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Rainfall timing and intensity jointly affect the survival and growth of seedling and juvenile *Poa crymophila* in alpine rangelands on the Qinghai-Tibetan Plateau

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Abstract

Background Rainfall intensity and timing may affect plant survival and growth differently across life stages. However, there is still a lack of studies that simultaneously examine these combined effects on plant performance, which largely limits our understanding of plant responses to climate change.

Methods Here, we examined the impacts of rainfall intensity (−75%, −50%, 0%, +50% and +75%) and rainfall timing (early growing season: June–July; late growing season: August–September) on the survival and growth of seedling and juvenile *Poa crymophila* Keng, which is a dominant grass and serves as an important forage for livestock on the alpine rangelands of Qinghai-Tibetan Plateau.

Results Rainfall intensity, timing, and plant life stage jointly affected the survival, growth, and biomass allocation of *P. crymophila*. Survival and growth increased with increasing rainfall, peaking under +50% rainfall for seedlings and under +75% rainfall for juveniles. Early-season rainfall promoted survival and growth far more than late-season rainfall, while early drought was more detrimental. Seedlings were more vulnerable to drought than juveniles but showed greater flexibility in biomass allocation.

Conclusions Our study provides new insights into how rainfall timing and intensity interact with plant life stage to jointly affect plant survival and growth. Our results underscore the importance of management measures to mitigate the detrimental effects of early-season drought during the seedling stage.

Keywords Rainfall regime, Life stage, Plant performance, Alpine rangeland

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Introduction

Climate change poses a pervasive threat to global biodiversity in recent decades, with at least 14% of species worldwide facing a high risk of extinction (Trew and Maclean 2021; IPCC 2022; Chai et al. 2025). It not only changes the mean annual rainfall intensity, but also strongly alters the timing of rainfall (Webster et al. 2021; IPCC 2022), which may affect plant performance in distinct ways (Yu et al. 2025; Anees et al. 2025a; Kaur et al. 2023). Changes in rainfall intensity directly affect water supply to plants, which further influence plants' water absorption and transportation, and consequently alter plants' morphology and biomass allocation strategy (Pastore 2022; Cui et al. 2023; Anees et al. 2025d). Previous studies have found that decreased rainfall may lead to reduced biomass accumulation (Kørup et al. 2017; Li et al. 2021; Shen-Tu et al. 2025; Mehmood et al. 2025b), lower plant height, and thinner and smaller leaves (Li et al. 2022a). By contrast, increased rainfall could significantly promote plant performance (Holdrege et al. 2020). However, previous studies have also reported that, when rainfall increased to a saturation point, a further increase may harm plant growth and lead to reduced total biomass due to anoxia stress and nutrient leaching (Zhang et al. 2018). Therefore, studies over a gradient of rainfall intensities are critical for a thorough understanding of the effects of rainfall variation on plant performance, to better inform biodiversity conservation in the face of climate change.

The effects of rainfall not only depend on the intensity, but also strongly rely on the timing (Zhang et al. 2026). Due to a higher water demand to support growth during the early growing season, plants may benefit more from an increase in rainfall earlier rather than later in the growing season. Similarly, drought in the early growing season might be more detrimental to plant survival and growth than that in the late growing season. Alternatively, an increase in rainfall during the late growing season may be less beneficial or even harmful to plant growth, because plants start to senesce and lack enough photosynthetically active tissues to quickly respond to a significant amount of water input (Parton et al. 2012). A previous study in a steppe system found that increased water supply in the early growing season promoted plant growth and the overall aboveground net primary production of the community (Derner et al. 2008). Similarly, Parton et al. (2012) reported that precipitation in June was more effective in promoting community production than precipitation in August. These findings suggest that not only the intensity of rainfall, but also the timing of rainfall may play an important role in shaping plants' performance under climate change. Therefore, studies to simultaneously examine the intensity and timing of rainfall are essential to better assess the consequences of changes in rainfall under climate change.

The response of plants to rainfall variation may depend on life stage (Jiang and Jin 2021). The amount of carbon storage varies across plant life stages, which may consequently affect plants' sensitivity and strategy to cope with rainfall variation (Song et al. 2020; Funk et al. 2021). For example, small seedlings have very limited resource reserves, which may make them highly sensitive to environmental variations affecting their photosynthesis (Bond 2000; Augustine and Reinhardt 2018). As a result, small seedlings may exhibit higher plasticity in biomass allocation to prioritize photosynthesis maintenance under environmental stresses (Bond 2000; Lum and Barton 2020). Alternatively, plants at later life stage, which have a larger size and higher carbon storage, may have a much higher tolerance to environmental stress and rely less on the changes in biomass allocation (Jiang et al. 2022; Song et al. 2020). A previous study by Cavender-Bares and Bazzaz (2000) in a forest system found that young seedlings of an oak tree species, *Quercus rubra*, were more sensitive to drought than mature individuals. Similarly, Meyer-Grünefeldt et al. (2015) found that the sensitivity of *Calluna vulgaris*, a perennial shrub species, exhibited a decreasing sensitivity to drought with progressing life history. These studies suggest that plants at early life stages are more sensitive than later life stages to changes in the amount of rainfall. However, despite these inferred responses to rainfall variation, it remains unknown how plants at different life stages may adjust their strategies to cope with concurrent changes in the timing and intensity of rainfall. So far, partly due to the substantial time and effort required to involve plants across different life stages, there is still a lack of studies that simultaneously examine the combined effects on plant performance.

Here we simultaneously examined the effects of changes in rainfall intensity and timing on the performance of an alpine perennial plant species, *Poa crymophila*, at seedling and juvenile stages on a rangeland of the Qinghai-Tibetan Plateau. The Qinghai-Tibetan Plateau has experienced considerable climate change in the past decades, with a warming rate of twice the global average (Xu et al. 2008). While rainfall in winter and spring has generally increased, it has fluctuated substantially in summer months during the past decades (Ding et al. 2024). Therefore, examining the effects of rainfall changes on plant growth and survival is critical to inform the management of rangelands on the Qinghai-Tibetan Plateau in the face of future climate change. We subjected *P. crymophila* at seedling stage (individuals germinated in the current spring) or juvenile stage (individuals germinated in the previous spring) to five intensities of rainfall made proportional to an ambient control [i.e., −75%, −50%, control (0%), +50% and +75%], which were either applied in early growing season (June–July) or late growing season (August–September). Specifically, we tested the following three hypotheses: (1) plant performance increases with the increase of rainfall, because water is an important limiting factor for plant survival and growth on the Qinghai-Tibetan Plateau; (2) changes in rainfall during the early growing season have more pronounced effects on plant performance than in the late growing season, i.e., the effect of drought will be more detrimental and the effects of increased rainfall will be more beneficial, because the demand of water for plants is higher in the early than in the late growing season; (3) seedlings are more responsive than juveniles to changes in rainfall, because younger individuals generally have lower carbon storage and thus are more sensitive to environmental variation.

Materials and methods

Study site

This study was conducted at the Research Station of Alpine Meadow Grassland Ecosystem of the Institute of Northwest Plateau Biology of the Chinese Academy of Sciences (37°36′ N, 101°19′ E, 3215 m a.s.l.), located in the northeastern part of the Qinghai-Tibetan Plateau (Fig. 1a). This area has a typical plateau continental climate, which is dominated by the Southeast Asian monsoon in summer and the Siberia high in winter. It is characterized by a short growing season from May to September and a long non-growing season from October to April (Wang et al. 2021). The mean annual air temperature is − 1.2 °C, with a minimum of − 14.5 °C in January and maximum of 10.4 °C in July. The mean annual precipitation is 485.3 mm, with more than 80% of the precipitation concentrated in the growing season (Wang et al. 2021). The study site is a typical alpine rangeland, and the vegetation is dominated by perennial herbaceous plants, including *Poa crymophila*, *Elymus nutans*, *Stipa aliena*, *Festuca ovina*, *Kobresia humilis*, *Carex przewalskii*, *Saussurea pulchra*, and *Gentiana straminea* (Liu et al. 2018). The main soil type is Mat Cryic Cambisols, typical of alpine rangeland soil (Yang et al. 2013).

Study species

Poa crymophila Keng is a perennial herbaceous species. It is widely distributed on the alpine rangelands with an altitude ranging 2000–4400 m on the Qinghai-Tibetan Plateau. This species can grow to 20–60 cm tall, with a lifespan of about 10 years. Its leaves are rolled or folded in half with a length of more than 10 cm. This species can reproduce both sexually and vegetatively. Its vegetative reproduction occurs mainly through tiller formation, whereby new shoots emerge from the base of the parent plant, allowing rapid colonization of available space (Wei et al. 2021). Its inflorescences are conical in shape, and the color of seeds turns brown when ripe in August–September. *Poa crymophila* is highly resistant to drought and cold environmental conditions, so it is widely reseeded for restoring degraded rangelands on the Qinghai-Tibetan Plateau. This species is highly palatable to livestock and contains 10–18% crude protein in its leaves, making it an important summer forage and a high-quality hay source for winter and spring feeding in pasture areas of the Qinghai-Tibetan Plateau (Zhou et al. 2010). Additionally, *P. crymophila* possesses an extensive root system that allows it to act as a competitive dominant, while it simultaneously functions as a facilitator by creating a protected microclimate within its dense tussocks (Li et al. 2022b). This dual role makes it an important species in alpine rangelands on Qinghai-Tibetan Plateau (Li et al. 2022c).

