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RESEARCH ARTICLE

Grasses, legumes and forbs respond differently to compound drought-heatwave events during establishment

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Abstract
Aims Climate change threatens agriculture worldwide, and grasslands must adapt to withstand and mitigate the effects of extreme climatic events. While plant diversity may boost resilience, grassland responses to compound drought-heatwave (CDHW) events remain unclear. As young plants are particularly vulnerable to stress, this study investigated the effects of climate extremes during grassland establishment.
Methods Two successive CDHWs, simulating average spring and summer stresses in western Europe, were applied to newly established plants from distinct functional groups: perennial ryegrass (*Lolium perenne* L.), white clover (*Trifolium repens* L.), and chicory (*Cichorium intybus* L.). Additionally, drought and heatwave components of CDHWs were tested separately to estimate their effects. Climate-controlled growth chambers ensured precise control of environmental conditions, allowing for accurate measurements of plants' morphological and physiological responses.
Results Yield responses to CDHW were driven by significant interaction among species, climate, and stress timing. Summer CDHW events reduced yields in white clover and chicory by 73% and 38%, respectively, with drought as the primary driver of stress. This trend was reversed with the occurrence of two successive CDHWs, resulting in an average 22% higher yield compared to summer CDHW alone, highlighting the importance of stress timing and recurrence in priming plants. Notably, chicory yield increased by 45% under spring CDHW conditions compared to control.
Conclusion This study underscores the importance of diversifying grassland systems to enhance resilience to climate change. It provides insights into the responses of different species to CDHW events, which can guide the design of multi-species mixtures for the future.

Keywords Multi-species swards · Climate extremes · Functional groups · Grassland · Establishment phase

Abbreviations

CDHW	Compound drought-heatwave event

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HW	Heatwave event
D	Drought event
Numbers 1, 2 and 12 accompanying treatment abbreviations	
1	Spring stress
2	Summer stress
12	Both spring and summer stresses
FG	Functional group

Introduction

Climate change poses a major threat to agriculture. The increasing frequency and intensity of extreme weather events, such as droughts, heavy rainfall and heatwaves, are expected to have a more profound impact on agricultural systems than gradual changes in average temperature (Arias et al. 2021; De Boeck et al. 2010). Among these events, simultaneous drought and heatwave occurrences, referred to as compound drought-heatwave (CDHW) events, are of particular concern due to their adverse effects on crop growth due to the simultaneously increased evapotranspiration rates and reduced precipitation (Tejedor et al. 2024). The frequency, intensity, and duration of CDHW events are projected to increase fourfold across 70% of global land areas under medium- and high-emission scenarios (Yin et al. 2023). Therefore, agricultural systems, particularly forage-based grasslands, must not only adapt to these changing climate conditions but also comply with emerging policies aimed at developing mitigation strategies to ensure future sustainability (Lambers and Cong 2022; Malisch et al. 2024; Martin et al. 2020).

Managed grasslands cover a significant portion of global agricultural land and are essential for livestock production, with demand for these products expected to double by 2050 (Rojas-Downing et al. 2017). When established as leys (i.e., temporary grasslands sown within crop rotations), they are an important tool to diversify cropping systems and thereby improve nutrient cycling, as well as mitigating carbon losses compared to monocropping of arable crops (Cong et al 2019; Lemaire et al. 2015). However, rising temperatures and shifting weather patterns threatens grassland productivity, with species composition and management practices playing a crucial role resilience (Lee et al. 2017; Loka et al. 2019; Tamboli et al. 2023). To address these challenges, diversifying grassland systems by incorporating different functional groups, such as grasses, legumes, and forbs, has been proposed as a promising strategy to enhance resilience (i.e., the ability to recover quickly and fully during periods of adequate environmental conditions following a stress event) and mitigate the negative effects of climate change (Grange et al. 2021; Haughey et al. 2023; Lüscher et al. 2022). Diverse plant communities can create synergistic interactions which improve the overall resistance (i.e., the degree of impairment during a stress event) of grassland swards to environmental stress (Finn et al. 2013; Haughey et al. 2023). For example, deep rooted species have been shown to actively shift their water uptake to deeper soil layers under drought (Hoekstra et al. 2015), and thereby contribute to hydraulic lift—a phenomenon where some of the water from deeper soil layers is redistributed to the topsoil, thereby benefiting plants without a deep rooting system (Oliveira et al. 2024). However, the specific roles of different species and functional groups in promoting these benefits, especially under climate extremes such as CDHW events, remain poorly understood.

Droughts and heatwaves result from complex interactions among physical processes that are heavily influenced by seasonal and region-specific climate variability (Yin et al. 2023). Although heatwaves are usually defined as temperature extremes, there's no universal definition (Marx et al. 2021; Perkins-Kirkpatrick et al. 2017; Perkins and Fischer 2013). In western Europe, heatwaves are closely linked to precipitation deficits, which can actually serve as a driving factor in their occurrence (Domeisen et al. 2023; Teuling 2018). In such scenarios, dry soils limit evapotranspiration, reduce convective cloud formation, increase sunshine, and ultimately drive higher maximum temperatures, further raising atmospheric demand (i.e., high vapor pressure deficit; VPD) (De Boeck et al. 2010; Hunt 2007). The complex interplay of these factors makes it difficult to quantify the combined effects of CDHW events, but existing research predicts amplifying impacts of drought and heatwave effects individually (Wang et al. 2024).

The seasonal timing and recurrence of CDHW events are, however, critical variables often overlooked in experimental designs (De Boeck et al. 2011; Jentsch et al. 2007; Shan et al. 2024). While many studies focus on climate extremes occurring in summer, CDHW events may also take place in other seasons, such as spring, resulting in different plant response dynamics (Craine et al. 2012; Shan et al. 2024; Qu et al. 2024). Spring CDHW events for instance, despite having lower absolute temperatures, can still cause significant stress, particularly in young plants at sensitive phenological stages (De Boeck et al. 2016). In spring-sown grassland leys, early CDHW events may stunt growth, although moderate early stress may also enhance resilience to future climatic events (Wang et al. 2024). Timing and recurrence add complexity, with intervals between CDHW events influencing their cumulative effects (Wang et al. 2024). Short intervals may exacerbate stress, while longer gaps might allow recovery, although excessively long intervals could reduce "stress memory," potentially weakening adaptive responses (Wohlgemuth et al. 2022). Some species acclimate to repeated events, while others experience compounded reductions in carbon uptake and respiration (Dong et al. 2022; Qu et al. 2024). The impacts of CDHW events, therefore, are context-dependent, driven by season, interval timing, plant species and phenological stages.

In this study, we simulated typical CDHW events for western Europe, along with their isolated components, drought and heatwave, under highly controlled conditions. Our primary objective was to assess how three forage species (*Lolium perenne* L., *Trifolium repens* L., and *Cichorium intybus* L., each representing a distinct functional group) respond to CDHW events during their establishment phase. Since biomass was harvested only once, at the end of the experiment rather than immediately after each stress event, this study primarily captures resilience rather than immediate resistance. Our specific objectives were to: (i) Analyze morphological (e.g., canopy cover, biomass production, allocation, and leaf area) and physiological (i.e., crop water stress index via infrared imaging) responses to CDHW events and determine whether species with contrasting functional traits exhibit distinct resilience under CDHW conditions, (ii) assess potential cultivar-level responses to these treatments, and (iii) determine whether the combined effects of drought and heatwaves (CDHW) differ from the sum of their isolated impacts. Furthermore, all climatic treatments were simulated as either a single event in spring or summer, or two repeated events in spring and summer, to examine whether early exposure to stress activates adaptive mechanisms or if the effects of multiple events accumulate, leading to greater reduction in productivity. This research contributes to the development of diversified, resilient grassland systems capable of maintaining productivity and sustainability under challenging climatic conditions.

Materials and methods

Plant material and growth conditions

Three plant species, each representing a distinct functional group commonly found in multispecies grassland leys, were selected for this experiment: perennial ryegrass (*Lolium perenne* L.; grass), white clover (*Trifolium repens* L.; legume), and chicory (*Cichorium intybus* L.; non-leguminous forb). Monocultures were sown in microcosms (10.5 cm diameter, 40 cm height), filled with a 50:50 (v/v) mixture of sand and topsoil (10% sand, 72% silt, 18% clay) sourced from agricultural fields in the Filderstatt region (Esslingen, Germany). The bulk density within the pots was adjusted to 1.14 g cm^{-3}. To represent each species, an equal-proportion mixture of cultivars was sown, with each cultivar clearly identified within the pots. The selected cultivars were as follows: *Lolium perenne* (two seeds per cultivar per pot: 'Abosan', 'Flinston', 'Nashota', 'Saqui'), *Cichorium intybus* (four seeds per cultivar per pot: 'Choice', 'Puna'), and *Trifolium repens* (three seeds per cultivar per pot: 'Brianna', 'Coolfin', 'Iona'). The sowing density was determined based on field seed application rates in Germany, ensuring that an equal proportion of cultivars was maintained within each pot. To account for potential variation in germination rates, seeds were sown in triplicate per hole. After germination, excess seedlings were carefully removed using tweezers to ensure that each pot contained the intended number of plants per species and cultivar.

