IMPACTS OF ATMOSPHERIC NITROGEN DEPOSITION ON VEGETATION AND SOILS AT JOSHUA TREE NATIONAL PARK

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Abstract. The western Mojave Desert is downwind of nitrogen emissions from coastal and inland urban sources, especially automobiles. The objectives of this research were to measure reactive nitrogen (N) in the atmosphere and soils along a N-deposition gradient at Joshua Tree National Park and to examine its effects on invasive and native plant species. Atmospheric nitric acid (HNO_3) and ozone (O_3) were elevated in western Joshua Tree National Park, and there were some high levels of atmospheric ammonia (NH_3) in the east that may be related to local sources. The central areas of Joshua Tree National Park were lowest in reactive atmospheric N; HNO_3 was higher in summer, while NH_3 was higher in winter. Extractable soil N was generally higher in sites that had higher atmospheric reactive N.

Invasive grasses and forbs, such as Mediterranean split grass (*Schismus barbatus*), red brome (*Bromus madritensis*), and stork's bill (*Erodium cicutarium*) have become more productive and widespread in the last two decades. To test the hypothesis that elevated N may be related to the success of invasive species, N fertilizer experiments were done at four sites in Joshua Tree National Park at levels of 5 and 30 kg N/ha for each of two years. Sites with higher

and lower atmospheric N deposition were selected, as well as low-elevation sites with creosote bush scrub and high-elevation sites with pinyon-juniper woodland. Non-native grass biomass increased significantly with 30 kg N/ha at three of the four sites but not with 5 kg/ha. The response of native forbs to N fertilizer was related to the amount of non-native grass present. The species richness of native forbs declined with fertilization at a site with high non-native grass cover, but native richness and cover increased with fertilization at a site with low non-native grass cover. Non-native grass cover was not related to atmospheric reactive N concentrations but is likely controlled by soil conditions such as soil texture and soil N-supply rate, as well as anthropogenic N inputs. This study provides evidence that atmospheric N deposition over time will increase the soil N to levels that may shift the community to a species-poor vegetation dominated by non-native grasses.

Key words: *Colorado Desert, diversity, invasive species, Joshua Tree National Park, Mojave Desert, native forbs, nitrogen deposition, nitrogen gradient*

INTRODUCTION

The western Mojave Desert is affected by air pollution generated in the Los Angeles air basin that moves inland with the predominant westerly winds (Edinger 1972, Fenn et al. 2003b). The pollution contains both oxidized and reduced forms of nitrogen (N), which are of concern because they are deposited on soil and plant surfaces and thus fertilize plants. Nitrogen deposition may affect plant productivity differentially; some studies have found that non-native grasses have higher rates of N-uptake and production than many native species (Allen et al. 1998; Yoshida and Allen 2001, 2004; Brooks 2003) while others have found that non-native grasses have similar N-uptake and production rates as natives (Padgett and Allen 1999, Salo et al. 2005). The number of non-native species and their abundance has increased in the desert in

the last two decades (Brooks 1999a, 1999b, *this volume*), and our objective was to determine whether this increase is related to elevated N deposition. As non-native grasses increase in productivity, native plants may become sparse (DeFalco et al. 2001; Brooks 2000, 2003, *this volume*). This is especially a concern in protected areas with rare species—areas such as Joshua Tree National Park (JTNP), which lies within both the Mojave and the Colorado Deserts. The wind patterns create N-deposition gradients that have been modeled and have the highest N levels on the west side of JTNP (Tonnesen et al. 2003). We selected sites along this gradient to make finer-scale field measurements of reactive atmospheric N, as well as soil extractable N, and to determine the response of non-native grass cover and native species diversity to elevated soil N.

