirmed that current dry periods do not represent a limiting factor for CO_2 and water vapour exchange in mountain grasslands. Given present and projected future trends of decreasing summer precipitation (Brunetti et al. 2006; Rotach et al. 1997; Smiatek et al. 2009), it is however uncertain whether the occurrence of more severe dry periods will affect ecosystems in the Alps in the foreseeable future.

In this study we aim to assess (i) the extent to which the present-day frequency and magnitude of soil drying causes stress to mountain grasslands in the Alps, (ii) whether representative mountain forb and graminoid plant species exhibit different degrees of sensitivity to progressive soil water shortage, and (iii) the vulnerability of mountain grasslands to reductions in summertime precipitation projected for the Alps. To this end laboratory leaf gas exchange measurements of typical mountain forb and graminoid plant species collected during a controlled soil drying experiment are combined with a 9-year record of eddy covariance net ecosystem CO_2 and H_2O flux measurements from a mountain grassland in Austria.

2 Methods

The study site is located near Neustift (47° 07' N, 11° 19' E) in the Stubai Valley (Austria) in the montane altitudinal zone at an elevation of 970 m a.s.l. The average annual temperature is 6.5 °C and average annual precipitation amounts to 852 mm. The vegetation has been classified as a Pastinaco-Arrhenatheretum, the soil as a Fluvisol (FAO classification) and is approximately 1 m deep. Below a thin (0.001 m) organic layer, an A horizon, with an organic volume fraction of approximately 14%, extends down to 0.02 m, followed by the B horizon, which is best described as a (sandy) loam. Roots reach down to 0.5 m, but 80% of them are concentrated in the upper 0.13 m of the soil. The site is managed as a hay meadow and is cut three times per year, typically by early June, beginning of August and the end of September.

Seeds of *Trifolium pratense* L., *Dactylis glomerata* L., *Ranunculus acris L., Taraxacum officinalis* Weber ex F.H.Wigg., four species that make up a major fraction of the local vegetation, were collected at the study site, germinated and grown to maturity in the glasshouse. Leaf gas exchange measurements (Von Caemmerer & Farquhar 1981) were collected from 5 ± 1 different plants for each of the investigated species using a commercial leaf gas exchange system (Li-6400, Li-Cor, Lincoln, NE, USA). Progressive soil water shortage was induced by withholding water and soil water content (SWC) of every single pot (at 0.05 m depth) was routinely measured before leaf gas exchange measurements using a soil water sensor (WET-1, Eijkelkamp **Agrisearch Equipment BV** Giesbeek, The Netherlands). When the measured SWC approached minimum values (< 0.01 m^3 m^{-3}) pots were re-watered to full capacity.

Eddy covariance flux measurements at this site began in 2001 and measurements continue as of this writing. Within this paper data from the growing seasons 2001-2009 are presented. Net ecosystem CO_2, latent and sensible energy exchange were measured by the eddy covariance method (Baldocchi et al. 1988) using the same instrumentation and following the procedures of the EUROFLUX project (Aubinet et al. 2000). For details regarding instrumentation and flux calculation procedures we refer to our earlier papers (Hammerle et al. 2008; Haslwanter et al. 2009; Wohlfahrt et al. 2008). In the following, negative fluxes represent transport from the atmosphere towards the surface, positive ones the reverse. Flux data acquisition was accompanied by measurements of the major physical environmental driving variables using a meteorological station.

3 Results and discussion

Precipitation amounts during the 9-year study period were quite variable (Figure 1) ranging from 582 mm (2006) to 984 mm (2002) with the average value over the period 1980–2000 amounting to 852 mm. During the main period of carbon uptake (April–September) rainfalls occurred on average each second day, or every three days if days with < 1 mm precipitation are classified as dry. Employing the latter definition, a total of 9 periods occurred with > 10 consecutive dry days. The longest dry period occurred in 2003 and lasted for 15 days. The standardized precipitation index (SPI; McKee et al. 1993) fell below –1 several times during the 9-year study period (Figure 1) indicating moderately dry conditions, once (2003) below –1.5 (severely dry) and once again (2006) even somewhat below –2 (extremely dry).

