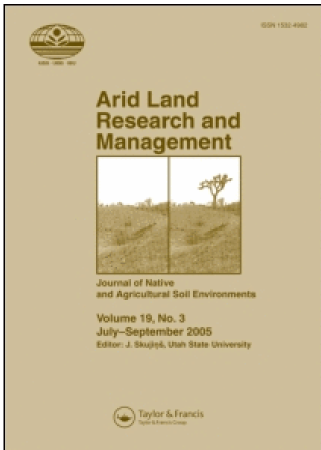

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Individual Performances and the Interaction Between Arid Land Plants Affected by the Growth Season Water Pulses

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Individual Performances and the Interaction Between Arid Land Plants Affected by the Growth Season Water Pulses

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Understanding the effects of rainfall pattern on the plant interactions is a prerequisite for anticipating the effects of climate change on communities and ecosystems. Effects of a change in growth-season rainfall pattern were tested on individual performances, and the interaction between arid land plants. Simulated rain events were applied either as two rains of 20 mm, or as four rains of 10 mm, on natural vegetation of steppe rangelands in Nasr-Abad, Yazd, Iran. Phenotype responses were assessed by measuring the density of annuals and current year growth of perennials. Facilitation effects were assessed by comparing density of annuals in open space and within the subcanopy of perennials. Competition between perennials was tested using target-neighbor designs. Effects of rain size were more significant than rain frequency. There were linear increases in performances of both annuals and perennials, as the magnitude of pulse sizes increased linearly from zero (control), to 10 and 20 ml per event. Larger rain events led to a shift in relationships between annual and perennials from facilitation to no interactions, and a change in the interaction between perennial plants from no relationship to the competition. Accordingly, arid land plant communities showed some potential to buffer the short time effects of climate change, which may occur as variations in the intra-annual rainfall pattern.

Keywords arid land vegetation, climate change, competition, facilitation, rain size

Arid and sem-arid regions are considered among the most sensitive to shifting climate conditions (Schlesinger et al., 1990; Hougheton et al., 1995), particularly to those which influence the intensity, frequency, and seasonal distribution of rainfall events (Ehleringer, Schwinning, and Gebauer, 1999). A change in rainfall pattern is thought to affect plant community composition by alternating competitive advantages over time (Chesson and Huntly, 1989). Therefore, understanding the effects of rainfall pattern on plant interactions is a prerequisite for anticipating the effects of climate change on arid-land communities and ecosystems (Schwinning, Starr, and

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Ehleringer, 2003). Furthermore, predicting the effects of climate change on community dynamics becomes more appealing if it is realized that the co-existing mechanisms between arid land plants are influenced by both facilitation and competition, and the fact that the relative importance of these interactions can change with time and resource availability (Bertness and Callaway, 1994; Greenlee and Callaway, 1996).

The purpose of this research was to investigate two important aspects of plant adaptation to pulse use that have gained less attention in the literature. In the first studies on plant adaptation to pulse use, the main attention has been on the individual plant responses (e.g., Ehleringer et al., 1999; Schwinning, Davis, Richardson, and Ehleringer, 2002; Huxman et al., 2004), while few experiments have measured possible effects of rainfall patterns on plant interactions (but refer to Weltizine and McPherson (2000) and Snyder et al. (2004), or few experiments have been conducted under field conditions. Under glasshouse experiments, pulses of water availability caused greater influence on competitive potential than individual growth of perennial grasses (Novoplansky and Goldberg, 2001), and pulses of ^{15}N caused greater impacts on juveniles than adults of an arid land grass (Jankju Borzelabad and Griffiths, 2006). Second, in the studies on the effects of rainfall pattern, only the total amount of annual rainfall has been considered (e.g., Bertness and Callaway, 1994; Greenlee and Callaway, 1996), while few works are done on assessing the effects of within season rainfall variability. The few experiments on the evaluation of the effect of rainfall size (Lauenroth, Sala, Milchunas, and Lathrop, 1987; Dougherty, Lauenroth, and Singh, 1996), or effects of shifting precipitation patterns (Grime, 2001; Knapp et al., 2002; Svejcar, Angell, and Miller, 2003, Bates, Svejcar, Miller, and Angell, 2006) have only measured productivity or composition in plant communities (e.g., Snyder et al., 2004, Weltzine and McPherson 2000), without giving any information on the effects of rainfall pattern or rain size on plant–plant interactions.

