# A conservative resource use strategy in agricultural grasslands counteracts lower productivity and water use efficiency under drought conditions

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## Abstract

Grassland response to changes in water availability is closely tied to the traits of the plant community which determine plant water uptake and resource use. Plants can adopt either moderate and efficient (conservative) or rapid and demanding (acquisitive) resource use strategies. These strategies combined with the plant interactions with microbes, such as arbuscular mycorrhiza fungi (AMF), determine the grassland productivity and efficiency. This study aims to compare the drought response of two agricultural grasslands that differ in their resource use strategies. In an experimental garden 12 small-scale lysimeters were installed with two different agricultural grassland types (conservative and acquisitive) and two different irrigation levels (wet and drought). We measured water fluxes, above- and belowground phytomass productivity and AMF spore productivity in these two grassland types throughout a drought of 64 days. Despite differing resource use strategies, both grassland types exhibited similar reductions in evapotranspiration and aboveground phytomass under drought. However, the conservative grassland showed higher water use efficiency (WUE) when considering only aboveground phytomass, and a less pronounced compositional shift towards greater grass phytomass. Furthermore, in acquisitive grasslands the root:shoot ratio of grasses and AMF spores abundance in the soil were greatly reduced than in conservative grasslands. We also identified differences in legume productivity, rooting system, and AMF spores community composition as key factors influencing WUE. In a changing climate with greater frequency and severity of droughts in the European Alps, opting for grassland mixtures with more species with conservative characteristics should be considered, as they i) reach the productivity of acquisitive grassland even under wetter conditions and ii) show higher efficiency and longer vitality under drought conditions.

## 1. Introduction

The presence and abundance of functional groups in grasslands have a significant influence on the quantity and quality of agricultural yield. Forb species increase the mineral content of forage and improve the palatability and digestibility of fodder (Evers, 2011). Legumes are particularly important as protein carriers and for nitrogen fixation from the air. Legumes improve the nitrogen supply of the entire canopy through infection of roots by effective *Rhizobium* strains, which causes the formation of functional root nodules (Reich et al., 2003). Farmers directly or indirectly determine the composition of plant species through management measures to build up economically and agro-production optimized grassland. Ideally, these should have a canopy with an optimal plant composition ratio of 60 to 70 % grasses and 30 to 40 % legumes and other forbs (Potsch, 1999; Sanderson et al., 2013; Knot et al., 2015). Such mixtures are also best suited to deliver high yields not only now, but also in a warmer climate of the future (Elgersma and Søegaard, 2016). Thus, the need for functionally optimized grasslands and to improve our knowledge of the reaction of species and functional groups to stresses like drought. Functional diversity may not only determine these responses, but also may itself be effected by drought (Miller et al., 2019; Tello-García et al., 2020) through changes in plant species composition (Griffin-

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Nolan et al., 2019), and simplification of communities, which may lead to species reduction (Peralta et al., 2019).

According to the individual traits involved in resource use, plants can range from fast/acquisitive to slow/conservative strategies (Diaz et al., 2004; Reich, 2014; Wright et al., 2004). Acquisitive species construct energetically cheap but short-lived tissues optimized for fast resource acquisition, whereas conservative species produce more resource-expensive but persistent tissues with a slower rate of return. Species following an acquisitive strategy are usually characterised by high specific leaf area (SLA), low leaf dry-matter content (Wright et al., 2004) and long, thin roots (Roumet et al., 2016; Reich, 2014). Fine roots make rapid use of resources with minimal biomass investment, resulting in high metabolic and growth rates under favourable conditions (Ostonen et al., 2007; Reich, 2014; Bergmann et al., 2020). Overall, acquisitive species have a high photosynthetic rate, but also high water consumption (Manzoni et al., 2013). Acquisitive traits may be detrimental under extreme drought conditions as such species are insensitive to progressive soil drying until very low soil water content is reached (e.g. the permanent wilting point) (Brilli et al., 2011). Conversely, conservative species typically have smaller, thicker leaves and shorter, coarser roots (Roumet et al., 2016; Tardy et al., 2017). Conservative species reduce water uptake earlier under drought, economise nutrients and use them slowly, which results in low growth rates under favourable conditions. Conservative and acquisitive strategies mark the ends of the spectrum, a wide range exists between them, defined by the specific traits of a species and its plasticity (Perez-Ramos et al., 2019).

Belowground components (e.g. root biomass and characteristics) have a significant impact on plant resources uptake, as they are in contact with the soil and are one of the main pathways for all resources (Ma et al., 2018; Mccormack and Iversen, 2019). Plant roots and associated rhizosphere organisms influence many important ecosystem processes, including nutrient and carbon storage in the soil, soil structural stability (e.g. erosion resistance and porosity (Bardgett et al., 2014)), water uptake (Gross et al., 2008), and interactions with other soil organisms. In this context, plants response to drought not only on their functional traits and position on the conservative-acquisitive spectrum but also on their associated rhizosphere. Belowground traits are intrinsically connected to the way plants benefit from soil microbes. Therefore, a deeper knowledge of root-associated mutualists, such as arbuscular mycorrhiza fungi (AMF), may partially account for variation along the spectrum (Bergmann et al., 2020).

AMF are obligate symbionts with plant roots meaning they obtain most of their required organic carbon from the host plant in return for inorganic N, P and water (Parniske, 2008). Moreover, AMF can alter plant traits, such as stomatal conductance, triggering mechanisms to protect the plant from drought (Augé, 2001). They improve plant growth even when root colonisation is reduced (Bahmani et al., 2018; Hartman and Tringe, 2019; Tuo et al., 2017; Zhang et al., 2018b). Decrease on AMF productivity includes reduced extraradical mycelial network and reproduction (i.e. sporulation) (Bahadur et al., 2019;

Hashem et al., 2019; Kilpeläinen et al., 2017; Maitra et al., 2019). Interestingly, AMF spore abundance is primarily influenced by seasonal climate and host-independent physico-chemical soil properties, and less so by the composition of host plants, as reported for Chilean Mediterranean-type ecosystems (Silva-Flores et al., 2019). Although AMF spore abundances may not be an accurate indicator for mycorrhizal activity, they can be useful as a proxy for stress. Under stress, the photobionts must reduce the amounts of nutrients provided to their mycorrhizal partner, thus limiting the seasonally induced AMF spore formation. Therefore, when comparing plant drought strategies in the same soil, we expect AMF spore abundance to decrease proportionally to the stress a plant community is experiencing.

The community-weighted mean (CWM) of the individual plant traits and plant interactions (i.e. with AMF) determine the strategy followed by the community under drought, and therefore the productivity and water use efficiency (WUE). Acquisitive plant species that can use water and nutrients quickly but wastefully during short wet periods are better prepared to cope with irregular rainfall (Querejeta et al., 2018). These traits may be advantageous for successful colonization in dry regions with extreme fluctuations in resource availability. However, in humid to semi-arid climates or in scenarios with brief but intense dry periods this strategy breaks down. The economical use of water of conservative species through dynamic control of water uptake via stomatal behaviour is more advantageous in the long term (Zhao et al., 2016; Lu et al., 2020; Brodribb et al., 2020). Therefore, the traits of the plant communities used in farming must be in accordance with the climatic conditions, as they will determine the tolerance of crops to drought and their productivity.

This study aimed to (i) compare the effects of drought on two grassland seed mixtures commonly sown in wet and dry sites in mountain farming in the European Alps, and to (ii) identify the main parameters affecting water use efficiency of these agricultural grasslands. The seed mixtures studied differed primarily on the resource use strategies of the plant community (i.e. more conservative or acquisitive). In addition, we wanted to understand any impacts on agricultural yields under dry conditions. To analyse the mechanisms behind the expected differences, we focused on the water fluxes, functional composition, phytomass productivity, and AMF spore productivity of these two grassland types in a drought experiment. We hypothesized that the agricultural grassland with more traits related to conservative strategies (hereafter referred to as conservative grassland) would show a faster response to drought. Expected responses included closing of stomata and higher investment in root and AMF sporulation. We expected that these responses would result in a higher WUE under drought conditions. In contrast, we expected that the grassland with more traits related to acquisitive strategies (hereafter referred to as acquisitive grassland) would be less responsive to drought. We expected plants to use the available water under drought more quickly and then have less time to produce phytomass and AMF biomass before wilting, resulting in a lower WUE.

## 2. Material and Methods

The experimental garden was established in the long-term socio-ecological research (LTSER) site “Stubai valley” (LTSER platform “Tyrolean Alps”), close to Neustift im Stubaital (Austria), located on the valley floor in the montane belt at 972 m above the sea level (WGS84: 47.115833 N, 11.320556 E) in a meadow used for hay production (Fig. 1). It has an annual mean temperature of 6.5 °C and annual mean precipitation of 1097 mm (Frenck et al., 2018). There, 12 small-scale lysimeters were installed with two different agricultural grassland types and two different irrigation levels. Investigations took place in 2018 during part of the growing season (June - August).

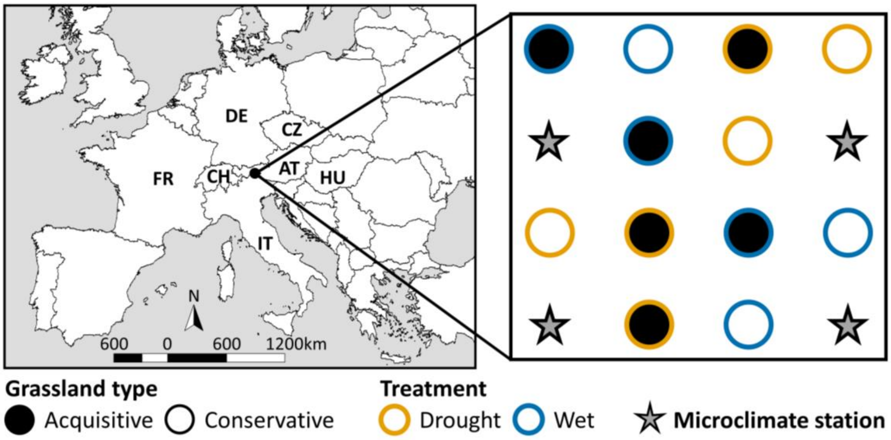

**Figure 1. Schematic overview of the experimental design. Three replicates were used for each combination of grassland type and irrigation level. © EuroGeographics for the administrative boundaries.**

### 2.1. Investigated grassland types: community composition and plant traits

We linked this investigation to applied grassland farming using two seed mixtures commonly sown in European Alpine grassland farming (Schwarzenberger Samen & Gartenbedarf, Austria). Both seed mixtures were sown directly in 12 small-scale lysimeters (Fig. 1). The highly productive ‘seed mixture for humid locations (SR037)’ is typically sown in more humid areas of the Central and Northern Alps (> 800 mm annual precipitation), and the ‘seed mixture for dry locations (SR032)’ is sown in the drier areas of the Southern Alps (< 800 mm annual precipitation). The two seed mixtures were characterized as acquisitive and conservative, respectively, based on their traits´ CWM being closer to one or another end of the resource use spectrum. For all species present in the mixtures (Table 1), main traits for resource use classification were searched in the literature (only data on traits from plants growing in favourable conditions were selected, and a mean was calculated when more than one paper or value was

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found): root-shoot ratio, shoot C:N ratio, SLA, leaf N concentration (LNC) and rooting index (Wright et al., 2004; Roumet et al., 2016; Diaz et al., 2016; Bu et al., 2018; Chacón-Madrigal et al., 2018; Reich, 2014). We then calculated a CWM proxy for each trait of the two seed mixtures (Table 1). Due to difficulties in differentiating species in their vegetative state, we calculated the CWM proxy based on the seed abundance in the mixture rather than on actual biomass or cover. The highly productive 'seed mixture for humid locations (SR037)' displayed higher SLA and LNC and lower rooting, C:N in shoots and root-shoot ratio; and therefore was defined as the acquisitive grassland. The 'seed mixture for dry locations (SR032)' with opposite traits was defined as the conservative grassland (Wright et al., 2004; Roumet et al., 2016). Plant biomass was cut and separated into functional groups prior to the start of the drought experiment to confirm the relation between biomass and seed share. Furthermore, SLA was calculated for the three main species of each grassland type to confirm that mean SLA in conservative grassland was lower (28.9 $m^2$ $kg^{-1}$) than in acquisitive grassland (33.9 $m^2$ $kg^{-1}$).

**Table 1** Plant species and corresponding functional group present in the seed mixtures with their respective plant traits, i.e. rooting index, specific leaf area (SLA), leaf nitrogen content (LNC), C:N ratio in shoots and root-shoot ratio; the share (%) of each species in the seed mixtures. Rooting index was calculated as the product of the root density (classes) × main rooting depth (m) × root lateral extension (m) based on species-specific data according to Tasser and Tappeiner (2005). The grassland types were characterised based on these two seed mixtures, utilising the community-weighted means, i.e. mean values of the traits and seed percentages.

