Thermography captures the differential sensitivity of dryland functional types to changes in rainfall event timing and magnitude

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Introduction

Climate warming is driving the intensification of the global hydrologic cycle, increasing the frequency and intensity of extreme weather events (Dai, 2013; Madaukumbura et al., 2019), with critical yet poorly known consequences for ecosystem structure and function (Weiskopf et al., 2020). In particular, drylands of the western United States are experiencing shifts toward larger, less frequent rainfall events interspersed by longer intervals of dry days (Bradford et al., 2020; Zhang et al., 2021). Drylands are predominately driven by water availability, and thus such ‘temporal repackaging’ of precipitation can profoundly alter the range, magnitude, and variability of ecosystem carbon uptake (i.e. gross primary productivity (GPP)), and water loss to the atmosphere (i.e. evapotranspiration (ET)). The seasonal and mechanistic controls on these key ecosystem functions are particularly difficult to elucidate in dryland ecosystems composed of heterogenous plant functional types (PFTs), pulse-driven moisture dynamics, and the diverse biological strategies for dealing with water stress (Kushwaha et al., 2011; Collins et al., 2014; Bradford et al., 2017).

Plant temperature is a promising trait for indexing GPP and ET because temperature is essential for optimum plant function (Farquhar et al., 1980; Guo et al., 2022) and is intrinsically connected to GPP, ET, and surface energy balance (Brown & Escombe, 1905; Farella et al., 2022). Dryland plants cool to a minimum temperature in response to rainfall pulse events due to increases in latent heat flux driven by soil evaporation and plant transpiration. They then warm to a maximum temperature with reductions in latent heat flux as soils dry, plant available water is depleted, and transpiration ceases (Noy-Meir, 1973; Fu et al., 2022b). High transpiration rates cool the plant surface

Summary

- Drylands of the southwestern United States are rapidly warming, and rainfall is becoming less frequent and more intense, with major yet poorly understood implications for ecosystem structure and function. Thermography-based estimates of plant temperature can be integrated with air temperature to infer changes in plant physiology and response to climate change. However, very few studies have evaluated plant temperature dynamics at high spatiotemporal resolution in rainfall pulse-driven dryland ecosystems.
- We address this gap by incorporating high-frequency thermal imaging into a field-based precipitation manipulation experiment in a semi-arid grassland to investigate the impacts of rainfall temporal repackaging.
- All other factors held constant, we found that fewer/larger precipitation events led to cooler plant temperatures (1.4°C) compared to that of many/smaller precipitation events. Perennials, in particular, were 2.5°C cooler than annuals under the fewest/largest treatment.
- We show these patterns were driven by: increased and consistent soil moisture availability in the deeper soil layers in the fewest/largest treatment; and deeper roots of perennials providing access to deeper plant available water. Our findings highlight the potential for high spatiotemporal resolution thermography to quantify the differential sensitivity of plant functional groups to soil water availability. Detecting these sensitivities is vital to understanding the ecohydrological implications of hydroclimate change.
relative to ambient conditions (Gates, 1968), whereas low rates of transpiration results in more energy partitioned to sensible heat flux, resulting in plant temperatures exceeding air temperature (Miller et al., 2021). Differences between plant and air temperature can therefore be used to infer plant water stress and downregulation of physiological processes and have been used to assess plant moisture stress across spatiotemporal scales (Anderson et al., 2007, 2008; Kustas et al., 2007). For instance, Green et al. (2022) used the ratio of remotely sensed land surface to near surface atmospheric temperatures (LST/$T_{air}$) to represent vegetation water stress. Using this index, they found GPP can be reduced by up to 80% in water limited regions when critical thresholds for precipitation and air dryness are exceeded simultaneously.

Plant temperatures are expected to remain relatively cooler for longer durations as rainfall pulse event size increases (Feldman et al., 2021). However, fluctuations in water availability within the soil profile may differentially influence PFTs with diverse hydraulic traits (Zhang et al., 2022). For example, PFTs in water-limited ecosystems were found to vary widely in rooting depth and distribution and to display differential sensitivity to soil moisture at different depths (Schwinning & Sala, 2004; Zhang et al., 2022). Deeper infiltration of precipitation into the soil profile under large rainfall pulses may favor deeper-rooted perennial plants over shallow-rooted annual grasses and forbs under prolonged dry intervals since root depth can produce important variation in water accessibility (Schwinning & Ehleringer, 2001). Plants that share common functional traits may, as a group, respond differently to precipitation variability relative to other groups, with the ecosystem response corresponding to the abundance-weighted response of the individual groups (Gherardi & Sala, 2015; Cooley et al., 2022). Yet, capturing plant temperature for multiple PFTs at relatively fine spatiotemporal scales and without background effect remains a major challenge.

