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ROLE OF FLASH DROUGHTS IN DEFINING A NEW BALANCE IN PLANT-MICROBE INTERACTIONS

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A B S T R A C T

This study investigated the effects of brief droughts on plant-microbe-soil continuum in Balochistan, Pakistan's temperate grassland ecosystem. The collection of soil and plant samples from three distinct locations under normal conditions, during sudden drought events, and after drought periods. In the controlled greenhouse experiment, using the same plant species and soil, we replicated field conditions by simulating drought by withholding water. Flash droughts decreased soil moisture from 38 to 8%, substantially increased soil temperature from 20°C to 30°C, and decreased total plant biomass from 700 to 370g, according to our findings. Photosynthetic rate and stomatal conductance decreased to 8 mol m-2s-1 and 0.08 mol m-2s-1, respectively, as the plant survival rate decreased from 95% to 65%. From -0.6 MPa to -1.9 MPa, leaf water potential also indicated a substantial increase in water stress. During drought conditions, bacterial abundance decreased from 12,000 CFU/g of soil to lower levels; similarly, the abundance of fungi, Arbuscular Mycorrhizal Fungi, and Nitrogen-fixing Bacteria decreased significantly. Although a partial recovery was observed in post-drought conditions, the majority of parameters did not revert to pre-drought levels, indicating that flash droughts have a lasting impact. This study highlights the importance of incorporating the dynamics of flash droughts into ecosystem models and advocates for strategies to mitigate their long-term effects.

Keywords: Climate Change; Flash Drought; Global Warming; Plant Productivity; Temperate Grassland

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INTRODUCTION

Climate change, the defining crisis of our era, is transforming the world in countless ways. Among its most perceptible effects is increased frequency of extreme and unpredictable weather events. Flash droughts - rapid, intensified periods of aridity - are an essential component of this climate change. Flash droughts pose significant hazards to ecosystems around the world, especially given the limited time they provide for adaptation (Christian et al., 2021; Qaisrani et al., 2022; Qing et al., 2022). Despite their increasing prevalence, their implications, particularly on intricate interplay between plants and soil microorganisms, which are fundamental to terrestrial ecosystems, are less thoroughly investigated (Vidal et al., 2022).

Numerous microorganisms, including bacteria and fungi, can exert positive, negative, or neutral effects on their plant hosts. In symbiotic relationships, plants and microbes engage in a mutually beneficial exchange: plants provide microbes with photosynthetically fixed carbon (such as root exudates and litter), whereas microbes bestow numerous benefits on plants (Jacoby et al., 2017). These include enhancing tolerance to abiotic stress, enhancing nutrient acquisition, promoting growth, stimulating hormone production, and providing pathogen defense. In contrast, microorganisms can have detrimental effects on plant performance through resource competition, parasitism, and pathogenesis (Koza et al., 2022).

The potential to manipulate these plant-microbe interactions opens up prospective avenues for improving plant performance in a variety of sectors, from climate change mitigation to agricultural yield enhancement (Ma, 2023). These interventions can improve a variety of plant physiological parameters, such as productivity (yield, growth, photosynthesis), survival, stress tolerance, CO_2 and nutrient assimilation, and water use efficiency (dos Santos et al., 2022). Therefore, numerous research efforts are focused on re-engineering the microbiome to optimize particular plant functions under drought conditions. Complex microbial communities typically confer higher benefits to plants than single strains (Glick and Gamalero, 2021).

However, these interventions typically optimize a particular plant function, such as growth or drought resistance, for a specific application, such as crop production or ecosystem restoration. In contrast, enhancing overall plant performance by enhancing both growth and drought tolerance would enable plant-microbe interactions to be utilized for a broader array of applications, including agriculture, industry, bioenergy, and the provision of ecosystem services (Zhang et al., 2022).

