THESIS

BELOWGROUND PLANT RESPONSES TO COMPOUND CLIMATE EXTREMES IN THE SHORTGRASS STEPPE

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ABSTRACT

BELOWGROUND PLANT RESPONSES TO COMPOUND CLIMATE EXTREMES IN THE SHORTGRASS STEPPE

Climate change is increasing the frequency and intensity of extreme precipitation events, resulting in greater variability in water availability across terrestrial ecosystems. Semi-arid grasslands are particularly sensitive to these changes because productivity and carbon cycling are strongly regulated by precipitation. While the impacts of drought on aboveground processes have been extensively studied, much less is known about how belowground productivity and root functional strategies respond to compound climate extremes, such as drought followed by extreme rainfall events. Understanding these responses is critical because roots represent a major pathway for carbon inputs into soils and strongly influence ecosystem resilience.

This study examined how prolonged drought and an extreme precipitation event (deluge) interact to influence belowground net primary productivity (BNPP) and root functional traits in the shortgrass steppe of northeastern Colorado. Using a manipulative field experiment at the Central Plains Experimental Range, we evaluated responses to ambient conditions, drought, deluge, and drought followed by deluge. Root ingrowth cores were used to quantify BNPP across soil depths (0–10, 10–20, and 20–30 cm), and root morphological traits, including specific root length (SRL) and root tissue density (RTD), were measured to assess shifts in belowground resource acquisition strategies.

Drought strongly reduced BNPP across the soil profile and shifted root traits toward a more conservative strategy characterized by lower SRL and higher RTD. The addition of a deluge during drought substantially increased root production but did not fully restore BNPP to ambient levels, indicating persistent drought legacy effects. Deluge responses varied with soil depth,

with increased root production occurring throughout the measured soil profile during drought and particularly strong responses in deeper soil layers during the post-deluge period. Additionally, deluge during drought reversed drought-induced trait shifts, increasing SRL and decreasing RTD, suggesting a transition toward a more acquisitive root strategy following increased water availability.

These results demonstrate that compound drought–deluge events influence not only the magnitude of belowground productivity but also the spatial distribution and functional strategies of root systems. While extreme rainfall events may partially offset drought impacts by stimulating root production, shifts toward acquisitive traits may increase root turnover and alter the fate of belowground carbon inputs. Incorporating root trait responses and drought legacy effects into ecosystem models will improve predictions of grassland carbon dynamics under increasingly variable precipitation regimes.

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1. INTRODUCTION

Ecosystems across the globe are experiencing profound changes as a result of climate change. Rising global temperatures are altering the hydrological cycle, leading to greater variability in precipitation and more frequent climate extremes, such as droughts and deluges (Donat et al., 2016; Stocker, 2014). followed by extreme precipitation events (i.e., deluges), often defined relative to the historical distribution of rainfall events for a given ecosystem (Hoover et al., 2022). Such compound climate extremes (CCE) are significantly altering ecosystem structure and function, posing new challenges to ecosystem resilience. Numerous studies demonstrate that drought reduces productivity in grassland ecosystems, whereas deluges can generate short-lived increases in productivity that may partially offset drought legacies (Hoover et al., 2022; Post and Knapp, 2020). Additionally, variation in precipitation timing, intensity, and duration can strongly regulate ecosystem responses independent of total precipitation amount (Knapp et al., 2015a; Padilla et al., 2019).

Hydrological extremes are especially impactful in grassland ecosystems, which cover approximately 22.8% of Earth's terrestrial surface and play a disproportionate role in global carbon cycling (Ahlström et al., 2015; MacDougall et al., 2026). More specifically, semi-arid grassland ecosystems are responsible for a large share of interannual variability in terrestrial carbon fluxes due to strong coupling between water availability and productivity (Ahlström et al., 2015; "Drought effects on soil carbon and nitrogen dynamics in global natural ecosystems," 2021). Because plant growth in these systems is primarily water-limited, relatively small changes in precipitation timing and magnitude can produce large changes in ecosystem function (Griffin-Nolan et al., 2018; Knapp and Smith, 2001). The shortgrass steppe of the western Great Plains of North America represents a model system for studying these dynamics due to its strong water limitation and sensitivity to precipitation variability. Projected increases in precipitation extremes are expected to alter soil water availability across depth, with subsequent effects on plant water uptake and productivity (Knapp et al., 2008; Nippert and Knapp, 2007).

However, recovery trajectories following extreme rainfall events remain highly variable and poorly understood, particularly for belowground processes (Guasconi et al., 2023; Hoover et al., 2022). Thus, prior drought conditions can create conditions that constrain ecosystem responses to subsequent precipitation events, potentially limiting recovery within the context of drought following a deluge event.

Despite increasing evidence that compound hydroclimatic extremes are becoming more frequent and intense under climate change, much of our understanding of ecosystem responses to these events is still derived from aboveground measurements, particularly aboveground net primary productivity (ANPP), which are more readily quantified than belowground measurements (Carroll et al., 2021; Knapp et al., 2015b). This aboveground bias overlooks the fact that a substantial proportion of ecosystem carbon is stored belowground in roots and soils, particularly in grassland systems . Belowground net primary productivity (BNPP) often equals or exceeds ANPP in semi-arid ecosystems, especially during dry years, and plays a central role in both short-term carbon allocation and long-term carbon storage (From et al., 2021; Sala et al., 1988). Furthermore, the vertical distribution of roots strongly influences where carbon enters and is stabilized in soils, with most root biomass concentrated in surface layers but deeper roots playing a critical role in accessing water during periods of stress, such as drought (Jackson et al., 1996; Jobbágy and Jackson, 2000). In addition to changes in root biomass and distribution, root functional traits provide insight into how plants acquire resources and respond to environmental stress. Root functional traits are morphological, physiological, or chemical characteristics that influence plant performance and ecosystem processes, linking belowground structure with functions such as water and nutrient acquisition, carbon allocation, and root turnover (Freschet et al., 2021a; Freschet et al., 2021b).

Drought is known to alter root biomass and morphological traits, but responses vary widely across systems, species, and environmental conditions (Guasconi et al., 2023; Pilon et al., 2013; Zhou et al., 2018). Global syntheses indicate that drought often reduces root length,

root length density, and biomass while increasing root diameter and root:shoot allocation, reflecting shifts toward more conservative strategies (Ranjan et al., 2022; Zhou et al., 2018). However, other studies report increases in fine-root production and higher specific root length (SRL), suggesting enhanced soil exploration under resource limitation (Chandregowda et al., 2023; Liu et al., 2020). These contrasting responses highlight strong context dependence, driven by factors such as drought intensity, duration, and plant functional type (Craine et al., 2013; Guasconi et al., 2023). Root responses are often more variable than aboveground responses, emphasizing the need for direct measurement of belowground processes (From et al., 2021; Wang et al., 2021).

Patterns in root trait shifts reflect underlying trade-offs in plant strategies that are often described within the framework of the plant economics spectrum, which links traits across leaves, stems, and roots along a continuum from resource acquisition to conservation (Reich, 2014). In roots, acquisitive strategies are typically characterized by high SRL and low root tissue density (RTD), whereas conservative strategies exhibit thicker, denser roots with longer lifespans (Freschet et al., 2021b). However, recent work suggests that root traits are multidimensional and do not align along a single axis, with different trait combinations representing multiple strategies for resource acquisition and stress tolerance (Herms et al., 2022; Valverde-Barrantes and Blackwood, 2016). These root traits not only reflect plant strategies but also influence ecosystem processes, including nutrient cycling, soil structure, and carbon dynamics (de Vries et al., 2016; Freschet et al., 2021a). However, interpretation of root traits requires consideration of variation both among and within species. While interspecific trait variation reflects differences in ecological strategies among plant species, intraspecific variation allows individual species to adjust root morphology and function in response to changing environmental conditions (Freschet et al., 2021a; Zhou et al., 2018). Additionally, root traits can vary with root developmental stage and age, as younger absorptive roots often differ in morphology, lifespan, and function compared to older root tissues (Freschet et al., 2021a;

McCormack et al., 2015). Because root traits are responsive to both environmental conditions and developmental processes, shifts in root morphology provide important insight into how plants adjust belowground growth strategies under stress. Changes in root biomass are often mechanistically linked to shifts in root morphological traits, indicating that trait plasticity plays a key role in mediating belowground responses to drought (Zhou et al., 2018).