Thermography, in other words, thermal infrared imaging, can be used to measure plant temperatures with high spatiotemporal frequency and has been utilized at scales ranging from towers (Kim et al., 2016; Johnston et al., 2021) and drones (Still et al., 2019; Javadian et al., 2022), to satellites (Bayat et al., 2018; Fisher et al., 2020). Previous studies have found that, when coupled with eddy covariance flux measurements of GPP, high accuracy and precision plant temperature measurements from thermal infrared cameras at the tower level can help identify plants experiencing heat and water stress and are crucial to differentiating plant and air temperature (Coates et al., 2015; Buitrago et al., 2016). For example, using thermal cameras on eddy covariance towers, Still et al. (2022) found the peak of GPP occurred when canopy leaves were warmer than air across four forest sites. Thermal imaging of plots in the context of global change experiments has the potential to reveal novel insights into dryland structural and functional responses, yet such imaging has been underutilized by the experimental community (Shilkomanov et al., 2019; Aparecido et al., 2020; Blonder et al., 2020).

Here, we address this research gap by integrating high spatiotemporal resolution thermography into an experimental manipulation evaluating the ecological consequences of a climatic shift toward fewer, larger precipitation events. We utilized the intensively instrumented Rainfall Manipulation facility in the Santa Rita Experimental Range (RainManSR) in Southern Arizona, USA, which was designed to fully control precipitation over 60 hydrologically isolated plots. Each plot initially contained relatively equal mixtures of multiple semi-arid PFTs, including annual and perennial grasses, forbs, and shrubs (Fig. 1). Following anticipated and already observed climatic changes, hydroclimate disturbance treatments focused on the consequences of fewer, larger vs more, smaller precipitation events without changing the mean seasonal precipitation of 205 mm (Zhang et al., 2022). The precipitation treatments are as follows: S1 (many/small with 3.5-d dry intervals), S2 (climatic normal average with 7-d dry intervals), S3 (few/large with 14-d dry intervals), and S4 (fewest/largest with 21-d dry intervals). We utilized measurements of surface radiant temperature from a high-resolution thermal camera with 2 mm spatial resolution and a daily temporal repeat frequency for the 3-d period following irrigation to capture in detail the plant temperature pulse response. We continued to collect thermal images at a reduced temporal frequency for the duration of the experiment resulting in an average frequency of 3 d. To facilitate comparison between plots and functional groups, we calculate and analyze relative anomalies in surface temperature over the irrigation pulse event. In addition, we incorporate ancillary data on PFT fractional cover, soil moisture at multiple depths, root area at multiple depths, and plot-level GPP and ET.

Our main objective with this research was to evaluate plant temperature dynamics at high spatiotemporal resolution in a rainfall pulse-driven dryland ecosystem. In our research, we explicitly tested the following three hypotheses. (1) Precipitation repackaging will change the soil water profile and result in significant differences in relative soil and plant temperature due to changes in evaporation and transpiration. (2) Irrigation-driven increases in GPP and ET will be associated with similar magnitude reductions in relative plant temperature due to associated increase in latent heat flux. (3) Perennial plants relative to annual plants will maintain higher rates of transpiration and relatively cooler plant temperatures under larger/fewer precipitation events since these events will result in more plant available water in deeper soil layers which perennials can access through relatively deeper roots.