Nitrogen deposition in the shrublands and forests of the Los Angeles air basin may be as high as 30-50 kg ha^{-1}yr^{-1} (Bytnerowicz et al. 1987; Fenn et al. 1998, 2003b). Most of this N arrives as dry deposition in gaseous, ionic, and particulate form during the dry summer season and is much more difficult to measure than wet deposition, which arrives in the form of rain, snow, etc. (Bytnerowicz et al. 2000). Relatively few estimates of N deposition have been done in the Mojave or Colorado Deserts. One study calculated a value of 8 kg ha^{-1}yr^{-1} for the Black Rock site (Fig. 1) in northwestern JTNP (Sullivan et al. 2001), and 12 kg ha^{-1}yr^{-1} in the northwestern Coachella Valley (Tonnesen et al., *unpublished data*). Total N deposition reported at the Clean Air Status and Trends Network (CASTNET) monitoring site near Black Rock ranged from 3.2 kg ha^{-1} yr^{-1} in 1995 to 5.9 kg ha^{-1} yr^{-1} in 2003 (CASTNET 2005). However, CASTNET underestimates dry deposition of N (Baumgardner et al. 2002, Fenn et al. 2003a), particularly in California sites where dry deposition of ammonia (NH$_3$) is a significant fraction of inorganic N deposition (Fenn et al., *submitted*). Short-term measurements at the western Salton Sea, which

are recalculated on a yearly basis, ranged from 0.4 to 6.6 kg ha^{-1}yr^{-1} for nitrate-N (NO$_3$-N) and

2.6 to 8.7 for ammonium-N (NH$_4^+$-N, Alonso et al. 2005), but such calculations are fraught with

assumptions about variations in short-term deposition rates and the spatial distribution of

deposition. The lack of actual measurements of N deposition in these deserts means that

observed vegetation changes cannot be explained with respect to air pollution, although field

observations and N fertilizer experiments suggest there may be a relationship (DeFalco et al.

2001, Brooks 2003).

Soil N gradients caused by anthropogenic deposition have been measured in western

Riverside County in coastal sage scrub vegetation (Padgett et al. 1999) and in the San Bernardino

Mountains in coniferous forest (Fenn et al. 2003b), with values for extractable N increasing 5-

fold across the gradients. This effect is especially pronounced when measurements are taken in

seasonally dry soils, when extractable N is highest, both from dry deposition and mineralization

(conversion into plant-available forms). Thus, soil surface N measurements during the dry season

can be used as another indicator of the accumulation of N from air pollution (Padgett et al.

1999).

The impacts of elevated N include changes in nutrient cycling as well as plant community

composition. The rate of nutrient cycling and N leakage has increased in mesic forests of the

eastern U.S. (Aber et al. 1998) as well as in seasonally dry, mixed coniferous forests in

California (Fenn et al. 2003b), but the rate of N loss is expected to be lower in arid or semi-arid

ecosystems (Wood et al. 2006). Studies from Europe have shown a loss of diversity of native

herbaceous species and an increase in native grass biomass with N deposition (Bobbink et al.

1998, Stevens et al. 2004). Nitrogen fertilizer studies in the Mojave Desert (Brooks 2003) and in

coastal sage scrub (Allen 2004) have shown increased productivity of invasive grasses and

decreased productivity and diversity of native species.

To control for the natural variability of climate, soils, and vegetation inherent in any gradient, we performed N fertilization experiments to determine the impacts of N on vegetation and soils using blocked, replicated designs. This was especially critical because the Mojave and Colorado Deserts have low N inputs compared to mesic climates, which would make a N response difficult to detect along a heterogeneous gradient. Air pollution measurements for the first phase of this study included ambient concentrations of ozone (O_3), nitric acid (HNO_3), and NH_3. We do not present data on N deposition (only on concentrations of atmospheric pollutants) although research on N deposition is underway. Ozone was measured because it co-varies with nitrogen oxides and has been reported at high levels in JTNP. Earlier work showed O_3 damage to native plants in the desert (Thompson et al. 1984, Bytnerowicz et al. 1988). The specific objectives of this research were to 1) measure gaseous N pollutant and O_3 concentrations along N-deposition gradients in JTNP using passive samplers, and determine extractable soil N concentrations along the same gradients, and 2) measure non-native grass biomass and cover, and native forb cover and species richness in N-fertilized and control plots at high and low N-pollution sites in creosote bush scrub and pinyon-juniper woodland.

