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RESEARCH ARTICLE

Recurrent summer drought affects biomass production and community composition independently of snowmelt manipulation in alpine grassland

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Abstract

1. Earlier snowmelt and more frequent summer drought due to climate warming are considered particularly influential for extratropical alpine plants, which are adapted to a short growing season and high water availability.
2. Here, we explored the combined effects of the two drivers with a field experiment in late-successional alpine grassland in the Swiss Alps (2500 m a.s.l.) over 6–7 years. We advanced and delayed snowmelt by removing and adding snow to experimental plots prior to natural snowmelt for 7 years and combined this treatment with 5 and 10 weeks of summer drought for 6 years. We measured plant biomass formation, community composition and ecosystem respiration, and monitored soil moisture as well as soil temperature.
3. Natural snowmelt dates varied by 42 days across years. Snow manipulations advanced and delayed snowmelt by 4.6 and 8.0 days on average but did not affect annual growth (peak biomass) above- nor below-ground. Interactions between snowmelt and drought were nonsignificant, implying that drought effects were independent of snowmelt.
4. Drought reduced total annual above-ground biomass in the 10-week treatment by 16 ± 7% across years, while the 5-week treatment lowered biomass in the last year only. This decline in biomass was accountable to high drought sensitivity of biomass production in a few forb and graminoid species. In contrast, drought did not affect the biomass production of the dominant sedge *Carex curvula*, whose proportion of total plant cover increased from 36% in controls to 48% in 10-week drought.
5. Below-ground biomass slightly increased under drought (5-week treatment only), resulting in a higher root mass fraction (both treatments). Despite continued root formation, drought reduced ecosystem respiration by 13%–23% per season, assessed nine times during three growing seasons. Since more than 85% of ecosystem respiration stemmed from below-ground activities and roots continued

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growing under drought, we assume that soil microorganisms were heavily constrained by the drought treatments.

6. *Synthesis*. We conclude that snowmelt timing is unrelated to productivity, while recurrent drought will shift biomass allocation from shoots to roots in this typical alpine grassland, with potential implications for grazers but also for nutrient and carbon cycling. Species-specific drought-sensitivity will considerably alter community composition under more frequent drought.

KEYWORDS
climate change, ecosystem respiration, high elevation, long-term, manipulative experiment, root mass fraction, root production, snowmelt

1 | INTRODUCTION

The effects of climate change are deemed especially pronounced in alpine regions, where plants are adapted to a cold environment (Körner, 2021) and temperature is rising above-average (Pepin et al., 2015, 2022). Beside temperature, other, indirect consequences of a warmer atmosphere may play a decisive role for plant functioning at high elevation, such as earlier snowmelt (Stewart et al., 2004; Vorkauf, Marty, et al., 2021) and restricted water availability during summer (Calanca, 2007; Gobiet et al., 2014; Kotlarski et al., 2023). In the Swiss Alps, snowmelt was already occurring 17 days earlier in 2019 than in 1958 and is projected to further advance by up to 1 month until the end of the 21st century (Vorkauf, Marty, et al., 2021). This will significantly extend the time available for growth of alpine plants, which are adapted to a growing season length of only 2–3 months (Körner, 2021). At the same time, summer drought is becoming more frequent in the Alps: the probability of a drought event of the same magnitude as the severe drought in 2003 was 4% in the 20th century but could rise to 25% in 2071–2100 (Calanca, 2007). Thus, shifted snowmelt and more frequent drought could potentially have a greater impact on alpine plants than a few degrees higher air temperature, especially considering the favourable microclimate in which alpine plants grow (Körner, 2021; Scherrer & Körner, 2010). Yet, to our best knowledge, experimental studies that address the combined consequences of altered snowmelt timing and recurrent summer drought on alpine grasslands do not exist.

Earlier snowmelt and reduced water availability may alter productivity and dry matter allocation of alpine grassland species, potentially impacting nutrient cycling, species interactions, and community composition. Moreover, herbivores on managed (e.g. sheep and other livestock) and unmanaged lands (e.g. grasshoppers, marmots, snow hares, chamois and ibex) depend on the annual biomass production of these grasslands (Blumer & Diemer, 1996; Jäger et al., 2020). As biomass production may correlate with growing season length (Kudo, 1992), earlier snowmelt was expected to enhance productivity (Rammig et al., 2010). However, experimental studies have provided little evidence of a stimulating effect of earlier snowmelt on biomass production so far (Baptist et al., 2010; Boyle et al., 2022; Darrouzet-Nardi et al., 2019; Möhl et al., 2022; Wipf et al., 2009). On the other hand, drought periods are known to reduce above-ground biomass production in different grassland types (Kahmen et al., 2005; Kröel-Dulay et al., 2022; Mackie et al., 2019), including subalpine meadows (Gilgen & Buchmann, 2009; Ingrisch et al., 2018). This effect could exacerbate with earlier snowmelt in the future, because a smaller fraction of the snow-free period profits from the high soil moisture following snowmelt. Given the high interannual variability of snowmelt dates, identifying interactions with drought requires several years of in-situ experimental data.

Longer term experimental studies (>5 years) on summer drought or snowmelt timing in alpine grassland are scarce, although the long-term aspect is a prerequisite for distinguishing between transient and permanent responses to environmental change (Lindenmayer et al., 2012). Our knowledge of how drought affects productivity of alpine vegetation stems mainly from short-term studies (1–2 seasons): 1–9 weeks of rain exclusion per season resulted in higher root:shoot ratios by reducing above-ground biomass (de Boeck et al., 2015; Johnson et al., 2011), while below-ground biomass remained unchanged (Gilgen & Buchmann, 2009). An increased root:shoot ratio in response to reduced precipitation (−50%) was also observed in grassland of the Tibetan Plateau (Liu et al., 2018), although in this case root biomass increased and above-ground biomass remained stable. Drought also lowers microbial activity (Schimel, 2018), plant carbon allocation to microbes (Karlowsky et al., 2018), and root respiration (Hasibeder et al., 2015), with pronounced effects on ecosystem respiration. Two 8-days water exclusions within 1 month led to reduced above-ground biomass, net CO_2 exchange, and ecosystem respiration in monoliths of *Nardus stricta* dominated grassland (Johnson et al., 2011). Similarly, soil and ecosystem respiration of subalpine grasslands was up to 60% lower after 6–9 weeks of rain exclusion (Hagedorn & Joos, 2014; Ingrisch et al., 2018) but recovered quickly or even surpassed controls during the recovery period. Most studies rely on daytime assessments of ecosystem respiration, despite the drawbacks associated with measuring respiration during the day, especially in alpine ecosystems with strong solar radiation. Sudden darkening can lead to strong microclimatic changes (light, temperature, humidity) and trigger substantially increased respiration in plants ('light-enhanced dark respiration', Atkin et al., 1998; up

to +30% in alpine grassland, T. Gross & E. Hiltbrunner, unpublished). Hence, in situ measurements of dark respiration are most reliable when conducted at night.

Alpine grasslands are often species-rich and the impacts of environmental changes are known to differ among grassland species (Suttle et al., 2007). Previous studies highlighted that mountain species belonging to different functional types (e.g. grasses and forbs) respond differently to climate change (Gilgen & Buchmann, 2009; Liu et al., 2018; Rosbakh et al., 2017). Plant species with high phenological flexibility may benefit from earlier snowmelt, while those species capable of forming dense root systems or symbiotic networks may gain an advantage during drought (Freschet et al., 2021; Jumpponen & Trappe, 1998). Such differential responses to snowmelt timing and drought may lead to future changes in community composition in alpine grassland (e.g. Liu et al., 2018). Despite that, species composition in late-successional subalpine and alpine grasslands was found to be stable in the face of the changing climate of recent decades with increasing air temperatures (Vittoz et al., 2009; Windmaißer & Reisch, 2013), but further environmental change and recurrent extremes may disrupt this stability.

We experimentally advanced and delayed the timing of snowmelt in a widespread alpine grassland type and combined these treatments with either 5 or 10 weeks of rain exclusion during the growing season. For six consecutive years (2017–2022), we measured above-ground biomass production at the species-level and assessed total root production using in-growth cores for two 2-year periods. In 2021, we additionally harvested standing root biomass to quantify net shifts in biomass allocation. We complemented these proxies for productivity with pointwise, night-time measurements of ecosystem respiration, which we conducted three times per season from 2019 to 2021. We hypothesise that (1) biomass declines above-ground and increases below-ground to compensate water shortage under both drought levels. (2) Night-time ecosystem respiration declines progressively with increasing drought duration. (3) Effects of snowmelt timing on biomass production materialize after several years only, while earlier snowmelt immediately amplifies adverse effects of summer drought. (4) We also expect that the response to snowmelt and drought differs between species and functional groups, and hence, leads to changes in community composition.

2 | MATERIALS AND METHODS

2.1 | Study site, vegetation and soil

Our experiment was located on a SW-oriented, slightly inclined (ca. 10°) slope at 2450 m a.s.l. in the Swiss Alps (46°33′47″ N, 8°23′28″ E; Figure S1; permission granted by the municipality of Obergoms). Vegetation is dominated by the sedge *Carex curvula* All. s.s. (referred to as *Carex*), which makes up around 30%–45% of annual biomass production above-ground (Möhl et al., 2020; Schäppi & Körner, 1996). This grassland community, termed *Caricetum curvulae* (Braun-Blanquet, 1948), is widespread in European mountain systems (Puşcaş & Choler, 2012) and the most frequent alpine grassland on acidic bedrock in the Swiss Alps (Landolt, 2012). At least 34 species grow at the site, 23 forbs and 11 graminoids. Beside the annual forb *Euphrasia* sp., all species are perennial, mostly of short stature and with below-ground shoot meristems. The soil is a ca. 60–80 cm deep, acidic, partly podzolic cambisol with a soil pH_{CaCl2} between 3.6 (0–10 cm) and 4.2 (10–20 cm). The soil C:N ratio is 11.7 at 0–10 cm depth and increases to 13.9 at 10–20 cm depth with 1.8 and 1.0 mg N per g dry soil in the two soil horizons, respectively. Skeleton content increases along the soil profile from a few percent in the top 15 cm to 10%–25% at 30 cm and >40% at ca. 70 cm depth. Root density is extremely high in the uppermost 10 cm, but decreases exponentially with soil depth (only few roots below 50 cm), which is typical for alpine grassland (Körner, 2021). The permanent wilting point, derived from replicated pF curves, is 10.1 vol-% at 10 cm and 8.8 vol-% at 30 cm soil depth (Vorkauf, Kahmen, et al., 2021). Precipitation during alpine summer amounts to roughly 100–150 mm per month (June–September) and snow load during winter reaches 2–4 m.

2.2 | Experimental treatments

We defined 45 plots (2 m × 2.5 m) across five replicated blocks (Figure S1). Each plot was assigned to one of three levels of snow manipulation and summer drought for the whole duration of the experiment (3 × 3 full factorial block design). Snow manipulations were conducted each spring from 2016 to 2022, a few weeks before snowmelt to prevent shovelled holes from being refilled by recent snowfall. Remaining depth of the melting snowpack amounted to ca. 1 m at this time. Snow height was experimentally reduced to 0.5 m to advance snowmelt and elevated to 2.2–2.5 m (2016; 2017) or 1.3 m (2019–2022) to delay snowmelt (Figure S1). In 2018, heavy thunderstorms delayed snowmelt manipulations and the remaining snow height was only 0.5 m. Therefore, we reduced it to 0.3 m in early snowmelt plots, while the thin snow pack only allowed raising snow height to 0.7 m in late snowmelt plots. Additionally, we covered the piled up snow with white fleece to further delay snowmelt (Datex KN 25; Fritz Landolt AG). The fleece covers worked well and this practice was thus continued in the following years (2019–2022), allowing us to lower the target snow height for late snowmelt to 1.3 m and still achieve similar or even longer delays in snowmelt as in the initial 2 years. Fleece covers were removed once controls became snow free, which was 10–30 days after snow manipulations.

We employed two rain-exclusion treatments that started after snowmelt and lasted for either 5 or 10 weeks ('moderate' and 'extreme' drought, respectively), which is in the range of previous studies in subalpine grassland (7–9 weeks in Gilgen & Buchmann, 2009; 6 weeks in Ingrisch et al., 2018). Drought was realized with tent-like rain-out shelters that exceeded the plots on all sides (2.5 m × 3 m; ridge height of 1.2 m; Figure S1), consisting of aluminium frames with UV-B permeable, transparent plastic foil (Lumisol AF clear with ca. 90% light transmission; Hortuna AG). From 2017 (1 year later than the first snow manipulations) to 2022, 15 plots were sheltered for

5 weeks per season, 15 plots for 10 weeks and the remaining 15 plots were never covered by rain-out shelters (controls). Shelters were installed immediately after snow had melted in all plots, which varied between years (Figure 1). In 2018, 2019 and 2022, naturally occurring drought periods forced us to water control plots on one to two occasions per season with 17 L m^{-2} per plot, which is enough to support normal evapotranspiration for 4–5 days (van den Bergh et al., 2013) and similar to an average rain event at this site (Figure 1). In each plot, we marked a central area of 1 × 1 m (central-m^2) that excludes edge effects (Figure S1).