The experiment was conducted using five climate-controlled chambers (Vötsch VB 1514/S, BioLine) at the Institute of Landscape and Plant Ecology, University of Hohenheim, and established on March 27 th, 2024. Each chamber had an internal area of 1.5 m^2, a total volume of 2.4 m^3 and internal dimensions of 1.4 m (height) ×0.750 m (depth) ×1.27 m (width). The climate profiles used were derived from weekly average data from Stuttgart Airport (years 1991 to 2005), allowing for regulation of temperature, CO$_2$

concentration, relative humidity and light intensity. These profiles were rotated weekly to simulate the spring establishment of grasslands, encompassing a growing season starting on March 31 st, until July 19 th. CO_2 concentration was maintained at 400 ppm throughout the experiment, and light intensity followed a diurnal course with a maximum photon flux density of 1000 µmol m^{-2} s^{-1} around noon. Fertilization was conducted shortly after seedling emergence, with a NPK solution applied according to German agricultural guidelines (Landwirtschaftskammer Niedersachsen 2020) and based on soil analysis results. The application rate, equivalent to 40% of the yearly recommended dose for a four-cut system, was 36 kg P ha^{-1}, 100 kg K ha^{-1}, and 60 kg N ha^{-1}. This rate corresponds to the first-dose application and was proportional to the experiment duration.

Experimental design and CDHW simulation

For the initial 56 days after sowing, all plants were grown under identical climate and watering conditions. Plants were kept near field capacity, monitored through the gravimetric method. Additionally, soil moisture sensors (ECH2O EC-TM, Decagon Devices, USA) were installed at depths of 15 cm and 30 cm in selected microcosms to track soil water content throughout the experiment. To minimize both between- and within-chamber effects, microcosms were rotated weekly among the climate chambers, and their positions were re-randomized within each chamber during rotation. Tinytag sensors (Gemini Data Loggers, UK) were deployed in each chamber to ensure uniform air temperature and relative air humidity levels, with recording intervals every 15 min.

Climatic treatments included a two-factor CDHW event, consisting of a simultaneous heatwave (HW) and edaphic drought (D) period. Additionally, isolated drought (D) and heatwave (HW) treatments were applied separately to investigate the isolated versus combined effects of these stressors. All treatments were implemented at two timepoints: starting on May 28 th (63 days after-sowing) to represent spring stress, and June 28 th (91 days after-sowing) to represent summer stress. Plants were exposed to either one of these stress periods or both (Table 1). The parameters for climatic modifications were adapted from De Boeck et al. (2010). Each single-factor HW lasted nine days, with maximum air temperatures increased by +8 °C, minimum temperatures by +3.4 °C, and humidity reduced by 17% relative to the base weekly climate profile (i.e., simulating increased atmospheric demand). This resulted in maximum calculated VPDs of 1.80 kPa during spring and 2.21 kPa during summer, compared to the control VPDs of 0.93 and 1.15 kPa, respectively. Drought-only treatments also lasted nine days (timed with the HW treatments) and involved halting irrigation from day one, with soil moisture monitored every 24 h to track reductions in water content. The same parameters were combined simultaneously to simulate the CDHW event. Importantly, for perennial ryegrass during the summer D and CDHW conditions, 100 ml of water was applied to the plants on July 2nd (95 days after-sowing) to prevent the pot's water content from dropping further. This was necessary as grasses exhibited more intense drought symptoms, and the water application was essential to prevent them from dying. Finally, after each CDHW, HW, or D event, plants were returned to optimal watering conditions, and the climate settings were reverted to the baseline values identical to the control.

The experiment lasted a total of 112 days. It included 90 microcosms, structured using a fractional factorial design: 3 climates (D, HW, CDHW) ×3 stress timings (spring, summer, both) ×3 plant species (perennial ryegrass, white clover, chicory) ×3 replicates, totaling 81 microcosms. Additionally, a well-irrigated baseline-climate control was included for comparison (1 control ×3 plant species ×3 replicates =9 microcosms), bringing the total to 90 microcosms.

Measurements

Canopy cover was measured weekly from photographs taken throughout the experiment, starting 49 days after sowing. Each pot was photographed individually from above, using a tripod set at a fixed height (1 m) to minimize variability and light influence. Canopy cover analysis was performed using ImageJ software (Schneider et al. 2012), with the pot diameter set as a reference scale. Plant surface area was selected by applying a color-based threshold optimized for plant material, effectively removing the background. The canopy cover area (cm^2) was then

Table 1 Summary of all climate treatments, detailing maximum and minimum temperatures, relative humidity levels, and maximum VPD for baseline and altered climate profiles during spring and summer stress simulations

Abbreviation	Treatment description	Timing of stress	Temperature (°C)		Relative humidity (%)		VPD (MAX) kPa
			Max	Min	Max	Min	
Control	Baseline-climate, well-irrigated plants during all experiment	Spring	16.9	10.8	78.7	51.5	0.93
		Summer	20.7	13.5	82.2	52.8	1.15
CDHW1	Compound drought-heatwave event simulated in spring	Spring	24.9	14.2	65.3	42.7	1.8
		Summer	20.7	13.5	82.2	52.8	1.15
CDHW2	Compound drought-heatwave event simulated in summer	Spring	16.9	10.8	78.7	51.5	0.93
		Summer	28.7	16.9	68.2	43.8	2.21
CDHW12	Compound drought-heatwave events simulated in spring and summer	Spring	24.9	14.2	65.3	42.7	1.8
		Summer	28.7	16.9	68.2	43.8	2.21
D1	Drought simulated in spring	Spring	16.9	10.8	78.7	51.5	0.93
		Summer	20.7	13.5	82.2	52.8	1.15
D2	Drought simulated in summer	Spring	16.9	10.8	78.7	51.5	0.93
		Summer	20.7	13.5	82.2	52.8	1.15
D12	Drought simulated during spring and summer	Spring	16.9	10.8	78.7	51.5	0.93
		Summer	20.7	13.5	82.2	52.8	1.15
HW1	Heatwave simulated in spring	Spring	24.9	14.2	65.3	42.7	1.8
		Summer	20.7	13.5	82.2	52.8	1.15
HW2	Heatwave simulated in summer	Spring	16.9	10.8	78.7	51.5	0.93
		Summer	28.7	16.9	68.2	43.8	2.21
HW12	Heatwaves simulated in spring and summer	Spring	24.9	14.2	65.3	42.7	1.8
		Summer	28.7	16.9	68.2	43.8	2.21

calculated based on pixel measurements and normalized by the pot's surface area (cm^2).

Additionally, thermal images were captured using an infrared camera (VarioCAM hr/S inspect 165 s, InfraTec, Dresden, Germany) at three time points: before, immediately after, and nine days post-CDHW events. The Crop Water Stress Index (CWSI) was calculated from these images using IRBIS® software (InfraTec, Dresden, Germany), following Costa et al. (2013). Emissivity was set at 0.96, and artificial references (filter paper) were used to define upper and lower temperature baselines. CWSI, derived from infrared imaging, serves as an indirect non-invasive indicator of plant gas exchange and stomatal regulation under stress (Costa et al. 2013). Under optimal conditions, plants dissipate heat through stomatal opening and transpiration, maintaining lower leaf temperatures and thus lower CWSI values. In contrast, stomatal closure restricts transpiration, limiting the plant's ability to regulate temperature under stress. This leads to elevated leaf temperatures due to the absence of transpirational cooling, resulting in higher CWSI values.

At the conclusion of the experiment, plants were harvested to measure total biomass, aboveground biomass, belowground biomass, and the root/shoot ratio for each species and treatment. To determine cultivar proportions within the species, the aboveground biomass was carefully harvested for each cultivar. Leaf area was measured using a portable leaf area meter (LI- 3000 C, with LI-3050 C Transparent Belt Conveyor Accessory, Licor, Lincoln, NE, USA). For belowground biomass, roots were washed according to standard procedures (Böhm 1979), dried on paper towels, and weighed for fresh biomass. Dry weights were recorded after drying plant material at 60 °C until constant weight.

Statistical analysis

All analyses were conducted in R (R Core Team 2024). A three-way linear model was used to assess the effects of climate treatment (Control, D, HW, CDHW), stress timing (Spring, Summer, Both), and species (*Lolium perenne*, *Trifolium repens*, *Cichorium intybus*) on yield. Due to the fractional factorial design of the experiment, the climate control group was assumed as the baseline across all timing levels to enable a complete analysis. This model tested for main effects and interactions, providing an overall assessment of yield responses to climate and timing treatments across species.

