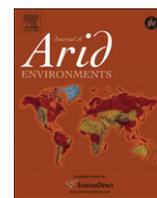




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Effects of enhanced summer monsoons, nitrogen deposition and soil disturbance on *Larrea tridentata* productivity and subsequent herbivory in the Mojave Desert

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ABSTRACT

Important global change factors in the Mojave Desert include altered precipitation, nitrogen deposition and soil disturbance. We examined the effects of enhanced summer monsoons, nitrogen deposition, and decreased nitrogen inputs via soil disturbance on *Larrea tridentata* productivity, reproduction, and herbivory. *Larrea* growth increased with summer monsoons in the dry years of 2004 and 2006, while *Larrea* growth decreased with summer monsoons in the wet year of 2005. Contrary to predictions, nitrogen addition only increased branch production in the summer of 2005. Combined treatments of monsoons and nitrogen did not result in enhanced growth or reproduction. Disturbance, which was intended to decrease N inputs from biological soil crust, decreased stem elongation in 2005. No treatments affected *Larrea* reproduction or insect herbivory. Substantial branch-level herbivory by mammals was observed, which significantly increased in the fall of 2005 and 2006, particularly with enhanced monsoons. While nitrogen addition alone had no effect, the addition of water and nitrogen significantly increased branch removal. Our results suggest that increased summer monsoons and nitrogen deposition may result in only small growth increases by *Larrea* in the Mojave Desert. However, any biomass gains are likely to be lost due to extensive mammalian herbivory with water and nitrogen additions.

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1. Introduction

Limited water and nutrient availability are primary reasons for low plant productivity in desert systems. The timing and amount of precipitation in deserts is intermittent and unpredictable, creating 'pulse-reserve' systems that require species to be resilient to sporadic precipitation (Noy-Meir, 1973; Reynolds et al., 2004). Nitrogen limitations also require desert species to optimize nitrogen use to maintain photosynthetic rates and productivity (Hooper and Johnson, 1999; Smith et al., 1997; Yahdjian et al., 2011). Global change models for desert ecosystems of the southwestern U.S. predict changes in precipitation, as well as altered nitrogen inputs, via nitrogen deposition and soil disturbance. The resulting impacts on plant growth and productivity are crucial to understanding desert ecosystems' response to climate change.

Although the exact patterns are unclear, future climate scenarios suggest extreme events in the hydrological cycle will likely become more frequent (Huntington, 2006). Indeed, Arriaga-Ramírez and

Cavazos (2010) reported extreme precipitation events increased from 1960 to 1997 in the southwestern US, with increasing extreme events occurring both in the summer and winter months. While Global Circulation Models (GCMs) suggest annual precipitation in the southwestern US will decrease in the future (Cayan et al., 2010; Seager et al., 2007), Anderson et al. (2010) found that the number, amount, intensity and coverage of summer rainfall events increased from 1931 to 2000 over the southwestern US. The increased expanse of summer rainfall events was primarily due to greater rainfall event coverage over areas that are more north of the typical summer monsoonal belt in the US.

Since deserts are water-limited, these ecosystems are expected to greatly respond to changes in precipitation, including extreme (large, infrequent) precipitation events (Huxman et al., 2004; Knapp et al., 2008). Thus, alterations in the El Niño–Southern Oscillation (ENSO) are likely to have consequences for plant productivity, consumer responses, and ecosystem structure and function (Holmgren et al., 2006). Precipitation patterns in the Mojave, Chihuahuan and Sonoran deserts are winter-dominated, summer-dominated, and bimodal, respectively; thus, changes in the monsoonal belt northward could create precipitation conditions in the Mojave Desert similar to the Sonoran Desert. Considering the three North American deserts have different precipitation

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regimes that strongly influence vegetation communities and phenology, alterations in the timing and amount of precipitation could redefine southwestern US desert boundaries (Smith et al., 1997).

Anthropogenic activities have substantially altered the global N cycle (Gruber and Galloway, 2008; Vitousek et al., 1997). Nitrogen deposition in the western United States is primarily via dry deposition originating from vehicle emissions, agriculture, and industry, with the highest rates of N deposition found downwind from agricultural and urban areas (Fenn et al., 2003a, 2003b). In contrast to nitrogen deposition, nitrogen loss could occur through soil disturbance in desert ecosystems. Biological soil crusts are a fragile mixture of lichens, mosses, cyanobacteria, and algae, which are easily destroyed by soil disturbance in deserts. Biological soil crusts play an important role in N cycling because some species fix nitrogen; therefore, biological soil crust is crucial in N-limited desert systems and nitrogen inputs could be reduced by soil and crust disturbance (Belnap, 2003).

LeBauer and Treseder (2008) reported a 53% and 60% increase in annual net primary productivity for grasslands and forests, respectively, with N addition, which would result in concomitant increases in carbon sequestration (Thomas et al., 2010). However, the LeBauer and Treseder (2008) meta-analysis found that deserts did not respond to N additions, although only three desert sites were examined. In another meta-analysis, nitrogen limitations were evident across semi-arid and arid ecosystems; in 68 N fertilization experiments, primary productivity increased 51% on average when N was added (Yahdjian et al., 2011). Variation in desert responses to N necessitate further study, particularly in drier deserts with less than 250 mm of mean annual precipitation, which were not represented in either meta-analysis.

Since water and nitrogen may both be limiting in desert systems, a combined change in water and/or nitrogen availability is likely to influence ecosystem structure and function (Phoenix et al., 2006; Xia and Wan, 2008; Yang et al., 2011). Furthermore, plant responses to altered water and nitrogen are likely to have cascading effects into higher trophic levels (Hadley and Szarek, 1981; Lightfoot and Whitford, 1987; Throop and Lerdau, 2004). While some have suggested that water and nitrogen are co-limiting in dryland ecosystems (Harpole et al., 2007; Hooper and Johnson, 1999), others have proposed water is the primary limiting factor with nitrogen as a secondary limiting factor (Seagle and McNaughton, 1993). Furthermore, the importance of water and N limitations likely vary over time in relation to one another (Niu et al., 2009; Yahdjian et al., 2011).