| | | Plant traits | | | | | Species abundance in seed mixture (%) | |
|---|---|---|---|---|---|---|---|---|
| Species | Functional group | Rooting index | SLA ($m^2$ $kg^{-1}$) | LNC (mg $g^{-1}$) | C:N of shoot | Root-shoot ratio | for dry locations (SR032) | for humid locations (SR037) |
| *Agrostis capillaris* L. | grass | $1.42^{a}$ | $29.31^{b,c,d}$ | $23.65^{d}$ | $20.32^{m}$ | $0.41^{aa,ab}$ | 0.0 | 4.1 |
| *Alopecurus pratensis* L. | grass | $0.81^{a}$ | $24.08^{b,c}$ | $41.50^{d}$ | $17.47^{m,n,o}$ | $0.39^{ac}$ | 0.0 | 6.1 |
| *Arrhenatherum elatius* P. Beauv. | grass | $4.62^{a}$ | $29.68^{e,f}$ | $29.62^{d}$ | $26.00^{o}$ | $0.74^{ab}$ | 4.4 | 0.0 |
| *Dactylis glomerata* L. | grass | $0.15^{a}$ | $24.35^{d,f,g,h,i}$ | $24.30^{d}$ | $19.63^{p}$ | $0.79^{ab,ad}$ | 6.7 | 7.0 |
| *Festuca arundinacea* Schreber | grass | $3.88^{a}$ | $17.40^{i,j}$ | $18.00^{d}$ | $36.33^{q,r,s}$ | $0.91^{ad}$ | 50.6 | 0.0 |
| *Festuca pratensis* Hudson | grass | $0.64^{a}$ | $22.29^{d,f}$ | $24.95^{d}$ | $20.00^{o}$ | $0.68^{ae}$ | 2.7 | 18.1 |
| *Festuca rubra* L. | grass | $0.64^{a}$ | $11.62^{d,g}$ | $34.00^{d}$ | $29.57^{t}$ | $0.43^{af}$ | 5.0 | 12.0 |
| *Lolium perenne* L. | grass | $0.66^{a}$ | $22.60^{f,l,j}$ | $33.00^{d}$ | $34.21^{t,u}$ | $0.70^{aa,ab,ad,ag}$ | 6.9 | 13.5 |
| *Lotus corniculatus* L. | legume | $0.25^{a}$ | $18.8^{d,e,k}$ | $28.98^{d}$ | $22.60^{v}$ | $0.62^{ah}$ | 0.0 | 2.5 |
| *Medicago sativa* L. | legume | $0.76^{a}$ | $28.50^{i,j}$ | $55.50^{d}$ | $21.60^{v}$ | $0.24^{ai,aj}$ | 3.9 | 0.0 |
| *Phleum pratense* L. | grass | $0.40^{a}$ | $28.41^{d,j,l}$ | $25.42^{d}$ | $18.30^{w}$ | $0.86^{ab}$ | 5.8 | 8.0 |
| *Poa pratensis* L. | grass | $0.31^{a}$ | $20.29^{d,l}$ | $34.50^{d}$ | $29.37^{t}$ | $0.67^{ad,ag}$ | 5.6 | 12.1 |
| *Trifolium hybridum* L. | legume | $0.84^{a}$ | $33.68^{g,i}$ | $43.20^{d}$ | $14.29^{x}$ | $0.27^{ak}$ | 0.0 | 4.0 |
| *Trifolium pratense* L. | legume | $0.21^{a}$ | $25.07^{d,g,j}$ | $34.86^{d}$ | $18.10^{v}$ | $0.30^{ad,ah}$ | 2.8 | 2.5 |
| *Trifolium repens* L. | legume | $0.84^{a}$ | $40.84^{d,g,i}$ | $49.10^{d}$ | $14.10^{y}$ | $0.36^{aa,ad}$ | 5.6 | 6.0 |
| *Trisetum flavescens* (L.) P. Beauv. | grass | $0.62^{a}$ | $29.00^{d,h}$ | $21.55^{d}$ | 17.75 | $0.81^{al}$ | 0.0 | 4.1 |
| Grassland type | | Community-weighted means | | | | | | |
| Conservative (seed mixture for dry location) | | 2.39 | 21.37 | 25.99 | 30.07 | 0.76 | | |
| Acquisitive (seed mixture for humid location) | | 0.59 | 23.67 | 31.61 | 23.24 | 0.60 | | |

Literature: a) Tasser and Tappeiner (2005), b) Kleyer et al. (2008), c) Kattge et al. (2020), d) Fontana et al. (2017), e) Freschet et al. (2015), f) Arredondo and Schnyder (2003), g) Wohlfahrt et al. (1999), h) Guyonnet et al. (2018), i) Prieto et al. (2017), j) Mason et al. (2016), k) Ordonez et al. (2010), l) Meziane

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and Shipley (2001), m) Baxendale et al. (2014), n) De Long et al. (2019), o) Arfin Khan et al. (2016), p) Ryser and Eek (2000), q) Chen et al. (2017), r) Jacob et al. (2020), s) Bowden et al. (2007), t) Evers et al. (2020), u) Shahzad et al. (2012), v) Talgre et al. (2017), w) Hempel et al. (2009), x) Davis (1991), y) Kaleeem Abbasi et al. (2015), z) Gubsch et al. (2011), aa) Cook et al. (1996), ab) Crush et al. (2005), ac) Gloser (1993), ad) Davidson (1969), ae) Malinowski (1995), af) Paterson et al. (2005), ag) Pande and Singh (1981), ah) Foulds (1977), ai) Philippot et al. (1991), aj) Zhang et al. (2018a), ak) Murray (2012), al) Baillard et al. (2020).

## 2.2. Experimental Set-up

Twelve small-scale lysimeters (Smart-Field-Lysimeter, UMS/Meter Group Munich, Germany) with a depth and diameter of 0.3 m were used for the experiment (Fig. 1). Each lysimeter was filled with a standard horticultural soil. The soil had 6.03 % ± 0.07 % of organic matter and a pH of 7.21 ± 0.07. More information on the soil characterization can be found in the appendice. All lysimeters were equipped with an independent bi-directional pumping system between the lysimeters and drainage containers, thus ensuring tension-controlled soil moisture conditions. An electronic weighing platform (PL-50, UMS/Meter Group Munich, Germany) under each lysimeter recorded the weight every minute. With the same frequency, the weight of each water drainage container was recorded (used electronic platform: PL-10, UMS/Meter Group Munich, Germany). Both measurements were applied for the calculation of evapotranspiration (ET). Soil water content (SWC) was recorded every 10 minutes by EC-5 sensors (Decagon Devices, Inc.), at a soil depth of 5, 15 and 25 cm (Frenck et al., 2018) and the daily mean of the three sensors was calculated per lysimeter. Sensors were calibrated for repeatability and accuracy over a period of one month prior to the start of the experiment. This ensured they consistently provided the same values under identical conditions, thus minimising random noise. To do this, they were calibrated to the mean as a reference by creating a sensor-specific linear calibration curve between the measured values and the mean values (see also Schwamback et al. (2023)). These sensor-specific calibration functions were then applied throughout the experiment.

The seed mixtures were sown in the lysimeters in the previous year and kept in a greenhouse at 20°C. After installation in the experimental garden, the lysimeters were managed according to the scheme of the surrounding meadow to settle (i.e. cutting, and exposed to the natural precipitation regime of the study site where mean annual precipitation is 1100 mm). The density of plant individuals at the time of the experiment was 2512.4 ± 349.4 ind. $m^{-2}$ (legumes: 589.5 ± 123.0 ind. $m^{-2}$, grasses:1922.9 ± 330.2 ind. $m^{-2}$). The experiment started directly after the first harvest of the season and all lysimeters were covered with a UV-transmissive transparent polyethylene film (Lumisol Clear AF. 88-92 % light transmission) to exclude natural precipitation. The shelters were approximately 2.5 m tall and were closed from 0.5 to 2.5 m, but open on the sides facing the main wind directions to account for typical wind conditions at the site. Lysimeters were subjected to two irrigation levels (i.e. wet and drought treatments, Fig. 1) from 8 June to 8 August (64 days). For the wet treatment, soil moisture was maintained at field capacity by controlled watering to avoid waterlogging and ensure sufficient water supply for maximum productivity. For the drought treatment, soil was maintained in a water deficit. For the first 26 days, the lower boundary was maintained at a constant matric potential of –1 kPa. This was achieved by a bi-directional pumping system that delivered water in and out of the lysimeter to mimic groundwater inflow and capillary rise from deeper soil layers. From thereon until the end of the experiment (3 July to 8 August), no watering was applied and extreme drought was simulated.

## 2.3. Measurements

*Water fluxes*

ET was calculated by the weight differences between the lysimeter and the drainage container, and applying the AWAT (Adaptive Window Adaptive Threshold) filter to separate significant from insignificant mass changes (Peters et al., 2014; Peters et al., 2016; Peters et al., 2017). The integrated WUE of the grasslands was calculated by dividing dry phytomass by the accumulated ET for the experimental period. Here, aboveground dry phytomass was used for calculating $\mathrm{WUE}_{\mathrm{ap}}$ and total dry phytomass (i.e., aboveground and belowground) was used to calculate $\mathrm{WUE}_{\mathrm{tp}}$ (Kirkham, 2005).

Starting on 3 July, weekly stomatal conductance measurements were taken on the leaf underside of grasses and legumes in the lysimeters using a DECAGON SC-1 Leaf Porometer (Decagon Devices; 2016) in four measurement cycles from 8:00 h to 18:00 h in sun-exposed individuals. The measurements could not be carried out at the species level due to the young age of the canopy and the resulting non-definitive species recognition. Three replicates per functional group in each lysimeter were used to calculate a daily mean, resulting in 12 single measurements per day for each functional group and lysimeter.

*Phytomass*

At the end of the experiment, individuals of grasses and legumes were counted. Between 5 and 20 individuals of legumes and grasses were randomly selected and excavated to determine the root-shoot ratio, depending on how strongly a group was represented in the lysimeter. Root extraction was done manually by washing the roots under running water. The low stand density and loose soil made individual roots easily distinguishable during washing, as they were not tightly intertwined. Afterwards, roots were dried at 80°C, and weighed to determine the average root weight per functional group in each lysimeter. The remaining aboveground phytomass in the lysimeters was harvested, separated into functional groups, dried at 80°C, and weighed. We included individuals used for root-shoot ratio assessment. Biomass and necromass proportions were visually estimated at five time points (19 June, 9 July, 18 July, 1 August, and 7 August) in each lysimeter during the experiment.

*Spore productivity of arbuscular mycorrhizal fungi*

The abundance of AMF spores in the initial soil mixture used represented the amount of available AMF inoculum in the soil at the beginning of the season. End-of-season sporulation was considered an approximation of AMF reproduction. The extraradical spores produced by AMF in the soil were extracted by the differential water-sucrose centrifugation method (Ianson and Allen, 1986). First, 30 g of 2 mm-sieved dry soil was mixed with 60 ml of water to allow rehydration, the solution was centrifuged at 2,000 rpm for 10 min, and the supernatant containing organic material was discarded. The soil was re-suspended in 60 ml of a 2 M sucrose solution with a dispersant (2 % Calgon) and centrifuged at 2,000 rpm at room temperature for 10 min. Next, to remove soil particles remaining in suspension, a sucrose-Calgon solution was added to the supernatant containing the AMF spores to reach an approximate volume of 20 ml. The mixture was sieved through a 500 µm sieve and centrifuged again for 10 min at 2,000 rpm. The material retained on the 500 µm sieve was examined under a stereo microscope to check for the presence of large AMF spores. To separate the spores into three additional size classes (i.e. 51 – 100 µm,100 – 200 µm, and 200 – 500 µm), the spore-containing supernatant was consecutively sieved through a 200 µm and then a 100 µm sieve cascade. The spores retained on each sieve were separately washed off with distilled water and poured into the filter funnel of a vacuum line covered with a 51 µm mesh tissue. Spores of each size class retained on the mesh were counted under the stereo microscope at 63-fold magnification. Size classes and pigmentation of AMF spores were recorded as they are common criteria for identification (Invam, 2023; Schüßler and Walker, 2010). Although no molecular AMF species classification was carried out, the main AMF classes could be discriminated by the combination of size and pigmentation. This allowed us to detect compositional changes in AMF communities. We considered small (51 - 100 µm), medium (100 – 200 µm), and large (200 - 500 µm) spore sizes and black, brown and yellow (pale) spore pigmentation. The density of AMF spores was expressed on a soil dry weight basis.

## 2.4. Data processing and statistics

Most of the statistical analyses were performed using the R statistical programming language (R Core Team, 2022). To compare SWC, ET, and necromass between irrigation levels and grassland types, ANCOVAs were used. Date was included as a covariate, and grassland type as well as irrigation levels were independent variables. In addition, interactions between variables were tested. For stomatal conductance, functional group was added as independent value. Finally, legumes and grasses stomatal conductance were tested also independently. ANOVAs with a significance level of 0.05 were performed to compare aboveground, belowground phytomass, abundance of AMF spores, $WUE_{ap}$, and $WUE_{tp,}$ between the different irrigation levels and grassland types. All ANOVAs included grassland type and irrigation levels as independent variables, and interactions between variables were tested. Above- and belowground phytomass also included plant functional groups as independent variables, whilst AMF spores included the different size and pigmentation classes of AMF spores. When interactions between variables were significant, a post hoc Tukey test was performed to test the differences between groups. The homogeneity of variances and distribution of residuals were analysed using residual plots. Additionally, the Levene test with "car" package (Fox and Weisberg, 2019) was used to examine the homogeneity of variances and Shapiro-Wilk's with "stats" package (R Core Team, 2022) was used for analysing distribution of residuals. Aboveground and belowground phytomass were log-transformed to meet the assumptions of normality and homogeneity of variances.

Finally, we estimated the relationship between WUE and the above- and belowground plant characteristics, parameters of the water balance and AMF. We ran a factor analysis using varimax rotation and reduced our 32 variables to five factors (Table S3). This allowed us to assess multicollinearities between the variables as well as in terms of trade-offs and redundancies. Linear regression analysis was then used to test the effect of these factors on $WUE_{ap}$ and $WUE_{tp}$. These analyses were performed in SPSS Statistics (IBM SPSS Statistics 28).

## 3. Results

### 3.1. Drought intensity and water fluxes

The drought treatment effectively induced a severe drought, where soil water content (SWC) decreased immediately after the start of the extreme drought (3 July) for both grassland types (Table S1, irrigation level, $p < 0.001$). However, the decrease was more pronounced in acquisitive grassland (up to 3.27 ± 0.62 %) than in conservative grassland (up to 6.76 ± 0.54 %; irrigation level * grassland type, $p < 0.001$) under drought. In contrast, lysimeters in wet treatment generally maintained high and similar SWC (Fig. 2a).