While drought responses have been widely studied (Guasconi et al., 2023; Lozano et al., 2020; Pilon et al., 2013; Zhou et al., 2018), far less is known about how root systems respond to extreme deluge events, particularly when they occur following periods of drought (Hoover et al., 2022; Post and Knapp, 2020). Pulse dynamics theory suggests that ecosystem responses to precipitation events depend strongly on event size and timing, with larger rainfall pulses producing deeper and longer-lasting soil moisture availability (Hoover et al., 2022; Post and Knapp, 2020; Schwinning and Sala, 2004). Experimental evidence indicates that root responses to precipitation pulses occur in multiple phases, with rapid physiological responses of existing roots followed by delayed increases in new root production (Lauenroth et al., 1987). In semi-arid grasslands, where dominant species such as blue grama (*Bouteloua gracilis*) typically rely on shallow soil water, deluge events may allow access to deeper soil moisture, potentially altering patterns of root growth and resource uptake (Hoover et al., 2022; Lee and Lauenroth, 1994; Nippert and Knapp, 2007; Post and Knapp, 2020). However, the extent to which these responses offset drought effects, particularly belowground, remains understudied.

Despite growing recognition of compound climate extremes, we still lack an understanding of how belowground productivity and root functional traits respond to co-occurring drought–deluge events, particularly across gradients of soil depth (Hoover et al., 2022; Post and Knapp, 2020). This limitation is important because inaccurate representation of belowground processes constrains our ability to predict carbon cycling and ecosystem resilience under future climate scenarios (Warren et al., 2015; Zhou et al., 2018). Also, most experimental studies examine drought and extreme rainfall in isolation, rather than as co-occurring events,

limiting our understanding of compound climate effects (Hoover et al., 2022; Padilla et al., 2019). To address these gaps in knowledge, this study investigated belowground responses to compound climate extremes in a semi-arid grassland ecosystem. Using a manipulative field experiment that combines multi-year drought with an experimentally imposed extreme deluge event, we quantify how these treatments influence BNPP and root morphological traits across soil depths using root ingrowth core methods. By linking changes in root production with trait-based responses, this work aims to clarify the mechanisms underlying belowground responses to sequential drought and deluge events and to improve predictions of carbon cycling in water-limited ecosystems under increasing climate variability.

Specifically, we tested three hypotheses examining how drought, deluge, and their interaction influence belowground productivity and root functional traits in a semi-arid grassland: (1) drought will reduce BNPP and shift root systems toward more conservative strategies, characterized by lower specific root length (SRL) and higher root tissue density (RTD), reflecting increased investment in stress tolerance; (2) deluge events under ambient conditions will stimulate BNPP and promote more acquisitive root traits, characterized by higher SRL and lower RTD, due to increased soil moisture availability; and (3) deluge events occurring during drought will partially offset drought-induced reductions in BNPP and shift root traits toward more acquisitive strategies, including higher SRL and lower RTD. Because large precipitation pulses can increase water availability deeper in the soil profile, we further predicted that BNPP and root trait responses would vary across soil depth, with stronger responses occurring in deeper soil layers following deluge treatments.

2. METHODS

2.1 Study Site and Experimental Design

This study was conducted during the 2025 growing season at the USDA-ARS Central Plains Experimental Range (CPER) located northeast of Nunn, Colorado. CPER is a Long-Term

Agroecosystem Research (LTAR) site managed by the USDA Agricultural Research Service and is representative of the shortgrass steppe (SGS) ecosystem of the western Great Plains. The region is a semi-arid grassland, receiving approximately 340 mm of mean annual precipitation (MAP), the majority of which occurs during the growing season (May-August) (Sala et al., 1988). High interannual variability in precipitation and high evaporative demand results in strong water limitation, making this ecosystem highly sensitive to changes in precipitation regimes (Knapp et al., 2008; Post and Knapp, 2020).

The plant community at CPER is characteristic of the shortgrass steppe and is dominated by the perennial C4 grasses blue grama (*Bouteloua gracilis*) and buffalo grass (*Bouteloua dactyloides*) (Lauenroth and Burke, 2008). Other vegetation includes perennial C3 grasses, cool-season annual grasses, forbs, and cacti, which contribute smaller proportions of the plant community. The site has a long history of ecological research on grassland dynamics, grazing, and climate variability, and is a well-established model system for studying ecosystem responses to drought and precipitation variability (Hoover et al., 2022; Post and Knapp, 2020).To test how drought, deluge, and their interaction influence belowground plant responses, we used a precipitation manipulation experiment that independently manipulated drought history and extreme precipitation events. This study was conducted within an existing multi-year precipitation manipulation experiment at CPER, referred to as the Compound Climate Extremes (CCE) experiment, which was designed to quantify the separate and interactive effects of drought and deluge events on ecosystem productivity and carbon cycling. The CCE experimental design is a randomized block split-plot design to account for spatial heterogeneity across the site (Fig. 1). The ten blocks consisted of two plots, each 4 x 12 m in size (n = 20 total). Plots within blocks were separated by 3 m, and the blocks were arrayed across the study site at least 5 m apart in relatively homogeneous vegetation. Each plot contained two 2 x 4 m subplots (n = 40 total) separated by a 3-m buffer. Each 2 x 4 m subplot was hydrologically isolated by trenching around plot boundaries and installing aluminum flashing (5-cm

aboveground and 15-cm belowground) to prevent later water movement between plots. Plots within each block were randomly assigned to either the ambient rainfall (control) or drought treatment, and subplots within each block were randomly assigned to either the deluge or no deluge (control) treatment. This resulted in four treatment combinations: control, control + deluge, drought, and drought + deluge. The drought treatment was imposed using passive rainout shelters (GrowSpan round cold frames, each 12 x 4 m in size) equipped with roofs consisting of strips of corrugated polycarbonate that excluded approximately 66% of incoming precipitation. The remaining ambient plots were unsheltered. The deluge treatment consisted of a 60-mm simulated rainfall event that was added in early July of the second growing season. The deluge amount was based on the long-term precipitation records from the study site, corresponding to a 98th percentile event size (Knapp et al., 2015b; Post and Knapp, 2020). The timing of the deluge addition was chosen based on historical timing of deluge events, and because previous studies have shown that this timing coincides with large effects on ecosystem functioning (Post and Knapp, 2020).

During the first year of the experiment (2024), drought treatments were implemented starting May 5th. The shelter roofs remained in place throughout the duration of the experiment, resulting in precipitation being manipulated year-round. Due to below-average precipitation during the 2024 growing season (~ 262-mm), supplemental water was applied as needed to both ambient (15-mm was added on June 12, 14, 20, 24, and 27, with another 9-mm addition on July 25, 2024) and drought plots (5-mm was added on June 12, 14, 20, 24, and 27, with another 3-mm addition on July 25, 2024) to maintain target precipitation levels, ensuring consistent treatment separation despite anomalously dry conditions. In the second year (~ 328-mm), ambient rainfall during the growing season was near average and thus supplemental water additions were not needed. The mid-season deluge treatment was added on July 9-10. The 60-mm deluge treatment was applied by hand with a watering wand attached to a pump, with a

digital flow meter used to track the amount of water added. Water was added at a rate to prevent pooling on the soil surface and allow soil infiltration to occur.

2.2 Soil Moisture

Soil moisture, expressed as percent volumetric water content (% VWC), was monitored at 15-minute intervals throughout the study in a subset of plots (n = 5 per treatment). Sensors (CS616 Water Content Reflectometers; Campbell Scientific, Logan, UT) were installed within one destructive sampling subplot of selected ambient and drought plots (n = 10 total). Soil moisture sensors were installed to measure integrated soil water availability across depth intervals rather than at discrete points within the soil profile. Sensors measuring the upper 0–15 cm of the soil profile were installed at a 45° angle relative to the soil surface. Data were recorded using a CR1000 datalogger (Campbell Scientific, Logan, UT) and downloaded biweekly. For analysis, soil moisture measurements collected during the 2025 growing season were averaged to daily values within plots.

