

Above- and belowground responses to nitrogen addition in a Chihuahuan Desert grassland

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Abstract Increased available soil nitrogen can increase biomass, lower species richness, alter soil chemistry and modify community structure in herbaceous ecosystems worldwide. Although increased nitrogen availability typically increases aboveground production and decreases species richness in mesic systems, the impacts of nitrogen additions on semiarid ecosystems remain unclear. To determine how a semiarid grassland responds to increased nitrogen availability, we examined plant community structure and above- and belowground net primary production in response to long-term nitrogen addition in a desert grassland in central New Mexico, USA. Plots were fertilized annually (10 g N m^{-2}) since 1995 and NPP measured from 2004 to 2009. Differences in aboveground NPP between fertilized and control treatments occurred in 2004 following a prescribed fire and in 2006 when precipitation was double the long-term average during the summer monsoon. Presumably, nitrogen only became limiting once drought stress was alleviated. Belowground

NPP was also related to precipitation, and greatest root growth occurred the year following the wettest summer, decreasing gradually thereafter. Belowground production was unrelated to aboveground production within years and unrelated to nitrogen enrichment. Species richness changed between years in response to seasonal precipitation variability, but was not altered by nitrogen addition. Community structure did respond to nitrogen fertilization primarily through increased abundance of two dominant perennial grasses. These results were contrary to most nitrogen addition studies that find increased biomass and decreased species richness with nitrogen fertilization. Therefore, factors other than nitrogen deposition, such as fire or drought, may play a stronger role in shaping semiarid grassland communities than soil fertility.

Keywords Semiarid grassland · N deposition · Aboveground production · Belowground production · Species richness

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Introduction

Human modifications to the N cycle and increased N deposition associated with urban development have altered ecosystem processes worldwide (Vitousek et al. 1997; Fenn et al. 2003a; Galloway et al. 2004). Many terrestrial ecosystems are N limited (Vitousek and Howarth 1991) and atmospheric deposition often increases nutrient availability, which typically increases aboveground net primary productivity (ANPP) and decreases species diversity (Baer et al. 2003; Chalcraft et al. 2008; Stevens et al. 2010). N deposition lowers diversity through competitive exclusion and may increase the abundance of non-native species (Tilman 1987; Rajaniemi 2002; Suding et al. 2005). Plant

community responses to N addition vary across ecosystems and are often co-determined with environmental conditions (Gough et al. 2000; Clark et al. 2007). In a meta-analysis of N addition experiments, deserts were poorly represented and appeared to be the only biome that did not exhibit N limitation (LeBauer and Treseder 2008). Yet, given evidence that desert soils are notoriously nutrient poor (Peterjohn and Schlesinger 1990; Zak et al. 1994; Hall et al. 2011), further investigation is required to determine if deserts are indeed N limited or if the perceived lack of N limitation is contingent upon other environmental factors.

Aridland ecosystems are characterized by low water availability and unevenly distributed precipitation within and between years. Thus, many arid ecosystems respond primarily to precipitation pulses with greatest plant growth occurring when soil water is available (Noy-Meir 1973; Schwinning and Sala 2004). The extent of plant responses to precipitation pulses varies geographically, seasonally and as a function of plant life-history traits (Ogle and Reynolds 2004). For example, within semiarid grasslands in the northern Chihuahuan Desert, peak grass production occurs following large summer rain events, whereas peak forb and shrub production, both of which are typically dominated by C₃ species, occur following winter rains (Muldavin et al. 2008; Xia et al. 2010).

Although desert plants are primarily limited by water, previous studies have indicated the potential for co-limitation by N in semiarid systems (Peterjohn and Schlesinger 1990; Hooper and Johnson 1999; Hall et al. 2011). N fertilization in other semiarid systems has led to both decreases (Carpenter et al. 1990) and increases (Ettershank et al. 1978) in ANPP of perennial species and, even within the same grassland, C₄ grasses can show variable responses to N addition (Báez et al. 2007; Collins et al. 2010). Experimental N fertilization of 3.2–10 g N m⁻² year⁻¹ in Mojave, Sonoran and Chihuahuan desert communities increased ANPP, especially by quickly responding annual plants during years of average to above average precipitation (Gutierrez and Whitford 1987; Gutierrez et al. 1988; Brooks 2003; Allen et al. 2009; Rao and Allen 2010; Rao et al. 2010). Thus, quick-growing annuals can respond to N additions, yet it remains unclear how communities composed mainly of longer-lived, herbaceous perennials, such as C₄ grasses, respond to chronic N addition.