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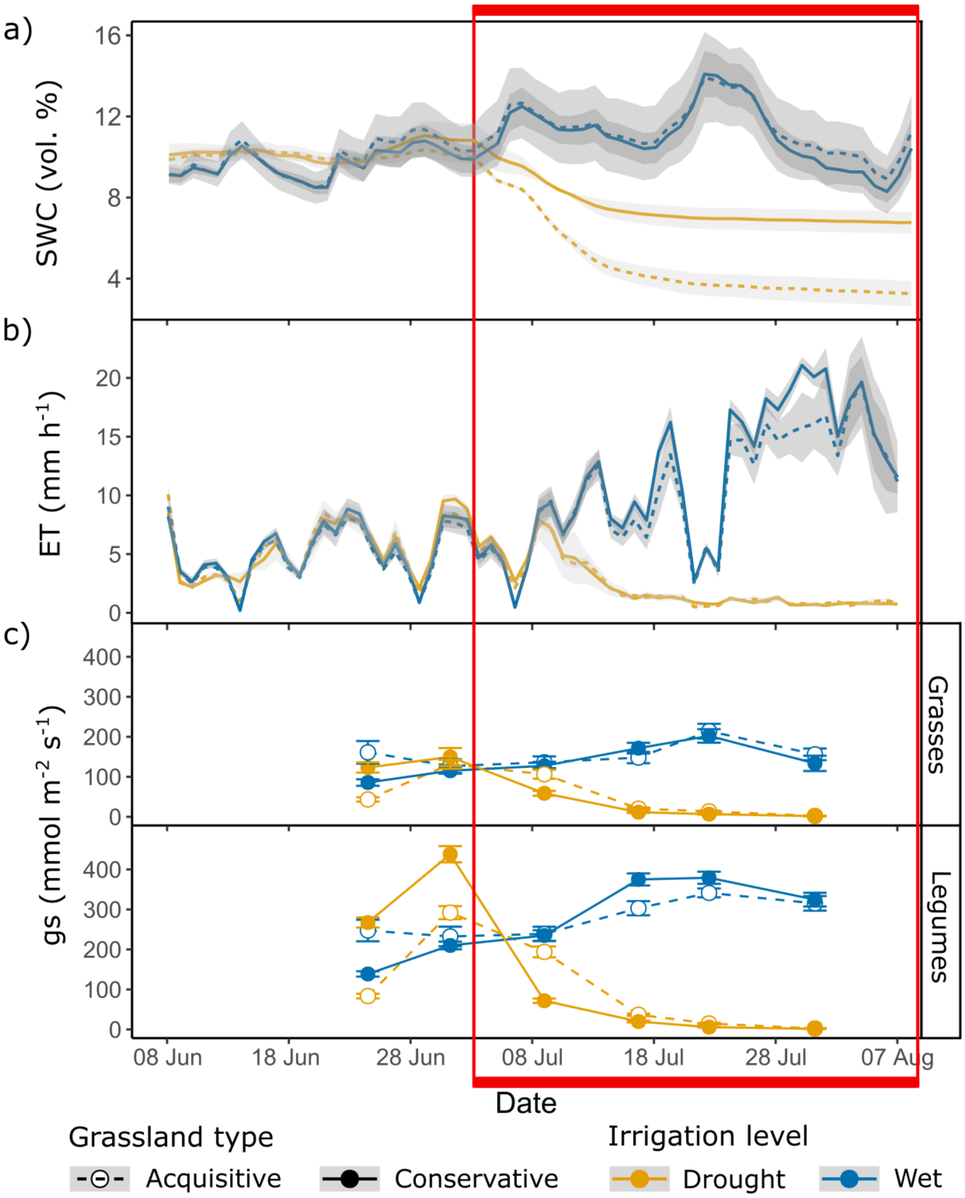

**Figure 2. a) Mean soil water content (SWC), b) evapotranspiration (ET) and, c) stomatal conductance ($g_s$) over the course of the experiment for conservative and acquisitive grasslands under wet and drought treatment. The shaded area represents the standard error and the red box indicates the duration of the extreme drought. Stomatal conductance values are presented as $\bar{x}$ ± s.e.**

Before the extreme drought event, evapotranspiration (ET) dynamics were similar between conservative and acquisitive grasslands, irrespective of the irrigation level (Fig. 2b). With the onset of the extreme drought, ET changed over time (Table S1, date, $p = 0.001$), and differed between irrigation levels ($p < 0.001$). Wet lysimeters exhibited increased ET, while drought lysimeters showed a decreased. The impact of the drought treatment on ET became evident on day 6 of the extreme drought (9 July) (Fig. 2b).

Measuring stomatal conductance throughout the experiment (Fig. 2c) revealed that legumes had higher conductance rates than grasses (Table S1, functional group, $p < 0.001$) and reacted differently to drought (irrigation level * functional group, $p < 0.001$). Legumes in acquisitive grassland only reduced their conductance after two weeks of extreme drought, whereas in conservative grassland substantial reductions were observed one week earlier (Table S1, irrigation level * grassland type, $p < 0.001$). For grasses, drought reduced stomatal conductance (Table S1, irrigation level, $p < 0.001$) after two weeks of extreme drought in both grassland types. We also observed that grasses in the conservative grassland tended to reduce stomatal conductance earlier, although this difference was smaller than that in legumes.

### 3.2. Aboveground and belowground impacts

In wet treatment, both grassland types produced similar aboveground phytomass ($1.01 \pm 0.15$ kg $m^{-2}$ and $1.00 \pm 0.11$ kg $m^{-2}$ for acquisitive and conservative grasslands, respectively). In the drought treatment, aboveground phytomass production dropped (Table S2, irrigation level, $p = 0.001$) to $0.26 \pm 0.03$ kg $m^{-2}$ in acquisitive and $0.38 \pm 0.03$ kg $m^{-2}$ in conservative grassland. Grasses and legumes differed significantly in their total aboveground phytomass (Fig. 3a, functional group $p < 0.001$), and on the grassland types (grassland type * functional group, $p = 0.004$), and they reacted differently to drought (irrigation level * functional group, $p < 0.001$). In conservative grassland, the proportion of grasses increased from 2.2 % in wet to 9.7 % in drought treatment, whilst in acquisitive grassland, it increased from 3.9 to 19.9 %. The proportion of legumes decreased with drought, with a smaller reduction in conservative grassland (7.5 % vs 16.0 % reduction from wet to drought treatment for conservative and acquisitive grassland, respectively).

Belowground phytomass did not differ between grassland types (Table S2, grassland type, $p = 0.46$). Acquisitive grassland reduced belowground phytomass from $1.45 \pm 0.26$ kg $m^{-2}$ in wet to $0.24 \pm 0.04$ kg $m^{-2}$ in drought treatment. Whilst conservative grassland reduced belowground phytomass from $1.39 \pm 0.20$ kg $m^{-2}$ to $0.37 \pm 0.03$ kg $m^{-2}$ between wet and dry treatments. However, legumes and grasses were affected differently by drought (functional group, $p < 0.001$). Legumes decreased their belowground phytomass after drought, while grasses increased it (Fig. 3a). Accordingly, the root-shoot ratio (Fig. 3b) increased for grasses and decreased for legumes (Table S2, irrigation level * functional group, $p = 0.043$). Additionally, grasses exhibited a higher root-shoot ratio in conservative than acquisitive grasslands (grassland type, $p = 0.052$), independently of the irrigation level.

At the end of the extreme drought period, the proportion of necromass aboveground in both grassland types affected by drought was more than 90 %. Almost all aboveground parts of the legumes and approximately 80 % of the grasses had died (Fig. 3c). Die-off commenced in the first third of the drought period and increased with duration (Table S1, date * irrigation level, $p < 0.001$). After two weeks of extreme drought (i.e. 18 July), the proportion of necromass in the conservative grassland was 13 %, and in the acquisitive grassland was 30 %.

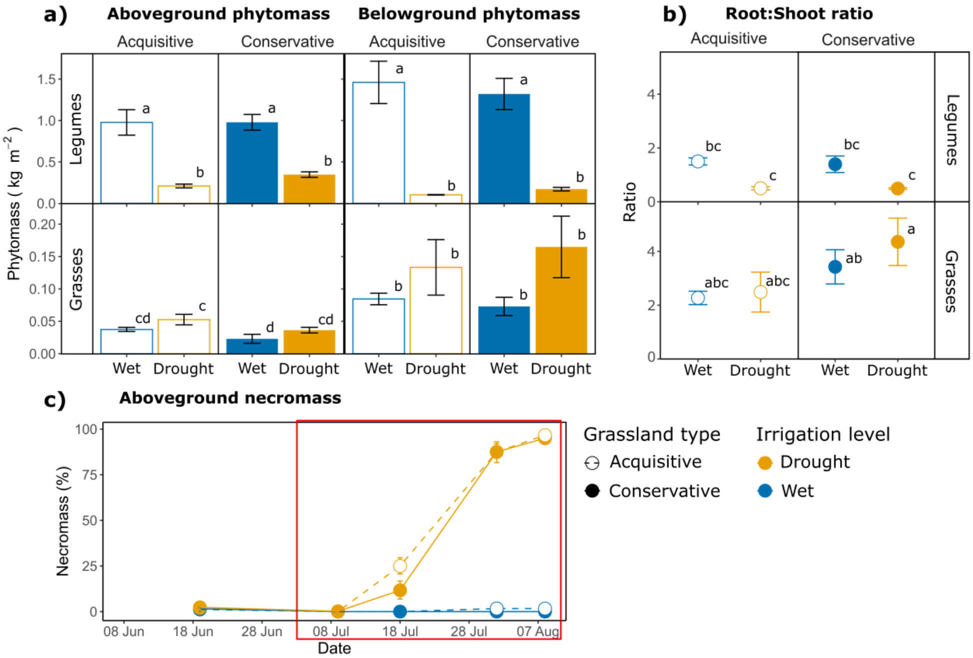

**Figure 3. a) Above- and belowground phytomass ($\bar{x}$ ± s.e.), b) root-shoot ratio ($\bar{x}$ ± s.e.), and c) proportion of necromass on the aboveground phytomass ($\bar{x}$ ± s.e.) of the conservative and acquisitive grasslands under wet versus drought treatments. The red box represents the duration of the extreme drought. Letters indicate the significant differences found by post-hoc analysis following three different ANOVAs ($p < 0.05$): i) aboveground phytomass, ii) belowground phytomass, and iii) root:shoot ratio.**

### 3.3. Arbuscular mycorrhizal fungi spore abundance

In all lysimeters, the total abundance of AMF spores increased over the course of the experiment compared to the initial AMF inoculum present in the soil (Fig. 4a). The drought treatment showed lower AMF spore abundance (Table S2, irrigation level, $p < 0.001$) and resulted in changes in the detected AMF size and pigmentation classes (Fig. 4b, irrigation level * size and pigmentation classes, $p = 0.008$). Results also indicated higher AMF spore productivity for the conservative grassland compared to acquisitive grassland after the drought treatment, but differences were not statistically significant (Fig. 4a).

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Nine different combinations of size and pigmentation in AMF spores were identified and AMF abundances significantly varied amongst classes (size and pigmentation classes, $p < 0.001$). Of these nine combinations, small and yellow spores were the most abundant (Fig. 4b). In conservative grassland, differences between irrigation levels were small. However, in acquisitive grassland, black and brown spores, especially the small-brown class, increased their abundance in drought conditions. The evenness of spore classes was high in the initial soil (0.81 ± 0.02), i.e. all abundances are the same when evenness is one. After the drought experiment, observed evenness generally decreased but this effect differed between irrigation levels and grassland types. Conservative grassland maintained similar evenness between irrigation levels (0.49 ± 0.03 for wet and 0.55 ± 0.06 for drought treatment). However, evenness of the AMF spores classes increased under drought in acquisitive grasslands from 0.52 ± 0.03 for wet to 0.66 ± 0.02 in drought (irrigation level, $p = 0.006$; grassland type, $p = 0.045$).

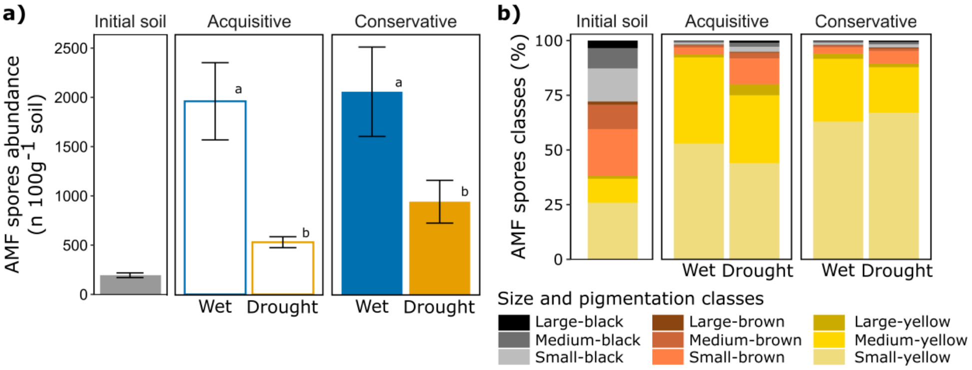

**Figure 4. a) Abundance of arbuscular mycorrhiza fungi (AMF) spores ($\bar{x} \pm$ s.e.) in conservative and acquisitive grasslands after drought or wet treatments. The initial soil corresponds to the AMF spores present in the standardized soil mixture used for the lysimeter setup. Spore counts are provided as AMF spores per 100 g of dry soil. Letters indicate the significant differences found by post-hoc analysis following ANOVAs ($p < 0.05$) comparing AMF spores numbers at the end of the experiment. b) Relative abundance of different AMF spore size and pigmentation classes in the soil of lysimeters with conservative or acquisitive grassland types under drought or wet treatment, and in the initial soil before the experiment. Size and pigmentation classes were combinations of small (51 - 100 µm), medium (100 – 200 µm), or large (200 - 500 µm) with black, brown and yellow.**

### 3.4. Water use efficiency (WUE) of two grassland types

The two calculated WUEs showed different trends (Fig. 5). Despite similarities in ET and aboveground phytomass productivity between grassland types under drought, a difference in $WUE_{ap}$ was found at the end of the experiment (Fig. 5a). Drought $WUE_{ap}$ decreased only in acquisitive grassland (Table S2, irrigation level * grassland type, $p = 0.038$), whilst conservative grassland showed no difference between wet and drought conditions. $WUE_{tp}$ decreased with drought treatment (Table S2, irrigation level, p =

0.004), regardless of the grassland type (Fig. 5b). However, the decrease is much larger for acquisitive (-54.6 %) than for conservative grassland (-22.2 %).