METHODS

Site description

The research was done at Joshua Tree National Park, with two additional locations to the west of JTNP to include areas of potentially higher N deposition (Fig. 1). JTNP has approximately 320,000 ha that span the boundary between the Mojave and Colorado Deserts. The dominant vegetation types include low-elevation creosote bush (*Larrea tridentata*) scrub, intermediate-elevation Joshua tree (*Yucca brevifolia*) woodland, and high-elevation pinyon-

juniper (*Pinus monophylla, Juniperus californica*) woodland, as well as smaller areas of riparian, grassland, and succulent vegetation types (Sawyer and Keeler-Wolfe 1995). Joshua Tree National Park has over 700 plant species identified to date. The elevation ranges from 500 to 1650 m. The geologic parent materials of JTNP consist primarily of granites with several areas of basaltic extrusions (Trent 1984). Air pollution has been increasing and visibility decreasing over the last four decades (Joshua Tree National Park 2004). Annual precipitation during the two years of study was 249 mm (2002-03) and 180 mm (2003-04) at the Black Rock Station (pinyon-juniper woodland), and 205 and 113 mm, respectively, at Hayfield (creosote bush scrub, Fig. 1). The data are reported for October 1-September 30, as the growing season is fall through spring, depending on elevation and yearly precipitation.

Air pollution measurements

Air samplers were deployed at 18 locations across JTNP (Fig. 1). The locations were chosen to cover JTNP, encompass the potential west to east gradient, and be accessible to roads (although not located near any well-traveled highways that might contribute to air pollution). They were placed within the dominant vegetation types (creosote bush scrub, Joshua tree woodland, pinyon-juniper woodland). Concentrations of ambient gaseous N pollutants [nitric oxide (NO), nitrogen dioxide (NO_2), NH_3 and O_3] were determined with passive samplers in the selected sites (Koutrakis et al. 1993). The passive samplers consisted of teflon cartridges with pollutant-collecting filters placed in inverted PVC protective cups 2 m above ground level. HNO_3 was collected on three nylon filters placed in double rings hung inside PVC caps to protect them from wind and rain (Bytnerowicz et al., 2001). Two-week average concentrations of the pollutants were determined three times during the dry season and two times during the wet season. Results are shown for the 14 days following February 10 and July 21, 2004, which were

precipitation-free periods (Figs. 2, 3, 4).

Soil sampling

Soil samples for extractable N analysis were collected from the same 18 sites as the air samples during July 2004, as well as from two additional sites outside JTNP to the west (Fig. 1). Dry-season samples are shown because prior analyses showed extractable N is greater in the dry season than in the winter rainy season (Padgett et al. 1999). Cores were taken 5 cm deep (n = 10) in the interspaces between shrubs or trees. Soils were extracted in potassium chloride (KCl), and ammonium (NH_4^+) and nitrate (NO_3^-) were measured colorimetrically using a Technicon Autoanalyzer.

Fertilization experiment

Fertilization was done at four sites, two on the west end of JTNP and two further to the east (Table 1, Fig. 1). These were in two vegetation types, creosote bush scrub in the Colorado Desert portion of JTNP, and pinyon-juniper woodland in the Mojave Desert. The two vegetation types represent two of the most abundant vegetation types in JTNP, as well as the extremes in elevation. The relative amounts of N deposition were hypothesized based on the model of Tonnesen et al. (2003), but actual rates of N deposition are not yet known for these sites (Table 1).

Two levels of fertilizer were used, 5 and 30 $kg\,ha^{-1}\,yr^{-1}$, plus an unfertilized control at each site. The higher rate was chosen because 30 kg N/ha increased biomass of Mediterranean split grass (*Schismus* spp.), red brome (*Bromus madritensis* ssp. *rubens*) and stork's bill (*Erodium cicutarium*) in another study within one growing season in the western Mojave Desert (Brooks 2003). However, composition of low-productivity vegetation is more sensitive to N inputs, and may experience shifts even with low levels of fertilization (Theodose and Bowman

1997, Bowman and Steltzer 1998). Therefore, the treatments also included a low level of N fertilizer (5 kg N/ha).

