

# Short-term soil inorganic N pulse after experimental fire alters invasive and native annual plant production in a Mojave Desert shrubland

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Received: 1 February 2007 / Accepted: 13 March 2010  
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**Abstract** Post-fire changes in desert vegetation patterns are known, but the mechanisms are poorly understood. Theory suggests that pulse dynamics of resource availability confer advantages to invasive annual species, and that pulse timing can influence survival and competition among species. Precipitation patterns in the American Southwest are predicted to shift toward a drier climate, potentially altering post-fire resource availability and consequent vegetation dynamics. We quantified post-fire inorganic N dynamics and determined how annual plants respond to soil inorganic nitrogen variability following experimental fires in a Mojave Desert shrub community. Soil inorganic N, soil net N mineralization, and production of annual plants were measured beneath shrubs and in interspaces during 6 months following fire. Soil inorganic N pools in burned plots were up to  $1 \text{ g m}^{-2}$  greater than unburned plots for several weeks and increased under

shrubs ( $0.5\text{--}1.0 \text{ g m}^{-2}$ ) more than interspaces ( $0.1\text{--}0.2 \text{ g m}^{-2}$ ). Soil  $\text{NO}_3^-$ -N (nitrate-N) increased more and persisted longer than soil  $\text{NH}_4^+$ -N (ammonium-N). Laboratory incubations simulating low soil moisture conditions, and consistent with field moisture during the study, suggest that soil net ammonification and net nitrification were low and mostly unaffected by shrub canopy or burning. After late season rains, and where soil inorganic N pools were elevated after fire, productivity of the predominant invasive *Schismus* spp. increased and native annuals declined. Results suggest that increased N availability following wildfire can favor invasive annuals over natives. Whether the short-term success of invasive species following fire will direct long-term species composition changes remains to be seen, yet predicted changes in precipitation variability will likely interact with N cycling to affect invasive annual plant dominance following wildfire.

**Keywords** Annual grass/fire cycle · Inorganic N · Plant interactions · Resource pulse · *Schismus*

Communicated by Hormoz BassiriRad.

**Electronic supplementary material** The online version of this article (doi:10.1007/s00442-010-1617-1) contains supplementary material, which is available to authorized users.

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## Introduction

The invasion of Mediterranean annual grasses such as red brome (*Bromus madritensis* L.), cheatgrass (*B. tectorum* L.), and split grass (*Schismus arabicus* Nees or *S. barbatus* L. Thell.) has increased fire frequency in North American deserts (Esque and Schwalbe 2002; Brooks and Matchett 2006). Invasive annual grasses have been ubiquitous in the Mojave Desert during the past 30 years (Hunter 1991; Brooks and Matchett 2006) resulting in fires that reduce the diversity and abundance of native species (Esque et al. 2004). Many native species that define desert mixed shrub and succulent communities do not survive exposure to even

moderate fires (McLaughlin and Bowers 1982; Brown and Minnich 1986; Esque and Schwalbe 2002).

In undisturbed Mojave Desert shrub communities, nutrient and water availability are greater beneath shrubs creating nutrient and moisture heterogeneity (Schlesinger et al. 1996; Titus et al. 2002). Loss of shrubs to invasive grasses and the periodic re-burning of previously burned sites promote annual grasslands and loss of physical structure and species richness (Billings 1990; D'Antonio and Vitousek 1992). The rate of conversion from shrubland to grassland often exceeds the rates that desert communities can recover or be effectively restored (Billings 1990). While these patterns of landscape and ecological change are well established, the mechanisms of invasion and community change are not well understood.

Fire causes profound structural, chemical and biotic change in ecosystems through a net loss or gain of standing mass and nutrients, or changes in nutrient and water cycling (Raison 1979; Whelan 1995). Soil  $\text{NH}_4^+$  pools often increase within hours to days after fire because heat converts organic N to  $\text{NH}_4^+$  and because  $\text{NH}_4^+$  is a component of ash (Christensen and Muller 1975; DeBano et al. 1998; Wan et al. 2001). Soil  $\text{NH}_4^+$  is also affected by microbial ammonification rates (conversion of organic N to  $\text{NH}_4^+$ ), which may briefly decrease if soil temperatures are sufficient to kill microorganisms (Dunn et al. 1979). In arid ecosystems, ammonification rates may decline more under shrub canopies where soil temperatures during fires are greater than in plant interspaces (Biederbeck et al. 1980). Following microbial recovery (or immediately if soil temperatures are not high enough to kill microorganisms), burned ecosystems often have elevated net ammonification rates for weeks to years before returning to pre-fire levels (Certini 2005). In contrast to  $\text{NH}_4^+$ , soil  $\text{NO}_3^-$  pools do not typically increase immediately after a fire, though they often increase several days to weeks after fire through microbial nitrification (Dunn et al. 1979; Blank et al. 1994; Wan et al. 2001). Over decades, repeated fires with temperatures  $>200^\circ\text{C}$  can deplete soil N reserves through gaseous losses (Wan et al. 2001). To date, little is known about how fire affects N dynamics in deserts (Schaeffer et al. 2003), even though fire–N dynamics could have large effects on desert plant communities.

Desert annual plant species may co-exist in landscapes because of differing N requirements or differing abilities to acquire N (Gutierrez and Whitford 1987), but the relationship between desert fires and alien annual grass invasions are complicated by changes in soil resource availability, including N, that affect plant interactions (Davis et al. 2000; D'Antonio et al. 2001; Davis and Pelsor 2001). Even brief increases in soil resources (e.g., moisture or N over several weeks) can cause dramatic changes in plant community dominance (Davis and Pelsor 2001).