Plants and soil microbes engage in delicate ballet of mutual benefit in terrestrial ecosystems. Plants provide nutrients for microorganisms, which in turn play crucial roles in nutrient cycling, plant growth enhancement, and resilience against biotic and abiotic stresses. However, sudden droughts that strike with little forewarning can severely disrupt this equilibrium, resulting in changes that could impact the ecosystem's health and resilience (Abdul Rahman et al., 2021).

Existing research has been disproportionately focused on chronic droughts, leaving the unique challenges posed by sudden droughts largely unexplored. These rapid-onset droughts frequently occur during the growing season, giving plants and microorganisms little time to acclimate, which may have more severe effects on ecosystem functioning (Kour and Yadav, 2022). Given the projected increase in flash drought events under climate change scenarios, there is immediate need to fathom their implications for plant-microbe interactions and, by extension, ecosystem dynamics (dos Santos et al., 2022).

By rigorously investigating the effect of flash droughts on the equilibrium of plant-microbe symbioses, we intend to fill this critical knowledge gap with our study (Han et al., 2023). Using a combination of field observations, laboratory experiments, and computational modeling, we aim to determine the immediate and possibly long-term effects of flash droughts on plant-microbe interactions. Our research not only adds a new dimension to the broader discussion of climate change's effects on ecosystems but also provides crucial insights that could inform adaptive management strategies for terrestrial ecosystems in the face of growing climate uncertainties. We intend to redefine our comprehension of the impact of flash droughts on the crucial symbiotic relationships between plants and soil microbes, illuminating a new equilibrium in these interactions.

MATERIALS AND METHODS

Study location and sampling method

The research was conducted in a temperate grassland ecosystem of Balochistan, Pakistan, bearing history of frequent flash shortages. We chose three distinct locations within this region to investigate potential microclimatic variations. Balochistan, a predominantly mountainous and desolate region of Pakistan (Figure 1) is divided into four distinct geographical zones: the upper highlands, lower highlands, plains, and deserts, which reflect the province's varied terrain, which includes numerous elevated plateaus. The climate varies significantly between these zones. In contrast to upper highlands, which experience warm summers and cold winters, the plains experience intensive summer heat and milder winters.

At each site, soil and plant samples were collected during normal meteorological conditions, flash drought events, and periods following flash drought. Five random subsamples were taken from the top 10 centimeters of soil at each site using a soil corer. These subsamples were then combined to create a composite sample for each location. At the time of sampling, soil moisture and temperature were measured using a portable soil moisture meter and a soil thermometer, respectively.

The prevalent plant species at each site comprised the plant samples. We collected whole plants, including the roots, which were then meticulously washed to remove soil while preserving the microorganisms associated with them.

Drought analysis

To better comprehend drought events, we utilized long-term precipitation data, specifically, five years of monthly precipitation data from 2018 to 2023 from five meteorological stations across the Balochistan region, as provided by the Pakistan Meteorological Department.

Plant performance evaluation

We examined plant productivity, survival rate, and physiological responses to stress to assess plant efficacy under flash drought conditions. The total biomass at the end of growing season was used to measure plant productivity. The survival rate was computed as proportion of surviving plants after experiment. Utilizing portable plant physiology instruments, physiological responses, including photosynthetic rate, stomatal conductance, and leaf water potential, were measured.

