

RESEARCH ARTICLE

Rooting depth and specific leaf area modify the impact of experimental drought duration on temperate grassland species

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Abstract

1. Due to climate change, temperate grasslands are being exposed to increasingly severe droughts. Concurrently, land-use intensification is altering grasslands' functional composition by promoting fast-growing, resource-acquisitive species with high specific leaf area (SLA).
2. How SLA affects the ability of grassland species to resist and recover from increasingly severe droughts and if deep roots improve their drought performance remains unclear. To investigate this, we established a common-garden field experiment including temperate grassland species with SLAs of 17.9–39.3 mm² g⁻¹ and maximal rooting depths of 16–252 cm. After 1.5 years, we simulated droughts for 0, 79, 134, 177 and 220 days.
3. Drought effects on plant performance increased with drought length, reducing the survival of green tissue and annual biomass by up to ~50% across all 32 species considered. As plant-available water remained in deep soil layers by the end of all treatments, deep roots mitigated the negative effect of increasing drought length on productivity in the later stage of drought and favoured productivity after a longer drought. The low-to-high SLA trait gradient among the 16 graminoid species seemed to represent alternative survival strategies ranging from dehydration tolerance to dehydration avoidance, rather than drought sensitivity. Variable drought responses along the SLA gradient of forbs imply that multiple other traits are related to drought resistance across evolutionarily distant species.
4. *Synthesis.* Our results suggest that deep roots are beneficial for temperate grassland species subjected to longer periods without rainfall when plant-available water is lacking in shallow soil layers but remaining in deep soil layers. In the face of increasing drought severity, we thus recommend (1) fostering deep-rooted species in intensive grasslands on deep, productive soil and (2) directing further studies towards identifying management practices that support deep rooting in semi-natural grasslands.

KEYWORDS

climate change, common garden, drought severity gradient, land-use, plant traits, precipitation exclusion

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1 | INTRODUCTION

Grasslands cover more than one third of the Earth's terrestrial habitats and 35% of agriculturally used land in Europe (Gibson & Newman, 2019; Smit et al., 2008). They provide essential goods and ecosystem services (Gibson & Newman, 2019) and include the biomes with the highest vascular plant-species richness at <50 m² scale (Boch et al., 2020; Wilson et al., 2012). Due to climate change, temperate grasslands will be exposed to more frequent and more severe droughts (Christidis et al., 2015; IPCC, 2014; Spinoni et al., 2018). At the same time, land-use intensification with massively increased fertilization rates, sowing of high-yielding forage species and consequential higher cutting frequency (Bosshard et al., 2010) is altering grasslands' functional composition by favouring fast-growing, resource-acquisitive species (Allan et al., 2015; Boch et al., 2021). To enable the multiple valuable goods and ecosystem services of temperate grasslands to be preserved under global change, it is crucial to understand how traits that are favoured by intensified land-use affect plant performance under increasingly severe drought. Furthermore, we need to identify traits that might improve plant performance under increasingly severe drought.

In previous studies, droughts have been found to reduce biomass production in temperate grasslands (Kreyling et al., 2017; Stampfli et al., 2018), soil respiration and ecosystem photosynthesis (Jentsch et al., 2011; Wu et al., 2011), and to change plant community structure (Stampfli et al., 2018; Tello-García et al., 2020). Kramp et al. (2022) showed that different traits explain plant responses to contrasting drought severities, consistent with the idea that favourable plant strategies might be contingent on the severity of a drought (Volaire et al., 2014). Further studies suggest that reductions in above-ground biomass become stronger with increasing precipitation reduction (Gao et al., 2019; Ingrisch et al., 2023; Kröel-Dulay et al., 2022; Oram et al., 2023; Wilcox et al., 2017). However, our understanding of how plant responses to drought change with increasing drought severity remains limited as across-site or across-study comparisons of different drought severities involve confounding drought severity with biotic and abiotic site conditions. Further, experiments simulating drought severity gradients within single sites are rare and, to the best of our knowledge, so far have manipulated severity in terms of different precipitation reductions over the same period of time (Ingrisch et al., 2023; Oram et al., 2023; Zhang et al., 2019), but not in terms of complete precipitation exclusion over different periods of time. This gap needs to be addressed because the way in which drought is simulated can affect plant responses, even if the total amount of excluded precipitation is similar (Carroll et al., 2021).

Functional trait-based approaches to investigating vegetation responses to environmental change have been widely recognized (Cornelissen et al., 2003). One decisive function for plant performance is water acquisition and the importance of deep roots for acquiring water from deep soil layers has been well-acknowledged in

trees (Burgess et al., 1998; Mackay et al., 2020; Maeght et al., 2013). However, whether deep roots are also important for grassland species under drought remains unclear, as previous studies have found both a positive effect of rooting depth on plant performance under drought (Zeiter et al., 2016) and also no such effect (Hoekstra et al., 2014; Hofer et al., 2017; Volaire, 2008). How rooting depth is related to land-use intensity in temperate grasslands is barely studied. However, there is evidence that land-use-driven changes in community composition affect rooting parameters, including rooting depth (Tasser et al., 2021).

A further important dimension of function is represented by the leaf economic spectrum, ranging from slow-growing, resource-conservative species to fast-growing, resource-acquisitive species (Díaz et al., 2016; Wright et al., 2004). Of the several traits involved in the leaf economic spectrum, specific leaf area (leaf area per mass, SLA) is probably one of the most widely used proxies for the position of a species along this slow-fast axis. Slow growth and resource-conservative traits (low SLA) are advantageous when resources are limited (Reich, 2014) and are thus expected to be favourable under drought (Harrison et al., 2015). On the other hand, fast-growing species with resource-acquisitive traits (high SLA) are favoured by land-use intensification and nutrient addition (Louault et al., 2005; Maskell et al., 2010; Ordoñez et al., 2009) and are expected to recover faster after a drought (Ingrisch et al., 2018). However, previous studies addressing the effect of SLA on plant performance under drought have reported mixed results (Dawson et al., 2022; Griffin-Nolan et al., 2019; Milbau et al., 2005; Pérez-Ramos et al., 2013, 2020; Volaire, 2008), probably because the droughts studied differed in severity. Hence, it remains unresolved how SLA relates to species performance during and after increasingly long-lasting periods without precipitation.

In this study, we investigated how rooting depth and SLA are related to plant performance under drought at the species level. Thereby, unravelling how SLA is related to species' drought performance will improve our mechanistic understanding of the combined effects of land-use intensification and climate change, that is, if and how the promotion of high SLA species by increased fertilization rates, seeding of fast-growing forage species and higher cutting frequency affects grassland performance under and after increasingly severe drought.

We established a common-garden field experiment with temperate grassland species that cover wide ranges of SLA and rooting depth values. By simulating four droughts of different lengths within one growing season and a control treatment, we tested the following hypotheses: (a) negative drought effects increase with increasing drought duration, (b) deeper roots mitigate the negative effects of longer droughts, and (c) lower SLA mitigates the direct negative effect of longer droughts, but higher SLA promotes regrowth post drought. To gain a comprehensive understanding of the effects, we considered abundance-based as well as productivity-based measures of plant performance over all species and separately for forbs and graminoids.