Few studies have measured the effects of N addition on belowground net primary production (BNPP), yet belowground growth and storage are important components of ecosystem productivity. Increased soil N availability can alleviate N limitation, leading to a decrease or altered patterns of belowground production. In other semiarid grasslands, addition of 10–20 g N m⁻² altered root growth patterns and increased shallow, fine root production (Stephens and Whitford 1993; Zeng et al. 2010). Although

potentially substantial, belowground production dynamics following N fertilization in semiarid grasslands remain largely unknown because of the limited number of studies and the challenges involved with measuring belowground NPP (Milchunas 2009).

Nitrogen addition also has variable effects on plant community composition and structure in arid environments. Changes in community composition can influence ecosystem processes and alter community response to disturbances. In more mesic grasslands, N addition generally leads to a decline in species richness and community heterogeneity (Gough et al. 2000; Chalcraft et al. 2008), primarily through competitive exclusion (Rajaniemi 2002). However, N addition may increase species richness and community heterogeneity in low productivity systems (Gutierrez and Whitford 1987; Chalcraft et al. 2008) because light is rarely limiting in these systems even with an increase in aboveground NPP (but see Zeng et al. 2010). Nevertheless, it remains unclear how long-term community dynamics and structure will respond to N addition in drier semiarid grasslands.

To determine how semiarid grasslands respond to increased N availability and precipitation variability, we examined above- and belowground productivity, and plant community composition, in response to long-term N fertilization from 2004 to 2009 in a native northern Chihuahuan Desert plant community. We hypothesized that N addition would (1) increase ANPP only during years of average to above average precipitation, (2) decrease BNPP only during years of average to above average precipitation because of higher soil resource availability, and (3) increase species richness and diversity, and the total abundance of perennial C₄ grasses.

Materials and methods

Study site

This research was conducted at the Sevilleta National Wildlife Refuge (SNWR) located in central New Mexico, USA, roughly 95 km south of Albuquerque. Annual precipitation is highly variable and averages 250 mm with the majority falling as large summer monsoon events (Gosz et al. 1995; Pennington and Collins 2007). Average annual temperature is 13.2°C with highest temperatures in June, 33.4°C, and lowest in January, 1.6°C (Collins et al. 2008). Several ecoregions occur within the SNWR, including the northern most extent of the Chihuahuan Desert grassland and southern extent of shortgrass steppe. Both grasslands contain a variety of forbs but are dominated by C₄ perennial grasses. Chihuahuan Desert grasslands, which occur throughout much of southern New Mexico and northern

Mexico, are dominated by *Bouteloua eriopoda*. Shortgrass steppe along the Colorado plateau to the north and east of SNWR is largely dominated by *Bouteloua gracilis* as well as other perennial C_4 grasses. This research was conducted in a transition zone containing a mixture of species from both Chihuahuan Desert and shortgrass steppe vegetation.

The growing season of this semiarid grassland is closely aligned with seasonal precipitation and temperature. Over 60% of annual precipitation occurs during the summer monsoon from June to September each year, while sporadic precipitation occurs throughout the winter and spring as a consequence of frontal systems from the west and northwest. This precipitation pattern results in two distinct growing seasons, spring and fall, with virtually all herbaceous plants dying or going dormant between the two seasons (Notaro et al. 2010). Since plant growth is highly dependent on water, the success of each growing season depends heavily on amount of precipitation for that season and legacy effects of previous precipitation events.

