

Precipitation amount and frequency affect seedling emergence and growth of *Reaumuria soongarica* in northwestern China postprint

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Abstract

Climate change is shifting the amount and frequency of precipitation in many regions, which is expected to affect seedling recruitment across ecosystems. However, the combined effects of precipitation amount and frequency on seedling recruitment remain largely unknown. An understanding of the effects of precipitation amount and frequency and their interaction on seedling emergence and growth of typical desert plants is vital for managing populations of desert plants. We conducted two experiments to study the effects of variation in precipitation on *Reaumuria soongarica* (Pall.) Maxim. First, greenhouse experiments were conducted to examine the effects of three precipitation amount treatments (ambient, +30%, and -30%) and two precipitation frequency treatments (ambient and -50%) on seedling emergence. Second, the morphological responses of *R. soongarica* to changes in precipitation amount and frequency were tested in a controlled field experiment. Stage-specific changes in growth were monitored by sampling in different growth seasons. Our results showed that precipitation amount significantly affected germination, seedling emergence, and growth of *R. soongarica*, and there was a larger effect with decreased precipitation frequency compared with ambient. Germination and seedling emergence increased as precipitation increased under the same frequency of precipitation. The highest emergence percentage was obtained with a 30% increase in precipitation amount and a 50% reduction in precipitation frequency. Compared with ambient precipitation, a 30% increase in precipitation amount increased above- and below-ground biomass accumulation of *R. soongarica* during the growth season. A decrease of 30% in precipitation amount also resulted in an increase in below-ground biomass and root/shoot ratio in the early stages of the growth season, however, above- and below-ground biomass showed the opposite results at the end of the growth season, with larger effects on above-ground than below-ground biomass under decreased precipitation frequency. When precipitation

frequency decreased by 50%, values of all growth traits increased for a given amount of precipitation. We concluded that precipitation frequency may be as important as precipitation amount to seedling emergence and growth of *R. soongarica*, and that understanding the effects of precipitation variability on seedling recruitment requires the integration of both precipitation amount and frequency. In particular, the combination of a 30% increase in precipitation amount and 50% reduction in precipitation frequency increased the emergence and growth of seedlings, suggesting that alteration of amount and frequency of precipitation caused by climate change may have significant effects on seedling recruitment of *R. soongarica*.

Full Text

Preamble

Precipitation Amount and Frequency Affect Seedling Emergence and Growth of *Reaumuria soongarica* in Northwestern China

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Abstract

Climate change is altering precipitation amount and frequency in many regions, which is expected to affect seedling recruitment across ecosystems. However, the combined effects of precipitation amount and frequency on seedling recruitment remain largely unknown. Understanding how these factors and their interactions influence seedling emergence and growth of typical desert plants is vital for managing desert plant populations. We conducted two experiments to investigate the effects of precipitation variation on *Reaumuria soongarica* (Pall.) Maxim. First, greenhouse experiments examined the effects of three precipitation amount treatments (ambient, +30%, and -30%) and two precipitation frequency treatments (ambient and -50%) on seedling emergence. Second, morphological responses of *R. soongarica* to changes in precipitation amount and frequency were tested in a controlled field experiment, with stage-specific growth changes monitored by sampling at different points in the growing season. Our results showed that precipitation amount significantly affected germination, seedling emergence, and growth of *R. soongarica*, with a larger effect observed under decreased precipitation frequency compared to ambient conditions. Germination and seedling emergence increased with precipitation amount under the same frequency. The highest emergence percentage occurred with a 30% in-

crease in precipitation amount combined with a 50% reduction in precipitation frequency.

Compared with ambient precipitation, a 30% increase in precipitation amount increased above- and below-ground biomass accumulation during the growth season. A 30% decrease in precipitation amount also resulted in increased below-ground biomass and root/shoot ratio during early growth stages; however, above- and below-ground biomass showed opposite results by the end of the growth season, with larger effects on above-ground biomass under decreased precipitation frequency. When precipitation frequency decreased by 50%, all growth trait values increased for a given precipitation amount. We conclude that precipitation frequency may be as important as precipitation amount for seedling emergence and growth of *R. soongarica*, and that understanding the effects of precipitation variability on seedling recruitment requires integrating both factors. In particular, the combination of a 30% increase in precipitation amount and 50% reduction in precipitation frequency enhanced seedling emergence and growth, suggesting that climate change-induced alterations in precipitation amount and frequency may have significant effects on seedling recruitment of *R. soongarica*.

