

Neighbourhood matters: implications of canopy structure on plant water-use strategies

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Zusammenfassung

Alpines Grasland bietet viele Ökosystemdienstleistungen (u.a. Wasserversorgung und Futterproduktion) und wird laut aktuellen Klimaszenarien in Zukunft öfter und mit intensiveren Trockenperioden konfrontiert werden. Ein Lysimeterexperiment auf dem sozio-ökologischen Langzeitforschungsstandort (LTSER) 'Stubaital' in Tirol untersucht die Reaktion auf Trockenheit von zwei unterschiedlichen Alpinen Graslandtypen. Kleinlysimeter (Smart Field lysimeters®, SFL, METER Group) wurden mit zwei Einsaatmischungen für Grasland (Dauerwiese für trockene und feuchte Lagen) bepflanzt. Sowohl bodenhydrologische Parameter als auch die stomatare Leitfähigkeit der funktionellen Gruppen wurden während einer Trockenperiode gemessen. Unter gemeinsamen Klimabedingungen und im gleichen standardisierten Boden, wiesen die beiden Graslandtypen verschiedene Wassernutzungsstrategien auf und unterschieden sich in ihrer Produktivität. Wir konnten Unterschiede in der Reaktion auf Trockenheit für die beiden Graslandtypen, für funktionelle Gruppen und innerhalb der funktionellen Gruppen nachweisen.

Schlagwörter: Smart-field-Lysimeter, Stomatare Leitfähigkeit, Klimawandel, Grünlandwirtschaft

Summary

In a future climate change scenario probabilities of drought periods in Alpine grasslands, which provide multiple ecosystem services (i.e. water provisioning and grassland productivity), will increase. To assess the reaction of Alpine grassland to drought conditions, two types of grassland seed mixtures (permanent meadow for dry and humid sites) were grown and investigated in a garden experiment at the long term socio-ecological research (LTSER) site 'Stubai Valley', Tyrol, Austria. Soil hydrology analyses were performed using high precision lysimeters (Smart Field lysimeters®, SFL, METER Group) and stomatal conductance of the main functional groups was measured during an extended drought period. Sharing a common environment and the same standardized soil, the two types of Alpine grassland showed different water-use strategies and productivity. Responses to drought revealed differences between grassland types, functional groups and even within functional groups present in both grassland types, although soil hydrology did not differ.

Keywords: Smart-field-lysimeter, stomatal conductance, climate change, grassland management

Introduction

Precipitation patterns will be modified and a change in water resources timing and amount is predictable worldwide (IPCC 2013), increasing the possibility of drought periods in Alpine grasslands, which generally have become sufficient water supply so far (van der Schrier et al. 2007). Alpine grasslands are biodiversity hotspots and provide multiple ecosystem services, which will be negatively affected by climate change, especially the ecosystem service 'forage production' (Jäger et al. (submitted)). Beyond the direct implications of water availability on biomass productivity, drought impacts on different types of Alpine grassland has been assessed and differences in water use strategies have been shown (Leitinger et al. 2015, Frenck et al. 2018), suggesting that species composition play an important role in the response to varying water supply. The composition of species in the community and the resulting functional structure adjust to varying drought conditions, optimizing water use according to different strategies and regulating the use and allocation of limiting resources (Peñuelas et al. 2004). At the individual level, water losses are controlled

by stomatal conductance, which varies among plant species depending on water availability (Silva 2015).

The importance of understanding water fluxes and the role of species composition in order to improve grassland management becomes evident. To address drought implications in Alpine grasslands, a network of automated small-scale lysimeters were used to emerge specific differences in the temporal dynamics of water fluxes of two different grassland seed mixtures (permanent meadow for dry and humid sites), as well as differences at plant functional group level, under an extended drought period. We hypothesize that water use strategies under persistent drought periods are specific for each functional group, and that different species composition will lead to a different water use strategies in Alpine grassland.