Larrea tridentata (DC.) Coville (hereafter referred to as “*Larrea*”) is an evergreen shrub which dominates the warm North American deserts, including the Mojave Desert (Fig. 1A). Part of *Larrea*'s success in warm deserts has been attributed to its drought stress tolerance, including maintenance of leaf area and photosynthesis during drought conditions (Smith et al., 1997). Photosynthetic responses of desert plants to precipitation also depend upon plant nitrogen status (Smith et al., 1997). Previous studies have investigated the effects of water and nitrogen additions on the ecophysiology, growth and reproduction of *Larrea* (Cunningham et al., 1979; Fisher et al., 1988; Lajtha and Whitford, 1989; Meinzer et al., 1988), but most studies occurred in the Chihuahuan Desert. Considering the Chihuahuan Desert's precipitation regime has peak rainfall in the summer, *Larrea*'s response to altered summer rain could differ in the Mojave Desert, where summer rainfall is sporadic in most years. *Larrea* growth responses to altered water and nitrogen could also affect insect and mammalian herbivory.

We examined the effects of enhanced summer monsoons, nitrogen deposition, and soil disturbance on the dominant shrub, *Larrea tridentata*, in the Mojave Desert in a multi-factor field

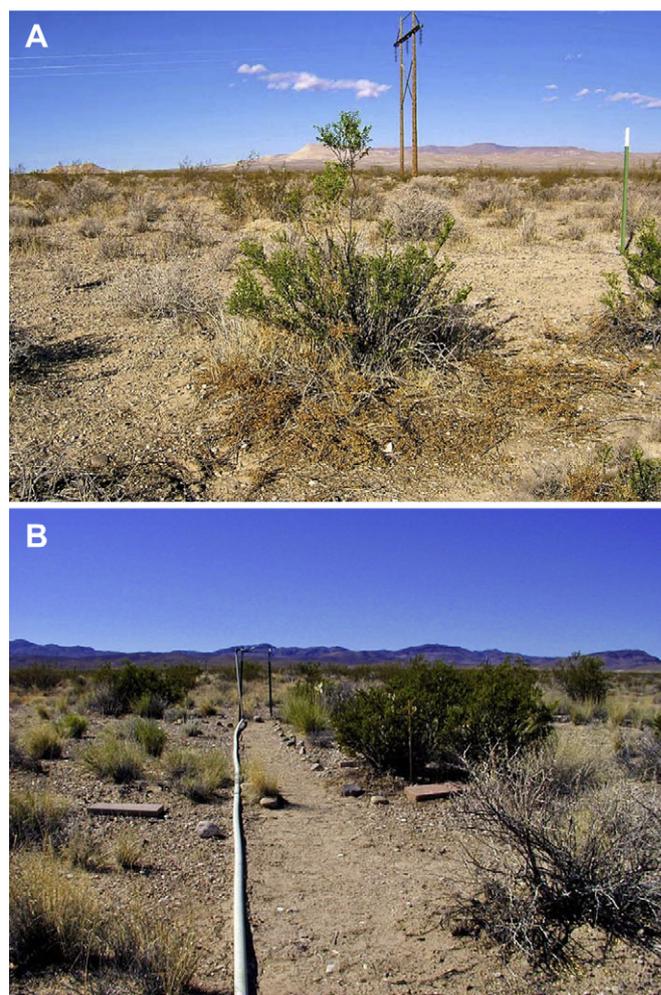


Fig. 1. (A) *Larrea tridentata* clipped by mammals. (B) Experimental plot (monsoons + 40 kg N/ha/yr + no disturbance) with central walkway, stepping-stones, and pipe for irrigation treatments. Photographs by B.A. Newingham.

experiment. Water, nitrogen, and surface soil disturbance were manipulated to answer the following question: *How do altered precipitation and nitrogen inputs affect Larrea growth and reproduction, as well as insect and mammalian herbivory?* We predicted that enhanced summer monsoons and nitrogen deposition would increase *Larrea* growth, reproduction and herbivory, with the greatest responses shown with combined summer monsoons and nitrogen addition. We predicted soil disturbance would negatively affect *Larrea* growth and reproduction, while having no significant effect on herbivory.

2. Materials and methods

2.1. Experimental design

The Mojave Global Change Facility (MGCF) is located in southern Nevada on the Nevada National Security Site (formerly Nevada Test Site; 36°45.5' N, 115°59.25' W, 970 m), where the public and livestock have been excluded for over 50 years. The MGCF lies in the northern Mojave Desert with mean annual precipitation at 143.2 mm. Most precipitation occurs in the winter months (~60% according to Blainey et al., 2007); however, summer monsoonal rains occur episodically. Soils at the MGCF consist of well-drained aridisols composed of loamy to coarse sands in texture (Titus

et al., 2002). Biological soil crusts cover approximately 35–65% of the soil surface; the rugose crust is dominated by cyanobacteria but also contains four species of lichen and three species of moss (Ustin et al., 2009).

The MGCF is a study site with a completely randomized block design where water, nitrogen deposition, and surface disturbance were manipulated each year commencing in 2001. The entire experiment was a $2 \times 3 \times 2$ factorial resulting in 12 treatments, each replicated in eight blocks; however, for this study we sampled a subset of treatments, which are listed below. Each study plot was 14×14 m (196 m^2) and treatments were applied to a 16×16 m area, allowing for a 1-m buffer around the plot. Access to plots was limited to pre-determined narrow walkways and brick stepping-stones to eliminate disturbance in the plots (Fig. 1B).

Water treatments were timed to increase summer monsoonal events in the Mojave Desert, which created a bimodal distribution of precipitation similar to the Sonoran Desert. Water was added to simulate summer monsoons via three pulse events consisting of 25-mm water applications through a central sprinkler system in each plot during June, July and August. The summer monsoon treatment (hereafter referred to as “monsoon”) provided a total of 75 mm per year, which resulted in a 50% increase in annual precipitation and about a three-fold increase in summer rain for the Mojave Desert (based on mean annual rainfall).

Nitrogen was applied in October of each year as 5 mm of an aqueous solution of $\text{Ca}(\text{NO}_3)_2$ through the central sprinkler system. Deposition rates were either 10 or 40 kg N $\text{ha}^{-1} \text{yr}^{-1}$ (hereafter referred to as “10N” and “40N”), which are slightly higher than the rate of nitrogen deposition recorded for a site in southern Nevada and a site east of Los Angeles (Bytnerowicz and Fenn, 1996), respectively. Soil disturbance (hereafter referred to as “disturbance”) was achieved by investigators scuffing their feet consistently throughout the plots in October before the application of $\text{Ca}(\text{NO}_3)_2$ and prior to germination of winter annuals. Soil disturbance broke up biological soil crusts without removing soil and therefore simulated nitrogen reduction by removing crust cover and activity. Additionally, soil disturbance may result in compaction and reduce water infiltration, so the annual scuffing treatment was conducted when soils were dry to minimize this potential effect.