Keywords: precipitation patterns; seedling emergence; biomass; root/shoot ratio; seedling recruitment

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1 Introduction

Climate change has altered precipitation patterns, leading to more extreme precipitation events and prolonged drought conditions (Diffenbaugh and Field, 2013; Westra et al., 2014), particularly in dryland areas (Miranda et al., 2011). These changes affect local hydrological processes, which ultimately influence soil water availability to plants (Craine et al., 2012; Zhang et al., 2013; Shi et al., 2014). However, the influence of precipitation amount and frequency on desert vegetation and plant responses to these changes remain unclear.

The regeneration stage is critical for plants to complete their life history, with seed germination, emergence, and seedling establishment forming the core of population regeneration (Fay and Schultz, 2009; Dalglish et al., 2010). Seedling emergence and growth are sensitive to precipitation amount and frequency (Dalglish et al., 2010; Zeppel et al., 2014; Zhu et al., 2014; Gao et al., 2015). Previous research has shown that increasing precipitation amount enhances seed germination (Torres-Martínez et al., 2017), seedling emergence (Robinson and Gross, 2010), and growth (Schneider et al., 2014; Didiano et al., 2016). Similar positive relationships between precipitation and seedling emergence and growth have been reported for the sandy desert shrub *Artemisia sphaerocephala* in the

Ordos Plateau, China (Yang et al., 2012), and for the dune grass *Leymus secalinus* in the Mu Us Sandy Land, China (Zhu et al., 2014). Some studies have determined that precipitation frequency is also a key factor affecting seedling emergence and growth (Schneider et al., 2014; Gao et al., 2015; Gibson-Forty et al., 2016), with both processes decreasing as precipitation frequency declines (Zhu et al., 2014). Additionally, shifts in precipitation patterns can have different and potentially greater ecological consequences for plants than changes in precipitation amount alone (Reyer et al., 2013; Robinson et al., 2013), particularly in desert ecosystems. Thus, exploring the effects of precipitation amount, frequency, and their interactions is necessary. However, current studies have focused on plants in grassland and forest ecosystems (Dalglish et al., 2010; Schneider et al., 2014; Didiano et al., 2016), while no studies have been conducted in desert ecosystems where plants are especially sensitive to moisture changes.

Phenotypic plasticity is the capacity for a given genotype to express different phenotypes under heterogeneous environments (Geange et al., 2017). Biomass allocation plasticity is a component of phenotypic plasticity that enables plants to cope with unpredictable environments. Recent studies report that altered precipitation trends, with less frequent and larger precipitation events, are expected to increase in the future (Yue et al., 2013). Such events will likely impact biomass accumulation and allocation (Hoover et al., 2014; Knapp et al., 2015; Wilcox et al., 2015). While some studies showed increased biomass accumulation with increasing precipitation variability (Wang et al., 2012; Kang et al., 2013; Li et al., 2014), others showed opposite responses (Gherardi and Sala, 2015). Furthermore, the influence of precipitation on biomass accumulation and allocation is typically documented through single-pulsed events in grassland ecosystems, while fewer studies in desert ecosystems manipulate precipitation patterns (such as amount and frequency) to illuminate how a series of pulse events affect desert plants (Thomey et al., 2011).

Reaumuria soongarica (Pall.) Maxim. is an extreme xerophytic and salt-tolerant semi-shrub that serves as a constructive and dominant species in desert shrub vegetation, widely distributed in desert regions including sand dunes and the Gobi desert of Central Asia (Shi et al., 2013). This species plays a major role in mitigating desertification and over-grazing effects and may be considered a keystone species and indicator of Gobi desert communities (Ma et al., 2007). Furthermore, *R. soongarica* is recognized as an important forage species and major source of salt for livestock (Yang et al., 2015). Previous studies on this species have focused on its morphology and anatomy (Liu et al., 2007; Wang et al., 2011a), genetic diversity (Yang et al., 2015), stress-resistance mechanisms (Xu et al., 2010), and adaptive strategies to desiccation (Wang et al., 2011b). Despite some work demonstrating links between seed germination, seedling emergence, and water availability in *R. soongarica*, the relationships among seedling emergence, growth, and recruitment with precipitation variability are not fully understood. We hypothesized that projected variation in precipitation amount and frequency caused by climate change will alter seedling emergence and growth

of *R. soongarica* seedlings, thereby significantly impacting recruitment of this species.