Experimental design

In late May 2022, we excavated 200 *P. crymophila* seedlings germinated in the current spring, with an average height of 3.90 ± 0.07 cm (mean ± S.E.) in a field near the Research Station of Alpine Meadow Grassland Ecosystem of the Institute of Northwest Plateau Biology. The seedlings had an average of 1.21 ± 0.03 leaves, and an average root length of 4.42 ± 0.11 cm (mean ± S.E.). In the same field, we excavated 200 individual juveniles of similar size that germinated from seeds sown in previous spring. The juveniles had an average height of 6.05 ± 0.06 cm (mean ± S.E.), an average number of leaves of 3.39 ± 0.03 and an average root length of 6.42 ± 0.14 cm (mean ± S.E.). Finally, we transplanted each individual plant into cylindrical polyvinyl chloride (PVC) pipes with a depth of 30 cm and a radius of 5 cm. We filled these PVC pipes with soil taken from the same field site where the excavated *P. crymophila* plants grew. The soil was sieved through a sieve with a mesh diameter of 1 cm to remove plant roots. For individuals that died during transplantation, we replaced them with individuals excavated from the same field site. All seedling and juvenile individuals in the PVC pipes received 0.9 L of water per day, an amount based on the mean June–September rainfall under field conditions at the study sites. This level of watering was sufficient for the full recovery of all individuals before the start of rainfall treatments.

We initiated rainfall treatments two weeks post-transplantation when the plants had recovered well. The experiment followed a factorial design with two levels of rainfall timing (early growing season vs. late growing season), five levels of rainfall intensity (−75%, −50%, 0%, +50%, +75%), and two life stages (seedlings

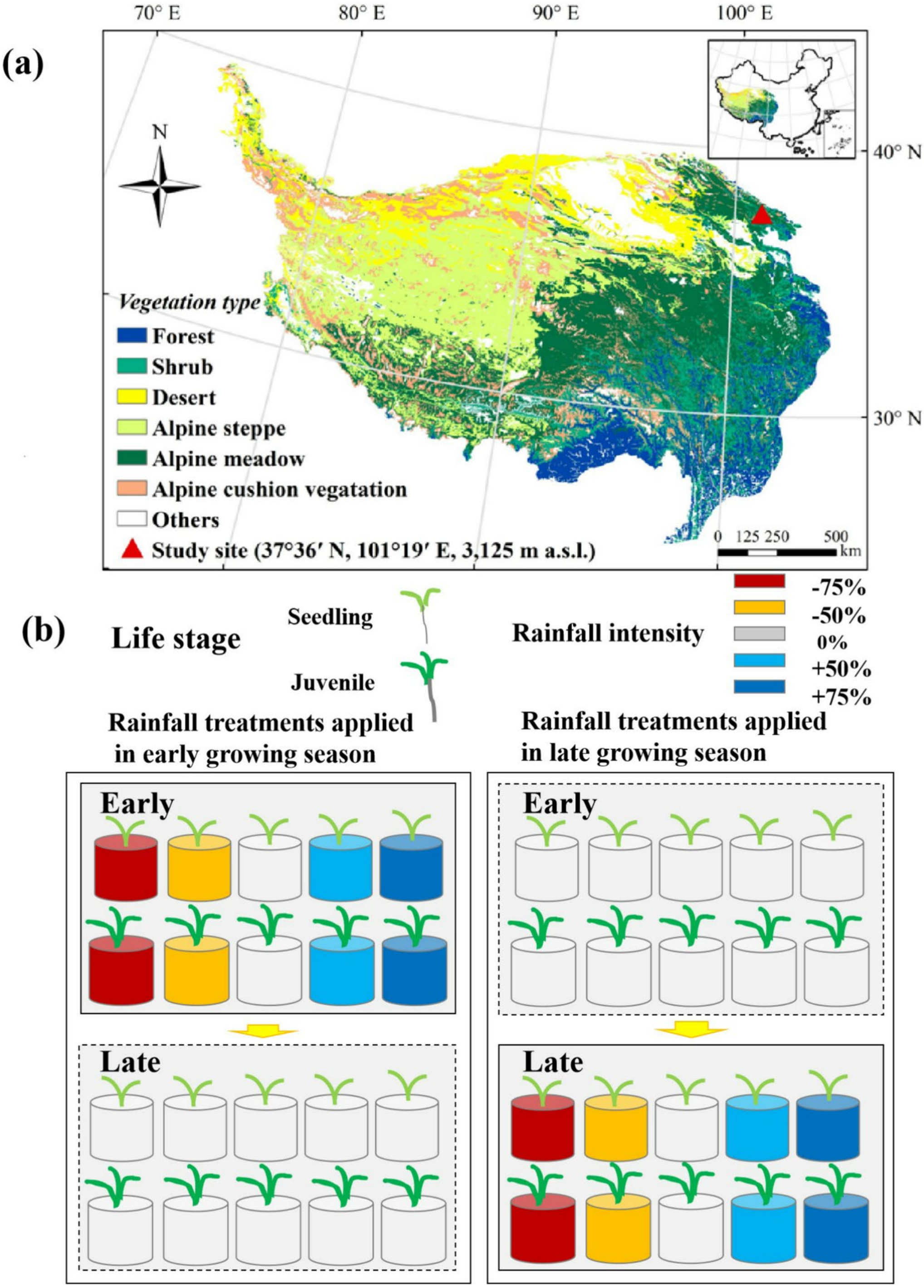

Fig. 1 Geographical location in the study site (**a**) and the schematic diagram of experimental design (**b**). In the field experiment, a randomized block design is adopted, in which life stages and rainfall treatments are assigned randomly. The early growing season rainfall treatments indicate that seedlings and juveniles first receive different levels of rainfall during the early growing season, followed by normal environmental rainfall during the late growing season. In contrast, the late growing season rainfall treatments indicate that seedlings and juveniles first receive normal environmental rainfall in the early growing season, followed by different levels of rainfall during the late growing season

vs. juveniles) (Fig. 1b). To compare the effects of different rainfall intensities on *P. crymophila*, we set five rainfall levels (−75%, −50%, 0%, +50%, +75% of the average rainfall level of the study area during the growing season). The ambient condition (0%) was based on the average growing season precipitation over the past five years (2015–2020) from the Research Station of Alpine Meadow Grassland Ecosystem at the study site (Table S1). The range of rainfall intensity (−75% to +75%) is designed to encompass the extreme precipitation anomalies recoded from 2015 to 2020 in the study region. Furthermore, to assess the effects of the timing of rainfall on plant performance, we conducted two treatments of rainfall timing: one during the early growing season (3 June–1 August), and the other during the late growing season (2 August–30 September). This classification is based on plants' phenological and developmental stages. Plants generally undergo rapid vegetative growth in June and July, followed by reproduction and the initiation of nutrient resorption in August and September. For the rest of the time without rainfall treatment during the whole experiment process, all plants received the same amount of water as the control. We watered plants at a frequency of every four days, which was set based on the rainfall data at the Research Station of Alpine Meadow Grassland Ecosystem. Additionally, to assess the effects of different life stages on the response of *P. crymophila* to changes in rainfall, we selected two life stages, which were seedlings that germinated in the current spring, and juveniles that germinated in the spring of previous year. Each treatment had 20 replicates, resulting in 400 pots (2 rainfall timing levels × 5 rainfall intensity levels × 2 life stages × 20 replicates). We arranged the 400 pots in 4 randomized blocks, with a distance of 50 cm between blocks. Each block contained 100 randomly arranged pots, comprising five replicates of all 20-treatment combinations. Pots were embedded into pre-excavated holes in the alpine grassland soil, with each hole precisely matching the depth of its corresponding pot. The pots were arranged in close proximity, with minimal spacing between them.

We simulated rainfall treatments by manual watering. To avoid the effects of ambient rainfalls, we built rainout shelters, which excluded 100% of ambient precipitation during the experiment period. The shelters had minimal shading effects (< 10% reduction in photosynthetically active radiation; wavelength range: 250–700 nm) and exerted little impact on air and soil temperature. The roofs of these shelters were 1.5 m high, allowing for near surface air exchange while avoiding greenhouse effects and disturbance of ambient rainfall. We fenced the experimental area with barbed wire net to avoid animal interference. The experiment treatment initiated on 3 June, 2022 and ended on 30 September, 2022, lasting for 120 days, which approximately covered the whole growing season of *P. crymophila* on Qinghai-Tibetan Plateau.

Sampling and measurements

We measured plant height, number of leaves and root length of each seedling and juvenile before transplanting. We measured plant height and number of leaves again when the experimental treatments were applied. During the experiment period, we checked the plants' survival status and measured the height, number of leaves and tillers and reproductive status of the surviving individuals every two weeks.

At the end of the experiment, we recorded the survival status of each individual, and measured the height, number of leaves and number of tillers for each living individual. Then, we separated each plant into leaves, culms and roots. We measured the root length, recorded images of the leaf samples of each individual using a high-resolution scanner (Uniscane 53, Qinghua Ziguang, Beijing, China), and measured the total leaf area of each individual by analyzing leaf images with ImageJ (v1.32j, National Institutes of Health, Bethesda, MD, USA) (Schneider et al. 2012). We oven dried the leaves, culms and roots separately at 65 °C to determine their dry biomass. We calculated the specific leaf area (SLA) by the ratio of leaf area to leaf dry mass. We classified the combined dry biomass of leaves and culms as aboveground biomass, and defined root dry biomass as belowground biomass. We estimated root to shoot ratio as the ratio of belowground biomass to aboveground biomass. We calculated the stage-specific survival rate under each treatment as the number of individuals alive at the end of the experiment divided by the number of individuals at the initiation of the treatments. We calculated the relative growth rates ($\mathrm{RGR_M}$) of plant performance (i.e., aboveground biomass, height, number of leaves, and number of tillers) from the beginning to the end of the experiment using the following equation:

$$RGR_M = \frac{\ln M_{t_2} - \ln M_{t_1}}{t_2 - t_1}$$

where M_{t_1} and M_{t_2} represent the values of the respective plant performance measured at start (t_1) and end (t_2) of the experiment, respectively, and $t_2 - t_1$ is duration of the experiment in days (Poorter 2001).