Methodology

The field site was established in the Long-Term Ecological Research (LTER) Austria site "Stubai", Neustift im Stubaital (Austria), located at the valley floor at 972 m a.s.l.

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(WGS84: 47.115833 N, 11.320556 E) in a meadow used for hay production. Investigations were carried out during part of the growing season (May-August) in the year 2018. Two grassland seed mixtures (Schwarzenberger 2018) with different plant species composition, commonly used when recultivating in two locations of the Alps which differ in their predominant climate, were cultivated. A permanent humid adapted type (type SR037), commonly used in the Stubai valley, which has a northern Central-European climate with high precipitation totals, many rainy days, and a distinct maximum of precipitation during summer with little interannual variability. The humid seed mixture was mainly composed by grasses (i.e. *Festuca pratensis*, *Festuca rubra*, *Lolium perenne*, *Poa pratensis*), legumes (*Trifolium hybridum*, *Trifolium pratense* and *Trifolium repens*) and herbs (*Lotus corniculatus*). Contrastingly, a drought adapted mixture (type DWi-r*), mostly composed by grasses (i.e. *Festuca arundinacea*, *Lolium perenne*, *Dactylis glomerata*) and legumes (*Medicago sativa*, *Trifolium pratense* and *Trifolium repens*). Drought seed mixture is commonly used in regions in South Tyrol, Italy, with a dry inner alpine climate, characterized by low precipitation total and a highly variable distribution of precipitation.

Seed mixtures were grown on standardized soils directly in 12 small-sale lysimeters with 0.3m diameter and depth. The lysimeters were distributed into four plots of 3.5 x 3.5 m. Lysimeters were equipped with soil water content, soil temperature and soil matric potential probes installed at 0.05, 0.15 and 0.25m depth. All plots which were subjected to drought treatment were closed using a UV permeable transparent polythene film (Lumisol Clear AF, 88% - 92% light transmittance).

At the field site, all experimental plots were managed congruently with the land-use scheme of the surrounding

meadow. Two cuts were made, before the drought experiment started (07.06.2018) and at the end of the experiment (08.08.2018) and it was fertilized once (19.04.2018). The experiment involved two different rainfall scenarios: a) moist treatment, i.e. Stubai Valley environment, plots were constantly irrigated and a bi-directional pumping system at the bottom of the lysimeter acted as groundwater supplier; b) drought treatment, where plots experienced an extensive drought period. We use the word 'drought' to refer to an experimental condition of volumetric water content (θ) that is low enough to cause a physiological response relative to plants at a higher θ . The drought treatment was divided in two phases, a first period (07.06.2018 – 02.07.2018) when shelters were installed preventing irrigation, but the pumping system supplied groundwater; and a second period (03.07.2018 – 08.08.2018) of extreme drought where the pumping system was switched off and there were neither irrigation nor groundwater supply.

Stomatal conductance of the functional groups present in both vegetation types (grasses and legumes) was measured with a DECAGON SC-1 Leaf Porometer (Decagon Devices 2016). Measurements were made on sunny days, approximately twice a week; each measurement was replicated three times per functional group and lysimeter, three or four times a day. The individuals analysed were always completely exposed to the sun. To assess productivity of each grassland type, biomass was determined by weighing harvested biomass after the cut. The harvested plant material was separated into functional groups.

Results

Changes in soil water content between moist and drought treatments are evident (*Figure 1*), verifying the proper functioning of the irrigation treatments. At the beginning of the