Therefore, this experiment was designed to assess the effects of the growth season rainfall pattern on the individual performance of, and the interaction between, arid land plants. The first hypothesis was that the small and more frequent rain events may only improve the establishment of shallow-rooted annuals, but the large and less frequent events will enhance the performance of both annual and perennial plants. The second hypothesis was that the balance between competition and facilitation can be affected by changes in the size or frequency of rain events. Results will show how contrasting plant phenotypes respond to a gradient of rain size events, and how plant-plant interaction may be affected by different patterns of the growth season water pulses.

Material and Methods

Study Site

This research was conducted on the natural vegetation of an arid rangeland, in Nasr-Abad, Yazd, Iran (latitude: 32 03 North, longitude: 53 33 East, and altitude 1990 m). Soil texture was silty clay, soil pH 7.2, EC 1.63 dS m^{-1} and maximum soil depth 35–40 cm, which was limited by a calcareous hard pan. Annual precipitation in year 2004 was 193 mm, which was lower than the average (i.e., 227.1 mm) of 38 years (1968–2004) data period. Most of the annual precipitation occurs during winter months, and only 16% of the rainfall (i.e., 35.9 mm) happens during

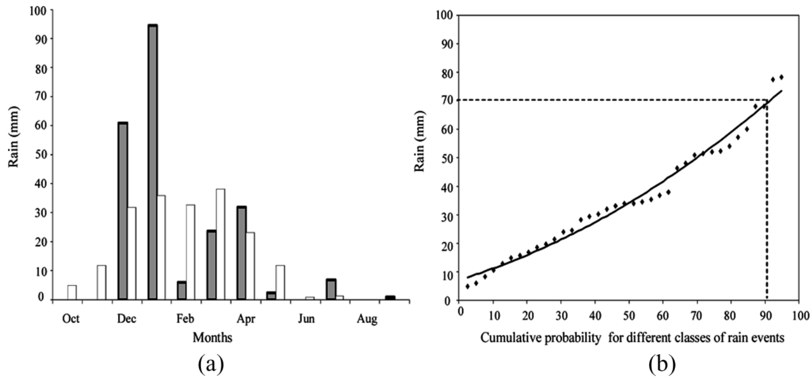

Figure 1. Rainfall pattern in Nasrabad area. (a) Monthly distribution of rainfall: as average of 38 years (□), or in the year of study (■). (b) Cumulative probability for different classes of April–May rains, based on data of 1968–2004 record period; probability for 70 mm or higher is indicated (i.e., $100 - 90 = 10\%$ or once ever 10 y).

April–May (Figure 1a). The active growth period for annuals and perennial geophytes is from early April till late May, and for perennial shrubs and woody plants from April till early October. The experiment site was dominated by relatively pure stands (>90%) of perennial semi-shrub *Artemisia aucheri* (Bois), with annual grass *Bromus tectorum (L.)* beneath the *Artemisia* canopy or in open spaces. Companion plant species were *Onobrychis cornuta* (*L. Desv*) *Stipa barbata* (*Desf.*), *Oryzopsis molinioides* (*Boiss.*), *Centaurea spp*, *Carex stenophylla* (*Wg*) *Tulipa biflora (Pall)*, and *Astragalus adscendens (Boiss. & Hausskn)*.

The sum of April–May rainfalls were calculated for data of 38 years record period. The return period for each rain event was calculated by using Weibull formula (Alizadeh, 2006):

$$\mathrm{P} = \frac{\mathrm{m}}{\mathrm{n} + 1}$$

where P is the probability for the return period of a specific rain size, m is the hierarchy for that rain size in the ascending arrangement, and n is the length of record period (here is 38). The probability for the return period of 70 mm or higher (i.e., control plus induced rains) rain was measured from the cumulative distribution function, in which the calculated possibility for occurrence of different rain events had been plotted against the rain amounts (Figure 1b).

Experimental Design

A specific amount of water was applied on natural vegetation, in treatments with different frequencies and intensities. For low-frequency, high intensity treatment (LF), two rains of 20 mm were applied on the 7th of April and the 14th of May, and for high-frequency, low intensity treatment (HF), four rains of 10 mm were applied on the 7th of April, the 29th of April, the 14th of May, and the 29th of May 2004. There was also a control treatment that received no additional water. Naturally, all treatments (LF, HF, and Control) were subjected to the ambient (control) rainfall that was 32.1 mm during April—May 2004 (the study time). Therefore, pulse treatments received 72.1 mm (40 mm added plus 32.1 mm natural rain in Control) rain during April to May.