Statistical analyses

To assess the effects of rainfall intensity, rainfall timing, and life stage on plant performance, we used mixed-effects models (MEMs). In these models, rainfall intensity, rainfall timing, life stage, and their interactions were treated as fixed effects, while block was included as a random effect. Survival was modeled using a binomial distribution with a logit link function. Growth (height, root length, number of leaves and tillers, leaf area and specific leaf area), biomass accumulation (aboveground, belowground, and total biomass), biomass allocation (root-shoot ratio), and relative growth rate (aboveground biomass, height, number of leaves, and number of tillers) were modeled using a Gaussian distribution with an identity link function. Models were fitted using the R package *lme4* (Bates et al. 2015). Fixed effects were evaluated using Wald chi-squared test from the R package *car* (Fox and Weisberg 2019), with significance determined via type-II test. When a fixed effect was significant ($P < 0.05$), post hoc pairwise comparisons among treatments were conducted using the Least Significant Difference (LSD) test on estimated marginal means derived from the mixed-effects model implemented in the R package *multcomp* (Bretz et al. 2010). The LSD test is a widely used post-hoc test to compare differences among treatment means, particularly when the number of comparisons is relatively small (Steel et al. 1997), as is the case in the current study. All analyses were performed using the software R 4.2.0 (R Core Team 2022).

Results

Survivorship

The survival of *P. crymophila* was significantly affected by life stage ($\chi^2 = 4.47$, $P = 0.047$) and marginally affected by the interaction between the intensity and timing of rainfall ($\chi^2 = 2.32$, $P = 0.08$; Table 1). The survival rate on average was significantly higher in juveniles than in seedlings (Fig. S1). In particular, the survival rate of juveniles was significantly higher than that of seedlings under the +75% treatment ($\chi^2 = 5.28$, $P = 0.03$). Furthermore, seedling survival peaked in the +50% rainfall treatment (Fig. 2a), whereas juvenile survival was highest in the +75% treatment (Fig. 2b).

Growth

Life stage significantly affected plant growth in terms of final height ($\chi^2 = 450.22$, $P < 0.001$), root length ($\chi^2 = 172.90$, $P < 0.001$), the number of leaves ($\chi^2 = 100.06$, $P < 0.001$) and tillers ($\chi^2 = 86.62$, $P < 0.001$), leaf area ($\chi^2 = 241.04$, $P < 0.001$), and the relative growth rate of height ($\chi^2 = 241.04$, $P < 0.001$; Table 1). In particular, while seedlings had a lower final height (5.28 ± 0.66 vs. 16.97 ± 1.28; Fig. S2A) and the relative growth rate of height (0.03 ± 0.004 vs. 0.09 ± 0.01; Fig. S3B) than juveniles, they had a higher number of leaves (45.86 ± 8.92 vs. 26.18 ± 3.52; Fig. S2D) and the relative growth rate of leaves (0.65 ± 0.11 vs. 0.23 ± 0.03; Fig. S3C) than juveniles by the end of the experiment. Rainfall intensity significantly affected final height ($\chi^2 = 10.89$, $P = 0.027$), root length ($\chi^2 = 11.53$, $P = 0.021$), the number of leaves ($\chi^2 = 23.33$, $P < 0.001$) and tillers ($\chi^2 = 21.07$, $P < 0.001$), leaf area ($\chi^2 = 21.67$, $P < 0.001$), the relative growth rate of height ($\chi^2 = 9.74$, $P = 0.044$), number of leaves ($\chi^2 = 25.87$, $P < 0.001$) and tillers ($\chi^2 = 21.12$, $P < 0.001$; Table 1). The height, root length, number of leaves and tillers, leaf area, and specific leaf area of juveniles increased with rainfall intensity, reaching their highest values under +75% rainfall treatment (Fig. 3b, d, f; Fig. 4b, d, f). In contrast, these growth metrics peaked under +50% rainfall in seedlings, but started to decline when rainfall was further increased to +75% (Fig. 3a, c, e; Fig. 4a, c, e). We did not detect any significant effects of rainfall timing when applied alone to any plant growth metrics (Table 1).

The interaction of life stage and rainfall intensity significantly affected the relative growth rate of leaves ($\chi^2 = 16.40$, $P = 0.002$; Table 1). In particular, the relative growth rate of height in juveniles significantly increased under +75% treatment (Fig. 5d), while the relative growth rate of leaves in seedlings significantly increased under +50% treatment (Fig. 5e). Furthermore, the interaction of rainfall timing and intensity significantly affected leaf area ($\chi^2 = 24.73$, $P < 0.001$), root length ($\chi^2 = 13.63$, $P = 0.008$), the number of leaves ($\chi^2 = 12.97$, $P = 0.011$) and tillers ($\chi^2 = 12.14$, $P = 0.016$), and the relative growth rate of leaves ($\chi^2 = 11.08$, $P = 0.025$) and tillers ($\chi^2 = 13.01$, $P = 0.011$; Table 1). With rainfall intensity held the same, drought that occurred in the early growing season had stronger negative effects on these measures than those in the late growing season, while early rainfall increase could more effectively improve these measures than late rainfall (Figs. 3–5).

Biomass accumulation and biomass allocation

Biomass accumulation, in terms of total, aboveground and belowground biomass, was jointly affected by life stage, rainfall intensity, and the interaction between timing and intensity of rainfall (Table 1). Overall, the biomass accumulation was significantly higher in juveniles than in seedlings ($\chi^2 = 6.17$, $P = 0.012$; Table 1; Fig. S4A–D). Furthermore, the biomass accumulation generally increased with rainfall intensity (Fig. 6). While the biomass accumulation in juveniles reached the maximum under +75% treatment (Fig. 6b, d, f), that of seedlings reached the maximum under +50% treatment and then remained stable or even started to decline with further increase in rainfall (Fig. 6a, e). Importantly, we found the effects of rainfall on biomass largely depended on the timing. With rainfall intensity held the same, drought that occurred at the early growing season was more harmful to biomass accumulation than that in later growing season (Fig. 6a–f), while early rainfall addition was more beneficial than late rainfall addition (Fig. 6a–f). The interaction of rainfall timing and intensity with life stage

Table 1 Results of mixed-effects models assessing the fixed effects of rainfall intensity, rainfall timing, life stages, and their interactions on plant performance (i.e., the total biomass, aboveground biomass, belowground biomass, root-shoot ratio, leaf area, specific leaf area, height, root length, and number of leaves and tillers) of *Poa crymophila*

Plant performance	**Intensity**		**Timing**		**Life stage**		**Intensity × timing**		**Intensity × life stage**		**Timing × life stage**		**Intensity × timing × life stage**	
	χ^2	*P*	χ^2	*P*	χ^2	*P*	χ^2	*P*	χ^2	*P*	χ^2	*P*	χ^2	*P*
Survival	0.94	0.462	1.33	0.262	4.47	0.047	2.32	0.080	0.98	0.438	0.04	0.849	0.34	0.848
Total biomass (g)	33.45	< 0.001	6.21	0.650	158.10	< 0.001	23.81	< 0.001	7.43	0.114	0.09	0.770	5.32	0.256
Aboveground biomass (g)	24.04	< 0.001	0.56	0.454	156.59	< 0.001	24.94	< 0.001	4.46	0.385	0.02	0.917	3.26	0.515
Belowground biomass (g)	27.04	< 0.001	0.61	0.435	150.23	< 0.001	22.31	< 0.001	8.20	0.081	0.17	0.679	6.91	0.140
Root-shoot ratio	0.84	0.933	0.95	0.330	6.17	0.012	8.62	0.051	2.68	0.612	1.19	0.275	16.96	0.001
Leaf area (cm^2)	21.67	< 0.001	0.05	0.825	241.04	< 0.001	24.73	< 0.001	3.95	0.413	0.02	0.909	4.95	0.292
Specific leaf area (cm^2/g)	3.57	0.467	0.23	0.632	1.16	0.281	2.45	0.653	1.85	0.763	0.18	0.675	0.38	0.983
Height (cm)	10.89	0.027	0.05	0.821	450.22	< 0.001	4.28	0.369	5.23	0.264	0.02	0.884	0.25	0.992
Root length (cm)	11.53	0.021	1.27	0.259	172.90	< 0.001	13.63	0.008	4.22	0.376	0.38	0.536	4.90	0.297
Number of leaves	23.33	< 0.001	1.83	0.176	100.06	< 0.001	12.97	0.011	8.84	0.065	0.78	0.375	5.76	0.218
Number of tillers	21.07	< 0.001	1.27	0.259	86.62	< 0.001	12.14	0.016	8.89	0.063	0.02	0.914	13.11	0.011
RGR of aboveground biomass	3.47	0.482	2.90	0.088	8845.95	< 0.001	8.10	0.058	1.20	0.877	3.90	0.048	5.65	0.227
RGR of height	9.74	0.044	0.96	0.326	139.45	< 0.001	7.25	0.123	3.27	0.513	0.91	0.340	1.35	0.853
RGR of leaves	25.87	< 0.001	1.83	0.176	331.34	< 0.001	11.08	0.025	16.40	0.002	1.17	0.279	9.33	0.053
RGR of tillers	21.12	< 0.001	2.12	0.145	265.09	< 0.001	13.01	0.011	9.41	0.051	0.12	0.732	11.32	0.023