2.2. Measurements

Site precipitation data were collected during 1996–2007 using HOBO rain gauges (model RG3-M; Onset Corp, Bourne, MA, USA) from a site approximately 1.5 km from the MGCF and are based on the hydrologic year (October 1st through September 30th). Growth measurements (stem elongation, leaf production, branch production, fruit production and leaf-level herbivory) were conducted in the following seven treatments: (1) control, (2) monsoon, (3) 10N, (4) 40N, (5) monsoon + 10N, (6) monsoon + 40N, and (7) disturbance. We randomly selected one *Larrea* individual in each plot, measured four shoot tips per plant, and sampled five blocks per treatment (4 shoot tips \times 1 plant \times 5 blocks; $n = 5$). To assess leaf production and leaf-level herbivory, four new 2-cm shoot tips were tagged prior to the start of the growing season using colored wire in 2004–2006. To assess stem elongation, branch production, and fruit production, four 5-cm shoot tips were tagged. Measurements were made on a monthly basis during 2004–2006, except leaf-level herbivory was measured in only 2005 and 2006. Stem elongation rates were incorporated into three growing seasons (spring, summer, and late summer) by using the following equation: $((\text{final stem length} - \text{initial stem length}) / \text{initial stem length}) / \text{\#days}$ (units are mm/day). Negative values indicate branch loss or die back. Leaf-level herbivory by insects was assessed by estimating the percent of

tissue missing from each leaf on a branch and adding up percentages when more than one leaf was damaged per stem.

Beginning in the fall of 2005, we observed large numbers of branches lying on the ground next to *Larrea* shrubs (Fig. 1A). Although both wood rats (*Neotoma lepida*) and black-tailed jackrabbits (*Lepus californicus*) could have clipped the *Larrea* branches, we assume the herbivores are jackrabbits since 1) they are the only reported mammals that browse *Larrea* in this region (Jaeger, 1948; Roth et al., 2007; Whitford, 2002), 2) jackrabbit branch removal was observed on the site (Newingham personal observation), and 3) the area was not typical wood rat habitat. Since this biomass removal likely has large impacts on the productivity of *Larrea*, we sampled branch-level herbivory by collecting all branches on the ground underneath the canopy of four *Larrea* individuals per plot. Furthermore, *Larrea* shrubs were grouped into three size classes (small = 0–20 cm, medium = 21–40 cm, and large > 40 cm), and we noted whether holes from other species of rodents were present underneath the canopy. The branch-level herbivory measurements were done in disturbed plots only, as these were the only plots we could walk in. We sampled eight blocks of the following six treatments for branch-level herbivory: (1) disturbance, (2) 10N + disturbance, (3) 40N + disturbance, (4) monsoon + disturbance, (5) monsoon + 10N + disturbance, and (6) monsoon + 40N + disturbance.

2.3. Statistical analyses

Growth and leaf-level herbivory variables were analyzed in a split plot design analysis of variance (ANOVA), where year, date within year (for fruits, herbivory, leaves, and branches; or season with a season-by-year interaction for stem elongation), and treatments were fixed effects in SAS 9.1 (PROC MIXED; SAS, 2002–2008). The experimental design was factorial for water and nitrogen but not for disturbance (treatments = control, monsoon, 10N, 40N, monsoon + 10N, monsoon + 40N, disturbance). The main effects of treatment, year, and season or date within year, plus appropriate two-way and three-way interactions, were included in the model as fixed effects. The models also included a block within treatment effect, with treatments considered between-block effects and all other fixed effects considered within-block effects. In some cases, residuals violated assumptions of the ANOVA model, so data were permuted to meet assumptions and produce alternative p -values. Permuted p -values closely matched the original p -values obtained by normal assumptions, so the original p -values are reported. Two separate sets of Tukey post-hoc tests were employed when ANOVA effects were significant ($\alpha = 0.05$). For the initial post-hoc tests involving treatment, the specific effects of monsoon, nitrogen, disturbance, and their interactions with year and season/date were considered. When these initial post-hoc tests were significant, Tukey pairwise comparisons were made to further explore patterns in the data. Fruit data were $\log_{10} + 1$ transformed to meet ANOVA assumptions; effect sizes and standard errors were back-transformed for reporting purposes.

Branch-level biomass data were $\log_{10} + 1$ transformed and analyzed with a mixed-model ANOVA in a split-plot design that included monsoon, nitrogen, time (i.e., month) and their interactions as fixed effects and block as the subject effect, with monsoon and nitrogen considered between-subject effects and time considered a within-subject effect. Significant main effects were subjected to a Tukey post-hoc test among pairs.

We used a categorical model (PROC CATMOD; SAS, 2002–2008) to analyze the effect of nitrogen and monsoon treatment, presence of rodent holes, and size of the shrub on the date when a shrub was first clipped. Shrub size was divided into three categories and was modeled as ordinal, whereas all other variables were nominal. The

categorical model included no interactions among main effects due to insufficient sample sizes in some combinations. Post-hoc comparisons were initiated for significant effects ($\alpha = 0.05$).

3. Results

3.1. Precipitation

Annual mean precipitation near the site from 1996 to 2007 was 143.2 mm with a minimum of 47 mm in the 2001–2002 hydrologic year and maximum precipitation of 328 mm in 1997–1998 (Fig. 2). Annual precipitation was slightly below average for 2003–04 (113 mm) and 2005–06 (123 mm), while annual precipitation was 75% above average during the El Niño year of 2004–05 (242 mm). Important differences in the timing of rain events occurred between the two average years: spring precipitation events in 2004 came earlier than in 2006, and there was a significant event in mid-August. In contrast, total precipitation was greater in the fall of 2005–06. Besides total amounts of precipitation, the wet year (2004–05) was characterized by higher fall and winter rains (but spring–summer rain closer to average) than in the two below-average rainfall years.