2.3 | Environmental conditions

Air temperature, radiation and precipitation were monitored 1.5 m above-ground every 10 min by two on-site weather stations during the growing season starting in 2017 (Vantage Pro2; Davis Instruments Corp.). In the central-m^2 of each plot, soil temperature was read once per hour at 3–4 cm depth (TidbiT v2 Temp; Onset Computer Corp.), which is close to most species' meristems. Soil temperatures were recorded year-round from 2016 to 2022 and allowed to accurately delineate snowmelt date in spring, defined as the first hour when mean temperature over 24 h rose above 3°C. Every autumn, T-sensors were read out and replaced if needed. In five cases (out of 315), T-sensors failed during winter and snowmelt timing was determined from webcam images or nearby plots with the same snowmelt treatment. We measured topsoil moisture content (0–5 cm) every 1–2 weeks in in each corner and in the centre of every plot during the growing season (Theta probe ML2 and ML3; Delta-T Devices). From 2018 onwards, soil moisture was simultaneously assessed at 5–10, 15–20, 25–30, and 35–40 cm depth in the centre of the plots (Profile probe PR2; Delta-T Devices; for simplicity referred to as 10, 20, 30, and 40 cm depth). To quantify reductions in irradiance due to the rain-out shelters, we placed light loggers (HOBO Pendant Temperature/Light Logger; Onset Computer Corp.) in three controls and three sheltered plots from 27 August until 23 September 2021, when shelters were removed. All light loggers remained in the field until 29 September to measure a reference period for standardization of logger readings.

2.4 | Above-ground biomass

We harvested peak biomass as a surrogate for annual biomass production above-ground, which is widely adopted in such grassland types where only a negligible amount of biomass is produced later in

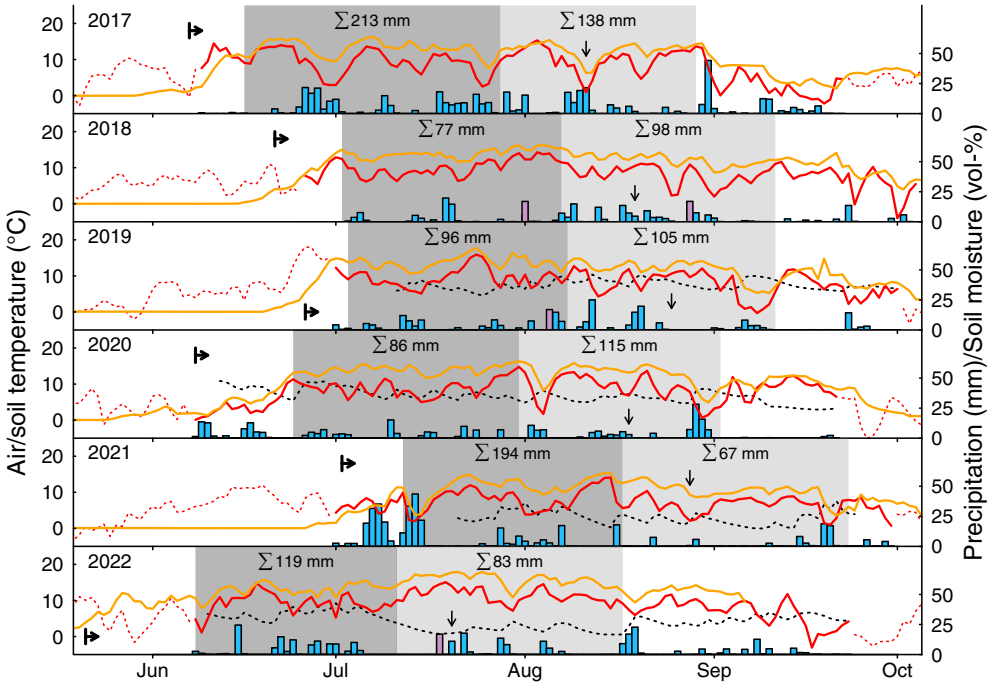


FIGURE 1 Weather conditions at the experimental site in 2017–2022. Blue bars show daily sums of precipitation, whereas red and orange lines show mean air (1.5 m above-ground) and soil temperature (3–4 cm depth, mean of control plots), respectively, measured on site. Red dotted lines at the start and end of the season show air temperature from the nearby research station (2 m above-ground). Dotted black lines (2019–2022) indicate topsoil moisture in control plots (vol-%, same y-axis as precipitation). Dark grey background indicates the sheltering period of the 5-week drought treatment and the entire grey background (dark + light grey) the duration of the 10-week treatment. Sums of excluded precipitation (Σ) were calculated for the 5-week period (dark grey) and the remaining time of the 10-week period (light grey). Horizontal arrows indicate the time of snowmelt in control plots (no snow manipulation), vertical arrows show the time of above-ground peak biomass harvest. Purple bars indicate artificial rain events (17 mm), where control plots (no rain-exclusion) were watered to counteract naturally occurring drought (two times in 2018, once in 2019 and 2022).

the season (e.g. Klug-Pümpel, 1989; Körner, 2021; Wang et al., 2020). Also, a transition from biomass to necromass (still attached to the plants) occurs after peak biomass and harvesting later would reduce the estimated annual biomass formation (Körner, 2021). From 2017 to 2022, we harvested above-ground phytomass in two 10×20 cm strips per plot that were not harvested before (Figure S1). Harvest took place during peak biomass usually within 1–2 weeks in early- to mid-August, except for 2022, when an extremely early season-start induced earlier growth and prompted us to harvest at the end of July. This practice implied that the harvested biomass experienced only 6–8 weeks of drought in the 10-week treatment and 5 weeks of drought plus 9–18 days of recovery in the 5-week treatment. However, the plants that were harvested were exposed to the full drought duration in all previous years, with potential legacy effects on biomass production. Freshly cut phytomass was stored at 4–6°C before sorting biomass to species-level. Each species was assigned to one of the functional groups of forbs, graminoids (comprising different grass-like species) and *Carex*. Although *Carex curvula* is a graminoid species, we treated it separately because of its dominance. Necromass was assigned to forbs and graminoids (including *Carex*). Leaves of *Carex* exhibit die-back from the tip downwards during senescence, leading to characteristic brown leaf tips that can be used as a proxy for senescence (Möhl et al., 2022). We cut these brown leaf tips of *Carex* at the yellow intersection to the green leaf and collected them separately as necromass in 2019–2022. Previous-year leaves, mainly of *Geum montanum* were assigned to necromass. In 2021, we quantified leaf area of 3–5 leaves per plot for five frequent species (*Carex curvula*, *Helictotrichon versicolor*, *Geum montanum*, *Leontodon helveticus* and *Potentilla aurea*). Leaves were fixed under a transparent acrylic plate and photographed beside a reference scale. Leaf area was extracted using Fiji (Schindelin et al., 2012) and specific leaf area (SLA) was determined after weighing oven-dried, single leaves. Lichens and mosses were not accounted for in the above-ground biomass harvests. However, in 2022, total lichen mass was assessed by collecting all lichens within the 20 cm-respiration rings (see paragraph on ecosystem respiration), without differentiating between species, biomass, necromass and age (unfeasible for lichen). Once sorting was complete, all biomass and necromass samples were oven-dried at 80°C for at least 12 h and then weighed.

2.5 | Root biomass in in-growth cores

At the start of the growing season in 2017 and 2020, three in-growth cores were installed per plot (Figure S1). We extracted soil cores to a depth of 20 cm (excluding the upper 1–2 cm of litter and raw humus with meristems) using a soil corer of 4.8 cm diameter. Soil collected from the study site was sieved to remove all roots and filled into the holes (same soil for all in-growth cores). The refilled hole was covered with a vegetation patch of the same diameter. We sampled roots in 2018 and 2021, after two growing seasons each, by removing the vegetation patch and extracting the filled-in soil with a 4.4 cm (2018) and 3.8 cm (2021) corer at the end of the growing season in September, when seasonal root growth was complete (Möhl et al., 2022). We split the core in two to get the 0–10 and 10–20 cm horizons. Different volumes of the soil cores were taken into account when root biomass was transformed to $g\,m^{-2}$.

2.6 | Standing root biomass

To assess whether our treatment affected standing root biomass, we harvested two soil cores (4.4 cm diameter, 20 cm depth) of intact root space in the central-m^2 of each plot in August 2021 (Figure S1). Cores were split into 0–10 and 10–20 cm and then stored at −20°C until processing. After thawing at 4°C, most roots were picked out with tweezers. Roots were then placed in a supersonic bath to loosen soil particles between fine roots and washed. The remaining soil-root mixture was sieved under running water (32 µm mesh size) to collect all other roots. Washed roots were oven-dried in the same way as above-ground biomass. Stone volume was determined by water displacement and subtracted from the soil volume before normalizing biomass to $g\,m^{-2}$.

2.7 | Community composition

We visually estimated plant cover (0%–100%) at species level in the central-m^2 of each plot in early August 2022. From the cover of vascular plants, we calculated two diversity indices: Shannon's index (Shannon, 1948) as an indicator of plant diversity (equally sensitive to rare and abundant species) and Simpson's index (Simpson, 1949) to assess changes in dominance (more sensitive to abundant species; Morris et al., 2014). Lichens and mosses were not determined to species level, but the majority of lichens belonged to *Cetraria* sp. and less frequently to *Cladonia* sp., while *Polytrichum sexangulare* Brid. was the most abundant moss.

2.8 | Ecosystem respiration

Total respirational CO_2 (auto- and heterotrophic, 'ecosystem respiration') was measured with two identical static chambers (Bader & Körner, 2010; Mildner et al., 2015). They consist of a grey polypropylene housing with a 20 cm diameter opening. A battery-driven 3V-ventilator ensured gentle mixing of the air while CO_2 concentration and temperature were measured in the chamber (GMP343 and HMP75; Vaisala). Prior to the first measurement, each plot was permanently equipped with a polypropylene ring (height×diameter: 5×20 cm) in the central-m^2 (Figure S1). The ring was inserted ca. 2.5 cm into the soil and served as a socket for air-tight chamber placement. Ecosystem respiration was measured in each plot during three measuring campaigns per season from 2019 to 2021. As measuring ecosystem respiration during the day can introduce significant error, we measured respiration during the night, starting 1 h after sunset and finishing 3–5 h later. After chamber placement on the

socket, the increase in CO_2 was monitored for 5 min. The first minute of CO_2 readings was discarded to avoid anomalies caused by chamber placement. For the last measurement of 2021 we only used the last 2 min of CO_2 readings of one chamber, because the fan was not working properly and the increase in CO_2 stabilized only towards the end. Comparing respiration rates from the two devices did not indicate any measurement error and analysing the data with and without these measurements yielded the same statistical and qualitative outcome. Soil temperature at 0–5 cm depth was measured simultaneously at two positions beside the socket ring (GTH175; Greisinger). In 2021, we additionally measured ecosystem respiration in 10 spots within the experimental site but outside of the treatment plots. These spots were measured a second time after above-ground biomass was cut to estimate the proportion of above- and below-ground respiration. Respiration rates were calculated from the linear regression slope of increasing CO_2 over time (ΔCO_2, ppm s^{-1}):

$$R = \frac{\Delta CO_2 \times 760 \times 273.15}{22.4 \times 1013.25 \times (273.15 + T_{air})} \times \frac{V_c}{A} \ (\mu mol\ m^{-2}\ s^{-1}),$$

where 22.4 (L mol^{-1}) is the molar volume of any gas at standard pressure and temperature, 760 (hPa) is the local air pressure at the study site, 1013.25 (hPa) is the air pressure at sea level, 273.15 (K) is the standard temperature and T_{air} is the air temperature in the chamber. V_c is the chamber volume (5.65 L) and A the area (0.0314 m^2). Four single measurements were discarded because the regression had an R^2 of less than 0.9. As mean soil temperature per campaign varied between 7.8°C and 13.4°C (lowest value of 5.8°C and highest of 15.9°C), R was then standardized to 10°C (R_{10}) using the modified Arrhenius function by Lloyd and Taylor (1994):

$$R_{10} = \frac{R_s}{e^{E_0\left(\frac{1}{283.15-T_0} - \frac{1}{T_{soil}-T_0}\right)}},$$

where R_s is the respiration rate of the sample, T_{soil} (in K) the concurrently measured soil temperature, and 283.15 K equals to 10°C. E_0 (308.56 K, 'activation energy') and T_0 (227.13 K) are fitted parameters (Lloyd & Taylor, 1994).

2.9 | Statistical analyses

All statistical analyses were performed using the statistical programming language R 4.0.5 (R Core Team, 2022). We fitted mixed effect models (R-package 'nlme'; Pinheiro et al., 2021) with block as random effect. In the case of repeated measures, we also included plot identity as random effect. Where levels of a predictor showed substantially different variance (e.g. above-ground biomass of different functional types), we included constant variance functions that differed between factor levels ('weights' argument of the lme function). R^2_m-values reported for mixed effect models reflect marginal R^2-values for fixed effects, derived with the package 'piecewiseSEM' (Lefcheck, 2016). Differences between treatments and species were computed using the *R*-package 'emmeans' (Lenth, 2021), which allows to perform *t*-tests on fitted values and thereby account for dependencies specified with random effects. Model assumptions regarding residual distribution were verified visually (quantile-quantile plots of residuals, residuals vs. fitted values). Multiple data points per plot were pooled prior to analysis (e.g. two harvest strips per plot, three ingrowth cores per plot and year). Correlations between below-ground biomass and total as well as species-specific above-ground biomass were investigated with least-absolute shrinkage (LASSO) regression ('glmnet'-package; Friedman et al., 2010), where coefficients of terms with low explanatory power shrink to zero. Resulting non-zero terms were then used to fit a linear mixed effect model. To assess whether above-ground biomass of the most common species (Table S1) responded to snowmelt timing and drought, we fitted individual regressions with 'year' and 'mean topsoil moisture between shelter placement and harvest' or 'day of snowmelt' as predictor variables, including interactions. Response variables were log or square-root transformed to improve the distribution of residuals in statistical models but back-transformed to report estimates on the original scale. If not stated otherwise, means ± SE are reported.