Given significant interactions among climate, timing, and species, a one-way ANOVA followed by Tukey's HSD test ($P \leq 0.05$) was conducted separately for each species to allow pairwise comparisons between key treatments (i.e., CDHW in spring, CDHW in summer, and CDHW in both seasons). The same approach was applied to leaf area, root biomass, root/shoot ratio, canopy cover, and thermal imaging data, adjusting the response variable accordingly. For time-series data (i.e., canopy cover and thermal imaging), ANOVA and Tukey's test were conducted at specific time points: canopy cover was analyzed at 105 days after sowing, while thermal imaging data were assessed at 63, 71, and 80 days after sowing (spring stress) and at 91, 99, and 108 days after sowing (summer stress).

To determine whether CDHW effects exceeded the expected additive response of individual drought and heatwave impacts, the initial three-way linear model was used to test for deviations from additivity. A contrast test was performed using the hypothesisTest package in R (R Core Team 2024) within each species and stress timing to compare CDHW biomass responses against the sum of drought- and heatwave-only treatments. This approach allowed us to determine whether CDHW effects were purely additive (i.e., matching the expected sum of drought and heatwave effects) or if interactions resulted in synergistic (greater than additive) or antagonistic (less than additive) effects.

Cultivar composition changes were analyzed by estimating the relative change (%) in aboveground biomass per cultivar compared to its expected biomass under control conditions. These values were analyzed within each species using ANOVA and Dunnett's test ($P \leq 0.05$) to determine whether climate treatments led to significant cultivar-level differences relative to the control. This helped assess whether species-level biomass responses to CDHWs were driven by uniform cultivar responses or specific cultivar contributions.

Results

Impact of CDHW events on plant growth and stress indicators

The progression of canopy cover throughout the experiment displayed distinct patterns among the species under different treatments. Growth rates declined across all species during the CDHW events, with more pronounced declines observed during the summer event (CDHW2) compared to the control (Fig. 1). Perennial ryegrass showed full recovery post-stress, resulting in no significant difference in canopy cover between CDHW-exposed and control treatments (Online Resource 1). In contrast, CDHW exposure induced more pronounced and lasting changes in the canopy growth of chicory and clover, resulting in significant differences over time.

At 105 days after-sowing, chicory exhibited one of the highest canopy cover measurements under the CDHW1 treatment, showing an increase of 47% ($P = 0.002$) relative to the control. However, chicory's canopy cover was lowest in the CDHW2 treatment, with a decrease of 39% ($P = 0.008$) compared to the control. White clover demonstrated reductions in canopy cover relative to the control at 105 days after-sowing: a non-significant decrease of 12% under CDHW1, and significant ($P \leq 0.05$) reductions of 73%, and 64% for CDHW2, and CDHW12, respectively. Notably, exposure to two consecutive stress periods (CDHW12) led to a non-significant higher canopy cover in chicory (25%) and clover (35%) compared to exposure to CDHW2 alone.

The Crop Water Stress Index (CWSI) results highlighted elevated stress levels in plants subjected to CDHW treatments. Significant differences in CWSI measurements were evident across all species at both the beginning (63 and 91 days after-sowing, respectively) and end (71 and 99 days after-sowing, respectively) of the stress periods compared to the control ($P \leq 0.05$; Fig. 1). Nine days post-stress, CWSI levels normalized across species, showing no significant difference from the control, indicating a return to baseline stress levels (Online Resource 1).

CDHW events effects on yield, resource allocation and leaf area

The three-way linear model indicated significant interactions between climate, timing, and species

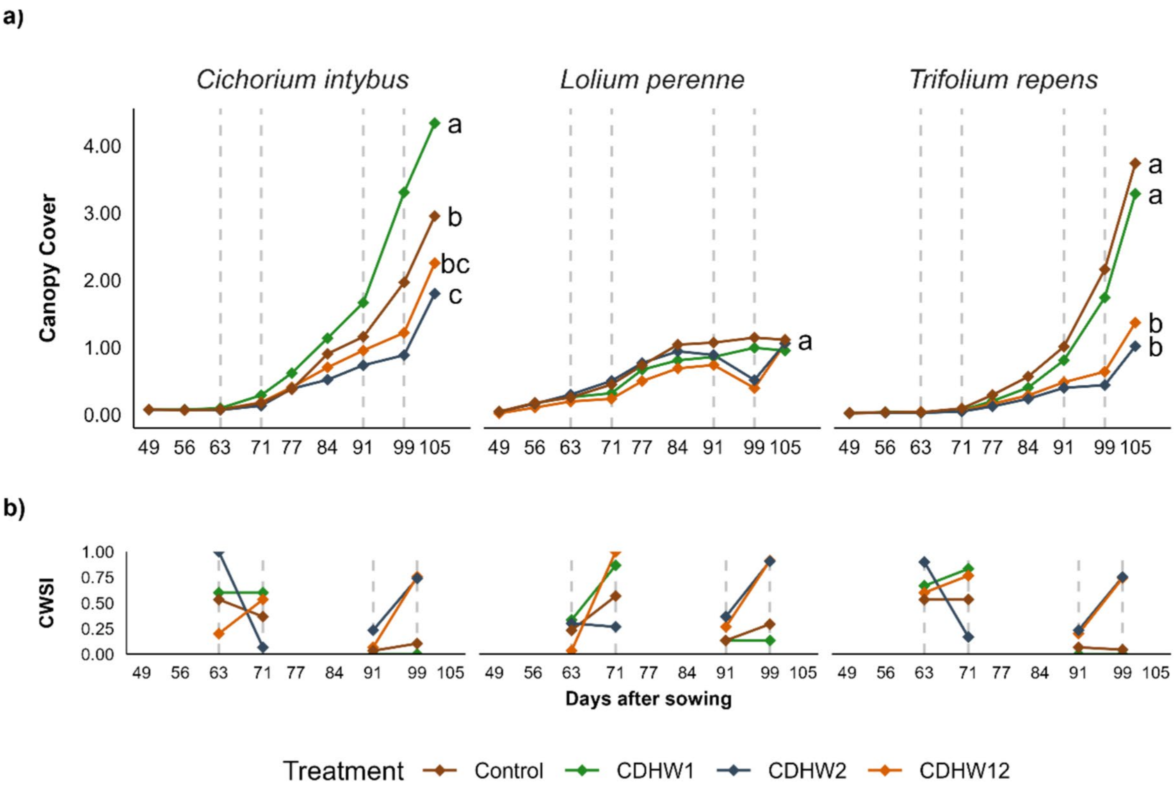

Fig. 1 Canopy cover and crop water stress index (CWSI) for different species under compound drought-heatwave (CDHW) treatments and control. CDHWs were applied in spring (1), summer (2) or both (1 and 2). **a)** Canopy cover progression throughout the experiment, different letters indicate significant ($P \leq 0.05$) differences among treatments within each functional group, based on Tukey's test; **b)** CWSI values before and after each stress period, indicated by vertical gray dashed lines

(F =17.86, $P<$ 0.001), highlighting that biomass responses to CDHW treatments were dependent on both species identity and stress timing. Overall biomass differed significantly among species, with perennial ryegrass exhibiting the highest biomass under control conditions (Estimate =6.46, SE =0.47, $P<$ 0.001), followed by white clover (Estimate =3.51, SE =0.67, $P<$ 0.001) and chicory (Estimate =2.35, SE =0.67, $P<$ 0.001). Although CDHW treatments generally reduced biomass, the magnitude of these reductions varied across species and stress timing, with greater declines observed in white clover and chicory. Timing effects were particularly evident, as biomass reductions under summer CDHW had a stronger impact on biomass compared to spring (Estimate =− 1.72, SE =0.95, $P=$ 0.073), while exposure across both seasons did not lead to additional reductions beyond those observed in summer alone.

Pairwise comparisons revealed that none of the CDHW treatments had a significant effect on yield of perennial ryegrass. In contrast, CDHWs significantly impacted the yields of chicory and white clover (Fig. 2). Especially in chicory, the timing of CDHWs significantly impacted the effect on yield, though, as CDHW1 resulted in a 45% (P =0.004) increase in aboveground biomass compared to the control, as well as a tendency to increase belowground biomass by 43% (P =0.16). Contrary to that, both CDHW2 and CDHW12 resulted in yield reductions of 38% and 26% (P =0.012 and $P=$ 0.075, respectively) compared to the control. For white clover, on the other hand, both CDHW2 and CDHW12 resulted in yield reductions of 73% (P =0.01) and 61% (P =0.012), respectively, whereas CDHW1 did not affect yield (P =0.74).