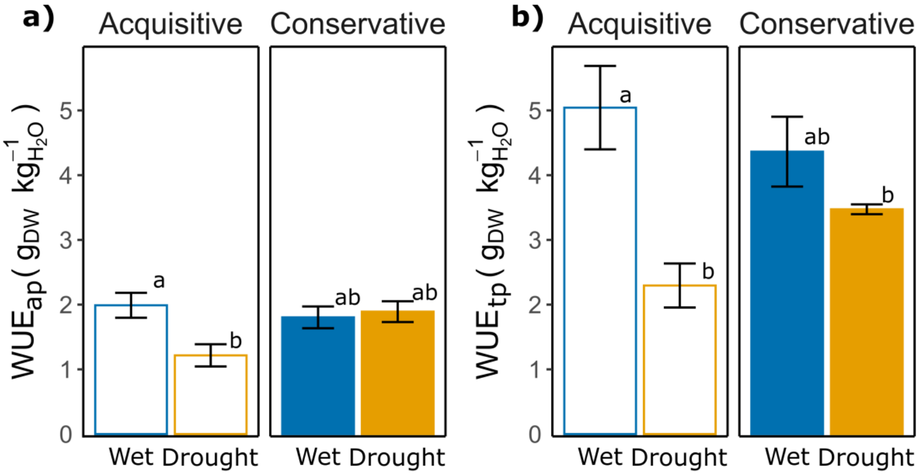

**Figure 5. Water use efficiency calculated at the end of the experiment as the amount of a) aboveground phytomass ($WUE_{ap}$) and b) total phytomass. Total phytomass is the sum of aboveground and belowground phytomass ($WUE_{tp}$) produced (gDW) per quantity of used water (kg $H_2O$) from conservative or acquisitive grasslands under drought and wet treatment ($\bar{x}$ ± s.e.). Letters indicate the significant differences found by post-hoc analysis following ANOVAs ($p < 0.05$).**

To estimate the relationship between WUE and the 32 potential driving variables (Table S3), firstly the variables were condensed into 5 factors: factor 1 related to high plant productivity, factor 2 related to a generally high abundance of AMF spores, factor 3 related to high productivity of grasses, factor 4 related to high stomatal conductance and factor 5 related to high abundance of large AMF spores. This grouping allowed us to see how AMF spores with specific size and pigmentation (e.g. small-black to medium-black spores) are associated with legumes, and others with grasses (small-brown spores). Secondly, the relationship of the factors with the two indices $WUE_{ap}$ and $WUE_{tp}$ were estimated. The results (Table S4, Fig. 6) show that $WUE_{ap}$ was strongly correlated with the created factors ($R^2 = 0.68$, $p = 0.027$). Factor 1 (high total productivity) was positively correlated, and factor 5 (high abundance of large AMF spores) was negatively correlated with $WUE_{ap}$ ($p = 0.005$ and $p = 0.020$, respectively). On the other hand, $WUE_{tp}$ was also well explained by the considered factors ($R^2 = 0.96$, $p < 0.001$) and it was positively correlated with overall high productivity (factor 1, $p < 0.001$) and a general high abundance of AMF (factor 2, $p = 0.001$). However, $WUE_{tp}$ was negatively correlated with the high abundance of large spores of AMF (factor 5, $p = 0.009$).

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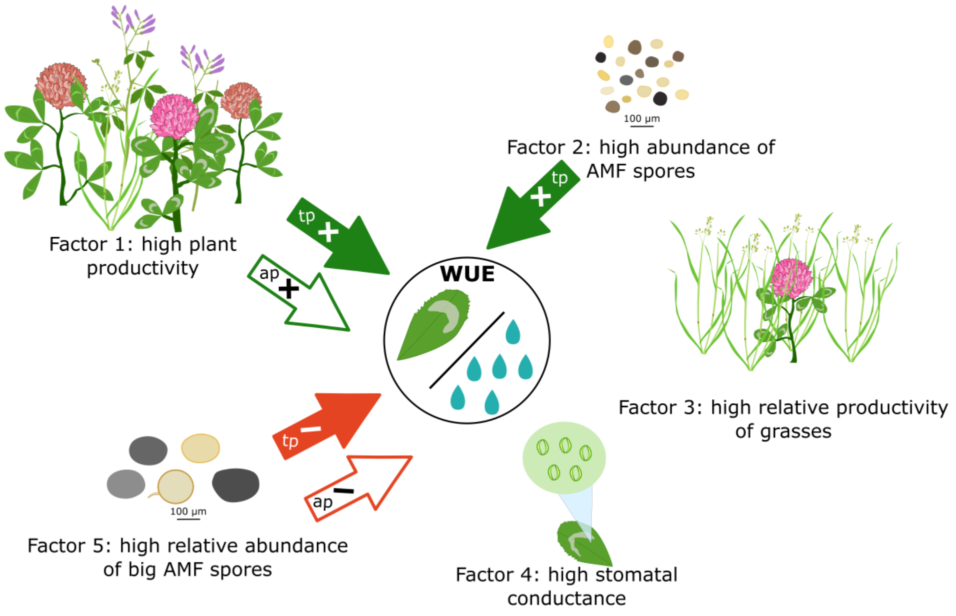

**Figure 6. Significant relationships between water use efficiency (WUE) and the five factors into which the indicators were condensed based on a factor analysis. Filled arrows represent the statistically significant correlations between the factor and WUEtp and empty arrows between the factor and WUEap. Green arrows indicate a positive relationship and red arrows show a negative relationship.**

## 4. Discussion

Our results provide experimental evidence of the effects of drought on two grassland types used for hay production in two climatically different areas of the European Alps. These two grasslands were classified as conservative and acquisitive according to their plant resource use strategies. In this study, the drought treatment provoked an extreme water deficit for the plants. The conditions simulated may not be observed in nature in the near future, however, as Reichstein et al. (2013) recommend, experiments towards climate extremes are necessary to better understand the ecosystem processes.

### 4.1. Consequences of water stress on aboveground productivity

Although there were some differences in ET between grassland types in wet conditions, ET generally increased over the season alongside the temperature and evaporative demand. In the drought treatment, ET dropped following the decrease in SWC at the start of the extreme drought. Although we could not find differences in how the two grassland types modulated ET to drought, differences were observed when we looked more closely at the stomatal conductance of the main functional groups. Reduction in stomatal conductance in both legumes and grasses within the conservative grassland preceded those in the acquisitive grassland. The first detected measure where individuals in the acquisitive grassland started limiting stomatal conductance occurred when SWC was approximately 4 %. In conservative grassland, the first observed reduction started at a SWC of approximately 9 %. In agreement with Leitinger et al. (2015) and Frenck et al. (2018), the acquisitive grassland type, which represents the one sown in humid areas of the European Alps, did not react to drought until water scarcity became severe. In other words, legumes in the acquisitive grassland showed little reduced stomatal conductance until the soil became very dry. However, the results did not show as great a difference as we would expect from seed mixtures specifically designed for such different climates.

The conservative grassland had numerically higher phytomass productivity than the acquisitive grassland in drought treatment. However, the differences were not statistically significant, possibly due to low sampling size (n = 3 per grassland type × irrigation level). Nevertheless, we found that plants wilt earlier in extreme drought conditions in acquisitive grassland. In this grassland type, stomatal conductance was restricted later, therefore a higher water loss was experienced, and an earlier death was expected (Martin-Stpaul et al., 2017). In this experiment, drought was long enough to provoke wilt in most of the grassland community, but in a scenario with shorter drought periods, conservative grassland would show higher living biomass.

The two grassland types studied in this paper differed from the seed mixture slightly on the percentage of grasses (typically more conservative) and legumes (typically more acquisitive). However, it must be noted that some grasses present in the acquisitive grassland showed traits that would be towards the acquisitive end of the gradient, e.g. *Agrostis capillaris* and *Alopecurus pratensis* (Table 1). As in the study by Tello-García et al. (2020), which utilised a commercial seed mixture typically used for intensively cultivated hay grasslands, drought favoured the grass species over legume species. This effect resulted in a shift towards a predominance of grasses in community composition. After drought, the conservative grassland had a higher proportion of legumes (98 %) than the acquisitive one (80 %). Legumes tend to use resources acquisitively, which may make them stronger competitors in favourable conditions but worse as the conditions get more severe (Thakur et al., 2022; Komainda et al., 2019; Carlsson et al., 2017). Accordingly, acquisitive grassland suffered a stronger decrease on SWC, which is expected to translate into greater physiological stress. Even if the proportion of legumes remains high, the decrease is evident and has a big impact on the total phytomass productivity. Legumes are plants known to enrich soil with nitrogen due to their mutualistic relationship with nitrogen-fixing bacteria, and thus provide valuable ecosystem services. These ecosystem services can be interrupted by drought (Dollete et al., 2023) and decreased by the reduction of legumes biomass. Hence, a greater loss of legumes results in i) a reduction in soil fertility (Ledgard and Steele, 1992; Wei et al., 2019); ii) greater loss of an important food source for grazing animals, affecting their diet (Cole et al., 2022); iii) stronger changes in plant community composition, possibly further declining soil fertility through species loss

(Spehn et al., 2002; Cong et al., 2014); and finally iv) greater loss of pollinators, as legumes are important food sources for pollinators including bees and butterflies (Cole et al., 2022).

### 4.2. Higher investment belowground for the conservative grassland

Aboveground components of both grassland types did not always differ significantly under drought conditions. This effect illustrates the importance of belowground components in shaping grasslands drought strategies. Young individuals, such those sown here, adapt particularly well to changing conditions so are especially well suited for such studies, as life-span plasticity decreases in the plant ageing process (Henn and Damschen, 2021). In addition, the root turnover in young individuals is generally short, meaning that rapid adaptations can also be recognised here (Sun et al., 2016; Wang et al., 2020).

Besides a general reduction of phytomass productivity, drought usually changes biomass allocation, and increases root-shoot ratio (Zhou et al., 2020). Investing in the root system under stress conditions increases the ability to absorb water and nutrients, as the results of the grasses in this study support. However, it is known that root responses to drought are very heterogeneous (Lozano et al., 2020). Accordingly, the opposite root system effect was also observed in the legumes in this experiment, as they drastically reduced root phytomass and thus the root-shoot ratio. Our findings confirm that legumes usually follow acquisitive strategies, using the available resources to build fast-growing and short-lived aboveground tissues, rather than larger root systems. A deeper analysis of the rooting system in the direction of architectural and morphological traits could allow us to link the functional groups or grassland rooting system to a higher or lower efficiency on carbon, nutrients input, plant uptake or mineralisation of nutrients (Bardgett et al., 2014).

The abundance of AMF spores in the soil was measured at the end of the season as an indicator of stress. Congruently, at the end of the drought experiment AMF spore abundance was significantly lower in both grassland types compared to the wet treatment. The presence of AMF is known to improve drought tolerance (Bahadur et al., 2019), and reduce plant stress and results in increased plant biomass (Sun et al., 2017; Jacott et al., 2017), rooting system (Ji et al., 2019) and plant fitness either via direct effects on stomatal conductance or enhanced nutrition and water-uptake (Hartman and Tringe, 2019). Although we could not causally link increased plant fitness with the productivity of AMF spores, our results imply that plants in the conservative grassland (with slightly higher biomass production) can allocate a greater proportion of their resources into their associated AMF partners under drought. This allows them to produce more spores (slightly higher spore abundance) than acquisitive grasslands. Other studies carried out with similar main plant species than in our lysimeters reported an increased fitness of plants with mycorrhiza symbionts under drought. This includes mycorrhized roots of *Trifolium repens* having higher concentrations of proline, soluble proteins, flavonoids (Tuo et al., 2017), and mycorrhized *Festuca arundinacea* leaves having a higher chlorophyll content and thus an enhanced nutrient uptake under drought (Mahdavi et al., 2018).

Besides a slightly higher number of AMF spores produced, the differences on AMF spore classes (defined based on spore size and pigmentation) provide insights in potential changes in AMF community composition due to stress or a different reaction of plants with different strategies. Although we did not further identify these classes to species level, we used this as a proxy for species composition, as AMF spores with different size and pigmentation typically represent different taxonomical units (Invam, 2023; Schüßler and Walker, 2010). Changes in the AMF community composition of acquisitive grassland under drought could cause the proportion of some specific spore classes to change and evenness to increase, indicating a homogenization of abundances. According to our results, these compositional changes may be related to changes in the functional group composition of each grassland type, as suggested by the factor analysis. AMF mutualism can be species-specific or genus-specific to associated plant species (Zafari et al., 2017; Ben Laouane et al., 2019; Bhandari et al., 2020). Thus, mycorrhizal fungal communities often follow plant compositional changes (Kruger et al., 2017). Another reason for this shift in community composition could be adaptation to drought. The species *Funneliformis mossae* and *Glomus margarita* (Ji et al., 2019) or taxa of the genus *Rhizophagus* (Emery et al., 2022) are examples of AMF with increased abundance under drought. Molecular identification on species level and further *in-vitro* experiments would help to better understand the changes on the AMF community and the factors causing these changes.

### 4.3. Conservative strategies lead to higher water use efficiency under drought

All plant traits and characteristics listed above (i.e. ET, stomatal conductance, plant productivity (aboveground and belowground) and AMF sporulation) respond to drought with the main goal of greater water use efficiency by balancing water consumption and phytomass productivity (e.g. stomatal closure (Brodribb et al., 2020), investing in root phytomass (Li et al., 2022), or maintaining AMF symbiosis (Zhao et al., 2015)). Conservative and acquisitive grasslands did not show all the significant differences we expected but followed different trends in some aspects. Conservative grassland under drought reduced stomatal conductance of legumes earlier, had higher root-shoot ratio of grasses and higher AMF activity. These trends were supported by the significant difference in $WUE_{ap}$ between both grassland types after drought. In conservative grassland, $WUE_{ap}$ was similar in wet and drought treatment. Therefore the grassland appeared to react to changes in water availability through specific mechanisms to maintain efficiency, as suggested by Lubbe et al. (2021). However, the acquisitive grassland did not react to the decrease in water availability, resulting in a drop in $WUE_{ap}$, which we expected to be caused by a high water loss by the later closing of the stomata (Brodribb et al., 2020). However, $WUE_{ap}$ was positively related to the total productivity led by legumes and AMF spores related to legumes (small- and medium-black, and large-brown), and negatively to some specific classes of large spores (black and yellow) (Fig. 6). We detected changes on the proportion of these spores at the different irrigation levels of the acquisitive grassland. Therefore, a deeper understand on the changes on the mycorrhizal community could help to disentangle the decrease on $WUE_{ap}$ in acquisitive grassland under drought.

However, when we expand the focus to the whole phytomass productivity and calculate $WUE_{tp}$, the greater efficiency of conservative grassland under drought is no longer clear. At this scale, differences in wet vs drought become higher, as expected for grasslands under severe drought (Gang et al., 2016; Zhao et al., 2020). Therefore, when interpreting the commonly used $WUE_{ap}$, we must consider that the relevant belowground part and the changes on phytomass allocation are missing (Quan et al., 2020). In addition, at least in this study, $WUE_{ap}$ for grasslands under drought was overestimated. This overestimation is obvious in our results as root phytomass was more strongly affected than aboveground phytomass and differences between wet and drought were greater. These responses on the belowground phytomass were not strong enough to equal $WUE_{tp}$ of the wet treatment, but pinpoint a higher $WUE_{tp}$ in conservative than in acquisitive grassland under drought treatment. Besides the factors related to $WUE_{ap}$, $WUE_{tp}$ is positively related to total AMF spores abundance and spores not linked to grasses nor legumes. This reinforces the potential importance of AMF on WUE in agricultural grasslands.

### 4.4. Implications for grassland farming

In addition to disentangling plant mechanisms during drought, we focus this study on productivity and efficiency which have the greatest impact on grassland management. We can confirm the decrease in productivity due to drought, but cannot statistically separate grassland types. However, two other results need to be considered: vitality and WUE. A more acquisitive strategy could result in less vigorous grassland with lower efficiency which should lead to a decline in productivity in the future. We should also point out that under wet treatment, conservative grassland reached similar productivity to acquisitive grassland. This finding is contrary to the expectations that acquisitive grassland would grow more and faster in favourable conditions (Reich, 2014).This may indicate a high plasticity of the conservative grassland. However, further analysis of the nutritional value and palatability of the forage would be interesting to ensure that quality is not reduced in more conservative grasslands.