3.2. Shoot tip measurements

Generally, stem elongation was significantly lower in 2006 compared to 2004 and 2005 (Fig. 3; Table A.1) signifying substantial die back in 2006. There were significant interactions between year and monsoon-by-N, as well as year and disturbance (Fig. 3; Table A.1). Treatment interactions with season-by-year were not significant, but there was low statistical power to test these effects. The effect sizes are therefore reported (Fig. 3) and significant differences are reported within each season for each year among N and monsoon treatments. In 2004, there were no significant monsoon or N effects on stem elongation in any season, although there was an overall qualitative trend toward an increase in stem elongation with monsoons (Fig. 3). In 2005, the trend reversed, where the monsoon only treatment resulted in significantly lower stem elongation in late summer compared to no monsoon, 10N, and 40N treatments; other combinations of monsoon and N were intermediate. In the following spring of 2006, the lowest stem elongation was observed in the control treatment compared to

monsoon and nitrogen addition treatments (Fig. 3). In 2006, the overall lower stem elongation in the control was related to low stem elongation in the spring, while overall low stem elongation in the monsoon + 40N treatment was due to low stem elongation in late summer (Fig. 3). Disturbance decreased stem elongation in 2005 only (Fig. 4).

The effects of monsoon and N addition on leaf production significantly differed among years and dates within years (Fig. 5; Table A.2). Monsoons positively affected leaf production during late summer 2004, but N addition had no impact (Fig. 5; Table A.2). In 2005 and 2006, monsoon and N addition interacted to influence leaf production, but no clear patterns emerged (Fig. 5; Table A.2). There was no significant effect of disturbance on leaf production; however, disturbance slightly decreased leaf production in the summer and fall of 2005 (Fig. 5).

Monsoon and N addition, but not disturbance, significantly impacted the number of branches produced (Table A.2). Monsoons led to significantly more branches at the end of the growing season in drier years (2004, 2006; Fig. 5; Table A.2); however, monsoons decreased branch production in the summer during the wetter year of 2005. Nitrogen addition led to more branches late in 2005, had no effect in 2004, and decreased branches in the summer in 2006 (Fig. 5; Table A.2). Overall three years, disturbance tended to decrease branch production, particularly in the drier years.

Fruit production varied by year with intermediate (1.0 ± 0.1), high (1.5 ± 0.1), and low (0.8 ± 0.1) numbers of fruits produced in 2004–2006, respectively. Although there was a significant overall treatment effect, significant differences corresponding to monsoon, N addition, or disturbance treatments were not observed (Table A.2).

3.3. Herbivory

Although leaf-level herbivory by insects was not affected by any treatments, it significantly varied by year and date within year (Table A.2). Leaf-level herbivory was higher on average in wet 2005 ($15 \pm 0.01\%$) than in dry 2006 ($11 \pm 0.01\%$). Leaf-level herbivory gradually declined throughout the season in both years with small increases in October/November (data not shown).

The amount of branch-level herbivory varied significantly by monsoon and date, where clipping was significantly higher during fall of both sampling years in the monsoon treatments (Fig. 6;

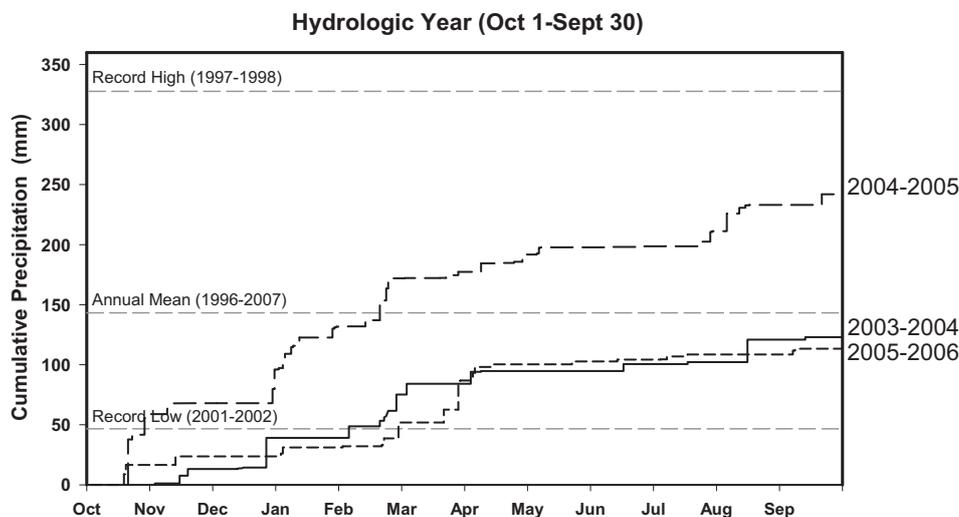


Fig. 2. Precipitation over three growing seasons corresponding with data from 2004–2006. The hydrologic year is defined as October 1 to September 30. Record highs and lows are noted for the time period of 1996–2007.