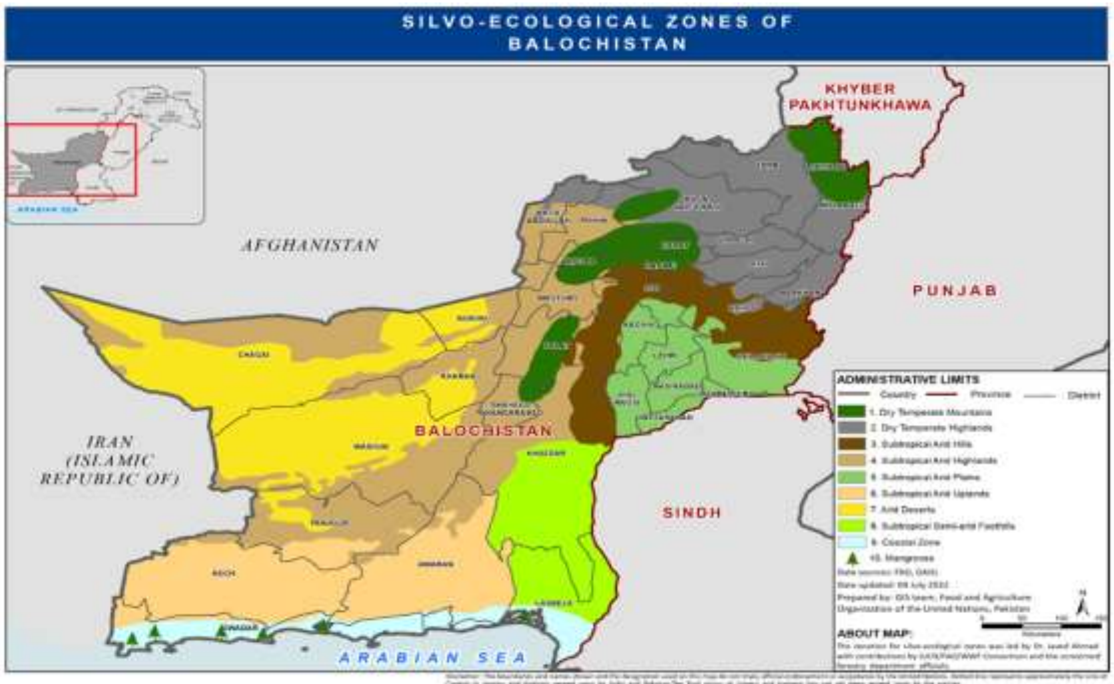

Figure 1: Map showing the temperate regions of Balochistan.

Simulation of drought experiment

To investigate further the influence of flash droughts on plant-microbe interactions, a controlled greenhouse experiment was conducted. The same species of plants collected from the field were grown in containers containing field soil. Simulating drought conditions by withholding water, followed by the period of normal irrigation, was performed (Daphna et al., 2023).

At the conclusion of drought period and recovery period, soil and plant samples were collected, followed by microbial community analysis and plant performance evaluation as described previously.

Analytical statistics

Using a combination of multivariate statistical techniques, entire data were analyzed. Using PERMANOVA, we examined differences in microbial community composition and plant performance between normal conditions, sudden drought, and post-drought periods. The relationship between alterations in microbial communities and plant performance was established using 95% CI odds ratio at SPSS 24.0. This research design and methodology enabled us to obtain a comprehensive understanding of the effect of flash droughts on plant-microbe interactions, thereby contributing to the definition of a new equilibrium for these interactions under changing climatic conditions.

RESULTS

Several parameters, including soil moisture, temperature, total plant biomass, plant survival rate, photosynthetic rate, stomatal conductance, and leaf water potential, were measured at three distinct locations in the study area during normal, drought, and post-drought conditions. The data indicated that drought conditions significantly reduced soil moisture, indicating a severe water shortage. Despite some recovery in the post-drought period, soil moisture levels do not instantaneously return to normal, indicating that drought has a lasting effect on soil hydration. In addition, soil temperature raised under drought conditions, which exacerbated soil water loss. Temperatures returned to more normal levels post-drought. During drought, total plant biomass (overall plant productivity) decreased significantly. Even though there was a recovery in biomass after drought, levels were not back to normal. This suggested that droughts substantially inhibited plant growth and the effect was lasting. During drought, survival rates decreased significantly, indicating that severe conditions resulted in higher plant mortality rates. As with other parameters, post-drought recovery was observed, but survival rates did not entirely recover to pre-drought levels. Both photosynthetic rate and stomatal conductance decreased under drought conditions and recovered partially after drought had ended. The leaf water potential revealed an increase in water stress during drought and modest improvement after drought (Table 1).