Although it appears in this study that a conservative strategy would be better to tolerate drought, it is known that diversity of strategies among coexisting species is more beneficial to the community (Pérez-Ramos et al., 2013). For example, Griffin-Nolan et al. (2019) and Blessing et al. (2018) revealed in different experiments that, on one hand, functional diversity decreased in dry years because conservative grasses grew more and maintained higher soil moisture. On the other hand, acquisitive species grew less or changed their phenology. However, in wet years or under short periods of drought, the acquisitive species grew faster, increasing aboveground phytomass production and functional diversity. This finding underlines that a mix of conservative and acquisitive species would be expected to perform better than communities where only conservative species remain, which would have very low productivity (Lavorel and Grigulis, 2012). We must consider that in this study the strategy attributed to each grassland type was calculated as the CWM proxy of all the species coexisting, which could be more acquisitive or conservative. Therefore, smaller differences would be expected than in other studies comparing communities of exclusively conservative/slow species versus acquisitive/fast species (Oram et al., 2023).

## 5. Conclusions

This study compares responses of two different grassland types to drought. We focus on their resource use strategies and the impact on water fluxes, productivity, and AMF spore productivity. Although some of the results are in line with our expectations and previous findings, (i.e. decrease of ET, phytomass productivity, vitality, and AMF spore abundance) our results showed that the selected grassland types differ in their reactions to drought according to their more acquisitive or conservative strategies. Our predominantly conservative grassland revealed earlier stomata closure in legumes, a higher percentage of legumes, slightly higher root-shoot ratio for grasses, and a slightly higher AMF spore productivity. In particular, differences in legume productivity and abundance of certain AMF spores resulted in greater WUE and prolonged vitality under extreme drought in comparison to the acquisitive grassland.

The use of seed mixtures adapted to prevailing climatic conditions should ensure high productivity in grassland management. Therefore, our results suggest that increasing the abundance of species with more conservative traits in a future climate with more frequent droughts should be considered. This recommendation is based on findings that i) under favourable conditions they achieve the productivity of acquisitive grassland, and ii) under drought conditions they show a lower yield loss, longer vitality and higher efficiency. Besides these findings, it also became evident that the apparent aboveground phytomass is not a good indicator of overall productivity or WUE. Therefore, root traits and plant-soil interactions must also be considered for an overall assessment of drought tolerance.

## 6. Data availability

The datasets generated are available in B2SHARE with DOI: 10.23728/b2share.33d070b2e3d541ab8d147e80ebba9eb4

## 7. Author contribution

The study was conceived by ET, GL and UT. GL, ET, UP and ETG conceived the paper. Field measurements, data collection and analysis were performed by ETG instructed by GL and ET on field measurements and by UP on laboratory analysis. The first draft of the manuscript was written by ETG and all authors commented on previous versions of the manuscript and made suggestions for its structural and scientific improvement. All authors read and approved the final manuscript.

## 8. Competing interests

The authors declare that they have no conflict of interest.

## 9. Acknowledgments

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## 10. References

Arfin Khan, M. A. S., Kreyling, J., Beierkuhnlein, C., and Jentsch, A.: Ecotype-specific improvement of nitrogen status in European grasses after drought combined with rewetting, Acta Oecologica, 77, 118-127, doi:10.1016/j.actao.2016.10.004, 2016.

Arredondo, J. T. and Schnyder, H.: Components of leaf elongation rate and their relationship to specific leaf area in contrasting grasses, New Phytologist, 158, 305-314, doi:10.1046/j.1469-8137.2003.00745.x, 2003.

Augé, R. M.: Water relations, drought and vesicular-arbuscular mycorrhizal symbiosis, Mycorrhiza, 11, 3-42, doi:10.1007/s005720100097, 2001.

Bahadur, A., Batool, A., Nasir, F., Jiang, S., Mingsen, Q., Zhang, Q., Pan, J., Liu, Y., and Feng, H.: Mechanistic insights into arbuscular mycorrhizal fungi-mediated drought stress tolerance in plants, International Journal of Molecular Sciences, 20, doi:10.3390/ijms20174199, 2019.

https://doi.org/10.5194/egusphere-2024-2435
Preprint. Discussion started: 12 August 2024

Bahmani, M., Naghdi, R., and Kartoolinejad, D.: Milkweed seedlings tolerance against water stress: Comparison of inoculations with Rhizophagus irregularis and Pseudomonas putida, Environmental Technology & Innovation, 10, 111-121, doi:10.1016/j.eti.2018.01.001, 2018.

Baillard, V., Sulmon, C., Bittebiere, A. K., Mony, C., Couee, I., Gouesbet, G., Delignette-Muller, M. L., Devin, S., and Billoir, E.: Effect of interspecific competition on species sensitivity distribution models: Analysis of plant responses to chemical stress, Ecotoxicology and Environmental Safety, 200, 110722, doi:10.1016/j.ecoenv.2020.110722, 2020.

Bardgett, R. D., Mommer, L., and De Vries, F. T.: Going underground: root traits as drivers of ecosystem processes, Trends in Ecology & Evolution, 29, 692-699, doi:10.1016/j.tree.2014.10.006, 2014.

Baxendale, C., Orwin, K. H., Poly, F., Pommier, T., and Bardgett, R. D.: Are plant-soil feedback responses explained by plant traits?, New Phytologist, 204, 408-423, doi:10.1111/nph.12915, 2014.

Ben Laouane, R., Meddich, A., Bechtaoui, N., Oufdou, K., and Wahbi, S.: Effects of arbuscular mycorrhizal fungi and rhizobia symbiosis on the tolerance of Medicago Sativa to salt stress, Gesunde Pflanzen, 71, 135-146, doi:10.1007/s10343-019-00461-x, 2019.

Bergmann, J., Weigelt, A., van der Plas, F., Laughlin, D. C., Kuyper, T. W., Guerrero-Ramirez, N., Valverde-Barrantes, O. J., Bruelheide, H., Freschet, G. T., Iversen, C. M., Kattge, J., McCormack, M. L., Meier, I. C., Rillig, M. C., Roumet, C., Semchenko, M., Sweeney, C. J., van Ruijven, J., York, L. M., and Mommer, L.: The fungal collaboration gradient dominates the root economics space in plants, Science Advances, 6, eaba3756, doi:10.1126/sciadv.aba3756, 2020.

Bhandari, K. B., West, C. P., and Acosta-Martinez, V.: Assessing the role of interseeding alfalfa into grass on improving pasture soil health in semi-arid Texas High Plains, Applied Soil Ecology, 147, 103399, doi:10.1016/j.apsoil.2019.103399, 2020.

Blessing, C. H., Mariette, A., Kaloki, P., and Bramley, H.: Profligate and conservative: water use strategies in grain legumes, Journal of Experimental Botany, 69, 349-369, doi:10.1093/jxb/erx415, 2018.

Bowden, C., Spargo, J., and Evanylo, G.: Mineralization and N fertilizer equivalent value of composts as assessed by tall fescue (Festuca arundinacea), Compost Science & Utilization, 15, 111-118, doi:10.1080/1065657X.2007.10702320, 2007.

Brilli, F., Hortnagl, L., Hammerle, A., Haslwanter, A., Hansel, A., Loreto, F., and Wohlfahrt, G.: Leaf and ecosystem response to soil water availability in mountain grasslands, Agricultural and Forest Meteorology, 151, 1731-1740, doi:10.1016/j.agrformet.2011.07.007 2011.

Brodribb, T. J., Sussmilch, F., and McAdam, S. A. M.: From reproduction to production, stomata are the master regulators, The Plant Journal, 101, 756-767, doi:10.1111/tpj.14561, 2020.

Bu, W., Huang, J., Xu, H., Zang, R., Ding, Y., Li, Y., Lin, M., Wang, J., and Zhang, C.: Plant functional traits are the mediators in regulating effects of abiotic site conditions on aboveground carbon stock-Evidence from a 30 ha tropical forest plot, Frontiers in Plant Science, 9, 1958, doi:10.3389/fpls.2018.01958, 2018.

Carlsson, M., Merten, M., Kayser, M., Isselstein, J., and Wrage-Mönnig, N.: Drought stress resistance and resilience of permanent grasslands are shaped by functional group composition and N fertilization, Agriculture, Ecosystems & Environment, 236, 52-60, doi:10.1016/j.agee.2016.11.009, 2017.

Chacón-Madrigal, E., Wanek, W., Hietz, P., and Dullinger, S.: Traits indicating a conservative resource strategy are weakly related to narrow range size in a group of neotropical trees, Perspectives in Plant Ecology, Evolution and Systematics, 32, 30-37, doi:10.1016/j.ppees.2018.01.003, 2018.

Chen, W., Liu, H., Wurihan, Gao, Y., Card, S. D., and Ren, A.: The advantages of endophyte-infected over uninfected tall fescue in the growth and pathogen resistance are counteracted by elevated CO(2), Scientific Reports, 7, 6952, doi:10.1038/s41598-017-07183-y, 2017.

Cole, L. J., Baddeley, J. A., Robertson, D., Topp, C. F. E., Walker, R. L., and Watson, C. A.: Supporting wild pollinators in agricultural landscapes through targeted legume mixtures, Agriculture, Ecosystems & Environment, 323, 107648, doi:10.1016/j.agee.2021.107648, 2022.

Cong, W.-F., van Ruijven, J., Mommer, L., De Deyn, G. B., Berendse, F., and Hoffland, E.: Plant species richness promotes soil carbon and nitrogen stocks in grasslands without legumes, Journal of Ecology, 102, 1163-1170, doi:10.1111/1365-2745.12280, 2014.

Cook, A., Marriott, C. A., Seel, W., and Mullins, C. E.: Effects of soil mechanical impedance on root and shoot growth of Lolium perenne L., Agrostis capillaris and Trifolium repens L, Journal of Experimental Botany, 47, 1075-1084, doi:10.1093/jxb/47.8.1075, 1996.

Crush, J. R., Waller, J. E., and Care, D. A.: Root distribution and nitrate interception in eleven temperate forage grasses, Grass and Forage Science, 60, 385-392, doi:10.1111/j.1365-2494.2005.00488.x, 2005.

Davidson, R. L.: Effect of root/leaf temperature differentials on root/shoot ratios in some pasture grasses and clover, Annals of Botany, 33, 561-569, doi:10.1093/oxfordjournals.aob.a084308, 1969.

Davis, M. R.: The comparative phosphorus requirements of some temperate perennial legumes, Plant and Soil, 133, 17-30, doi:10.1007/BF00011895, 1991.

De Long, J. R., Semchenko, M., Pritchard, W. J., Cordero, I., Fry, E. L., Jackson, B. G., Kurnosova, K., Ostle, N. J., Johnson, D., Baggs, E. M., and Bardgett, R. D.: Drought soil legacy overrides maternal effects on plant growth, Functional Ecology, 33, 1400-1410, doi:10.1111/1365-2435.13341, 2019.

Diaz, S., Kattge, J., Cornelissen, J. H., Wright, I. J., Lavorel, S., Dray, S., Reu, B., Kleyer, M., Wirth, C., Prentice, I. C., Garnier, E., Bonisch, G., Westoby, M., Poorter, H., Reich, P. B., Moles, A. T., Dickie, J., Gillison, A. N., Zanne, A. E., Chave, J., Wright, S. J., Sheremet'ev, S. N., Jactel, H., Baraloto, C., Cerabolini, B., Pierce, S., Shipley, B., Kirkup, D., Casanoves, F., Joswig, J. S., Gunther, A., Falczuk, V., Ruger, N., Mahecha, M. D., and Gorne, L. D.: The global spectrum of plant form and function, Nature, 529, 167-171, doi:10.1038/nature16489, 2016.

Diaz, S., Hodgson, J. G., Thompson, K., Cabido, M., Cornelissen, J. H. C., Jalili, A., Montserrat-Marti, G., Grime, J. P., Zarrinkamar, F., Asri, Y., Band, S. R., Basconcelo, S., Castro-Diez, P., Funes, G., Hamzehee, B., Khoshnevi, M., Perez-Harguindeguy, N., Perez-Rontome, M. C., Shirvany, F. A., Vendramini, F., Yazdani, S., Abbas-Azimi, R., Bogaard, A., Boustani, S., Charles, M., Dehghan, M., de

Torres-Espuny, L., Falczuk, V., Guerrero-Campo, J., Hynd, A., Jones, G., Kowsary, E., Kazemi-Saeed, F., Maestro-Martinez, M., Romo-Diez, A., Shaw, S., Siavash, B., Villar-Salvador, P., and Zak, M. R.: The plant traits that drive ecosystems: Evidence from three continents, Journal of Vegetation Science, 15, 295-304, doi:10.1111/j.1654-1103.2004.tb02266.x, 2004.

Dollete, D., Lumactud, R. A., Carlyle, C. N., Szczyglowski, K., Hill, B., and Thilakarathna, M. S.: Effect of drought stress on symbiotic nitrogen fixation, soil nitrogen availability and soil microbial diversity in forage legumes, Plant and Soil, doi:10.1007/s11104-023-06348-1, 2023.

Elgersma, A. and Søegaard, K.: Effects of species diversity on seasonal variation in herbage yield and nutritive value of seven binary grass-legume mixtures and pure grass under cutting, European Journal of Agronomy, 78, 73-83, doi:10.1016/j.eja.2016.04.011, 2016.

Emery, S. M., Bell-Dereske, L., Stahlheber, K. A., and Gross, K. L.: Arbuscular mycorrhizal fungal community responses to drought and nitrogen fertilization in switchgrass stands, Applied Soil Ecology, 169, 104218, doi:10.1016/j.apsoil.2021.104218, 2022.

Evers, G. W.: Forage legumes: forage quality, fixed nitrogen, or both, Crop Science, 51, 403-409, doi:10.2135/cropsci2010.06.0380, 2011.

Evers, M., Kroon, H., Visser, E., and Caluwe, H.: Carbon accumulation of cool season sports turfgrass species in distinctive soil layers, Agronomy Journal, 112, 3435-3449, doi:10.1002/agj2.20231, 2020.

Fontana, V., Kohler, M., Niedrist, G., Bahn, M., Tappeiner, U., and Frenck, G.: Decomposing the land-use specific response of plant functional traits along environmental gradients, Science of The Total Environment, 599-600, 750-759, doi:10.1016/j.scitotenv.2017.04.245, 2017.