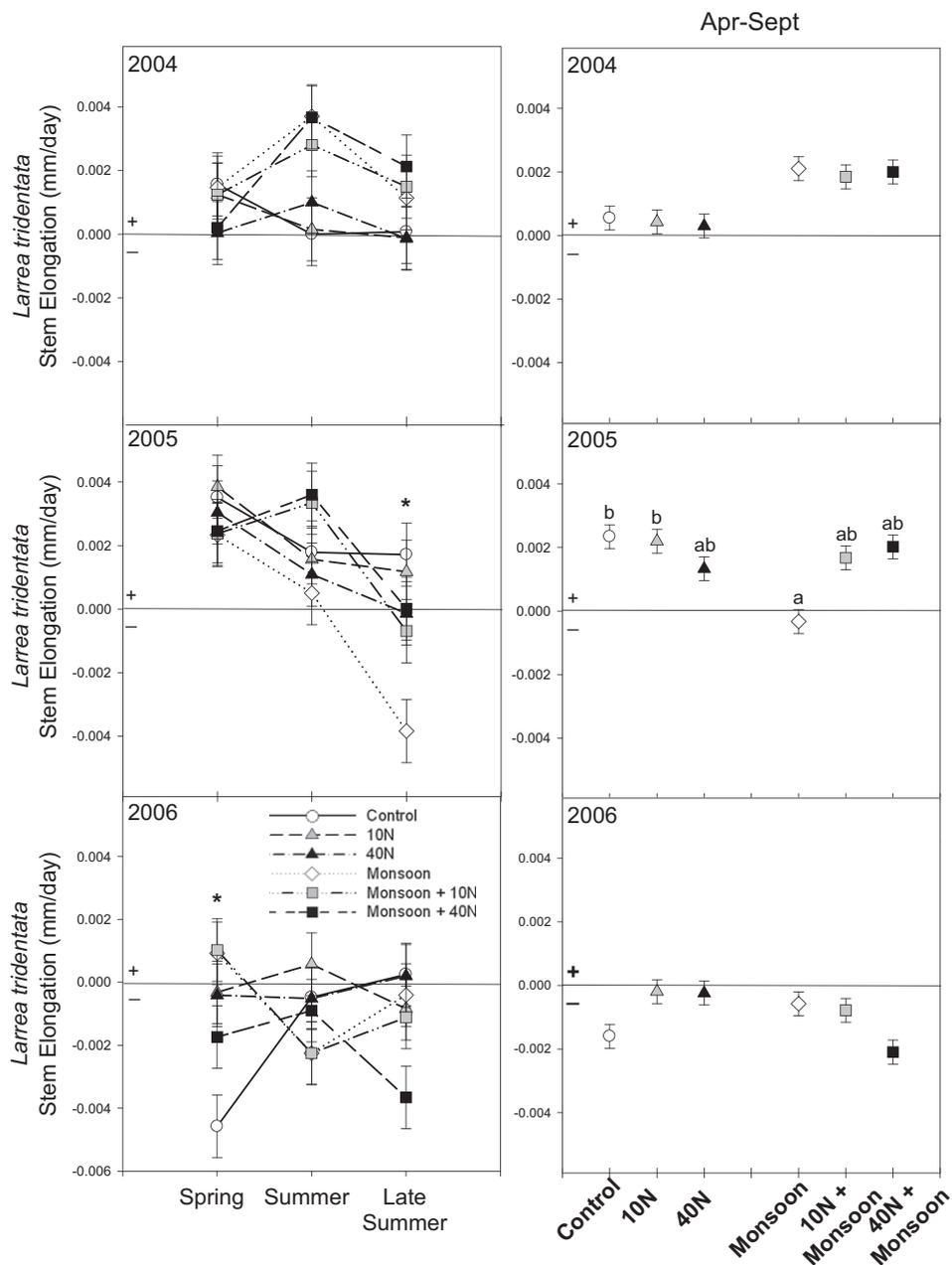


Fig. 3. Stem elongation of *Larrea tridentata* in response to simulated summer monsoons and nitrogen addition (CaNO_3). Measurements were taken on 50 mm growing tips, which were marked each spring. Error bars represent ± 1 standard error.

$F_{1,294} = 25.08$, $P_{\text{monsoon}} < 0.0001$; $F_{7,294} = 107.40$, $P_{\text{date}} < 0.0001$; $F_{7,294} = 8.24$, $P_{\text{monsoon} \times \text{date}} < 0.0001$). There was also a monsoon-by-N interaction, in which N addition had no impact on clipping in the no-monsoon treatments, but higher N inputs facilitated greater clipping under the monsoon treatment ($F_{2,294} = 2.98$, $P_N = 0.05$; $F_{2,294} = 3.39$, $P_{\text{monsoon} \times N} = 0.04$; Fig. 7).

The date of first clipping was significantly influenced by monsoon ($\chi^2_{14} = 26.79$, $P = 0.02$) and N addition ($\chi^2_7 = 21.46$, $P = 0.003$), as well as existing shrub size ($\chi^2_7 = 31.78$, $P < 0.0001$) and proximity to rodent holes ($\chi^2_7 = 14.13$, $P = 0.05$). Plants with the highest N supplementation had disproportionately more plants clipped by December 2005 ($\chi^2_2 = 8.29$, $P = 0.02$; Table A.3), which was shortly after N was applied; plants with no N addition were disproportionately clipped during June 2006 ($\chi^2_2 = 6.42$, $P = 0.04$; Table A.3). Other trends suggested that plants near rodent holes

were preferred in spring 2006 ($\chi^2_1 = 6.12$, $P = 0.01$; Table A.3), whereas those further from rodent holes were first clipped in October 2006 ($\chi^2_1 = 5.28$, $P = 0.02$; Table A.3). The smallest shrubs were more likely to be clipped in fall 2005 (beginning of experiment) than expected ($\chi^2_2 = 39.45$, $P < 0.01$; Table A.3), but there were otherwise no significant differences or trends in size of shrubs clipped.

4. Discussion

4.1. Monsoon, nitrogen and disturbance effects on plant growth

Although others have applied water to study growth in *Larrea*, our study is unique in altering the seasonality of precipitation, adding summer precipitation to a desert ecosystem that historically

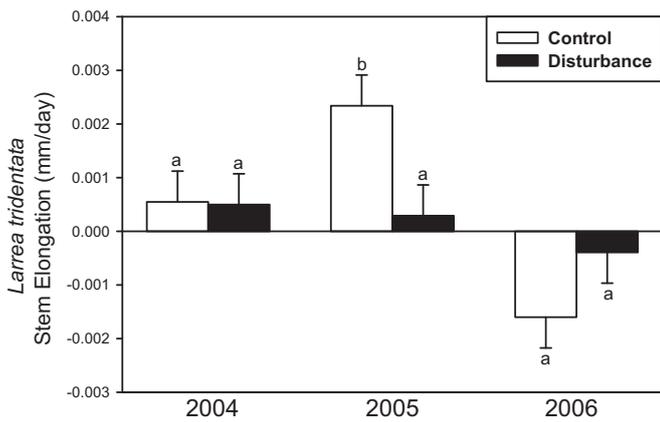


Fig. 4. Stem elongation of *Larrea tridentata* in response to soil disturbance. Measurements were taken on 50 mm growing tips, which were marked each spring. Error bars represent ± 1 standard error. Different letters indicate significant differences at $P < 0.05$ within years.