Fixed effects were evaluated using Wald chi-squared tests, with significance determined via type-II tests

RGR stands for relative growth rate

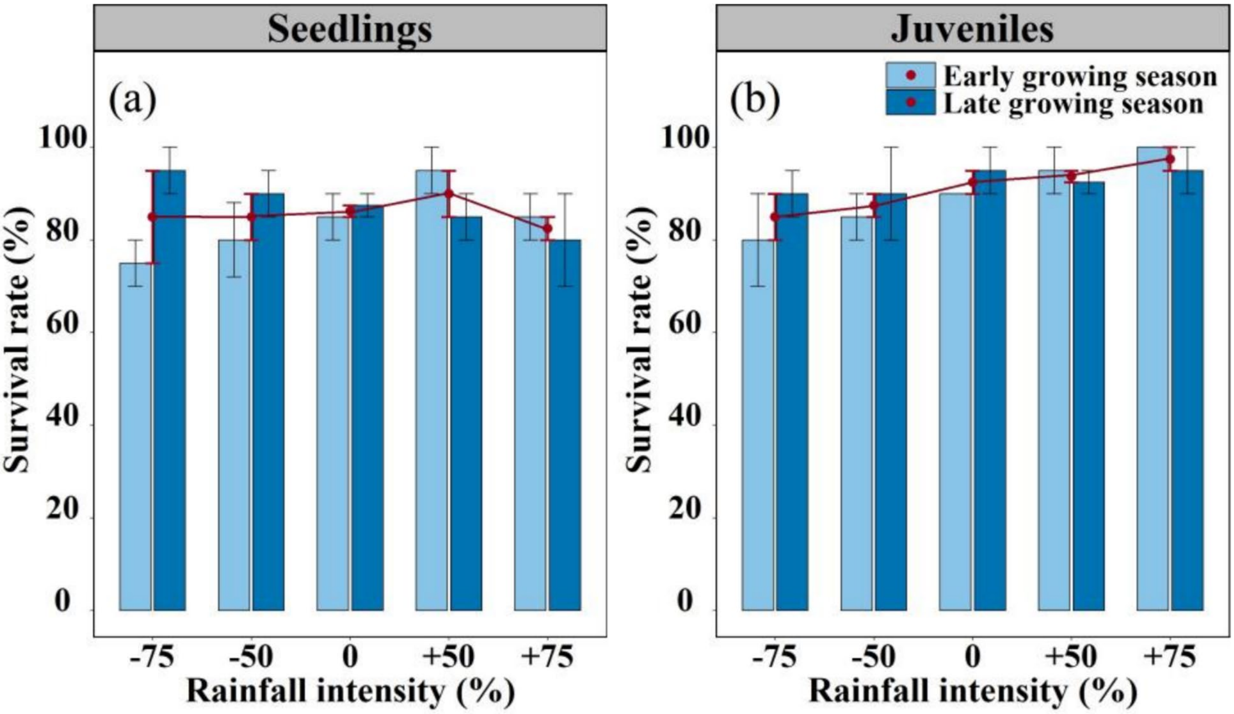

Fig. 2 Effects of rainfall intensity and timing on the survival rate in seedlings (**a**) and juveniles (**b**) of *Poa crymophila*. Error bars represent standard errors

had a significant effect on biomass allocation ($\chi^2 = 16.96$, $P = 0.001$; Table 1). Seedlings increased belowground biomass allocation to adapt to drought. Specifically, seedlings exhibited a higher root-shoot ratio under the −50% rainfall treatment when applied in the early growing season than when applied in the late growing season (Fig. 6g). In contrast, rainfall intensity and timing did not show any significant effect on the root-shoot ratio in juveniles (Fig. 6h).

Discussion

Understanding how timing and intensity of rainfall may differently affect plant performance at different life stages is critical to inform biodiversity conservation under different climate scenarios (Anees et al. 2025c; Mehmood et al. 2025a). Here we simultaneously examined the effects of changes in rainfall intensity and timing on the survival and growth of the seedlings and juveniles of *P. crymophila*, a dominant plant species on the Qinghai-Tibetan Plateau. We found that plant performance declined with reduced rainfall, but such effects were strongly regulated by the timing of rainfall. While earlier drought had more severe effects on growth, increased rainfall in the early growing season more effectively improved plant performance than comparable changes later in the season. Furthermore, we found that the threshold of increase in rainfall to benefit plant growth differed between life stages, highlighting the importance of taking life stage into account for grassland conservation under climate change.

The effects of rainfall intensity on survival and growth

Rainfall intensity is an important environmental factor for this alpine species. In our study, the survival and growth of *P. crymophila* generally increased with rainfall intensity, with the highest values observed in juveniles under the +75% treatment—the maximum rainfall level tested—supporting our hypothesis 1. High-intensity rainfall can enhance water infiltration into deeper soil layers (Bargués-Tobella et al. 2020; Haughey et al. 2020; Bauman et al. 2022). Juveniles possess significantly longer roots and a larger photosynthetic apparatus (e.g., leaf area) than seedlings. This advantage promotes water uptake with deeper root systems, and efficiently converts the abundant resources into substantial growth and biomass accumulation (Bargués-Tobella et al. 2020; Haughey et al. 2020). However, although seedling performance initially improved with increasing rainfall, it declined once rainfall exceeded +50%. This pattern suggests that seedlings may have reached water saturation at +50%, and further increases in rainfall could become detrimental to establishment, contradicting hypothesis 1. The relatively short root systems and limited photosynthetic capacity of seedlings restrict their ability to absorb and utilize

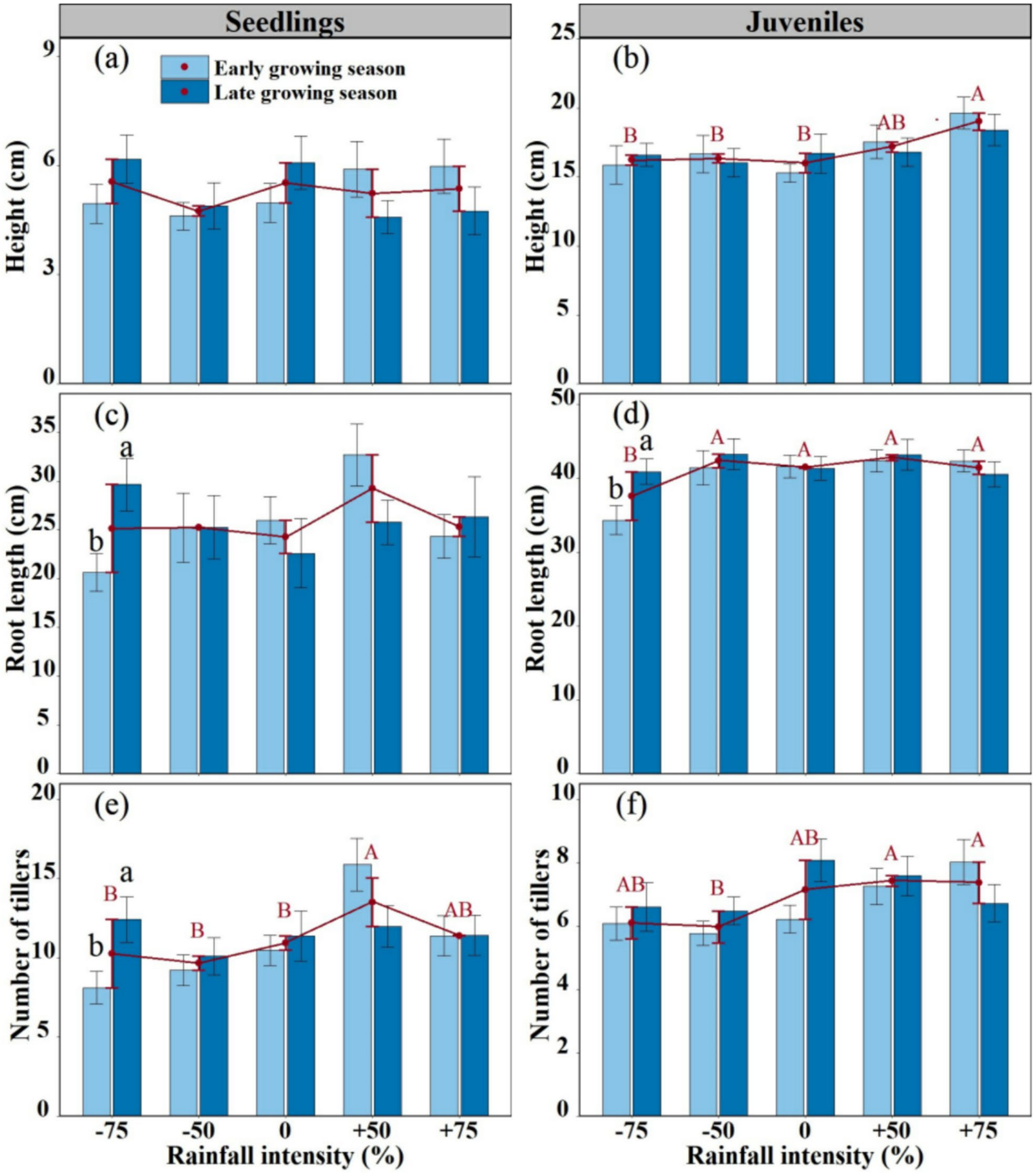

Fig. 3 Effects of rainfall intensity and timing on plant height (**a**, **b**), root length (**c**, **d**), and number of tillers (**e**, **f**) in seedlings and juveniles of *Poa crymophila*. Error bars represent standard errors. Different uppercase letters indicate significant differences among different rainfall intensity treatments. Different lowercase letters indicate significant differences between different rainfall timing treatments

resources (Poorter et al. 2012). Therefore, excess water is known to limit root oxygen availability and impair root function, nutrient uptake, and physiological activity, thereby suppressing plant growth (Reyer et al. 2013; Yang et al. 2014). For instance, O'Brien et al. (2024) reported a 48% reduction in productivity and a 92% reduction