We aimed to answer the following questions: (1) How do *R. soongarica* seedling emergence and growth respond to altered rainfall events? (2) Can less-frequent and larger precipitation events enhance seedling emergence and growth of *R. soongarica* and thus promote seedling recruitment? (3) Which traits—seedling emergence, germination index, vigor index, relative growth rate, above- and below-ground biomass, or root-shoot ratio—are most impacted by changes in precipitation patterns?

2.1 Experimental Site and Seed Collection

The experiment was conducted during the 2014 growth season of *R. soongarica* at the Linze Inland River Basin Research Station, Chinese Academy of Sciences, located at the southern edge of the Badain Jaran Desert (39°19' -39°21' N, 100°02' -100°21' E), the third largest desert in China by area. The region has a temperate arid desert climate with average annual precipitation of 117 mm and mean annual evaporative demand >2390 mm; over 80% of precipitation occurs between May and September. From 2005 to 2015, precipitation amount and frequency decreased and exhibited substantial inter-annual fluctuations [Figure 1: see original paper]. During growth seasons (May to October) from 2005 to 2015, the mean annual number of rainy days was 31 d, with a mean interval between precipitation events of 5.9 d [Figure 2: see original paper]. Annual average temperature was 7.6°C, with a maximum of 39°C and minimum of -27°C. The frost-free period lasted approximately 165 d.

During the 2014 growth season, monthly mean temperature was 18.2°C and total rainfall was 98.6 mm based on meteorological records from the Linze Inland River Basin Research Station. Capsules of *R. soongarica* were collected in October 2013 from natural populations in the Gobi desert near the station. In the laboratory, capsules were laid open at room temperature for approximately 4 weeks for natural air drying and after-ripening. Thereafter, capsules were manually shaken to obtain seeds, which were stored in closed cotton bags at -18°C until use.

2.2 Experimental Design

Two experiments were conducted: one on seedling emergence and another on subsequent seedling growth. The same treatments were applied to both experiments.

Seedling emergence experiments were conducted in a non-heated greenhouse. Initially, 360 healthy, average-sized seeds were selected and soaked in water for 24 h at 25°C to break dormancy. Plastic pots (height × top diameter × bottom diameter = 20 cm × 25 cm × 18 cm) were filled with native soil to within 1 cm of the top. Twenty seeds were placed in each pot, with 3 pots (replicates) per

treatment. Emergence was recorded daily and defined as the presence of two leaves 5 mm above the soil surface. A few seedlings emerged during days 1–6, while the majority emerged on day 7.

We employed a fully factorial, randomized complete block design to examine precipitation amount and frequency effects on seedling growth. Eighteen plots were demarcated across approximately 48 m² (6 m × 8 m) at the study site in May 2014 [Figure 2: see original paper]. Each plot (1 m × 1 m) was situated at least 0.2 m from other plots in the same block. Impermeable plastic film buried to 1 m depth prevented seepage between neighboring plots. Seeds were soaked in water at 25°C for 24 h to break innate dormancy on 20 May 2014. Eighty seeds were sown at 0.5–1.0 cm depth in a grid pattern spaced 0.2 m apart, with 5 seeds sown at each grid junction. After emergence, 50 seedlings were retained per plot, and simulated precipitation began after 1 month.

Natural precipitation was diverted by shelters constructed with sloping wooden roofs covered with transparent polycarbonate sheets (1.1 m × 1.1 m). The plastic sheeting was transparent and did not affect illumination. Shelters were deployed over all blocks when rain was forecasted from 1 July to 31 October 2014, placed at a minimum height of 0.5 m to allow near-surface air exchange, thus avoiding greenhouse effects. Shelters were removed on rainless days to minimize effects on other environmental variables.

2.3 Precipitation Pattern

Average annual precipitation in this region was 117 mm during 1967–2008 based on records from the Linze Inland River Basin Research Station. Inter-annual variation in precipitation amount over 50 years ranged from -29% to +36%, prompting our use of a 30% alteration in precipitation amount. We established a precipitation gradient of 70% (30% decrease), 100% (ambient), and 130% (30% increase), designated as W-, W, and W+, respectively.

Current climate change predictions indicate a 50% increase in the interval between precipitation events (i.e., precipitation frequency reduced by half) can be expected (IPCC, 2014). The Badain Jaran Desert climate has changed tremendously over the past 50 years, particularly in precipitation patterns (Ma et al., 2011). Climate models forecast reductions in annual precipitation and increased prevalence of extreme events, including longer intervals between precipitation events and fewer rainy days (Yue et al., 2013). Meteorological records at the Linze Inland River Basin Research Station show mean monthly precipitation frequency during the growth season is 5.9 events (31 total events from May to October). Thus, each precipitation amount had two frequency treatments: (1) ambient (6 times per month during the growth season), designated as T, and (2) 3 times per month, designated as T-. Simulated precipitation was evenly distributed among events each month.