An area of 1500 m^2 was enclosed from animal grazing. The area was divided into three main blocks of 500 m^2. Each block was equally divided into three subblocks, which were devoted to the LF, HF, or Control treatments. Thus, each treatment was replicated three times. Water for irrigation was melted snow and obtained from a nearby river. A pressurized system including a pump, several pipes, and nozzles were used to produce the simulated rainfalls. Induced rain intensity was $0.15\,m^3\,m^{-2}\,s^{-1}$, slightly higher than natural rainfall in the area. To prevent runoff, rainfall places were constantly being changed and also rain application had to be stopped every 15–45 minutes. The total time for rain application (including stoppage times) was varied between 3–6 h.

Measurements

Performances and Interactions of Annual Plants

The performance of annual plants was assessed on the 6th of June, when the major annual grass *Bromus tectorum* had begun the seed ripening stage. For assessing annual performances, 30 quadrates of 2 m^2 were established within LF, HF, and Control treatments (10 for each) in a random-systematic method (Brown, 1954). The total number of annual plants was counted, and separately recorded for those growing in open space or under a canopy of perennials. For assessing facilitation effects, the canopy area of perennial plants within each quadrate was measured, to be related on the density of annuals growing under their canopy. The canopy area of shrubs was calculated by using the average diameter; and it was the mean of the longest length and width of each shrub canopy.

Performances and Interactions of Perennial Plants

The performance of perennial plants was assessed on the 23–27th of September, when the major dominant perennial plant *Artemisia aucheri* had begun the flowering stage. At this time, all annual plants had completed their growth stage and were dead or had disappeared. Thirty quadrates (10 for each treatment) of 10 m^2 area were established in a randomized systematic method. The current year growth of *Artemisia aucheri*, the dominant perennial, was measured for assessing the effects of watering treatments. To study the interaction between perennials plants, one individual of *Artemisia* was considered as the target in the center of each quadrate, and all other perennials were considered as neighbors. All plants were cut 2 cm above the ground, then taken to a laboratory where dead and living parts, current and previous year's growth were separated. All plant materials were dried in an oven at 75–80°C for 48 h and then weighed.

Data Analysis

Data analysis was performed to evaluate the effects of watering treatments on annual establishment, perennial growth, and plant–plant interactions. Data on annual establishment and perennial growth were analyzed through Analysis of Variance (ANOVA) and the Duncan statistical test, using SPSS software, Chicago, IL. Because of a wide variation observed in sizes of *Artemisia* individuals, the natural logarithm of the actual data was used in the statistical analysis.

For studying the interaction between annuals and perennials, regression models were fitted between the size (weight or dimensions) of perennials and density of annuals co-existing under their canopy. Also, for assessing the interaction between perennials, regression models were fitted between current year growth of the target at each plot and the sum of total shoot weight of all neighboring plants inside the same plot. The significance of regression relationships was tested by ANOVA, using SPSS software.

Results

Responses of Annuals to Water Pulses

The total number of annual plants per plot was higher in the areas that received additional rain pulses (LF, HF), than in the control plots that received only ambient natural rainfall (Figure 2a). However, a statistically significant increase was found only under the treatment in which rainfall regimes had been applied as big pulses of low frequent (LF), rather than the shorter and more frequent (HF) rain applications.

Response of annual plants to the induced rain treatments was also affected by their position inside the experimental plots. Annuals growing under the canopy of perennial plants did not show a significant response to the induced rain treatments. As a result, their density was not significantly different under the LF, HF, and control conditions (Figure 2b). In contrast, a positive response to the induced rain pulses was found for annuals growing in open areas, in a way that their density increased significantly under the LF and relatively under the HF regimes (Figure 2c).

Responses of Perennials to Water Pulses

The current year growth and total dry weight of perennial plants were increased under the experimental rain regimes (LF and HF) as compared to the control condition (Figure 3). However, the only statistically significant increase was