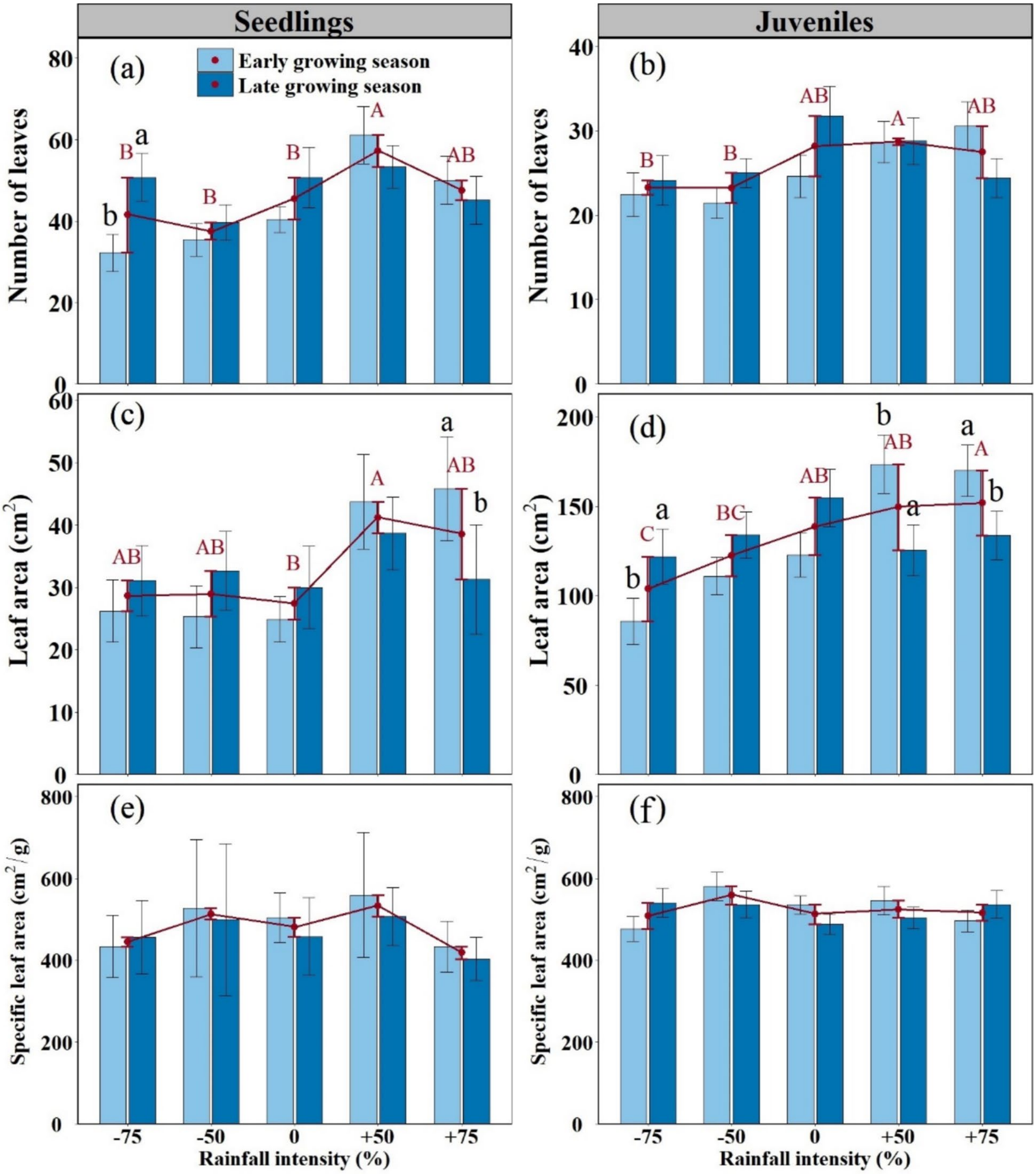

Fig. 4 Effects of rainfall intensity and timing on number of leaves (**a**, **b**), leaf area (**c**, **d**), and specific leaf area (**e**, **f**) in seedlings and juveniles of *Poa crymophila*. Error bars represent standard errors. Different uppercase letters indicate significant differences among different rainfall intensity treatments. Different lowercase letters indicate significant differences between different rainfall timing treatments

in individual survival during periods of high rainfall. Together, these findings indicate that the shift from positive to negative effects occurs at different thresholds across life stages. Our results, along with previous studies, highlight the need to evaluate rainfall changes across a gradient of intensities and multiple developmental stages.

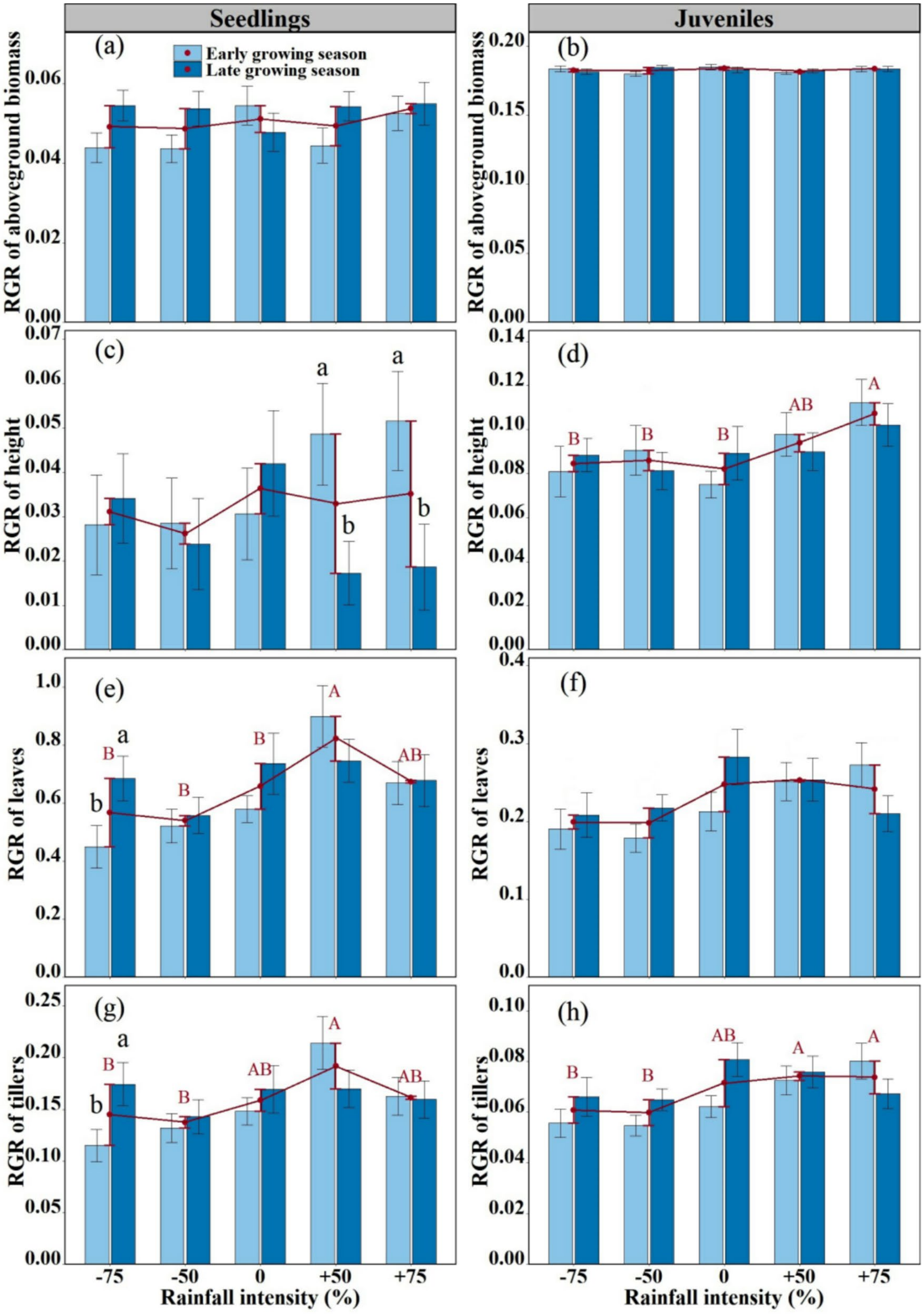

Fig. 5 Effects of rainfall intensity and timing on the relative growth rate of aboveground biomass (**a**, **b**), height (**c**, **d**), leaves (**e**, **f**), and tillers (**g**, **h**) in seedlings and juveniles of *Poa crymophila*. Error bars represent standard errors. Different uppercase letters indicate significant differences among different rainfall intensity treatments. Different lowercase letters indicate significant differences between different rainfall timing treatments