Materials and Methods

Site description and experimental setup

This experiment was conducted at the Rainfall Manipulation in the Santa Rita Experimental Range (RainManSR) experimental facility (31.79°N, 110.90°W, 1075 m asl). The mean annual temperature (2004–2018) is c. 19.0°C, with daytime maximum temperature often exceeding 35°C in June (Scott et al., 2009; Zhang et al., 2022). The mean annual precipitation (2004–2018) is 384 mm, c. 50–60% of which arrives during the summer growing season associated with the North American Monsoon (July–September) (Roby et al., 2020). Soils at the site are deep,
well-drained sandy loams (72% sand, 13% clay, and 15% silt) and do not vary considerably across the site, where all experimental plots were within 140 m of one another. The extant ecosystem is savanna, with widely spaced *Prosopis velutina*, *Senegalia greggii*, and *Celtis pallida* the most common woody species and a sparse understory of non-native and native C₄ perennial bunchgrasses (*Eragrostis lehmanniana*, *Digitaria californica*, *Heteropogon contortus*) interspersed with a seasonally dynamic community of C₄ annual grasses (*Bouteloua barbata*, *B. aristidoides*, *Aristida adscensionis*) and C₃ forbs (*Evolvulus arizonicus*, *Solanum elaeagnifolium*, *Eriogonum abertianum*, *Machaeranthera tanacetifolia*) (Zhang et al., 2022). All experimental blocks are located in grassland community spaces between woody plants. The experiment used a randomized block design, with each of five rainout shelters considered a block, and 4 target plots from 12 plots, measuring 1.2 m × 1.5 m, spatially randomized under each shelter with a total of 20 target plots that include five from each precipitation treatment (Supporting Information Fig. S1).

Experimental shelters (GrowSpan Greenhouse Structures), built in 2019, utilized a semi-circular 'hoop house' style with dimensions of 4.3 m in width, 22 m in length, and a maximum height of 2.5 m. These shelters were covered with a transparent greenhouse film (Lumite Inc.) that allowed for 92% of photosynthetically active radiation to penetrate and all plots were sheltered uniformly. We also installed flashing to a depth of 1 m around all plots to ensure hydraulic isolation. In addition, hardware fabric with a 1.2 cm mesh was installed around each shelter up to a height of 1 m and a depth of 0.3 m below the surface to prevent disturbance from rodents and lagomorphs, while still allowing access to small reptiles, arthropods, and soil macroinvertebrates. The rainout shelters had a minimal environmental impact, as demonstrated by the slight changes in air temperature and relative humidity (Fig. S2). The shelters were equipped with gutters to collect precipitation, which was subsequently utilized for all irrigation treatments (Zhang et al., 2022).

This experiment only altered the dry interval duration and frequency of precipitation events while maintaining constant summer monsoon season precipitation of 205 mm, equivalent to the c. 45-yr mean (1975–2019). Within the context of a 45-yr climate record for this location, the durations of dry intervals were fixed for each precipitation treatment as follows: 3.5 d (S1, many/small), 7 d (S2, 30-yr climatic normal), 14 d (S3, few/large), and 21 d (S4, fewest/largest). For a complete site description and the experimental setup, see Zhang et al. (2022).
Data collection
Thermal imaging Thermal infrared imagery of 20 selected plots (Fig. S1) was captured during 20 d of summer 2021 using an ICI 9640 thermal camera with a 2 m stand. We focused the experiment on a rainfall pulse event occurring near the peak of the growing season over the period August 16, 2021 to September 22, 2021. We utilized a daily image collection at the start of the irrigation pulse to capture the rapid response of the vegetation, and then reduced the image collection frequency to every 2 to 3 d as pulse sensitivity diminished (Table S1). Thermal images of House 1, 3, 5, 4, and 2 were captured at 9:15 h, 9:45 h, 10:15 h, 10:45 h, and 11:15 h, respectively, during the entire experiment (Table S2). While each plot had a different image capturing time, the mean capturing time for each treatment was 10:15 h to avoid time-of-day bias and capture peak diurnal grass function. Fixed plot sampling times were utilized to minimize the impact of diurnal canopy temperature dynamics on our estimates of multi-day irrigation pulse response. The camera spectral range was 7–14 μm, pixel resolution was 640 × 512, thermal sensitivity was 0.02°C, focal length was 12.5 mm, and sensor width was 7.5 mm. The spatial resolution of the thermal images on the ground was 2 mm (calculated using: stand height × sensor width/focal length × image width). To estimate surface temperature, we applied a fixed emissivity value of 0.97 for all thermal images collected over the duration of the study. We derived this value from previous measurements of emissivity within a grassland site (Qin & Karnieli, 1999; Meng et al., 2017). We point out that the primary focus of this study is variation of plant temperature over time for a given set of grassland species, rather than the absolute temperature difference across grassland species. As a result, any variations in emissivity across plant types do not impact the findings of our analysis. The camera’s accuracy was assessed using the ICI portable IR calibrator as a temperature reference source device in the laboratory. This sophisticated tool functions as a black body with a target temperature below 70°C, ensuring precise and reliable temperature measurements. The camera was consistently underestimating the temperature by 1.1°C at a 2 m distance from the objects. We applied this correction for all measurements. Our main objective was to determine the average ΔT differences between the treatments, and thus, any potential biases in the estimated surface temperatures would not significantly affect the study outcome. In addition, half-hourly air temperature was measured at 0.9 m height inside one shelter using a HMP45C (Campbell Scientific, Logan, UT, USA) and assumed to be representative of air temperature above all plots. We calculated the difference ‘ΔT’ = Radiant − Air temperature’ using thermal camera imagery and air temperature.