3 | RESULTS

3.1 | Environmental conditions

Over the study duration, interannual variation in snowmelt date (2016–2022) spanned 42 days in control plots (2 July in 2020 and 21 May in 2022; Figures 1 and 2a). Snow removal led to an average advance of snowmelt by 4.6 ± 0.8 days and snow addition delayed snowmelt by 8.0 ± 1.9 days, with a maximum difference of 20 days between the two in 2020. Snow manipulations had minor effects on soil moisture, and only plots with delayed snowmelt were slightly moister (+2.1 ± 0.8 vol-%; Figure S2) during the first 5 weeks ($p = 0.018$) but not afterwards. Rain-out shelters excluded an average of 131 mm (32%–51% of the growing season's total) in the 5-week and 232 mm in the 10-week drought treatment (69%–90%). The drought treatment led to a steady decline in water availability (Figures S2 and S3). Soil moisture in the topsoil (0–5 cm) was reduced from 27.3 ± 0.7 vol-% in controls to 19.6 ± 0.7 vol-% in droughted plots (mean of the first 5 weeks), with a mean minimum value of 13.8 ± 0.6 vol-% (Figure 2b; no difference between the 5- and 10-week treatment). During the second 5 weeks mean soil moisture dropped to 15.6 ± 0.6 vol-% in the 10-week treatment and recovered to 21.5 ± 0.7 vol-% in the 5-week treatment, where the rain-out shelters were already removed (Figure 2c). Still droughted plots had a mean minimum soil moisture of 13.2 ± 0.5 vol-% during that period. Mean soil moisture within treatments always remained above the permanent wilting point, although topsoil moisture dropped regularly below that threshold in individual plots under drought (Figure 2). Expectedly, differences in soil moisture were highest in the topsoil and declined with increasing soil depth (no difference at 40 cm depth, Figure 2d,e). From 2019 to 2022, we measured early-season soil moisture prior to the setup of rain-out shelters, which showed that the previous years' drought treatment left a signal in

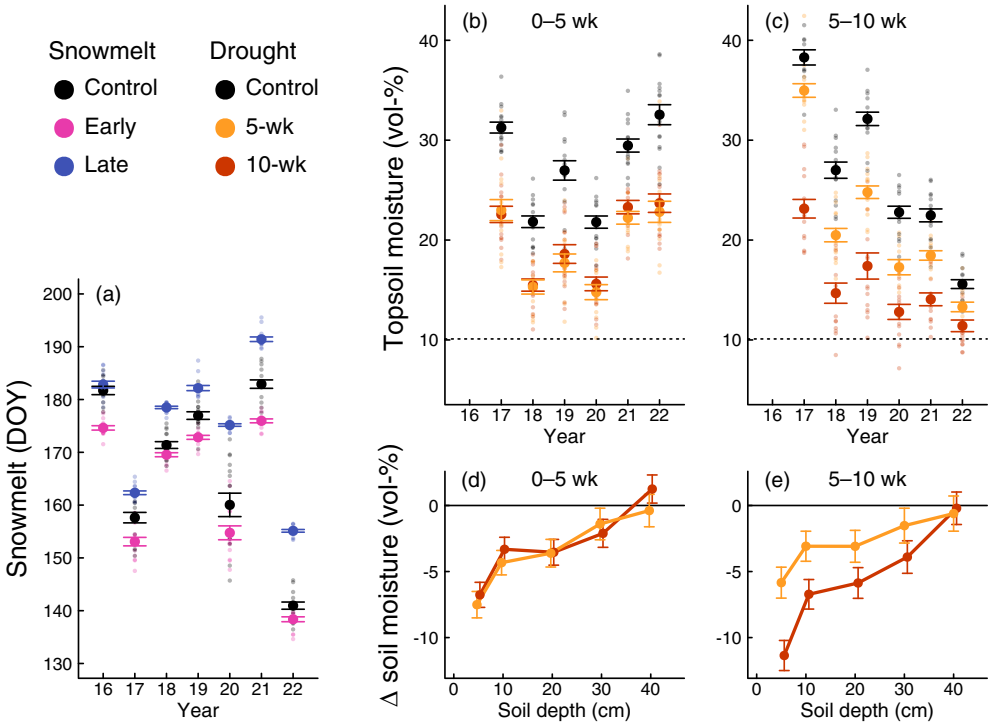


FIGURE 2 (a) Day of year of snowmelt (2016–2022) and (b, c) mean topsoil (0–5 cm) moisture for each experimental year (2017–2022, first rain-out shelters in 2017). Small points depict values for each plot and bigger points show means ± SE for each treatment. DOY of 140 is equal to 21 May, DOY of 200 to 20 July. Topsoil moisture is split in two periods: from 0 to 5 weeks plots of both drought treatments (5- and 10-week) were sheltered from rain, while from 5 to 10 weeks only the 10-week plots were sheltered. Dashed line indicates soil moisture at the permanent wilting point. (d, e) Difference in soil moisture between the two drought treatments and controls (horizontal black line) across soil depths, averaged over all seasons (Figure S3 for continuous soil moisture values at 0–5 and 10 cm depth).

the topsoil even right after snowmelt (−3.6 ± 0.9%, $p < 0.001$, no difference between 5- and 10-week). Mean soil temperature (at 3–4 cm depth) during the drought treatment varied between 11.0°C (2021) and 14.6°C (2022) in controls and was on average 0.7 K higher in droughted plots during the first 5 weeks (Figure S4). During the second 5 weeks, when soils were even drier in plots with rain-out shelters, this temperature difference increased to 1.2 K, suggesting less transpirational cooling under drought. Mean irradiance was 13.0 ± 3.1% lower under rain-out shelters.

3.2 | Above-ground biomass

Annual peak above-ground biomass in controls was 122 ± 6 g m^{-2} a^{-1} across all years and, aside from the first 2 years, biomass was remarkably similar between years (Figure 3). Total community biomass was unaffected by snowmelt date (Table 1) and including the interannual variation of snowmelt in the analysis by replacing snow treatment with the date of snowmelt in our model did not indicate a significant effect of snowmelt timing on total above-ground biomass production either ($p = 0.78$). Drought, however, decreased total biomass significantly in the 10-week treatment (−16.0 ± 7%, $p = 0.011$). This effect was absent in the first year but then persisted during the following years (Figure 3). The response to the 5-week treatment varied significantly across years (Table 1), with a trend towards lower biomass in 2019 ($p = 0.12$) and a significant reduction in the final year 2022 ($p = 0.008$, Figure 3). This reduction in biomass was unrelated to the precipitation that the plants received between removal of the 5-week rain-out shelters and harvest, which amounted to 50–110 mm (and corresponding increases in soil moisture; Figure S3) in 2017–2020 but only <15 mm in 2021 and 2022.

Although total community biomass was not affected, snowmelt timing did exert differential biomass effects among functional groups (Table 1). Later snowmelt reduced biomass in graminoids (without *Carex*) by 9.6 ± 4.3% ($p = 0.029$), but had no effect on *Carex* or forbs. When including the interannual variation of snowmelt in the analysis, the grass *Helictotrichon* was the only species of the 10 most abundant ones that was affected by snowmelt timing, with more than doubled peak biomass (from 4.2 ± 1.2 to 9.6 ± 2.1 g m^{-2} a^{-1}) when snowmelt occurred at DOY 160 compared to 180 ($p = 0.027$, Figure S5).

Under drought, forbs and graminoids had lower biomass in the 10-week treatment, explaining the observed difference at the community level. In contrast, the dominant sedge *Carex* did not suffer from drought, and even produced slightly more biomass in the 5-week treatment ($p = 0.031$, Figure 3), increasing the proportion of *Carex* from 42 ± 2% in controls to 51 ± 2% in droughted plots ($p < 0.001$, no difference between 5- and 10-week). Regression analysis of the above-ground biomass in response to mean soil moisture between rain-out shelter placement and harvest confirmed these patterns, with less biomass in drier soil for the total community, forbs and

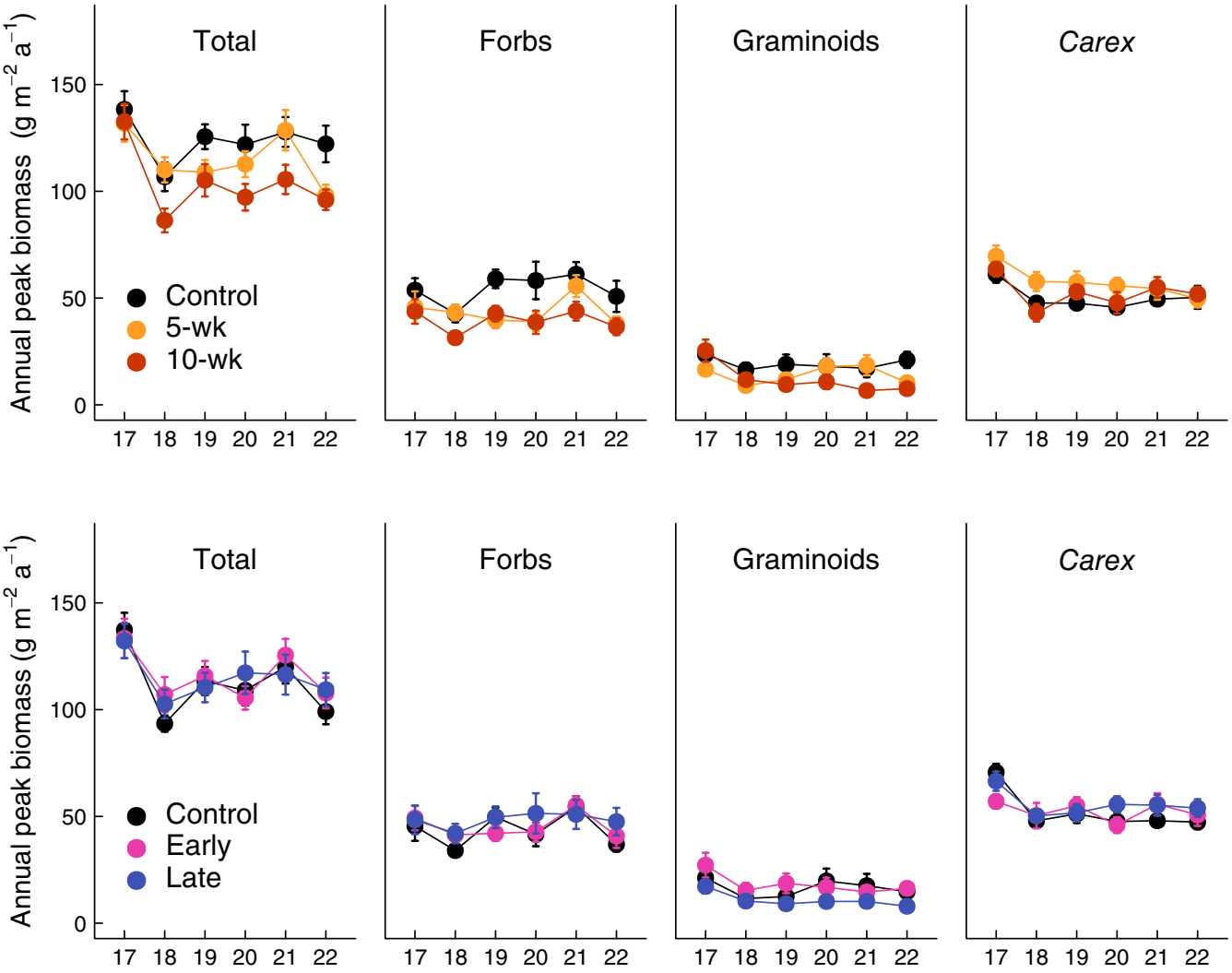


FIGURE 3 Annual peak above-ground biomass (2017–2022) by drought treatment (top) and snow manipulation (bottom). Biomass is further split into functional groups of forbs, graminoids and *Carex* (the only sedge). Points and error bars indicate means ± SE per treatment. As there was no interaction between snowmelt timing and drought (Table 1), we averaged across all snowmelt plots in the case of drought and vice versa ($n = 15$).

graminoids, but not *Carex* (Figure S6). Analysing the 10 most abundant species (together comprising >95% of total biomass) revealed that lower soil moisture significantly reduced biomass production in *Geum*, *Helictotrichon* and *Agrostis*, and marginally significant in *Ligusticum* (Figure 4). From the fitted models, we predicted average square-rooted biomass at 30 and 15 vol-% soil moisture and back-transformed the resulting values, which indicated a biomass reduction by 62 ± 21% for *Geum*, 54 ± 22% for *Helictotrichon*, 78 ± 24% for *Agrostis* and 50 ± 34% for *Ligusticum*. In contrast, biomass of *Leontodon* seemed to benefit from drier soil (+53 ± 32%; marginally significant, Figure 4). There was substantial variation in the lichen mass per plot, varying between 5 and 517 g m^{-2} (d. w.) with an average of 282 ± 36 g m^{-2} in controls. Drought significantly reduced lichen mass to 180 ± 31 g m^{-2} in the 5-week and to 130 ± 22 g m^{-2} in the 10-week treatment.

Necromass averaged at 38 ± 2.7 g m^2 a^{-1} in controls, varying between 26 and 52 g m^2 a^{-1} between years. There was marginally more necromass when snowmelt occurred earlier (42 ± 2.4 g m^2 a^{-1}, $p = 0.061$) and less under late snowmelt (31 ± 1.2 g m^2, $p < 0.001$) across all years (Table S2). Drought reduced total necromass by 13 ± 5% (10-week only, $p = 0.020$), similar to the effect on above-ground biomass. Consequently, the ratio of necro- to biomass was unaffected by drought ($p = 0.479$). The response of necromass to snowmelt timing and drought was not significantly different between forbs and graminoids (including *Carex* here; Table S2). Snowmelt timing had a similar effect on the dead fraction of *Carex* leaves as on total necromass: brown tips amounted to 22% of the green leaf mass in snow-controls, 26% under early ($p = 0.003$) and 16% under late snowmelt ($p < 0.001$). Drought also reduced this fraction by 3% ($p = 0.003$, no difference between 5- and 10-week). Measured in five abundant species in 2021, SLA responded to drought only, with an average decline by 6.5 ± 2.6% in the 10-week treatment (Figure S7, $p = 0.014$, no interaction between drought and species).

TABLE 1 Linear mixed effect models testing for the effects of summer drought and altered snowmelt date on above- and below-ground biomass, plant cover and ecosystem respiration.