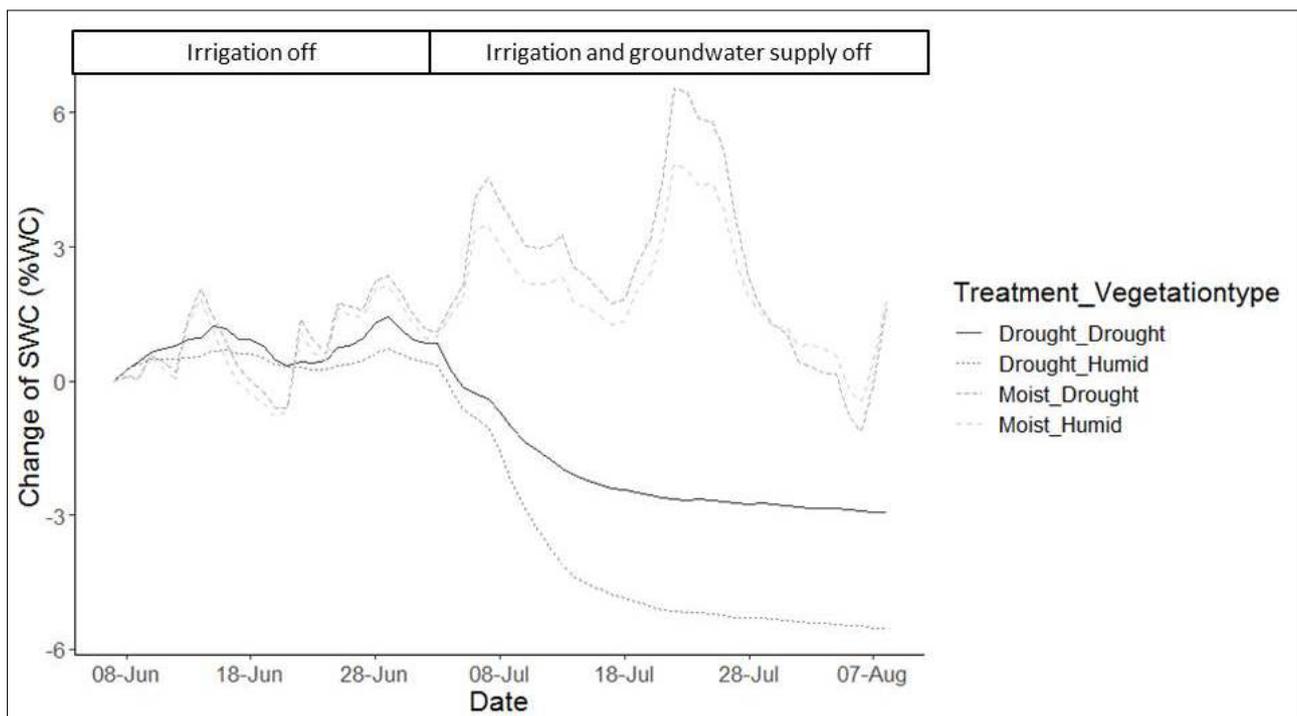


Figure 1. Changes of soil water content (SWC) (%WC) during the experiment.

Table 1. Differences on stomatal conductance between moist and drought treatments for each functional group present in drought or humid adapted vegetation at the first three porometer measurement days of the drought experiment. After day 18.07.2018 results remain the same. Significant p values in bold.

Date	Vegetation type	Functional group	Treatment P
02.07.2018	Humid	Grasses	0.833
		Legumes	0.517
	Drought	Grasses	0.179
		Legumes	<0.001
09.07.2018	Humid	Grasses	0.061
		Legumes	0.0445
	Drought	Grasses	<0.001
		Legumes	<0.001
18.07.2018	Humid	Grasses	<0.001
		Legumes	<0.001
	Drought	Grasses	<0.001
		Legumes	<0.001

drought, when groundwater supply was still possible, there were no differences between moist and drought treatment. Since the beginning of the extreme drought (03.07.2018), lysimeters under moist and drought treatments differed. Vegetation types showed a different reaction to severe drought ($p < 0.001$). Humid adapted vegetation reacted faster and decreased 6% in water content; however drought adapted vegetation lost 3% of soil water content. The loss of water in moist conditions at the end of the project could be explained by the exceptional drought and heat of summer 2018. Similarly to soil water content, stomatal conductance showed significantly different trends for lysimeters under moist or drought treatment, whereby the difference between treatments increased with time ($p < 0.001$). The functional groups legumes and grasses showed different stomatal conductance in moist treatment, legumes showed higher rates of conductance than grasses ($p < 0.001$). Although when drought was severe, the stomatal conductance of both functional groups dropped to minimum and there was no difference between them. Additionally, differences within the functional group legumes in drought adapted vegetation were found for the moist treatment ($p < 0.001$). *Medicago sativa* showed higher conductance rates than species from genus *Trifolium*, while in drought treatment conductance rates were similar.

