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Short Communication

Effects of simulated storm sizes and nitrogen on three Chihuahuan Desert perennial herbs and a grass

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ABSTRACT

Establishment and growth of three perennial herbs and a small tussock grass were studied in an experiment that provided simulated rainfall of 6 mm week^{-1} or 25 mm once per month and nitrogen fertilization in combination with the different simulated rainfall regimes. Wild onion, *Allium macropetalum*, failed to establish in plots receiving 25 mm month^{-1} simulated rainfall. The perennial composite, *Bahia absinthifolia*, occurred at higher densities in plots that were not irrigated but there were no differences in biomass in any of the irrigation or fertilization treatments. Desert holly, *Perezia nana*, failed to establish in nitrogen fertilized plots and developed higher abundance and biomass in plots receiving 25 mm month^{-1}. Nitrogen fertilization had either no effect or an adverse effect on the perennial herbs. The tussock grass, *Dasychloa pulchella* exhibited highest abundance and biomass with 6 mm week^{-1} added water plus nitrogen. Since global climate change will affect both rain storm frequency and size and atmospheric nitrogen deposition, the results of this study are applicable to understanding vegetation responses climate change.

1. Introduction

The main driver of primary production in arid ecosystems is rainfall which is considered to be the trigger in the “pulse-reserve” conceptual model (Noy-Meir, 1973). Discrete rainfall events trigger plant and soil responses at short temporal scales and are sensitive to the amount, timing, and intensity of storms (Schwinning and Sala, 2004; Sponseller, 2007). Rainfall in arid regions is extremely variable both spatially and temporally. Precipitation pulse size and frequency are important controllers of biological processes in arid ecosystems (Huxman et al., 2004; Reynolds et al., 2004). In the Chihuahuan Desert, small rains (1–5 mm/event) are insufficient to provide effective soil moisture during hot, dry period from May through September because of high rates of evaporation from the soil and plant canopies. In the Chihuahuan Desert, rainfalls of 6 mm–12 mm accounted for between 10% and 22% of the total number of rain events while rainfalls of 12 mm–25 mm accounted for between 2% and 9% of the total number of rain events (Whitford, 2002). Since rain events of 12 mm–25 mm generate surface run-off in inter-shrub spaces, soil water content is generally lower in the inter-shrub spaces than under shrub canopies. Therefore it was hypothesized that perennial herbs and grasses growing in the shrub inter-space would exhibit higher rates of establishment and growth with frequent simulated rain events of 6 mm than with infrequent simulated events of 25 mm.

Although water is the obvious limiting factor for primary production in arid ecosystems, available nitrogen can be almost as important (Whitford, 2002). In arid ecosystems, shrubs have been documented to represent “islands of fertility” especially with respect to nitrogen (Garcia-Moya and McKell, 1970; Charley and West, 1975; Garner and Steinberger, 1989). Nitrogen mineralization has been shown to vary with the amount of rainfall per event (Fisher and Whitford, 1995). Since available nitrogen is a function of nitrogen mineralization rates, there should be higher rates of N mineralization with larger rain events in soil patches with high organic matter. Therefore, application of nitrogen fertilizer should have a greater effect on herbaceous perennials and grasses growing in the inter-shrub spaces than species growing under shrub canopies.

The most abundant perennial herb in creosotebush shrubland is *Bahia absinthifolia* (Compositae) which grows under the canopy of *Larrea tridentata*. Other less abundant perennial herbs are the wild onion, *Allium macropetalum*, (Liliaceae) and desert holly, *Perezia nana* (Compositae), which are found at the edge of *L. tridentata* canopies or in the bare, inter-shrub spaces. The perennial grass, *Dasyochloa pulchella*, is a small, short-lived tussock grass of the inter-

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shrub spaces and under the canopy margins of *L. tridentata*. It was hypothesized that perennial species in the inter-shrub spaces would develop higher abundance and biomass in response to frequent simulated rain events of 6 mm per week than to a simulated event of 25 mm once per month and that perennial species in the inter-shrub spaces would exhibit higher abundance and biomass with nitrogen fertilization than with no fertilization. Since the soils under *L. tridentata* canopies are nitrogen rich islands (Schlesinger et al., 1996), *B. absinthifolia* should be less responsive to nitrogen fertilization than perennials growing in the inter-shrub spaces. We therefore hypothesized that the inter-shrub space perennials develop the greatest abundance and biomass in response to small, frequent rainfall coupled with nitrogen fertilization. An experimental study was designed to test these hypotheses.