Variable	df	χ^2	*p*	Variable	df	χ^2	*p*
Above-ground BM by FG (g d.w.)				Ingrowth root mass (g d.w.)			
2017–2022				2018, 2021			
Year	5	47.3	**<0.001**	Year	1	9.0	**0.003**
FG	2	1127.4	**<0.001**	Depth	1	48.4	**<0.001**
Drought	2	7.9	**0.019**	Drought	2	4.4	0.110
Snow	2	0.5	0.787	Snow	2	0.4	0.825
Year × FG	10	20.8	0.023	Year × depth	1	<0.1	0.993
Year × drought	10	8.6	0.574	Year × drought	2	2.7	0.261
Year × snow	10	6.2	0.801	Year × snow	2	1.7	0.432
FG × drought	4	38.6	**<0.001**	Depth × drought	2	2.5	0.279
FG × snow	4	18.7	**0.001**	Depth × snow	2	0.9	0.624
Drought × snow	4	3.0	0.564	Drought × snow	4	2.1	0.722
Total above-ground BM (g d.w.)				Standing root mass (g d.w.)			
2017–2022				2021			
Year	5	68.6	**<0.001**	Depth	1	256.1	**<0.001**
Drought	2	10.7	**0.005**	Drought	2	<0.1	0.995
Snow	2	0.8	0.672	Snow	2	<0.1	0.981
Year × drought	10	19.9	**0.030**	Depth × drought	2	0.8	0.682
Year × snow	10	8.9	0.545	Depth × snow	2	2.4	0.300
Drought × snow	4	3.2	0.522	Drought × snow	4	2.0	0.734
Plant cover (%)				Ecosystem respiration (μmol C m^{-2} s^{-1})			
2022				2019–2021			
FG	2	319.5	**<0.001**	Date	8	959.0	**<0.001**
Drought	2	8.7	**0.013**	Drought	2	20.1	**<0.001**
Snow	2	1.3	0.534	Snow	2	1.4	0.486
FG × drought	4	15.0	**0.005**	Date × drought	16	112.2	**<0.001**
FG × snow	4	8.4	0.077	Date × snow	16	60.5	**<0.001**
Drought × snow	4	1.4	0.848	Drought × snow	4	0.3	0.987

Abbreviations: BM, biomass; depth, soil depth (0–10 and 10–20 cm); FG, functional group (forbs, graminoids, *Carex*). Year was treated as a categorical factor. Values in bold indicate significance at $p < 0.05$.

3.3 | Below-ground biomass

The total amount of newly formed roots in in-growth cores (0–20 cm depth) was unaffected by snowmelt (Table 1) and amounted to 304 ± 14 g m^{-2} a^{-1} in controls, with ca. 25% more roots at 0–10 cm soil depth compared to 10–20 cm (Figure 5). Drought increased root biomass in in-growth cores by 13 ± 6% in the 5-week treatment ($p = 0.035$) and this effect was independent of soil depth. Comparing the annual peak above-ground harvest with root growth in in-growth cores (both in g m^{-2} a^{-1}) revealed an increase in the root mass fraction of (root mass / total mass) under drought ($p = 0.009$). It was 70.7 ± 1.5% in controls and rose to 73.5 ± 1.4% in the 5-week and 75.2 ± 1.2% in the 10-week drought. Standing root biomass (incl. older roots and rhizomes) was influenced neither by drought nor by snowmelt timing (Table 1) and amounted to 1045 ± 36 g m^{-2}, with 762 ± 34 g m^{-2} in the upper and 283 ± 12 g m^{-2} in the lower soil horizon across all treatments (Figure 5). Fine roots with diameters <1 mm contributed ca. 95% to total below-ground biomass, irrespective of treatment. Model selection using least-absolute shrinkage regression revealed that plots with more *Carex* above-ground biomass had significantly more below-ground biomass in the 0–10 cm soil layer (+9.5 ± 2.8 g below-ground biomass per g *Carex* above-ground biomass; $p = 0.006$), while total below-ground biomass was unrelated to total above-ground biomass.

3.4 | Community composition

Seven years of snow manipulation had no significant effects on plant cover, species richness, or diversity indices (Tables 1 and 2). Also, 6 years of recurring drought had no effect in the 5-week treatment, but total plant cover was reduced by 12 ± 4% in the 10-week

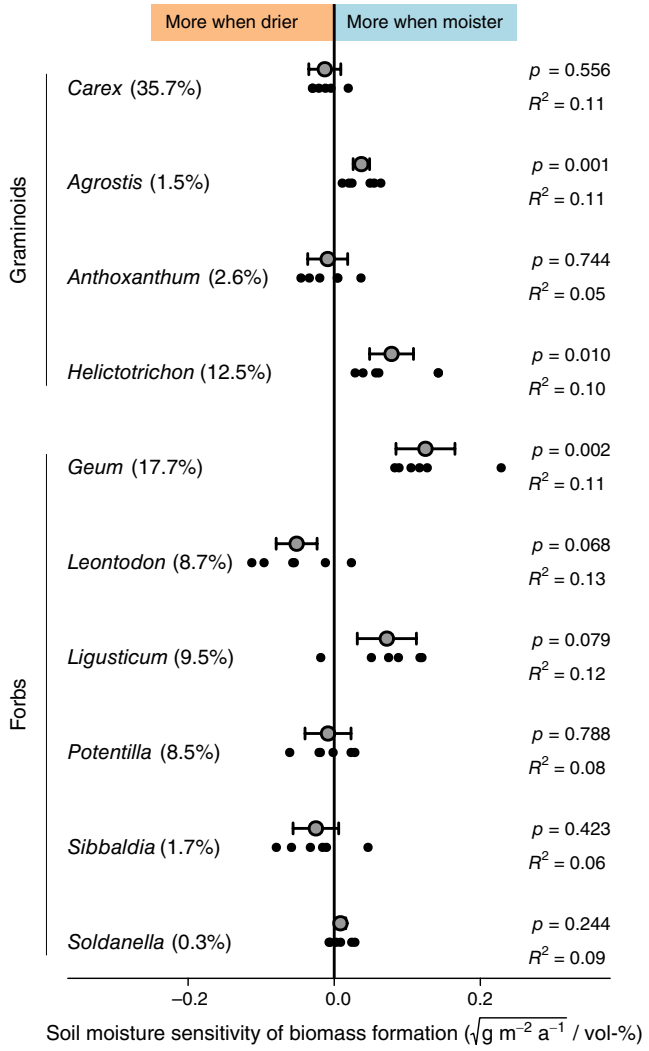


FIGURE 4 Species-specific soil moisture sensitivity of annual peak biomass in the 10 most frequently occurring species (ordered alphabetically within functional groups). Percentage numbers in brackets indicate the fraction of biomass per species across all control plots. Points indicate regression slopes of peak biomass (square-rooted, $\sqrt{g\,m^{-2}a^{-1}}$) against mean topsoil moisture (0–5 cm, vol-%) between the placement of rain-out shelters and harvest. Negative values (to the left) indicate more biomass in drier soil and vice versa. Small points depict slopes for each of the 6 years, while bigger points show the mean ± SE across all years. Marginal R^2-values are reported.

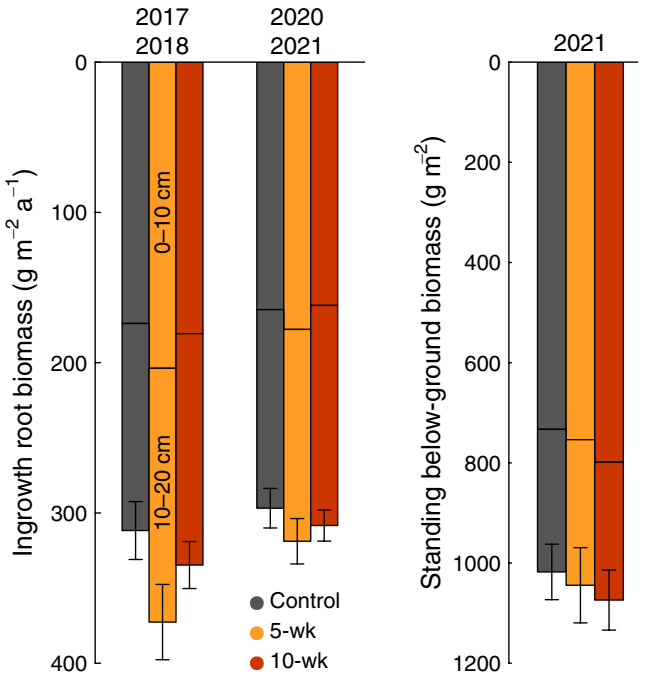


FIGURE 5 Below-ground biomass in response to drought treatments. Left: Fine root biomass of in-growth cores, collected after 2 years of incubation (2017/2018 and 2020/2021). Right: Standing below-ground biomass (note different *y*-axis dimension) including fine roots (>95% of total), thicker roots (>1 mm) and rhizomes, collected in 2021. Total bar size indicates mean ± SE per treatment. The upper and lower part of each bar shows the biomass at 0–10 cm and 10–20 cm soil depth, respectively.

drought treatment ($p = 0.005$; Table 2). This reduction was accountable to a decline in the cover of graminoids (−7 ± 2%, $p < 0.001$) and forbs (−9 ± 4%, $p = 0.030$). Plant cover of individual species reflected the species-specific declines in biomass production under drought (Table S1). In contrast, both drought levels had no negative effect on *Carex* cover, and the 5-week treatment even induced a trend towards higher cover (+6%, $p = 0.10$). Owing to the decrease in biomass of forbs and grasses, the relative contribution of *Carex* to total plant cover increased by 12 ± 4% in the 10-week drought treatment (36% in controls vs. 48% in 10-week; $p = 0.003$). Higher dominance of *Carex* was also reflected by the Simpson's index, which was significantly higher in the 10-week treatment compared to controls ($p = 0.026$; Table 2). In line with this, Shannon diversity decreased, although not significantly. Snowmelt and drought had no effect on moss cover, but lichen cover was nearly halved by the 10-week drought (from 6.9% to 3.6%; $p = 0.001$; Table 2).

3.5 | Ecosystem respiration

Ecosystem respiration varied from 1.12 ± 0.08 to 1.71 ± 0.08 μmol CO_2 $m^{-2}s^{-1}$ between single dates in controls (Figure 6). Plots that melted out earlier than controls had a higher respiration in the two measurements conducted already in July, by 12 ± 6% in 2020 ($p = 0.054$) and by 21 ± 6% in 2021 ($p = 0.002$). This effect disappeared later in the season. Over all dates, drought on average reduced ecosystem respiration by 13 ± 5% in the 5-week ($p = 0.015$) and by 23 ± 5% in the 10-week treatment ($p < 0.001$). The strength of this effect varied between measurement dates, depending on whether plots were still under drought. Under rain-out shelters, the deviation from controls increased with drought duration (up to 40%; $p < 0.001$, $R^2 = 0.80$; Figure 6d) and as the difference in soil moisture content became more pronounced ($p = 0.03$, $R^2 = 0.49$; Figure 6e). Removal of above-ground foliage before the measurement reduced ecosystem respiration by 13 ± 4% in early season of 2021 (July), but this difference disappeared

TABLE 2 Estimated marginal means (± SE) of plant and lichen cover, species richness, and two diversity indices (Shannon's and Simpson's).

	Snow			Drought		
	Control	Early	Late	Control	5-week	10-week
Total plant cover (%)	74.5 ± 2.9	74.9 ± 2.9	72.1 ± 2.9	77.8 ± 3.2	78.4 ± 3.0	**65.6 ± 2.5**
Plant cover by FG (%)						
Forbs	32.3 ± 2.7	32.6 ± 2.7	38.1 ± 2.9	37.5 ± 2.8	36.7 ± 3.1	**29.0 ± 2.5**
Graminoids (w/o *Carex*)	7.7 ± 1.4	8.3 ± 1.5	4.6 ± 1.1	10.7 ± 1.6	6.6 ± 1.4	**3.8 ± 1.0**
Carex	32.3 ± 2.4	31.2 ± 2.3	28.1 ± 2.2	27.6 ± 2.1	33.2 ± 2.6	30.8 ± 2.3
Lichen cover (%)	6.3 ± 0.8	5.6 ± 0.7	4.6 ± 0.8	6.9 ± 0.7	6.0 ± 1.0	**3.6 ± 0.6**
Species richness	12.3 ± 0.6	12.3 ± 0.7	11.2 ± 0.7	11.9 ± 0.7	11.9 ± 0.7	12.0 ± 0.7
Shannon's index	1.59 ± 0.08	1.58 ± 0.08	1.61 ± 0.06	1.68 ± 0.05	1.60 ± 0.07	1.50 ± 0.10
Simpson's index	0.29 ± 0.03	0.30 ± 0.03	0.27 ± 0.02	0.24 ± 0.01	0.28 ± 0.02	**0.33 ± 0.03**

Note: In the case of plant cover, estimates and standard errors were back-transformed from the square-root values, meaning that cover by functional group (FG) does not sum up exactly to total plant cover. Values in bold differ significantly ($p < 0.05$) from controls.