2 | MATERIALS AND METHODS

2.1 | Study site

The experiment was conducted in an arable field designated for agricultural experiments next to the Bern University of Applied Sciences campus in Zollikofen, Switzerland (46°59'38" N, 7°27'57" E). Therefore, our fieldwork did not require permission beyond the consent of the school. The area is situated in the Swiss Central Plateau at an elevation of 559 m a.s.l. and has a temperate climate with a mean annual temperature of 9.3°C and a mean annual precipitation of 1022 mm; the mean precipitation sum from April to October is 685 mm (reference period 1991–2020, MeteoSwiss).

The soil is a slightly acid Cambisol (pH = 6.1, measured in water) with an estimated average clay content of 18% and an estimated average silt content of 25%–30% in the top 40–45 cm. Sand, silt and clay fractions were manually sensed in comparison with calibration standards by a soil expert. The plant-available water-holding capacity (AWC) of the soil varies between medium and high (129–162 mm), based on estimates of texture class, rooted space and coarse fraction of soil samples extracted to a depth of ca. 110 cm from nine places across the experimental site in January 2021. For the 2 years preceding our experiment, potatoes and oats had been cultivated at the site.

2.2 | Species and experimental design

To investigate the effects of SLA and rooting depth on drought response metrics of temperate grassland species, we aimed at a set of study species covering wide trait ranges (Table S1). We therefore selected 48 species from four functionally different semi-natural or agricultural Swiss grasslands that have been shaped by very low to high land-use intensity. These reference grasslands, representing different vegetation types (names follow Ellenberg and Leuschner (2010)) were (1) an unfertilized steppe grassland, *Festucion valesiacae* (FES), that is cut once per year for haymaking, (2) an unfertilized semi-dry meadow, *Bromion erecti* (BRO), that is cut twice per year for haymaking, (3) an unfertilized French ryegrass meadow, *Arrhenatherion elatioris* (ARR), that is cut three times per year for haymaking and (4) an English ryegrass mowing pasture, *Cynosurion cristati* (CYN), that is fertilized twice per year with liquid manure, cut four times per year and grazed early and late in the season. Consistent with the findings of Tasser et al. (2021), community-weighted mean (CWM) maximal rooting depth (MRD) was highest in the least intensively managed reference grassland (FES), and lowest in the most intensively managed reference grassland (CYN) (Figure S1a). CWM SLA was lowest in the least intensively managed reference grassland (FES) and highest in the most intensively managed reference grasslands (ARR and CYN) (Figure S1b). Our aim was to include the most abundant perennial species based on frequency recordings in each reference grassland in May 2019. We allocated the 48 species to four subplot

types (FES, BRO, ARR, CYN), according to their prevalence in the reference grasslands to avoid that species chosen from the more productive reference grasslands would overgrow species from the less productive grasslands (Table S1).

The experiment was established under the scaffolding of four adjacent greenhouse tunnels covering a total area of 22 × 24 m. In the summer 2019, the area under the four tunnels was ploughed and 15 plots (3 × 3 m) were established (Figure S2). Each plot comprised four subplots (45 × 120 cm), which were randomly assigned to the four subplot types (FES, BRO, ARR, CYN). For the sowing (or planting of adult plants in the case of *Carex caryophyllea*) in autumn 2019, we divided each subplot into 24 contiguous squares (15 × 15 cm) with a thread grid. Each of the 12 species of the respective subplot type was then sowed (or planted in the case of *C. caryophyllea*) into two randomly assigned squares per subplot, mainly using commercially available seeds (see Appendix S1 for details). The random assignments of subplot type to subplot and species to squares were determined separately for each greenhouse tunnel.

We let the plants establish for 1.5 years under ambient weather conditions with additional watering in a dry and hot period in summer 2020 before we started the drought treatments in spring 2021. Throughout the experiment, plant species other than those studied were repeatedly removed from all plots. On 24 March 2021, we covered the scaffolding above our experimental site with greenhouse plastic (UV M 42, Window high diffuse, gvz-rossat ag, Otelfingen, Switzerland) to hold off rainwater from entering the plots. As the experimental area is slightly sloped (~5°), we dug a pond liner 1-m deep vertically into the ground along the upper side of the experimental area to prevent underground water input.

2.3 | Drought length gradient

We simulated droughts of four different lengths by omitting the regular irrigation of the respective plots while holding off ambient rainfall with the plastic roof from March to October 2021. The four drought treatments were to last for c. 12 weeks (t1), 18 weeks (t2), 24 weeks (t3) and 32 weeks (t4). Each treatment period was started in a staggered fashion, so that all treatments reached mid-drought in the first week of July 2021. The fifth treatment was the control, in which regular watering was provided without interruption while the experiment was covered with a plastic roof. The treatments were randomly allocated to plots ($n = 3$). Arrangements in which a t3 or t4 treatment was placed directly below a control or t1 treatment were rejected to reduce the possibility of incidental flows of irrigation water to these longer drought treatments (Figure S2).

Regular irrigation should prevent edaphic water stress in plots except for periods of drought. We continuously measured soil water potential 15 cm below ground in two control plots (Figure 1) using TEROS 21 soil water potential sensors (METER Group, Pullman, WA, USA and Munich, Germany) and volumetric soil water content 15 cm below ground in one or two plots per treatment using TEROS 11 soil moisture sensors (METER Group, Pullman, WA, USA and Munich,