Precipitation pulses influence N availability to plants, and the timing of these pulses can affect the survival and competitive ability of desert plants (James and Richards 2006; DeFalco et al. 2007; Rao and Allen 2009). The timing of resource pulses and the consequent response by plants may be altered by wildfire but has not been documented for desert systems. In the Mojave Desert, N fertilizer additions increased density and biomass of the alien species *B. madritensis*, *Schismus* spp., and *Erodium cicutarium* ((L.) L'Her), but decreased density, biomass, and richness of native species (Brooks 2003). Invasive species such as *B. madritensis* extract water and N more efficiently than some common native annual plant species (DeFalco et al. 2003), ultimately resulting in greater biomass of invasives than natives (Brooks 2003; DeFalco et al. 2003). Desert fires reduce the abundance of perennial vegetation (Brown and Minnich 1986), thus increasing soil resource availability for alien annual species. Alternatively, *Schismus* abundance can be affected by the timing and amount of moisture and N pulses, and on the phenological status of neighboring native shrubs (James et al. 2009). Thus, pulse dynamics, timing of resource availability, and the condition of the plant community all play roles in the trajectory of vegetation communities.

To increase our understanding of the grass/fire cycle in the Mojave Desert, this paper assesses relationships among fire, N, shrub canopies, and annual plant communities. We tested whether experimental fire alters the short-term spatial distribution of inorganic N and net N mineralization and how native and alien annual plants respond to changes in plant available N during 6 months following fire. We addressed the following research questions: (1) how does soil inorganic N beneath plant canopies and interspaces respond over time to fire; and (2) do changes in inorganic N correlate with post-fire changes in species composition (i.e. native or alien) or shoot production of desert annual plants?

## Materials and methods

### Study site

This study was conducted at Grand Canyon-Parashant National Monument, Arizona ( $36^\circ25'\text{N}$ ,  $113^\circ55'\text{W}$ ) in Mojave Desert shrubland on a volcanic mesa 800–1,000 m above mean sea level. Soils on the mesa are in the Winkel series of loamy-skeletal, mixed, superactive, thermic, shallow Calcic Petrocalcids. The typical surface soil pH is 8.8 for this series. Depth to the petrocalcic layer is  $<300$  mm at the south end of the study area grading into soils  $>500$  mm deep at the north end. Long-term average annual precipitation between 1957 and 1992 was 208 mm for nearby Littlefield, Arizona (NOAA 2003). *Larrea*

*tridentata* (DC) Cov. and *Ambrosia dumosa* (A. Gray) Payne are co-dominant, with *Yucca brevifolia* Engelm. as a conspicuous sub-dominant species. Winter and summer annual floras are distinct and respond to specific combinations of precipitation and temperature (Beatley 1974). In 1999, wet N deposition ( $\text{NH}_4^+ - \text{N} + \text{NO}_3^- - \text{N}$ ) at the nearest National Atmospheric Deposition Program sites west (site NV00) and east (site AZ03) of our study area were 0.10 and 0.15 g N m<sup>-2</sup>, respectively.

A total of 101 mm of rain fell 1 July through 30 September 1999 (147% of the previous 16-year average), but almost 80% occurred just prior to the experimental fires and was irrelevant to the winter annuals studied in these experiments. In October through December of 1999, no measurable precipitation occurred on the study site and only 4 mm of rain fell in January 2000 (4% of the 16-year average for October through January). Effective precipitation for spring annual plant production (October through April) in 2000 was 97 mm (56% of the 16-year average). Therefore, precipitation that was relevant to the winter annual plants included in these experiments came very late in the growth season. During the 15 years prior to this experiment, seasonal drought of this magnitude never occurred (unpublished BLM climate records).

### Research design

Study plots were established at six locations (blocks) dispersed evenly along 7 km of a graded road with sufficient distance from the road to eliminate visible roadside effects. Within each block, six *Larrea* canopy, six *Ambrosia* canopy, and six shrub interspace microhabitats were selected. Plots with 2 m × 2 m dimensions were centered on the *Larrea* and *Ambrosia* shrubs and >0.5 m from canopy edges for the interspace plots. Three of each of the microhabitats were randomly assigned burned and three assigned unburned treatments. The responses of the three samples for each burn and microsite combination were collected within each block and pooled for a total of 6 blocks × 3 microsities × 2 burn treatments × 3 replicates ( $n = 108$ ) for each time period sampled.

We added hay consisting of Sudan grass and Bermuda grass (*Sorghum sudanense* L. Pers./*Cynodon dactylon* L. Pers.) at an amount near the upper limit for spring annual shoot production for the region (Esque 2004). The fuel was spread by hand in the amount of 3,175 kg ha<sup>-1</sup> (2,833 lbs ac<sup>-1</sup>) 30 min prior to ignition as determined from preliminary trials to simulate the flame length and duration observed in wildfires. Plots were burned on 22 July 1999 during the local fire season.

Flame length was photographed and the speed with which fire fronts moved was observed on each experimental fire. Fire temperature and residence times were

recorded using Type K (24 gauge) high temperature glass thermocouple wire rated to 700°C in combination with a Campbell Scientific CR10X datalogger. Temperatures were recorded at -5, -2, -0.1, +0.1, 10, 25, and 50 cm in relation to the soil surface. Temperatures were recorded in shrub interspaces, *Larrea* and *Ambrosia* crowns, and control sites outside the burned area. Measurements were replicated on five different experimental fires spread across the study area.

Fire behavior associated with the experimental fires was typical of wildfires during calm conditions with high fuel loads in Mojave Desert scrub (T. Esque, personal observation). Fire fronts moved at 1 m min<sup>-1</sup> with flame lengths of 2–3 m on shrubs and 0.5–1 m across interspaces. Mean peak temperatures were highly variable, and the hottest microsite was at +1 cm above soil surface within *Ambrosia* crowns (Electronic supplementary material, ESM, Table S1). Peak temperatures lasted less than 30 s in all cases; however, the stumps of some *Larrea* burned for hours but were not recorded at temperature recording stations and were generally rare. Study plots where experimental fires occurred were 100% scorched, killing the above-ground parts of perennial plants.