We observed that *R. soongarica* seeds germinated in May, with germination lasting one month (Zeng et al., 2004). Therefore, average May precipitation

from 1967 to 2008 was used as ambient precipitation in the seedling emergence experiment. Ambient precipitation amounts each month for seedling growth were based on average monthly precipitation from July to October (1967-2008), corresponding to the main growth season of *R. soongarica*.

Shelters were arranged to collect natural precipitation for irrigation near the test plots. Irrigation was applied from 19:00 to 20:00 (LST) using a modified sprinkler system with simulated precipitation amounts and frequencies for different treatments.

2.4 Seedling Emergence and Growth Measurements

Seedling emergence was monitored daily starting on 10 May. The experiment was terminated when the total number of seedlings remained constant. Soil was then removed from pots, and the number of germinated seeds was carefully checked. We used four indices to describe seedling emergence: (1) emergence rate, representing the speed of seedling emergence (shown as the slope of dynamic curves); (2) percentage of seedling emergence (seedlings emerged compared to total seeds); (3) germination index (GI); and (4) vigor index (VI). GI and VI were calculated using Equations 1 and 2 from Boscagli and Sette (2001), respectively:

$$GI = \sum(G_t/D_t)$$

where G_t is the number of seeds germinated on day t and D_t is the number of germination days.

$$VI = GI \times S$$

where S is the average total seedling length (cm), measured with Vernier calipers.

To evaluate effects of precipitation pattern changes on *R. soongarica* seedlings during the growth season, we destructively sampled plots 4 times on 25 July, August, September, and October. During each sampling, we harvested 18 saplings (1 plant per plot), totaling 72 saplings. Before sampling, we recorded stem length and canopy and branch diameters with a tape measure and Vernier calipers. We carefully excavated complete root systems using the skeleton method (Böhm, 1979): after specimen selection, a trench (length \times width \times depth = 0.5 m \times 0.3 m \times 0.6 m) was dug on the north side to prevent root exposure to direct sunlight, then the root system was exposed by carefully removing soil downward from the surface with a small shovel until the entire root system was revealed. All plant material was transported to the laboratory, soil was brushed from roots, and above- and below-ground parts were separated. Both sections were oven-dried at 105°C for 2 h, then maintained at 60°C for 48 h before weighing biomass with an analytical balance. Root/shoot ratio was calculated from above- and below-ground biomass. Relative growth rates (RGR) were calculated using Equation 3 from Poorter (1999):

$$RGR = (\ln W_2 - \ln W_1) / \Delta t$$

where W_1 is initial biomass (g), W_2 is final biomass (g), and Δt is the time interval between measurements.

2.5 Statistical Analysis

Data in all figures are expressed as arithmetic mean \pm SE. Differences among treatments for above- and below-ground biomass, root/shoot ratio, seedling emergence percentage, GI, VI, and RGR were analyzed using two-way or one-way ANOVA. Multiple comparisons were conducted to determine differences between treatments when ANOVA showed significant effects. Tukey's honestly significant difference (HSD) tests at $P < 0.05$ were used to identify which sample means differed. All analyses were conducted using SPSS version 15.0 for Windows (SPSS Inc., Chicago, USA).

3.1 Seedling Emergence

Cumulative seedling emergence at both precipitation frequencies was higher in W+ than in W or W- during the 28-day experiment [Figure 3: see original paper]. The highest emergence (approximately 70%) was observed in W+ at 3 times per month frequency (W+T-). Under this pattern, cumulative seedling emergence quickly reached 38.33% on day 8 after sowing, producing a steep germination curve.

Two-way ANOVA showed that final seedling emergence percentage was significantly affected by precipitation amount ($P < 0.05$;) but not by precipitation frequency or their interaction. Seedling emergence in W+ was significantly higher than in W or W- ($P < 0.05$; [Figure 3: see original paper]), but did not differ significantly between W and W- ($P > 0.05$; [Figure 3: see original paper]). Seedling emergence percentage increased by an average of 45.7% in W+ compared to W.

GI and VI were significantly affected by precipitation amount ($P < 0.001$;). Both indices increased with precipitation amount under the same frequency [Figure 4: see original paper]. GI and VI in W+ were significantly higher than in W or W- ($P < 0.05$; [Figure 5: see original paper]), but did not differ significantly between W and W- ($P > 0.05$; [Figure 4: see original paper]). Under decreased precipitation frequency, the largest GI and VI were obtained with W+, with values of 1.57 (± 0.033) and 7.54 (± 0.36), respectively.