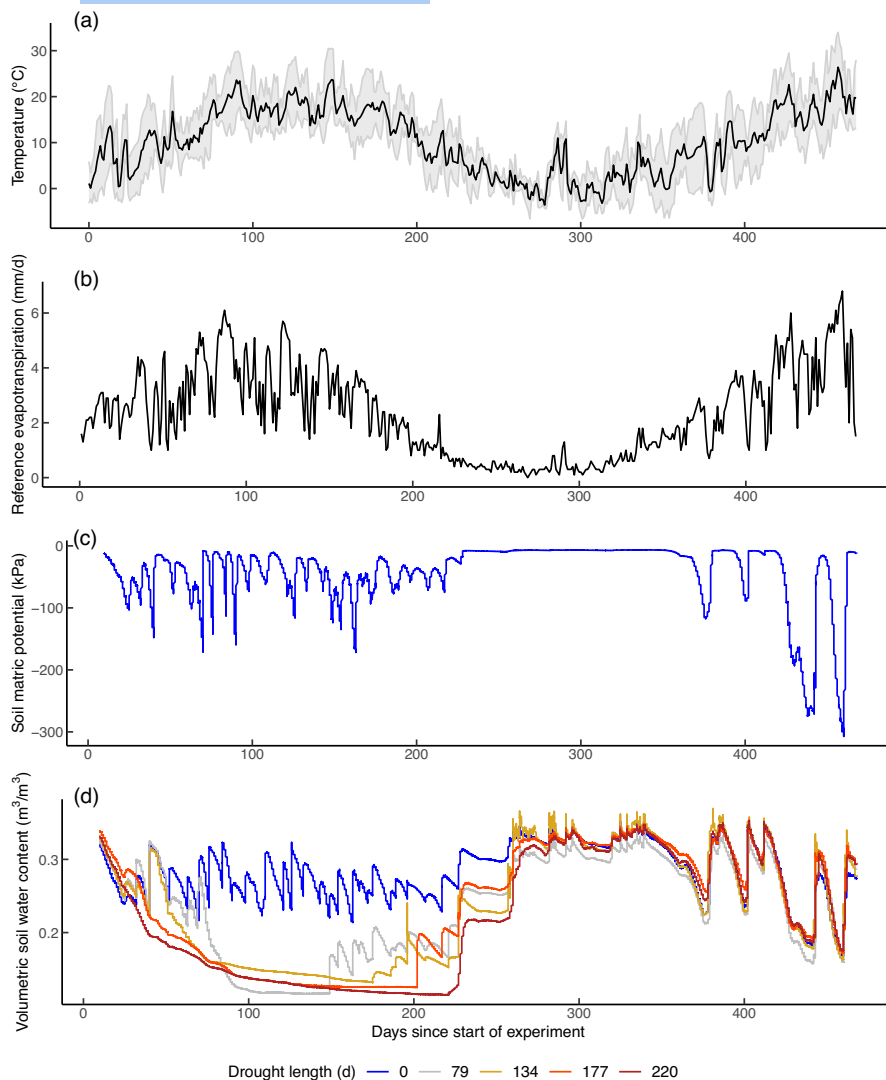


FIGURE 1 Climatic variability and soil moisture during common-garden drought experiment between 19 March 2021 (day 0) and 30 June 2022 (day 468). (a) Daily mean (black line), minimum and maximum (grey ribbon) air temperature 2 m above ground and (b) reference evapotranspiration based on measurements at a distance of 350 m from the experimental site (MeteoSwiss data). (c) Soil matric potential in control plots, continuously measured at 15 cm below ground. (d) Volumetric water content, continuously measured at 15 cm below ground in treatments differing in drought length (mean of two sensors for drought lengths of 0 and 220 days; values of the single sensor for other treatments).

Treatment	Period of suspended watering	Drought length (day)	Water added (L/m ²)	Water balance (L/m ²)
Control	—	0	587	−55
t1	28 May 2021–15 August 2021	79	356	−287
t2	29 April 2021–10 September 2021	134	176	−467
t3	14 April 2021–08 October 2021	177	72	−571
t4	20 March 2021–26 October 2021	220	0	−643

Note: Water added during the irrigation period (20 March 2021–26 October 2021). Water balance is water added minus total evapotranspiration (ET_0) measured at Bern-Zollikofen (MeteoSwiss) during the irrigation period.

Germany). We irrigated plots whenever soil water potential in control plots approached or fell below -100 kPa. This method resulted in realized drought lengths of 0–220 days from the last irrigation before to the first irrigation after the simulated drought and 29 irrigations of 12 – 32 L/m² (Table 1). For the first three irrigations, we used watering cans and then sprinklers. We placed one sprinkler in

the centre of each plot and set the water pressure at 0.25 bar with pressure-reducing valves. In this way, we ensured that the irrigated area was large enough to provide equal irrigation rates within irrigated plots but small enough to avoid water input into neighbouring plots. Within 12 days before the end of the drought treatments t2, t3 and t4, we extracted soil samples for five 20-cm sections of a

TABLE 1 Characterization of the four drought levels in comparison to the control.

1-m-deep drill core next to all subplots of the respective treatment to measure soil matrix potentials (Appendix S2).

At the end of October 2021, we removed the greenhouse plastic roof, irrigated all plots with 20 L/m² and re-exposed them to ambient weather conditions until the end of the experiment. After rewetting, the soil never dehydrated below −310 kPa until July 2022 (Figure 1c). We retrieved air temperature (measured 2 m above-ground) from MeteoSwiss and daily reference evapotranspiration (Allen, 1998) calculated by MeteoSwiss from temperature, solar radiation, humidity, and wind speed for the whole experimental period. All this data from MeteoSwiss was measured at a distance of 350 m from the experimental site (Figure 1a,b).

2.4 | Plant traits

Specific leaf area was calculated based on leaf area (using a leaf area meter LI-3000C, LI-COR Biosciences) and dry weight measured on 12–14 relatively young but fully expanded leaves without obvious signs of herbivory, pathogens, or senescence of 6–12 adult individuals per species in control plots in May 2021 according to Cornelissen et al. (2003) and Garnier et al. (2001). For species with both rosette and stem leaves, we measured stem leaves if available and we included all petioles and stipules into the measurements. We checked and completed our SLA measurements in June 2022 (see Appendix S3 for more details on SLA measurements). We used maximal rooting depth (MRD) values compiled for a previous study (Stampfli et al., 2018) from the TRY database (Kattge et al., 2011), Kutschera et al. (1982, 1992) and references cited therein, and from Fort et al. (2017) and Guerrero-Campo et al. (2006) for *Potentilla verna*. MRD and SLA of our study species were not significantly correlated ($r = -0.29$, $p = 0.11$; Figure 2). Within our set of species, forbs had deeper roots than graminoids (101 cm vs. 50 cm, $t_{15} = 2.5$, $p = 0.02$), whereas SLA did not differ significantly between forbs and graminoids ($t_{29} = -1.7$, $p = 0.09$). To account for additional sources of variation in species' drought survival and post-drought regrowth,

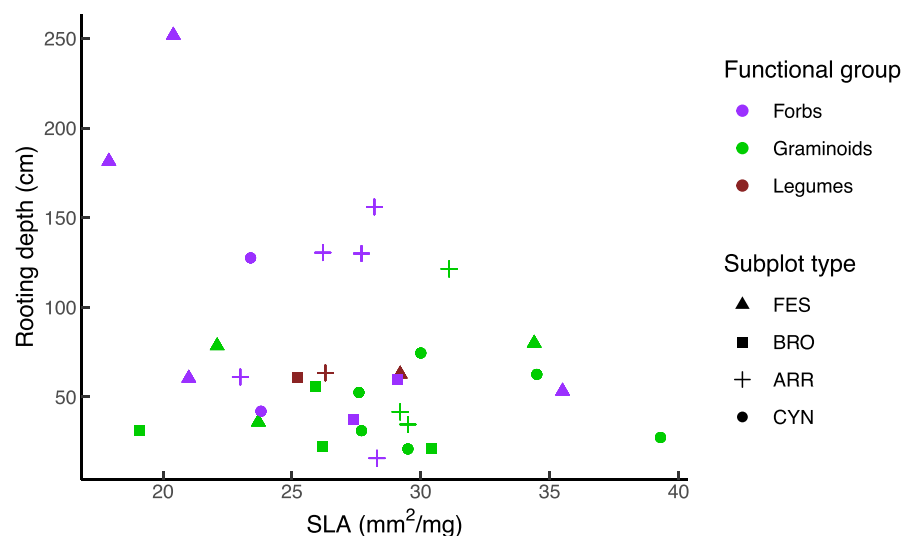
we compiled information about storage organs and forms of vegetative dispersal in our study species from *Flora indicativa* (Landolt & Bäumler, 2010). For the analyses, we summarized the categories of storage organs therein into absence and presence of noticeable storage organs like root swellings, thick rhizomes, hypocotyl tubers, thick lignified main roots, or many thick non-lignified roots. The categories of vegetative dispersal therein were summarized into long distance, short distance, and none (see Appendix S3). To account for size-related variation in species productivity responses to drought, we compiled the maximum height of our study species from *Flora Helvetica* (Lauber et al., 2018). All considered traits of our study species are compiled in Table S1.