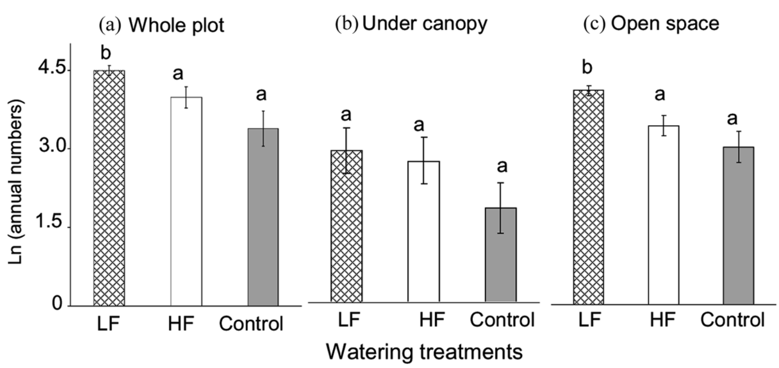

Figure 2. (a) Total number of annuals as affected by watering treatments. (b–c) Effect of spatial position (under canopy of perennials vs. open spaces) of annuals on their response to watering treatments. LF = low frequent-high volume; HF = high frequent-low volume; Control, no watering. Means ±SD are reported, total replications for each treatment was 10. Treatment combinations with different letters were significantly different as determined by Tukey's HSD at $P < 0.05$.

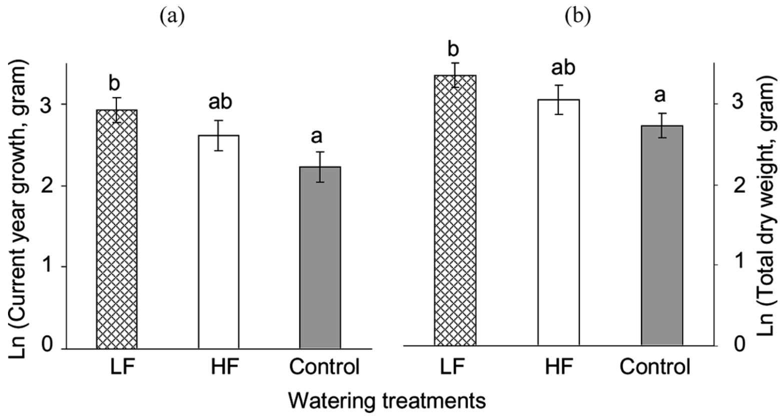

Figure 3. (a) Current year growth and (b) total dry weight of perennial plants as affected by watering treatments. LF-low frequent-high volume; HF-high frequent-low volume; Control, no watering.

observed under LF treatment, where plants received water as low frequent-high volume rain pulses.

Interaction Between Annual and Perennials

There was a positive correlation between the total canopy area of perennial plants and the density of annuals under their canopy (Figure 4). The greatest correlation coefficient was found in the control treatment ($R^2 = 0.73$), where plants received no additional rain. The correlation coefficient was correspondingly decreased under the high frequent-low volume (HF, $R^2 = 0.52$), and low frequent-high volume (LF, $R^2 = 0.31$) treatments. Therefore, by increasingly available soil moisture, annual plants were less dependent on the microclimate conditions created under the canopy cover of perennials.

Interactions Between Perennials

Where plants had only received the ambient natural precipitation (control treatment), there was no significant correlation ($R^2 = 0.0008$) between the current year growth of a perennial target plant in the plot and the shoot dry weight of all neighboring plants inside the same plot. However, a negative correlation occurred where plants received additional simulated rainfalls (Figure 5). The strength of the competitive correlations was observed based on the size and frequency of the added rain pulses. The negative correlation was more pronounced and significant where rain was applied as big pulses of low frequent (LF, $R^2 = 0.56$) compared with the treatments that received small and high frequent rain events (HF, $R^2 = 0.039$). This means that simulated rain pulses could change plant interaction, having no relation to the competitive relationship. The strength of this relationship was dependent on the size of the applied pulses.