Foulds, W.: The physiological response to moisture supply of cyanogenic and acyanogenic phenotypes of Trifolium repens L. and Lotus corniculatus L, Heredity, 39, 219-234, doi:10.1038/hdy.1977.62, 1977.

Fox, J. and Weisberg, S.: An {R} Companion to  Applied Regression, Sage [code], 2019.

Frenck, G., Leitinger, G., Obojes, N., Hofmann, M., Newesely, C., Deutschmann, M., Tappeiner, U., and Tasser, E.: Community-specific hydraulic conductance potential of soil water decomposed for two Alpine grasslands by small-scale lysimetry, Biogeosciences, 15, 1065-1078, doi:10.5194/bg-15-1065-2018, 2018.

Freschet, G. T., Swart, E. M., and Cornelissen, J. H.: Integrated plant phenotypic responses to contrasting above- and below-ground resources: key roles of specific leaf area and root mass fraction, New Phytologist, 206, 1247-1260, doi:10.1111/nph.13352, 2015.

Gang, C., Wang, Z., Chen, Y., Yang, Y., Li, J., Cheng, J., Qi, J., and Odeh, I.: Drought-induced dynamics of carbon and water use efficiency of global grasslands from 2000 to 2011, Ecological Indicators, 67, 788-797, doi:10.1016/j.ecolind.2016.03.049, 2016.

Gloser, J.: Growth rate and total nonstructural saccharides content inAlopecurus pratensis L, Biologia Plantarum, 35, 37-42, doi:10.1007/BF02921116, 1993.

Griffin-Nolan, R. J., Blumenthal, D. M., Collins, S. L., Farkas, T. E., Hoffman, A. M., Mueller, K. E., Ocheltree, T. W., Smith, M. D., Whitney, K. D., and Knapp, A. K.: Shifts in plant functional composition following long-term drought in grasslands, Journal of Ecology, 107, 2133-2148, doi:10.1111/1365-2745.13252, 2019.

Gross, N., Robson, T. M., Lavorel, S., Albert, C., Le Bagousse-Pinguet, Y., and Guillemin, R.: Plant response traits mediate the effects of subalpine grasslands on soil moisture, New Phytologist, 180, 652-662, doi:10.1111/j.1469-8137.2008.02577.x, 2008.

Gubsch, M., Buchmann, N., Schmid, B., Schulze, E. D., Lipowsky, A., and Roscher, C.: Differential effects of plant diversity on functional trait variation of grass species, Annals of Botany, 107, 157-169, doi:10.1093/aob/mcq220, 2011.

Guyonnet, J. P., Cantarel, A. A. M., Simon, L., and Haichar, F. E. Z.: Root exudation rate as functional trait involved in plant nutrient-use strategy classification, Ecology and Evolution, 8, 8573-8581, doi:10.1002/ece3.4383, 2018.

Hartman, K. and Tringe, S. G.: Interactions between plants and soil shaping the root microbiome under abiotic stress, Biochemical Journal, 476, 2705-2724, doi:10.1042/BCJ20180615, 2019.

Hashem, A., Kumar, A., Al-Dbass, A. M., Alqarawi, A. A., Al-Arjani, A. F., Singh, G., Farooq, M., and Abd Allah, E. F.: Arbuscular mycorrhizal fungi and biochar improves drought tolerance in chickpea, Saudi Journal of Biological Sciences, 26, 614-624, doi:10.1016/j.sjbs.2018.11.005, 2019.

Hempel, S., Stein, C., Unsicker, S. B., Renker, C., Auge, H., Weisser, W. W., and Buscot, F.: Specific bottom-up effects of arbuscular mycorrhizal fungi across a plant-herbivore-parasitoid system, Oecologia, 160, 267-277, doi:10.1007/s00442-009-1294-0, 2009.

Henn, J. J. and Damschen, E. I.: Plant age affects intraspecific variation in functional traits, Plant Ecology, 222, 669-680, doi:10.1007/s11258-021-01136-2, 2021.

Ianson, D. C. and Allen, M. F.: The effects of soil texture on extraction of vesicular-arbuscular mycorrhizal fungal spores from arid sites, Mycologia, 78, 164-168, doi:10.1080/00275514.1986.12025227, 1986.

INVAM: Species descriptions from reference cultures. International culture collection of (vesicular) arbuscular mycorrhizal fungi: https://invam.ku.edu/species-descriptions, last access: July 2023.

Jacob, V., Zhang, H., Churchill, A. C., Yang, J., Choat, B., Medlyn, B. E., Power, S. A., and Tissue, D. T.: Warming reduces net carbon gain and productivity in Medicago sativa L. and Festuca arundinacea, Agronomy, 10, 1601, doi:10.3390/agronomy10101601, 2020.

Jacott, C., Murray, J., and Ridout, C.: Trade-offs in arbuscular mycorrhizal symbiosis: Disease resistance, growth responses and perspectives for crop breeding, Agronomy, 7, 75, doi:10.3390/agronomy7040075, 2017.

Ji, L., Tan, W., and Chen, X.: Arbuscular mycorrhizal mycelial networks and glomalin-related soil protein increase soil aggregation in Calcaric Regosol under well-watered and drought stress conditions, Soil and Tillage Research, 185, 1-8, doi:10.1016/j.still.2018.08.010, 2019.

Kaleeem Abbasi, M., Mahmood Tahir, M., Sabir, N., and Khurshid, M.: Impact of the addition of different plant residues on nitrogen mineralization–immobilization turnover and carbon content of a soil incubated under laboratory conditions, Solid Earth, 6, 197-205, doi:10.5194/se-6-197-2015, 2015.

Kattge, J. and Bonisch, G. and Diaz, S. and Lavorel, S. and Prentice, I. C. and Leadley, P. and Tautenhahn, S. and Werner, G. D. A. and Aakala, T. and Abedi, M. and Acosta, A. T. R. and Adamidis, G. C. and Adamson, K. and Aiba, M. and Albert, C. H. and Alcantara, J. M. and Alcazar, C. C. and Aleixo, I. and Ali, H. and Amiaud, B. and Ammer, C. and Amoroso, M. M. and Anand, M. and Anderson, C. and Anten, N. and Antos, J. and Apgaua, D. M. G. and Ashman, T. L. and Asmara, D. H. and Asner, G. P. and Aspinwall, M. and Atkin, O. and Aubin, I. and Baastrup-Spohr, L. and Bahalkeh, K. and Bahn, M. and Baker, T. and Baker, W. J. and Bakker, J. P. and Baldocchi, D. and Baltzer, J. and Banerjee, A. and Baranger, A. and Barlow, J. and Barneche, D. R. and Baruch, Z. and Bastianelli, D. and Battles, J. and Bauerle, W. and Bauters, M. and Bazzato, E. and Beckmann, M. and Beeckman, H. and Beierkuhnlein, C. and Bekker, R. and Belfry, G. and Belluau, M. and Beloiu, M. and Benavides, R. and Benomar, L. and Berdugo-Lattke, M. L. and Berenguer, E. and Bergamin, R. and Bergmann, J. and Bergmann Carlucci, M. and Berner, L. and Bernhardt-Romermann, M. and Bigler, C. and Bjorkman, A. D. and Blackman, C. and Blanco, C. and Blonder, B. and Blumenthal, D. and Bocanegra-Gonzalez, K. T. and Boeckx, P. and Bohlman, S. and Bohning-Gaese, K. and Boisvert-Marsh, L. and Bond, W. and Bond-Lamberty, B. and Boom, A. and Boonman, C. C. F. and Bordin, K. and Boughton, E. H. and Boukili, V. and Bowman, D. and Bravo, S. and Brendel, M. R. and Broadley, M. R. and Brown, K. A. and Bruelheide, H. and Brumnich, F. and Bruun, H. H. and Bruy, D. and Buchanan, S. W. and Bucher, S. F. and Buchmann, N. and Buitenwerf, R. and Bunker, D. E. and Burger, J. and Burrascano, S. and Burslem, D. and Butterfield, B. J. and Byun, C. and Marques, M. and Scalon, M. C. and Caccianiga, M. and Cadotte, M. and Cailleret, M. and Camac, J. and Camarero, J. J. and Campany, C. and Campetella, G. and Campos, J. A. and Cano-Arboleda, L. and Canullo, R. and Carbognani, M. and Carvalho, F. and Casanoves, F. and Castagneyrol, B. and Catford, J. A. and Cavender-Bares, J. and Cerabolini, B. E. L. and Cervellini, M. and Chacon-Madrigal, E. and Chapin, K. and Chapin, F. S. and Chelli, S. and Chen, S. C. and Chen, A. and Cherubini, P. and Chianucci, F. and Choat, B. and Chung, K. S. and Chytry, M. and Ciccarelli, D. and Coll, L. and Collins, C. G. and Conti, L. and Coomes, D. and Cornelissen, J. H.

C. and Cornwell, W. K. and Corona, P. and Coyea, M. and Craine, J. and Craven, D. and Cromsigt, J. and Csecserits, A. and Cufar, K. and Cuntz, M. and da Silva, A. C. and Dahlin, K. M. and Dainese, M. and Dalke, I. and Dalle Fratte, M. and Dang-Le, A. T. and Danihelka, J. and Dannoura, M. and Dawson, S. and de Beer, A. J. and De Frutos, A. and De Long, J. R. and Dechant, B. and Delagrange, S. and Delpierre, N. and Derroire, G. and Dias, A. S. and Diaz-Toribio, M. H. and Dimitrakopoulos, P. G. and Dobrowolski, M. and Doktor, D. and Drevojan, P. and Dong, N. and Dransfield, J. and Dressler, S. and Duarte, L. and Ducouret, E. and Dullinger, S. and Durka, W. and Duursma, R. and Dymova, O. and A, E. V. and Eckstein, R. L. and Ejtehadi, H. and Elser, J. and Emilio, T. and Engemann, K. and Erfanian, M. B. and Erfmeier, A. and Esquivel-Muelbert, A. and Esser, G. and Estiarte, M. and Domingues, T. F. and Fagan, W. F. and Fagundez, J. and Falster, D. S. and Fan, Y. and Fang, J. and Farris, E. and Fazlioglu, F. and Feng, Y. and Fernandez-Mendez, F. and Ferrara, C. and Ferreira, J. and Fidelis, A. and Finegan, B. and Firn, J. and Flowers, T. J. and Flynn, D. F. B. and Fontana, V. and Forey, E. and Forgiarini, C. and Francois, L. and Frangipani, M. and Frank, D. and Frenette-Dussault, C. and Freschet, G. T. and Fry, E. L. and Fyllas, N. M. and Mazzochini, G. G. and Gachet, S. and Gallagher, R. and Ganade, G. and Ganga, F. and Garcia-Palacios, P. and Gargaglione, V. and Garnier, E. and Garrido, J. L. and de Gasper, A. L. and Gea-Izquierdo, G. and Gibson, D. and Gillison, A. N. and Giroldo, A. and Glasenhardt, M. C. and Gleason, S. and Gliesch, M. and Goldberg, E. and Goldel, B. and Gonzalez-Akre, E. and Gonzalez-Andujar, J. L. and Gonzalez-Melo, A. and Gonzalez-Robles, A. and Graae, B. J. and Granda, E. and Graves, S. and Green, W. A. and Gregor, T. and Gross, N. and Guerin, G. R. and Gunther, A. and Gutierrez, A. G. and Haddock, L. and Haines, A. and Hall, J. and Hambuckers, A. and Han, W. and Harrison, S. P. and Hattingh, W. and Hawes, J. E. and He, T. and He, P. and Heberling, J. M. and Helm, A. and Hempel, S. and Hentschel, J. and Herault, B. and Heres, A. M. and Herz, K. and Heuertz, M. and Hickler, T. and Hietz, P. and Higuchi, P. and Hipp, A. L. and Hirons, A. and Hock, M. and Hogan, J. A. and Holl, K. and Honnay, O. and Hornstein, D. and Hou, E. and Hough-Snee, N. and Hovstad, K. A. and Ichie, T. and Igic, B. and Illa, E. and Isaac, M. and Ishihara, M. and Ivanov, L. and Ivanova, L. and Iversen, C. M. and Izquierdo, J. and Jackson, R. B. and Jackson, B. and Jactel, H. and Jagodzinski, A. M. and Jandt, U. and Jansen, S. and Jenkins, T. and Jentsch, A. and Jespersen, J. R. P. and Jiang, G. F. and Johansen, J. L. and Johnson, D. and Jokela, E. J. and Joly, C. A. and Jordan, G. J.