2.5 | Metrics of plant performance during and after drought

We used a frame with 24 contiguous 15 × 15 cm grid squares at fixed positions and recorded for each species in each subplot the grid squares in which the species rooted. These records were taken at the start of the experiment (8–26 April 2021), at the start and the end of the respective drought treatment and in spring post drought (12 April–6 May 2022). In the control plots, we also recorded species at the start and the end of drought in the t1, t3 and t4 treatments. Grid squares were only counted if plants of the respective species rooted therein had some green tissue left. At the start of the experiment, all species included in the analyses were present with green tissue in all 15 plots. Seedlings were not considered in any measure.

From this data, we calculated three variables representing drought response at different time stages: The proportion of surviving green tissue (number of grid squares occupied by a species at the end of the drought treatment, not counting squares that were newly occupied during the drought period, divided by the number of occupied squares at the start of the drought treatment), the proportion of regrowth post drought (number of squares that were not occupied by the respective species at the end of the drought treatment

FIGURE 2 Correlation between specific leaf area (SLA) and maximal rooting depth of grassland species studied. Correlation across all species ($r = -0.29$) and species within functional groups is not significant. Species were assigned to different subplot types (shapes) according to the reference grassland from which they were selected: Steppe grassland, *Festucion valesiacae* (FES), semi-dry meadow, *Bromion erecti* (BRO), French ryegrass meadow, *Arrhenatherion elatioris* (ARR), and English ryegrass mowing pasture, *Cynosurion cristati* (CYN).



but occupied in the spring after the drought, divided by the number of squares that were not occupied by the respective species at the end of the drought treatment) and abundance in spring post drought (proportion of occupied squares in spring 2022). To calculate the survival of green tissue in control plots, we used the number of occupied squares recorded concurrently with t4. To calculate the regrowth post drought in the control plots, we used the number of occupied squares recorded concurrently with t1.

We measured biomass production of each plot with control, t2, t3 or t4 treatment for three harvests during the period of experimental droughts, h1 (June 2021), h2 (July–August 2021) and h3 (September 2021) and a fourth harvest in the year after the experimental droughts, h4 (June 2022). In each harvest, we cut the vegetation of the entire plot 4 cm above ground and sorted the biomass by species. Before weighing, all biomass samples were dried at 80°C for at least 24 h. We considered four biomass-related response variables in our analyses: Biomass in the year of drought (h1 + h2 + h3), which was composed of biomass in the first half of drought (h1) and biomass in the second half of drought (h2 + h3), and biomass in summer post drought (h4).

2.6 | Statistical analyses

Our analyses are based on 32 of 48 species, 16 graminoids, 13 non-leguminous forbs and three legumes (Table S1). Eleven species had only poorly established, for two species adequate maximal rooting depth values were not available, for two species we could not measure SLA adequately (Appendix S3) and one species had to be weeded when it started to overgrow other species in the subplot.

All statistical analyses were performed using R software version 4.3.0 (R Core Team, 2023). We tested the effects of the continuous variables drought length (DL), SLA and maximal rooting depth (MRD), as well as the interactions between drought length and SLA (DL × SLA) and drought length and maximal rooting depth (DL × MRD) on all metrics of plant performance. We fitted generalized linear mixed models (GLMMs) with a binomial distribution and logit link function to analyse proportions (survival of green tissue, regrowth post drought and abundance in spring post drought) and linear mixed effect models (LMMs) to analyse effects on biomass-related response variables using the lme4 package (Bates et al., 2015). Before fitting the models, we transformed biomass values from x to $\log_{10}(x + 1)$ and $\log_{10}$ -transformed MRD values to improve the normality of errors and homoscedasticity. Further, the variables DL, SLA, MRD and maximum height were standardized to a mean of 0 and a standard deviation of 1. We included the variables DL, SLA, MRD, SLA × DL and MRD × DL in all models as fixed effects, and subplot and species as random effects. We further included the covariable number of occupied grid squares at the start in all models except the ones with the response variable survival of green tissue, to account for between-plot heterogeneity in species' abundances. We included the covariable maximum height in all models with biomass-related response variables to account for size-related differences in species' productivity

responses. We included the covariable storage organ in models with the response variable survival of green tissue or abundance in spring post drought, to account for possible variation in drought survival related to these structures. We included the covariable vegetative dispersal in models with the response variables regrowth post drought or abundance in spring post drought to account for possible variation in post-drought colonisation of previously unoccupied grid squares through vegetative dispersal organs. The full models were then simplified by removing non-significant fixed effects with a backward model selection based on AIC.

After fitting these models for the complete set of species, we fitted separate models for forbs and graminoids. For the among-forbs and among-graminoids models, we used the same fixed and random effects in the full models as described above. In all models for the effects on the abundance in spring post drought and in the model for the effects on biomass summer post drought within forbs, the random factor subplot had a variance ≤ 0.00001 and was dropped to avoid singularity. As our final species set included only three legume species with narrow ranges of both SLA and MRD (Figure 2), we did not fit separate models for legumes.

For significant SLA × DL or MRD × DL interactions, we tested the significance of the relationships between SLA or MRD on measures of plant performance for DL levels of 0, 79, 134, 177 and 220 days separately using the emtrends() function from the emmeans package (Lenth, 2023).

We used a LMM to test the effects of the fixed factors drought length, soil layer (0–20, 20–40, 40–60, 60–80 and 80–100 cm below surface) and their interaction on soil matric potential at the end of the drought treatments. The $\log_{10}$ notation (pF) was used for soil matric potential in hPa (Appendix S2). The random structure of this model was subplot nested in plot.

3 | RESULTS

During the droughts, volumetric soil-water content in the topsoil declined from ~ 0.33 to $\sim 0.12 \text{ m}^3/\text{m}^3$ (Figure 1d). This decline was strongest at the start of the respective drought and had markedly slowed down or almost ceased shortly before the middle of the drought treatments, around day 100 (Figure 1d). Due to the staggered ending of our drought treatments, plots with shorter droughts were rewetted earlier in the season, which coincided with warmer and dryer weather compared to later in the season when plots with longer drought treatments were rewetted (Figure 1). This explains why topsoil in plots subjected to shorter drought treatments took longer to reach the moisture level of the control plots (Figure 1d). However, we observed that plants started to regrow immediately after rewetting also in plots subjected to shorter drought, in which soil moisture had increased only slowly. At the end of the droughts, soil matric potential differed significantly among soil layers (Table S6): While the upper soil layers had dried out below the wilting point, water was still available for plants in soil layers deeper than 60 cm below ground (Figure S3).