2.3 Root Ingrowth Core Installation and Collection

To test how drought and deluge treatments affected belowground productivity across soil depths, root ingrowth cores were used to quantify BNPP during the second year (2025) of the experiment. Root ingrowth cores were used to quantify BNPP and root trait responses to experimental treatments in the second year (2025) of the experiment only. Roots from ingrowth cores were not separated by species and therefore represent community-level root production and trait responses. Given the dominance of perennial C4 grasses at CPER, root samples likely primarily reflect responses of the dominant grass species (*Bouteloua gracilis* and *Bouteloua dactyloides*), although contributions from other species cannot be excluded. Cores were constructed from 2 mm fiberglass mesh and formed into cylindrical units approximately 33 cm in

length and 5 cm in diameter. The mesh was sealed along seams to maintain structural integrity while allowing space for roots to penetrate. Soil used to fill ingrowth cores was collected adjacent to experimental plots and transported to the laboratory for processing. Soil was sieved to 500 μm to remove coarse fragments and existing roots, and remaining fine root material was manually removed to produce root-free substrate for core installation.

In the field, cylindrical holes were created in designated destructive sampling areas within each subplot using a stainless-steel soil auger to a depth of approximately 30 cm. This depth was selected because the majority of root biomass in grassland ecosystems occurs within the upper 30 cm of soil (Jackson et al., 1996; Jobbágy and Jackson, 2000). Ingrowth cores were inserted into these holes such that approximately 3 cm of mesh extended above the soil surface to facilitate retrieval. Cores were then filled with sieved, root-free soil using a funnel and gently packed to approximate in situ soil bulk density, ensuring continuity with surrounding soil conditions.

Two sets of ingrowth cores were installed to distinguish between seasonal and event-driven root production. Full-season cores (n = 39) were installed on May 29th, 2025, to capture cumulative BNPP across the growing season. One plot could not be sampled due to physical limitations preventing core installation. A second set of mid-season cores (n = 40) was installed on July 8, 2025, immediately prior to the deluge treatment, to isolate root production responses to the precipitation pulse. Cores were installed at one location per plot for each exposure type (total n = 79 ingrowth cores).

All ingrowth cores were harvested at the end of the growing season in late October (starting on October 27th and ending on November 3rd). Cores were excavated using a soil knife to a depth of approximately 30 cm and carefully removed by hand. In cases where soil compaction impeded removal, surrounding soil was loosened to minimize damage. Additional cores were lost during extraction and excluded from subsequent analyses, resulting in final recovered sample sizes of 8 ambient, 5 ambient + deluge, 7 drought, and 8 drought + deluge

cores for the full-season sampling period, and 8 ambient, 10 ambient + deluge, 6 drought, and 7 drought + deluge cores for the mid-season sampling period. Following removal, cores were placed in sealed plastic bags, labeled by plot and exposure type, and placed in coolers during transport to the laboratory and stored at 4°C until further processing.

2.4 Root Processing and BNPP Estimation

Following collection, ingrowth cores were processed to quantify BNPP. Each core was sectioned into three depth increments (0–10, 10–20, and 20–30 cm) using a knife and ruler to ensure consistent segment lengths. Soil and root material from each increment were separated and processed individually. Samples were transferred to trays, and large soil aggregates were gently broken apart by hand to facilitate root separation. Roots protruding from the exterior of the mesh cores were trimmed and excluded from analysis to ensure that only roots grown within the ingrowth cores were quantified.

Root material was separated from soil using a wet-sieving procedure with stacked 1 mm and 500 µm sieves under running water. Soil was removed as thoroughly as possible, and roots retained on the sieves were collected using forceps and transferred to a water-filled container. Remaining roots were rinsed from the sieves into the same container. Within the container, roots were carefully isolated from organic debris and non-root material by hand to ensure accurate biomass and trait measurements.

Cleaned root samples were then transferred to 15 mL centrifuge tubes containing a ~50% ethanol solution and stored at 4°C until further processing. Prior to drying, all root samples were scanned to quantify morphological traits (see Section 2.4). Following scanning, root samples were dried at 60°C for 72 hours and weighed using a digital analytical balance with a precision of 0.0001 grams. BNPP was calculated as the dry mass of roots produced within each ingrowth core and subsequently scaled to units of g m^{-2} based on core dimensions.

2.5 Root Trait Measurements

To evaluate whether drought and deluge treatments altered root functional strategies, root morphological traits were quantified using an image analysis system (WinRHIZO, Regent Instruments Inc., Quebec, Canada).Prior to scanning, root samples were removed from the ~50% ethanol solution and rinsed with deionized (DI) water to remove residual ethanol and debris. Roots were transferred to a shallow, water-filled scanning tray and arranged to minimize overlap. Water was added to fully submerge the roots while preventing excessive movement, allowing roots to settle at the bottom of the tray. Roots were gently teased apart using forceps to further reduce overlap and improve image clarity.

All samples were scanned using a flatbed scanner (EPSON Perfection V800/V850) at high resolution and analyzed using WinRHIZO software (version 2021a). Each sample was initially scanned once, and image quality was assessed to ensure accurate root detection. Samples were rescanned as needed if excessive overlap or poor image quality was observed. Root measurements included total root length (cm), average root diameter (mm), and root volume (cm^3) for each sample. Derived root traits were calculated from these measurements. SRL was calculated as root length per unit dry mass ($m\ g^{-1}$), and RTD was calculated as dry mass per unit root volume ($g\ cm^{-3}$).

2.6 Statistical Analysis

All statistical analyses were performed in R version 4.5.1 (R Core Team, 2025). Data processing and visualization were conducted using the tidyverse package (Wickham et al., 2019). Linear mixed-effects models were fit using the lme4 package (Bates et al., 2015), with significance tests conducted using lmerTest (Kuznetsova et al., 2017). Post-hoc pairwise comparisons were performed using estimated marginal means from the emmeans package (Lenth, 2025). Statistical significance was evaluated using an alpha value of $\alpha = 0.05$.

Model assumptions were evaluated prior to inference using residual diagnostic plots. Normality and homogeneity of variance were assessed through visual inspection of quantile-quantile plots and residual versus fitted plots. Visual diagnostics were used because they directly evaluate model assumptions and are commonly recommended for mixed-effects models, where formal tests can be overly sensitive to small deviations from normality. Response variables were log-transformed when necessary to improve model fit.

Separate linear mixed-effects models were used to analyze full-season BNPP, mid-season BNPP, SRL, and RTD. For BNPP analyses, drought, deluge, depth, and their interactions were included as fixed effects. Random effects accounted for the split-plot design, with block, whole plot (block × drought), and core identity included to account for experimental structure and repeated measurements across depths. Whole-core BNPP was analyzed by summing biomass across depths prior to analysis and included drought, deluge, and their interaction as fixed effects, with block included as a random effect.

Root trait analyses were conducted on mid-season cores using drought, deluge, and their interaction as fixed effects. Significant treatment effects were further evaluated using Tukey-adjusted pairwise comparisons of estimated marginal means.

3. RESULTS

3.1 Soil Moisture

Soil moisture differed among treatments throughout the 2025 growing season (Fig. 2). Prior to the deluge event, drought treatments generally maintained lower soil moisture than control treatments, indicating that the drought treatment reduced soil water availability. During the 7-day period prior to the deluge, mean soil moisture was 24.3% VWC in control plots, 23.3% VWC in control + deluge plots, 21.9% VWC in drought plots, and 19.7% VWC in drought + deluge plots. Following the 60-mm deluge addition on July 9–10, soil moisture increased sharply in both deluge treatments. Control + deluge plots reached a peak of 47.1% VWC on July 11, representing a 23.8% increase relative to pre-deluge conditions. Drought + deluge plots

reached a peak of 36.4% VWC on July 14, representing a 16.6% increases. In contrast, plots without deluge did not show comparable increases over the same period. Thus, the deluge produced a large but transient increase in soil water availability during the mid-growing season, with greater absolute soil moisture in control + deluge plots but substantial rewetting of previously droughted soils following the deluge event.

3.2 Belowground Net Primary Productivity (BNPP)

3.2.1 Full-season BNPP

Drought had a strong negative effect on full-season BNPP (Fig. 3). Whole-core BNPP was approximately 86% lower under drought compared to the control (153.9 vs. 21.7 g m^{-2}; $p < 0.001$). Under ambient conditions, applying a deluge did not change BNPP (13% increase; $p = 0.73$). When a deluge was applied during drought, however, BNPP increased substantially, rising from 21.7 to 91.6 g m^{-2} ($p < 0.001$), representing a ~322% increase relative to drought alone. Despite this large increase, BNPP remained lower in plots receiving a deluge during drought than in control plots.