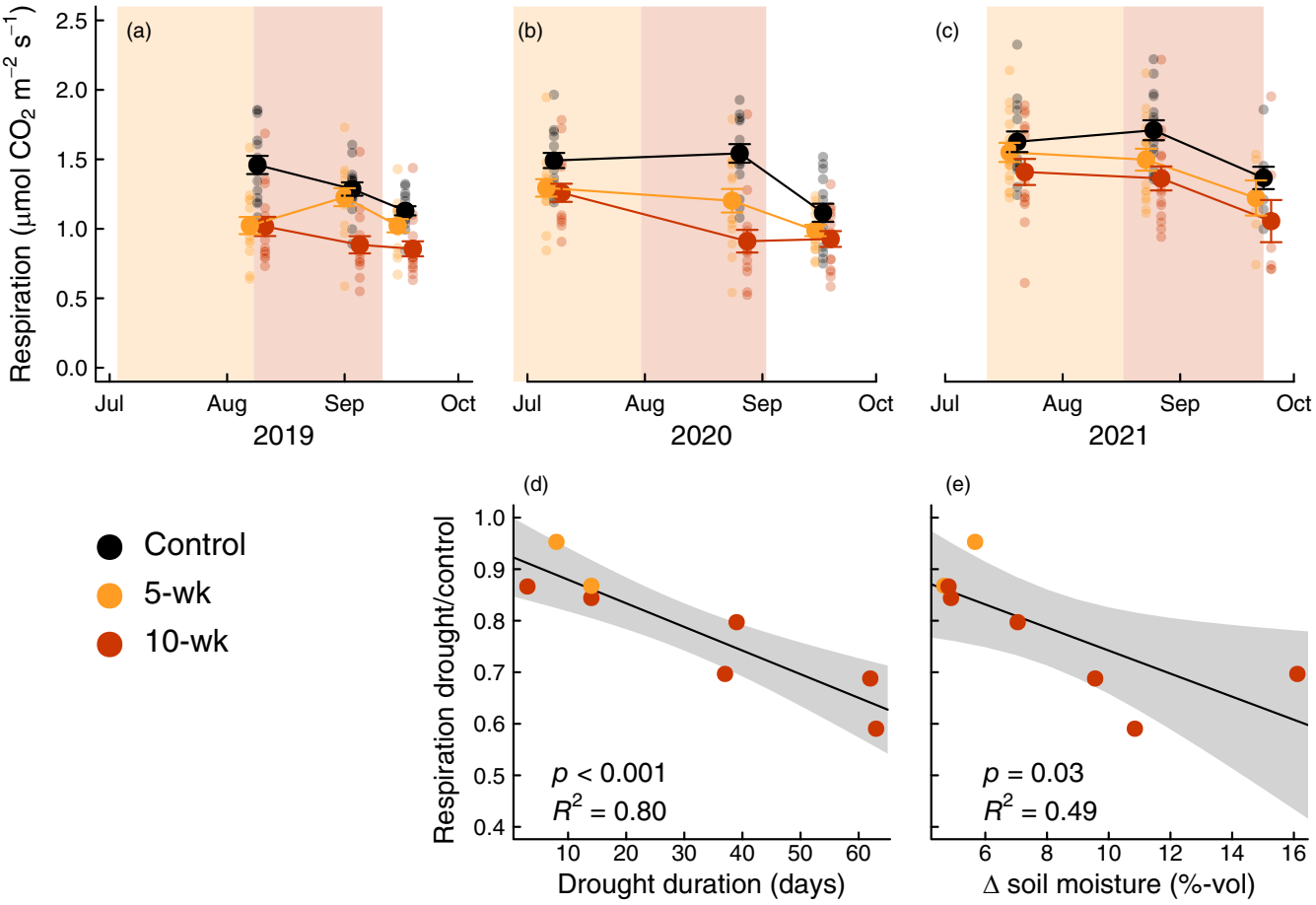


FIGURE 6 (a–c) Ecosystem respiration in response to 5- and 10-week of recurring summer drought, normalized to 10°C soil temperature. Coloured background indicates the sheltering periods of the 5- and 10-week drought treatment. Light-coloured points indicate values for each plot and dark-coloured, bigger points show means ± SE for each drought treatment (no interaction with snowmelt, $n = 15$). Points of the three treatments are slightly shifted to improve visibility. (d, e) Respiration (mean, 95%-CI in grey) in droughted plots as a fraction of control plots across all three seasons. The fraction declines with increasing drought duration (d) and/or with larger soil moisture difference between control and droughted plots (e).

later in the season (−3 ± 4% in August and +1 ± 6% in September, *n.s.*). Thus, >85% of ecosystem respiration stemmed from below-ground activities, underpinning the overarching importance of respiration originating from below-ground biomass (including microbes).

4 | DISCUSSION

We aimed at deciphering the effects of climate change on the productivity of this late-successional alpine grassland and employed a unique experimental approach where we combined manipulated snowmelt timing with recurrent summer drought over 6 years. Most importantly, recurrent drought reduced above-ground biomass, increased the root mass fraction and shifted the community composition towards the already dominant *Carex curvula*, which proved to be highly drought-resistant. In contrast, shifting snowmelt by 13 days on average between early and late snowmelt had little effects on any of the measured traits, underlining recent findings that snowmelt timing (and by that, season length) has little predictive value for biomass production in this type of alpine grassland (Möhl et al., 2022). Our results also highlight the differential controls over growth and reproduction: in contrast to growth, flowering phenology was mainly affected by snowmelt timing, while summer drought played a minor role in a previous study from the same experiment (Vorkauf, Kahmen, et al., 2021).

4.1 | Treatment effectiveness

Snow-removal and -addition in spring altered snowmelt timing by 13 days on average (maximum of 20 days), which represents a significant shift for the activity of alpine plants. However, this range is much smaller than the natural year-to-year variation in snowmelt (42 days), which is a characteristic of most snowmelt manipulation experiments (Rixen et al., 2021), as interannual variability in snowmelt is generally large in mountain areas (Vitasse et al., 2017). Together, snow manipulation and inter-annual variation in the snowmelt date allowed us to test a large gradient of snowmelt timing of more than 50 days. Rain-out shelters effectively reduced soil moisture, with the strongest effects in the topsoil and observable differences down to 30 cm soil depth. This includes most of the rooted space in such grasslands (Greinwald et al., 2021; Hitz et al., 2001; Mezhunts et al., 2005). Beside precipitation, fog and dew formation during cold nights is a minor source of moisture, amounting to 2–6 mm per month (Groh et al., 2018; Riedl et al., 2021; van den Bergh et al., 2018), although rain-out shelters partly inhibit dew formation as radiative cooling during nights is reduced.

4.2 | Less biomass above-ground but more below-ground

Reduced above-ground biomass production in droughted grasslands has frequently been observed (Gao et al., 2019) across different land-use intensities and from low to subalpine elevation (Gilgen & Buchmann, 2009; Kröel-Dulay et al., 2022; Stampfli et al., 2018). As expected, our data show that alpine grassland is no exception, and peak above-ground biomass declined by 16% under recurring drought of 10 weeks per season. Interestingly, biomass was clearly not reduced by the 10-week drought in the first year of treatment, pointing towards drought effects on developmental processes after peak biomass (such as preformation of leaf buds) that might reduce biomass production in the following year. Because necromass was also lower under drought, the decline in biomass does not reflect increased or faster die-back but evidently a reduced biomass production. In contrast, a shorter drought of 5 weeks reduced peak biomass in the final year only, indicating some leeway for compensatory growth during drought recovery (Hahn et al., 2020). Yet, the time available for compensatory growth was obviously short, given that senescence and leaf die-back starts already 5–7 weeks after snowmelt in this vegetation type (Möhl et al., 2022). Topsoil desiccation during drought was more pronounced in 2022 and remained close to the permanent wilting point in the 5-week drought plots even during the recovery phase before harvest (Figure S3), possibly contributing to the lower biomass production in that year. The biomass decline we observed is less severe than that previously reported for a single-season drought experiment in a similar vegetation type, where 17 days of rain exclusion reduced above-ground production by 40% (de Boeck et al., 2015). However, this study used excavated monoliths that were decoupled from the soil continuum, which may explain the strong drought effect. Lower above-ground biomass under drought may counteract projected increases in growth due to warmer growing season temperatures (Rammig et al., 2010; Rumpf et al., 2022) and reduce food resources for various herbivores.

We also observed a massive reduction in the cover and mass of lichens (mainly *Cetraria* sp. and with lower abundance *Cladonia* sp.) under drought, although lichens are generally considered robust against harsh life conditions, including desiccation (Kranner et al., 2008). Very little is known about the effects of recurrent drought on ground-dwelling lichens in situ. We assume a massive dieback in *Cetraria* sp. but also increased dislocation by strong winds as dry thalli are less embedded in the less dense plant canopy under drought.

Low water availability can directly affect biomass production of plants by reducing turgor and impairing cell growth and biochemistry (Hsiao et al., 1976; Muller et al., 2011) but also indirectly by dampening nutrient uptake and availability in the soil (Da Silva et al., 2011). Though soil moisture remained above the permanent wilting point for most of the experiment, we expect that both reduced water (through low turgor pressure) and nutrient availability caused much of the observed decline in biomass. It is known that growth of alpine grasslands is often limited by soil nutrients—in fact, a study conducted in the same vegetation type and close to our site found that above-ground biomass production increased by 50% when NPK-fertilizer (45 kg ha^{-1}) was applied (Schäppi & Körner, 1996).

The reduction of SLA in droughted plants along with reduced biomass and vegetation density (cover) in the 10-week drought treatment also points to a reduced leaf area index (LAI), contributing to community wide water savings (Chaves et al., 2003). A lowering of SLA in response to drought at high elevation had been observed earlier (Rosbakh et al., 2017), although a drought treatment with intermittent irrigation elicited only weak responses in SLA (Hamann et al., 2017). A meta-analysis of temperate grasslands at lower elevation found that SLA of grasses responds more strongly to drought than forbs (Wellstein et al., 2017). Yet, we could not confirm this pattern for the five alpine plants tested here. Another way to maintain the balance between water uptake and transpiration is to invest in below-ground tissues and improve access to soil water.

In general, drought stimulates root growth relative to shoot growth to balance resource acquisition (Bloom et al., 1985), especially in species-rich grasslands (Kahmen et al., 2005). Four seasons with 50% less precipitation resulted in nearly 30% more root biomass (in-growth cores) in alpine grassland on the Tibetan Plateau (Liu et al., 2021). Another study reported that below-ground biomass remained unchanged under drought, while above-ground production declined in subalpine grassland (Gilgen & Buchmann, 2009). Whether or not below-ground biomass was enhanced, the root mass fraction increased in all these studies, similar to our findings. A more productive alpine grassland, exposed to three seasons with 6–12 weeks of experimental drought showed an increased root biomass in in-growth cores by up to 40% in calcareous and 24% in siliceous sloping terrain (Schmid, 2017). Hence, we suppose that more frequent droughts in the future will further increase the already high root mass fraction in alpine ecosystems. Potential consequences include increased resource allocation to roots with unchanged or even reduced decomposition rates, which may increase root-derived carbon in alpine soils (Liu et al., 2021).

In our grassland, annual above-ground biomass production—approximated by peak biomass—amounted to ca. 120 g m^{-2}, while below-ground production was 300 g m^{-2} to a soil depth of 20 cm, indicating that the large below-ground fraction of alpine grasslands is not only due to high root longevity but also a result of substantially more below-ground investments. Notably, we compared peak above-ground harvests with end-of-season below-ground harvests because roots grow for a much longer period than leaves in this ecosystem and harvesting in-growth cores together with peak above-ground biomass may underestimate annual below-ground production by up to 50% (Möhl et al., 2022).

We aimed at identifying longer-term effects of climate change on biomass formation, but did not observe any duration-related trends over 6 years of combined snow manipulation and drought treatments. Biomass responses were either fairly stable or fluctuated between years with no clear trend. We assume that the absence of additive effects of recurring drought is a consequence of the large influx of water during snowmelt, which largely reset the system. Nonetheless, we found that control plots were moister than droughted plots right after snowmelt in the last 3 years, suggesting a legacy effect, namely that drought reduced soil field capacity over the course of the experiment. This implies changes in soil structure and properties under recurring drought, for instance, increased water repellency (hydrophobicity) due to a change in the structure of soil particles (Goebel et al., 2011; Robinson et al., 2016), which could affect nutrient relations and plant growth in the long term under more frequent drought.

4.3 | Reduced ecosystem respiration under drought

We observed efflux rates of 1–2 µmol CO_2 m^{-2} s^{-1} during the growing season, which is low compared to lower elevation grasslands (e.g. Burri et al., 2018: 4–8 µmol CO_2 m^{-2} s^{-1}), but typical for high-elevation vegetation with low soil temperature and productivity (Bahn et al., 2008; Diemer, 1994). Year-round eddy covariance measurements at a nearby alpine grassland site yielded ecosystem respiration rates in a similar range (0–5 µmol CO_2 m^{-2} s^{-1} during the growing season; Scholz et al., 2018). The biggest fraction (>85%) of respiration was accountable to below-ground activity, as cutting above-ground tissues reduced respiration by no more than 15%, which is nearly equal to the portion of total biomass (incl. roots) made up by above-ground tissues in our experiment (14.2% in controls).

As expected, drought resulted in consistently lower ecosystem respiration in plots with rain-out shelters compared to controls, implying that reduced above-ground biomass and dry soil constrain plant and microbial activity (Hasibeder et al., 2015; Schimel, 2018). However, given that drought did not reduce root biomass in our case, we hypothesize a stronger negative drought effect on soil microbes than on plant organs. Such results are consistent with reduced soil respiration in other drought experiments in lowland (non-alpine) grassland ecosystems (e.g. Bloor & Bardgett, 2012; Burri et al., 2018; Harper et al., 2005) and in managed subalpine grassland (Hagedorn & Joos, 2014; Ingrisch et al., 2018). While droughted plots respired less during each of the nine measurement campaigns between 2019 and 2022, we might have missed ephemeral respiratory bursts due to rewetting immediately after removal of the rain-out shelters (Barnard et al., 2020; Ingrisch et al., 2020; Schimel, 2018). Such bursts can result from rapid mineralization of litter and soil organic matter upon rewetting and may, beside stimulating microbial growth, also increase plant nutrient uptake and growth (Karlowsky et al., 2018). Especially in the 5-week drought treatment, such a burst of nutrients due to rewetting may have contributed to biomass recovery. CO_2 efflux rates during recovery from drought increased to the level of controls but never exceeded them. A 3-year drought study in managed subalpine grassland measured soil respiration at higher temporal resolution but found no indications for higher respiration after rewetting (Hagedorn & Joos, 2014). On the other hand, respiration was stimulated by rewetting after a 6-week drought in managed and abandoned subalpine grassland (Ingrisch et al., 2020). It awaits further research to explore whether the reduced rates of respiration

under drought are compensated during wetter periods, particularly during the 8–9 months lasting winter period at our site.