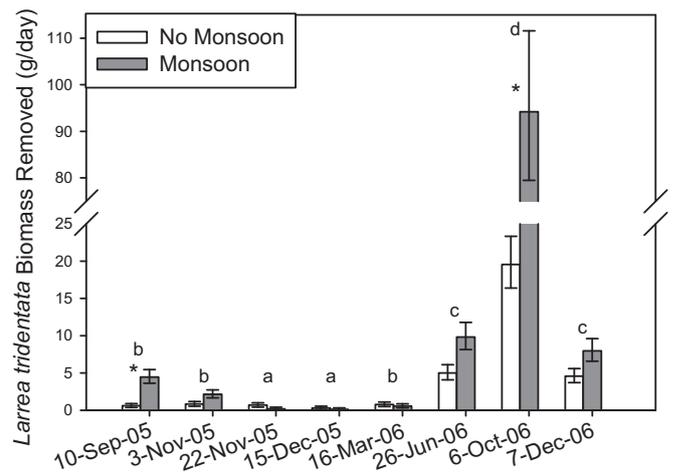


Fig. 6. *Larrea tridentata* mean branch biomass removed by mammals in response to simulated summer monsoons in 2005 and 2006. Error bars represent ± 1 standard error on back-transformed means. Asterisks represent significant differences between no monsoon and monsoon within date ($P < 0.0001$). Letters signify significant differences among dates.

received most precipitation in the winter. In contrast to other irrigation studies in the Chihuahuan Desert that found positive effects on *Larrea* growth (Cunningham et al., 1979; Fisher et al., 1988), we found both positive and negative effects of our summer monsoon treatments on *Larrea* growth in the Mojave Desert. Summer monsoons in the dry years yielded mixed

responses from *Larrea*, from nearly doubling the plants' growth rates in 2004 to barely perceptible growth responses in 2006. Even though annual precipitation in 2004 and 2006 was similar, seasonality differed substantially. In 2006, annual precipitation

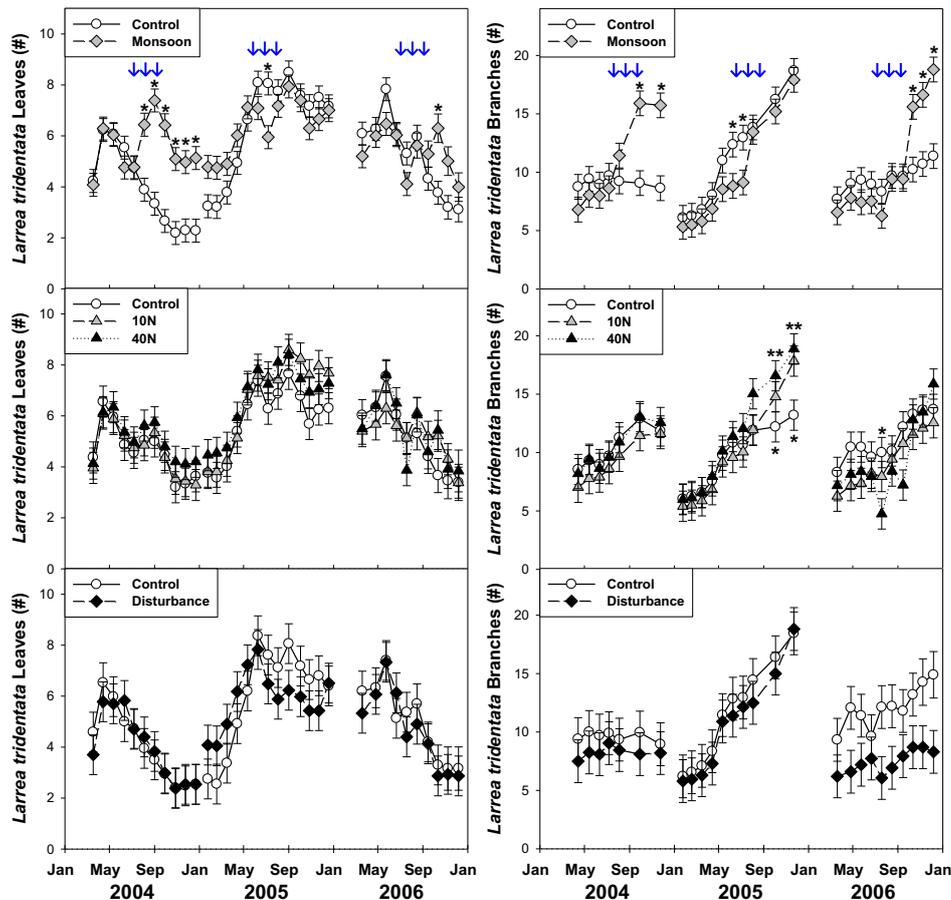


Fig. 5. Number of *Larrea tridentata* leaves and branches in response to simulated summer monsoons, nitrogen addition (CaNO_3) and soil disturbance. Main effects are separated for ease of viewing treatment effects. Error bars represent ± 1 standard error. Arrows indicate when monsoon treatments were applied. Treatments were compared within date. Asterisks above points in each date denote the number of means (starting with the highest in rank) significantly different from the lowest means, denoted by asterisks below points in each date.

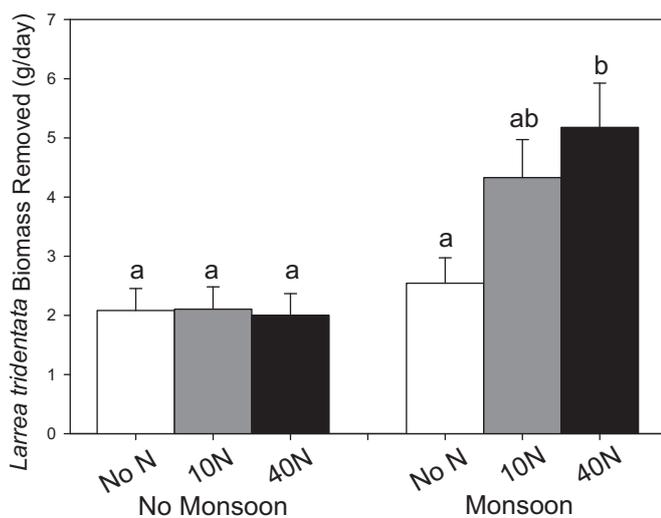


Fig. 7. *Larrea tridentata* mean branch biomass removed by mammals in response to simulated summer monsoons overall nitrogen treatments. Error bars represent ± 1 standard error on back-transformed means. Letters represent significant differences among treatments ($P < 0.0001$).

lagged behind that of 2004 until mid-April. This delay in early season precipitation caused substantial branch die back that was not entirely reduced by our monsoon treatments. In addition, the positive effects of monsoons on *Larrea* growth were evident only directly after application during the summer months; Barker et al. (2006) also found strong responses in leaf-level CO_2 assimilation and stomatal conductance directly after water application at this same site.