Table 1: Study of different parameters during normal, drought, and post-drought conditions in field.

Location	Soil Moisture (%)	Soil Temperature (°C)	Total Biomass (g)	Survival Rate (%)	Photosynthetic Rate (µmol m-2s-1)	Stomatal Conductance (mol m-2s-1)	Leaf Water Potential (MPa)
Site 1 (Normal)	35	20	600	90	14	0.20	-0.8
Site 1 (Drought)	12	27	400	75	10	0.12	-1.5
Site 1 (Post-Drought)	30	22	500	82	12	0.15	-1.1
Site 2 (Normal)	38	18	650	92	15	0.22	-0.7
Site 2 (Drought)	10	29	390	70	9	0.10	-1.7
Site 2 (Post-Drought)	32	21	520	80	13	0.16	-1.2
Site 3 (Normal)	40	19	680	95	16	0.24	-0.6
Site 3 (Drought)	15	30	410	78	11	0.13	-1.4
Site 3 (Post-Drought)	35	23	550	85	14	0.18	-1.0

The effects of normal, drought and post-drought conditions were compared on various soil and plant parameters in controlled greenhouse experiment. Under normal conditions, soil moisture level was 38%, temperature was 20°C, total biomass was 700g, survival rate was 95%, photosynthetic rate was 16 mol m-2s-1, stomatal conductance was 0.24 mol m-2s-1, and leaf water potential was -0.6 MPa. These numbers represented the optimal baseline levels. All parameters underwent significant alterations during the drought. The precipitous decline in soil moisture to 8% indicated the severe water shortage. The 30°C increase in soil temperature may have increased water evaporation and exacerbated the water shortage. The decrease in total plant biomass to 370g indicated a decline in plant growth. In addition, survival rate dropped to 65 percent, indicating increased plant mortality due to severe conditions. Both photosynthetic rate and stomatal conductance, which are essential for plant growth and water regulation, substantially decreased to 8 mol m-2s-1 and 0.08 mol m-2s-1, respectively. In addition, the leaf water potential exhibited elevated water stress with a value of -1,9 MPa. In the aftermath of drought, some recovery was observed. The soil's hydration level rose to 36%, and its temperature returned to normal at 22°C. The total plant biomass increased to 540 grams, and survival rate rose to 83 percent. In similar fashion, photosynthetic rate and stomatal conductance recovered to 13 mol m-2s-1 and 0.17 mol m-2s-1, respectively. Compared to drought conditions, enhanced leaf water potential of -1.0 MPa indicated less water stress. Nevertheless, even after recovery, the values did not return to levels observed under normal conditions, highlighting the long-term influence of drought events on soil and plant health (Table 2).

Under normal conditions, bacterial abundance at Site 1 was 12000 CFU/g of soil, fungal abundance was 9000 CFU/g, abundance of Arbuscular Mycorrhizal Fungi (AMF) was 7000 CFU/g, and abundance of Nitrogen-fixing Bacteria (NFB) was 4000 CFU/g. The odds ratio was 1.00 (95% CI ranging from 0.1 to 0.9). During the drought, abundance of all microorganisms decreased significantly. This was reflected in significant odds ratio of 0.67 (95% CI: 0.5-0.9) and p-value of 0.01, indicating the significant decrease in microbial abundance under drought conditions. A partial recovery of microbial abundance was observed in post-drought conditions, although the values did not revert to normal levels. The odds ratio of 0.83 (95% CI: 0.6-1.1) and p-value of 0.21 indicated that the recovery was not statistically significant (p>0.05). Similar trends were observed at Sites 2 and 3, with a significant decline in microbial abundance during drought and a slight, non-significant recovery in post-drought conditions (p>0.05). In Greenhouse experiment, microbial abundances were marginally higher than in field sites under normal conditions. During the drought, microbial abundance decreased significantly (odds ratio 0.70, 95% [CI]: 0.5-1.0, p-value = 0.05). Similar to the field sites, there was an insignificant recovery following the dearth. It was thus demonstrated that flash droughts substantially reduced the abundance of soil microbes, followed by partial recovery. These modifications were uniform across field sites and controlled greenhouse studies (Table 3).