The hay that was used as fuel for the experimental fires was 40.6 ± 0.05% C and 1.7 ± 0.04% N by mass prior to burning (means ±1 SE,  $n = 5$ ). After burning, the ash from the hay was 18.08 ± 0.32% C and 0.90 ± 0.03% N representing a 50% loss of C and N by mass. Thus, the burned hay potentially resulted in as much as 2.4 g m<sup>-2</sup> of N and 60.5 g m<sup>-2</sup> of C being added to plots. However, most of the ash resulting from experimental fires was blown from the sampling areas on the study plots immediately following the fires (T. Esque, personal observation). Study plots were isolated within unburned areas; thus, ash that blew away was not replaced from nearby sites resulting in lower ash levels than available in a large burned area. Experimental fires fueled by cereal straw have similar heating patterns above and below the ground surface (Biederbeck et al. 1980) including those we observed on companion studies at this site (Esque 2004).

Trade-offs between the structure of the alien annual grasses and the hay we used for artificial fuel made differences in the amount of fuel necessary for mimicking wildfire behavior. First, the stems of the fine-textured alien annual grasses are predicted to be more flammable than the coarse hay stems. Second, although great care was taken to spread the hay adequately, the hay was piled several stems deep in contrast to the erect, individual stems of the alien annual grasses exposed maximally to atmosphere and flames. Finally, because fine fuels dry more quickly (Whelan 1995), artificial fuel was somewhat moist compared to the alien annual grasses, and the stout hay stems

were more resistant to incineration than the finer alien annual grass stems.

Soils for inorganic N soil content were collected 1 day (23 July 1999), 7 days (29 July 1999), 14 days (5 August 1999), 30 days (21 August 1999), 112 days (11 November 1999), and 172 days (10 January 2000) after the experimental fires ( $n = 6$  blocks  $\times$  3 microsites  $\times$  2 burn treatments  $\times$  6 dates = 216). Within sampling microsites, soil cores were subsampled on the cardinal points within shrub canopies and a parallel set of sites at each open microsite (i.e. this resulted in four subsamples from under one *Larrea* canopy or similar site, and those subsamples were pooled for that sampling site to create one sample). Soils were collected with a 2-cm-diameter corer to 5 cm depth to capture the highest inorganic N values in the soil column (Blank et al. 1994) and because desert annual plants have shallow roots (Romney et al. 1978). In the field, 100 mL of 2 M KCl solution were added to a  $20 \pm 0.5$  g subsample of soil and then placed on ice for transport to the laboratory within 8 h of collection. In the laboratory, samples were shaken vigorously by hand for 20 s, left to settle overnight, filtered through pre-leached #1 Whatman filter paper, and frozen until  $\text{NH}_4^+$ -N and  $\text{NO}_3^-$ -N concentrations were determined by flow injection colorimetry. Following extraction, residual soils were sieved and the  $>2$  mm fraction was collected, dried, and subtracted from the sample mass. Soil water content was determined gravimetrically on a separate subsample of the field collected sample by weighing  $10 \pm 0.5$  g of dry-sieved ( $<2$  mm fraction) soil from each sample and drying for 24 h at  $100^\circ\text{C}$ .

Nitrification, ammonification, and net mineralization rates were determined using wet and dry laboratory incubations. Incubations were conducted 1, 112, and 172 days following burning ( $n = 6$  blocks  $\times$  3 microsites  $\times$  2 burn treatments  $\times$  2 incubation moisture treatments  $\times$  3 dates = 216). Field-collected soil samples were placed on ice and transported to the laboratory for incubation. For incubations, samples were collected dry and weighed, randomly assigned wet or dry treatment and placed in the dark at  $20$ – $25^\circ\text{C}$  for 30 day. Wet treatments were maintained at field capacity for the length of the incubation. Dry treatments were maintained without moisture addition. At the conclusion of incubations,  $\text{NH}_4^+$  and  $\text{NO}_3^-$  were extracted (100 mL of 2 M KCl as described above) and compared to initial samples from the field. Net ammonification was calculated as extractable  $\text{NH}_4^+$ -N in the incubated sample minus extractable  $\text{NH}_4^+$ -N in the field-extracted sample. Net nitrification was calculated in the same manner for extractable  $\text{NO}_3^-$ , and net N mineralization was calculated as the sum of  $\text{NH}_4^+$  +  $\text{NO}_3^-$  in the incubated samples minus field-extracted samples. The volume of KCl and the mass, moisture content, rock content, and bulk density of

the extracted soil were used to convert N concentrations to  $\text{g N m}^{-2}$ . We measured bulk density by collecting a volumetric soil core ( $122 \text{ cm}^3$ ) at each nitrogen-sampling site and determining the rock-free oven dry mass of soil in each core.

Above-ground annual plant shoot production was sampled on 2–3 May 2000 using  $20 \text{ cm} \times 50 \text{ cm}$  quadrats ( $0.10 \text{ m}^2$ ) in the growth season following the fires. Each quadrat was placed on the north side of each shrub plot where N was sampled. For *Ambrosia* and *Larrea*, the quadrats were placed as close to the base of the shrub as possible. Current year's shoot growth of annual plants was harvested, sorted by species, dried at  $60^\circ\text{C}$  to a constant mass, and weighed.

### Statistical analyses

Pool sizes of  $\text{NO}_3^-$ -N and  $\text{NH}_4^+$ -N, as well as net ammonification, net nitrification, and net N mineralization were each analyzed in a random complete block design with repeated measures. Burn treatment (burned vs unburned), and microsite (*Larrea*, *Ambrosia*, or interspace), and incubation type were fixed factors, and block was a random effect. Normality and variance assumptions for ANOVA were examined and transformations were performed when necessary. Post hoc analyses were conducted using Tukey's HSD at  $\alpha = 0.05$ .