Belowground biomass production showed similar patterns to aboveground biomass, maintaining a relatively stable root/shoot ratio across all species

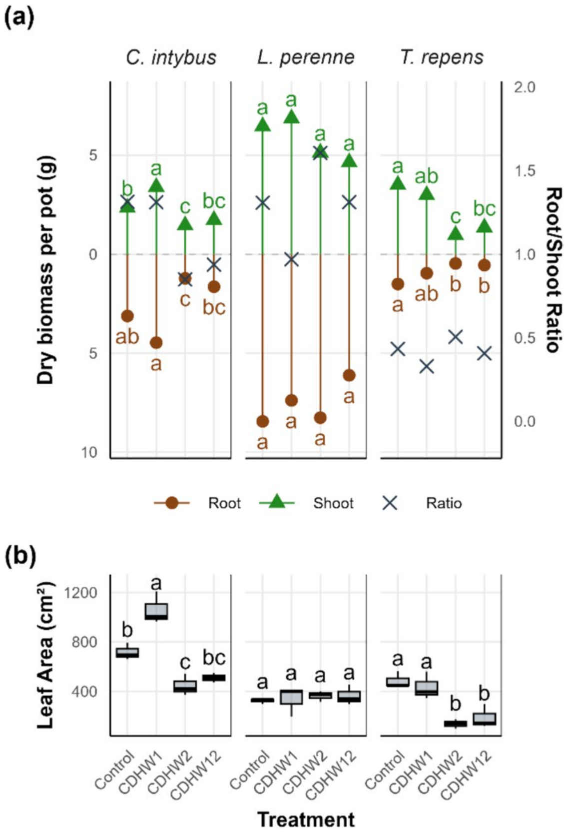

Fig. 2 **a)** Aboveground biomass (green), belowground biomass (brown), and root/shoot ratio (X) across all compound drought-heatwave (CDHW) treatments and control. **b)** Boxplot showing leaf area measurements for CDHW treatments and control. Numbers 1, 2 or 1 and 2 following the treatment abbreviations represent the timing of stress applied: spring, summer or spring and summer, respectively. Letters indicate significant ($P \leq 0.05$) differences among treatments within each functional group, based on Tukey's test results for **a)** aboveground (green letters), belowground biomass (brown letters) and **b)** leaf area

and CDHW treatments when compared to the control. However, a slight reduction in the root/shoot ratio was observed for chicory under the CDHW2 treatment compared to the control, decreasing from 1.31 to 0.84, respectively (Tukey test, $P = 0.068$). Similarly, pairwise comparisons indicated a marginal decrease in root/shoot ratio, noted for both white clover and chicory when comparing CDHW1 to CDHW2. Specifically, white clover's root/shoot ratio declined from 0.50 to 0.32 ($P = 0.066$), while chicory's ratio decreased from 1.31 to 0.84 ($P = 0.07$).

Leaf area results from pairwise comparisons also seemed to mirror the trends observed in yield. For perennial ryegrass, leaf area remained unchanged across all CDHW treatments compared to the control. Chicory, however, showed the greatest increase in leaf area under CDHW1, with a 41% increase relative to the control ($P = 0.005$). The lowest leaf area for chicory was observed under CDHW2, showing a significant 38% reduction ($P = 0.021$), while the reduction under CDHW12 (29%) was not statistically significant compared to the control ($P = 0.076$). For white clover, significant reductions in leaf area were recorded under both CDHW2 (72%, $P = 0.004$) and CDHW12 (62%, $P = 0.01$), with no significant difference between these two treatments.

Isolated effects of drought and heatwaves

The combined effects of heatwaves and drought had a more pronounced impact on yield compared to each stressor individually (Fig. 3), but the magnitude and direction of these interactions varied by species and stress timing (three-way linear model: F = 17.86, $P < 0.01$). Among the affected species (i.e., white clover and chicory), CDHW treatments led to significant biomass reductions, primarily driven by drought, which alone reduced biomass by 31% on average but was not statistically significant ($P = 0.64$). In contrast, heatwaves alone had neutral or even positive effects on yield.

For perennial ryegrass, the three-way linear model showed that neither drought nor heatwaves alone significantly reduced biomass at any timing. In fact, heatwaves had a significant positive effect ($P = 0.017$). The hypothesis test assessing whether CDHW effects exceeded the sum of individual stressor effects was non-significant in spring (F = 0.31, $P = 0.589$), summer (F = 3.38, $P = 0.103$), and across both seasons (F = 1.54, $P = 0.248$). The combined effect of drought and heatwaves did not exceed the expected additive response, showing no synergistic interaction for perennial ryegrass.

For white clover, the three-way linear model indicated no significant effect of drought ($P = 0.320$) or heatwaves ($P = 0.391$) alone. The hypothesis test for CDHW was non-significant in spring, but significant in summer (F = 5.87, $P = 0.042$) and across both seasons (F = 5.32, $P = 0.050$). Biomass loss

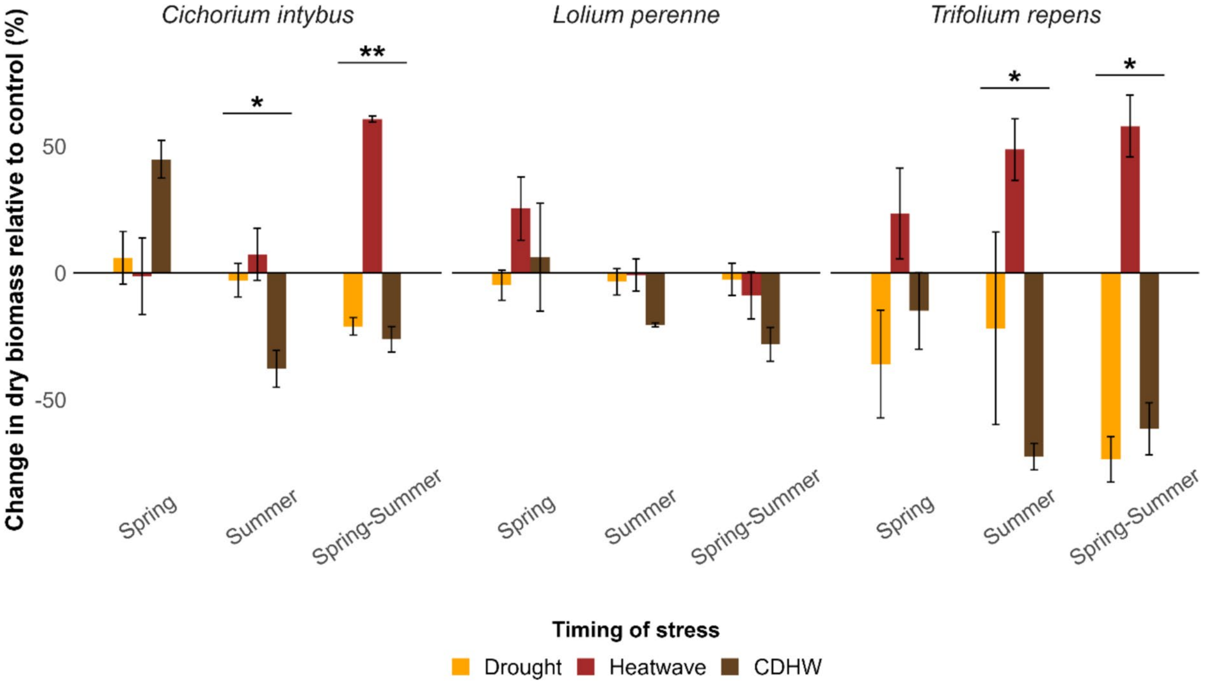

Fig. 3 Reduction in yield for different species and seasons induced by compound drought-heatwave events (CDHW) and its individual components—drought and heatwave. Yield reduction was calculated as the relative change (%) in dry aboveground biomass compared to the well-irrigated baseline climate control, and is presented for visualization purposes only. Statistical analyses were conducted on absolute dry aboveground biomass values. Asterisks (*) indicate significant interactions where the combined effect of drought and heatwave (CDHW) exceeded the additive expectation of individual stressors, based on the hypothesis test (drought + heatwave $\neq$CDHW, $P \leq 0.05$)

under CDHW was higher than the expected additive response in these seasons, with a significant deviation from additivity.

For chicory, the three-way linear model showed that neither drought nor heatwaves alone significantly affected biomass. The hypothesis test for CDHW indicated a non-significant effect in spring (F = 3.83, $P = 0.086$) but a significant effect in summer (F = 7.78, $P = 0.024$) and across both seasons (F = 64.05, $P < 0.001$). Similar to white clover, the significant deviation from an additive response suggests a synergistic interaction, where the combined stressors resulted in biomass losses that were disproportionately greater than expected.