Field experiment

In 1995, twenty 10 m \times 5 m plots were established within the transition between Chihuahuan Desert grassland and shortgrass steppe to examine impacts of N enrichment on above- and belowground processes (Johnson et al. 2003). Ten of the plots were randomly assigned to the fertilizer treatment and ten plots served as controls. In March and June of each year since 1995, 5 g N m⁻² as NH₄NO₃ has been applied to the ten treatment plots. This level of N addition was chosen to reflect potential rates of atmospheric deposition near urban areas in the US Southwest (Fenn et al. 2003b). A management fire was allowed to burn through all the plots in June 2003, a time of year when lightning strikes and natural wildfires are common (Parmenter 2008).

In 1997, cover of each species was visually estimated in two randomly located 1-m² subplots in each treatment and control plot. Starting in 2004, vegetation within four 1-m² subplots in each treatment and control plot was measured during the peak spring and fall growing seasons for species composition and ANPP. For every subplot, the biomass of each species was determined allometrically from cover and height size classes following Muldavin et al. (2008). Regressions of weight-to-volume were developed by harvesting various sizes of each species from adjacent areas. A positive change in green biomass from one season to the next in each subplot was used as a measure of ANPP.

Starting in 2005, belowground net primary production (BNPP) was measured using root ingrowth donuts following Milchunas et al. (2005). A comprehensive comparison of BNPP sampling methods determined root ingrowth donuts to be a reliable and repeatable method

with limited soil disturbance that can yield conservative measurements of annual BNPP (Milchunas 2009). One root donut was located in the center of each plot to measure annual root growth within shallow (0–15 cm) and deep (15–30 cm) soil layers. To create a root ingrowth donut, a 20-cm-diameter by 30-cm-deep cylinder of soil was excavated with a custom-made auger and the soil was sieved to remove all roots. The surface wall of the hole from which the soil core was removed was lined with 2 mm \times 2 mm mesh plastic cross-stitch fabric. A 15-cm-diameter by 30-cm-tall cylinder of PVC pipe was then inserted into the center of the soil core to take up space, and filled with bags of sand to hold it in place. Root-free sieved soil was then poured into the remaining space between the PVC cylinder and the cross-stitch fabric, creating a root ingrowth donut. Donuts were harvested yearly by removing the sand bags and PVC cylinder, cutting the internal soil adjacent to the cross-stitch fabric with a sharp kitchen knife, and collecting the soil and root materials. This was done at two depths, 0–15 and 15–30 cm. Newly collected soil from adjacent areas from 0 to 30 cm depth was then sifted and used to reconstruct the root ingrowth donut for the next annual harvest. Following each sample period, the volume of collected soils was measured by depth, roots were sifted and floated out of each sample, collected, dried at 60°C for 48 h, and weighed.

Detailed meteorological data from Sevilleta LTER Meteorological station 54, located 1,200 m from the site, were used to relate measures of community structure and dynamics to seasonal and annual climate variables.

Statistical analysis

To test our first hypothesis, we compared ANPP between fertilizer treatments and years using a repeated measures analysis of variance (RMANOVA). To test hypothesis two, BNPP was evaluated separately at each depth (0–15 and 15–30 cm) and collectively for total BNPP. We used three separate RMANOVAs to compare BNPP between treatments and years. To test hypothesis three, we first examined treatment effects on species richness, evenness, and Shannon diversity through time with three separate RMANOVAs. Additionally, forb:grass ratios of ANPP were evaluated with a RMANOVA to determine if fertilizer differentially influenced functional groups. All statistical tests were run using SAS v.9.2 and results reported using Wilk's Lambda statistics with $\alpha = 0.05$.

We used PERMANOVA to determine if fertilized and control plots differed significantly in composition. The PERMANOVA procedure analyzes distance measures in any linear model with categorical factors, such as fertilizer treatments, and tests for significance by permutation of the distance matrix (Anderson 2001; Anderson and Ter Braak

2003). PERMANOVA procedures were run on the complete data set as well as on data from each year individually. Finally, we ran SIMPER (similarity percentage) analyses which uses Bray–Curtis dissimilarity values as a post hoc test to determine which species contributed the most to differences between treatment and control plots. SIMPER analyses were performed on the complete matrix as well as separately on data from each year. PERMANOVA and SIMPER were performed with PRIMER-e v.6.