RGB imaging High-resolution (4000 × 6000 pixels) nadir RGB images of each plot were collected using a digital camera (Nikon D3500 DSLR; Nikon Corp., Tokyo, Japan) mounted on a 2-m portable stand. We used these images to classify green vegetation, brown vegetation, and bare soil within each plot (Fig. 1). A support vector machine (SVM) supervised classification method was applied using 60 training polygons per class in each RGB image (Cortes & Vapnik, 1995) (Fig. 1b,d). To perform image registration, we carefully selected recognizable objects from the RGB images that were clearly visible in the thermal images. These objects included the corners and centers of tubes and instruments as well as other narrow features that we could confidently identify (Fig. S3). Because the spatial resolution of the RGB images was higher than that of the thermal images, we upsampled the RGB images to accurately extract the corresponding thermal pixel temperatures. We were able to effectively align the two image types and ensure accurate temperature measurements at both the plot and plant scale using this approach.

Plot-level GPP and ET Whole-plot CO₂ fluxes were measured in light and dark conditions with a closed static chamber (1.3 m wide, 1.0 m tall, 1.6 m long), using an infrared gas exchange analyzer configured for closed-loop measurements (IRGA; LI-6400; Li-Cor Inc.) fitted inside (Huxman et al., 2004; Potts et al., 2006). NEE, GPP, and ET were calculated from these measurements described in Zhang et al. (2022).

Soil moisture In nine selected plots, half-hourly soil moisture and temperature at three depths were measured by time domain reflectometry sensors (12 cm tines, CS655; Campbell Scientific) inserted from the soil surface at a 30° from the nadir, providing an integrated measurement over the top 10 cm of soil, and horizontally into the soil column at 25 and 75 cm depths. Due to cost constraints for the sensors, we prioritized the extreme treatments (S1 and S4) and the intermediate treatment S2.

Root area Root area was measured using a minirhizotron camera. The minirhizotron tubes were installed in 2019, providing a 2-yr period of equilibration prior to the observation period. This interval allows for the necessary adjustment following the initial disturbance associated with tube installation. In all, 32 images were taken to construct a depth profile in all 60 plots using the BTC I-Cap software. The pictures were taken inside of a clear tube that is embedded into the soil at an angle of 45°, reaching a depth of 45 cm. Minirhizotron images were collected to analyze how root structures in each plot change over time. The root data were measured on July 2, July 8, July 22, and August 6, 2021. All 4 d of data have been used in this study.

PFT fractional cover The point frame rests over the entire treatment plot (152 cm × 122 cm). In all, 81 points were determined using string in a 9 × 9 matrix with 12.2 cm spacing between columns and 15.2 cm between rows. At each point, a pin was dropped perpendicular to the soil surface, and the functional type of any plant tissue intercepted from the top of the canopy to the soil surface was recorded. If the pin intercepted leaves from different plants, the functional type of the highest and lowest interception was recorded separately (i.e. ‘top layer’, ‘lower layer’). Each individual plant was only recorded once per point; however, different individuals of the same species/function type can be recorded at the same point. If the pin intercepted no vegetation, only a soil cover type was recorded. We used a single collection
Plant temperature of different PFTs
We defined a region of interest (ROI) dominated by different PFTs inside each plot. We combined the PFTs into two groups: (1) perennial plants including perennial forb and perennial grass; and (2) annual plants including annual forb and annual grass. We excluded shrubs from this life-history classification scheme, since shrubs were relatively infrequent and only present in a few experimental plots. We selected ROIs with at least 10 green vegetation temperature grids (i.e., the pixels that classified as ‘Green Vegetation’ in the classification) during the experiment, and that are not mixed with other PFTs. Due to this limitation in PFT ROIs, we only defined ROIs in four target plots of House 3 (rain out shelter no. 3). Then, using the high-resolution RGB image classification, we extracted the green vegetation temperature inside of each ROI to obtain pure PFT temperatures. The ROIs were constant during the 36 d of the experiment. However, using dynamic RGB image classification from 11 d during the experiment, we were able to consider changes in PFT covers.