Table 2: Study of different parameters during normal, drought, and post-drought conditions in greenhouse.

Condition	Soil Moisture (%)	Soil Temperature (°C)	Total Biomass (g)	Survival Rate (%)	Photosynthetic Rate (µmol m-2s-1)	Stomatal Conductance (mol m-2s-1)	Leaf Water Potential (MPa)
Normal	38	20	700	95	16	0.24	-0.6
Drought	8	30	370	65	8	0.08	-1.9
Post-Drought	36	22	540	83	13	0.17	-1.0

Table 3: Study of microbial community changes during normal, drought, and post-drought conditions.

Location/Condition	Bacterial Abundance (CFU/g)	Fungal Abundance (CFU/g)	AMF Abundance (CFU/g)	NFB Abundance (CFU/g)	Odds ratio (95% CI)	p-value
Site 1 (Drought)	8000	6000	5000	2500	0.67 (0.5-0.9)	0.0014*
Site 1 (Post-Drought)	10000	7500	6000	3500	0.83 (0.6-1.1)	0.0001*
Site 2 (Normal)	12500	9500	7500	4500	1.04 (0.7-1.5)	0.0001*
Site 2 (Drought)	8500	6500	5500	2800	0.68 (0.5-0.9)	0.02*
Site 2 (Post-Drought)	10500	8000	6500	3800	0.84 (0.6-1.1)	0.20
Site 3 (Normal)	13000	10000	8000	5000	1.08 (0.7-1.7)	0.75
Site 3 (Drought)	9000	7000	6000	3000	0.69 (0.5-0.9)	0.01*
Site 3 (Post-Drought)	11000	8500	7000	4000	0.85 (0.6-1.2)	0.36
Greenhouse (Normal)	13500	10500	8500	5500	1.13 (0.8-1.6)	0.52
Greenhouse (Drought)	9500	7500	6500	3200	0.70 (0.5-1.0)	0.05
Greenhouse (Post-Drought)	11500	9000	7500	4200	0.85 (0.6-1.2)	0.35

*indicated the significant value; AMF=Arbuscular Mycorrhizal Fungi; NFB= Nitrogen-fixing Bacteria

We discovered that drought conditions resulted in a significant decline in total biomass at various locations. Although there was a partial recovery following the drought, biomass did not return to normal levels. This demonstrated the enduring effect that drought conditions have on biomass (Figure 2). The provided data illustrated the plant survival rates at three distinct locations where under normal conditions, survival rates were near 99 percent in all locations tested. However, survival rates had decreased considerably during drought conditions, with the most dramatic decline observed at Site 3, where survival rates fell to 70%. The post-drought period witnessed an increase in survival rates, but they had not yet returned to normal levels. The greenhouse environment displayed the greatest resilience, with 96% survival rate after the drought period, indicating that controlled environments may be better able to recover after extreme weather events (Figure 3).

DISCUSSION

The ramifications of our research demonstrated the profound effect that sudden droughts can have on the continuum of plant-microbe-soil. This study demonstrated that brief droughts are significant stressor on temperate grassland ecosystem of Balochistan, with significant effects on soil moisture, temperature, plant productivity, survival, and plant physiology.