Results

Common in arid systems, annual precipitation greatly varied between years. Lowest annual precipitation (153 mm) occurred in 2003, the year prior to vegetation sampling and the greatest annual precipitation (392 mm) occurred in 2006. All other years received roughly average precipitation (250 mm), based on the 20-year average from this site (Fig. S1). Aboveground production strongly corresponded to monsoon precipitation and both were lowest in 2005 and greatest in 2006. Duration of monsoon season also varied between years with 2005 experiencing a short, late monsoon season, and a long monsoon season with consistent precipitation occurred in 2006. Fertilizer treatments began in 1995 and percent cover data from 1997 provided background information about community composition before the managed burn in 2003. Total vegetation cover was higher in fertilized plots than in control plots (57 vs. 42%). In 1997, grasses dominated both fertilized and unfertilized communities, and *Bouteloua gracilis* was the most abundant species. Collectively, grasses comprised 80% of plant cover in both fertilized and control plots.

Aboveground NPP varied between years ($p < 0.0001$, $F_{5,14} = 21.86$) and corresponded well with the current year's precipitation. Lowest ANPP occurred in 2005 when the monsoon season was late and short, and there was a several fold increase in ANPP during 2006, a year with a long and above average monsoon season (Figs. 1; S1). A significant interaction between time and fertilizer treatment indicated differences in ANPP between treatments among years ($p = 0.0452$, $F_{5,14} = 3.06$). ANPP was greater in fertilized plots during 2006 ($p = 0.0002$, $F_{1,18} = 21.02$, $r^2 = 0.539$). Nitrogen fertilization accounted for 50% of the increased production in fertilized plots. Slightly greater ANPP in fertilized plots was also present in 2004, the year following the management burn ($p = 0.0332$, $F_{1,18} = 5.32$, $r^2 = 0.228$). ANPP did not vary between fertilized and control plots in 2005, 2007, 2008 and 2009 ($p = 0.857$, $p = 0.657$, $p = 0.5335$, $p = 0.1742$; Fig. 1).

Belowground NPP was also linked to precipitation but unlike aboveground production there was no effect of N fertilization on belowground production at shallow soils,

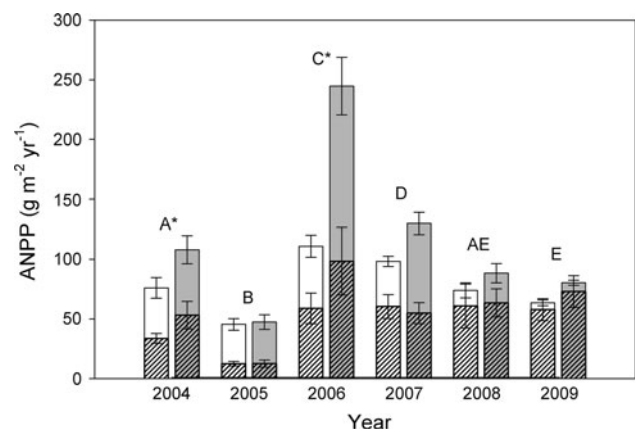


Fig. 1 Annual ANPP in control (white) and N fertilized (gray) plots, separated into grass (striped) and forb (solid) components. With regard to total ANPP, letters indicate significant differences between years and an asterisk indicates significant differences between treatments for that year. Error bars $\pm 1SE$

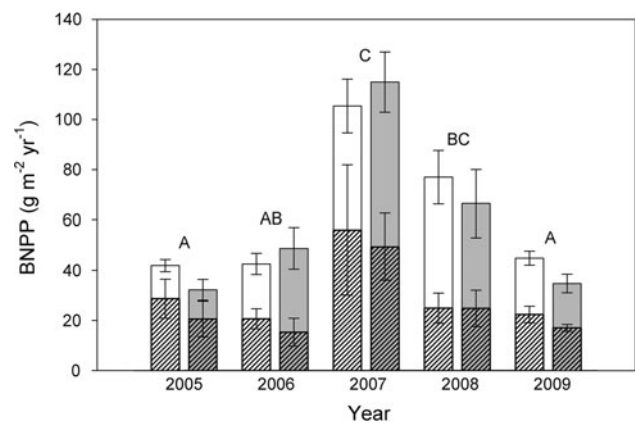


Fig. 2 Annual BNPP within the top 30 cm of soil in control (white) and N fertilized (gray) plots. Soil profile is separated into BNPP in the top 0–15 cm of soil (striped) and 15–30 cm of soil (solid). Letters indicate years with significantly different BNPP. There was no significant difference between fertilized and control plots. Error bars $\pm 1SE$