2. Methods

Nine experimental plots were established in a nearly monotypic creosotebush, *L. tridentata*, shrubland on the mid-slope of a piedmont on the Chihuahuan Desert Rangeland Research Center, 40 km NNE of Las Cruces, New Mexico (32 °30′N, 106 °45′N).The soil is a deep sand alluvium. The *L. tridentata* shrubs in this area were fairly uniform in size: average height − 112 cm; average canopy diameter − 76 cm. Prevailing winds in this area are from the southwest. The 7 × 15 m plots were fenced with chicken mesh to exclude rabbits but plots were accessible to small rodents. Three plots were assigned at random to above canopy sprinkler irrigation of 6 mm week^{-1}, three plots were assigned to irrigation of 25 mm every fourth week, and three plots received no irrigation. The irrigation schedule was applied for 18 months prior to the initial measurements of perennial herb and grass density and biomass and continued on that schedule for the duration of the study. Irrigation water was obtained from a concrete water storage pool that was supplied with well water. Water retained in the pool supported algae and aquatic insects. The water was pumped from the storage pool into a water tank that was pulled to the experimental plots that were approximately 4 km from the water storage pool. Granular nitrogen fertilizer (NH_4NO_3) was applied by a hand-held spreader at a rate of 100 kg ha^{-1} on the down-slope half of each plot four months prior to the plant measurements.

The densities of perennial herbs and the grass, *D. pulchella*, were estimated in late May 1982, at the beginning of the growing season, and in late September at the end of the growing season. Six, 1 m^2 quadrats were placed at random under the canopy of random *L. tridentata* shrubs and on the up-slope inter-shrub space of each split plot (half fertilized, half not fertilized). This stratified sampling design was employed to adequately sample the *B. absinthifolia* which was restricted to areas below the shrub canopies, and to sample those species that occurred primarily in the bare, inter-shrub spaces. Random placement of quadrats under *L. tridentata* canopies avoided differences due to aeolian redistribution of resources. Biomass production was estimated by harvesting the perennial herbs and *D. pulchella* within the quadrats in the September sampling. The harvested perennials were returned to the laboratory and dried to a constant weight.

Natural rainfall was recorded by a tipping bucket rain gauge located 500 m from the experimental plots. Data were analyzed by Analysis of Variance. Significant differences among treatments were indicated by Tukey's HSD test (Steel and Torrie, 1980).

3. Results

The natural rainfall during the growing season (99.5 mm) was below the long-term average of 175 mm and was characterized only four rainfalls greater than 5.0 mm: two in July and one in the months of August and September (Table 1). The absence of effective natural rainfall from March through June confirms that the early growth of the perennial herbs and grass was primarily stimulated by the irrigation regimes.

A. macropetalum was present in May but absent from all plots in September. Available nitrogen had no effect on the density or biomass production of *A. macropetalum*. *A. macropetalum* emerges in March and grows through June (Kearney and Peebles, 1960). The above-ground stems are not present in mid-summer and autumn. There were no differences in density and biomass of *A. macropetalum* that were not irrigated or provided with simulated rainfall of 6 mm/week (Tables 2 and 3). However when simulated rainfall of 25 mm every month was added to the natural rainfall, the wild onion, *A. macropetalum* was eliminated or failed to establish (Table 2).

In May *B. absinthifolia* occurred at lower densities in the plots that were not irrigated, but fertilized with NH_4NO_3 and in the 6 mm/week irrigated plots than in the other treatments ($F_{5,30} = 20.1$, $p < 0.0001$). The density of *B. absinthifolia* in late September was the same as May in the non-irrigated-nitrogen fertilized plots. Densities of *B. absinthifolia* increased in the unfertilized plots during the growing season (Table 2). The differences in density did not result in increased biomass production (Table 2).

Simulated rainfall of frequent, small events (6 mm/week) plus nitrogen fertilization resulted in the highest densities and biomass of fluff grass, *D. pulchella* ($F_{5,12} = 8.5$, $p < 0.01$). There was a significant increase in the density of *D. pulchella* in the 6 mm/week irrigation supplement to natural rainfall plots during the growing season but a decrease in density of fluff grass in the 25 mm/month supplement plus nitrogen treatment (Table 2). Simulated rainfall of 6 mm/week resulted in higher biomass production of *D. puchella*, while simulated rainfall of 25 mm/month resulted in biomass production equal to no irrigation (Table 3). Nitrogen fertilization of plots receiving 25 mm/month supplementary water increased biomass production of fluff grass sufficient to equal the biomass production in plots treated with 6 mm/week irrigation with no added nitrogen treatment (Table 3).