Statistical analysis
All analyses were performed in Python v.3.10 (Rossum, 1995). Analysis of variance (ANOVA) test was used to determine statistical significance (Kaufmann & Schering, 2014). ANOVA is a statistical test used to determine whether there is a significant difference among the means of three or more groups. It does this by comparing the variance between groups to the variance within groups. If the variance between groups is significantly greater than the variance within groups, then there is evidence that the means of the groups are different. In this study, significant differences were identified using one-way ANOVA and P values, followed by a pairwise Tukey Honest Significant Differences (Tukey HSD) post-hoc test to compare the effects for each treatment (Tukey, 1949). We chose a confidence level of 0.1 for the pairwise Tukey HSD test to ensure the detection of meaningful differences between treatments in our study on responses to rainfall pulses considering the limitations of our sample size and the objective of our research. To enhance the clarity and rigor of our multivariate analysis, we implemented a standardization process using Z-scores to account for substantial variations in variable ranges across treatments by subtracting the sample mean from the individual measurements and then dividing the difference by the standard deviation across all treatments. The visual comparison of these variables would have otherwise been challenging. By standardizing the variables, we ensured fair and accurate comparisons, enabling us to visualize and interpret the relative differences between treatments with greater precision.

The Plot-level radiant temperature analysis and Plant temperature and ecosystem function analysis are based on 20 target plots from all five houses, but Plant temperature dynamics of key functional types analysis is based on four target plots in House 3 using 11 d of the experiment.

Results
Plot-level radiant temperature
Temporal repackaging of precipitation significantly altered the radiant temperature minus air temperature (ΔT) of green vegetation, brown vegetation, and bare soil (Fig. 2; Table S3). Rainfall treatments did not significantly influence ΔT in S1 and S2 (P>0.1 within treatments, Fig. 2a,b), while it significantly influenced ΔT in S3 and S4 (P<0.05 within treatments, Fig. 2c,d). There was a clear increasing trend through time of ΔT between rainfall pulses in S3 and S4 in which ΔT values were low immediately after rainfall and increased through the interstorm period. For example, the average increase in green vegetation ΔT between two rainfall events was 4.5°C and 6.6°C for S3 and S4, respectively (Fig. 2c,d). The general temporal patterns of different cover classes ΔT were similar to each other, but the average increase in ΔT between two rainfall events was higher in bare soil than the vegetation classes across all rainfall treatments (P<0.05). Among the vegetation classes, the average increase in ΔT between two rainfall events was higher in brown vegetation than in green vegetation.

Fewer/larger precipitation events (S3 and S4) led to cooler plant temperatures (Fig. 2e). In the S3 and S4 treatments, green vegetation ΔT was on average 1.7°C and 1.2°C cooler than S1, respectively (P<0.1). Conversely, many/small precipitation events raised the plant and soil temperature in comparison to fewer/larger precipitation events (P<0.1, Fig. 2e). Across all treatments, green vegetation temperature was 4.1°C and 2.3°C cooler than bare soil and brown vegetation, respectively (P<0.001). We also observed higher temporal variability (SD) in bare soil ΔT than in vegetation classes (P<0.001).

Plant temperature and ecosystem function
Plant temperature dynamics were strongly related to whole plot measurements of ET and GPP (Fig. 3a-d). After the irrigation pulse, green vegetation ΔT decreased significantly in all treatments, and ET increased due to some combination of soil evaporation and plant transpiration. Meanwhile, GPP reached its peak value 1–4 d later than the ET peak, likely because stomatal process upregulation is delayed with respect to abiotic evaporation. Green vegetation ΔT dynamics were significantly correlated with concurrent ET (r = −0.71, P<0.001) and with GPP with one lag in measurement time (r = −0.71, P<0.001).