Within-species variation in stress response

The overall amount of dry biomass produced per cultivar within species remained relatively consistent across treatments, with a few notable exceptions (Fig. 4). In white clover, the cultivar 'Iona' yielded significantly more under heatwave (HW) treatments compared to the control, with relative increases in yield of 168% ($P = 0.034$), 234% ($P = 0.001$), and 188% ($P = 0.013$) for HW1, HW2, and HW12, respectively. Similarly, in chicory, the cultivar 'Choice' showed a non-significant yield increase of 86% under HW12 compared to the control ($P = 0.061$).

Discussion

The escalating frequency and intensity of compound drought–heatwave (CDHW) events represent a growing challenge for agricultural systems, including grasslands, where responses to these events remain poorly understood (Craine et al. 2012; Huang et al. 2024). The CDHW scenarios in this study were based on current climate profiles for Germany, derived from

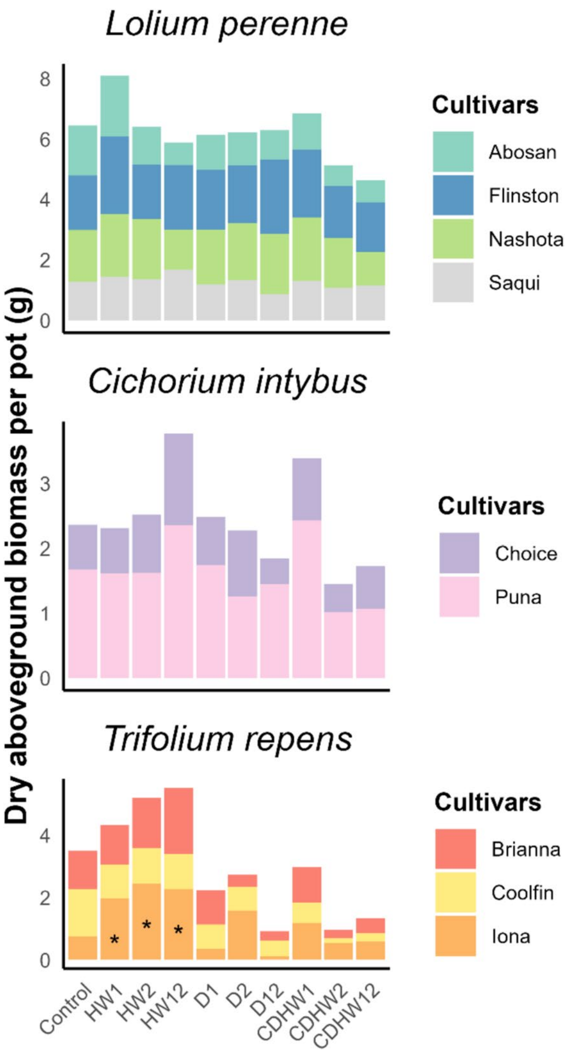

Fig. 4 Dry biomass of cultivars contributing to yield across drought (D), heatwave (HW), compound drought-heatwave (CDHW) treatments, and control. CDHWs were applied in spring (1), summer (2) or both (1 and 2). Distinct colors represent individual cultivars within each species. Asterisks (*) indicate significant effects from Dunnett's test, assessing relative changes in biomass values against the control ($P \leq 0.05$)

average data, and simulated following the climatic characteristics of European heatwaves described by De Boeck et al. (2010). These scenarios offer a realistic framework for assessing grassland responses to extreme climate events. Our study demonstrates that grassland species in the establishment phase exhibited varied responses to CDHW events, highlighting the importance of species-specific traits in determining resilience and/or resistance to climate extremes. Among the tested species, perennial ryegrass showed the highest resilience to CDHW stress, white clover the lowest, and chicory exhibited mixed responses that fluctuated with the seasonality of stress. These differences observed in yield likely stem from species-specific characteristics that influence resilience and resistance, which may also extend to the functional group (FG) level; variation in drought tolerance among FGs can play a greater role in grassland resilience than species diversity alone (Komainda et al. 2020; Mackie et al. 2019).

Grasses, for instance, have relatively shallow roots, making them more susceptible to prolonged drought; however, they can demonstrate rapid recovery following stress events (Haughey et al. 2023; Hofer et al. 2017a; Hoover et al. 2014; Volaire et al. 2014). Narrow leaves in grasses may also reduce evaporative pressure, supporting resilience by minimizing water loss. In our experiment, perennial ryegrass seemed unaffected by the CDHW events, likely due to the relatively short duration of stress. The rapid establishment and root expansion characteristics of grasses probably enabled perennial ryegrass to establish quickly within the microcosms, enhancing resilience (Volaire et al. 2014). However, it is also important to acknowledge that our model did not explicitly account for cultivar diversity as a predictor, which could have influenced species-level responses. Perennial ryegrass had the highest cultivar diversity (four cultivars), followed by white clover (three) and chicory (two), which may have contributed to its greater stability under stress. Additionally, the controlled conditions of our study and the water applied during the summer stress (95 days after-sowing) likely contributed to this resilience, thus larger-scale studies with prolonged stress might reveal different outcomes. Forbs possess unique traits, such as deep tap-root systems and higher root/shoot ratios, which support water uptake from deeper soil layers and make them well-suited to drought conditions (De Boeck et al. 2016; Hofer et al. 2016; Mackie et al. 2019). The effect of rooting depth is, however, less relevant in the establishment period, thereby limiting the benefits from a deep root. Chicory is frequently reported as highly drought-tolerant and is increasingly used in temperate mixtures (Haughey et al. 2018), though its response in our study varied with event timing. A previous study based on both greenhouse and field experiments determined, however, that chicory can normally be considered successfully established after 40–50 days after-sowing, thereby indicating that our chicory plants were sufficiently mature by the time the stress treatments were started (Sanderson and Elwinger 2000). The mixed results are likely a result from the generally beneficial effect of elevated temperatures, combined with the detrimental effects of drought.

White clover, in contrast, consistently showed reduced yield under all CDHW treatments. It was particularly vulnerable to water stress, likely due to its shallow roots and lower root/shoot ratio (Hoekstra et al. 2015; Hofer et al. 2017b). While legumes in general can benefit from nitrogen fixation, which can enhance water-use efficiency and resistance to stress (Hofer et al. 2017a, b), white clover struggled in our experiment, possibly due to the early-stage stress application. The Crop Water Stress Index (CWSI) results add further evidence to our findings, indicating elevated stress levels across all species under CDHW treatments, with no significant differences in CWSI observed between the tested species. This suggests that despite experiencing similar stress levels, species and/or FG-specific traits played a crucial role in determining the observed differences in stress responses. CWSI is an indirect measure of plant gas exchange rate, and therefore photosynthetic capacity (Hernanda et al. 2024). Under optimal conditions, plants can cool their surfaces through stomatal opening and transpiration. However, under stress conditions plants close their stomata to save water, losing their ability to regulate temperature, which leads to increased CWSI values and decreased photosynthesis (Grossiord et al. 2020). Importantly, while CWSI measurements during summer CDHWs were consistent, showing high values in stressed plants and low values in unstressed ones, spring measurements were highly variable. This variability could be due to smaller plants during spring, as the influence of environmental variability on plant tissue may confound thermal imaging data at this stage (Costa et al. 2013; Still et al. 2019).

Similar to other studies, our findings emphasize the potential of plant diversity as a key strategy for managing and determining resilience to climate stress (Bloor and Bardgett 2012; Isbell et al. 2015; Kahmen et al. 2005; Lüscher et al 2022). Multispecies mixtures that combine grasses for rapid recovery, deep-rooted forbs for drought tolerance, and nitrogen-fixing legumes for improved water-use efficiency can enhance resilience to CDHW conditions (Hofer et al. 2016, 2017b). Diversification, however, can extend across scales, going beyond FGs and species to cultivar-level diversity (Pollnac et al. 2014). Due to unique breeding conditions, variations in stress tolerance between cultivars can add an important layer of resilience (Reiss and Drinkwater 2018; Wang et al. 2007). Increasing intraspecific genetic variation through cultivar mixtures or varieties with broader genetic bases, has shown to improve stability of yields and ecosystem services, particularly under stress conditions (Deng et al. 2021; Prieto et al. 2015; Wolff et al. 2024). In grasslands, genotypic diversity within dominant species enhanced ecosystem resilience, microbial diversity, and soil health, sometimes even exceeding the benefits of interspecific diversity (De Boeck et al. 2018; Des Roches et al. 2018; Jiang et al. 2022). Exceptions in our study were observed for cultivars ’Iona’ (white clover) and ’Choice’ (chicory), that showed significant yield increases under stress treatments relative to their control performance, despite equal numbers of individuals per cultivar in all pots. This suggests that species-level yield increases under heatwave treatments were not uniformly driven by all cultivars but were influenced by specific cultivars contributing disproportionately to the total biomass increase. The short and intense stress periods, however, may have limited further differentiation in yield performance among cultivars. Existing literature supports that prolonged stress, particularly during the establishment phase, can magnify differences in cultivar performance, thereby amplifying the role of cultivar-level diversification in building resilience (Dodd et al. 2001; Egan et al. 2021; Ghanaatiyan and Sadeghi 2017; Wang et al. 2023).