Nitrogen fertilization resulted in the death of desert holly, *P. nana*, and in the failure of *P. nana* to establish (Table 2). Supplemental rainfall of 25 mm/month resulted in higher density ($F_{5,12} = 5.5$, $p < 0.007$) and biomass ($F_{2,6} = 7.9$, $p < 0.02$) of *P. nana*. However there were no significant differences in densities of desert holly during the growing season.

4. Discussion

Perennial herbs responded to small, frequent simulated rains and large infrequent simulated rainfall differently than the evergreen shrub, *L. tridentata*. *L. tridentata* exhibited higher biomass production with frequent small rain events than with the 25 mm per month events and both rain simulations stimulated higher biomass production than no supplemental water (Fisher et al., 1988). Nitrogen fertilization added to the supplemental rainfall effects on biomass production of *L. tridentata*. The mixed response of the perennial herbs to the rainfall supplementation suggests

Table 1
Rainfall amounts and number of rain events during the growing season at the experimental plots. The numbers after the/are the number of rain events contributing to the total for the <3.0 mm events and the >5.0 mm events.

Rainfall	Mar	Apr	May	Jun	Jul	Aug	Sep
Total	0	0	9.5	4.5	28.0	30.9	26.6
<3.0 mm	0	0	4.7/5	0	1.9/2	9.6/10	6.0/4
>5.0 mm	0	0	0	0	26.7/2	12.5/1	19.8/1

Table 2
Mean densities ± SD of the perennials Alma (*A. macropetalum*), Baab (*B. absinthifolia*), Dapu (*D. pulchella*), and Pena, (*P. nana*) in plots irrigated at 6 mm/week, 25 mm/month, or no irrigation (0 mm) and plots receiving the irrigation treatments plus NH_4NO_3 Values followed by different letters are significantly different at $p < 0.05$. Significant differences in density between May and September indicated by*.

Species-Date	0 mm	0 mm + N	6 mm	6 mm + N	25 mm	25 mm + N
Alma-May	0.4 ± 0.02a	0.2 ± 0.03a	0.2 ± 0.04a	0.2 ± 0.05a	0	0
Baab-May	1.7 ± 0.4a	0.2 ± 0.07b	0.4 ± 0.07b	1.7 ± 1.6a	1.3 ± 0.3a	1.8 ± 0.1a
Baab-Sep	3.7 ± 0.4a*	0.2 ± 0.02b	1.0 ± 0.3c*	1.5 ± 0.5c	2.4 ± 0.2c*	1.9 ± 0.2c
Dapu May	1.2 ± 0.6c	1.2 ± 0.8c	3.1 ± 1.0c	15.1 ± 1.2a	8.4 ± 0.9b	4.1 ± 1.4c*
Dapu-Sep	2.5 ± 0.4c	1.2 ± 0.4c	7.5 ± 1.5b*	16.5 ± 2.3a	6.7 ± 1.9b	2.0 ± 0.2c
Pena-May	0.8 ± 0.2b	0	0.4 ± 1b	0	1.4 ± 0.5a	0
Pena-Sep	1.5 ± 0.5b	0	1.1 ± 1.2b	0	3.0 ± 0.8a	0

species specific water requirements or differences in microhabitat distribution of soil water. The small tussock, fluff grass, *D. pulchella* exhibited a dramatic response to nitrogen fertilization and to small frequent irrigations. This response was very different from the large tussock, black grama grass, *Bouteloua eriopoda*. *B. eriopoda* productivity was not affected by nitrogen fertilization but did increase in plots receiving 12.5 mm irrigation at two week intervals (Stephens and Whitford, 1993). The differences in responses to additional water and nitrogen fertilization of these grasses are probably due to life span differences and habitat differences. *B. eriopoda* is a long-lived grass (more than a decade) while *D. pulchella* is short-lived (2–5 years). Life span may affect root turnover rates thereby affecting nitrogen mineralization and immobilization processes (Tongway and Whitford, 2002). *D. pulchella* is a component of many desert plant communities including creosotebush and tarbush, *Florensia cernua*, shrublands, mesquite, *Prosopis glandulosa* shrublands and coppice dunes, and several desert grasslands including black grama, *B. eriopoda*, grasslands. Since soils of *L. tridentata* shrublands are lower in nitrogen than other ecosystems of the northern Chihuahuan Desert (Whitford et al., 1987) nitrogen limitation of growth and establishment of *D. pulchella* in that habitat explains the response of this grass to nitrogen fertilization in the creosotebush shrubland.