3.2 Growth

Above- and below-ground biomass were affected by precipitation amount ($P < 0.05$;), increasing in W+ at both frequency levels [Figure 5: see original paper]. The highest above-ground biomass occurred in W+ at 3 times per month frequency across sampled growth stages (W+T-) [Figure 5a: see original paper].

Early in the growth season (July), below-ground biomass in W- was significantly higher than in W at both frequencies ($P < 0.05$; [Figure 5b: see original paper]). Compared with W, W- resulted in increased or equivalent below-ground biomass in mid-season (August and September), followed by decreases toward the end (October) [Figure 5b: see original paper].

Root/shoot ratio was affected by precipitation amount ($P < 0.001$;). Compared with ambient precipitation, it significantly increased in W- at the same frequency levels in July and August. In September and October, root/shoot ratio was significantly increased in W- compared to W at frequency T, but was equivalent between W- and W at frequency T- [Figure 6: see original paper]. The highest root/shoot ratio occurred with W- and T [Figure 6: see original paper].

RGR was affected by precipitation amount, frequency, and their interaction ($P < 0.05$;). RGR of above-ground, below-ground, and total biomass increased significantly with precipitation amount under the same frequency ($P < 0.05$; [Figure 7: see original paper]). Compared with ambient precipitation, RGR of above-ground, below-ground, and total biomass increased by averages of 52.88% ($\pm 6.36 \pm 4.39 \pm 4.98 \pm 7.52 \pm 2.67 \pm 6.58\%$), respectively.

4.1 Germination and Seedling Emergence

Germination and seedling emergence can be altered by water availability changes in arid and semi-arid areas, where rainfall constitutes the primary water source for these processes (Li et al., 2012; Funk et al., 2014). Global climate change is gradually altering precipitation patterns, with less frequent and larger precipitation events predicted for the future (Diffenbaugh and Giorgi, 2012). Previous studies indicate that increased precipitation amount promotes germination and seedling emergence in some desert plants (Yang et al., 2012; Zhu et al., 2014). In our study, germination and seedling emergence of *R. soongarica* were affected by precipitation amount changes , with stronger effects when precipitation frequency decreased from 6 to 3 times per month. Similar results have been reported for herbs at the northern edge of the Great Plains in Canada (Ambrose and Wilson, 2003) and at Shapotou in northwestern China (Tobe et al., 2005). These observations support the well-defined positive relationship between germination/seedling emergence and precipitation amount, attributable to increased soil moisture after high precipitation.

With a 30% decrease in precipitation amount, germination and seedling emergence of *R. soongarica* decreased [FIGURE:3 and FIGURE:4], indicating that reduced precipitation may have intensified soil moisture loss, causing drought stress and decreasing reproductive success. These results are consistent with Gómez-Aparicio et al. (2008) and Hovenden et al. (2008). Heavier precipitation events have been predicted to increase during summers in this region (Yue et al., 2013). Since *R. soongarica* germinates in summer, seedling emergence would be expected to increase and improve reproductive success with greater precipitation in a future climate. However, germination and seedling emergence may

be determined mainly by additional precipitation in late spring and evenness of precipitation distribution rather than precipitation amount alone (Barchuk et al., 2005). Therefore, increasing our understanding of varying precipitation pattern effects on germination and seedling emergence is critical.

Germination and seedling emergence were also affected by precipitation frequency (Schneider et al., 2014; Gao et al., 2015; Gibson-Forty et al., 2016). Zhu et al. (2014) demonstrated that germination and seedling emergence of the dune grass *Leymus secalinus* increased with precipitation frequency under the same precipitation amount. A similar positive relationship between seedling emergence and precipitation frequency was reported for annual plants *Bassia dasyphylla* and *Agriophyllum squarrosum*, while *Aristida adscensionis* favored lower precipitation frequency (Tobe et al., 2005). We found that *R. soongarica* seedling emergence increased when precipitation frequency decreased under the same amount [Figure 3: see original paper]. Maximum emergence (70%) occurred when precipitation increased by 30% and frequency decreased. This discrepancy likely reflects species-specific effects of precipitation frequency changes, possibly related to the high water requirement for seed germination in *R. soongarica* (Zeng et al., 2004); lower-frequency, higher-amount rain events may better meet this requirement. Precipitation patterns in arid areas may become more unpredictable in the future (Zhu et al., 2014). Therefore, less frequent precipitation events with higher amounts will enhance seedling emergence in this species. Our results suggest that effects of changing precipitation patterns on seedling emergence are complex and require considerable changes in both amount and frequency magnitude to predict how population regeneration will respond to variable precipitation.