deeper soils, or collectively ($p = 0.5528$; $p = 0.9922$; $p = 0.4792$, respectively; Fig. 2). Both current and past annual precipitation played an equally important role in belowground production. BNPP significantly varied through time and highest BNPP occurred in 2007, a year with average precipitation following a year with above-average precipitation ($p = 0.0008$, $F_{4,12} = 10.24$; Fig. 2). Within deeper soils (15–30 cm), BNPP did not significantly change between years ($p = 0.0712$) and variation between years was largely driven by root growth in the top 15 cm of soil ($p < 0.0001$, $F_{3,14} = 26.56$).

Fertilizer effects on Shannon's diversity were only present in 2007 and diversity was higher in fertilized plots ($p = 0.025$, $F_{1,18} = 5.99$, $r^2 = 0.25$; Table 1). The increase in diversity was driven by increased evenness in

Table 1 Shannon's diversity (D) and evenness (E) from 2004 to 2009

| | 2004 | | 2005 | | 2006 | | 2007 | | 2008 | | 2009 | |
|---------------|-------|-------|-------|-------|-------|-------|--------------|--------------|-------|-------|-------|-------|
| | D | E | D | E | D | E | D | E | D | E | D | E |
| Control | 1.928 | 0.639 | 1.736 | 0.635 | 1.764 | 0.592 | 1.875 | 0.618 | 1.484 | 0.608 | 1.283 | 0.506 |
| Fertilized | 1.648 | 0.561 | 1.697 | 0.635 | 1.706 | 0.596 | 2.194 | 0.741 | 1.443 | 0.585 | 1.358 | 0.549 |
| Control SE | 0.126 | 0.029 | 0.097 | 0.034 | 0.100 | 0.027 | 0.086 | 0.029 | 0.161 | 0.053 | 0.154 | 0.043 |
| Fertilized SE | 0.091 | 0.025 | 0.064 | 0.021 | 0.095 | 0.025 | 0.098 | 0.018 | 0.206 | 0.055 | 0.206 | 0.047 |

Significant differences between fertilized and control plots are indicated in bold

fertilized plots ($p = 0.002$, $F_{1,18} = 12.91$, $r^2 = 0.42$) and not a change in richness between treatments. Neither total species richness, grass richness nor forb richness were related to N fertilization ($p = 0.576$, $p = 0.911$, $p = 0.613$). Species richness significantly varied between years ($p < 0.0001$, $F_{5,14} = 86.49$) and was greatest in 2004 and 2007, primarily due to an increase in annual forbs (Fig. 3). The decline in species richness in 2008, which persisted in 2009, was largely driven by a loss of forbs. Forbs formed the majority of ANPP until 2007 when a switch in community composition resulted in grasses becoming more abundant than forbs from 2008 onwards (Fig. 1). This compositional switch, measured as a decrease in forb:grass ratio of ANPP, occurred in all plots and was unaffected by fertilizer treatment ($p = 0.4448$).

PERMANOVA followed by a pos-hoc SIMPER analysis provided a more direct test of fertilizer effects on species composition over time. PERMANOVA on the full dataset showed a significant overall difference in species composition of N fertilized and control plots (pseudo $F = 3.76$, $p = 0.003$) and year (pseudo $F = 9.21$, $p = 0.001$), but the treatment times year interaction was not significant. Yearly analyses found significant differences in composition between treatment and control plots in 2005–2007, but not in 2004, 2008 or 2009. SIMPER results showed that overall differences in composition between treatment and control plots primarily reflected strong differences in species abundances in response to fertilization (Table 2). In general, the two most abundant C_4 grasses, *Bouteloua gracilis* and *Pleuraphis jamesii*, along with the annual forbs *Kallstroemia parviflora* and *Salsola tragus*, had much higher abundances on fertilized compared to control plots. In contrast, the C_4 perennial grasses *B. eriopoda* and *Aristida purpurea* had higher abundances on plots that did not receive additional N.