The different responses of perennials growing in the inter-shrub spaces to large infrequent and small frequent simulated rainfalls and to available nitrogen shows that the establishment and growth of perennial forbs and of fluff grass are species specific with respect to these variables. The failure of *B. absinthifolia* to increase in density or biomass in the nitrogen fertilized plots suggests that the below-canopy soil concentration of nitrogen is sufficient for establishment and growth and supports the "island of fertility" hypothesis for *L. tridentata*. The lack of differences in densities and biomass of *B. absinthifolia* among rainfall treatments is probably the result of reduced evaporation due to the litter layer and shade under *L. tridentata*. There was higher biomass of herbaceous annuals under *L. tridentata* canopies in the plots receiving 25 mm supplemental water per month than in the plots receiving 6 mm irrigation per week, and biomass of herbaceous annuals was lower in control plots than in irrigated plots (Gutierrez and Whitford, 1987). Competition for water may account for the different growth patterns of *B. absinthifolia* in the irrigation treatments.

The perennial herbs in the shrub inter-spaces of the *L. tridentata* shrubland appear to be well adapted to the low available nitrogen characteristic of the inter-shrub spaces. Adaptation to low available nitrogen is evidenced by the absence of increased growth or establishment of *A. macropetalum* in the nitrogen fertilized plots. The lack of increased densities or biomass of *A. macropetalum* in the nitrogen fertilized plots show that this species is not nitrogen limited. The absence of *A. macropetalum* in plots receiving pulses of 25 mm simulated rainfall per month suggests that one or more essential nutrients may have been leached out of the upper soil layers thereby inhibiting germination, establishment and survival of this species.

The absence of *P. nana* in the nitrogen fertilized plots suggests nitrogen toxicity because *P. nana* was present all of the unfertilized plots. Because *P. nana* achieved higher density and biomass in the 25 mm per month rainfall supplement plots than in the 6 mm per week rainfall supplements or no rainfall supplement plots, suggests that the large events did not leach essential nutrients to levels below the requirements of this species. The differences in responses of *A. macropetalum* and *P. nana* to 25 mm monthly supplemental rainfall are probably the effect of the different rooting depths of these plants. *A.maropetalum* roots are concentrated in the top 10 cm and *P. nana* taproots extend to more than 30 cm.

It is possible that the responses of the perennial forbs to nitrogen amendments would be different if the plots had been fertilized when the irrigation program was initiated. Fertilizer application at the beginning of the growing season was instituted to avoid different levels of available N at the beginning of the growing season due to differential leaching of nitrates by the simulated rainfall. Nitrogen fertilization at the initiation of the irrigation program would have exposed the highly mobile nitrate to differential leaching out of the root zone of one or more of the plant species.

The higher density and biomass of fluff grass in irrigated, nitrogen fertilized plots provides partial support for earlier findings of higher biomass production of *D. pulchella* with nitrogen fertilization (Ettershank et al., 1978). However, in this study *D. pulchella* did not respond to nitrogen fertilization by increased density or biomass in the unwatered, nitrogen fertilized plots. Fluff grass exhibited a response to the supplemental rainfalls similar to that of perennial black grama grass, *B. eriopoda* (Stephens and Whitford, 1993). The growth responses of *D. pulchella* require rejection of the hypothesis that large infrequent rainfalls are more effective than small frequent events. The responses of *D. pulchella* demonstrate that the interactions between rainfall event size, nitrogen availability and growth

Table 3
Mean biomass ± SD of of the perennials Alma (*A. macropetalum*), Baab (*B. absinthifolia*), Dapu (*D. pulchella*), and Pena, (*P. nana*) in plots irrigated at 6 mm/week, 25 mm/month, or no irrigation (0 mm) and plots receiving the irrigation treatments plus NH_4NO_3. Values followed by different letters are significantly different at $p < 0.05$.

Species-Date	0 mm	0 mm + N	6 mm	6 mm + N	25 mm	25 mm + N
Alma	0.4 ± 0.1a	0.2 ± 0.1a	0.2 ± 0.1a	0.2 ± 0.1a	0	0
Baab	2.3 ± 0.1a	1.2 ± 1.2a	0.2 ± 0.5a	0.6 ± 0.2a	2.6 ± 0.9a	0.8 ± 0.1a
Dapu	0.8 ± 0.3c	0.2 ± 0.1c	3.1 ± 2.0b	15.1 ± 7.9a	0.9 ± 0.2c	2.3 ± 2.1b
Pena	0.2 ± 0.1b	0	0.1 ± 0.03b	0	0.6 ± 0.2a	0

and establishment are not linear or predictable based on earlier studies that did not examine the rainfall-nitrogen availability interactions. In conclusion, the results of this study provide evidence that, in arid ecosystems, size and frequency of rain events affect availability of soil nutrients, which can produce unexpected growth responses of perennial herbs and grasses.

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