Disentangling the individual contributions of CDHW components to plant stress responses remains a complex challenge due to their intertwined effects, with some studies suggesting their combined impacts often exceed the sum of individual factors (De Boeck et al. 2016; Perkins 2015; Shtai et al. 2024; Wang et al. 2024). In our study, summer and spring–summer CDHW events significantly reduced yield by at least 26% in affected species, whereas individual stressors did not. The hypothesis testing revealed that CDHW effects exceeded the sum of individual drought and heatwave effects in chicory, indicating a synergistic response in summer and across both seasons (spring–summer). In white clover, biomass reductions under CDHW also showed a significant deviation from additivity in these seasons, suggesting a mild synergistic effect rather than a purely additive response. Drought consistently emerged as the dominant factor limiting yield during CDHWs, while heatwaves alone had milder or even positive effects. Heatwave effects are typically temperature-driven, acting either directly or indirectly (Mathieu et al. 2014; Wang et al. 2016). Direct thermal damage to photosynthetic machinery was unlikely in our study, particularly during spring, as temperatures remained below critical thresholds (Mueller and Seneviratne 2012; Zhao et al. 2023). Instead, the positive effects of heatwaves observed in some treatments suggest that elevated temperatures during spring may have temporarily enhanced photosynthesis by bringing leaf temperatures closer to photosynthetic optima (Craine et al. 2012). Although high VPD can lead to stomatal closure even when enough water is available in the soil (Koehler et al. 2024; Merilo et al. 2018), the positive effects observed in heatwave-only treatments suggest that plants maintained transpiration, resulting in increased biomass.

However, when coupled with drought, heatwaves exacerbated stress through increased evaporative demand (high VPD), amplifying water loss, similarly to other studies (Craine et al. 2012; De Boeck et al. 2016; Zhao et al. 2023). This was particularly evident in both chicory and white clover, where CDHW significantly reduced biomass beyond the expected additive effects of drought and heatwaves, suggesting greater physiological strain under combined stress. These interactions were further reflected in soil moisture responses during CDHWs. During spring events, soil water content dropped more under CDHW treatments compared to drought-only, likely due to the added atmospheric demand of heatwaves (Online Resource 2). Interestingly, during summer events, we observed minimal differences in soil water content between CDHW and drought-only treatments, with a slight tendency for the drought-only treatment to lose water more rapidly in the initial days (Online Resource 2). This could indicate that, under summer CDHW conditions, plants detected the combined stress earlier and activated coping mechanisms sooner. In contrast, under drought-only conditions, soil moisture continued to drop further, indicating continued plant transpiration, which is in line with previous research, suggesting that plants tend to respond more quickly to edaphic drought when VPD is high (Koehler et al. 2024).

The relative importance of soil water content over VPD is evident above critical soil moisture thresholds. However, as soil dries, the increasing influence of VPD amplifies plant stress (Berauer et al. 2024). This dynamic is closely tied to seasonality (i.e., timing of stress), as summer CDHWs with higher temperature extremes amplify stress effects, whereas spring CDHWs often occur under milder conditions that may prevent rapid soil moisture depletion (Hahn et al. 2021; Wang et al. 2024). In our study, soil water levels were higher after CDHW1 compared to CDHW2 (Online Resource 2). Correspondingly, spring CDHWs enhanced chicory biomass, whereas summer CDHWs significantly reduced biomass in both chicory and white clover. Nevertheless, spring extremes are not uniformly advantageous, as the phenological stage of plants at the time of stress adds complexity to their responses (De Boeck et al. 2011; Denton et al. 2017; Hahn et al. 2021). Early CDHW events in spring-sown grasslands can be particularly harmful, as younger plants with underdeveloped root systems are more vulnerable. In some cases, early-season stress may necessitate reseeding, delaying establishment and increasing production costs. Similarly, this sensitivity also extends to post-cut regrowth, when plants are particularly vulnerable to stress (Vogel et al. 2012).

Furthermore, our investigation of single versus repeated CDHW events revealed that repeated stress can influence the impact on plant biomass. Chicory and white clover plants exposed to both spring and summer CDHW events showed 16% and 28% greater yields than those experiencing only summer stress, respectively. This outcome could reflect a priming effect, where early stress exposure induces physiological or epigenetic changes that enhance the plant's ability to withstand subsequent stresses. Such priming, or "stress memory", has been well-documented in the literature, with mechanisms including modifications in gene expression, accumulation of stress-related proteins, and phenotypic plasticity to optimize stress response (Bruce et al. 2007; Walter et al. 2011). Recurrent stress, when paired with sufficient recovery intervals, can enhance plant resilience; notably, in grasses, this effect endured even after complete aboveground biomass was harvested and regrown (Walter et al. 2011; Wang et al. 2024). However, excessively frequent stress without sufficient recovery can lead to cumulative damage, diminished photosynthetic efficiency, and reduced yield (Tombesi et al. 2018; Walter et al. 2013). Conversely, prolonged intervals between stress events may erode the benefits of prior acclimatization, reducing a plant's ability to leverage its"stress imprint"effectively (Wohlgemuth et al. 2022). Future research should focus on identifying optimal recovery intervals and exploring the physiological and molecular pathways underpinning stress resilience in grassland species with varied tolerance mechanisms.

In summary, this study underscores the importance of diversity as a strategy for enhancing resilience to climate extremes in grasslands. By examining responses across species, FGs, and cultivars under both isolated and compound drought–heatwave stresses, we discuss key traits that can be leveraged in designing grassland mixtures. Our findings highlight that the timing and recurrence of CDHW events significantly influence outcomes, emphasizing the need for multispecies mixtures and cultivar diversity to sustain productivity and resilience under increasing climate variability. While the use of climate chambers in our study allowed for precise control over climatic variables, the limited space within microcosms may have constrained plant growth and stress responses compared to field conditions (Hill et al. 2024). However, focusing on the establishment phase likely minimized these effects, as the soil volume and depth provided were sufficient to support early-stage growth. Similarly, while the simulated drought duration was relatively short, it reflected the average length of CDHW events in western Europe, providing a realistic scenario, although longer droughts could exacerbate stress responses in certain species such as perennial ryegrass (Hofer et al. 2017b; Mackie et al. 2019). Given the inherent variability of climate extremes—spanning geographical distribution, timing, intensity, and recurrence—no single experiment can comprehensively simulate all possible scenarios. Future research should explore CDHW events under varying stress intensities, durations, and recurrence intervals to deepen our understanding of how timing and "stress memory" interact. Investigating FG-specific responses will be particularly valuable for optimizing grassland resilience and productivity. Additionally, studies addressing stress during the early establishment phase and post-cut regrowth could clarify how early-season stress primes plants for future events or hinders development, providing critical insights for timing-based management strategies to advance grassland resilience science.

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Data availability Data is available on request.

Declarations

Competing interests The authors have no conflict of interest to disclose.

References

Arias PA, Bellouin N, Coppola E et al (2021) Technical Summary. In: Masson-Delmotte V, Zhai P, Pirani A et al (eds) Climate Change 2021: The Physical Science Basis

Contribution of Working Group I to the Sixth Assessment Report of the Intergovernmental Panel on Climate Change. Cambridge University Press, Cambridge, pp 33–144

Berauer BJ, Steppuhn A, Schweiger AH (2024) The multidimensionality of plant drought stress: The relative importance of edaphic and atmospheric drought. Plant Cell Environ 47:3528–3540. https://doi.org/10.1111/pce.15012

Bloor JMG, Bardgett RD (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. Perspect Plant Ecol Evol Syst 14:193–204. https://doi.org/10.1016/j.ppees.2011.12.001

Böhm W (1979) Techniques of Root Washing. In: Böhm W (ed) Methods of Studying Root Systems. Springer Berlin, Heidelberg, pp 115–124

Bruce TJA, Matthes MC, Napier JA, Pickett JA (2007) Stressful "memories" of plants: Evidence and possible mechanisms. Plant Sci 173:603–608. https://doi.org/10.1016/j.plantsci.2007.09.002

Cong WF, Christensen BT, Eriksen J (2019) Soil nutrient levels define herbage yield but not root biomass in a multispecies grass-legume ley. Agric Ecosyst Environ 276:47–54. https://doi.org/10.1016/j.agee.2019.02.014

Costa JM, Grant OM, Chaves MM (2013) Thermography to explore plant–environment interactions. J Exp Bot 64:3937–3949. https://doi.org/10.1093/jxb/ert029

Craine JM, Nippert JB, Elmore AJ et al (2012) Timing of climate variability and grassland productivity. Proc Natl Acad Sci 109:3401–3405. https://doi.org/10.1073/pnas.1118438109