Full-season BNPP by depth was influenced by drought, deluge, and soil depth (Fig. 5). Across all depths, BNPP was lower under drought than under ambient conditions ($p < 0.001$), and values declined with depth. Under control conditions, applying a deluge did not affect BNPP in the 0–10 cm or 10–20 cm layers, but increased BNPP in the 20–30 cm layer ($p = 0.048$). When a deluge was applied during drought, BNPP increased at all depths (Fig. 5), increasing from 0.068 to 0.211 g at 0–10 cm, 0.034 to 0.118 g at 10–20 cm, and 0.005 to 0.057 g at 20–30 cm. These increases were statistically significant across all depths ($p < 0.01$).

3.2.2 Post-deluge BNPP

Mid-season BNPP varied with drought, deluge, and soil depth (Fig. 4), with distinct patterns between ambient and drought conditions. Averaged across soil depths, deluge increased BNPP under both ambient and drought conditions, although the magnitude and

significance of these responses differed by depth. Under ambient conditions, BNPP was highest in the shallow soil layer (0–10 cm), and applying a deluge increased BNPP at all depths (Fig. 4; all $p < 0.01$). These increases were significant, with BNPP rising by approximately 195% in the 0–10 cm layer, 458% in the 10–20 cm layer, and nearly 950% in the 20–30 cm layer. Across these treatments, the largest BNPP values occurred in the shallowest layer.

Under drought conditions, total root biomass was very low across all depths in the absence of a deluge, with values near zero at 20–30 cm (Fig. 4). Applying a deluge during drought increased BNPP across all soil depths, although this response was only statistically significant in the 20–30 cm layer ($p = 0.029$). BNPP increased by approximately 136% in the 0–10 cm layer, 827% in the 10–20 cm layer, and substantially in the 20–30 cm layer following the deluge treatment. The largest BNPP values under drought occurred in the deepest soil layer in plots receiving a deluge.

3.3 Root Trait Responses

3.3.1 Specific Root Length (SRL)

Specific root length (SRL) differed among treatments depending on previous moisture conditions (Fig. 6). Under ambient conditions, SRL did not differ between plots with and without a deluge ($p > 0.05$). Under drought conditions, however, applying a deluge resulted in substantially higher SRL compared to drought alone ($p < 0.001$), with increases of approximately 700–800%. SRL was also lower in drought plots than in ambient plots under no-deluge conditions ($p < 0.001$).

3.3.2 Root Tissue Density (RTD)

Root tissue density (RTD) responded to deluge differently under ambient and drought conditions (Fig. 7). Under ambient conditions, RTD increased by approximately 85% in response to a deluge ($p < 0.01$). In contrast, when a deluge was applied during drought, RTD

decreased by approximately 50–55% relative to drought alone ($p < 0.01$). RTD was also higher in drought plots than in ambient plots under no-deluge conditions ($p = 0.007$).

4. DISCUSSION

In this study, we examined how compound climate extremes, specifically an extreme deluge event occurring during the second year of extreme drought, affected belowground productivity and root functional traits across soil depths in the semi-arid shortgrass steppe, an ecosystem highly sensitive to variation in precipitation regimes Belowground responses to these treatments revealed three primary patterns. First, prolonged drought strongly suppressed BNPP and shifted root systems toward more conservative strategies, characterized by lower specific root length (SRL) and higher root tissue density (RTD), consistent with increased resource limitation. Second, the addition of a deluge during drought substantially increased BNPP and reversed drought-induced trait shifts, promoting more acquisitive root strategies. However, BNPP remained lower than ambient levels, indicating the lack of complete recovery following the deluge event. Finally, root responses to deluge varied with soil depth and moisture history, with shallow soils responding most strongly under ambient conditions and deeper soils responding more strongly under drought. Overall, these results demonstrate that compounded drought-deluge events influence not only the magnitude of belowground productivity, but also the spatial distribution and functional strategies of root systems, highlighting the overriding importance of drought in shaping ecosystem responses to climate variability.

4.1 Drought reduces BNPP and promotes conservative root traits

An experimentally induced, two-year drought substantially reduced BNPP relative to the control treatment. This pattern is consistent with previous work showing that drought suppresses productivity in grasslands and can reduce root biomass, root length, and belowground production, especially when droughts are intense or sustained over longer periods

(Hoover et al., 2022; Poorter et al., 2012; Slette et al., 2023; Zhou et al., 2018). In the shortgrass steppe, ecosystem responses are tightly linked to soil moisture dynamics, and previous work at CPER has shown that drought dramatically reduces ecosystem productivity and carbon cycling responses relative to ambient precipitation conditions (Hoover et al., 2022; Knapp et al., 2015a).

Drought effects on BNPP were also evident across soil depth. In both mid-season and full-season cores, BNPP declined with depth under drought, with very limited root production in deeper soil layers. Some decline with depth is expected in grasslands, where root biomass and production are often concentrated near the soil surface (Gill and Jackson, 2000; Jackson et al., 1996). However, the near absence of deeper root biomass under drought suggests that deeper soil layers were especially affected. These findings are consistent with pulse-based frameworks for semi-arid ecosystems, where small precipitation events often wet shallow soil layers but may not recharge deeper portions of the rooting zone, especially under high evaporative demand (Knapp et al., 2008; Sala et al., 1988; Schwinning and Sala, 2004).

Drought also shifted root traits toward a more conservative strategy, with lower SRL and higher RTD relative to ambient conditions. These traits are widely used to describe root functional strategies, where higher SRL reflects greater efficiency in soil exploration and resource acquisition per unit biomass, while higher RTD indicates greater structural investment and longer tissue persistence (Freschet et al., 2021b; Garbowski et al., 2023; Lupini et al., 2018). Such shifts are consistent with drought tolerance strategies, where plants invest in denser, longer-lived root tissues that enhance persistence and reduce turnover under prolonged water limitation, rather than maximizing rapid resource uptake. Similar drought-induced shifts toward increased root diameter, reduced SRL, or greater structural investment have been observed across grassland systems, although responses are highly variable depending on species identity and environmental context (Lozano et al., 2020; Ostonen et al., 2007; Ryser, 2006; Zhou et al., 2018). This variability highlights that root trait responses do not follow a single

axis, but instead reflect multiple strategies, with plants shifting between drought avoidance and drought tolerance depending on the severity and duration of water stress.

4.2 Deluge during drought stimulated root productivity and reversed drought-induced trait shifts

A mid-season deluge significantly increased BNPP when applied during drought. Despite this increase, BNPP remained below ambient levels and did not rescue productivity as hypothesized. A similar response was reported in a compound drought–deluge experiment, where a large precipitation event stimulated ecosystem processes but did not fully offset productivity losses associated with drought (Hoover et al., 2022). Large precipitation events have been shown to stimulate productivity in semi-arid grasslands (Knapp et al., 2008; Post and Knapp, 2020; Schwinning and Sala, 2004; Wilcox et al., 2015), but the results of this study demonstrate that the magnitude and distribution of that response can depend strongly on antecedent conditions, event timing, and the continuation of drought conditions after the deluge event.

Deluge effects also varied strongly with soil depth during drought conditions. In full-season cores, deluge during drought increased BNPP across the entire 0–30 cm profile, indicating that the pulse stimulated root production throughout the measured rooting zone. This pattern aligns with previous work in the same system showing that large precipitation pulses can increase soil moisture deeper in the rooting zone, whereas smaller precipitation events primarily influence surface soil layers (Hoover et al., 2022). More broadly, dryland pulse frameworks suggest that larger events generate deeper and longer-lasting soil moisture availability, allowing biological activity to extend beyond surface soils (Knapp et al., 2008; Schwinning and Sala, 2004).

The mid-season cores showed a more deluge-driven response. Under drought, deluge significantly increased BNPP only in the deepest layer, suggesting that deeper soil layers were

most responsive during the shorter post-deluge window. This pattern reflects the importance of pulse duration, as deeper soil layers often retain water longer than surface soils (Knapp et al., 2008; Schwinning and Sala, 2004). Additionally, short-lived pulses may primarily enhance activity of existing root systems rather than drive substantial new root production, limiting responses in shallow soils when moisture is rapidly lost (Lauenroth et al., 1987).

In contrast, mid-season ambient plots responded across all depths, with the strongest response in the shallowest layer, indicating that prior moisture conditions influenced where in the soil profile root production responded most strongly to the pulse. Under ambient conditions, where roots were less water-limited, the addition of water may have been more readily utilized in surface soils, resulting in a stronger shallow response compared to drought conditions (Hoover et al., 2022; Knapp et al., 2008; Schwinning and Sala, 2004).