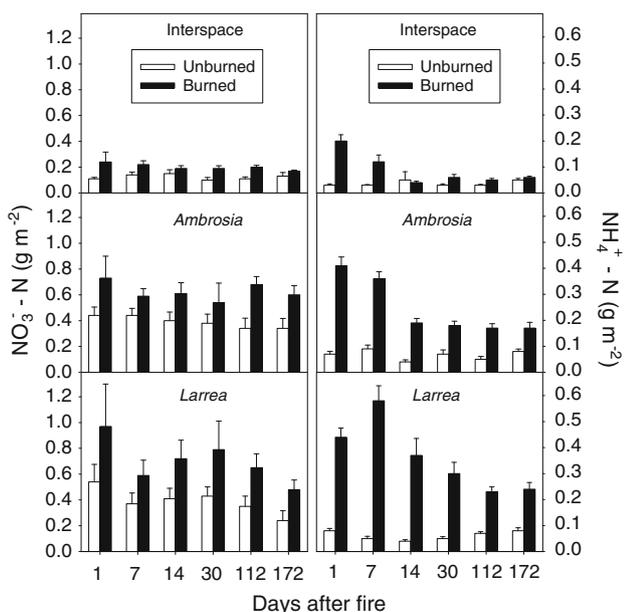
Annual plant production was analyzed in a three-way ANCOVA (burn  $\times$  microsite  $\times$  total inorganic N on day 172). We used the inorganic N pool at day 172 because this was the closest to when the winter annuals were growing. Native and alien annual plant production was compared to soil inorganic N availability using linear regression. All statistical analyses were conducted using SAS statistical software (SAS Institute 2004).

## Results

### Inorganic N response to burning

Soil  $\text{NO}_3^-$ -N pools were almost twice as large as  $\text{NH}_4^+$ -N, but the response of  $\text{NH}_4^+$ -N to burning was relatively stronger and more variable through time (Fig. 1). Burning increased the  $\text{NO}_3^-$ -N pool size overall and was greater beneath *Larrea* and *Ambrosia* than interspaces (Tukey's HSD  $< 0.05$ ), but  $\text{NO}_3^-$ -N levels were similar up to 172 day following fire (Table 1). Burning also increased  $\text{NH}_4^+$ -N pools more under the shrubs than in interspaces, but this increased  $\text{NH}_4^+$ -N diminished through time (Fig. 1; Table 1).

Laboratory incubations conducted at ambient soil moisture levels (hereafter referred to as "dry") had net



**Fig. 1** Field measures of  $\text{NO}_3^-$ -N and  $\text{NH}_4^+$ -N pools in response to burning, microsite, and time since plots were burned in Mojave Desert shrub habitat of the Pakoon Basin, Grand Canyon-Parashant National Monument, Arizona in July 1999 through February 2000. *Days after fire* designates time elapsed since burning and corresponds as follows: 1 = 23 July; 7 = 29 July; 14 = 5 August; 30 = 21 August; 112 = 11 November; 172 = 10 January

ammonification rates near zero, but significantly greater ( $F_{1,150} = 36.1$ ;  $P < 0.01$ ; Fig. 2) than net ammonification in soils that were experimentally wetted in the laboratory (hereafter referred to as “wet”). Under dry incubation conditions, net ammonification was not affected by burning, but interspaces had more negative net ammonification than either *Larrea* or *Ambrosia* canopies (Tukey’s HSD  $< 0.05$ ; Fig. 2). Dry net ammonification became less negative through time (Table 2). In contrast, net ammonification in wet laboratory incubations was greater in unburned plots than burned plots and this difference was greater on day 1 (immediately after fire) than on day 172 (Table 2; Fig. 2). Unburned plots had positive or near-zero

net ammonification rates, while burned plots had negative net ammonification (i.e. net N immobilization). Interspaces had significantly greater wet net ammonification than *Larrea* or *Ambrosia* (Table 2; Tukey’s HSD  $\alpha < 0.05$ ).

Dry soils had lower net nitrification than wetted soils (Fig. 2). Dry net nitrification was nearly zero and did not differ between burned and unburned treatments or among microsites; net nitrification only became less negative through time (Table 2). Under wet laboratory incubation conditions, burning also did not change net nitrification (Fig. 2). Wet net nitrification was greater under shrubs than interspaces and declined through time (Table 2). Net mineralization rates (Figure S1) had treatment and time patterns and statistical effects (ESM, Table S2) that were similar to net nitrification rates.

Annual plant production in relation to burning

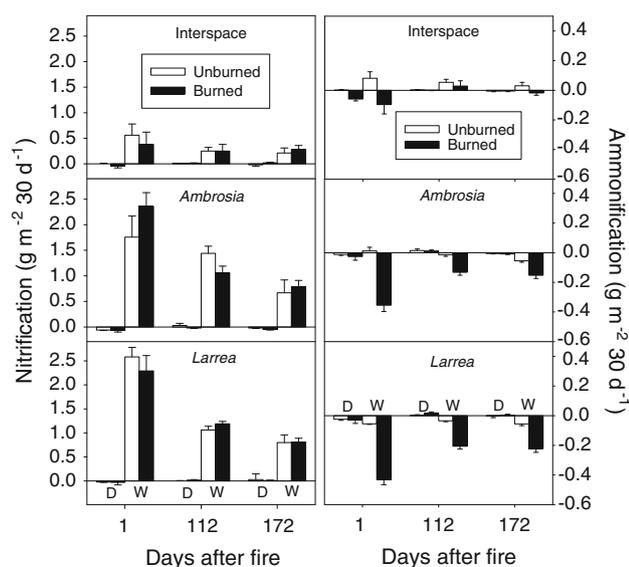
Burning increased annual plant production in *Ambrosia* but not in interspaces or *Larrea* microsites (microsite  $\times$  burn,  $F_{2,97} = 6.34$ ,  $P < 0.01$ ; Fig. 3). Total annual plant production during the growing season was positively yet weakly correlated with greater total inorganic N at day 172 ( $F_{1,34} = 5.3$ ,  $P = 0.03$ ,  $r^2 = 0.14$ ). Production of the predominant invasive *Schismus* spp. was positively correlated with total soil inorganic N pools at day 172 ( $F_{1,32} = 19.5$ ,  $P < 0.01$ ; Fig. 4) with the highest production where shrub canopies were burned. In contrast, native annual plant production decreased with increasing soil inorganic N on the same plots ( $F_{1,32} = 13.2$ ,  $P < 0.01$ ; Fig. 4). Greater production of annuals was not, however, related to integrated seasonal soil moisture (day 1 through 172) for either invasive ( $F_{1,100} = 0.56$ ,  $P = 0.46$ ,  $r^2 = 0.01$ ) or native taxa ( $F_{1,77} = 1.25$ ,  $P = 0.27$ ,  $r^2 = 0.02$ ).