4.4 | Weak effects of snowmelt timing

We hypothesized that earlier snowmelt could lead to higher above-ground biomass after several years. To our surprise, even over 7 years of snow manipulation, altered snowmelt timing had hardly any effects on the vegetation. Several studies in arctic tundra and alpine vegetation observed a similar unresponsiveness in productivity to earlier snowmelt, both above- and below-ground (Baptist et al., 2010; Boyle et al., 2022; Darrouzet-Nardi et al., 2019). It was previously argued that adverse effects of freezing temperatures during earlier snowmelt outweigh beneficial effects of a longer growing season (Wipf et al., 2009) but particularly graminoids exhibit a high freezing resistance even in a fully active state (von Büren & Hiltbrunner, 2022). In addition, internal controls over growth and senescence could restrain plants from extending growth when the season prolongs (Körner et al., 2023), as recently evidenced for alpine *Carex curvula* grassland (Möhl et al., 2022). Nevertheless, a remote sensing study on alpine grasslands between 2000 and 2600 m elevation in the Alps found a correlation between growing season length (snowmelt timing) and NDVI-derived gross primary production (Choler, 2015). However, the higher integrated NDVI signal in seasons with earlier snowmelt stemmed mainly from an extension of the senescence period, as peak NDVI always occurred ca. 50 days after snowmelt. This indicates that remaining green tissues, rather than new growth, were responsible for the observed correlation. In absence of direct effects, the timing of snowmelt is assumed to influence plant growth mainly through changes in community composition, as plant species (other than *Carex*) with already longer growing phases may become more competitive in a future climate with much earlier snowmelt. While the average shift in snowmelt of 13 days was not enough to affect community composition, the substantial advance in snowmelt of up to 1 month projected for the end of the 21st century (Vorkauf, Marty, et al., 2021) will push snowmelt largely out of the range of its current interannual variation, and could therefore exert greater pressure on the prevailing plant community. Although the Alps have become greener (higher NDVI) at montane and alpine elevations during the last four decades, this greening was associated with warmer temperatures rather than a decline in snowcover during summer months (Rumpf et al., 2022).

Manipulated snowmelt timing also had no effect on the drought treatment, except for the slightly higher soil moisture in the first 5 weeks under delayed snowmelt. It appears that the consequences of the two treatments were largely independent and that our drought-related findings are representative of future conditions with earlier snowmelt. One reason for the consistency of drought effects among snowmelt treatments could be that we initiated both drought levels immediately after snowmelt. Growth of alpine plants tightly tracks snowmelt (Choler, 2015; Vitasse et al., 2017), and starts whenever temperature is suitable for growth. Consequently, the main phase of biomass production always occurs in the first weeks of the season (Möhl et al., 2022) and drought is expected to affect biomass production most during this phase. This also means that drought later in the season may affect productivity of alpine grassland to a lesser extent or only for species that still grow later in the season (e.g. *Helictotrichon versicolor* or *Potentilla aurea*; Möhl et al., 2022).

4.5 | Species identity matters

Graminoids and forbs differ in many aspects such as plant architecture, metabolism, or dispersal strategy (Wullschleger et al., 2014) and therefore respond differently to environmental change. For example, a study on the Tibetan Plateau reported stronger effects of drought on the abundance of forbs and sedges, while the abundance of grasses (*Stipa aliena*, *Elymus nutans*, *Helictotrichon tibeticum* and others) increased over 4 years of experimentally reduced precipitation (Liu et al., 2018). In our study, biomass of both forbs and graminoids other than *Carex* declined in the 10-week drought treatment. It is striking that biomass production of the dominant species, *Carex curvula*, was not affected by drought and even slightly increased in the 5-week drought treatment. After 6 years of treatment the dominance of *Carex* in droughted plots was indeed higher. Therefore, the consequences of drought in this alpine grassland appear to be specific to species rather than to functional groups and thus, depend substantially on the local species pool.

Carex curvula appears to have a very conservative growth control, with above-ground biomass hardly responding to varying environmental conditions such as elevated CO_2 (Schäppi & Körner, 1996), shading (Möhl et al., 2020) and as revealed here to summer drought. In part, low growth rates, preformed leaf buds and tiller endurance of several years may confer this high resistance to variable life conditions. Its below-ground dominance through substantial root longevity (Budge et al., 2011; Leifeld et al., 2015) may considerably add to the high drought tolerance (Mähr & Grabherr, 1983), which fits our observation that standing root biomass correlates with *Carex* cover. Interestingly, *Carex curvula* roots are known to be heavily colonized by dark septate fungal endophytes (DSE), quite a different group of fungi than those forming VA mycorrhizas (Read & Haselwandter, 1981). Whether these dark-septate fungi mediate the enhanced drought resistance in this species has not been explored so far. DSE isolated from roots of an epiphytic orchid and inoculated to seedlings of the same species increased their drought resistance (Liu et al., 2022), underpinning the role of DSE for the hosts.

In contrast to *Carex*, two of the most abundant species—the forb *Geum montanum* and the grass *Helictotrichon versicolor*—which together accounted for about 30% of total biomass production, turned out to be sensitive to drought. A study with 11 alpine species from the Rocky Mountains and the Sierra Nevada grown from seed revealed differential growth responses to drought, with those species from drier sites being less affected (Peterson & Billings, 1983). Although *Geum* and *Helictotrichon* are not known for preferring moist habitats (both have an Ellenberg moisture indicator of 5; Ellenberg

& Leuschner, 2010), water shortage may render them less competitive within this plant community, reducing their abundance under future drought scenarios. In contrast, the low sensitivity to drought suggests that *Carex* will become even more dominant in the future.

5 | CONCLUSIONS

Despite our expectations, we found almost no evidence of interactive effects between snowmelt timing and summer drought in this ecosystem. Our results show that several weeks of summer drought reduce biomass production of this alpine grassland, with consequences for grazers on managed- and unmanaged land under continued climate change. While most of the biomass of alpine grassland is already below-ground, the proportion of root mass will further increase in the future should drought conditions become more frequent, underscoring the need to understand root and soil processes as well as their interaction in these ecosystems. Drought appears to have hampered soil microbial activity in the most active soil horizon, which could limit nutrient and carbon cycling and lead to temporal discrepancies between nutrient availability and plant demand. We find it remarkable that experimental drought increased the dominance of *Carex curvula* in only 6 years, despite the recognized persistence and longevity of such dense, late-successional vegetation with predominantly clonal growth (Vittoz et al., 2009; Windmaißer & Reisch, 2013). A major outcome of this study is therefore that the dominant species profits from the simulated scenarios, perhaps explaining the several millennia of persistence of individual *Carex* clones in this grassland (de Witte et al., 2012). Given the unresponsiveness of biomass production to variable snowmelt dates, our study warns against projections that assume proportionality between biomass production and season length (see Körner et al., 2023). In contrast to drought, systematic variation of snowmelt date did not affect species composition, a surprising result in view of the classical species gradients across snowmelt gradients. Either, late successional communities represent an end point of species assemblage that is far more robust than the species composition of snowbeds, or such 'timing effects' take longer than drought effects to materialize, given the natural variation of snowmelt timing.

AUTHOR CONTRIBUTIONS

Erika Hiltbrunner designed and initiated the study. Patrick Möhl, Maria Vorkauf and Erika Hiltbrunner collected data. Patrick Möhl analysed the data and wrote the manuscript in close consultation with Erika Hiltbrunner and with input from the other authors. All authors revised the manuscript and approved the final version.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

PEER REVIEW

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DATA AVAILABILITY STATEMENT

All relevant data used in this study are available from the Figshare repository https://doi.org/10.6084/m9.figshare.20529678 (Möhl et al., 2023).

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REFERENCES

Atkin, O. K., Evans, J. R., & Siebke, K. (1998). Relationship between the inhibition of leaf respiration by light and enhancement of leaf dark respiration following light treatment. *Functional Plant Biology*, *25*, 437–443. https://doi.org/10.1071/pp97159

Bader, M. K.-F., & Körner, C. (2010). No overall stimulation of soil respiration under mature deciduous forest trees after 7 years of CO_2 enrichment. *Global Change Biology*, *16*, 2830–2843. https://doi.org/10.1111/j.1365-2486.2010.02159.x

Bahn, M., Rodeghiero, M., Anderson-Dunn, M., Dore, S., Gimeno, C., Drösler, M., Williams, M., Ammann, C., Berninger, F., Flechard, C., Jones, S., Balzarolo, M., Kumar, S., Newesely, C., Priwitzer, T., Raschi, A., Siegwolf, R., Susiluoto, S., Tenhunen, J., … Cernusca, A. (2008). Soil respiration in European grasslands in relation to climate and assimilate supply. *Ecosystems*, *11*, 1352–1367. https://doi.org/10.1007/s10021-008-9198-0

Baptist, F., Flahaut, C., Streb, P., & Choler, P. (2010). No increase in alpine snowbed productivity in response to experimental lengthening of the growing season. *Plant Biology*, *12*, 755–764. https://doi.org/10.1111/j.1438-8677.2009.00286.x

Barnard, R. L., Blazewicz, S. J., & Firestone, M. K. (2020). Rewetting of soil: Revisiting the origin of soil CO_2 emissions. *Soil Biology and Biochemistry*, *147*, 107819. https://doi.org/10.1016/j.soilbio.2020.107819

Bloom, A. J., Chapin, F. S., III, & Mooney, H. A. (1985). Resource limitation in plants—An economic analogy. *Annual Review of Ecology and Systematics*, *16*, 363–392. https://doi.org/10.1146/annurev.es.16.110185.002051

Bloor, J. M. G., & Bardgett, R. D. (2012). Stability of above-ground and below-ground processes to extreme drought in model

grassland ecosystems: Interactions with plant species diversity and soil nitrogen availability. *Perspectives in Plant Ecology, Evolution and Systematics*, *14*, 193–204. https://doi.org/10.1016/j.ppees.2011.12.001

Blumer, P., & Diemer, M. (1996). The occurrence and consequences of grasshopper herbivory in an alpine grassland, Swiss Central Alps. *Arctic and Alpine Research*, *28*, 435–440. https://doi.org/10.1080/00040851.1996.12003196

Boyle, J. S., Angers-Blondin, S., Assmann, J. J., & Myers-Smith, I. H. (2022). Summer temperature—But not growing season length—Influences radial growth of *Salix arctica* in coastal Arctic tundra. *Polar Biology*, *45*, 1257–1270. https://doi.org/10.1007/s00300-022-03074-9

Braun-Blanquet, J. (1948). *La Végétation alpine des Pyrénées Orientales, étude de phyto-sociologie comparée*. Monografías de la Estación de Estudios Pirenaicos y del Instituto Español de Edafología, Ecología y Fisiología Vegetal 9.

Budge, K., Leifeld, J., Hiltbrunner, E., & Fuhrer, J. (2011). Alpine grassland soils contain large proportion of labile carbon but indicate long turnover times. *Biogeosciences*, *8*(7), 1911–1923. https://doi.org/10.5194/bg-8-1911-2011

Burri, S., Niklaus, P. A., Grassow, K., Buchmann, N., & Kahmen, A. (2018). Effects of plant productivity and species richness on the drought response of soil respiration in temperate grasslands. *PLoS ONE*, *13*, e0209031. https://doi.org/10.1371/journal.pone.0209031

Calanca, P. (2007). Climate change and drought occurrence in the alpine region: How severe are becoming the extremes? *Global and Planetary Change*, *57*, 151–160. https://doi.org/10.1016/j.gloplacha.2006.11.001

Chaves, M. M., Maroco, J. P., & Pereira, J. S. (2003). Understanding plant responses to drought — from genes to the whole plant. *Functional Plant Biology*, *30*(3), 239–264. https://doi.org/10.1071/fp02076

Choler, P. (2015). Growth response of temperate mountain grasslands to inter-annual variations in snow cover duration. *Biogeosciences*, *12*, 3885–3897. https://doi.org/10.5194/bg-12-3885-2015

Da Silva, E. C., Nogueira, R., Da Silva, M. A., & De Albuquerque, M. B. (2011). Drought stress and plant nutrition. *Plant Stress*, *5*, 32–41.

Darrouzet-Nardi, A., Steltzer, H., Sullivan, P. F., Segal, A., Koltz, A. M., Livensperger, C., Schimel, J. P., & Weintraub, M. N. (2019). Limited effects of early snowmelt on plants, decomposers, and soil nutrients in Arctic tundra soils. *Ecology and Evolution*, *9*, 1820–1844. https://doi.org/10.1002/ece3.4870

de Boeck, H. J., Bassin, S., Verlinden, M., Zeiter, M., & Hiltbrunner, E. (2015). Simulated heat waves affected alpine grassland only in combination with drought. *The New Phytologist*, *209*, 531–541. https://doi.org/10.1111/nph.13601

de Witte, L. C., Armbruster, G. F. J., Gielly, L., Taberlet, P., & Stöcklin, J. (2012). AFLP markers reveal high clonal diversity and extreme longevity in four key arctic-alpine species. *Molecular Ecology*, *21*, 1081–1097. https://doi.org/10.1111/j.1365-294x.2011.05326.x

Diemer, M. W. (1994). Mid-season gas exchange of an alpine grassland under elevated CO_2. *Oecologia*, *98*, 429–435. https://doi.org/10.1007/bf00324233

Ellenberg, H., & Leuschner, C. (Eds.) (2010). Zeigerwerte der Pflanzen Mitteleuropas. In *Vegetation Mitteleuropas mit den Alpen* (Vol. *72*, pp. 706). Utb.