These changes in productivity were accompanied by clear shifts in root functional traits. Deluge during drought strongly shifted root traits toward more acquisitive strategies, with substantial increases in SRL and simultaneous decreases in RTD relative to drought alone. Together, these changes reflect increased investment in resource acquisition following the pulse. Similar responses have been observed under increased resource availability, where plants often produce thinner, less dense roots associated with greater resource uptake capacity (Freschet et al., 2021b; Ostonen et al., 2007; Poorter et al., 2012; Ryser, 2006; Valverde-Barrantes and Blackwood, 2016). The strength and coordination of this response suggest that roots were highly responsive to the temporary increase in water availability and appeared to maximize exploration for resources.

Ambient plots showed no change in SRL and an increase in RTD following deluge, indicating that trait responses did not uniformly shift toward acquisition when water was not strongly limiting. This contrast reinforces that trait responses to precipitation pulses depend strongly on antecedent conditions. More broadly, root traits are increasingly recognized as multidimensional, with SRL and RTD not always varying together or along a single acquisitive–

conservative axis (Freschet et al., 2021a; Garbowski et al., 2020; Kramer-Walter et al., 2016; Lozano et al., 2021; Valverde-Barrantes et al., 2017; Zhou et al., 2018), which helps explain why responses differed between drought and ambient treatments.

4.3 Limitations

While our results show clear differences in BNPP and root trait responses to drought-deluge conditions when compared to deluge alone or ambient conditions, it is important to consider several potential limitations when interpreting the results from this study. First, the use of root ingrowth cores likely introduced some degree of soil disturbance, which may have influenced estimates of belowground productivity. Installation of cores disrupts existing root systems and soil structure, potentially reducing root growth during the early stages of recolonization. This effect was likely most pronounced in the mid-season cores, which were installed immediately prior to the deluge and had a relatively short period for root development. As a result, the low root production observed in these cores under both drought and ambient conditions may partially reflect methodological constraints rather than purely ecological responses. In contrast, full-season cores were installed earlier in the growing season, allowing surrounding root systems more time to re-establish and acclimate to the disturbed soil environment. Although there is also evidence that longer-term cores can potentially overestimate BNPP (Milchunas, 2009; Neill, 1992), we do not believe that this was likely given the amounts we observed were comparable to other studies in this system (Hoover et al., 2022; Post and Knapp, 2020).

An additional limitation relates to the experimental simulation of the deluge event. Although water was applied to approximate a large precipitation pulse, this approach likely does not fully replicate natural rainfall. Water was added over a relatively short period to reach a target amount, rather than following the temporal patterns typical of natural precipitation events. Also, the application occurred during sunny conditions, where evaporative demand may have

been relatively high compared to conditions during natural storm events. These factors may have influenced how water was retained and distributed in the soil, potentially affecting the magnitude and duration of soil moisture availability. As a result, the productivity and root trait responses observed with our study may differ from those generated by natural rainfall events of similar magnitude and during naturally occurring drought events.

Another important consideration is that root morphological traits can vary with root developmental stage and age, which may influence interpretations of belowground functional strategies (Freschet et al., 2021; Valverde-Barrantes and Blackwood, 2016). Because ingrowth cores measure newly produced roots during a defined sampling period, observed differences in traits may partially reflect differences in root ontogeny rather than solely treatment-induced shifts in root strategies. This consideration may be particularly relevant for mid-season cores, where roots had a shorter growth period following installation and may represent younger root populations compared to full-season cores. However, because all treatments were sampled over the same time period, relative differences among treatments likely reflect responses to altered water availability. Future studies incorporating direct measurements of root age, lifespan, and turnover would provide additional insight into how drought-deluge events influence belowground carbon dynamics (Gill et al., 2002; Freschet et al., 2021).

4.4 Implications and Future Directions

The results of this study show that compounded drought-deluge conditions can fundamentally alter belowground productivity, an important component of carbon cycling, in semi-arid grasslands. The shift toward more acquisitive root traits under drought followed by a large precipitation pulse, specifically higher specific root length and lower root tissue density, suggests a transition toward root systems that are shorter-lived and more dynamic. Roots with higher specific root length and lower tissue density are generally associated with faster turnover and shorter lifespans (Freschet et al., 2021a; McCormack et al., 2015). In shortgrass steppe

systems, root longevity varies strongly with morphology, with finer roots exhibiting substantially shorter lifespans and higher turnover rates than thicker roots (Gill et al., 2002). These patterns suggest that carbon entering the soil through root production under these conditions may cycle more rapidly rather than being retained long-term. Because soil carbon storage is governed by the balance between carbon inputs and turnover rates (Todd-Brown et al., 2013), increases in root turnover may reduce carbon residence time even when belowground production increases. While root-derived carbon is often considered an important and relatively stable component of soil organic matter (Rasse et al., 2005), these results suggest that faster cycling may limit long-term carbon storage under compound climate extremes. More broadly, this points to a potential decoupling between belowground productivity and soil carbon storage, where increases in root production do not necessarily translate to greater carbon accumulation due to faster turnover rates.

Antecedent drought conditions also play a central role in shaping the belowground responses to deluge events. Even after the deluge, belowground productivity did not return to ambient levels, indicating that prior drought conditions continued to constrain plant function. Similar patterns have been observed in other systems, where drought reduces root production, with those effects persisting beyond the duration of the drought (Slette et al., 2023). These results suggest that while semi-arid grasslands may respond rapidly to precipitation pulses, their capacity for full recovery (or rescuing of functioning) in the context of prolonged drought is limited. This combination of strong pulse responses and incomplete recovery may lead to even greater interannual variability in ecosystem productivity, which is a signal that has been observed more broadly for dryland ecosystems globally (Schwalm et al., 2012). These findings also highlight a limitation of using belowground productivity alone as an indicator of ecosystem carbon storage. While precipitation pulses can increase BNPP, the fate of these inputs depends on turnover rates and subsequent processing in the soil. As a result, increases in belowground

production do not necessarily indicate increased carbon storage, particularly in situations where shifts in root traits may lead to rapid root turnover.

There are several clear directions for future work that result from this study. First, while specific root length and root tissue density are useful measurements, they do not fully capture root function. Root traits are multidimensional, and these traits can vary independently depending on environmental drivers (Valverde-Barrantes et al., 2017). Future studies should incorporate a broader set of traits, including root diameter distributions, branching structure, lifespan, and chemical composition, to better link root structure to processes such as turnover and decomposition.

Second, it is important to better understand how drought intensity and duration influence these responses. Root responses to drought vary widely depending on the severity and duration of water limitation (Guasconi et al., 2023). The drought imposed in this study was severe, and it is possible that plants approached a threshold where root production was strongly constrained. Future experiments that manipulate both drought intensity and duration would help identify these thresholds and clarify how systems transition from functional resilience to physiological limitation.

Additionally, incorporating mycorrhizal fungi into future work would add an important component that is not captured here. Root traits are strongly influenced by interactions with soil microbial communities, particularly mycorrhizal fungi, which can alter root morphology, extend resource acquisition, and influence belowground carbon allocation (Sweeney et al., 2021). There is growing recognition that integrating mycorrhizal dynamics into root trait studies is necessary to fully understand belowground function, as plant–fungal interactions can substantially influence both resource uptake and carbon cycling. Including measures of mycorrhizal colonization and fungal community composition would provide a more mechanistic understanding of the patterns observed in this study.

These findings also have implications for grassland management under increasingly variable precipitation regimes. Semi-arid grasslands have historically experienced severe drought events, such as the Dust Bowl, that can alter plant community composition and reduce forage availability for extended periods. Our results suggest that while large precipitation events may stimulate belowground production following drought, they may not fully eliminate drought legacies within a single growing season. Therefore, management decisions following drought, such as expectations of ecosystem recovery and forage availability, should consider not only immediate precipitation responses but also the potential for persistent belowground effects. Understanding how drought history influences recovery following large rainfall events may improve predictions of grassland resilience and inform adaptive management strategies under future climate variability.

Finally, these results suggest that current ecosystem and Earth system models may not adequately capture drought legacy effects, depth-dependent root production responses, or trait-mediated shifts in root turnover following drought-deluge events. Incorporating these processes into models will be important for improving predictions of carbon cycling under increasingly variable precipitation regimes. At the ecosystem scale, increasing climate variability may shift semi-arid grasslands toward systems characterized by faster carbon cycling, stronger pulse dependence, and incomplete recovery following stress. Understanding how these processes interact will be critical for predicting ecosystem function under a future climate dominated by hydroclimatic extremes.