The most frequently encountered species were *Schismus* (35 of 36 plots), *Erodium* (34 of 36 plots), *Bromus* (15 of 36 plots), and the native species *Plantago* (26 of 36 plots) and *Eriophyllum* (23 of 36 plots). Species richness was not

**Table 1** Nitrate–N and ammonium–N pools for research plots at Grand Canyon-Parashant National Monument

	Nitrate–N			Ammonium–N			
	<i>df</i>	<i>F</i>	<i>P</i>	<i>df</i>	<i>F</i>	<i>P</i>	
Burn	1.30	13.6	<0.01	Burn	1.31	126.0	<0.01
Microsite	2.30	19.1	<0.01	Microsite	2.31	25.8	<0.01
Burn $\times$ microsite	2.30	1.5	0.24	Burn $\times$ microsite	2.31	3.4	0.05
Time	5.30	2.3	0.07	Time	5.87	287.2	<0.01
Burn $\times$ time	5.30	1.2	0.32	Burn $\times$ time	5.87	9.3	<0.01
Microsite $\times$ time	10.30	1.6	0.14	Microsite $\times$ time	10.87	2.2	0.02
Burn $\times$ microsite $\times$ time	10.30	0.6	0.84	Burn $\times$ microsite $\times$ time	10.87	1.6	0.10

Nitrate–N and ammonium–N were measured as  $\text{g m}^{-2}$



**Fig. 2** Laboratory net nitrification and net ammonification for dry (D) and wet (W) incubations on burned and unburned treatments for three microsites. Samples were collected in a Mojave Desert shrub community, Grand Canyon-Parashant National Monument, Arizona. Days after fire designates time elapsed since burning and corresponds as follows: 1 = 23 July 1999; 7 = 29 July 1999; 14 = 5 August 1999; 30 = 21 August 1999; 112 = 11 November 1999; 172 = 10 January 2000. Note different scales for net nitrification and net ammonification

correlated with differences in the amount of total inorganic N 172 day after burning ( $F_{1,24} = 0.11$ ,  $P = 0.74$ ) or microsite ( $F_{1,24} = 0.78$ ,  $P = 0.47$ ). Burning reduced species

richness in *Larrea* and *Ambrosia* sites ( $F_{1,24} = 8.00$ ,  $P < 0.01$ ), but there was little difference between unburned and burned interspaces.

## Discussion

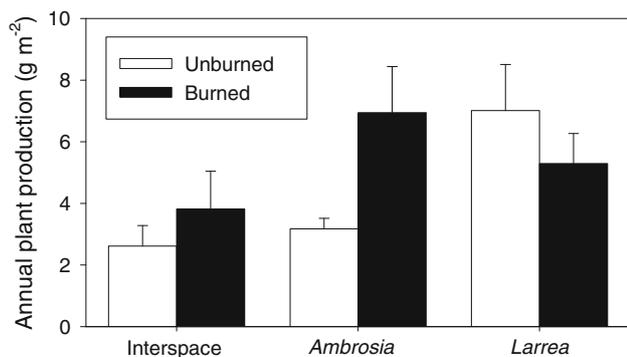
### Conditions resulting from experimental fires

Due to the high supplemental fuel loads, the experimental fires described here were moderate intensity and slow moving because of calm wind conditions. These conditions are within the range of conditions frequently observed during desert wildfires (T. Esque, personal observation) and typically lead to the most severe fire damage by a single burning event in this vegetation type. In related experiments, using the identical fuel loads to create similar fire characteristics, the highest peak temperatures occurred under *A. dumosa*, followed by *L. tridentata* and open sites (Esque 2004). Using very light fuels, Brooks (2002) found similar microsite patterns except that all peak temperatures were lower than ours. In the Arizona upland of the Sonoran Desert, microsite differences in temperatures were observed during experimental fires (Patten and Cave 1984). The heat generated during wildland fires can result in chemical and physical changes to the soil surface that affect water infiltration, potentially leading to changes in soil moisture holding capacity and erosion (MacDonald and Huffman 2004). Although these changes can be highly

**Table 2** Results of dry and wet incubations to determine nitrification, ammonification, and net mineralization potential from soils collected at Grand Canyon-Grand Canyon-Parashant National Monument, Arizona in 1999 and 2000

	Nitrification				Ammonification		
	df	F	P		df	F	P
<b>Dry Incubation</b>							
Burn	1.30	0.3	0.58	Burn	1.10	3.2	0.10
Microsite	2.30	1.4	0.27	Microsite	2.10	7.3	0.01
Burn × microsite	2.30	0.3	0.72	Burn × microsite	2.10	2.8	0.11
Time	2.30	4.5	0.02	Time	2.24	71.9	<0.01
Burn × time	2.30	0.1	0.88	Burn × time	2.24	0.0	1.0
Microsite × time	4.30	0.4	0.78	Microsite × time	4.24	0.0	1.0
Burn × microsite × time	4.30	0.6	0.69	Burn × microsite × time	4.24	0.0	1.0
<b>Wet Incubation</b>							
Burn	1.30	0.6	0.45	Burn	1.90	65.2	<0.01
Microsite	2.30	10.2	<0.01	Microsite	2.90	28.3	<0.01
Burn × microsite	2.30	0.8	0.46	Burn × microsite	2.90	1.3	0.28
Time	2.30	13.1	<0.01	Time	2.90	2.1	0.13
Burn × time	2.30	0.8	0.47	Burn × time	2.90	13.4	<0.01
Microsite × time	4.30	2.1	0.11	Microsite × time	4.90	2.2	0.07
Burn × microsite × time	4.30	2.0	0.12	Burn × microsite × time	4.90	0.2	0.92