De Boeck HJ, Dreesen FE, Janssens IA, Nijs I (2010) Climatic characteristics of heat waves and their simulation in plant experiments. Glob Change Biol 16:1992–2000. https://doi.org/10.1111/j.1365-2486.2009.02049.x

De Boeck HJ, Dreesen FE, Janssens IA, Nijs I (2011) Whole-system responses of experimental plant communities to climate extremes imposed in different seasons. New Phytol 189:806–817. https://doi.org/10.1111/j.1469-8137.2010.03515.x

De Boeck HJ, Bassin S, Verlinden M et al (2016) Simulated heat waves affected alpine grassland only in combination with drought. New Phytol 209:531–541. https://doi.org/10.1111/nph.13601

De Boeck HJ, Bloor JMG, Kreyling J et al (2018) Patterns and drivers of biodiversity–stability relationships under climate extremes. J Ecol 106:890–902. https://doi.org/10.1111/1365-2745.12897

Deng M, Liu W, Li P et al (2021) Intraspecific trait variation drives grassland species richness and productivity under changing precipitation. Ecosphere 12:e03707. https://doi.org/10.1002/ecs2.3707

Denton EM, Dietrich JD, Smith MD, Knapp AK (2017) Drought timing differentially affects above- and belowground productivity in a mesic grassland. Plant Ecol 218:317–328. https://doi.org/10.1007/s11258-016-0690-x

Des Roches S, Post DM, Turley NE et al (2018) The ecological importance of intraspecific variation. Nat Ecol Evol 2:57–64. https://doi.org/10.1038/s41559-017-0402-5

Dodd MB, Sheath GW, Wedderburn ME, Tarbotton IS (2001) Long-term performance of white clover cultivars oversown into summer-dry hill country. Proc N Z Grassl Assoc 85–89. https://doi.org/10.33584/jnzg.2001.63.2435

Domeisen DIV, Eltahir EAB, Fischer EM et al (2023) Prediction and projection of heatwaves. Nat Rev Earth Environ 4:36–50. https://doi.org/10.1038/s43017-022-00371-z

Dong X, Qu L, Dong G et al (2022) Mowing mitigated the sensitivity of ecosystem carbon fluxes responses to heat waves in a Eurasian meadow steppe. Sci Total Environ 853:158610. https://doi.org/10.1016/j.scitotenv.2022.158610

Egan L, Hofmann R, Nichols S et al (2021) Transpiration Rate of White Clover (Trifolium repens L.) Cultivars in Drying Soil. Front Plant Sci 12. https://doi.org/10.3389/fpls.2021.595030

Finn JA, Kirwan L, Connolly J et al (2013) Ecosystem function enhanced by combining four functional types of plant species in intensively managed grassland mixtures: a 3-year continental-scale field experiment. J Appl Ecol 50:365–375. https://doi.org/10.1111/1365-2664.12041

Ghanaatiyan K, Sadeghi H (2017) Differential responses of chicory ecotypes exposed to drought stress in relation to enzymatic and non-enzymatic antioxidants as well as ABA concentration. J Hortic Sci Biotechnol 92:404–410. https://doi.org/10.1080/14620316.2017.1286235

Grange G, Finn JA, Brophy C (2021) Plant diversity enhanced yield and mitigated drought impacts in intensively managed grassland communities. J Appl Ecol 58:1864–1875. https://doi.org/10.1111/1365-2664.13894

Grossiord C, Buckley TN, Cernusak LA et al (2020) Plant responses to rising vapor pressure deficit. New Phytol 226:1550–1566. https://doi.org/10.1111/nph.16485

Hahn C, Lüscher A, Ernst-Hasler S et al (2021) 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

Haughey E, Suter M, Hofer D et al (2018) Higher species richness enhances yield stability in intensively managed grasslands with experimental disturbance. Sci Rep 8:15047. https://doi.org/10.1038/s41598-018-33262-9

Haughey E, McElwain JC, Finn JA (2023) Annual yields of multispecies grassland mesocosms outperformed monocultures across a drought gradient due to complementarity effects and rapid recovery. Grassl Res 2:309–321. https://doi.org/10.1002/glr2.12064

Hernanda RAP, Lee H, Cho J et al (2024) Current trends in the use of thermal imagery in assessing plant stresses: A review. Comput Electron Agric 224:109227. https://doi.org/10.1016/j.compag.2024.109227

Hill D, Conte L, Nelson D et al (2024) Investigating the water availability hypothesis of pot binding: small pots and infrequent irrigation confound the effects of drought stress in potato (Solanum tuberosum L.). Front Plant Sci 15. https://doi.org/10.3389/fpls.2024.1399250

Hoekstra NJ, Suter M, Finn JA et al (2015) Do belowground vertical niche differences between deepand shallow-rooted species enhance resource uptake and drought resistance in grassland mixtures? Plant Soil 394:21–34

Hofer D, Suter M, Haughey E et al (2016) Yield of temperate forage grassland species is either largely resistant or resilient to experimental summer drought. J Appl Ecol 53:1023–1034. https://doi.org/10.1111/1365-2664.12694

Hofer D, Suter M, Buchmann N, Lüscher A (2017a) Nitrogen status of functionally different forage species explains resistance to severe drought and post-drought overcompensation. Agric Ecosyst Environ 236:312–322. https://doi.org/10.1016/j.agee.2016.11.022

Hofer D, Suter M, Buchmann N, Lüscher A (2017b) Severe water deficit restricts biomass production of Lolium perenne L. and Trifolium repens L. and causes foliar nitrogen but not carbohydrate limitation. Plant Soil 421:367–380. https://doi.org/10.1007/s11104-017-3439-y

Hoover DL, Knapp AK, Smith MD (2014) Resistance and resilience of a grassland ecosystem to climate extremes. Ecology 95:2646–2656. https://doi.org/10.1890/13-2186.1

Huang Y, Lei H, Duan L (2024) Resistance of grassland productivity to drought and heatwave over a temperate semi-arid climate zone. Sci Total Environ 951:175495. https://doi.org/10.1016/j.scitotenv.2024.175495

Hunt BG (2007) A Climatology of Heat Waves from a Multi-millennial Simulation. J Clim 20:3802–3821. https://doi.org/10.1175/JCLI4224.1

Isbell F, Craven D, Connolly J et al (2015) Biodiversity increases the resistance of ecosystem productivity to climate extremes. Nature 526:574–577. https://doi.org/10.1038/nature15374

Jentsch A, Kreyling J, Beierkuhnlein C (2007) A new generation of climate-change experiments: events, not trends. Front Ecol Environ 5:365–374. https://doi.org/10.1890/1540-9295(2007)5[365:ANGOCE]2.0.CO;2

Jiang M, He L, Fan B et al (2022) Intraspecific more than interspecific diversity plays an important role on Inner Mongolia grassland ecosystem functions: A microcosm experiment. Sci Total Environ 826:154134. https://doi.org/10.1016/j.scitotenv.2022.154134

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

Koehler T, Botezatu Á, Murugesan T et al (2024) The transpiration rate sensitivity to increasing evaporative demand differs between soil textures, even in wet soil. Plant Stress 12:100506. https://doi.org/10.1016/j.stress.2024.100506

Komainda M, Küchenmeister F, Küchenmeister K et al (2020) Drought tolerance is determined by species identity and functional group diversity rather than by species diversity within multi-species swards. Eur J Agron 119:126116. https://doi.org/10.1016/j.eja.2020.126116

Lambers H, Cong WF (2022) Challenges providing multiple ecosystem benefits for sustainable managed systems. Front Agr Sci Eng 9:170–176. https://doi.org/10.15302/J-FASE-2022444

Landwirtschaftskammer Niedersachsen (2020) Empfehlungen zur Grunddüngung. Landwirtschaftskammer Niedersachsen, Geschäftsbereich Landwirtschaft. Avaiable at: https://www.lufa-nord-west.de/index.cfm/action/downloadcenter?file=08E6CC. Accessed 07 May 2024

Lee MA, Davis AP, Chagunda MGG, Manning P (2017) Forage quality declines with rising temperatures, with implications for livestock production and methane emissions. Biogeosciences 14:1403–1417. https://doi.org/10.5194/bg-14-1403-2017

Lemaire G, Gastal F, Franzluebbers A, Chabbi A (2015) Grassland-cropping rotations: an avenue for agricultural diversification to reconcile high production with environmental quality. Environ Manage 56:1065–1077. https://doi.org/10.1007/s00267-015-0561-6

Loka D, Harper J, Humphreys M et al (2019) Impacts of abiotic stresses on the physiology and metabolism of cool-season grasses: A review. Food Energy Secur 8:e00152. https://doi.org/10.1002/fes3.152