Survival of green tissue ($\text{survival}_{\text{gt}}$) across all species decreased by 53% as drought length (DL) increased from 0 to 220 days, independently of SLA or maximal rooting depth (MRD) of the species (Figure 3a–c; Table S2). Among forbs, increasing SLA reduced the negative effect of drought length on $\text{survival}_{\text{gt}}$ (Figure S4a–c; Table S2). Among graminoids, increasing SLA increased the negative effect of DL on $\text{survival}_{\text{gt}}$, while increasing MRD reduced the negative effect of DL on $\text{survival}_{\text{gt}}$ (Figure 4a–c; Table S2). The opposite SLA $\times$ DL effect between forbs and graminoids was due to two species at the low end of our SLA range (*Plantago lanceolata* and *Peucedanum oreoselinum*), for which survival of green tissue was strongly negatively affected by increasing drought length and two species at the high end of our SLA range (*Thymus pulegioides* and *Euphorbia cyparissias*) for which survival of green tissue was hardly affected by increasing drought length. Without these four species, the SLA $\times$ DL effect was significantly negative also within the remaining nine forbs (13 non-leguminous forbs were considered in total).

Regrowth post drought across all species was not affected by drought length (Figure 3d; Table S2). However, the negative DL $\times$ MRD interaction suggests that the effect of drought length on regrowth changed from positive to negative with increasing MRD of the species (Figure 3f; Table S2). On the other hand, the positive DL $\times$ SLA interaction suggests that the effect of drought length on regrowth changed from negative to positive with increasing SLA of the species (Figure 3e; Table S2). Among forbs, regrowth decreased with increasing DL, independently of SLA but more strongly with increasing MRD (Figure S4d–f; Table S2). In contrast, regrowth increased with increasing DL among graminoids, independently of SLA or MRD (Figure 4d–f; Table S2).

Abundance in spring post drought ($\text{abundance}_{\text{pd}}$) across all species decreased by 30% as DL increased from 0 to 220 days, independently of MRD (Figure 3g,i; Table S2). However, with increasing SLA, this decrease became weaker (–40% for an SLA of $18 \text{ mm}^2 \text{ g}^{-1}$ vs. –15% for an SLA of $39 \text{ mm}^2 \text{ g}^{-1}$) (Figure 3h; Table S2). Among forbs, $\text{abundance}_{\text{pd}}$ decreased by 40% as DL increased from 0 to 220 days, whereas $\text{abundance}_{\text{pd}}$ decreased only by 13% among graminoids. Among both functional groups, the negative effect of DL on $\text{abundance}_{\text{pd}}$ was independent of SLA and MRD (Figure S4g–i; Figure 4g–i; Table S2).

Biomass in the year of drought ($\text{bm}_{\text{drought}}$) across all species decreased by 49%, as DL increased from 0 to 220 days, independently of SLA and MRD (Figure 5a–c; Table S3). Forbs (–47%) and graminoids (–51%) mirrored this pattern found across all species (Figures S5a–c and S6a–c; Table S3).

Biomass of the first half of the drought ($\text{bm}_{1^{\text{st}} \text{ halfdrought}}$) across all species and species among functional groups was not affected by DL, nor by an interaction with SLA or MRD (Figures S6–S8a–c; Table S3). This suggests that until the middle of the applied drought treatments in July 2021, most plants were still able to extract enough water from the soil to maintain their biomass production without significant losses, which is supported by our soil moisture measurements (Figure 1d, see above).

Biomass of the second half of drought ($\text{bm}_{2^{\text{nd}} \text{ halfdrought}}$) decreased by 93% across all species as DL increased from 0 to 220 days, by 86% among forbs and by 99% among graminoids (Figures S6–S8d; Table S3). Across all species, the negative effect of DL on $\text{bm}_{2^{\text{nd}} \text{ halfdrought}}$ decreased both with increasing SLA and with increasing MRD (Figure S7e,f; Table S3). Thereby, the DL $\times$ MRD interaction was mirrored among forbs (Figure S8f; Table S3) and the DL $\times$ SLA interaction was mirrored among graminoids (Figure S9e; Table S3).

Biomass in the summer post drought ($\text{bm}_{\text{post drought}}$) across all species was not affected by DL, nor by an interaction between DL and SLA. However, the significant DL $\times$ MRD interaction suggests that the effect of drought length on $\text{bm}_{\text{post drought}}$ changed from negative to positive with increasing MRD of the species (Figure 5d–f; Table S3). While graminoids mirrored this pattern found across all species (Figure S6d–f; Table S3), $\text{bm}_{\text{post drought}}$ increased by 50% as DL increased from 0 to 220 days among forbs, independently of SLA or MRD (Figure S5d–f; Table S3).

4 | DISCUSSION

4.1 | Declining plant performance with increasing drought duration

Consistent with our hypothesis, across all species survival of green tissue and biomass in the year of drought were negatively affected by increasing drought length (Figures 3a and 5a). Moreover, species' abundance was still negatively related to drought length in spring post drought, whereby higher SLA moderated this negative effect (as species with higher SLA decreased less in abundance after longer drought than species with lower SLA) (Figure 3g,h). This suggests that increasing drought severity, achieved by increasing durations of precipitation exclusion in this study, not only amplifies negative effects on plant productivity during drought (Gao et al., 2019; Kröel-Dulay et al., 2022; Wilcox et al., 2017), but also has the potential to exacerbate changes in community composition post drought.

The strong negative effect on abundance during drought was only weakly translated to the next year (Figure 3a,g). Probably, this is mainly due to low mortality, as previously reported for temperate grassland species (Jung et al., 2020). In our study, plant-available water was left in deeper soil layers even after 7 months without precipitation. Possibly, the linear negative relationship between plant performance and drought length suggested by our study only applies up to the point where water is still available in the soil. Beyond this point, drought duration would constitute a critical threshold of abrupt decline in physiological performance (Ingrisch et al., 2023; Oram et al., 2023) or population size. Such a critical threshold is reached earlier when droughts are accompanied by heatwaves, when water reserves are lacking on shallow or sandy soils, or after deficient precipitation in winter.

Our results suggest that on deep soils with medium to high available water content, even a drought that spans almost an entire