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and Joseph, G. S. and Junaedi, D. and Junker, R. R. and Justes, E. and Kabzems, R. and Kane, J. and Kaplan, Z. and Kattenborn, T. and Kavelenova, L. and Kearsley, E. and Kempel, A. and Kenzo, T. and Kerkhoff, A. and Khalil, M. I. and Kinlock, N. L. and Kissling, W. D. and Kitajima, K. and Kitzberger, T. and Kjoller, R. and Klein, T. and Kleyer, M. and Klimesova, J. and Klipel, J. and Kloeppel, B. and Klotz, S. and Knops, J. M. H. and Kohyama, T. and Koike, F. and Kollmann, J. and Komac, B. and Komatsu, K. and Konig, C. and Kraft, N. J. B. and Kramer, K. and Kreft, H. and Kuhn, I. and Kumarathunge, D. and Kuppler, J. and Kurokawa, H. and Kurosawa, Y. and Kuyah, S. and Laclau, J. P. and Lafleur, B. and Lallai, E. and Lamb, E. and Lamprecht, A. and Larkin, D. J. and Laughlin, D. and Le Bagousse-Pinguet, Y. and le Maire, G. and le Roux, P. C. and le Roux, E. and Lee, T. and Lens, F. and Lewis, S. L. and Lhotsky, B. and Li, Y. and Li, X. and Lichstein, J. W. and Liebergesell, M. and Lim, J. Y. and Lin, Y. S. and Linares, J. C. and Liu, C. and Liu, D. and Liu, U. and Livingstone, S. and Llusia, J. and Lohbeck, M. and Lopez-Garcia, A. and Lopez-Gonzalez, G. and Lososova, Z. and Louault, F. and Lukacs, B. A. and Lukes, P. and Luo, Y. and Lussu, M. and Ma, S. and Maciel Rabelo Pereira, C. and Mack, M. and Maire, V. and Makela, A. and Makinen, H. and Malhado, A. C. M. and Mallik, A. and Manning, P. and Manzoni, S. and Marchetti, Z. and Marchino, L. and Marcilio-Silva, V. and Marcon, E. and Marignani, M. and Markesteijn, L. and Martin, A. and Martinez-Garza, C. and Martinez-Vilalta, J. and Maskova, T. and Mason, K. and Mason, N. and Massad, T. J. and Masse, J. and Mayrose, I. and McCarthy, J. and McCormack, M. L. and McCulloh, K. and McFadden, I. R. and McGill, B. J. and McPartland, M. Y. and Medeiros, J. S. and Medlyn, B. and Meerts, P. and Mehrabi, Z. and Meir, P. and Melo, F. P. L. and Mencuccini, M. and Meredieu, C. and Messier, J. and Meszaros, I. and Metsaranta, J. and Michaletz, S. T. and Michelaki, C. and Migalina, S. and Milla, R. and Miller, J. E. D. and Minden, V. and Ming, R. and Mokany, K. and Moles, A. T. and Molnar, A. t. and Molofsky, J. and Molz, M. and Montgomery, R. A. and Monty, A. and Moravcova, L. and Moreno-Martinez, A. and Moretti, M. and Mori, A. S. and Mori, S. and Morris, D. and Morrison, J. and Mucina, L. and Mueller, S. and Muir, C. D. and Muller, S. C. and Munoz, F. and Myers-Smith, I. H. and Myster, R. W. and Nagano, M. and Naidu, S. and Narayanan, A. and Natesan, B. and Negoita, L. and Nelson, A. S. and Neuschulz, E. L. and Ni, J. and Niedrist, G. and Nieto, J. and Niinemets, U. and Nolan, R. and Nottebrock, H. and Nouvellon, Y. and Novakovskiy, A. and Nutrient, N. and Nystuen, K. O. and

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O'Grady, A. and O'Hara, K. and O'Reilly-Nugent, A. and Oakley, S. and Oberhuber, W. and Ohtsuka, T. and Oliveira, R. and Ollerer, K. and Olson, M. E. and Onipchenko, V. and Onoda, Y. and Onstein, R. E. and Ordonez, J. C. and Osada, N. and Ostonen, I. and Ottaviani, G. and Otto, S. and Overbeck, G. E. and Ozinga, W. A. and Pahl, A. T. and Paine, C. E. T. and Pakeman, R. J. and Papageorgiou, A. C. and Parfionova, E. and Partel, M. and Patacca, M. and Paula, S. and Paule, J. and Pauli, H. and Pausas, J. G. and Peco, B. and Penuelas, J. and Perea, A. and Peri, P. L. and Petisco-Souza, A. C. and Petraglia, A. and Petritan, A. M. and Phillips, O. L. and Pierce, S. and Pillar, V. D. and Pisek, J. and Pomogaybin, A. and Poorter, H. and Portsmuth, A. and Poschlod, P. and Potvin, C. and Pounds, D. and Powell, A. S. and Power, S. A. and Prinzing, A. and Puglielli, G. and Pysek, P. and Raevel, V. and Rammig, A. and Ransijn, J. and Ray, C. A. and Reich, P. B. and Reichstein, M. and Reid, D. E. B. and Rejou-Mechain, M. and de Dios, V. R. and Ribeiro, S. and Richardson, S. and Riibak, K. and Rillig, M. C. and Riviera, F. and Robert, E. M. R. and Roberts, S. and Robroek, B. and Roddy, A. and Rodrigues, A. V. and Rogers, A. and Rollinson, E. and Rolo, V. and Romermann, C. and Ronzhina, D. and Roscher, C. and Rosell, J. A. and Rosenfield, M. F. and Rossi, C. and Roy, D. B. and Royer-Tardif, S. and Ruger, N. and Ruiz-Peinado, R. and Rumpf, S. B. and Rusch, G. M. and Ryo, M. and Sack, L. and Saldana, A. and Salgado-Negret, B. and Salguero-Gomez, R. and Santa-Regina, I. and Santacruz-Garcia, A. C. and Santos, J. and Sardans, J. and Schamp, B. and Scherer-Lorenzen, M. and Schleuning, M. and Schmid, B. and Schmidt, M. and Schmitt, S. and Schneider, J. V. and Schowanek, S. D. and Schrader, J. and Schrodt, F. and Schuldt, B. and Schurr, F. and Selaya Garvizu, G. and Semchenko, M. and Seymour, C. and Sfair, J. C. and Sharpe, J. M. and Sheppard, C. S. and Sheremetiev, S. and Shiodera, S. and Shipley, B. and Shovon, T. A. and Siebenkas, A. and Sierra, C. and Silva, V. and Silva, M. and Sitzia, T. and Sjoman, H. and Slot, M. and Smith, N. G. and Sodhi, D. and Soltis, P. and Soltis, D. and Somers, B. and Sonnier, G. and Sorensen, M. V. and Sosinski, E. E., Jr. and Soudzilovskaia, N. A. and Souza, A. F. and Spasojevic, M. and Sperandii, M. G. and Stan, A. B. and Stegen, J. and Steinbauer, K. and Stephan, J. G. and Sterck, F. and Stojanovic, D. B. and Strydom, T. and Suarez, M. L. and Svenning, J. C. and Svitkova, I. and Svitok, M. and Svoboda, M. and Swaine, E. and Swenson, N. and Tabarelli, M. and Takagi, K. and Tappeiner, U. and Tarifa, R. and Tauugourdeau, S. and Tavsanoglu, C. and Te Beest, M. and Tedersoo, L. and Thiffault, N. and Thom, D. and Thomas, E. and Thompson, K. and Thornton, P.

E. and Thuiller, W. and Tichy, L. and Tissue, D. and Tjoelker, M. G. and Tng, D. Y. P. and Tobias, J. and Torok, P. and Tarin, T. and Torres-Ruiz, J. M. and Tothmeresz, B. and Treurnicht, M. and Trivellone, V. and Trolliet, F. and Trotsiuk, V. and Tsakalos, J. L. and Tsiripidis, I. and Tysklind, N. and Umehara, T. and Usoltsev, V. and Vadeboncoeur, M. and Vaezi, J. and Valladares, F. and Vamosi, J. and van Bodegom, P. M. and van Breugel, M. and Van Cleemput, E. and van de Weg, M. and van der Merwe, S. and van der Plas, F. and van der Sande, M. T. and van Kleunen, M. and Van Meerbeek, K. and Vanderwel, M. and Vanselow, K. A. and Varhammar, A. and Varone, L. and Vasquez Valderrama, M. Y. and Vassilev, K. and Vellend, M. and Veneklaas, E. J. and Verbeeck, H. and Verheyen, K. and Vibrans, A. and Vieira, I. and Villacis, J. and Violle, C. and Vivek, P. and Wagner, K. and Waldram, M. and Waldron, A. and Walker, A. P. and Waller, M. and Walther, G. and Wang, H. and Wang, F. and Wang, W. and Watkins, H. and Watkins, J. and Weber, U. and Weedon, J. T. and Wei, L. and Weigelt, P. and Weiher, E. and Wells, A. W. and Wellstein, C. and Wenk, E. and Westoby, M. and Westwood, A. and White, P. J. and Whitten, M. and Williams, M. and Winkler, D. E. and Winter, K. and Womack, C. and Wright, I. J. and Wright, S. J. and Wright, J. and Pinho, B. X. and Ximenes, F. and Yamada, T. and Yamaji, K. and Yanai, R. and Yankov, N. and Yguel, B. and Zanini, K. J. and Zanne, A. E. and Zeleny, D. and Zhao, Y. P. and Zheng, J. and Zheng, J. and Zieminska, K. and Zirbel, C. R. and Zizka, G. and Zo-Bi, I. C. and Zotz, G. and Wirth, C.: TRY plant trait database - enhanced coverage and open access, Global Change Biology, 26, 119-188, doi:10.1111/gcb.14904, 2020.

Kilpeläinen, J., Barbero-López, A., Vestberg, M., Heiskanen, J., and Lehto, T.: Does severe soil drought have after-effects on arbuscular and ectomycorrhizal root colonisation and plant nutrition?, Plant and Soil, 418, 377-386, doi:10.1007/s11104-017-3308-8, 2017.

Kirkham, M. B., Hillel, D. (Ed.): Water-use efficiency, Encyclopedia of Soils in the Environment Elsevier, Oxford2005.

Kleyer, M., Bekker, R. M., Knevel, I. C., Bakker, J. P., Thompson, K., Sonnenschein, M., Poschlod, P., van Groenendael, J. M., Klimeš, L., Klimešová, J., Klotz, S., Rusch, G. M., Hermy, M., Adriaens, D., Boedeltje, G., Bossuyt, B., Dannemann, A., Endels, P., Götzenberger, L., Hodgson, J. G., Jackel, A. K., Kühn, I., Kunzmann, D., Ozinga, W. A., Römermann, C., Stadler, M., Schlegelmilch, J., Steendam, H.

J., Tackenberg, O., Wilmann, B., Cornelissen, J. H. C., Eriksson, O., Garnier, E., and Peco, B.: The LEDA Traitbase: a database of life-history traits of the Northwest European flora, Journal of Ecology, 96, 1266-1274, doi:10.1111/j.1365-2745.2008.01430.x, 2008.

Knot, P., Skladanka, J., Hrabe, F., Slama, P., Nawrath, A., and Kvasnovsky, M.: Changes in the species diversity of grassland communities during secondary succession, Bulgarian Journal of Agricultural Science, 21, 822–828, 2015.

Komainda, M., Küchenmeister, K., Küchenmeister, F., Breitsameter, L., Wrage-Mönnig, N., Kayser, M., and Isselstein, J.: Forage legumes for future dry climates: Lower relative biomass losses of minor forage legumes compared toTrifolium repensunder conditions of periodic drought stress, Journal of Agronomy and Crop Science, 205, 460-469, doi:10.1111/jac.12337, 2019.

Kruger, C., Kohout, P., Janouskova, M., Puschel, D., Frouz, J., and Rydlova, J.: Plant communities rather than soil properties structure arbuscular mycorrhizal fungal communities along primary succession on a mine spoil, Frontiers in Microbiology, 8, 719, doi:10.3389/fmicb.2017.00719, 2017.

Lavorel, S. and Grigulis, K.: How fundamental plant functional trait relationships scale-up to trade-offs and synergies in ecosystem services, Journal of Ecology, 100, 128-140, doi:10.1111/j.1365-2745.2011.01914.x, 2012.

Ledgard, S. F. and Steele, K. W.: Biological nitrogen fixation in mixed legume/grass pastures, Plant and Soil, 141, 137-153, doi:10.1007/BF00011314, 1992.

Leitinger, G., Ruggenthaler, R., Hammerle, A., Lavorel, S., Schirpke, U., Clement, J. C., Lamarque, P., Obojes, N., and Tappeiner, U.: Impact of droughts on water provision in managed alpine grasslands in two climatically different regions of the Alps, Ecohydrology, 8, 1600-1613, doi:10.1002/eco.1607, 2015.

Li, W., Wang, L., Qian, S., He, M., Cai, X., and Ding, J.: Root characteristics explain greater water use efficiency and drought tolerance in invasive Compositae plants, Plant and Soil, 483, 209-223, doi:10.1007/s11104-022-05734-5, 2022.

Lozano, Y. M., Aguilar-Trigueros, C. A., Flaig, I. C., and Rillig, M. C.: Root trait responses to drought are more heterogeneous than leaf trait responses, Functional Ecology, 34, 2224-2235, doi:10.1111/1365-2435.13656, 2020.

Lu, Y., Duursma, R. A., Farrior, C. E., Medlyn, B. E., and Feng, X.: Optimal stomatal drought response shaped by competition for water and hydraulic risk can explain plant trait covariation, New Phytologist, 225, 1206-1217, doi:10.1111/nph.16207, 2020.

Lubbe, F. C., Bitomský, M., Hajek, T., de Bello, F., Doležal, J., Jandová, V., Janeček, Š., Bartušková, A., Lanta, V., and Klimešová, J.: A tale of two grasslands: how belowground storage organs coordinate their traits with water-use traits, Plant and Soil, 465, 533-548, doi:10.1007/s11104-021-05031-7, 2021.

Ma, Z., Guo, D., Xu, X., Lu, M., Bardgett, R. D., Eissenstat, D. M., McCormack, M. L., and Hedin, L. O.: Evolutionary history resolves global organization of root functional traits, Nature, 555, 94-97, doi:10.1038/nature25783, 2018.

Mahdavi, S. M. E., Salehi, H., and Zarei, M.: Can arbuscular mycorrhizal fungi ameliorate the adverse effects of deficit irrigation on tall fescue (Festuca arundinacea Schreb.)?, Journal of Soil Science and Plant Nutrition, 0-0, doi:10.4067/s0718-95162018005001902, 2018.

Maitra, P., Zheng, Y., Chen, L., Wang, Y.-L., Ji, N.-N., Lü, P.-P., Gan, H.-Y., Li, X.-C., Sun, X., Zhou, X.-H., and Guo, L.-D.: Effect of drought and season on arbuscular mycorrhizal fungi in a subtropical secondary forest, Fungal Ecology, 41, 107-115, doi:10.1016/j.funeco.2019.04.005, 2019.

Malinowski, D.: Rhizomatous ecotypes and symbiosis with endophytes as new possibilities of improvement in competitive ability of meadow fescue (Festuca pratensis Huds.). Doctoral Thesis, Swiss Federal Institute of Technology, Zürich, doi:10.3929/ethz-a-001575829, 1995.

Manzoni, S., Vico, G., Palmroth, S., Porporato, A., and Katul, G.: Optimization of stomatal conductance for maximum carbon gain under dynamic soil moisture, Advances in Water Resources, 62, 90-105, doi:10.1016/j.advwatres.2013.09.020, 2013.

Martin-StPaul, N., Delzon, S., and Cochard, H.: Plant resistance to drought depends on timely stomatal closure, Ecology Letters, 20, 1437-1447, doi:10.1111/ele.12851, 2017.

Mason, N. W., Orwin, K., Lambie, S., Woodward, S. L., McCready, T., and Mudge, P.: Leaf economics spectrum-productivity relationships in intensively grazed pastures depend on dominant species identity, Ecology and Evolution, 6, 3079-3091, doi:10.1002/ece3.1964, 2016.

McCormack, M. L. and Iversen, C. M.: Physical and functional constraints on viable belowground acquisition strategies, Frontiers in Plant Science, 10, 1215, doi:10.3389/fpls.2019.01215, 2019.

Meziane, D. and Shipley, B.: Direct and indirect relationships between specific leaf area, leaf nitrogen and leaf gas exchange. Effects of irradiance and nutrient supply, Annals of Botany, 88, 915-927, doi:10.1006/anbo.2001.1536, 2001.

Miller, J. E. D., Li, D., LaForgia, M., and Harrison, S.: Functional diversity is a passenger but not driver of drought-related plant diversity losses in annual grasslands, Journal of Ecology, 107, 2033-2039, doi:10.1111/1365-2745.13244, 2019.