Plant temperature dynamics of key functional types
Temporal repackaging of precipitation effects on plant temperature differed significantly between annual and perennial plants (Fig. 4; Table S4). In the S2 (climatic normal) treatment, there were no significant differences between annual and perennial PFTs ΔT means (P>0.1, Fig. 4b). By contrast, many/small rainfall events (S1) caused annual plants’ ΔT to be 1.8°C cooler on average than those of perennials (P<0.001, Fig. 4a). However,
fewer/larger rainfall events in the S3 and S4 treatments caused annual plants’ $\Delta T$ to be 0.9°C and 2.5°C warmer on average than perennials, respectively ($P<0.1$, Fig. 4c,d). There was a clear gradient of mean $\Delta T$ in annual and perennial plants from S1 to S4 (Fig. 4e). For annual plants, mean $\Delta T$ increased by 1.2°C from S1 to S4, while in perennial plants it decreased by 3.1°C from S1 to S4 ($P<0.1$, Fig. 4e). In other words, the patterns of $\Delta T$ we observed indicate that many/small rainfall events may favor annual plants, whereas fewer/larger rainfall events may be more favorable to perennials. We also observed a higher temporal standard deviation of $\Delta T$ in annual plants than in perennial plants ($P<0.001$).
Plant temperatures, water availability, and roots

To examine whether larger, less frequent storms resulted in deeper soil water availability that may favor perennial over annual grasses, we examined how rooting depth and soil moisture differed across the treatments. The root area in the deeper soil zone (34–44 cm) was greater in S4 than in S1 and S2 (Figs 5, S4). However, the root area in the shallow root zone (0–11 cm) was greater in S1 and S2 than in S4. Soil water content in the deeper zone was significantly greater in S4 than in S1 and S2 due to the larger irrigation volumes (Figs 5, S4). GPP and ET rates were also higher in S4 than in S1.

Discussion

Our study showed that temporal repackaging of seasonal precipitation, when precipitation total was held constant, had significant...
impacts on semi-arid grassland canopy temperature dynamics. Specifically, less frequent and greater depth (fewest/largest) precipitation events led to cooler plant temperatures relative to more frequent and less intense (many/small) precipitation events (supporting hypothesis 1). In dryland ecosystems, larger storms tend to wet the entire root zone, and these soil moisture pulses can be the main drivers of plant growth and ecosystem function (Noy-Meir, 1973; Huxman et al., 2004). Likewise, we observed more soil moisture in deeper soil, more GPP, and more ET in the S4 rainfall treatment (fewest/largest) (Fig. 5). Consistent with greater deep soil moisture, the latent heat followed by more transpiration in S4 resulted in cooler plants in fewest/largest precipitation events than many/small precipitation events. Moreover, we observed less variability of $\Delta T$ in more frequent and less intense

Fig. 4 Radiant temperature minus air temperature ($\Delta T$) of annual (red line) and perennial plant (green line) functional types in (a) S1 (many/small), (b) S2 (climatic normal), (c) S3 (few/large), and (d) S4 (fewest/largest) treatments. Colored bars show the timing of S1–S4 precipitation events, and the height of the bar shows their relative magnitude. (e) Mean radiant temperature minus air temperature ($\Delta T$) of annual and perennial plant functional types over the course of the experiment. Treatments with significantly different mean $\Delta T$ lack a common letter ($P < 0.1$, Tukey HSD). The bars represent the mean value of each treatment. Error bars represent standard error over each treatment.
(many/small) precipitation events, which suggests many/small rainfalls could help to avoid extreme plant temperatures in some species.

Plant temperature dynamics were closely associated with plot-level ET and GPP dynamics (supporting hypothesis 2). Plant temperature was highly correlated with instantaneous ET, but its relationship with GPP was only significant with a 1–4 d delay. The initial large contribution of soil evaporation to ET following a rainfall event likely drove the near-instantaneous plant temperature–ET correlation (Scott et al., 2006; Xie et al., 2020). By contrast, the lagged relationship between plant temperature and GPP may be explained by a delay in plant soil water uptake and physiological upregulation of photosynthesis following rainfall (Huxman et al., 2004; Feldman et al., 2021). Our findings are consistent with other efforts revealing that thermal observations are key in tracking plant water stress and ecosystem function (Duffková, 2013; Kim et al., 2016; Pau et al., 2018; Javadian et al., 2022). For instance, Kim et al. (2016) found a strong relationship between daily/sub-daily plant temperature and net ecosystem CO₂ exchange at a ponderosa pine forest site. Moreover, Yi et al. (2020) found notable differences among their study species in the sensitivities of canopy temperature and VPD at the canopy surface to rising air temperature and atmospheric water demand, which was closely related to species-specific hydraulic traits in a temperate mixed forest. However, this is the first time to our knowledge that these plant temperature dynamics have been revealed in the highly dynamic environment of a pulse-driven semi-arid grassland. With thermal imaging, it becomes possible to map the temperature of individual plants or entire ecosystems and identify areas experiencing water stress attributed to the reduction in transpiration and evaporative cooling caused by the closure of stomata, resulting in elevated plant temperatures. Our findings suggest high spatiotemporal resolution thermal imaging is a powerful tool for improved understanding and monitoring of plant functional response to rapid
hydroclimatic change being experienced across drylands of the western United States (Zhang et al., 2021) and globally (Stevenson et al., 2022) as it can provide detailed information on plant temperature and water stress in response to changes in hydroclimate.