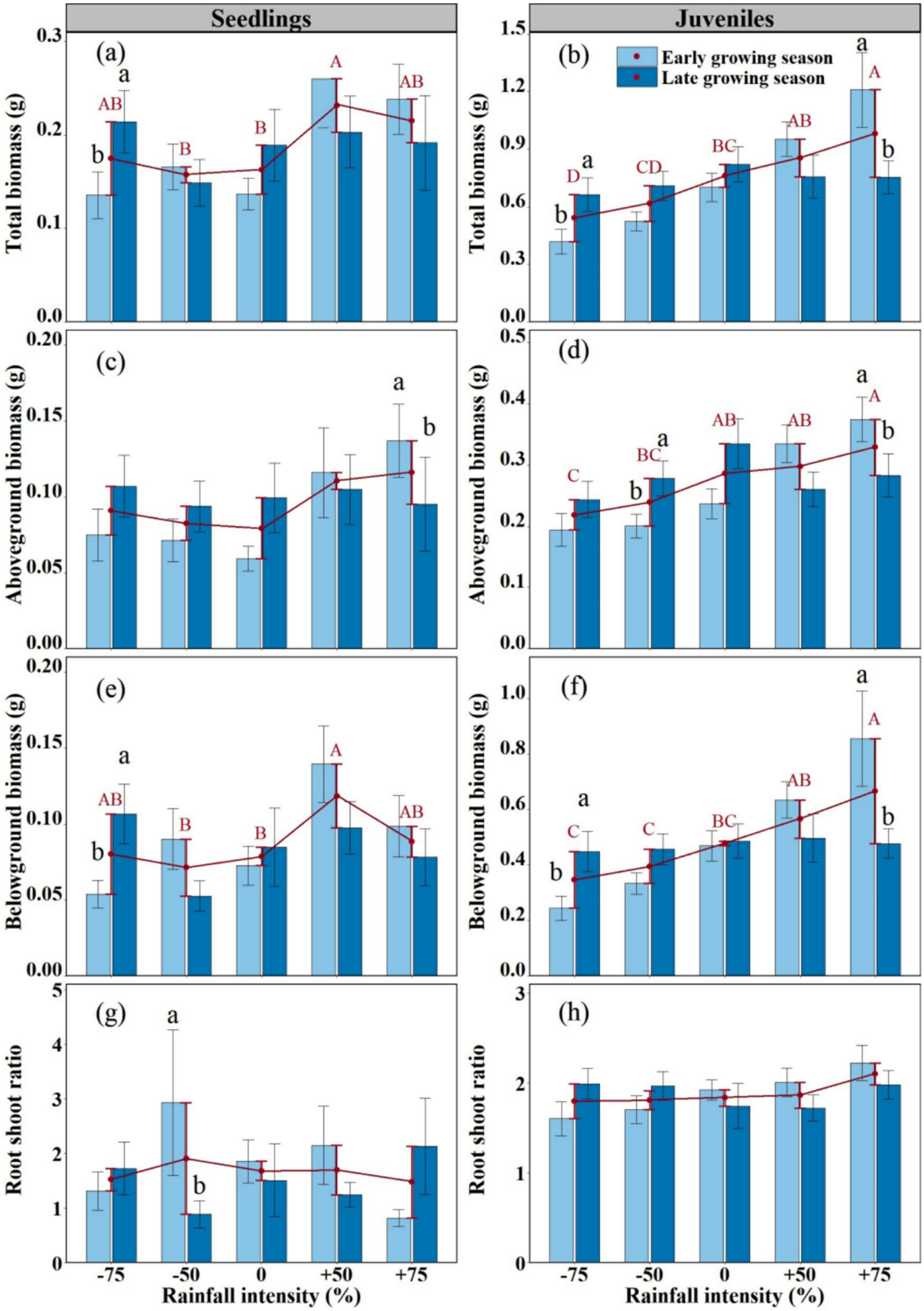

Fig. 6 Effects of rainfall intensity and timing on total biomass (**a**, **b**), aboveground biomass (**c**, **d**), belowground biomass (**e**, **f**), and root-shoot ratio (**g**, **h**) in seedlings and juveniles of *Poa crymophila*. Error bars represent standard errors. Different uppercase letters indicate significant differences among different rainfall intensity treatments. Different lowercase letters indicate significant differences between different rainfall timing treatments

The effects of rainfall timing on survival and growth

The effects of rainfall on plant performance may depend on its timing (Volder et al. 2013; Hovenden et al. 2017; Anees et al. 2025b). We found that increased rainfall in the early growing season more effectively promoted *P. crymophila* growth, whereas early drought was more detrimental. These findings support our second hypothesis that plants are more sensitive to rainfall changes in the early growing season. Plants tend to have higher demand and competition for water in the early growing season due to higher metabolic activity and growth rate at this time (Zhang et al. 2019). Adequate water availability at this time promotes deeper rooting, improves hydraulic architecture, and enhances photosynthesis and carbohydrate accumulation (Sperry and Love 2015), while early drought can reduce photosynthesis via stomatal closure, thereby suppressing growth (Wu et al. 2022; Yuan et al. 2025). Conversely, by the late growing season plants may have accumulated sufficient carbohydrate reserves and reached a stable phase of nutrient reabsorption, reducing their overall water demand (Hawkes et al. 2016; Feng et al. 2023). In addition, most leaves have entered the senescence stage during this period (Parton et al. 2012; Hermance et al. 2015), and are photosynthetically less active, which may limit a plant's ability to respond quickly to increased water input (Flexas and Medrano 2002; Funk et al. 2021). As a result, plants may respond less strongly to rainfall variation during the late growing season. This result was also consistent with findings on total community biomass (Post and Knapp 2019) and on leaf or fruit development (Misson et al. 2010). Previous studies have also found that early-season rainfall is critical for vegetation green-up and growth (Shaw et al. 2021; Mehmood et al. 2025c) and later rewatering may not offset the negative impacts of early-season drought on plant development (Hawkes et al. 2016), consistent with findings on community-level biomass responses (Hossain and Beierkuhnlein 2018; Shaw et al. 2021). Our results indicate that abundant water is more conducive to plant growth during early growing season, whereas acute water shortage during this time is more likely to lead to mortality or decreased growth (Walter et al. 2011). Our study emphasizes the importance of taking timing into account when studying the effects of rainfall variation under future climate change. Furthermore, because rangelands are widely used as livestock pastures, our findings suggest that avoiding heavy grazing is crucial to prevent additional negative impacts on plant survival and growth during early-season drought. Additionally, because the present study focused on a single species, it did not incorporate the effects of species interactions such as competition. Future experiments that explicitly include species interactions may therefore offer more comprehensive guidance for rangeland management under variable rainfall conditions.

The effects of life stage on survival and growth under variable rainfall

Plants at different life history stages may adopt different growth and biomass allocation strategies to cope with rainfall variation. In our study, seedlings allocated more biomass to roots under earlier drought, while juveniles maintained constant biomass allocation regardless of rainfall intensity or timing. These findings support our third hypothesis that seedlings are more responsive than juveniles to changes in rainfall in terms of adjustment of biomass allocation. By increasing their belowground biomass allocation, seedlings can improve their water absorption capacity in deep soil layers and thus increase their water supply to support growth under drought (Ramírez-Valiente et al. 2019). Contrastingly, juveniles with a relatively higher carbon storage may be less susceptible to water stress, which may therefore allow them to maintain a stable biomass allocation under drought. Previous studies also found that seedlings were more responsive than later life stages to changes in water supply in terms of a higher plasticity in biomass allocation (Meyer-Grünefeldt et al. 2015). Therefore, our findings together with previous studies highlight the importance of simultaneously considering the effects of the timing and intensity of rainfall, as well as the plant's developmental stage when designing conservation measures for the rangelands on the Qinghai-Tibetan Plateau.

Supplementary Information

The online version contains supplementary material available at https://doi.org/10.1186/s13717-026-00671-y.

Additional file1 (DOCX 583 KB)

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Author contributions

The study was conceived by Shou-Li Li, Yu-Kun Hu and Xue-Yan Wang. Experimental treatments, data collection and analysis were performed by Xue-Yan Wang, Shuai Jiang, Dan-Dan Li and Hai-Tao Miao. The first draft of the manuscript was written by Xue-Yan Wang. Xue-Yan Wang and Yu-Kun Hu contributed equally to this work. All authors contributed substantially to revisions. All authors read and approved the final manuscript.

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Availability of data and material

The data included in the current study are available from the corresponding author on reasonable request.

Declarations

Ethics approval and consent to participate

Not applicable.

Consent for publication

All authors approved the manuscript for publication in Ecological Processes.