In order to minimise confounding effects, pooled net ecosystem CO_2 exchange (NEE) and evapotranspiration (ET) data from 2001–2009 have been filtered for dry sunny conditions with high evaporative demand and well-developed plant canopies, i.e. PAR > 1,500 μmol m^{-2} s^{-1}, vapour pressure deficit (VPD) > 1 kPa, no precipitation and green area index (GAI) 5-6 m^2 m^{-2}, when restrictions due to soil drying would be expected to be most evident. NEE became more negative with decreasing SWC (0.55 μmol m^{-2} s^{-1} for a 0.1 m^3 m^{-3} change in SWC, respectively), while ET declined with progressively limiting SWC (Figure 2). Linear regressions shown in Figure 2 were all significantly different from zero, however changes in SWC explained less than 5 % of the variability in the data and we thus interpret Figure 2 to indicate that no correlations exist with between ecosystem-scale CO_2 and H_2O exchange and SWC.

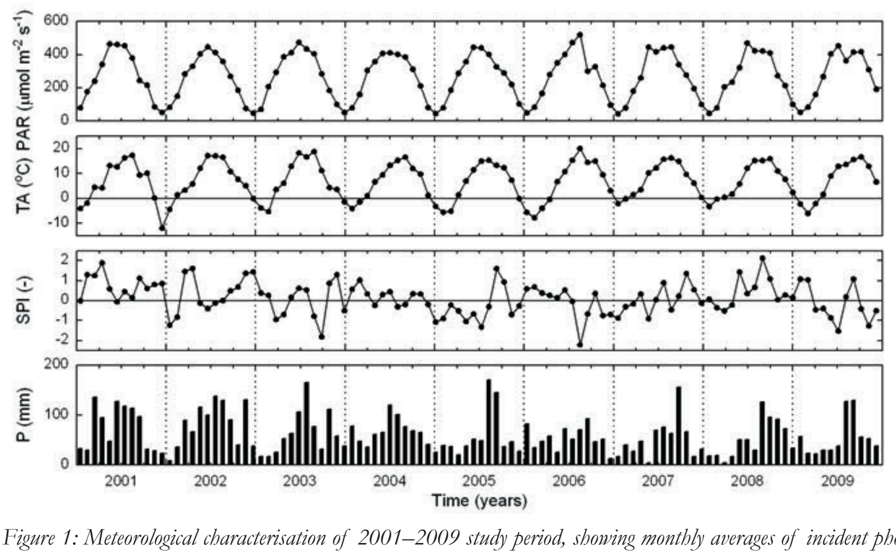

Figure 1: Meteorological characterisation of 2001–2009 study period, showing monthly averages of incident photosynthetically active radiation (PAR), air temperature (TA), the Standardised Precipitation Index (SPI; McKee et al. 1993) and monthly totals of precipitation (P).