Freschet, G. T., Roumet, C., Comas, L. H., Weemstra, M., Bengough, A. G., Rewald, B., Bardgett, R. D., de Deyn, G. B., Johnson, D., Klimešová, J., Lukac, M., McCormack, M. L., Meier, I. C., Pagès, L., Poorter, H., Prieto, I., Wurzburger, N., Zadworny, M., Bagniewska-Zadworna, A., … Stokes, A. (2021). Root traits as drivers of plant and ecosystem functioning: Current understanding, pitfalls and future research needs. *The New Phytologist*, *232*, 1123–1158. https://doi.org/10.1111/nph.17072

Friedman, J., Hastie, T., & Tibshirani, R. (2010). Regularization paths for generalized linear models via coordinate descent. *Journal of Statistical Software*, *33*, 1–22.

Gao, J., Zhang, L., Tang, Z., & Wu, S. (2019). A synthesis of ecosystem aboveground productivity and its process variables under simulated drought stress. *Journal of Ecology*, *107*, 2519–2531. https://doi.org/10.1111/1365-2745.13218

Gilgen, A. K., & Buchmann, N. (2009). Response of temperate grasslands at different altitudes to simulated summer drought differed but scaled with annual precipitation. *Biogeosciences*, *6*, 2525–2539. https://doi.org/10.5194/bg-6-2525-2009

Gobiet, A., Kotlarski, S., Beniston, M., Heinrich, G., Rajczak, J., & Stoffel, M. (2014). 21st century climate change in the European Alps—A review. *Science of the Total Environment*, *493*, 1138–1151. https://doi.org/10.1016/j.scitotenv.2013.07.050

Goebel, M., Bachmann, J., Reichstein, M., Janssens, I. A., & Guggenberger, G. (2011). Soil water repellency and its implications for organic matter decomposition—Is there a link to extreme climatic events? *Global Change Biology*, *17*, 2640–2656. https://doi.org/10.1111/j.1365-2486.2011.02414.x

Greinwald, K., Dieckmann, L. A., Schipplick, C., Hartmann, A., Scherer-Lorenzen, M., & Gebauer, T. (2021). Vertical root distribution and biomass allocation along proglacial chronosequences in Central Switzerland. *Arctic, Antarctic, and Alpine Research*, *53*, 20–34. https://doi.org/10.1080/15230430.2020.1859720

Groh, J., Slawitsch, V., Herndl, M., Graf, A., Vereecken, H., & Pütz, T. (2018). Determining dew and hoar frost formation for a low mountain range and alpine grassland site by weighable lysimeter. *Journal of Hydrology*, *563*, 372–381. https://doi.org/10.1016/j.jhydrol.2018.06.009

Hagedorn, F., & Joos, O. (2014). Experimental summer drought reduces soil CO_2 effluxes and DOC leaching in Swiss grassland soils along an elevational gradient. *Biogeochemistry*, *117*, 395–412. https://doi.org/10.1007/s10533-013-9881-x

Hahn, C., Lüscher, A., Ernst-Hasler, S., Suter, M., & Kahmen, A. (2020). Timing of drought in the growing season and strong legacy effects determine the annual productivity of temperate grasses in a changing climate. *Biogeosciences*, *18*, 585–604. https://doi.org/10.5194/bg-18-585-2021

Hamann, E., Kesselring, H., & Stöcklin, J. (2017). Plant responses to simulated warming and drought: A comparative study of functional plasticity between congeneric mid and high elevation species. *Journal of Plant Ecology*, *11*, 364–374. https://doi.org/10.1093/jpe/rtx023

Harper, C. W., Blair, J. M., Fay, P. A., Knapp, A. K., & Carlisle, J. D. (2005). Increased rainfall variability and reduced rainfall amount decreases soil CO_2 flux in a grassland ecosystem. *Global Change Biology*, *11*, 322–334. https://doi.org/10.1111/j.1365-2486.2005.00899.x

Hasibeder, R., Fuchslueger, L., Richter, A., & Bahn, M. (2015). Summer drought alters carbon allocation to roots and root respiration in mountain grassland. *The New Phytologist*, *205*, 1117–1127. https://doi.org/10.1111/nph.13146

Hitz, C., Egli, M., & Fitze, P. (2001). Below-ground and above-ground production of vegetational organic matter along a climosequence in alpine grasslands. *Journal of Plant Nutrition and Soil Science*, *164*, 389–397. https://doi.org/10.1002/1522-2624(200108)164:4<;389::aid-jpln389>3.0.co;2-a

Hsiao, T. C., Acevedo, E., Fereres, E., & Henderson, D. W. (1976). Water stress, growth and osmotic adjustment. *Philosophical Transactions of the Royal Society of London. Series B, Biological Sciences*, *273*, 479–500. https://doi.org/10.1098/rstb.1976.0026

Ingrisch, J., Karlowsky, S., Anadon-Rosell, A., Hasibeder, R., König, A., Augusti, A., Gleixner, G., & Bahn, M. (2018). Land use alters the drought responses of productivity and CO_2 fluxes in mountain grassland. *Ecosystems*, *21*, 689–703. https://doi.org/10.1007/s10021-017-0178-0

Ingrisch, J., Karlowsky, S., Hasibeder, R., Gleixner, G., & Bahn, M. (2020). Drought and recovery effects on belowground respiration dynamics and the partitioning of recent carbon in managed and abandoned grassland. *Global Change Biology*, *26*, 4366–4378. https://doi.org/10.1111/gcb.15131

Jäger, H., Peratoner, G., Tappeiner, U., & Tasser, E. (2020). Grassland biomass balance in the European Alps: Current and future ecosystem service perspectives. *Ecosystem Services*, *45*, 101163. https://doi.org/10.1016/j.ecoser.2020.101163

Johnson, D., Vachon, J., Britton, A. J., & Helliwell, R. C. (2011). Drought alters carbon fluxes in alpine snowbed ecosystems through contrasting impacts on graminoids and forbs. *The New Phytologist*, *190*, 740–749. https://doi.org/10.1111/j.1469-8137.2010.03613.x

Jumpponen, A., & Trappe, J. M. (1998). Dark septate endophytes: A review of facultative biotrophic root-colonizing fungi. *The New Phytologist*, *140*, 295–310. https://doi.org/10.1046/j.1469-8137.1998.00265.x

Kahmen, A., Perner, J., & Buchmann, N. (2005). Diversity-dependent productivity in semi-natural grasslands following climate perturbations. *Functional Ecology*, *19*, 594–601. https://doi.org/10.1111/j.1365-2435.2005.01001.x

Karlowsky, S., Augusti, A., Ingrisch, J., Akanda, M. K. U., Bahn, M., & Gleixner, G. (2018). Drought-induced accumulation of root exudates supports post-drought recovery of microbes in mountain grassland. *Frontiers in Plant Science*, *9*, 1593. https://doi.org/10.3389/fpls.2018.01593

Klug-Pümpel, B. (1989). Phytomasse und Nettoproduktion naturnaher und anthropogen beeinflusster alpiner Pflanzengesellsschaften in den hohen Tauern. In A. Cernusca (Ed.), *Struktur und Funktion von Graslandökosystemen im Nationalpark Hohe Tauern* (Vol. *13*, pp. 331–356).

Körner, C. (2021). *Alpine plant life: Functional plant ecology of high mountain ecosystems* (3rd ed.). Springer.

Körner, C., Möhl, P., & Hiltbrunner, E. (2023). Four ways to define the growing season. *Ecology Letters*, *26*, 1277–1292.

Kotlarski, S., Gobiet, A., Morin, S., Olefs, M., Rajczak, J., & Samacoïts, R. (2023). 21st century alpine climate change. *Climate Dynamics*, *60*, 65–86. https://doi.org/10.1007/s00382-022-06303-3

Kranner, I., Beckett, R., Hochman, A., & Nash, T. H. (2008). Desiccation-tolerance in lichens: A review. *Bryologist*, *111*, 576–593. https://doi.org/10.1639/0007-2745-111.4.576

Kröel-Dulay, G., Mojzes, A., Szitár, K., Bahn, M., Batáry, P., Beier, C., Bilton, M., de Boeck, H. J., Dukes, J. S., Estiarte, M., Holub, P., Jentsch, A., Schmidt, I. K., Kreyling, J., Reinsch, S., Larsen, K. S., Sternberg, M., Tielbörger, K., Tietema, A., … Peñuelas, J. (2022). Field experiments underestimate aboveground biomass response to drought. *Nature Ecology and Evolution*, *6*, 540–545. https://doi.org/10.1038/s41559-022-01685-3

Kudo, G. (1992). Effect of snow-free duration on leaf life-span of four alpine plant species. *Canadian Journal of Botany*, *70*, 1684–1688. https://doi.org/10.1139/b92-207

Landolt, E. (2012). *Unsere Alpenflora* (8th ed.). SAC-Verlag.

Lefcheck, J. S. (2016). piecewiseSEM: Piecewise structural equation modelling in r for ecology, evolution, and systematics. *Methods in Ecology and Evolution*, *7*, 573–579. https://doi.org/10.1111/2041-210x.12512

Leifeld, J., Meyer, S., Budge, K., Sebastia, M. T., Zimmermann, M., & Fuhrer, J. (2015). Turnover of grassland roots in mountain ecosystems revealed by their radiocarbon signature: Role of temperature and management. *PLOS ONE*, *10*(3), e0119184. https://doi.org/10.1371/journal.pone.0119184

Lenth, R. V. (2021). *Emmeans: Estimated marginal means, aka least-squares means*. R package version 1.6.2-1.

Lindenmayer, D. B., Likens, G. E., Andersen, A., Bowman, D., Bull, C. M., Burns, E., Dickman, C. R., Hoffmann, A. A., Keith, D. A., Liddell, M. J., Lowe, A. J., Metcalfe, D. J., Phinn, S. R., Russell-Smith, J., Thurgate, N., & Wardle, G. M. (2012). Value of long-term ecological studies. *Austral Ecology*, *37*, 745–757. https://doi.org/10.1111/j.1442-9993.2011.02351.x

Liu, H., Lin, L., Wang, H., Zhang, Z., Shangguan, Z., Feng, X., & He, J. S. (2021). Simulating warmer and drier climate increases root production but decreases root decomposition in an alpine grassland on the Tibetan plateau. *Plant and Soil*, *458*, 59–73. https://doi.org/10.1007/s11104-020-04551-y

Liu, H., Mi, Z., Lin, L., Wang, Y., Zhang, Z., Zhang, F., Wang, H., Liu, L., Zhu, B., Cao, G., Zhao, X., Sanders, N. J., Classen, A. T., Reich, P. B., & He, J. S. (2018). Shifting plant species composition in response to climate change stabilizes grassland primary production. *Proceedings of the National Academy of Sciences of the United States of America*, *115*, 4051–4056. https://doi.org/10.1073/pnas.1700299114

Liu, N., Jacquemyn, H., Liu, Q., Shao, S. C., Ding, G., & Xing, X. (2022). Effects of a dark septate fungal endophyte on the growth and physiological response of seedlings to drought in an epiphytic orchid. *Frontiers in Microbiology*, *13*, 961172. https://doi.org/10.3389/fmicb.2022.961172

Lloyd, J., & Taylor, J. A. (1994). On the temperature dependence of soil respiration. *Functional Ecology*, *8*, 315. https://doi.org/10.2307/2389824

Mackie, K. A., Zeiter, M., Bloor, J. M. G., & Stampfli, A. (2019). Plant functional groups mediate drought resistance and recovery in a multisite grassland experiment. *Journal of Ecology*, *107*, 937–949. https://doi.org/10.1111/1365-2745.13102

Mähr, E., & Grabherr, G. (1983). Wurzelwachstum und -produktion in einem Krummseggenrasen (Caricetum curvulae) der Hochalpen. In W. Bohm, L. Kutschera, & E. Lichtenegger (Eds.), *Wurzelkökologie und ihre Nutzanwendung*. Ein Beitrag zur Erforschung der Gesamtpflanze (pp. 405–416). Bundesanstalt für alpenländische Landwirtschaft.

Mezhunts, B. K., Britt, C., McMillan, S., & Givens, D. (2005). The distribution of root biomass and energy yields in mountain grasslands in Armenia. *Electronic Journal of Natural Sciences*, *4*, 1–5.

Mildner, M., Bader, M. K.-F., Baumann, C., & Körner, C. (2015). Respiratory fluxes and fine root responses in mature *Picea abies* trees exposed to elevated atmospheric CO_2 concentrations. *Biogeochemistry*, *124*, 95–111. https://doi.org/10.1007/s10533-015-0084-5

Möhl, P., Hiltbrunner, E., & Körner, C. (2020). Halving sunlight reveals no carbon limitation of aboveground biomass production in alpine grassland. *Global Change Biology*, *26*, 1857–1872. https://doi.org/10.1111/gcb.14949

Möhl, P., von Büren, R. S., & Hiltbrunner, E. (2022). Growth of alpine grassland will start and stop earlier under climate warming. *Nature Communications*, *13*, 7398. https://doi.org/10.1038/s41467-022-35194-5

Möhl, P., Vorkauf, M., Kahmen, A., & Hiltbrunner, E. (2023). Recurrent summer drought affects biomass production and community composition independently of snowmelt manipulation in alpine grassland. *Figshare*, https://doi.org/10.6084/m9.figshare.20529678

Morris, E. K., Caruso, T., Buscot, F., Fischer, M., Hancock, C., Maier, T. S., Meiners, T., Müller, C., Obermaier, E., Prati, D., Socher, S. A., Sonnemann, I., Wäschke, N., Wubet, T., Wurst, S., & Rillig, M. C. (2014). Choosing and using diversity indices: Insights for ecological applications from the German Biodiversity Exploratories. *Ecology and Evolution*, *4*, 3514–3524. https://doi.org/10.1002/ece3.1155

Muller, B., Pantin, F., Génard, M., Turc, O., Freixes, S., Piques, M., & Gibon, Y. (2011). Water deficits uncouple growth from photosynthesis, increase C content, and modify the relationships between C and growth in sink organs. *Journal of Experimental Botany*, *62*, 1715–1729. https://doi.org/10.1093/jxb/erq438

Pepin, N., Bradley, R. S., Diaz, H. F., Baraer, M., Caceres, E. B., Forsythe, N., Fowler, H., Greenwood, G., Hashmi, M. Z., Liu, X. D., Miller, J. R., Ning, L., Ohmura, A., Palazzi, E., Rangwala, I., Schöner, W., Severskiy, I., Shahgedanova, M., Wang, M. B., … Yang, D. Q. (2015). Elevation-dependent warming in mountain regions of the world. *Nature Climate Change*, *5*, 424–430. https://doi.org/10.1038/nclimate2563

Pepin, N. C., Arnone, E., Gobiet, A., Haslinger, K., Kotlarski, S., Notarnicola, C., Palazzi, E., Seibert, P., Serafin, S., Schöner, W., Terzago, S., Thornton, J. M., Vuille, M., & Adler, C. (2022). Climate changes and

their elevational patterns in the mountains of the world. *Reviews of Geophysics*, *60*, e2020RG000730. https://doi.org/10.1029/2020rg000730

Peterson, K. M., & Billings, W. D. (1983). Growth of alpine plants under controlled drought. *Environmental Science & Technology*, *14*, 189–194. https://doi.org/10.2307/1551151

Pinheiro, J., Bates, D., DebRoy, S., Sarkar, D., & R Core Team. (2021). *{nlme}: Linear and nonlinear mixed effects models*.