Competing interests

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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References

Anees SA, Mehmood K, Khan WR, Shahzad F, Zhran M, Ayub R, Alarfaj AA, Alharbi SA, Liu QJ (2025a) Spatiotemporal dynamics of vegetation cover: integrative machine learning analysis of multispectral imagery and environmental predictors. Earth Sci Inform 18(1):152. https://doi.org/10.1007/s12145-024-01673-0

Anees SA, Mehmood K, Luo M, Abuelgasim A, Pan SA, Shahzad F, Muhammad S, Khan WR (2025b) Advancing forest fire burn severity and vegetation recovery assessments using remote sensing and machine learning approaches. Ecol Inform 92(9):103466. https://doi.org/10.1016/j.ecoinf.2025.103446

Anees SA, Mehmood K, Muhammad S, Luo M, Shahzad F, Khan WR (2025c) Spatiotemporal dynamics and environmental drivers of fractional vegetation cover in a semi-arid region using machine learning. Theor Appl Climatol 156:475(9). https://doi.org/10.1007/s00704-025-05696-5

Anees SA, Mehmood K, Rehman A, Ur Rehman N, Muhammad S, Shahzad F, Hussain K, Luo M, Alarfaj AA, Alharbi SA, Khan WR (2025d) Unveiling fractional vegetation cover dynamics: a spatiotemporal analysis using MODIS NDVI and machine learning. Environ Sustain Indic 24:100485. https://doi.org/10.1016/j.indic.2024.100485

Augustine SP, Reinhardt K (2018) Differences in morphological and physiological plasticity in two species of first-year conifer seedlings exposed to drought result in distinct survivorship patterns. Tree Physiol 39(8):1446–1460. https://doi.org/10.1093/treephys/tpz048

Bargués-Tobella A, Hasselquist NJ, Bazié HR, Bayala J, Laudon H, Ilstedt U (2020) Trees in African drylands can promote deep soil and groundwater recharge in a future climate with more intense rainfall. Land Degrad Dev 31(1):81–95. https://doi.org/10.1002/ldr.3430

Bates D, Mächler M, Bolker BM (2015) Fitting linear mixed-effects models using lme4. J Stat Softw 67:1–48

Bauman D, Fortunel C, Cernusak LA, Bentley L, McMahon SM, Rifai SW, Aguirre Gutiérrez J, Oliveras I, Bradford M, Laurance SGW, Delhaye G, Hutchinson MF, Dempsey R, McNellis BE, Santos-Andrade PE, Ninantay-Rivera HR, Paucar JRC, Phillips OL, Malhi Y (2022) Tropical tree growth sensitivity to climate is driven by species intrinsic growth rate and leaf traits. Glob Change Biol 28(4):1414–1432. https://doi.org/10.1111/gcb.15982

Bond BJ (2000) Age-related changes in photosynthesis of woody plants. Trends Plant Sci 5(8):349–353. https://doi.org/10.1016/s1360-1385(00)01691-5

Bretz F, Hothorn T, Westfall P (2010) Multiple comparisons using R. CRC Press, Boca Raton

Cavender-Bares J, Bazzaz FA (2000) Changes in drought response strategies with ontogeny in *Quercus rubra*: implications for scaling from seedlings to mature trees. Oecologia 124(1):8–18. https://doi.org/10.1007/pl00008865

Chai YF, Miao CY, Slater L, Berghuijs WR, Chen TX, Huntingford C (2025) Underestimating global land greening: future vegetation changes and their impacts on terrestrial water loss. One Earth 8(2):101176. https://doi.org/10.1016/j.oneear.2025.101176

Cui SY, Xiao YS, Zhou Y, Peng FW, Cui LQ, Guo Z (2023) Variations in diversity, composition, and species interactions of soil microbial community in response to increased N deposition and precipitation intensity in a temperate grassland. Ecol Process 12:35. https://doi.org/10.1186/s13717-023-00445-w

Derner JD, Hess BW, Olson RA, Schuman G (2008) Functional group and species responses to precipitation in three semi-arid rangeland ecosystems. Arid Land Res Manage 22(1):81–92. https://doi.org/10.1080/15324980701784274

Ding Z, Ha Y, Huangfu JL, Zhong Z (2024) What distinguishes summer extreme precipitation from non-extreme precipitation over the Tibetan Plateau? Geophys Res Lett 51(20):e2024GL11119. https://doi.org/10.1029/2024gl111192

Feng SM, Zhang ZK, Zhao SH, Guo XY, Zhu WY, Das P (2023) Time lag effect of vegetation response to seasonal precipitation in the Mara River Basin. Ecol Process 12:49. https://doi.org/10.1186/s13717-023-00461-w

Flexas J, Medrano H (2002) Drought-inhibition of photosynthesis in C_3 plants: stomatal and non-stomatal limitations revisited. Ann Bot 89(2):183–189. https://doi.org/10.1093/aob/mcf027

Fox J, Weisberg S (2019) An R companion to applied regression, 3rd edn. SAGE Publications Inc, Christopher Hare

Funk JL, Larson JE, Vose G (2021) Leaf traits and performance vary with plant age and water availability in *Artemisia californica*. Ann Bot 127(4):495–503. https://doi.org/10.1093/aob/mcaa106

Haughey E, McElwain JC, Finn JA (2020) Variability of water supply affected shoot biomass and root depth distribution of four temperate grassland species in monocultures and mixtures. J Plant Ecol 13(5):554–562. https://doi.org/10.1093/jpe/rtaa044

Hawkes CV, Fierer N, Goulden ML (2016) The role of water availability in plant nutrient resorption. Oecologia 182:767–778

Hermance JF, Augustine DJ, Derner JD (2015) Quantifying characteristic growth dynamics in a semi-arid grassland ecosystem by predicting short-term NDVI phenology from daily rainfall: a simple four parameter coupled-reservoir model. Int J Remote Sens 36(22):5637–5663. https://doi.org/10.1080/01431161.2015.1103916

Holdrege MC, Beard KH, Kulmatiski A (2020) Woody plant growth increases with precipitation intensity in a cold semiarid system. Ecology 102(1):e03212. https://doi.org/10.1002/ecy.3212

Hossain ML, Beierkuhnlein C (2018) Enhanced aboveground biomass by increased precipitation in a central European grassland. Ecol Process 7:37. https://doi.org/10.1186/s13717-018-0149-1

Hovenden MJ, Newton PCD, Porter M (2017) Elevated CO_2 and warming effects on grassland plant mortality are determined by the timing of rainfall. Ann Bot 119(7):1225–1233. https://doi.org/10.1093/aob/mcx006

IPCC (2022) Summary for policymakers. In: Climate change 2022: impacts, adaptation and vulnerability. Contribution of working group II to the sixth assessment report of the intergovernmental panel on climate change. Cambridge University Press, Cambridge

Jiang F, Jin GZ (2021) Functional traits influence plant survival depending on environmental contexts and life stages in an old-growth temperate forest. J Plant Ecol 14(5):981–994. https://doi.org/10.1093/jpe/rtab049

Jiang F, Cadotte MW, Jin G (2022) Size- and environment-driven seedling survival and growth are mediated by leaf functional traits. Proc R Soc B Biol Sci 289(1983):20221400. https://doi.org/10.1098/rspb.2022.1400

Kaur N, Hui D, Riccuito DM, Mayes MA, Tian HQ (2023) Response patterns of simulated corn yield and soil nitrous oxide emission to precipitation change. Ecol Process 12:17. https://doi.org/10.1186/s13717-023-00429-w

Kørup K, Laerke PE, Baadsgaard H, Andersen MN, Kristensen K, Münnich C, Didion T, Jensen ES, Mårtensson LM, Jørgensen U (2017) Biomass production and water use efficiency in perennial grasses during and after drought stress. GCB Bioenergy 10(1):12–27. https://doi.org/10.1111/gcbb.12464

Li XY, Zuo XA, Yue P, Zhao XY, Hu Y, Guo XX, Guo AX, Xu C, Yu Q (2021) Drought of early time in growing season decreases community aboveground biomass, but increases belowground biomass in a desert steppe. Ecol Evol 21(1):106. https://doi.org/10.1186/s12862-021-01842-5

Li C, Han H, Ablimiti M, Liu R, Zhang H, Fan JL (2022a) Morphological and physiological responses of desert plants to drought stress in a man-made landscape of the Taklimakan desert shelter belt. Ecol Indic 140:109307. https://doi.org/10.1016/j.ecolind.2022.109037

Li W, Wang LW, Qian SF, He MY, Cai XJ, Ding JQ (2022b) Root characteristics explain greater water use efficiency and drought tolerance in invasive Compositae plants. Plant Soil 483(1–2):209–223. https://doi.org/10.1007/s11104-022-05734-5

Li Y, He M, Du YZ, Wang XP, Zhang H, Dai ZC, Wan JSH, Sun JQ, Wang CY, Du DL (2022c) Indigenous PGPB inoculant from Qinghai-Tibetan Plateau soil confer drought-stress tolerance to local grass *Poa annua*. Int J Environ Res 16(5):85. https://doi.org/10.1007/s41742-022-00470-1

Liu HY, Mi ZR, Lin L, Wang YH, Zhang ZH, Zhang FW, Wang H, Liu LL, Zhu B, Cao GM, Zhao XQ, Sanders NJ, Classen AT, Reich PB, He JS (2018) Shifting plant species composition in response to climate change stabilizes grassland primary production. PNAS 115(16):4051–4056. https://doi.org/10.1073/pnas.1700299114

Lum TD, Barton KE (2020) Ontogenetic variation in salinity tolerance and ecophysiology of coastal dune plants. Ann Bot 125(2):301–314. https://doi.org/10.1093/aob/mcz097

Mehmood K, Anees SA, Muhammad S, Albasher G, Shahzad F, Hussain K, Liu QJ, Ayub R, Khan WR (2025a) Spatial and temporal vegetation dynamics from 2000 to 2023 in the Western Himalayan regions. Stoch Environ Res Risk Assess 39(6):2309–2330. https://doi.org/10.1007/s00477-025-02971-9

Mehmood K, Anees SA, Shahzad F, Muhammad S, Liu QJ, Khan WR, Shah M, Jamjareegulgarn P (2025b) Exploring vegetation health in Southern Thailand under climate stress from temperature and water impacts between 2000 and 2023. Sci Rep 15(1):30491. https://doi.org/10.1038/s41598-025-16293

Mehmood K, Anees SA, Muhammad S, Shahzad F, Liu QJ, Khan WR, Shrahili M, Ansari MJ, Dube T (2025c) Machine learning and spatio temporal analysis for assessing ecological impacts of the Billion Tree Afforestation Project. Ecol Evol 15(2):e70736. https://doi.org/10.1002/ece3.70736.