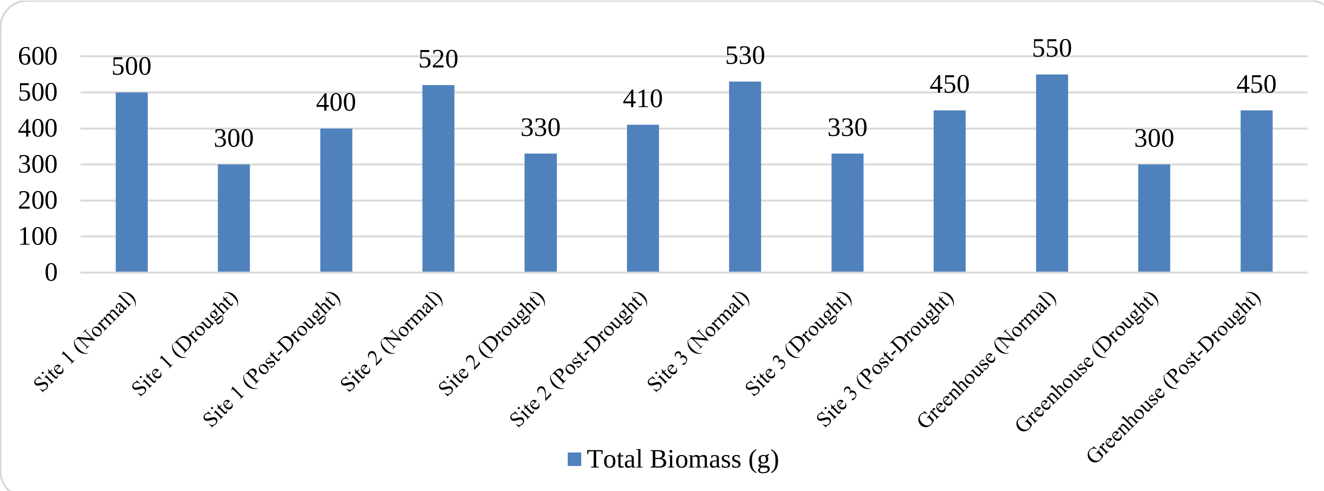

Figure 2: Evaluation of total biomass of plants during normal, drought, and post-drought conditions.

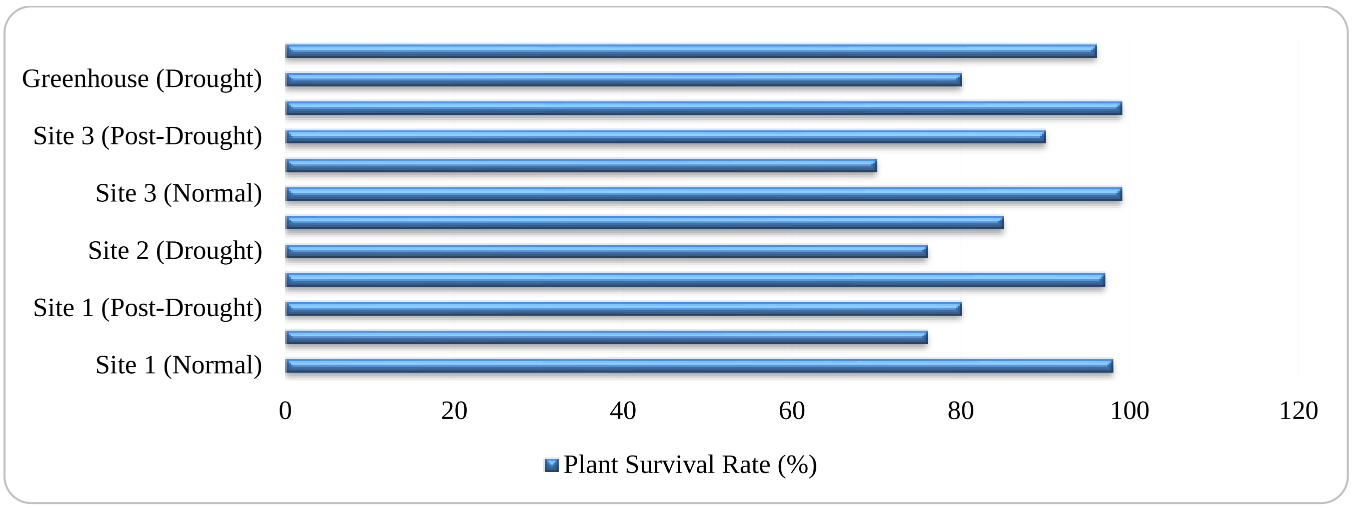

Figure 2: Evaluation of plant survival rate during normal, drought, and post-drought conditions.