Lüscher A, Barkaoui K, Finn JA et al (2022) Using plant diversity to reduce vulnerability and increase drought resilience of permanent and sown productive grasslands. Grass Forage Sci 77:235–246. https://doi.org/10.1111/gfs.12578

Mackie KA, Zeiter M, Bloor JMG, Stampfli A (2019) Plant functional groups mediate drought resistance and recovery in a multisite grassland experiment. J Ecol 107:937–949. https://doi.org/10.1111/1365-2745.13102

Malisch CS, Finn JA, Eriksen J et al (2024) The importance of multi-species grassland leys to enhance ecosystem services in crop rotations. Grass Forage Sci 79:120–134. https://doi.org/10.1111/gfs.12670

Martin G, Durand J-L, Duru M et al (2020) Role of ley pastures in tomorrow's cropping systems A review. Agron Sustain Dev 40:17. https://doi.org/10.1007/s13593-020-00620-9

Marx W, Haunschild R, Bornmann L (2021) Heat waves: a hot topic in climate change research. Theor Appl Climatol 146:781–800. https://doi.org/10.1007/s00704-021-03758-y

Mathieu A-S, Lutts S, Vandoorne B et al (2014) High temperatures limit plant growth but hasten flowering in root chicory (*Cichorium intybus*) independently of vernalisation. J Plant Physiol 171:109–118. https://doi.org/10.1016/j.jplph.2013.09.011

Merilo E, Yarmolinsky D, Jalakas P et al (2018) Stomatal VPD Response: There Is More to the Story Than ABA. Plant Physiol 176:851–864. https://doi.org/10.1104/pp.17.00912

Mueller B, Seneviratne SI (2012) Hot days induced by precipitation deficits at the global scale. Proc Natl Acad Sci 109:12398–12403. https://doi.org/10.1073/pnas.1204330109

Oliveira BA, López IF, Cranston LM et al (2024) 18O isotopic labelling and soil water content fluctuations validate the hydraulic lift phenomena for C3 grass species in drought conditions. Plant Stress 11:100414. https://doi.org/10.1016/j.stress.2024.100414

Perkins SE (2015) A review on the scientific understanding of heatwaves—Their measurement, driving mechanisms, and changes at the global scale. Atmos Res 164–165:242–267. https://doi.org/10.1016/j.atmosres.2015.05.014

Perkins SE, Fischer EM (2013) The usefulness of different realizations for the model evaluation of regional trends in heat waves. Geophys Res Lett 40:5793–5797. https://doi.org/10.1002/2013GL057833

Perkins-Kirkpatrick SE, Fischer EM, Angélil O, Gibson PB (2017) The influence of internal climate variability on heatwave frequency trends. Environ Res Lett 12:044005. https://doi.org/10.1088/1748-9326/aa63fe

Pollnac FW, Smith RG, Warren ND (2014) Cultivar diversity as a means of ecologically intensifying dry matter production in a perennial forage stand. Ecosphere 5:art115. https://doi.org/10.1890/ES14-00139.1

Prieto I, Violle C, Barre P et al (2015) Complementary effects of species and genetic diversity on productivity and stability of sown grasslands. Nat Plants 1:1–5. https://doi.org/10.1038/nplants.2015.33

Qu L-P, Chen J, Xiao J et al (2024) The complexity of heatwaves impact on terrestrial ecosystem carbon fluxes: Factors, mechanisms and a multi-stage analytical approach. Environ Res 240:117495. https://doi.org/10.1016/j.envres.2023.117495

R Core Team (2024) R: A language and environment for statistical computing. R foundation for statistical computing, Vienna, Austria. https://www.R-project.org/. Accessed 20 Sept 2024

Reiss ER, Drinkwater LE (2018) Cultivar mixtures: a meta-analysis of the effect of intraspecific diversity on crop yield. Ecol Appl 28:62–77. https://doi.org/10.1002/eap.1629

Rojas-Downing MM, Nejadhashemi AP, Harrigan T, Woznicki SA (2017) Climate change and livestock: Impacts, adaptation, and mitigation. Clim Risk Manag 16:145–163. https://doi.org/10.1016/j.crm.2017.02.001

Sanderson MA, Elwinger GF (2000) Seedling development of chicory and plantain. Agron J 92:69–74. https://doi.org/10.2134/agronj2000.92169x

Schneider CA, Rasband WS, Eliceiri KW (2012) NIH Image to ImageJ: 25 years of image analysis. Nat Methods 9:671–675. https://doi.org/10.1038/nmeth.2089

Shan B, Verhoest NEC, De Baets B (2024) Identification of compound drought and heatwave events on a daily scale and across four seasons. Hydrol Earth Syst Sci 28:2065–2080. https://doi.org/10.5194/hess-28-2065-2024

Shtai W, Asensio D, Kadison AE et al (2024) Soil water availability modulates the response of grapevine leaf gas exchange and PSII traits to a simulated heat wave. Plant Soil 501:537–554. https://doi.org/10.1007/s11104-024-06536-7

Still C, Powell R, Aubrecht D et al (2019) Thermal imaging in plant and ecosystem ecology: applications and challenges. Ecosphere 10:e02768. https://doi.org/10.1002/ecs2.2768

Tamboli P, Chaurasiya AK, Upadhyay D, Kumar A (2023) Climate Change Impact on Forage Characteristics: An Appraisal for Livestock Production. In: Singhal RK, Ahmed S, Pandey S, Chand S (eds) Molecular Interventions for Developing Climate-Smart Crops: A Forage Perspective. Springer Nature, Singapore, pp 183–196

Tejedor E, Benito G, Serrano-Notivoli R et al (2024) Recent heatwaves as a prelude to climate extremes in the western Mediterranean region. Npj Clim Atmospheric Sci 7:1–7. https://doi.org/10.1038/s41612-024-00771-6

Teuling AJ (2018) A hot future for European droughts. Nat Clim Change 8:364–365. https://doi.org/10.1038/s41558-018-0154-5

Tombesi S, Frioni T, Poni S, Palliotti A (2018) Effect of water stress “memory” on plant behavior during subsequent drought stress. Environ Exp Bot 150:106–114. https://doi.org/10.1016/j.envexpbot.2018.03.009

Vogel A, Scherer-Lorenzen M, Weigelt A (2012) Grassland Resistance and Resilience after Drought Depends on Management Intensity and Species Richness. PLoS ONE 7:e36992. https://doi.org/10.1371/journal.pone.0036992

Volaire F, Barkaoui K, Norton M (2014) Designing resilient and sustainable grasslands for a drier future: Adaptive strategies, functional traits and biotic interactions. Eur J Agron 52:81–89. https://doi.org/10.1016/j.eja.2013.10.002

Walter J, Nagy L, Hein R et al (2011) Do plants remember drought? Hints towards a drought-memory in grasses. Environ Exp Bot 71:34–40. https://doi.org/10.1016/j.envexpbot.2010.10.020

Walter J, Jentsch A, Beierkuhnlein C, Kreyling J (2013) Ecological stress memory and cross stress tolerance in plants in the face of climate extremes. Environ Exp Bot 94:3–8. https://doi.org/10.1016/j.envexpbot.2012.02.009

Wang Y, Yu S, Wang J (2007) Biomass-dependent susceptibility to drought in experimental grassland communities. Ecol Lett 10:401–410. https://doi.org/10.1111/j.1461-0248.2007.01031.x

Wang D, Heckathorn SA, Mainali K, Tripathee R (2016) Timing Effects of Heat-Stress on Plant Ecophysiological Characteristics and Growth. Front Plant Sci 7:1629. https://doi.org/10.3389/fpls.2016.01629

Wang J, Ren B, Shao J et al (2023) Impact of plant community structure and its diversity on richness and abundance of arthropod aphidophagous natural enemy community. Urban Urban Green 81:127850. https://doi.org/10.1016/j.ufug.2023.127850

Wang C, Li Z, Chen Y et al (2024) Characteristic changes in compound drought and heatwave events under climate change. Atmospheric Res 305:107440. https://doi.org/10.1016/j.atmosres.2024.107440

Wohlgemuth T, Jentsch A, Seidl R (eds) (2022) Disturbance Ecology. Springer International Publishing, Cham

Wolff B, Julier B, Louarn G (2024) Impact of intraspecific genetic variation on interspecific competition: a theoretical case study of forage binary mixtures. Front Plant Sci 15. https://doi.org/10.3389/fpls.2024.1356506

Yin J, Gentine P, Slater L et al (2023) Future socio-ecosystem productivity threatened by compound drought–heatwave events. Nat Sustain 6:259–272. https://doi.org/10.1038/s41893-022-01024-1

Zhao Z, Wang X, Li R et al (2023) Impacts of climate extremes on autumn phenology in contrasting temperate and alpine grasslands in China. Agric for Meteorol 336:109495. https://doi.org/10.1016/j.agrformet.2023.109495