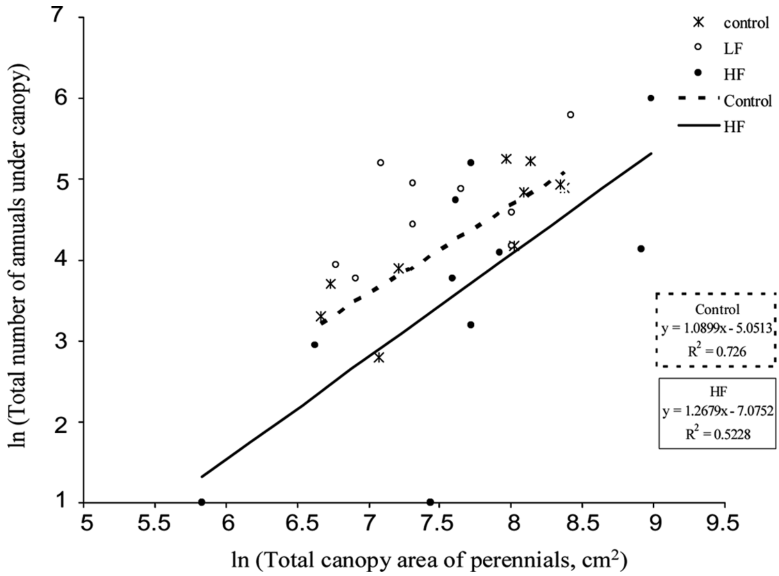

Figure 4. Regression between canopy cover of perennial plants and number of annuals growing beneath them, indicating facilitative effect by perennials on annuals. Significant regressions were only found for Control ($df_{total} = 9$, $P = 0.002$) and for high frequency low volume (HF, $df_{total} = 9$, $P = 0.018$). LF = low frequency-high volume rain events.

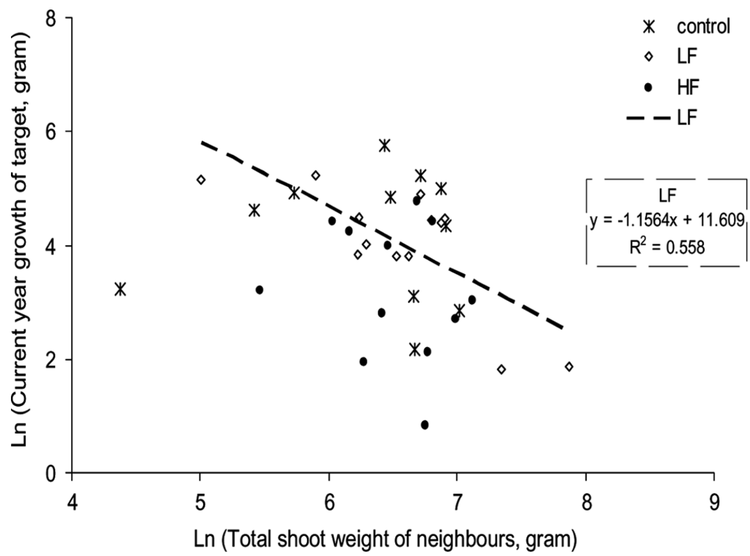

Figure 5. Regression between current year weight of a target plant (in the center of $10\,m^2$ plots) and total shoot dry weight of all neighboring plants, indicating competitive interactions. The only significant regression ($df_{total} = 9$, $P = 0.005$) was found in low frequent-high volume (LF) treatment. HF = high frequent-low volume rain events; Control means no watering.

Discussion

Effects of Rain Pattern

By applying the simulated pulse events, rain input (during April–May) increased from 32.1 in control to 72.1 mm in the HF and LF treatments. Although the amount of added rain exceeds the average (i.e., 35.92 mm) of 38 years data record of Nasrabad station, such an increase is not impossible. According to the cumulative distribution functions, the possibility for occurrence of 70 mm or higher rainfall amount during April–May in Nasrabad area is once every 10 years (Figure 1b). Therefore, the application of pulse treatments in this experiment has created an opportunity for comparing the responses of arid land plants to the rainfalls of a normal year (Control) with an above-average year (Control plus induced rains), as well as an opportunity for testing plant responses to the changes in the within-season rainfall patterns.

Among the rain characteristics studied in this experiment, the effects of rain size were more important than those of rain frequency. The big pulses of low frequent (20 ml, LF regime) rain events resulted in higher influence on individual plant performance and plant interaction, as compared to the high frequent and smaller rain events (10 ml, HF regime). It seems that the high frequency of the small rain events was disadvantaged by a high evaporation during interpulse periods. Small rainfall events moisten only the uppermost layer of the soil, where a large fraction of soil moisture is lost by direct evaporation due to high temperatures and low root densities (Noy-Meir, Kemp, Ogle, 1973; Reynolds and Fernandez, 2004). Since the small pulse events persist for a short period, they may only trigger the surface processes such as proliferation of those species of soil micro-fauna and micro-flora that show fast response and have a high tolerance for low resource levels. In contrast, large pulses (> 10–15 mm) are needed to trigger processes such as gas exchange metabolism of plants or annual germination. By increasing pulse size, evaporation and vapor diffusion rates decline, while a larger fraction of precipitation leave via transpiration and contribute to the primary productivity of higher plants (Huxman et al., 2004; Schwinning and Sala, 2004).