Puşcaş, M., & Choler, P. (2012). A biogeographic delineation of the European alpine system based on a cluster analysis of *Carex curvula*-dominated grasslands. *Flora—Morphol Distribution Funct Ecol Plants*, *207*, 168–178. https://doi.org/10.1016/j.flora.2012.01.002

R Core Team. (2022). *R: A language and environment for statistical computing*. Version 4.2.2. R Foundation for Statistical Computing. https://www.R-project.org/

Rammig, A., Jonas, T., Zimmermann, N. E., & Rixen, C. (2010). Changes in alpine plant growth under future climate conditions. *Biogeosciences*, *7*, 2013–2024. https://doi.org/10.5194/bg-7-2013-2010

Read, D. J., & Haselwandter, K. (1981). Observations on the mycorrhizal status of some alpine plant communities. *The New Phytologist*, *88*, 341–352. https://doi.org/10.1111/j.1469-8137.1981.tb01729.x

Riedl, A., Li, Y., Eugster, J., Buchmann, N., & Eugster, W. (2021). Technical note: High-accuracy weighing micro-lysimeter system for long-term measurements of non-rainfall water inputs to grasslands. *Hydrology and Earth System Sciences*, *26*, 91–116. https://doi.org/10.5194/hess-26-91-2022

Rixen, C., Høye, T. T., Macek, P., Aerts, R., Alatalo, J. M., Anderson, J. T., Arnold, P. A., Barrio, I. C., Bjerke, J. W., Björkman, M. P., Blok, D., Blume-Werry, G., Boike, J., Bokhorst, S., Carbognani, M., Christiansen, C. T., Convey, P., Cooper, E. J., Cornelissen, J. H. C., … Zong, S. (2021). Winters are changing: Snow effects on Arctic and alpine tundra ecosystems. *Arctic Science*, *8*, 572–608. https://doi.org/10.1139/as-2020-0058

Robinson, D. A., Jones, S. B., Lebron, I., Reinsch, S., Domínguez, M. T., Smith, A. R., Jones, D. L., Marshall, M. R., & Emmett, B. A. (2016). Experimental evidence for drought induced alternative stable states of soil moisture. *Scientific Reports-UK*, *6*, 20018. https://doi.org/10.1038/srep20018

Rosbakh, S., Leingärtner, A., Hoiss, B., Krauss, J., Steffan-Dewenter, I., & Poschlod, P. (2017). Contrasting effects of extreme drought and snowmelt patterns on mountain plants along an elevation gradient. *Frontiers in Plant Science*, *8*, 1478. https://doi.org/10.3389/fpls.2017.01478

Rumpf, S. B., Gravey, M., Brönnimann, O., Luoto, M., Cianfrani, C., Mariethoz, G., & Guisan, A. (2022). From white to green: Snow cover loss and increased vegetation productivity in the European Alps. *Science*, *376*, 1119–1122. https://doi.org/10.1126/science.abn6697

Schäppi, B., & Körner, C. (1996). Growth responses of an alpine grassland to elevated CO_2. *Oecologia*, *105*, 43–52. https://doi.org/10.1007/bf00328790

Scherrer, D., & Körner, C. (2010). Infra-red thermometry of alpine landscapes challenges climatic warming projections. *Global Change Biology*, *16*, 2602–2613. https://doi.org/10.1111/j.1365-2486.2009.02122.x

Schimel, J. P. (2018). Life in dry soils: Effects of drought on soil microbial communities and processes. *Annual Review of Ecology, Evolution, and Systematics*, *49*, 1–24. https://doi.org/10.1146/annurev-ecolsys-110617-062614

Schindelin, J., Arganda-Carreras, I., Frise, E., Kaynig, V., Longair, M., Pietzsch, T., Preibisch, S., Rueden, C., Saalfeld, S., Schmid, B., Tinevez, J. Y., White, D. J., Hartenstein, V., Eliceiri, K., Tomancak, P., & Cardona, A. (2012). Fiji: An open-source platform for biological-image analysis. *Nature Methods*, *9*, 676–682. https://doi.org/10.1038/nmeth.2019

Schmid, S. (2017). *Impacts of climate change on alpine grassland ecosystems: Responses in structure and function* (Dissertation). ETH Zürich Research Collection. https://doi.org/10.3929/ethz-b-000224238

Scholz, K., Hammerle, A., Hiltbrunner, E., & Wohlfahrt, G. (2018). Analyzing the effects of growing season length on the net ecosystem production of an alpine grassland using model–data fusion. *Ecosystems*, *21*, 982–999. https://doi.org/10.1007/s10021-017-0201-5

Shannon, C. E. (1948). A mathematical theory of communication. *Bell System Technical Journal*, *27*, 379–423. https://doi.org/10.1002/j.1538-7305.1948.tb01338.x

Simpson, E. H. (1949). Measurement of diversity. *Nature*, *163*, 688. https://doi.org/10.1038/163688a0

Stampfli, A., Bloor, J. M. G., Fischer, M., & Zeiter, M. (2018). High land-use intensity exacerbates shifts in grassland vegetation composition after severe experimental drought. *Global Change Biology*, *24*, 2021–2034. https://doi.org/10.1111/gcb.14046

Stewart, I. T., Cayan, D. R., & Dettinger, M. D. (2004). Changes in snowmelt runoff timing in Western North America under a 'business as usual' climate change scenario. *Climatic Change*, *62*, 217–232. https://doi.org/10.1023/b:clim.0000013702.22656.e8

Suttle, K. B., Thomsen, M. A., & Power, M. E. (2007). Species interactions reverse grassland responses to changing climate. *Science*, *315*, 640–642. https://doi.org/10.1126/science.1136401

van den Bergh, T., Inauen, N., Hiltbrunner, E., & Körner, C. (2013). Climate and plant cover co-determine the elevational reduction in evapotranspiration in the Swiss Alps. *Journal of Hydrology*, *500*, 75–83. https://doi.org/10.1016/j.jhydrol.2013.07.013

van den Bergh, T., Körner, C., & Hiltbrunner, E. (2018). Alnus shrub expansion increases evapotranspiration in the Swiss Alps. *Regional Environmental Change*, *18*, 1375–1385. https://doi.org/10.1007/s10113-017-1246-x

Vitasse, Y., Rebetez, M., Filippa, G., Cremonese, E., Klein, G., & Rixen, C. (2017). 'Hearing' alpine plants growing after snowmelt: Ultrasonic snow sensors provide long-term series of alpine plant phenology. *International Journal of Biometeorology*, *61*, 349–361. https://doi.org/10.1007/s00484-016-1216-x

Vittoz, P., Randin, C., Dutoit, A., Bonnet, F., & Hegg, O. (2009). Low impact of climate change on subalpine grasslands in the Swiss northern Alps. *Global Change Biology*, *15*, 209–220. https://doi.org/10.1111/j.1365-2486.2008.01707.x

von Büren, R. S., & Hiltbrunner, E. (2022). Low winter temperatures and divergent freezing resistance set the cold range limit of widespread alpine graminoids. *Journal of Biogeography*, *49*, 1562–1575. https://doi.org/10.1111/jbi.14455

Vorkauf, M., Kahmen, A., Körner, C., & Hiltbrunner, E. (2021). Flowering phenology in alpine grassland strongly responds to shifts in snowmelt but weakly to summer drought. *Alpine Botany*, *131*, 73–88. https://doi.org/10.1007/s00035-021-00252-z

Vorkauf, M., Marty, C., Kahmen, A., & Hiltbrunner, E. (2021). Past and future snowmelt trends in the Swiss Alps: The role of temperature and snowpack. *Climatic Change*, *165*, 44–62. https://doi.org/10.1007/s10584-021-03027-x

Wang, H., Liu, H., Cao, G., Ma, Z., Li, Y., Zhang, F., Zhao, X., Zhao, X., Jiang, L., Sanders, N. J., Classen, A. T., & He, J. S. (2020). Alpine grassland plants grow earlier and faster but biomass remains unchanged over 35 years of climate change. *Ecology Letters*, *23*, 701–710. https://doi.org/10.1111/ele.13474

Wellstein, C., Poschlod, P., Gohlke, A., Chelli, S., Campetella, G., Rosbakh, S., Canullo, R., Kreyling, J., Jentsch, A., & Beierkuhnlein, C. (2017). Effects of extreme drought on specific leaf area of grassland species: A meta-analysis of experimental studies in temperate and sub-Mediterranean systems. *Global Change Biology*, *23*, 2473–2481. https://doi.org/10.1111/gcb.13662

Windmaißer, T., & Reisch, C. (2013). Long-term study of an alpine grassland: Local constancy in times of global change. *Alpine Botany*, *123*, 1–6. https://doi.org/10.1007/s00035-013-0112-9

Wipf, S., Stoeckli, V., & Bebi, P. (2009). Winter climate change in alpine tundra: Plant responses to changes in snow depth and snowmelt

timing. *Climatic Change*, *94*, 105–121. https://doi.org/10.1007/s10584-009-9546-x

Wullschleger, S. D., Epstein, H. E., Box, E. O., Euskirchen, E. S., Goswami, S., Iversen, C. M., Kattge, J., Norby, R. J., van Bodegom, P. M., & Xu, X. (2014). Plant functional types in earth system models: Past experiences and future directions for application of dynamic vegetation models in high-latitude ecosystems. *Annals of Botany-London*, *114*, 1–16. https://doi.org/10.1093/aob/mcu077

SUPPORTING INFORMATION

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

Table S1. Plant cover of the most frequent species (ordered by functional types of forbs and graminoids), assessed in 2022.

Table S2. Mean annual necromass (NM, in $g\,m^{-2}$) at peak biomass, averaged per drought or snowmelt treatment (mean ± SE; $n = 15$ each). Values significantly different from controls are in bold ($p < 0.05$).

Figure S1. Left: Rain-out shelters in summer and snowmelt treatment in spring (snow removal in the front and snow addition in the back). Right: Outline of one plot, with the black dotted lines indicating the area covered by the rain-out shelter and by the central-m^2 (red, plant composition survey). Symbols indicate where meristem/soil temperature (3–4 cm), moisture (Theta probe 0–5 cm, PR2 profile probe 10–40 cm), ecosystem respiration (area of lichen harvest in 2022) and plant biomass (aboveground harvest, ingrowth cores, SRBM = standing root biomass) were quantified.

Figure S2. Volumetric soil moisture for snow treatments in each growing season (2017–2022) measured in the topsoil (top; 0–5 cm depth, Theta probe) and at 10 cm depth (bottom; profile probe, note the different *y*-axis). PR2 profile probe measurements started in 2018. Coloured background indicates the sheltering period of the 5- and 10-week treatment. Points = raw data, lines and shaded area = means ± SE, dashed line indicates soil moisture content at the permanent wilting point. Vertical arrows indicate aboveground harvests.

Figure S3. As Fig. S2 but for drought treatments.

Figure S4. Soil temperature (at 3–4 cm depth) in drought treatments (mean ± SE). Note that the difference between controls and droughted plots increases from 0–5 to 5–10 weeks in the 10-week drought treatment, while soil temperature in the 5-week treatment recovered after removal of the shelters (5–10 weeks period).

Figure S5. Species-specific snowmelt sensitivity of biomass formation in the ten most frequently occurring species (ordered alphabetically within functional groups). Percentage numbers in brackets indicate the fraction of biomass per species across all control plots. Points indicate regression slopes of biomass (square rooted) against day of year of snowmelt. Negative values (to the left) indicate more biomass with earlier snowmelt and *vice versa*. Small points depict slopes for each of the 6 years, while bigger points show the mean ± SE across all years. Marginal R^2-values are reported.

Figure S6. Aboveground biomass production in response to soil moisture (vol-%, 0–5 cm). Panels separate biomass data by total community and functional types (rows) and year (columns), while colors differentiate between drought treatments (black = control, yellow = 5-week, red = 10-week). Note the change in *y*-axis dimensions between total biomass (0–300 $g\,m^{-2}$) and functional types (0–200 $g\,m^{-2}\,a^{-1}$). Mean soil moisture was calculated for the period between placement of rain-out shelters and harvest. Linear model fits ± SE are shown as black lines with grey bands.

Figure S7. Specific leaf area (SLA) in response to drought, measured in 2021 for five of the most abundant species growing at the experimental site. Light-coloured points depict values for each plot and dark-coloured, bigger points show means ± SE for each drought treatment. Full species names: *Carex curvula*, *Helictotrichon versicolor*, *Geum montanum*, *Leontodon helveticus*, *Potentilla aurea*.

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