5. FIGURES

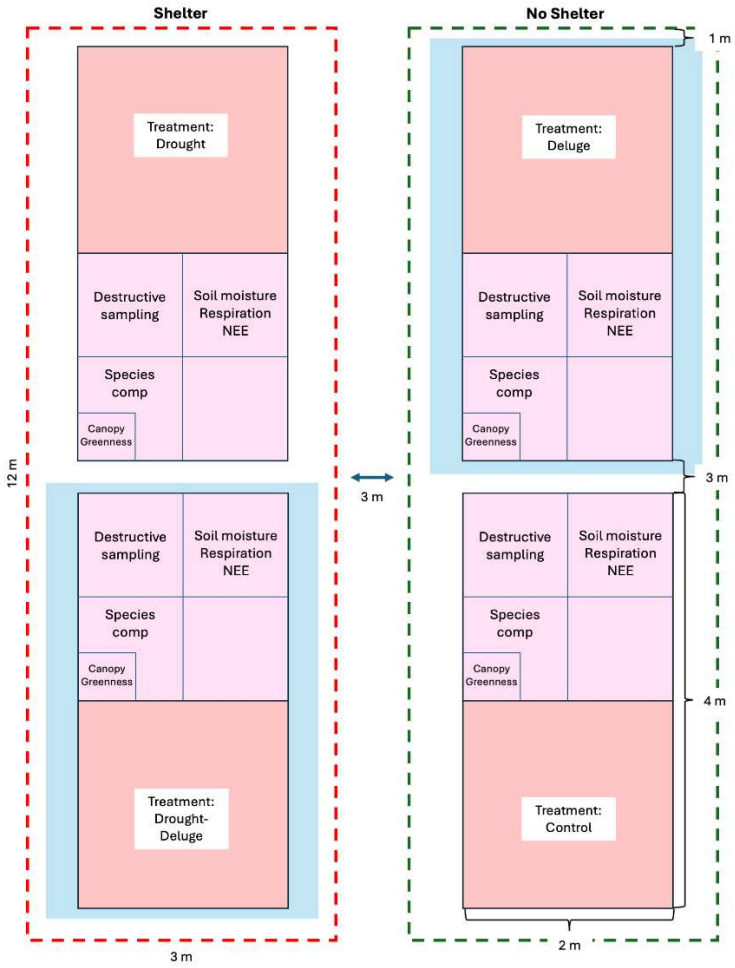

Figure 1. Schematic representation of one of ten experimental blocks in the compound climate extremes experiment at the Central Plains Experimental Range (CPER), Colorado, USA. Treatment locations were randomized within each block. The experiment consisted of four precipitation treatments arranged in a randomized complete block design: control (ambient precipitation), deluge, drought, and drought + deluge. Rainout shelters were installed over drought and drought + deluge plots (dashed red line) to reduce incoming precipitation by approximately 67%, while control and deluge plots remained unsheltered (dashed green line). Each experimental plot measured 2 × 4 m and was subdivided into subplots used for destructive sampling, soil moisture and respiration measurements, net ecosystem exchange (NEE), species composition surveys, and canopy greenness measurements. Plots within shelter and no-shelter treatments were separated by buffer areas to minimize hydrological interference among treatments.

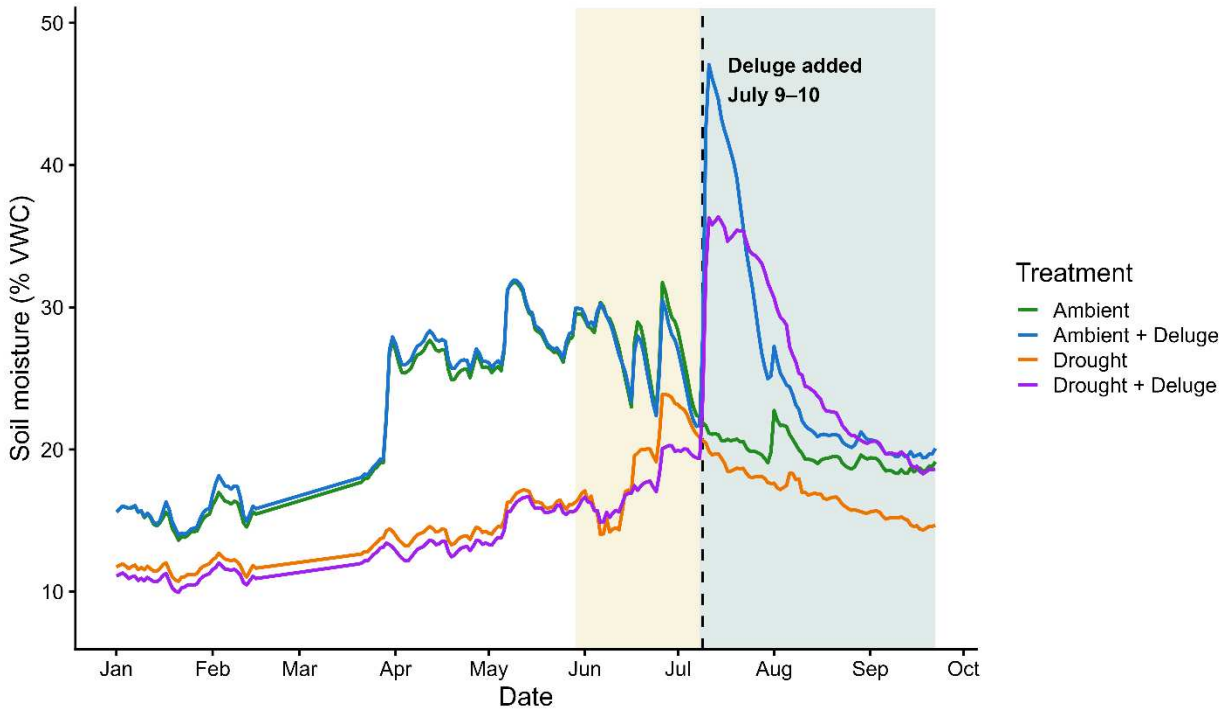

Figure 2. Daily mean soil moisture (% volumetric water content, VWC) across control and drought treatments with and without a deluge addition during the 2025 growing season. Lines represent treatment means averaged across soil moisture sensors installed within each treatment. The pale yellow shaded region indicates the full-season ingrowth core incubation period beginning May 29, while the pale blue shaded region indicates the mid-season ingrowth core incubation period beginning July 8. The dashed vertical line marks the timing of the simulated 60-mm deluge event applied on July 9–10.

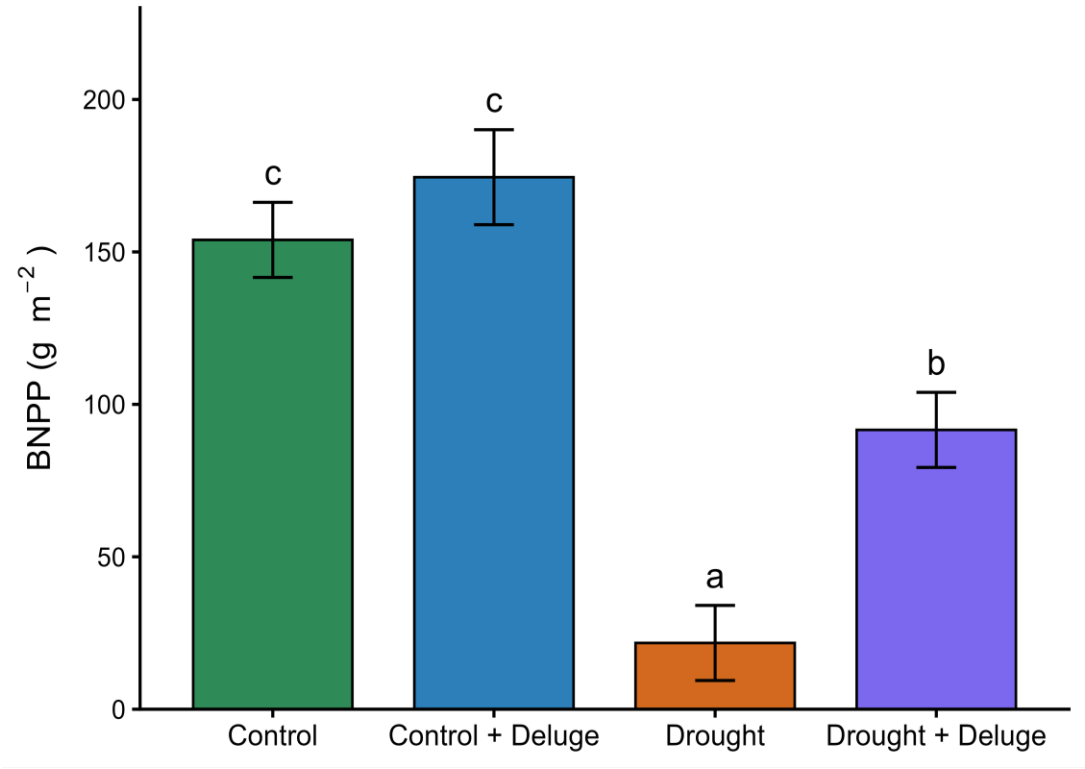

Figure 3. Full-season whole-core belowground net primary productivity (BNPP; g m^{-2}) across treatments. Bars represent mean ± SE. Different letters indicate significant differences among treatments ($p < 0.05$).