Discussion

Similar to many terrestrial systems (Gough et al. 2000; LeBauer and Treseder 2008), N addition resulted in increased aboveground production in some years indicating potential N limitation within this semiarid grassland.

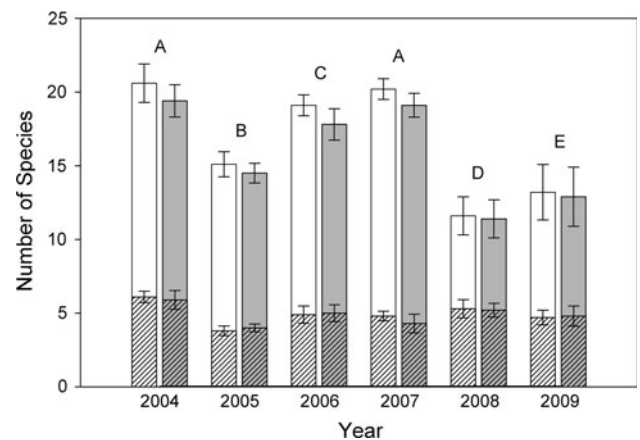


Fig. 3 Species richness per 4 m² in control (white) and N fertilized (gray) plots separated into grass (striped) and forb (open) components. Letters indicate significant differences between years. There were no significant differences between fertilizer and control treatments. Error bars $\pm 1SE$

Although present, N limitation only occurred during periods of above-average precipitation, adding further support to the claim that semiarid systems are primarily water limited and secondarily N limited (Gutierrez et al. 1988; Carpenter et al. 1990; Gutierrez 1992; Brooks 2003; Allen et al. 2009; Rao and Allen 2010; Rao et al. 2010). Although apparent aboveground, N fertilization did not increase belowground production nor did it drive directional changes in plant community diversity, composition or dynamics.

Aboveground production was positively related to seasonal precipitation, with highest production (250 g m⁻²) occurring in 2006 on fertilized plots following a summer of record high rainfall. In contrast, ANPP was < 50 g m⁻² on fertilized and control plots in 2005 when summer rains were 75% below the long-term average. Also, N addition significantly increased total aboveground production in 2004, the year following fire, when N fertilization may have restored some of the N lost through volatilization from burning. Overall, a strong N effect on ANPP only occurred during above average monsoon precipitation in 2006. Grass production was 66% higher and forb production nearly 300% higher on fertilized compared to control plots. However, greater aboveground production on

Table 2 Average abundance of dominant species in fertilized and control plots from 2004 through 2009 based on SIMPER analysis