Nitrification and ammonification were measured as  $\text{g m}^{-2} 30 \text{ day}^{-1}$



**Fig. 3** Annual plant production among microsites in a Mojave Desert shrub community in response to experimental treatments of burning at Grand Canyon-Parashant National Monument, Arizona. Burning occurred 22 July 1999. Production sampling occurred in April 2000

variable depending on temperature range, duration, and the materials that are combusted, we did not observe such changes due to the dry conditions during the study period.

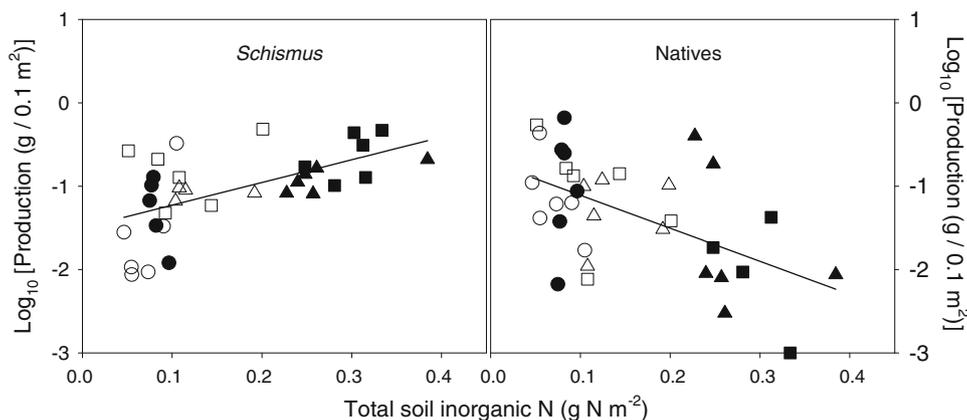
Soil inorganic N beneath plant canopies and interspaces following fire

Inorganic N concentrations that we measured in unburned interspaces and under shrubs were similar to previously published values for the Mojave Desert (Romney et al. 1978; Schaeffer et al. 2003). We found that late summer fire can double soil inorganic N content immediately after fire, and this elevated N availability can persist for 6 months, thus encompassing the time when invasive and native winter annual plants germinate (Beatley 1974). The magnitude of this inorganic N enrichment varied spatially after fires, with larger increases in soil inorganic N under burned shrub canopies than in plant interspaces.

In other ecosystems, increased soil  $\text{NH}_4^+$  following fire has been attributed to direct abiotic effects of fire (heat and ash deposition) and indirect effects of fire on microbial ammonification rates (Covington and Sackett 1986; Kaye and Hart 1998; Certini 2005). Because soils at the time of our fire were dry ( $<0.03 \text{ g H}_2\text{O g}^{-1}$  oven dry soil) and laboratory net ammonification in dry soils was near zero or negative, our data suggest that abiotic, rather than microbial, processes were responsible for increased soil  $\text{NH}_4^+$ -N pools following the fire. However, laboratory incubations are not always good predictors of field ammonification rates, and more detailed field studies are required to identify the source of  $\text{NH}_4^+$  that appears in these soils following fire.

The decrease in field soil  $\text{NH}_4^+$  pools with time likely results from microbial immobilization and  $\text{NH}_3$  emissions. Our dry laboratory incubations, and gross  $\text{NH}_4^+$  transformation measurements elsewhere in the Mojave (Jin and Evans 2007), suggest that immobilization by heterotrophic microorganisms is a sink for  $\text{NH}_4^+$  even in dry soils. Likewise, soil-atmosphere  $\text{NH}_3$  fluxes can deplete  $\text{NH}_4^+$  pools in dry Mojave soils, and, based on fluxes in McCalle and Sparks (2008), it is plausible that  $0.05 \text{ g m}^{-2}$  of  $\text{NH}_4^+$ -N were lost from soils via  $\text{NH}_3$  emissions between the time of the fire and our last soil  $\text{NH}_4^+$ -N pool size measurement. In contrast, for reasons outlined in the following paragraphs, we do not expect that nitrification contributed to the declines in soil  $\text{NH}_4^+$  pools with time since fire.

Most of the increase in soil inorganic N following our fires resulted from an increase in soil  $\text{NO}_3^-$ , which was quantified within 1 day following fire. In past studies in arid and semi-arid ecosystems, increases in soil  $\text{NO}_3^-$  have not occurred immediately following fire; there is generally



**Fig. 4** Biomass of the predominant alien annual species (left panel) and native annual plant species (right panel) in relation to total soil inorganic nitrogen. Open symbols represent unburned plots and solid symbols denote burned plots, for *Ambrosia* (open diamond, filled

diamond), *Larrea* (open square, filled square), and interspace (open circle, filled circle).  $\text{Log}_{10}$  *Schismus* spp. biomass =  $-1.4889 + 2.6785 \times \text{total soil inorganic N}$  ( $r^2 = 0.33$ );  $\text{Log}_{10}$  native biomass =  $-0.7080 - 3.9822 \times \text{total soil inorganic N}$  ( $r^2 = 0.29$ )