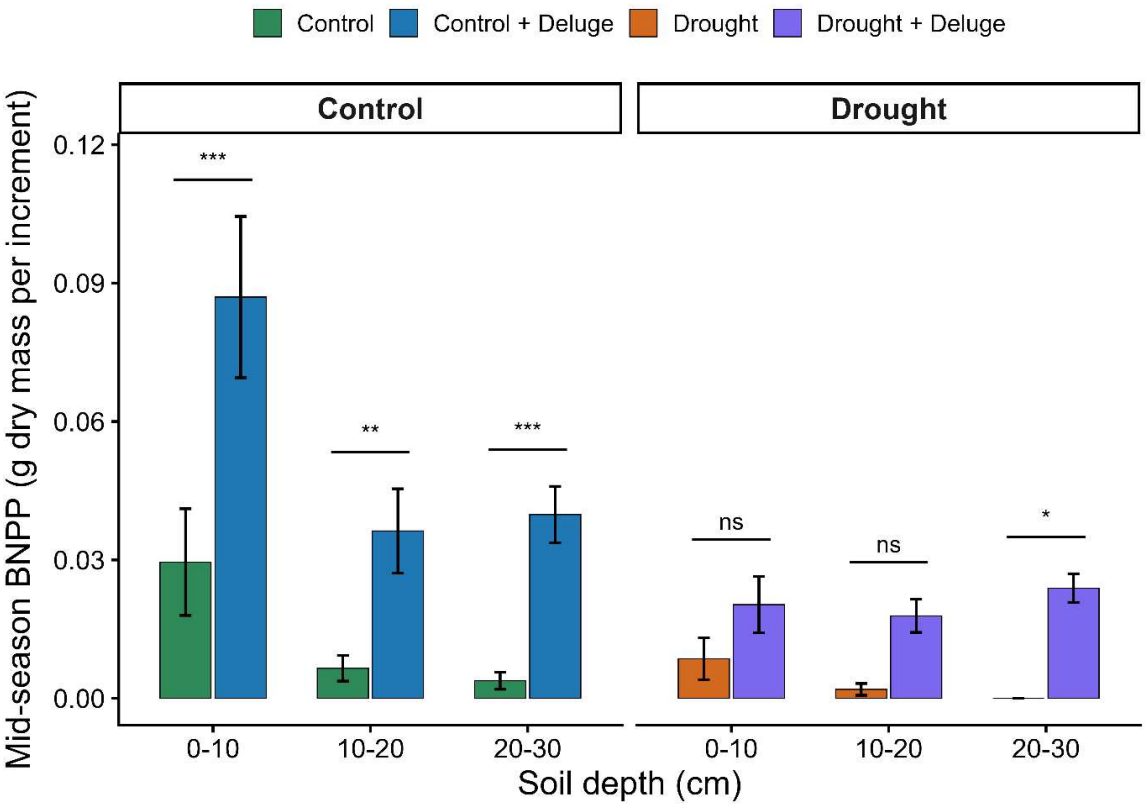

Figure 4. Mid-season belowground net primary productivity (BNPP; g dry mass per increment) across soil depths (0-10, 10-20, and 20-30 cm) under ambient (Control) and drought conditions with and without a deluge treatment. Bars represent mean ± SE. Asterisks indicate significant differences between deluge and non-deluge treatments within each depth and moisture condition (*p < 0.05, **p < 0.01, ***p < 0.001; ns = not significant).

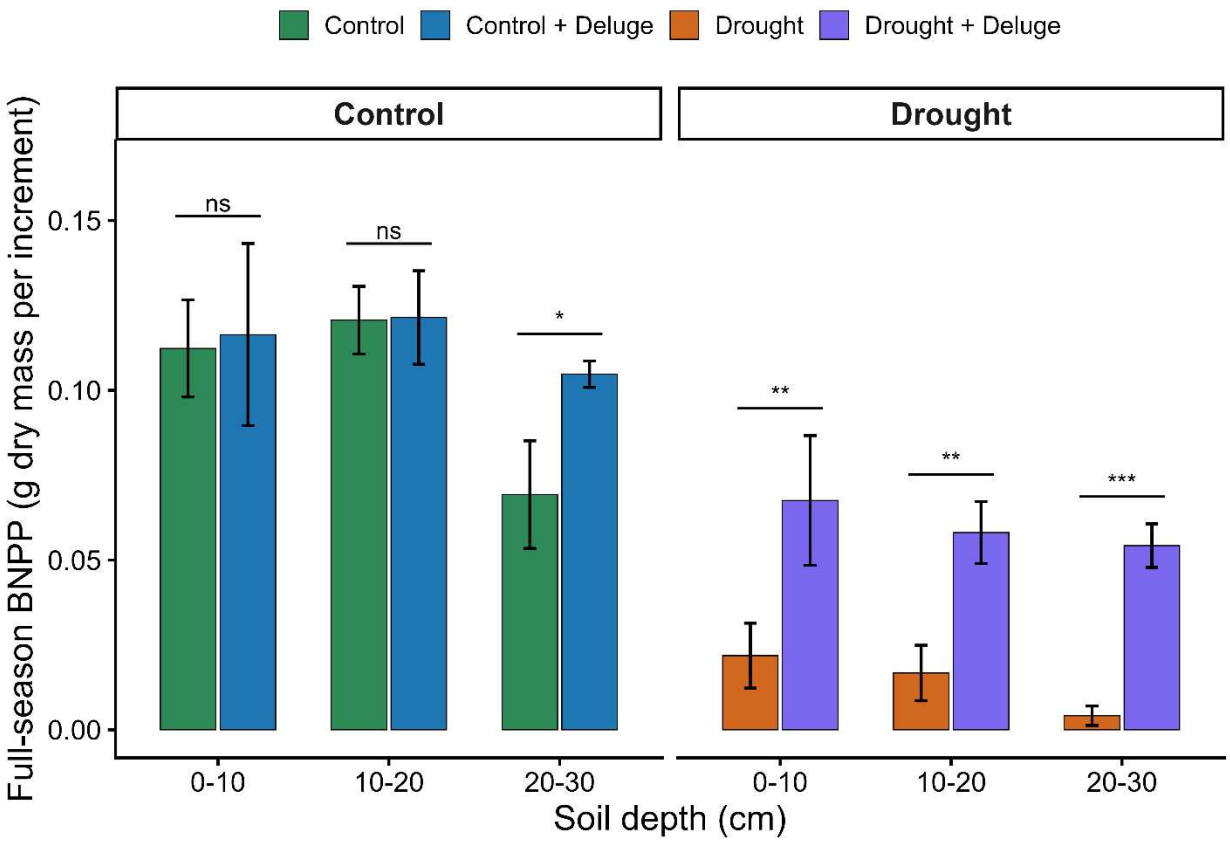

Figure 5. Full-season belowground net primary productivity (BNPP; g dry mass per increment) across soil depths (0-10, 10-20, and 20-30 cm) under ambient (Control) and drought conditions with and without a deluge treatment. Bars represent mean ± SE. Asterisks indicate significant differences between deluge and non-deluge treatments within each depth and moisture condition (*p < 0.05, **p < 0.01, ***p < 0.001; ns = not significant).