Drought and humid adapted vegetation types showed similar stomatal conductance in moist conditions, although in drought conditions stomata reaction of grasses and legumes was influenced by the vegetation type ($p < 0.001$, $p = 0.009$, respectively). Analyzing temporal changes on conductance reaction of both functional groups along the drought treatment (Table 1), it was shown that legumes in drought vegetation differed earlier (02.07.2018), when drought is not extreme, while legumes in the humid adapted vegetation responded later (09.07.2018), six days after the severe drought started. Grasses showed a later stomata reaction than legumes, differences of grass conductance between treatments was shown since 09.07.2018 for humid vegetation, and even later for drought adapted vegetation (18.07.2018; 15 days after the severe drought started). It suggested that drought adapted vegetation (both functional groups) reacted faster to drought conditions than humid

adapted vegetation. Additionally, functional groups showed the same trend in both treatments, with legumes reacting faster to drought conditions than grasses.

The biomass weighted at the end of the experiment showed that lysimeters subjected to a drought period differed from those well irrigated ($p = 0.018$ for drought adapted vegetation and $p = 0.042$ for humid adapted vegetation). Drought and humid adapted vegetation showed similar biomass productivity under moist conditions. Although, they differed in drought conditions ($p = 0.042$), suggesting that drought adapted biomass had a higher amount of standing biomass. Legumes were the most abundant functional group, covering a range of 92-94% in well irrigated lysimeters and 79-86% in lysimeters after drought treatment. Remainder biomass was represented by grasses and herbs were negligible, showing a maximum of 0.7%. Alternatively to total biomass, grass productivity did not show any differences neither between vegetation types nor between irrigation treatments (Figure 2). Legumes, since they represented most of the vegetation, showed the same trend as total biomass.

Discussion

Sharing a common environment and soil type, drought and humid adapted grassland types seem to differ in their water use strategies in drought conditions. Results of this experiment reveal a divergence in the stomatal conductance of the two Alpine grassland communities in drought conditions. In line with Leitinger et al. (2015) and Frenck et al. (2018), humid adapted vegetation did not react to the absence of water supply until drought is severe. It follows a water spending strategy; i.e. it hardly reduces transpiration with decreasing water availability until close to the wilting point. In contrast, drought adapted vegetation restrict stomatal conductance when drought is moderate. Therefore, it follows a water saving strategy; i.e. it implies a strict regulation of the stomata with decreasing water availability. Strategies followed by both types of vegetation become more evident when analyzing soil hydrology. Humid adapted vegetation has a greater loss of soil water content than drought vegetation during the drought period. It becomes more evident when the groundwater supply is off and the severe drought begins. The analysed water fluxes from the interface soil-plant-atmosphere in the lysimeter scale to some degree with productivity and total biomass of the vegetation, where consequences of water use strategies are evident. Humid-adapted vegetation risks hydrological failure and does not reduce transpiration since the beginning of the severe drought, resulting in lower biomass productivity and a high decrease of soil water content. However, drought adapted vegetation produces more biomass efficiently. Understanding the differences in plant water use strategies of varying vegetation types is important for grassland management strategies, in terms of increasing the productivity.