A shift to fewer/larger precipitation events (S3 and S4) resulted in perennial plant temperatures $2.5 \pm 1.2^\circ C$ cooler than that of annual plants (supporting hypothesis 3). Conversely, many/small precipitation events (S1) resulted in annual plant temperatures that were $1.8 \pm 1.1^\circ C$ cooler than that of perennials. This reversal in annual and perennial PFT response to precipitation variability was likely driven by contrasting soil water availability below the plants and correspondingly different root distributions. Specifically, we found that under the less frequent and more intense rainfall treatment, annual plant cover, surface soil moisture, and surface root area were increased (Fig. 5). Therefore, changes in water available across the distribution of soil water may differentially impact the physiological performance of these PFTs. Increased precipitation intensity has been shown to shift plant available water downward in the soil profile, potentially explaining the positive effect on deep-rooted perennials (Hess et al., 2018; Singh et al., 2021). In addition to the location of soil water, these contrasting rooting patterns determine the volume of soil explored by each plant type. Perennials explore a relatively large volume of soil where water from wet years can be stored, whereas annuals not only explore a smaller volume of soil but excess water percolating from top layers during wet years recharges the portion of the soil typically more explored by perennials (Roumet et al., 2006). Our findings are supported by a recent analysis that showed deeper-rooted shrubs are likely to outcompete grasses in a more extreme hydroclimate (Gherardi & Sala, 2015) and in drought conditions (Winkler et al., 2019). Here we show for the first time to our knowledge that when deployed at the high spatiotemporal resolution, thermal imaging can reveal PFT water acquisition strategies, root traits, and physiological performance and thereby provide an early indication of critical ecosystem threshold responses such as community composition transitions and mortality events. Zhang et al. (2021) found that over the past four decades drylands of southwest US are experiencing shifts toward larger, less frequent rainfall events interspersed by longer intervals of dry days. This suggests that for areas of similar soil type to our study site, this shift toward more intense precipitation events but longer dry intervals may provide a competitive advantage for deeper rooted functional types that can access increasing plant available water at depth in the soil profile. Further research across larger spatial scales, PFTs, and soil types is needed as a next step to test this extrapolation of our site-level results. The study was focused on tracking the response of key PFTs to rainfall pulses without considering minor microclimate differences between the treatments. However, differences in solar radiation absorption by different PFTs and minor microclimate differences associated with different rainfall pulses can affect plant temperature changes (Lian et al., 2017; Still et al., 2021; Guo et al., 2023). It is important to recognize the potential impact of these variables, as they have the potential to significantly influence plant temperature and, consequently, plant growth and development. Future attempts to consider microclimate impacts using distributed meteorological sensors are needed to understand the impacts of differing microclimates in the results.

Interestingly, we found in the climatic normal treatment (S2), annuals, and perennials had similar temperature responses (Fig. 4b). This suggests ecosystem adaptation in which all functional types maintain roughly equal access to moisture under the historical rainfall regime. Interestingly, different shifts in precipitation timing (i.e., shifts to smaller/more frequent compared to larger/less frequent shifts) had opposing effects on this balance for annual vs perennial plants, with important implications for ecosystem structure and function. It should be noted that soil type significantly impacts the soil moisture threshold of plant water stress and the depth distribution of soil moisture and how it responds to precipitation (Bassiouni et al., 2020; Fu et al., 2022a) and thus these findings are specific to the site soil type. Therefore, PFTs’ temperature might have a different response to precipitation changes in a different soil type. Future work is required to create a predictive framework for understanding PFTs’ temperature responses to rainfall pulses as a function of various soil types.