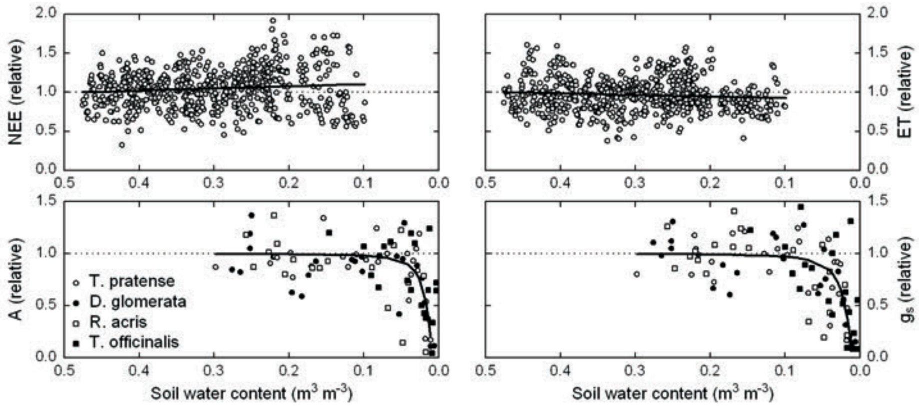

Figure 2: Daytime net ecosystem CO_2 exchange (NEE; upper left panel), evapotranspiration (ET; upper right panel), leaf net photosynthesis (A; lower left panel) and leaf stomatal conductance (g_s; lower right panel) as a function of volumetric soil water content (SWC; 0.05 m depth). Symbols in the upper panels indicate half-hourly eddy covariance measurements from the period 2001–2009 filtered for PAR (> 1,500 µmol m^{-2} s^{-1}), VPD (> 1 kPa), GAI (5–6 m^2 m^{-2}) and no precipitation. Symbols in the lower panels refer to leaf gas exchange measurements on the four investigated species. Data have been normalised with their average values at non-limiting SWC. Note that the values on the x-*axis are in descending order.*

Leaf net photosynthesis and stomatal conductance of all investigated plant species were insensitive to developing drought stress conditions until SWC approached very low values (< 0.10 m^3 m^{-3}), which resulted in a sudden drop of both net photosynthesis and stomatal conductance (Figure 2). Interestingly, our measurements revealed only minor differences between plant species when comparing the kinetic of photosynthetic carbon assimilation and stomatal conductance responses to decreasing SWC (Figure 2).

Our results highlight that the natural occurrence of moderately to extremely dry periods identified by the SPI (McKee et al. 1993) and ensuing low SWCs during the past 9 years (2001–2009) did not lead to substantial reductions of the net ecosystem CO_2 and H_2O exchange in the investigated mountain grassland ecosystem. Laboratory measurements confirmed that the four investigated key grassland plant species are insensitive to progressive drought conditions until a very low SWC is achieved, a threshold that was never reached in the field during the study period.

Our results indicate that the productivity of the investigated mountain grassland ecosystem is resilient to present-day magnitudes and durations of soil drying, but may be vulnerable to the projected increased frequency and severity of summertime dry periods (Rotach et al. 1997; Smiatek et al. 2009). Assuming typical average daily evapotranspiration rates on the order of 3 mm d^{-1} (Wieser et al. 2008) and given an active soil volume down to a depth of 0.4 m (where > 99 % of the roots are located), it can be estimated that once soil water content reaches a threshold of 0.1 m^3 m^{-3}, at least 10 additional rainless days are required before major limitations to net photosynthesis and stomatal conductance occur. This simple calculation is likely to represent an underestimation as it does not account for vertical water redistribution due to capillary rise and for higher SWCs at lower depths and may be put into perspective with the longest observed consecutive dry periods (i.e. 15 days in 2003). It is thus reasonable to speculate that soil water shortage is not going to impair the productivity of the investigated mountain grassland in the foreseeable future. As a consequence, mountain grasslands are expected to provide a negative (cooling) feedback effect on air temperature under present-day combined dry and heat episodes (Teuling et al. 2010). However, once critical low SWCs are reached, our results suggest a rapid and dramatic decline in both ecosystem CO_2 assimilation and evapotranspiration (Teuling et al. 2010). Additional drought experiments, both in the laboratory as well as in the field, are required in order to asses the response of photosynthesis and transpiration to prolonged very dry conditions in order to understand whether the results from this study can be simply extrapolated and to what extent adaptation processes may confound the reaction of plants to prolonged drought.

In conclusion, the aggressive use of water resources by the investigated grassland plant species may have important consequences for the future role of the Alps as the "water towers of Europe" (Viviroli et al. 2007). As shown by Wieser et al. (2008), grassland mountain ecosystems evapotranspire 50–60% of precipitation during wet, but up to 90% during dry years. In other words, the amount of water available for deep drainage and run-off is dramatically reduced during dry years, partially due to the observed low water use efficiency exhibited by the grassland vegetation under present-day conditions. Although river discharge from the Alps is also fuelled by run-off of water from non-grassland areas, such as glaciers (Pellicciotti et al. 2010) and forests (Teuling et al. 2010), the "water spending" strategy employed by the plant species of the investigated mountain grassland ecosystem may contribute to the recession of stream flow during dry periods and thus affect the water supply to the low-land areas surrounding the Alps (Viviroli et al. 2007; Vanham et al. 2009).

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