Meyer-Grünefeldt M, Friedrich U, Klotz M, Von Oheimb G, Härdtle W (2015) Nitrogen deposition and drought events have non-additive effects on plant growth-evidence from greenhouse experiments. Plant Biosyst 149(2):424–432. https://doi.org/10.1080/11263504.2013.853699

Misson L, Limousin JM, Rodriguez R, Letts MG (2010) Leaf physiological responses to extreme droughts in Mediterranean *Quercus ilex* forest. Plant Cell Environ 33(11):1898–1910. https://doi.org/10.1111/j.1365-3040.2010.02193.x

O'Brien MJ, Hector A, Ong R, Philipson D (2024) Tree growth and survival are more sensitive to high rainfall than drought in an aseasonal forest in Malaysia. Commun Earth Environ 5(1):179. https://doi.org/10.1038/s43247-024-01335-5

Parton W, Morgan J, Smith D, Grosso SD, Prihodko L, LeCain D, Kelly R, Lutz S (2012) Impact of precipitation dynamics on net ecosystem productivity. Glob Change Biol 18(3):915–927. https://doi.org/10.1111/j.1365-2486.2011.02611.x

Pastore MA (2022) Bringing the underground to the surface: climate change stressors negatively affect plant growth, with contrasting above and belowground physiological responses. Plant Cell Environ 45(8):2267–2270. https://doi.org/10.1111/pce.14379

Poorter L (2001) Light-dependent changes in biomass allocation and their importance for growth of rain forest tree species. Funct Ecol 15(1):113–123. https://doi.org/10.1046/j.1365-2435.2001.00503.x

Poorter H, Niklas KJ, Reich PB, Oleksyn J, Poot P, Mommer L (2012) Biomass allocation to leaves, stems and roots: meta-analyses of interspecific variation and environmental control. New Phytol 193(1):30–50. https://doi.org/10.1111/j.1469-8137.2011.03952.x

Post AK, Knapp AK (2019) Plant growth and aboveground production respond diferently to late-season deluges in a semi-arid grassland. Oecologia 191(3):673–683. https://doi.org/10.1007/s00442-019-04515-9

R Core Team (2022) R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna

Ramírez-Valiente JA, Aranda I, Sanchéz-Gómez D, Rodríguez-Calcerrada J, Valladares F, Robson TM (2019) Increased root investment can explain the higher survival of seedlings of 'Mesic' *Quercus suber* than 'xeric' *Quercus ilex* in sandy soils during a summer drought. Tree Physiol 39(1):64–75. https://doi.org/10.1093/treephys/tpy084

Reyer CPO, Leuzinger S, Rammig A, Wolf A, Bartholomeus PB, Bonfante BA, de Lorenzi F, Dury M, Gloning P, Jaoudé RA, Klein T, Kuster TM, Martins M, Niedrist G, Riccardi M, Wohlfahrt G, de Angelis P, de Dato G, François L, Menzel A, Pereira M (2013) A plant's perspective of extremes: terrestrial plant responses to changing climatic variability. Glob Change Biol 19(1):75–89. https://doi.org/10.1111/gcb.12023

Schneider CA, Rasband WS, Eliceiri KW (2012) NIH image to ImageJ: 25 years of image analysis. Nat Methods 9(7):671–675. https://doi.org/10.1038/nmeth.2089

Shaw EA, White CT, Silver WL, Suding KN, Hallett LM (2021) Intra-annual precipitation effects on annual grassland productivity and phenology are moderated by community responses. J Ecol 110(1):162–172. https://doi.org/10.1111/1365-2745.13792

Shen-Tu XL, Hu YK, Shea K, Gascoigne SJL, Wei Q, Tang LC, Li DD, Li SL (2025) Seedling size affects the strategy of dune seedlings responding to rainfall variation. Ann Bot 135(6):1125–1134. https://doi.org/10.1093/aob/mcaf017

Song ZP, Liu YH, Su HX, Hou JH (2020) N-P utilization of *Acer mono* leaves at different life history stages across altitudinal gradients. Ecol Evol 10(2):851–862. https://doi.org/10.1002/ece3.5945

Sperry JS, Love DM (2015) What plant hydraulics can tell us about responses to climate-change droughts. New Phytol 207(1):14–27. https://doi.org/10.1111/nph.13354

Steel RGD, Torrie JH, Dickey DA (1997) Principles and procedures of statistics: a biometrical approach, 3rd edn. McGraw-Hill, New York

Trew BT, Maclean IMD (2021) Vulnerability of global biodiversity hotspots to climate change. Glob Ecol Biogeogr 30(4):768–783. https://doi.org/10.1111/geb.13272

Volder A, Briske DD, Tjoelker MG (2013) Climate warming and precipitation redistribution modify tree-grass interactions and tree species establishment in a warm-temperate savanna. Glob Change Biol 19(3):843–857. https://doi.org/10.1111/gcb.12068

Walter J, Nagy L, Hein R, Rascher U, Beierkuhnlein C, Willner E, Jentsch A (2011) Do plants remember drought? Hints towards a drought-memory in grasses. Environ Exp Bot 71(1):34–40. https://doi.org/10.1016/j.envexpbot.2010.10.020

Wang H, Liu HY, Huang N, Bi J, Ma XL, Ma ZY, Shangguan ZJ, Zhao HF, Feng QS, Liang TG, Cao GM, Schmid B, He JS (2021) Satellite-derived ndvi underestimates the advancement of alpine vegetation growth over the past three decades. Ecology 102(12):e03518. https://doi.org/10.1111/ele.13474

Webster CL, Kilminster KL, Alarcón MS, Bennett K, Strydom S, McNamara S, Lavery PS, McMahon KM (2021) Population-specific resilience of *Halophila ovalis* seagrass habitat to unseasonal rainfall, an extreme climate event in estuaries. J Ecol 109(9):3260–3279. https://doi.org/10.1111/1365-2745.13648

Wei L, Zhang CP, Dong QM, Yang ZZ, Chu Y, Yu Y, Yang XX (2021) Effects of temperature and water potential on seed germination of 13 *Poa* L. species in the Qinghai-Tibetan Plateau. Glob Ecol Conserv 25:e01442. https://doi.org/10.1016/j.gecco.2020.e01442

Wu T, Tan ND, Tissue DT, Huang J, Duan HL, Su W, Song YT, Liu XJ, Liu Y, Li X, Lie ZY, Yang SM, Zhou SYD, Yan JH, Tang XL, Liu SZ, Chu GW, He XH, Liu JX (2022) Physiological traits and response strategies of four subtropical tree species exposed to drought. Environ Exp Bot 203:105046. https://doi.org/10.1016/j.envexpbot.2022.105046

Xu ZX, Gong TL, Li JY (2008) Decadal trend of climate in the Tibetan Plateau: regional temperature and precipitation. Hydrol Process 22(16):3056–3065. https://doi.org/10.1002/hyp.6892

Yang YF, Gao Y, Wang SP, Xu DP, Yu H, Wu LW, Lin QY, Hu YG, Li XZ, He ZL, Deng Y, Zhou JZ (2013) The microbial gene diversity along an elevation gradient of the Tibetan grassland. ISME J 8(2):430–440. https://doi.org/10.1038/ismej.2013.146

Yang QY, Zhao WZ, Liu B, Hu L (2014) Physiological responses of *Haloxylon ammodendron* to rainfall pulses in temperate desert regions, Northwestern China. Trees 28(3):709–722. https://doi.org/10.1007/s00468-014-0983-4

Yu LX, Liu Y, Shen MG, Yu ZC, Li X, Liu HJ, Lyne V, Jiang M, Wu CY (2025) Extreme hydroclimates amplify the biophysical effects of advanced green-up in temperate China. Agric For Meteorol 363:110421. https://doi.org/10.1016/j.agrformet.2025.110421

Yuan JF, Gao ST, Fang YT, Wang AY, Liu DW, Yu LZ, Zhang T, Yan QL, Li RP (2025) Drought aggravates the negative effects of warming on the growth of drought-intolerant tree seedlings in temperate forests. Ecol Process 14:81. https://doi.org/10.1186/s13717-025-00645-6

Zhang ZZ, Shan LS, Li Y (2018) Prolonged dry periods between rainfall events shorten the growth period of the resurrection plant *Reaumuria soongorica*. Ecol Evol 8(2):920–927. https://doi.org/10.1002/ece3.3614

Zhang XL, Manzanedo RD, D'Orangeville L, Rademacher TT, Li JX, Bai XP, Hou MT, Chen ZJ, Zou FH, Song FB, Pederson N (2019) Snowmelt and early to mid-growing season water availability augment tree growth during rapid warming in southern Asian boreal forests. Glob Change Biol 25(10):3462–3471. https://doi.org/10.1111/gcb.14749

Zhang WC, Zhao Y, Frouz J, Xue PF, Li JB, Suo LZ, Song B, Wang HX (2026) The impact of precipitation on N_2O emissions during the freeze-thaw cycle in a typical grassland in Inner Mongolia. Soil Tillage Res 255:106774. https://doi.org/10.1016/j.still.2025.106774

Zhou WS, Wu N, Bao WK (2010) Growth and potential reproduction of *Poa crymophila* in response to season precipitation shortage in the Eastern Tibetan Plateau. China. Russ J Ecol 41(2):147–152. https://doi.org/10.1134/s1067413610020062

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