Interestingly, *Larrea* had negative growth in 2005 in response to monsoons even though it was a relatively wet year. It is possible that such highly abundant soil moisture throughout the growing season in 2005 allowed other species to gain a competitive advantage. For example, drought-deciduous shrubs and winter annuals have earlier phenologies and may have reduced *Larrea*'s ability to fully respond to our treatments later on in the season. Bamberg et al. (1976) found that species that have earlier phenology, such as *Lycium* spp. and *Ambrosia dumosa*, benefitted more from increased spring precipitation than *Larrea*. Thus, while we predicted growth to always increase in response to additional summer precipitation, it is possible that other factors, such as spring precipitation, temperature, nutrient conditions, and biotic interactions, may further influence *Larrea*'s response to summer monsoons.

Although growth was affected by our monsoon treatments, reproductive output was not. This is in contrast to other studies, which found that increases in *Larrea* growth come at the cost of reproduction with additional summer rain (Cunningham et al., 1979; Fisher et al., 1988). It may be that our growth responses were not large enough to cause resource limitations to reproduction.

Summer monsoons had a larger effect on growth than nitrogen additions. While nitrogen addition slightly increased branch production in 2005, there was no strong increase in production with additional nitrogen, which corroborates *Larrea* physiological data (Barker et al., 2006). We predicted that low nutrient availability in this desert ecosystem would cause *Larrea* to strongly respond to nitrogen addition. Therefore, our results were surprising since most studies have found positive effects of N additions on productivity of desert plants (Harpole et al., 2007; LeBauer and Treseder, 2008; Xia and Wan, 2008; Yahdjian et al., 2011),

including *Larrea* (Fisher et al., 1988). Nitrogen was added in October to precede winter rains and facilitate N movement into the soil profile, which would approximate accumulated dry N deposition prior to predictable winter rainfall in this ecosystem. Leaf ^{15}N showed that N addition was taken up by *Larrea*, but it did not increase leaf N (Barker et al., 2006). Yahdjian et al. (2011) examined aridland responses to N additions along precipitation and temperature gradients; they found that aridlands with low mean annual precipitation responded less to N additions than those with higher precipitation. Furthermore, arid and semi-arid systems with higher mean annual temperatures also responded less than systems with lower temperature. Considering the Mojave Desert is at the extremes in the Yahdjian et al. (2011) study for high temperatures and low precipitation, our results fall within the scope of their meta-analysis and provide another much-needed data point at the extremes.

We predicted the combination of enhanced summer monsoons and nitrogen deposition would result in the greatest increase in *Larrea* growth. However, our findings agree with other work from a temperate steppe in China (Niu et al., 2009) in not finding additive effects of water and nitrogen. While the monsoon-nitrogen interaction was significant at times, there was no consistent pattern. Previous studies have found that gaseous N losses were highest with wet soil and high temperatures at this site (McCalley and Sparks, 2008, 2009). Although we presume N efflux rates were minimal during nitrogen application in October when soil temperatures are lower, it is possible that N efflux played variable roles throughout the experiment resulting in inconsistent patterns.

Soil disturbance, which was intended to decrease N inputs by biological soil crusts, had negative effects on *Larrea* stem elongation but only in the wet year. Since continuous hydration is necessary for the highest growth and N-fixation of biological soil crusts (Stark et al., 2011), it is possible that treatment differences were seen only in the wet year due to higher activity by the biological soil crusts in the undisturbed plots. During the drier years of 2004 and 2006, both treatments probably had low N-fixation rates, which may have eliminated our ability to see treatment differences.

4.2. Herbivore responses

Herbivore responses to treatments varied depending on the type of herbivory. First, leaf-level herbivory by insects was not affected by any of the experimental treatments in this study. Lightfoot and Whitford (1987) found that water and N additions increase foliage arthropod abundance; however, they determined most of the insects were sap suckers rather than leaf chewers. Our data only reflect leaf chewers that remove part of the leaf and thus do not represent other insect functional groups that could respond to our treatments. In stark contrast, although insect herbivory was not affected by our treatments, there were marked responses by mammalian herbivores.

Substantial branch biomass was removed, which could far outweigh biomass gains through leaf or branch production with added summer monsoons. Seasonal patterns revealed most branch biomass removal occurred during the fall/winter of both years, with more branch biomass being removed in the drier year of 2006. During the fall/winter months only, plants in monsoon addition plots had higher branch biomass removal. Jackrabbits graze primarily on *Larrea* in the Mojave Desert from July–March, and it has been suggested that they eat stems to obtain water, discarding the twigs and leaves (Hayden, 1966). Steinberger and Whitford (1983) suggested that jackrabbits select stems with higher water content during the dry season and will prefer plants that have been irrigated. Barker et al. (2006) found that stem water potential was

higher in monsoon plots. Therefore, an increase in *Larrea* water availability may alter the frequency and intensity of jackrabbit herbivory.

Nitrogen addition led to greater branch biomass removal of *Larrea* but only when summer monsoons were added. Many studies have found that nitrogen addition positively affects leaf nitrogen, which would increase food quality for herbivores (Throop and Lerdau, 2004). Earlier results at this site showed that nitrogen addition increased *Larrea*'s leaf nitrogen only when the monsoon treatment was also applied (Barker et al., 2006). These results combined suggest that both water and nitrogen additions create tissue chemistry that is favorable for mammalian herbivory. There were also differences in the initiation of clipping based on monsoons, nitrogen, the presence of rodent holes and the size of shrub. While the patterns are not entirely clear, these results suggest there are complex interactions happening in relation to mammalian herbivory. Considering the complexity of these responses and the potential impact on *Larrea*, further study is warranted on mammalian herbivore-*Larrea* interactions.

5. Conclusion

Our results suggest that in drier years increased summer monsoons in the Mojave Desert are likely to have positive effects on *Larrea* growth, assuming spring precipitation is adequate to avoid branch die back in late summer. However, our results also imply that *Larrea*'s response may be more complicated in wet years or in wet-dry or dry-wet sequences. Considering *Larrea* is highly adapted to low water conditions, it is possible that monsoons had limited effect in this winter rainfall desert. *Larrea* lacked strong growth responses to nitrogen addition or soil disturbance designed to decrease soil nitrogen. The absence of growth responses to nitrogen addition were surprising considering that this desert is thought to be nitrogen-limited; lack of responses to N additions may be complicated by low water availability and N efflux.