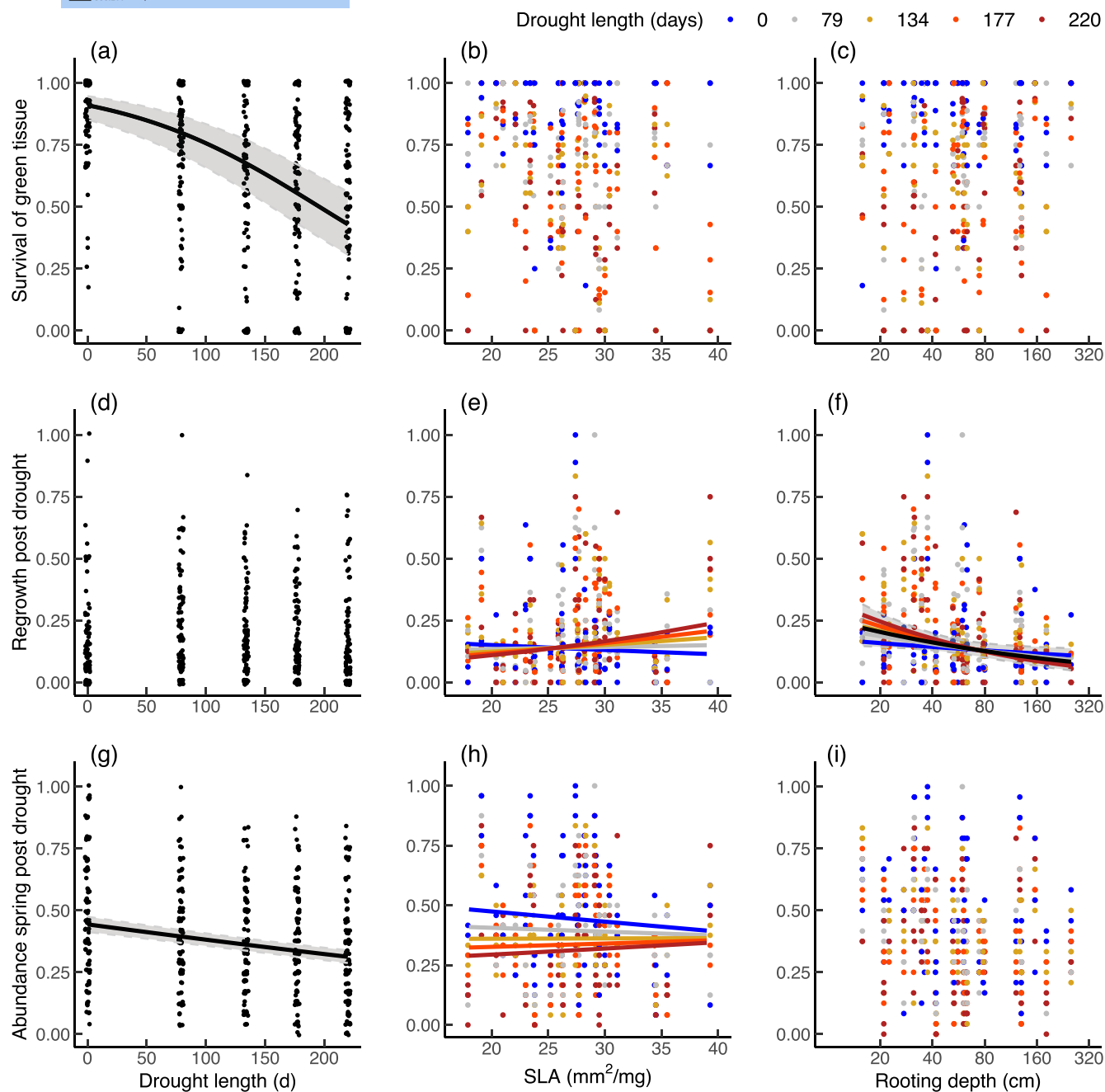


FIGURE 3 Relationships between drought length, specific leaf area (SLA) or maximal rooting depth and abundance-based drought response metrics, (a–c) proportion of green tissue surviving end of drought, (d–f) proportion of regrowth post drought, and (g–i) abundance (proportion of occupied squares out of totally 24 grid squares) in spring post drought across 32 grassland species (dots, $n=3$ subplots per species and treatment) in the drought experiment. A small amount of random variation is added to the location of dots in (a), (d) and (g) to reduce the overlap of datapoints. Lines are fitted with GLMM with logit link function and binomial distribution. Significant main effects (solid black line), 95% confidence intervals (grey ribbon), significant interaction with drought length (coloured lines). Note logarithmic scale of the x-axes in (c), (f) and (i). See [Table S2](#) for full statistical output and [Table S4](#) for significances of single coloured lines.

growing season does not necessarily push abundant species of temperate Swiss grassland beyond a critical threshold of mortality. However, experimental studies like ours may underestimate drought effects, for example by not controlling for evaporative demand associated with high temperature, low humidity or clear sky, often associated with droughts (Kröel-Dulay et al., 2022). Nevertheless, the high resilience of our mesic grassland species to

extremely long drought is in line with the findings of a global study suggesting that mesic sites are less vulnerable to extreme droughts than arid sites (Smith et al., 2024).

Even though drought length negatively affected post-drought abundance across all species, post-drought biomass across all species was not affected by drought length. This indicates that after longer drought, fewer plants of larger size remained. Thereby,