a lag time of days to months after the fire before soil  $\text{NO}_3^-$  increases (Dunn et al. 1979; Christensen and Muller 1975; Covington et al. 1991; Blank et al. 1994). Elevated  $\text{NO}_3^-$  following this post-fire lag time is typically attributed to the microbial process of chemoautotrophic nitrification. Several lines of evidence suggest that nitrification was not responsible for the pulse of  $\text{NO}_3^-$  that we observed following fire. First, the amount of  $\text{NO}_3^-$ -N that appeared within 1 day of the fire (up to  $1 \text{ g m}^{-2}$  of  $\text{NO}_3^-$ -N) is nearly twice as much as the highest reported daily gross nitrification rate for grasslands (Booth et al. 2005). Second, field soil moisture ( $<0.03 \text{ g H}_2\text{O g}^{-1}$  oven dry soil) following the fire was at levels that substantially constrain the growth of nitrifying bacteria (Stark and Firestone 1995; Paul and Clark 1996) and gross nitrification rates in Mojave Desert soils (Jin and Evans 2007). Finally, net  $\text{NO}_3^-$  immobilization in our dry laboratory incubations suggest that microbial processes likely diminished rather than increased the amount of  $\text{NO}_3^-$  in soil within 1 day of the fire. These three points combined provide strong evidence that fire-related abiotic processes generated the post-fire pulse of  $\text{NO}_3^-$  that we observed.

While ours is the first report of substantial increases in soil  $\text{NO}_3^-$  immediately following fire, there are laboratory data showing that soil heating generates  $\text{NO}_3^-$ . Mroz et al. (1980) heated O horizon soil ( $400^\circ\text{C}$  for 30 min) from three conifer forests, and  $\text{NO}_3^-$  concentrations increased in all forests and doubled in one case. The authors attributed the new  $\text{NO}_3^-$  to oxidation of soil organic N. Heating field-collected soils to a temperature range of  $100$ – $250^\circ\text{C}$  for  $<5$  min increased the concentration of  $\text{NO}_3^-$  in desert soils (Blank et al. 1994). These temperatures are similar to our field conditions where the highest mean peak temperatures in the top 1 cm of soil were below  $250^\circ\text{C}$  except for *Ambrosia* ( $\sim 325^\circ\text{C}$  at the soil surface). The durations of peak temperatures were less than 30 s; however, acutely high temperatures ( $>100^\circ\text{C}$ ) lasted for as long as 1 min (Esque 2004). These temperatures and durations are greater than low intensity fires (Brooks 2002), but they span the range of temperature exposure and heating duration likely to occur in Mojave Desert shrub community fires. In addition to heat-induced  $\text{NO}_3^-$  formation within soils,  $\text{NO}_3^-$  is also present in low concentrations in ash of burned plant material (Christensen and Muller 1975). We acknowledge that, while the majority of the ash blew off of plots immediately following the experimental burn, the small amount of ash that remained could have contributed to differences in inorganic N associated with the experimental fire. Measurements of ash  $\text{NO}_3^-$  inputs and field net and gross nitrification measurements are needed to test our hypothesis that microbial nitrification is not responsible for the pulse of  $\text{NO}_3^-$  we observed  $<1$  day following fire.

Ambient conditions during this experiment were on the dry end of the precipitation spectrum, and increased fall or winter precipitation more typical of recent conditions in the Mojave Desert might produce very different results following summer fires. There is a substantial literature describing changes in soil C and N cycling following rain pulses in arid ecosystems (reviewed by Austin et al. 2004). In general, these studies show that dry soils contain large pools of inorganic N (especially  $\text{NO}_3^-$ ) and labile C, and that upon rewetting, microbial growth responds rapidly and supports greatly elevated rates of C and N mineralization. The duration of the period of elevated mineralization rate depends on many factors, including the size of the rain event and labile C availability (Austin et al. 2004; Saetre and Stark 2005). As soils dry again, microbial death replenishes the labile C pool, and with low plant and microbial uptake inorganic N accumulates again in soils. Our wet laboratory incubation data are fully consistent with this general pattern, and lead us to expect that rain following fire would lead to greater N availability under shrubs than in plant interspaces.

While wetting soils increased laboratory net mineralization rates beneath shrubs more than interspaces in our soils and in soils from Patagonia (Mazzarino 1996), other research has shown that precipitation can have the opposite effect—increasing N availability beneath invasive annual grasses more than native shrubs (Saetre and Stark 2005). The difference among these studies likely is related to differences in the C:N ratio of microbial substrates between canopies and plant interspaces. Where invasive annuals generate soil substrates with lower C:N ratios than native shrubs, invasion will likely increase mineralization pulses following precipitation (Austin et al. 2004; Saetre and Stark 2005). Precipitation patterns will also affect fuel loads and post-fire C inputs that affect soil microbial activity and nutrient dynamics (Schaeffer et al. 2003; Saetre and Stark 2005).

#### Post-fire inorganic N influences annual plant composition and production

Total annual plant production increased in response to total inorganic N, and, when analyzed separately, the invasive annual grass *Schismus* spp. significantly increased in response to elevated inorganic N while native annual plant biomass decreased. Experiments in the Sonoran Desert resulted in  $\text{NH}_4^+$ -N and  $\text{NO}_3^-$ -N increases for up to 11 months after burning, and increases in annual production on burned sites persisted for at least 3 years (Loftin 1987). *Schismus* has previously been shown to rapidly increase in abundance in response to N supplementation in the Mojave Desert compared with native species (Williams and Bell 1981; Brooks 2003; James and Richards 2006).

Displacement of native annuals by alien species has also been demonstrated after N addition in the Mojave Desert (Brooks 2003). Based on the results of those fertilization trials, we hypothesize that invasive annuals in our plots were better at capturing the pulse of fire-induced N availability than were the native annual species (DeFalco et al. 2003). Our data show correlations between invasive annual growth (primarily *Schismus* spp.) after rains and soil N pools during the preceding drought. This result is consistent with recent (Collins et al. 2008) versions of the “pulse-reserve” model of arid ecosystem function in which reserves of soil resources (in this case inorganic N) affect ecosystem responses to small rain events.