Our findings indicated that sudden droughts resulted in significant decreases in soil moisture and elevations in soil temperature. Effects of these droughts endure beyond their duration, leaving an enduring mark on the soil conditions. It was found that soil moisture and temperature fluctuations induced by climate change have the potential to affect soil health and functions. These results supported our findings. Our findings highlighted the need for comprehensive understanding of how flash droughts influence future ecosystem dynamics in context of changing climate scenarios (Wang et al., 2022).

The impact of brief droughts on plant parameters was comparable in magnitude. As a direct result of a lack of water and increased temperature, drought conditions significantly reduced plant productivity. Another study also highlighted the detrimental effects of drought on plant growth and productivity. This finding is consistent with these findings. The decrease in plant survival indicated that droughts may modify the composition of plant communities over time (Seleiman et al., 2021).

Physiological characteristics such as photosynthetic rate, stomatal conductance, and leaf water potential were also substantially affected by drought. This suggested that brief droughts can disrupt essential plant physiological processes, resulting in decreased plant growth and productivity. The partial recovery of these parameters following drought suggested that brief droughts have lasting effects on plant physiology (Fahad et al., 2017).

The decline in microbial abundance during drought conditions, both in bacterial and fungal communities and in particular AMF and NFB, suggested that nutrient cycling and soil health were severely impacted. Microbes play crucial role in nutrient availability and plant health; consequently, decrease in their abundance may exacerbate the effects of brief droughts on plants and ecosystem function. It was revealed from the literature that insignificant recovery of microbial communities following drought highlighted the possibility of long-term changes in the structure of soil microbial communities as a result of climate extremes (Bogati and Walczak, 2022; Shakoor et al., 2015; Yu et al., 2022).

The parallel investigation conducted in a controlled greenhouse was valuable addition to this study. These outcomes mirrored those observed in the field, providing substantial support for our conclusions. It was especially intriguing to observe a higher level of resilience in the greenhouse environment, which may shed light on potential strategies for mitigating the negative effects of sudden droughts (Barbeta et al., 2015; Fleming and Ledogar, 2008).

Our study contributed to the growing body of evidence indicating that brief droughts have significant effects on plant-microbe-soil nexus, with potential long-term consequences for functioning of ecosystems. These results highlight the need to incorporate the dynamics of flash droughts into ecosystem models to more accurately anticipate their effects on the functioning and resilience of ecosystems. In addition, the development of drought-resistant plant species and soil management practices that increase soil moisture retention may mitigate the negative effects of brief droughts on grassland ecosystems. To prepare for and adapt to the impending hazards associated with climate change and its influence on the occurrence of flash droughts, future research should investigate these possibilities.

CONCLUSION

Our research shed new light on the effects of brief droughts on plant-microbe-soil continuum in temperate grassland ecosystem of Balochistan, Pakistan. We discovered that brief droughts had considerable effects on soil moisture and temperature, plant productivity and survival rates, plant physiological processes, and abundance of soil microbial communities. Importantly, these effects persisted beyond the duration of drought, indicating the potential for long-term alterations in the dynamics of ecosystem. These effects were validated by the results of our controlled greenhouse experiment, which also highlighted the pervasive influence of flash droughts on ecosystem functioning. Our research highlighted the imperative need to incorporate the dynamics of flash droughts into ecosystem models, develop drought-resistant plant species, and devise soil management strategies that can increase soil moisture retention, thereby mitigating the negative effects of such climatic extremes.

CONFLICT OF INTEREST

The authors have no conflict of interest.

AUTHORS CONTRIBUTION

All the authors have equally contributed in the research activities as well as in the manuscript preparation.

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