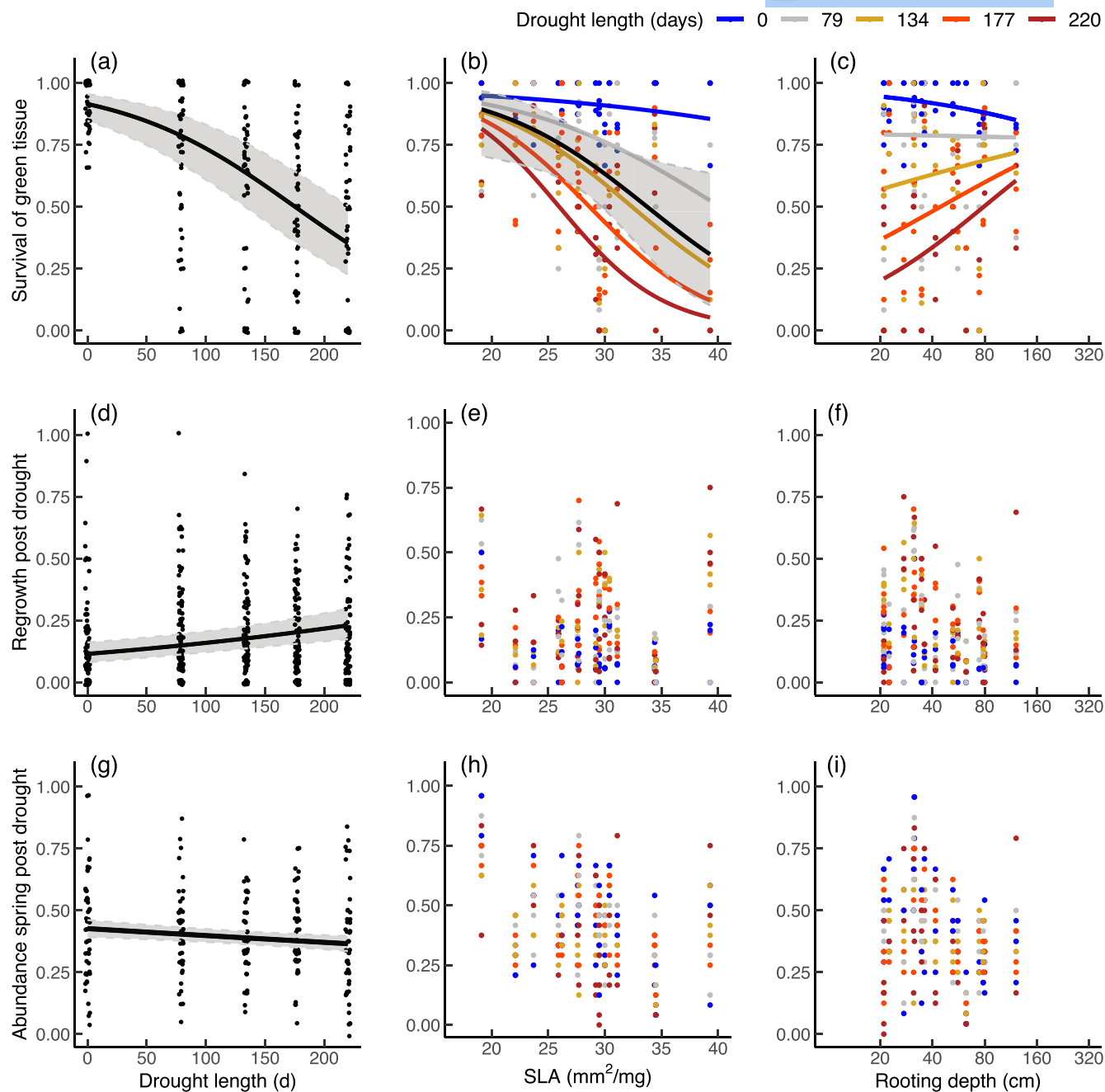


FIGURE 4 Relationships between drought length, specific leaf area (SLA) or maximal rooting depth and abundance-based drought response metrics: (a)–(c) proportion of green tissue surviving end of drought, (d)–(f) proportion of regrowth post drought, and (g)–(i) abundance (proportion of occupied squares out of totally 24 grid squares) in spring post drought across 16 GRAMINOID species (dots, $n=3$ subplots per species and treatment) in the drought experiment. A small amount of random variation is added to the location of dots in (a), (d) and (g) to reduce the overlap of datapoints. Lines are fitted with GLMM with logit link function and binomial distribution. Significant main effects (solid black line), 95% confidence intervals (grey ribbon), significant interaction with drought length (coloured lines). Note the logarithmic scale of the x-axes in (c), (f) and (i). See [Table S2](#) for full statistical output and [Table S4](#) for the significances of single coloured lines.

abundance reductions post drought were more strongly amplified for forbs than graminoids ([Table S2](#)), while post-drought biomass showed a positive drought legacy for forbs, but not for graminoids ([Table S3](#)). This indicates that the trend towards fewer but bigger plants was more pronounced in forbs than in graminoids. The weaker reduction in abundance after longer drought in

graminoids than in forbs was due to opposing drought length effects on regrowth post drought: While forb re-sprouting was hampered, graminoid re-sprouting was favoured by longer droughts ([Table S2](#)). This is in line with the previously described better ability of grasses to rapidly re-sprout from basal meristematic tissue (Stampfli et al., 2018; Volaire et al., 2014).

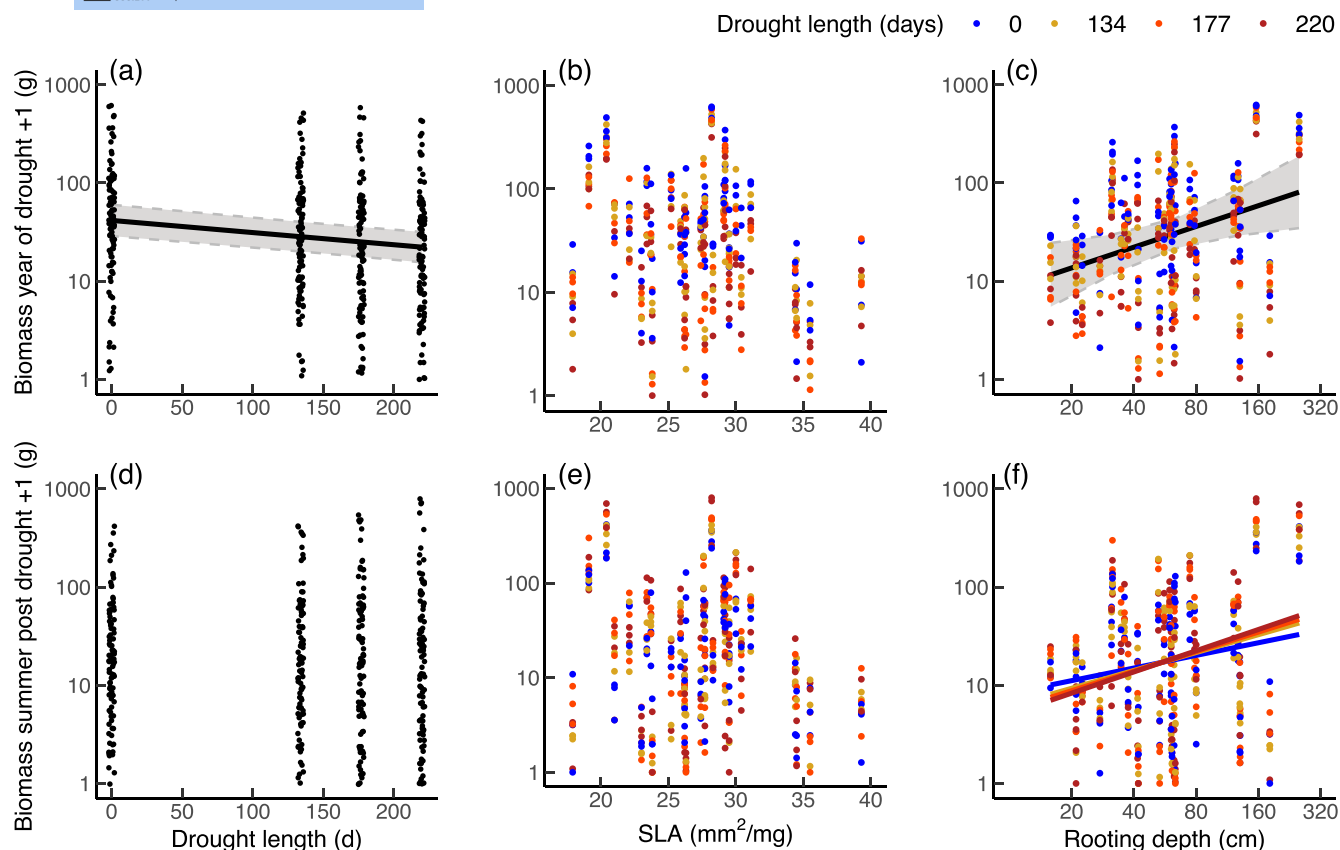


FIGURE 5 Relationships between drought length, specific leaf area (SLA) or maximal rooting depth and (a)–(c) biomass in the year of drought and (d)–(e) biomass in summer post drought across 32 species (dots, $n=3$ subplots per species and treatment) in the drought experiment. A small amount of random variation is added to the location of dots in (a) and (d) to reduce the overlap of datapoints. Lines are fitted with LMM. Significant main effects (solid black line), 95% confidence intervals (grey ribbon), significant interaction with drought length (coloured lines). Note the logarithmic scale of all y axes and the x axes in (c) and (f). See Table S3 for full statistical output and Table S5 for the significances of single coloured lines.

4.2 | Mitigation of drought-length effects by deep roots

Our results across all species suggest that deep roots mitigated the negative effects of longer drought duration on productivity in the second half of the drought (Figure S7f) when water became deficient in topsoil and limited plant growth. Through access to water remaining in deep soil layers, deeper roots obviously contributed better to avoiding dehydration than shallow roots (Volaire, 2018). This is consistent with our hypothesis and in line with the idea that deep roots might become important under extreme droughts (Hofer et al., 2016). However, other variables, like root distribution and hydraulic conductivity across depth, as well as root plasticity, interact with MRD to determine plants' water uptake across soil depth (Nippert & Holdo, 2015) and under less extreme drought conditions, high root plasticity may be more beneficial for plant performance than rooting depth (Hoekstra et al., 2014). Also, deep roots may not be useful under chronic reduction of precipitation, such as press droughts (Hoover et al., 2015) involving small precipitation events that only wet the upper soil layer (Ocheltree et al., 2020).