Most global change studies have focused on soil and plant responses and little is known how higher trophic levels might respond. Additionally, few studies have considered the combined

effects of multiple changes on herbivores. Our study suggests that browsing by mammalian herbivores will substantially increase with increased summer monsoons and nitrogen deposition, which could have substantial impacts on *Larrea* productivity in this ecosystem. Thus, higher trophic level responses should be incorporated into our understanding of ecosystem responses to global change.

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Appendix A

Table A.1

ANOVA table for stem elongation of *Larrea tridentata* in 2004–2006. Stem elongation was calculated during three seasons: spring, summer, and late summer. Degrees of freedom (d.f.) are expressed as numerator, denominator. Treatment effects and interactions involving treatment are reported for monsoon, nitrogen, and disturbance when significant for clarity. Bold numbers signify when $P < 0.05$.

Effect	d.f.	F	P
Treatment	6, 28	0.65	0.69
Season	2, 224	8.78	<0.001
Treatment*Season	12, 224	1.48	0.13
Year	2, 224	30.79	<0.001
Year*Season	4, 224	6.32	<0.001
Monsoon*Year	1, 224	5.76	0.02
Nitrogen*Year	1, 224	1.57	0.21
Monsoon*Nitrogen*Year	1, 224	10.16	0.002
Disturbance*Year	1, 224	7.00	0.009
Monsoon*Season*Year	1, 224	1.74	0.19
Nitrogen*Season*Year	1, 224	1.11	0.29
Monsoon*Nitrogen*Season*Year	1, 224	0.40	0.53
Disturbance*Season*Year	1, 224	0.09	0.77

Table A.2

ANOVA table for branch number, leaf number, fruit number and % leaf-level herbivory on *Larrea tridentata* in response to seven treatments in 2004–2006. Degrees of freedom (d.f.) are expressed as numerator, denominator. Treatment effects and interactions involving treatment are reported for monsoon, nitrogen, and disturbance when significant for clarity. Bold numbers signify when $P < 0.05$.

Effect	Branch number			Leaf number			Fruit number			% leaf-level herbivory		
	d.f.	F	P	d.f.	F	P	d.f.	F	P	d.f.	F	P
Treatment	6, 28	0.94	0.48	6, 28	1.57	0.19	6, 28	0.79	0.59	6, 28	0.81	0.57
Year	2, 699	0.07	0.93	2, 896	134.14	<0.001	2, 252	30.08	<0.001	1, 588	12.55	<0.001
Date(Year)	24, 699	20.48	<0.001	31, 896	19.98	<0.001	7, 252	91.11	<0.001	21, 588	7.66	<0.001
Year*Treatment	12, 699	7.78	<0.001	12, 896	6.58	<0.001	12, 252	1.90	0.03	6, 588	0.56	0.76
Monsoon*Year	1, 699	50.26	<0.001	1, 896	26.96	<0.001	1, 252	0.10	0.76			
Nitrogen*Year	1, 699	15.20	<0.001	1, 896	6.34	<0.001	1, 252	0.00	0.99			
Monsoon*Nitrogen*Year	1, 699	0.07	0.79	1, 896	0.06	0.80	1, 252	0.56	0.46			
Disturbance*Year	1, 699	1.10	0.30	1, 896	0.00	0.95	1, 252	0.01	0.92			
Treatment*Date(Year)	144, 699	1.35	0.01	186, 896	1.85	<0.001	42, 252	0.70	0.92	126, 588	1.15	0.15
Monsoon*Date(Year)2004	1, 699	29.56	<0.001	1, 896	99.98	<0.001						
Monsoon*Date(Year)2005	1, 699	7.87	0.005	1, 896	26.05	<0.001						
Monsoon*Date(Year)2006	1, 699	19.78	<0.001	1, 896	31.31	<0.001						
Nitrogen*Date(Year)2004	1, 699	0.08	0.77	1, 896	0.84	0.36						
Nitrogen*Date(Year)2005	1, 699	7.92	<0.001	1, 896	4.80	0.03						
Nitrogen*Date(Year)2006	1, 699	1.81	0.18	1, 896	14.25	<0.001						
M*N*Date(Year)2004	1, 699	0.01	0.91	1, 896	3.05	0.08						
M*N*Date(Year)2005	1, 699	7.10	0.008	1, 896	15.21	<0.001						
M*N*Date(Year)2006	1, 699	6.14	0.01	1, 896	15.88	<0.001						
Dist*Date(Year)2004	1, 699	0.01	0.91	1, 896	0.40	0.53						
Dist*Date(Year)2005	1, 699	6.48	0.01	1, 896	2.37	0.12						
Dist*Date(Year)2006	1, 699	0.22	0.64	1, 896	0.28	0.60						

Table A.3

Proportion of plants first clipped on dates of the study. Categories group plants in four ways: (1) near or far from rodent holes, (2) those with or without water supplementation, (3) for three levels of nitrogen supplementation, and (4) across shrub size. Bold denotes a significantly larger proportion of plants first clipped on a date relative to the corresponding value(s) within that category.

Date	No rodent hole	Rodent hole	No monsoon	Monsoon	0N	10N	40N	Small	Medium	Large
09/10/05	0.06	0.04	0.05	0.06	0.07	0.05	0.05	0.24	0.04	0.02
11/03/05	0.36	0.33	0.31	0.39	0.29	0.40	0.35	0.24	0.34	0.41
11/22/05	0.07	0.10	0.11	0.05	0.07	0.05	0.13	0.02	0.09	0.09
12/15/05	0.03	0.05	0.05	0.03	0.03	0.03	0.05	0.05	0.04	0.03
03/16/06	0.09	0.16	0.16	0.08	0.13	0.14	0.09	0.14	0.12	0.12
06/26/06	0.28	0.23	0.22	0.30	0.34	0.22	0.23	0.19	0.27	0.27
10/06/06	0.11	0.05	0.08	0.09	0.08	0.09	0.08	0.14	0.09	0.05
12/07/06	0.01	0.03	0.02	0.01	0.01	0.01	0.02	0.00	0.02	0.01

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