Murray, L. K.: Early development characteristics of different clover species during establishment, Lincoln University, Christchurch, New Zealand, 2012.

Oram, N. J., Ingrisch, J., Bardgett, R. D., Brennan, F., Dittmann, G., Gleixner, G., Illmer, P., Praeg, N., and Bahn, M.: Drought intensity alters productivity, carbon allocation and plant nitrogen uptake in fast versus slow grassland communities, Journal of Ecology, doi:10.1111/1365-2745.14136, 2023.

Ordonez, J. C., van Bodegom, P. M., Witte, J. P., Bartholomeus, R. P., van Hal, J. R., and Aerts, R.: Plant strategies in relation to resource supply in mesic to wet environments: does theory mirror nature?, American Naturalist, 175, 225-239, doi:10.1086/649582, 2010.

Ostonen, I., Püttsepp, Ü., Biel, C., Alberton, O., Bakker, M. R., Lõhmus, K., Majdi, H., Metcalfe, D., Olsthoorn, A. F. M., Pronk, A., Vanguelova, E., Weih, M., and Brunner, I.: Specific root length as an indicator of environmental change, Plant Biosystems - An International Journal Dealing with all Aspects of Plant Biology, 141, 426-442, doi:10.1080/11263500701626069, 2007.

Pande, H. and Singh, J. S.: Comparative biomass and water status of four range grasses grown under two soil water conditions, Society for Range Management, doi:10.2307/3898103, 1981.

Parniske, M.: Arbuscular mycorrhiza: the mother of plant root endosymbioses, Nature Reviews Microbiology, 6, 763-775, doi:10.1038/nrmicro1987, 2008.

Paterson, E., Thornton, B., Midwood, A. J., and Sim, A.: Defoliation alters the relative contributions of recent and non-recent assimilate to root exudation from Festuca rubra, Plant, Cell & Environment, 28, 1525-1533, doi:10.1111/j.1365-3040.2005.01389.x, 2005.

Peralta, A. M. L., Sánchez, A. M., Luzuriaga, A. L., Bello, F., and Escudero, A.: Evidence of functional species sorting by rainfall and biotic interactions: A community monolith experimental approach, Journal of Ecology, 107, 2772-2788, doi:10.1111/1365-2745.13210, 2019.

Perez-Ramos, I. M., Matias, L., Gomez-Aparicio, L., and Godoy, O.: Functional traits and phenotypic plasticity modulate species coexistence across contrasting climatic conditions, Nature Communications, 10, 2555, doi:10.1038/s41467-019-10453-0, 2019.

Pérez-Ramos, I. M., Volaire, F., Fattet, M., Blanchard, A., and Roumet, C.: Tradeoffs between functional strategies for resource-use and drought-survival in Mediterranean rangeland species, Environmental and Experimental Botany, 87, 126-136, doi:10.1016/j.envexpbot.2012.09.004, 2013.

Peters, A., Nehls, T., and Wessolek, G.: Technical note: Improving the AWAT filter with interpolation schemes for advanced processing of high resolution data, Hydrology and Earth System Sciences, 20, 2309-2315, doi:10.5194/hess-20-2309-2016, 2016.

Peters, A., Nehls, T., Schonsky, H., and Wessolek, G.: Separating precipitation and evapotranspiration from noise – a new filter routine for high-resolution lysimeter data, Hydrology and Earth System Sciences, 18, 1189-1198, doi:10.5194/hess-18-1189-2014, 2014.

Peters, A., Groh, J., Schrader, F., Durner, W., Vereecken, H., and Pütz, T.: Towards an unbiased filter routine to determine precipitation and evapotranspiration from high precision lysimeter measurements, Journal of Hydrology, 549, 731-740, doi:10.1016/j.jhydrol.2017.04.015, 2017.

Philippot, S., Allirand, J. M., Cartier, M., and Gosse, G.: The role of different daily irradiations on shoot growth and root/shoot ratio in lucerne (Medicago sativa L.), Annals of Botany, 68, 329-335, doi:10.1093/oxfordjournals.aob.a088260, 1991.

Potsch, M. E.: Kreisslaufwirtschaft im Alpenländischen Grünlandbetrieb, Ökosoziales Forum und BAL Gumpenstein, Vienna1999.

Prieto, I., Litrico, I., Violle, C., and Barre, P.: Five species, many genotypes, broad phenotypic diversity: When agronomy meets functional ecology, American Journal of Botany, 104, 62-71, doi:10.3732/ajb.1600354, 2017.

Quan, Q., Zhang, F., Meng, C., Ma, F., Zhou, Q., Sun, F., and Niu, S.: Shifting biomass allocation determines community water use efficiency under climate warming, Environmental Research Letters, 15, 094041, doi:10.1088/1748-9326/aba472, 2020.

Querejeta, J. I., Prieto, I., Torres, P., Campoy, M., Alguacil, M. M., and Roldán, A.: Water-spender strategy is linked to higher leaf nutrient concentrations across plant species colonizing a dry and nutrient-poor epiphytic habitat, Environmental and Experimental Botany, 153, 302-310, doi:10.1016/j.envexpbot.2018.06.007, 2018.

R Core Team: R: A language and environment for statistical computing. R Foundation for Statistical Computing [code], 2022.

Reich, P. B.: The world-wide 'fast-slow' plant economics spectrum: a traits manifesto, Journal of Ecology, 102, 275-301, doi:10.1111/1365-2745.12211, 2014.

Reich, P. B., Buschena, C., Tjoelker, M. G., Wrage, K., Knops, J., Tilman, D., and Machado, J. L.: Variation in growth rate and ecophysiology among 34 grassland and savanna species under contrasting

N supply: a test of functional group differences, New Phytologist, 157, 617-631, doi:10.1046/j.1469-8137.2003.00703.x, 2003.

Reichstein, M., Bahn, M., Ciais, P., Frank, D., Mahecha, M. D., Seneviratne, S. I., Zscheischler, J., Beer, C., Buchmann, N., Frank, D. C., Papale, D., Rammig, A., Smith, P., Thonicke, K., van der Velde, M., Vicca, S., Walz, A., and Wattenbach, M.: Climate extremes and the carbon cycle, Nature, 500, 287-295, doi:10.1038/nature12350, 2013.

Roumet, C., Birouste, M., Picon-Cochard, C., Ghestem, M., Osman, N., Vrignon-Brenas, S., Cao, K. F., and Stokes, A.: Root structure-function relationships in 74 species: evidence of a root economics spectrum related to carbon economy, New Phytologist, 210, 815-826, doi:10.1111/nph.13828, 2016.

Ryser, P. and Eek, L.: Consequences of phenotypic plasticity vs. interspecific differences in leaf and root traits for acquisition of aboveground and belowground resources, American Journal of Botany, 87, 402-411, doi:10.2307/2656636, 2000.

Sanderson, M. A., Brink, G., Stout, R., and Ruth, L.: Grass–legume proportions in forage seed mixtures and effects on herbage yield and weed abundance, Agronomy Journal, 105, 1289-1297, doi:10.2134/agronj2013.0131, 2013.

Schüßler, A. and Walker, C.: The Glomeromycota. A species list with new families and new genera., Gloucester, England2010.

Schwamback, D., Persson, M., Berndtsson, R., Bertotto, L. E., Kobayashi, A. N. A., and Wendland, E. C.: Automated low-cost soil moisture sensors: trade-off between cost and accuracy, Sensors (Basel), 23, 10.3390/s23052451, 2023.

Shahzad, T., Chenu, C., Repinçay, C., Mougin, C., Ollier, J.-L., and Fontaine, S.: Plant clipping decelerates the mineralization of recalcitrant soil organic matter under multiple grassland species, Soil Biology and Biochemistry, 51, 73-80, doi:10.1016/j.soilbio.2012.04.014, 2012.

Silva-Flores, P., Bueno, C. G., Neira, J., and Palfner, G.: Factors affecting arbuscular mycorrhizal fungi spore density in the Chilean Mediterranean-type ecosystem, Journal of Soil Science and Plant Nutrition, 19, 42-50, doi:10.1007/s42729-018-0004-6, 2019.

Spehn, E. M., Scherer-Lorenzen, M., Schmid, B., Hector, A., Caldeira, M. C., Dimitrakopoulos, P. G., Finn, J. A., Jumpponen, A., O'Donnovan, G., Pereira, J. S., Schulze, E. D., Troumbis, A. Y., and Körner, C.: The role of legumes as a component of biodiversity in a cross-European study of grassland biomass nitrogen, Oikos, 98, 205-218, doi:10.1034/j.1600-0706.2002.980203.x, 2002.

Sun, K., McCormack, M. L., Li, L., Ma, Z., and Guo, D.: Fast-cycling unit of root turnover in perennial herbaceous plants in a cold temperate ecosystem, Scientific Reports, 6, 19698, doi:10.1038/srep19698, 2016.

Sun, X., Shi, J., and Ding, G.: Combined effects of arbuscular mycorrhiza and drought stress on plant growth and mortality of forage sorghum, Applied Soil Ecology, 119, 384-391, doi:10.1016/j.apsoil.2017.07.030, 2017.

Talgre, L., Roostalu, H., Mäeorg, E., and Lauringson, E.: Nitrogen and carbon release during decomposition of roots and shoots of leguminous green manure crops, Agronomy Research, 15, 594-601, 2017.

Tardy, F., Damour, G., Dorel, M., and Moreau, D.: Trait-based characterisation of soil exploitation strategies of banana, weeds and cover plant species, PLoS One, 12, e0173066, doi:10.1371/journal.pone.0173066, 2017.

Tasser, E. and Tappeiner, U.: New model to predict rooting in diverse plant community compositions, Ecological Modelling, 185, 195-211, doi:10.1016/j.ecolmodel.2004.11.024, 2005.

Tello-García, E., Huber, L., Leitinger, G., Peters, A., Newesely, C., Ringler, M.-E., and Tasser, E.: Drought- and heat-induced shifts in vegetation composition impact biomass production and water use of alpine grasslands, Environmental and Experimental Botany, 169, 103921, doi:10.1016/j.envexpbot.2019.103921, 2020.

Thakur, M. P., Risch, A. C., and van der Putten, W. H.: Biotic responses to climate extremes in terrestrial ecosystems, iScience, 25, 104559, doi:10.1016/j.isci.2022.104559, 2022.

Tuo, X.-Q., He, L., and Zou, Y.-N.: Alleviation of drought stress in white clover after inoculation with arbuscular mycorrhizal fungi, Notulae Botanicae Horti Agrobotanici Cluj-Napoca, 45, 220-224, doi:10.15835/nbha45110709, 2017.

Wang, P., Huang, K., and Hu, S.: Distinct fine-root responses to precipitation changes in herbaceous and woody plants: a meta-analysis, New Phytologist, 225, 1491-1499, doi:10.1111/nph.16266, 2020.

Wei, X., Reich, P. B., and Hobbie, S. E.: Legumes regulate grassland soil N cycling and its response to variation in species diversity and N supply but not CO(2), Global Change Biology, 25, 2396-2409, doi:10.1111/gcb.14636, 2019.

Wohlfahrt, G., Bahn, M., Haubner, E., Horak, I., Michaeler, W., Rottmar, K., Tappeiner, U., and Cernusca, A.: Inter-specific variation of the biochemical limitation to photosynthesis and related leaf traits of 30 species from mountain grassland ecosystems under different land use, Plant, Cell & Environment, 22, 1281-1296, doi:10.1046/j.1365-3040.1999.00479.x, 1999.

Wright, I. J., Reich, P. B., Westoby, M., Ackerly, D. D., Baruch, Z., Bongers, F., Cavender-Bares, J., Chapin, T., Cornelissen, J. H., Diemer, M., Flexas, J., Garnier, E., Groom, P. K., Gulias, J., Hikosaka, K., Lamont, B. B., Lee, T., Lee, W., Lusk, C., Midgley, J. J., Navas, M. L., Niinemets, U., Oleksyn, J., Osada, N., Poorter, H., Poot, P., Prior, L., Pyankov, V. I., Roumet, C., Thomas, S. C., Tjoelker, M. G., Veneklaas, E. J., and Villar, R.: The worldwide leaf economics spectrum, Nature, 428, 821-827, doi:10.1038/nature02403, 2004.

Zafari, M., Ebadi, A., and Jahanbakhsh Godehkahriz, S.: Effect of seed inoculation on alfalfa tolerance to water deficit stress, Notulae Botanicae Horti Agrobotanici Cluj-Napoca, 45, 82-88, doi:10.15835/nbha45110424, 2017.

Zhang, C., Shi, S., Wang, B., and Zhao, J.: Physiological and biochemical changes in different drought-tolerant alfalfa (Medicago sativa L.) varieties under PEG-induced drought stress, Acta Physiologiae Plantarum, 40, doi:10.1007/s11738-017-2597-0, 2018a.

Zhang, T., Hu, Y., Zhang, K., Tian, C., and Guo, J.: Arbuscular mycorrhizal fungi improve plant growth of Ricinus communis by altering photosynthetic properties and increasing pigments under drought and salt stress, Industrial Crops and Products, 117, 13-19, doi:10.1016/j.indcrop.2018.02.087, 2018b.

Zhao, J., Xu, T., Xiao, J., Liu, S., Mao, K., Song, L., Yao, Y., He, X., and Feng, H.: Responses of water use efficiency to drought in Southwest China, Remote Sensing, 12, 199, doi:10.3390/rs12010199, 2020.

Zhao, R., Guo, W., Bi, N., Guo, J., Wang, L., Zhao, J., and Zhang, J.: Arbuscular mycorrhizal fungi affect the growth, nutrient uptake and water status of maize ( Zea mays L.) grown in two types of coal mine spoils under drought stress, Applied Soil Ecology, 88, 41-49, doi:10.1016/j.apsoil.2014.11.016, 2015.

Zhao, W., Liu, B., Chang, X., Yang, Q., Yang, Y., Liu, Z., Cleverly, J., and Eamus, D.: Evapotranspiration partitioning, stomatal conductance, and components of the water balance: A special case of a desert ecosystem in China, Journal of Hydrology, 538, 374-386, doi:10.1016/j.jhydrol.2016.04.042, 2016.

Zhou, L., Hong, Y., Li, C., Lu, C., He, Y., Shao, J., Sun, X., Wang, C., Liu, R., Liu, H., Zhou, G., and Zhou, X.: Responses of biomass allocation to multi-factor global change: A global synthesis, Agriculture, Ecosystems & Environment, 304, 107115, doi:10.1016/j.agee.2020.107115, 2020.