The negative effect of longer drought was still noticeable in the lower growth of shallow-rooted species, while deep-rooted species

thrived in summer post drought (Figure 5f). As post-drought abundance declined independently of MRD (Figure 3g,i), this positive effect of long drought on biomass suggests that deep-rooted species became larger but not more abundant than shallow-rooted species post drought. As biomass integrates both abundance and size, this positive effect still suggests a net gain from deeper roots for plant performance after increasingly severe drought. Due to the staggered ending of our experimental droughts, plants that experienced longer droughts had a shorter time to recover. Thus, the positive effect of deeper roots under longer drought is probably rather underestimated in our study.

After the rewetting of dried soil, nutrient pulses can feed back to plant productivity (Bloor & Bardgett, 2012; Borken & Matzner, 2009; Mackie et al., 2019). In a previous study, such topsoil nutrient pulses have been shown to favour the more resource-acquisitive grasses at the expense of the deeper-rooted forbs (Stampfli et al., 2018), suggesting that higher capacity of acquiring resources post drought outweighed any beneficial effects of deeper roots during drought. In our study, however, the benefit of better surviving severe drought on water in deep soil layers enabled deep-rooted species to better take advantage of rewetted soil and higher light availability (Perronne et al., 2020) post drought. As drought effects on post-drought productivity were not related to SLA, we

conclude that increased nutrient availability did not play a major role in post-drought productivity in our study.

The mitigative effect of MRD on green tissue survival under increasingly long drought was only found among graminoids (Figure 4c; Figure S6f), but not among forbs (Figures S4c and S5c,f). This can be explained by differences in rooting depth between these functional groups in our study, as most forbs, but only about a third of the graminoid species, had sufficiently deep roots to reach plant-available water in deep soil layers (Figure 2).

4.3 | Modification of drought-length effects by specific leaf area

The hypothesis that resource-conservative traits are favourable during drought (Harrison et al., 2015) was not supported by our results across all species. On the contrary, under limiting water availability in the second half of the drought, plant growth decreased less for higher-SLA than for lower-SLA species (Figure S7e). Further, increasing drought length favoured the post-drought abundance of species with higher SLA (Figure 3h). This mitigative effect of higher SLA was not due to resistance during drought, as green tissue survived independently of SLA (Figure 3a,b), but to recovery post drought when species with higher SLA gained in abundance with longer drought duration (Figure 3e). This is in line with our hypotheses and earlier evidence that high-SLA species better recover after a drought than low-SLA species (Ingrisch et al., 2018; Stampfli et al., 2018).

However, while high SLA was beneficial for species' abundances after longer drought, we found no such effect on post-drought biomass (no significant $DL \times SLA$ interaction on biomass in summer post drought, Figure 5e). This suggests that while higher-SLA species were less reduced in abundance after longer drought, they gained less in size than lower-SLA species. Our biomass measure integrates both abundance and size of the respective species in a subplot and is therefore a more comprehensive proxy for overall plant performance than abundance alone. Our results thus suggest that opposing effects of SLA on plant size and abundance after longer drought offset each other, resulting in no net effect of SLA on plant performance after longer drought. Therefore, our study at the species level does not provide evidence for the idea that the promotion of high SLA species by intensified land-use affects grassland performance in response to increasingly severe drought. The mixed evidence in the literature for SLA as a predictor of sensitivity to drought may not result from different drought durations but rather from different performance measures or observation periods during or after drought.

The negative effect of higher SLA on green tissue survival during longer droughts combined with trait-independent abundance reductions post drought among graminoids (Figure 4b,g,h) suggest that survival of green tissue exhibits different survival strategies (dehydration tolerance vs. dehydration avoidance, Voltaire, 2018), rather than whole-plant survival. Under severe drought, leaf senescence can contribute to plant survival by reducing plant-water

loss (Munné-Bosch & Alegre, 2004) and thus prevent dehydration of the meristems, which are the key organs for plant survival (Voltaire et al., 2014). Hence, the SLA gradient across our graminoid species does not represent drought sensitivity but a dehydration tolerance-avoidance trade-off (Pérez-Ramos et al., 2013; Voltaire, 2018). However, these alternative strategies might be related to performance under even longer or more severe droughts than simulated in our study, with either the most drought-tolerant traits or, as recent studies suggest, drought-avoidance and drought-escape traits becoming advantageous (Knapp et al., 2024).

In our study, some forb species with specific traits, such as lignification (*Thymus pulegioides* and *Euphorbia cyparissias*), short lifespan (*Plantago lanceolata*) or longer time to maturation (*Peucedanum oreoselinum*), reversed the pattern between SLA and green tissue among forbs compared to the negative relationship among graminoids. This is in line with the notion that greater evolutionary distance increases the likelihood that other traits complicate the functional importance of any individual trait (Anderegg, 2023), as forbs were represented by eight, but graminoids only by three families in our study. Hence, we support the suggestion that multiple traits need to be studied when searching for trait-drought resistance relationships (Anderegg, 2023; Knapp et al., 2024).

With our biomass harvesting regime of cutting all plants to the same height, we simulated common mowing practices, rather than grazing. Further studies are needed to investigate if processes related to grazing, like selective consumption of high SLA species (Pauler et al., 2020) or nutrient input by livestock faeces would change the relations between SLA and drought performance measures observed in our study.

5 | CONCLUSIONS

By including species representing wide ranges of SLA and MRD in a common-garden experiment and exposing them to a gradient of drought length, we found that plant-available water can remain in deeper layers of soils with high water-holding capacity even after 7 months without precipitation. Thus, across all species, increasing drought length favoured the post-drought biomass of species with deep roots, a measure that integrates drought effects on the abundance and size of plants. Our results further suggest that the low-to-high SLA trait gradient represents different drought survival strategies from dehydration tolerance to dehydration avoidance rather than sensitivity of species to drought, especially within graminoids.

In the face of climate change, which is exposing temperate grasslands to increasingly severe droughts, and in consideration of the positive effects of deep roots on plant performance during and after increasingly severe droughts, we recommend including more deep-rooted species in intensively managed grasslands on productive soils. This is especially important as rooting depth can be negatively related to the intensity of grassland management (Tasser et al., 2021). Further studies should therefore investigate which management practices best support deep rooting in semi-natural grasslands.

AUTHOR CONTRIBUTIONS

All authors conceived and designed the experiment. Yvonne Künzi and Andreas Stampfli performed the experiment. Yvonne Künzi analysed the data. Yvonne Künzi wrote the first draft of the manuscript; Andreas Stampfli and Michaela Zeiter contributed to revisions; Markus Fischer provided editorial advice.

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CONFLICT OF INTEREST STATEMENT

The authors declare that they have no conflict of interest.

PEER REVIEW

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DATA AVAILABILITY STATEMENT

Data available from the Dryad Digital Repository: <https://doi.org/10.5061/dryad.5mkwh7g4> (Künzi et al., 2024).

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

Appendix S1: Additional information on seed provenance and estimation of required seed numbers.

Appendix S2: Measurement of soil matric potential at end of drought treatments.

Appendix S3: Additional information on plant traits.

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