Annual plant production in the Mojave Desert is inherently variable as it depends on the amount and timing of precipitation and nutrients in relation to temperatures throughout the growing season (Beatley 1974). Even when “average” rainfall occurs, there is variability in the composition and production of annual plants due to temperature and nutrient variability that affect germination from the seed bank (Esque 2004). One study at the northern boundary of the Mojave Desert reported annual production ranging from 0 to over 80 g m<sup>-2</sup> during 19 years of observation (Hunter 1991). We described a year that was quite dry through about one-half of the available winter growing season, and then received sufficient rainfall to establish some annual plants.

In experiments related to the work presented here, seed losses were evident as a result of the experimental fires, but they do not directly explain the pattern in N and annual plant production (Esque 2004). Peak fire temperatures were not significantly different among microsites, but were all sufficient to cause seed bank mortality. Seeds for invasive species were an order of magnitude more abundant than the native seeds prior to fire, and had disproportionately greater seed losses (>20%) due to fire. Shrub microsites had more abundant seeds than open areas prior to fire, but after the experimental fires, seed densities between microsites were similar. Seed responses to fire varied by species. The invasive annual species *Schismus* was overwhelmingly abundant before and after fires, and the most abundant native was *Plantago*, yet production of neither species was different among microsites in the growth season immediately succeeding experimental fires.

Species richness was not affected significantly by burning and N variability. This result is consistent with previous studies in which a year of below average plant production resulted in low species richness. In contrast, during a year of average plant production (associated with more precipitation), a decline in species richness might occur as has been found with N additions to the soil (Brooks 2003). In the Chihuahuan Desert, plots with the highest soil N concentrations had higher diversity, but

greater biomass and plant density occurred on plots with high soil moisture and low soil N conditions (Gutierrez and Whitford 1987). Although inorganic N increased after burning and was greater under shrubs than in the open, the limitation of water had an overriding effect on the trajectory of plant production in the post-fire environment we observed.

One important question that remains unanswered by this experiment is whether the horizontal distribution of soil nutrients changes over time with the loss of perennial plant cover (Evans et al. 2001), or if the fertile islands that form under perennial plants maintain their integrity over time. Although we demonstrated a short-term increase in inorganic N pools, we predict that repeated fire and the subsequent loss of perennial plants that are focal points for nutrient re-distribution and concentration (Titus et al. 2002) would result in increased homogeneity of soil nutrients and ultimately losses due to run-off and wind erosion (Romney et al. 1978; Evans et al. 2001). Disintegration of fertile islands would likely cause a chronic shortage of N in this community (Romney et al. 1978). This degradation could have unexpected consequences for invasive and native plants in arid systems.

Our experiment occurred during a year that had insufficient precipitation during the early winter season to trigger annual plant germination (Beatley 1974). No precipitation fell during three critical growth months (i.e. October, November, and December). The lack of precipitation during the entire fall growth period resulted in a lack of annual plant germination and production until late in the spring growth period (T. Esque, personal observation). Although we did not collect soil nitrogen values at the time when annual plant production values were collected, we feel that the lack of seed germination prior to day 172 (the last date we collected nitrogen data) justifies using the soil nitrogen data from that date to correlate with annual production. Subsequently, early spring precipitation (February and March) was sufficient to stimulate germination and establishment very late in the growth season. The late season precipitation patterns can afford advantages to different functional groups depending on the timing and the amount of resources available during the pulse versus inter-pulse periods (James and Richards 2006; James et al. 2009). Invasive Mojave Desert annuals have the potential to use water and N more rapidly than native annual species (DeFalco et al. 2003); however, invasive annuals established in response to later season rainfall have less competitive potential (James and Richards 2006; DeFalco et al. 2007). While moisture availability may be more influential during other years, our data show that N availability was correlated with native and invasive annual plant production under seasonal drought.

In conclusion, our results suggest an important mechanism in the grass/fire cycle. D'Antonio and Vitousek

(1992) reviewed evidence from a variety of ecosystems showing that the proliferation of invasive annual grasses promoted fires that, in turn, favored the growth of invasive grasses over native species. Our results suggest that N availability plays a role in this feedback in the Mojave Desert. Because the link between N availability and plant growth was correlative in our study, future research that directly manipulates N availability is needed to test the hypothesis that N availability augmented by burning favors invasive plants over native species in post-fire landscapes. Furthermore, our study occurred during a protracted drought that occurred throughout the Southwest desert region in 1998–2004 (Cook et al. 2007; Quiring and Goodrich 2008). Future climate scenarios include greater prevalence of protracted La Niña events in part due to already drier baseline conditions than previously measured in the American Southwest (Hoerling and Kumar 2002; Seager et al. 2007). The soil N–invasive plant–fire dynamics that we documented during our study illustrate the potential response of this arid system to future pulses followed by drying that is expected for the region (Seager et al. 2007; Allan and Soden 2008; Hughes and Diaz 2008; Gergis and Fowler 2009) and may become the norm rather than the exception. Research that considers how post-fire plant communities are shaped by the seasonality of resource availability and resource acquisition among functional groups will provide insights into the trajectories for vegetation recovery on disturbed desert sites in the future.

**Acknowledgments** We thank D. Haines, R. Schwarz, and S.J. Scoles for their hard work establishing study plots, and exchange of ideas during this research project. Comments from J. Yee, J.E. Keeley, K. Phelps, K. Nolte and three anonymous reviewers improved the manuscript. D. Binkley inspired this experiment and provided laboratory space for biogeochemistry analyses. The US Department of Interior, Bureau of Land Management in Arizona and Utah provided partial funding and logistical support. L. Evers and the fire fighters on engines 147, 154, 163, 711, and 712 provided coordination, technical assistance, and logistical support for the experimental fires. T. Duck supported this research for the duration of the project. Staff at the Grand Canyon-Parashant National Monument provided research permits and encouragement. The US Geological Survey, Invasive Species Program provided primary financial and logistical support. Any use of trade, product, or firm names in this publication is for descriptive purposes only and does not imply endorsement by the U.S. government. The experiments described here comply with all rules and regulations pertaining to the land and resources in the country where they were performed.

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