| Species | Fertilized abundance | Control abundance | Average dissimilarity | Percentage contribution | Cumulative contribution |
|-----------------------------------|----------------------|-------------------|-----------------------|-------------------------|-------------------------|
| <i>Pleuraphis jamesii</i> | 31.62 | 19.04 | 12.51 | 16.26 | 16.26 |
| <i>Bouteloua gracilis</i> | 28.12 | 13.97 | 11.22 | 14.58 | 30.84 |
| <i>Kallstroemia parviflora</i> | 14.53 | 3.31 | 5.00 | 6.51 | 37.35 |
| <i>Salsola tragus</i> | 10.84 | 6.19 | 4.98 | 6.48 | 43.83 |
| <i>Sphaeralcea wrightii</i> | 10.74 | 2.59 | 4.82 | 6.26 | 50.09 |
| <i>Cryptantha crassisepala</i> | 8.11 | 5.38 | 4.78 | 6.21 | 56.29 |
| <i>Gutierrezia sarothrae</i> | 3.81 | 9.57 | 4.44 | 5.77 | 62.07 |
| <i>Bouteloua eriopoda</i> | 3.66 | 9.53 | 4.31 | 5.61 | 67.67 |
| <i>Oenothera caespitosa</i> | 5.09 | 1.28 | 2.03 | 2.64 | 70.31 |
| <i>Aristida purpurea</i> | 1.42 | 5.16 | 2.03 | 2.63 | 72.95 |
| <i>Melampodium leucanthum</i> | 2.27 | 2.92 | 1.90 | 2.46 | 75.41 |
| <i>Tidestromia lanuginosa</i> | 4.06 | 0.84 | 1.79 | 2.33 | 77.74 |
| <i>Astragalus nuttallianus</i> | 2.48 | 2.45 | 1.54 | 2.00 | 79.74 |
| <i>Euphorbia exstipulata</i> | 1.97 | 2.52 | 1.38 | 1.80 | 81.54 |
| <i>Machaeranthera pinnatifida</i> | 1.37 | 2.12 | 1.19 | 1.55 | 83.09 |
| <i>Solanum elaeagnifolium</i> | 2.23 | 1.14 | 1.18 | 1.53 | 84.62 |
| <i>Chaetopappa ericoides</i> | 0.84 | 2.21 | 1.03 | 1.34 | 85.96 |
| <i>Sporobolus flexuosus</i> | 1.64 | 0.73 | 0.93 | 1.21 | 87.17 |
| <i>Sporobolus contractus</i> | 1.25 | 1.21 | 0.90 | 1.16 | 88.33 |
| <i>Sporobolus cryptandrus</i> | 1.36 | 1.17 | 0.79 | 1.03 | 89.36 |
| <i>Sphaeralcea hastulata</i> | 1.15 | 0.53 | 0.78 | 1.01 | 90.37 |

fertilized plots did not persist. The results supported our first hypothesis that these desert grasslands are N limited and that N limitation only becomes evident following periods of above average rainfall as well as when N is depleted following fire. Average precipitation, however, is not sufficient to alleviate drought stress as N limitations were not present in the four years with average rainfall.

Over the 5 years of measurement, belowground production averaged $57.02 \text{ g m}^{-2} \text{ year}^{-1}$, which although low is still within the range of root production reported for other semiarid systems ($30\text{--}443 \text{ g m}^{-2} \text{ year}^{-1}$; Pavon 2005). Our measurement of belowground production underestimates actual root production because fine root turnover likely occurred between annual belowground sampling periods. Nevertheless, our results are certainly comparable across plots and years, and differences in root production were apparent over time. The greatest belowground production occurred in 2007, the year following the record monsoon rainfall, and declined gradually over time. A majority of increased production occurred in the top 15 cm of soil, a region of high root production (Bhark and Small 2003). Presumably, BNPP increased following the wet year, supporting aboveground production from the previous year. These results demonstrate that belowground production occurs on multiple-year cycles in response to above average precipitation, and provide the mechanism by

which these grasslands were a net carbon source in 2007 and 2008 despite relatively high aboveground and belowground production during those years (Xia et al. 2010; Anderson-Teixeira et al. 2011). In addition, these results indicate that high aboveground production in a given year does not correspond with high belowground production.

Even when N limitation was detectable aboveground, N fertilization did not stimulate belowground production, a result counter to our second hypothesis. Instead, belowground production was most responsive to ANPP from the previous year. Although we did not see an influence of N on belowground productivity, fertilization has been shown to affect shallow root biomass and growth patterns in other desert systems. Xeric shrubs in the central valley of Mexico reduced fine root production with N enrichment (Pavon 2005), and fertilization led to shorter roots in *B. eriopoda* in another Chihuahuan Desert grassland (Stephens and Whitford 1993). In contrast, fine root biomass increased in a semiarid sand–shinnery oak ecosystem in response to water and N additions (Zhang and Zak 1998). In many terrestrial systems, belowground production decreased with nitrogen addition because plants allocated more resources aboveground to compete for light (Hautier et al. 2009). In desert grasslands, however, light is generally abundant and plant cover is patchy such that aboveground competition for light is minimal even during periods of high

aboveground production. Overall, our results suggest that root production in our system is driven primarily by soil water availability and not by competition for soil nitrogen.