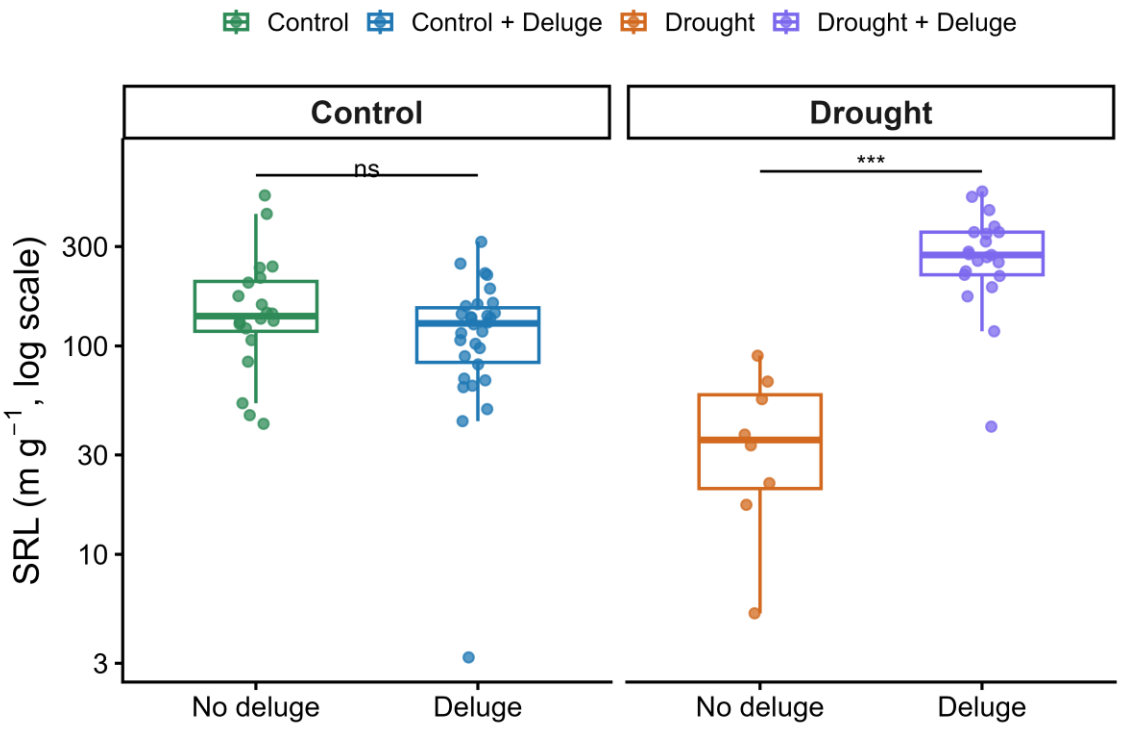

Figure 6. Specific root length (SRL; m g^{-1}, log scale) under ambient (Control) and drought conditions with and without a deluge treatment. Boxplots show median, interquartile range, and individual observations. Asterisks indicate significant differences between deluge and non-deluge treatments within each moisture condition (***$p < 0.001$; ns = not significant).

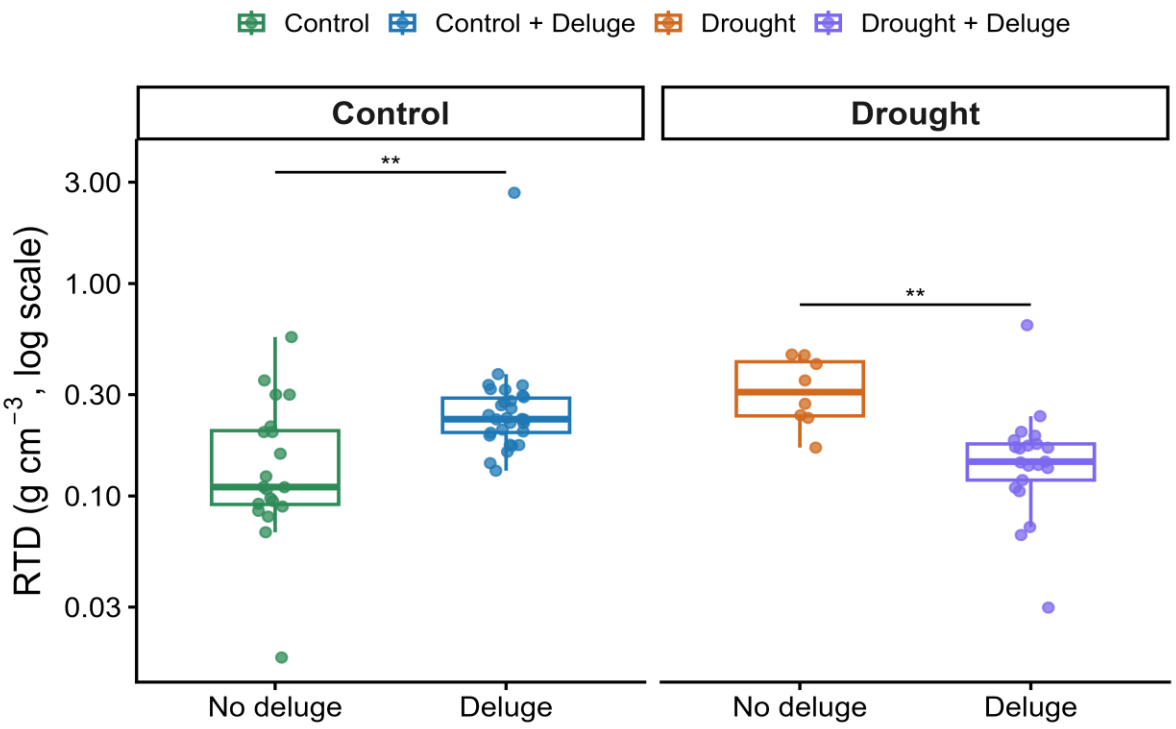

Figure 7. Root tissue density (RTD; g cm^{-3}, log scale) under ambient (Control) and drought conditions with and without a deluge treatment. Boxplots show median, interquartile range, and individual observations. Asterisks indicate significant differences between deluge and non-deluge treatments within each moisture condition (**p < 0.01).

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APPENDIX

Table A1. Type III ANOVA results from linear mixed-effects models examining the effects of drought, deluge, and soil depth on belowground net primary productivity (BNPP), specific root length (SRL), and root tissue density (RTD). Full-season whole-core BNPP was analyzed at the core level, while full-season and mid-season BNPP by depth were analyzed across soil depth increments. Numerator degrees of freedom (Num df), denominator degrees of freedom (Den df), sums of squares (Sum Sq), F-values, and p-values are shown for fixed effects. SRL and RTD were log-transformed prior to analysis.

Source	Num df	Den df	Sum Sq	F-value	p-value
Full-season BNPP by depth					
Drought	1	29.00	0.047	66.31	<0.001
Deluge	1	29.00	0.008	11.72	0.002
Depth	2	58.00	0.008	5.93	0.005
Drought × Deluge	1	29.00	0.002	3.49	0.072
Drought × Depth	2	58.00	0.002	1.64	0.203
Deluge × Depth	2	58.00	0.002	1.32	0.275
Drought × Deluge × Depth	2	58.00	0.001	0.57	0.567
Full-season whole-core BNPP					
Drought	1	29.00	80458.346	66.31	<0.001
Deluge	1	29.00	14224.868	11.72	0.002
Drought × Deluge	1	29.00	4231.060	3.49	0.072
Mid-season BNPP by depth					
Drought	1	36.80	0.005	14.42	<0.001
Deluge	1	36.80	0.008	26.15	<0.001
Depth	2	73.82	0.010	15.32	<0.001
Drought × Deluge	1	36.80	0.001	4.25	0.046
Drought × Depth	2	73.82	0.007	10.52	<0.001
Deluge × Depth	2	73.82	0.001	0.95	0.391
Drought × Deluge × Depth	2	73.82	0.002	2.66	0.076
Root tissue density					
Drought	1	34.00	0.185	0.72	0.402
Deluge	1	34.00	0.061	0.24	0.628
Drought × Deluge	1	34.00	4.605	17.94	<0.001
Specific root length					
Drought	1	36.92	1.213	2.80	0.103
Deluge	1	36.92	10.291	23.75	<0.001
Drought × Deluge	1	36.92	17.120	39.51	<0.001