Phenotypes and Responses to Pulse Sizes

The initial hypothesis in this research was that the small and more frequent rain events (HF) may only improve the establishment of shallow-rooted annuals, but the large and less frequent events (LF) will enhance the performance of both annual and perennial plants. However, the results of this experiment suggest that plant phenotype differences in water use tend to be more gradual rather than categorical. Both the density of annuals and the current-year growth of perennials was enhanced as the magnitude of pulse sizes increased linearly from 0, to 10 and 20 ml per event, in the Control, HF, and LF regimes, respectively. Schwinning et al. (2003) also found a linear increase in plant responses to the applied pulses (2–20 mm) of deuterium labelled irrigation water by four plant species of the Colorado Plateau.

As expected, annual plants (e.g., *Bromus tectorum*) were highly responsive to the simulated rain pulses. These plants contain morphological and/or physiological traits such as shallow root systems, low root/shoot ratio, and high stomatal conductance, which lower response thresholds to the sporadic rainfall (Schwinning and

Ehleringer 2001; Snyder et al., 2004). The response of annual plants to the applied pulses re-emphasize the observations that open spaces are important recruitment niches (Gillespie and Loik, 2004). The annual plants showed higher responses to the applied water pulses when growing in open spaces, as compared with those under the canopy of *Artemisa*. Therefore, an increase in the magnitude of rain sizes under future climate conditions (Easterling et al., 2000) may create potential for establishment of annuals in open spaces of desert areas, where the high temperature and low moisture usually restrict most of the biological activities.

The responses of perennial plants to the HF and LF treatments of this experiment also emphasize the impacts of winter precipitation. Whereas perennial shrubs are usually known as less responsive to the pulsed water and more dependent on the water stored in the deeper soil layers (Schwinning and Ehleringer, 2001), the dominant shrub *Artemisia aucheri* was highly responsive to both small and large pulses of this experiment. This possibly could be due to a precedent wet winter. A wet winter may be responsible for maintaining the leaf area index (LAI) of shrub community throughout the year, and this will subsequently increase the ability to use summer precipitation (Schwinning et al., 2002). There was a large amount of snowfall during December 2003 and January 2004 (Figure 1a), which could have raised soil moisture storage, and subsequently the leaf area index of the perennial shrub *Artemisia aucheri*. Alternatively, a high responsiveness of *Artemisia aucheri* to water pulses can be due to its intensive root system in the soil profile, as the soil layers were limited by a calcareous hardpan at the depth of 35–40 cm.

Plant Interactions and Response to Pulses

Extrapolating results of this experiment to the whole community level may not be widely applicable, because of the experiment being conducted in only one growing season. However, these results are valuable, as they combine results of few researches that have been conducted under field condition or studies on plant-plant interaction. In a field experiment, Bates et al. (2006) tested responses of individual plants to climate perturbation and found the resilience of the *Artemisia tridentate* community, as many of the vegetation shifts did not begin until 4 years after treatments. In glasshouse experiments (e.g., Novoplansky and Goldberg, 2001; Jankju Borzelabad and Griffiths, 2006) simulated pulses caused greater influence on competitive potential than individual growth of perennial grasses.

As expected by the second hypothesis, a change in intra-annual rainfall pattern altered the co-existing relationships between the plant species. As pulse sizes varied from 0 to 10 and 20 ml per event (i.e., Control, HF, and LF regimes, respectively), the relationship between annuals and perennials was shifted from facilitation towards no interactions, and the interaction between perennial plants shifted from no relationship to the competition. Accordingly, a decrease in the intensity of competition between perennials, under drier conditions (Control) or under small rainfall regime (HF), may be interpreted as adaptive strategies of arid communities against harsh climatic conditions in such ecosystems (e.g., Chesson, and Huntly, 1989). For annuals, however, facilitative effects may preserve them under the canopy of perennials. On the other hand, in years when large rain events are more frequent, there is greater opportunity for the perennial shrubs to increase biomass or reproduction yield. Large rain events also provide favorable conditions for the establishment of annuals (Figure 2), and possibly the seedlings of perennials in open spaces of desert areas, while hot and dry soil surface decrease the chance of the establishment for new arrivals within the existing communities (see also Gillespie and Loik, 2004; Loik, Breshears, Lauenroth, and Benlap, 2004). Accordingly, results of this and previous researches (e.g., Bates et al., 2006; Brooker 2006; Schwinning et al., 2003) imply that arid land plant communities may buffer the possible effects of climate change via linear responses to rain size events and through shifting type and/or intensity of the plant-plant interactions. Therefore, short term changes in the intra-annual rainfall regime may not lead to the significant changes in the community composition of arid land plants.

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