4.2 Growth and Allocation

Plasticity in plant performance (biomass, root/shoot ratio, and relative growth rate) under changing precipitation patterns exhibits short-term adaptation and promotes long-term evolution (Matesanz et al., 2010; Nicotra et al., 2010; Didiano et al., 2016). In our study, seedling growth and biomass accumulation were explained more by precipitation amount than frequency; increased precipitation amount significantly enhanced plant growth and biomass accumulation [Figure 5: see original paper]. However, a 30% decrease in ambient precipitation increased below-ground biomass and root/shoot ratio at both frequency levels during early growth stages [Figure 5: see original paper], indicating that roots may respond quickly to precipitation pattern changes during water stress in early growth. At the end of the growth season, a 30% decrease in ambient precipitation reduced above- and below-ground biomass, while root/shoot ratio was significantly increased under ambient frequency and remained unchanged under decreased frequency. This indicates that long-term precipitation reduction inhibited above- and below-ground biomass accumulation, with larger effects on above-ground biomass under decreased precipitation frequency. Our results reveal that growth and biomass allocation exhibited strong plasticity in response

to precipitation amount variability, enhancing plant survival and reproduction in unpredictable arid region environments and supporting the well-defined positive vegetation response to precipitation (Ponce-Campos et al., 2013; Yue et al., 2016). However, White et al. (2000) found that additional precipitation either did not affect or might decrease biomass, possibly because water gradients in their studies did not differ sufficiently to reflect actual differences.

Our results showed that decreased precipitation frequency increased plant growth and biomass accumulation under the same precipitation amount at the end of the growth season. The highest above- and below-ground biomass and RGR occurred with a 30% increase in precipitation amount and 50% decrease in precipitation frequency (less frequent but larger-volume events). This finding is consistent with results for other plants in arid and semi-arid regions (Heisler-White et al., 2009). Soil water infiltration is greater and high soil moisture persists longer under this precipitation pattern, especially at deeper soil depths where evaporation is low (Schwinning and Sala, 2004). Therefore, plants, particularly desert plants with deeper roots, have greater access to water resources that promote growth. This could explain why many desert plants with deep root systems showed the greatest response to low-frequency, high-precipitation events.

Reaumuria soongarica is a typical constructive xerophytic species for which water stress is the limiting factor for survival and growth (Yang et al., 2015). In this experiment, we created larger precipitation events by decreasing frequency for a given amount, which provided more biologically-available water and more effectively improved survival and establishment of *R. soongarica* seedlings than more frequent events. As a result, water was available to seedlings across the soil profile from surface to deep layers, improving establishment. Thus, precipitation frequency plays an ecologically important role in successful seedling establishment by advancing growth, which will be important for future climate change scenarios. These results indicate that we should compare interactive effects of precipitation amount and frequency on plant growth rather than single parameters of water availability (often mean precipitation amount) when attempting to describe climate-driven precipitation pattern effects on plant regeneration (Schneider et al., 2014).

5 Conclusions

This study demonstrates that *R. soongarica* seedling emergence adapted to a combination of 30% increased precipitation amount and 50% reduced precipitation frequency in late spring. Increased precipitation enhanced seedling emergence and growth in *R. soongarica*, with larger effects at lower than ambient frequency. Increased precipitation amount enhanced plant growth and biomass accumulation. However, a 30% decrease in ambient precipitation increased below-ground biomass and root/shoot ratio during early growth stages. At the end of the growth season, a 30% decrease in ambient precipitation reduced above- and below-ground biomass, while root/shoot ratio was significantly increased

under ambient frequency and unchanged under decreased frequency. When precipitation frequency decreased by 50%, all growth trait values increased under the same precipitation amount. Our results suggest that precipitation frequency may be as important as precipitation amount for seedling emergence and growth of *R. soongarica*. Therefore, understanding precipitation variability effects on seedling recruitment requires integrating both amount and frequency. The plastic response of *R. soongarica* growth to precipitation pulses exhibited strong adaptation to present-day unpredictable environments and may continue to do so under increased future climate unpredictability. Climate change-induced precipitation variability may thus have profound effects on seedling emergence and growth of *R. soongarica*.

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