Furthermore, it has been suggested that the degree of isohydry, a measure of stomatal closure, could be estimated using thermal imagery (Pignon et al., 2021). Previous studies have used changes in vegetation optical depth and plant temperature to estimate isohydricity, as more isohydric species are expected to exhibit more rapid stomatal closure and therefore experience more warming in the afternoon (Konings & Gentile, 2017). However, estimating isohydry from thermal imagery requires careful consideration of confounding factors such as diurnal radiation effects and changes in nearby soil temperature. While this approach could provide valuable insights into the water use strategies of different plant species, our study was more focused on daily variations and did not include diurnal sampling to estimate stomatal closure. Thus, future studies could build upon our findings using a multiscale approach to quantify stomatal behavior and determine the degree of isohydry across different temporal and spatial scales.

Our results show that the high spatiotemporal resolution of thermography can better uncover the interstorm pulse dynamics of physiological performance across an entire growing season among PFTs. It offers a new way of assessing coupled water and carbon cycles and, in some cases, may have advantages over other indirect measures of plant functioning (e.g., isotopes, plant water status, and manual leaf gas exchange measurements) due to its higher frequency, large number of samples, and nondestructive approach. This could be very helpful in disaggregating fluxes at plot studies and eddy covariance sites (from deserts to tropical forests). The results of this study highlight the need for high spatiotemporal resolution thermal imagery, for example, that could be obtained from satellites for a global study. Satellite observations complement limitations in spatial representation and global coverage of site-based measurements and can produce spatially continuous estimates of thermal data from regional to global.
scales based on different approaches (Li et al., 2021). Thermal imagery from Moderate Resolution Imaging Spectroradiometer and Landsat satellites have long been utilized to investigate vegetation ecohydrological traits (Smith et al., 2019). The ECOSystem Spaceborne Thermal Radiometer Experiment on Space Station (ECOSTRESS), launched in 2018, is one of the recent thermal missions that can capture high-resolution images at different times of day, which makes it the first satellite capable of detecting sub-daily vegetation water stress at field scales (Fisher et al., 2020). Despite their global coverages and other advancements, these satellite products remain unable to address some key ecohydrological questions due to: too coarse spatiotemporal resolutions for dryland ecosystem dynamics; and atmosphere and cloud impacts on thermal data, especially during rainfall events. These limitations indicate the benefit of a next generation, high spatiotemporal resolution thermal sensor capable of tracking diurnal surface temperature dynamics. To partially address this, NASA’s planned mission for Surface Biology and Geology (SBG) is expected to include 5 thermal infrared bands with spectral ranges of 8–12 µm and 3–5 µm, 40–60 m spatial resolution, 3 d revisit time, and global coverage (Cawse-Nicholson et al., 2021). The planned Hydrosat constellation may also be capable of breaking through current barriers to provide 5 thermal infrared (TIR) and visible near infrared data multiple times per day every day (Lalli & Soenen, 2021). Although geostationary satellites such as Geostationary Operational Environmental Satellite (GOES-R) series have high-frequency diurnal sampling, the coarse spatial resolution (for example, 2 km for TIR bands) produces mixed pixels containing plant species or individuals with different diurnal cycles (Xiao et al., 2021). As a result, future efforts that fuse SBG, ECOSTRESS, Hydrosat, and/or GOES toward a high spatiotemporal land surface temperature product could lead to the development of a high-resolution land surface temperature product with a detailed spatiotemporal coverage. This integrated approach has the potential to advance our understanding of ecohydrological processes in vegetation and the dynamics of water stress in ecosystems worldwide (Anderson et al., 2011, 2021; Smith et al., 2019; Javadian et al., 2022).

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Competing interests

None declared.

Author contributions

MJ, WKS, RLS and JAB designed the research. MJ collected the thermal images. MJ, WKS, FZ and JAB analyzed the data. MJ, WKS, RLS and JAB wrote the manuscript with the substantial contributions of FZ, JBF, SCR, DLP, MLV and AFF.

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Data availability

The data that support the findings are publicly available at doi: 10.5281/zenodo.7555147.

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Supporting Information

Additional Supporting Information may be found online in the Supporting Information section at the end of the article.

Fig. S1 The experimental design.

Fig. S2 The daily relative humidity (RH%) and air temperature (°C).

Fig. S3 Visualization of a sample of thermal and RGB image registration.

Fig. S4 Standardized boxplot of the variables based on Z Score during the experiment days.

Table S1 The sampling frequency of different datasets collected in the study in year 2021.

Table S2 Time of thermal infrared image collection for each plot.

Table S3 Absolute plant and air temperature of annual and perennial plant functional types.

Table S4 Average of Fig. S4 boxplot data.

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