In contrast to our third hypothesis, we observed no consistent impact of N enrichment on species composition over time. Although composition in treatment and control plots differed significantly in some years, composition of treatment and control plots did not differ during the final year of the study. Although N additions did not have large impacts on species abundances at our site, N fertilization has altered community dynamics in other desert systems. Other semiarid fertilization studies indicate decreases in species richness, a switch from C_4 to C_3 species, or influences that scale directly with amount of precipitation (Carpenter et al. 1990; Zeng et al. 2010; Hall et al. 2011). Site-specific differences may account for the differing results, as the degree of aridity and community composition varied between sites and may impact how plants respond to precipitation and N addition.

Although composition changed from a predominantly forb rich community into a grass dominated system, this change occurred on both fertilized and control plots. Thus, the increase in grass abundance relative to forbs probably reflects time since burning (Parmenter 2008). Fires occur in this system during summer months when conditions are windy and hot, and adequate dry fuel is available. Fires alter nutrient distribution locally and may promote grass dominance and reverse land degradation (Ravi et al. 2009; Ravi and D'Odorico 2009). Species abundance data collected in these plots in 1997, 2 years after the start of the fertilizer treatments, indicated roughly 50% cover of grass and <10% forbs. Response to fire varies among life forms (Parmenter 2008). Initially forbs dominate following fire, although *Bouteloua gracilis* recovered by the next season and it also responded favorably to N addition. *Bouteloua eriopoda*, on the other hand, is not well adapted to fire and can take 7–11 years to return to pre-fire abundance, depending on precipitation (Gosz and Gosz 1996; Parmenter 2008). N addition also appeared to suppress growth of *B. eriopoda*, perhaps through competition with other grasses that increased growth in fertilized plots (Table 2). Above average precipitation in summer 2006 enhanced recovery of *B. eriopoda*, and the increase in abundance of competitive perennial grasses likely decreased forb abundance and diversity. Thus, fire and nitrogen combined to affect community dynamics in this desert grassland.

Although N addition may constantly shape many terrestrial communities, N addition has restricted, sporadic impacts in this semiarid system. Several factors may lead to these varied dynamics. First, when compared to other systems, N deposition is relatively low in semiarid regions, except near densely populated areas. For example, N deposition at the SNWR is currently $0.2 \text{ g N m}^{-2} \text{ year}^{-1}$ compared to an

estimated $0.4\text{--}3 \text{ g N m}^{-2} \text{ year}^{-1}$ in the Phoenix metropolitan area (Fenn et al. 2003b; Báez et al. 2007; Hall et al. 2011), but N deposition at SNWR continues to increase over time. Population growth and urbanization projected for the southwestern US will likely increase N deposition even further, making continued studies of the effects of N enrichment on aridland ecosystems necessary. Despite the potential for higher rates of deposition in the future, N retention in aridland ecosystems is low (Peterjohn and Schlesinger 1990; McCalley and Sparks 2009), suggesting that impacts of N deposition may be periodic but ephemeral. Aridland soils lose considerable N through abiotic as well as biotic processes (Peterjohn and Schlesinger 1990; Walvoord et al. 2003; McCalley and Sparks 2009). Indeed, following 9–10 years of fertilization, the soils in both control and fertilized plots in our experiment had roughly the same low N content ($\sim 0.05\%$; Zeglin et al. 2007) showing that nitrogen is not accumulating in these soils. Thus, even with additional inputs of N through deposition, desert soils may not retain N, and nitrogen availability may continue to limit aboveground production during years of above average precipitation.

Many press and pulse factors (Smith et al. 2009) interact to shape community dynamics in plant communities. Press factors chronically influence the community while pulse factors occur in discrete events. In semiarid ecosystems, drought remains a persistent and frequent press disturbance, continually stressing plants and shaping community structure and ecosystem processes. Fire, although a less frequent pulse disturbance, quickly alters community composition, and leads to slow recovery by some dominant species. Nitrogen deposition is an increasing press disturbance that does not currently play a large role in shaping semiarid grassland structure and function but has the potential to increasingly affect aridland ecosystems in the future. Currently, unlike mesic systems (Tilman 1987; Gough et al. 2000; Stevens et al. 2004), water limitation remains the key driving force in arid and semiarid vegetation with nitrogen availability as a secondary factor, but one that may temporarily favor some dominant species over others, primarily in response to periods of above average water availability during the growing season.

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