Different influences of soil properties can be discarded in this case because the same standardized soil was used for all lysimeters. Therefore, differences between the studied grasslands seem to be driven by plant community assembly. As hypothesized, stomatal conductance differ between functional group and even there are differences between species. The presence of *Medicago sativa* in drought vegetation could be decisive for the water use strategy chosen

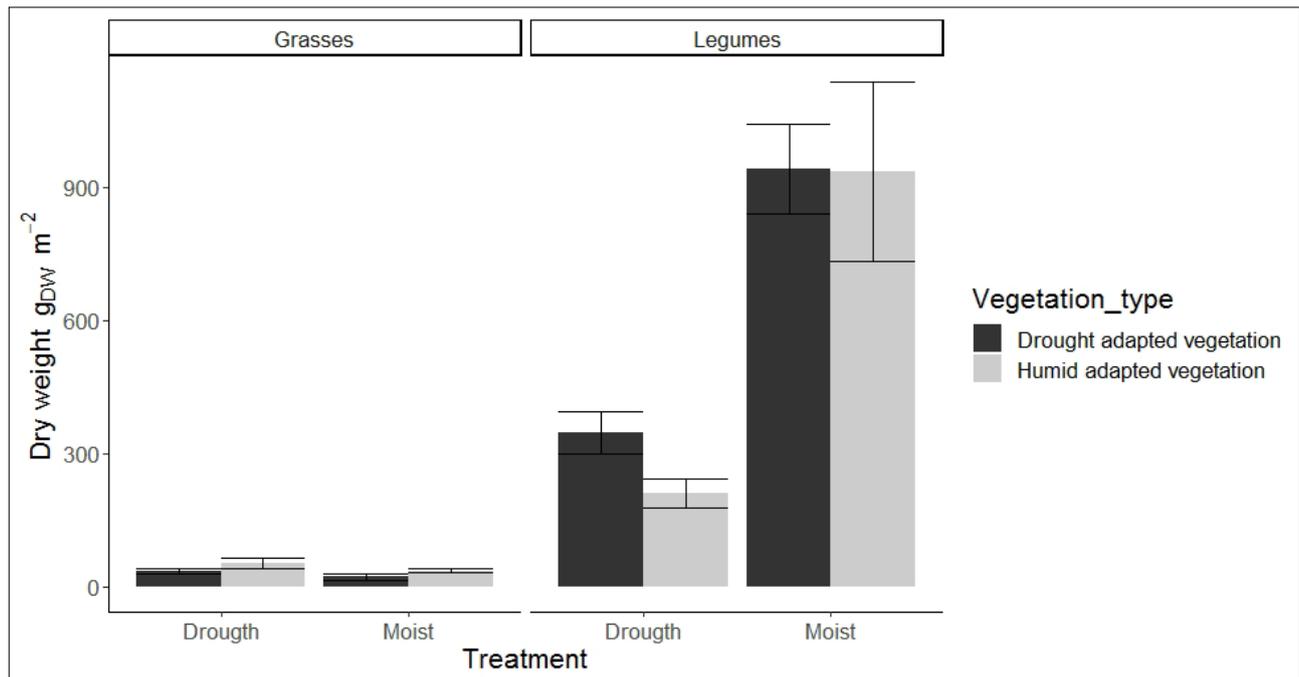


Figure 2. Average biomass dry weight (\pm SD) (gDW m⁻²) of grasses and legumes present in humid and drought adapted vegetation after moist and drought treatments.

because of its preference for moderately dry soils (Landolt et al. 2010); while *Trifolium hybridum*, only present in humid vegetation, and *Trifolium pratense*, abundant in both vegetation types, show a preference for moderately humid soils. Additionally, *Festuca arundinacea*, a grass species abundant in drought adapted vegetation, is mainly settled in wet meadow, although due to its good rooting, it is considered to be very drought resistant (Landolt et al. 2010). Thus, species exclusive for each vegetation type differ in their irrigation preferences and it could be decisive in the water use strategy of the vegetation.

Conclusion

The reduction of water availability reduces stomatal conductance and biomass productivity, and increase the loss of soil water for both Alpine grassland types. Drought adapted vegetation follows a water saving strategy that implies more efficient biomass productivity, while humid vegetation does not adapt fast enough to the lack of water supply. Hence, plant community composition could be an important factor in future grassland management, at least at the level of functional groups. Further studies would be needed to determine the variety in water-use strategies at species level.

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