Individual shrubs or trees were fertilized by broadcasting ammonium nitrate (NH_4^+-NO_3) granular fertilizer, into an area encompassing the tree canopy. Plot size was determined by the shrub or tree size, with 6 x 6 m for creosote bush, 8 x 8 m for juniper, and 10 x 10 m for pine. Each shrub or tree species was fertilized, and plots were selected across the landscape as 10 replicate blocks, each block containing each of the two N-fertilizer levels plus a control. Fertilizer levels were chosen because the results could be compared with the results from a previous study in the Mojave Desert, which showed a increased productivity by non-native grasses (Brooks 2003). The lower levels were chosen to determine if N would accumulate in soils in a dry climate and eventually promote a response by non-native plants. The low level (5 $kg\,ha^{-1}\,yr^{-1)}$ was similar to the highest known level of 8 $kg\,ha^{-1}\,yr^{-1}$ at the Black Rock Station, calculated by the Environmental Protection Agency (Sullivan et al. 2001). Plots were fertilized in December 2002 and again in December 2003. The N deposition model of Tonnesen et al. (2003) indicates that more NO_3 than NH_4 is deposited in southern California, but the relative amount deposited at each of our sites is not known. Prior analyses have shown that soil NH_4 and NO_3^- concentrations are high in December due to accumulated dry deposition during the summer/fall dry season and remaining mineralized N from the end of the prior rainy season (Padgett et al. 1999). Soil cores were collected to 5 cm deep to determine N levels after fertilization. Growing season (March-May) and dry season (July) samples were taken. July values are shown, as these were higher in extractable soil N, and represent the soil N that is available to plants for uptake at the onset of fall rains (Fig. 6).

Vegetation sampling

Vegetation cover was monitored at the four fertilization sites in 1.0 x 0.5 m quadrats placed just outside the dripline, to the north and south, of each shrub or tree. The percent cover of each species was estimated in a gridded frame with gridlines at 5, 10, and 25 cm intervals and estimates to the nearest 1% between 1-20%, and the nearest 5% between 20-100%; north and south sides of shrubs or trees were measured separately. Vegetation cover on the north side was, on average, higher than the south side, but there were no statistical interactions between the N fertilizer effect on the two sides, so the mean values of the two sides are shown (Table 2). Non-native grasses were clipped and measured for biomass in 10 replicate, 0.25 x 0.50 m (0.125 m^2) plots within each fertilizer level to develop regressions of grass biomass with percent cover. Clippings were dried at 65° to constant mass. Total grass biomass for the 0.5 m^2 quadrats was calculated from percent cover data based on these regressions. Biomass of native vegetation was not assessed to avoid destructive harvesting of native species, which included 77 herbaceous species (Table 2). Vegetation was monitored in March-May in 2003 and 2004, the date depending on peak-plant production according to elevation. Data are shown for 2004 only.

RESULTS

Air pollution

Nitric acid had higher atmospheric concentrations across Joshua Tree National Park (JTNP) in July than in February (Fig. 2), but the reverse was true for ammonia (NH_3), which had higher concentrations in February (Fig. 3). Ozone followed a pattern similar to that of nitric acid (HNO_3, Fig. 4). The concentrations of HNO_3 ranged from 1.0 to 5.0 $\mu g/m^2$ in February and from 2.0 to 9.0 $\mu g/m^2$ in July (Fig. 2). The concentrations fell along a gradient of high to low HNO_3 from west to east; the higher concentrations in the west are likely explained by the closer proximity to the prevailing winds that bring air pollutants from the Los Angeles basin. In winter,

the highest HNO_3 value was at Key's View (Fig. 1), a popular visitor overview on the ridge of the Little San Bernardino Mountains. This site had a higher value in the summer, although the highest summertime exposure was at Wide Canyon, one of the four experimental N fertilization sites.

Atmospheric concentrations of NH_3 ranged from 4.0 to 8.5 $\mu g/m^2$ in February, with lower values of 2.5 to 7.0 $\mu g/m^2$ in July (Fig. 3). The summer concentrations of NH_3 followed the same west to east gradient as the HNO_3, but the winter pattern was different, with an area of high concentration at the east end of JTNP at the Lily Preserve site (Figs. 1, 3). The sites in the interior of JTNP were the lowest in NH_3.

Spatial and temporal patterns of ozone (O_3) concentrations were similar to HNO_3, with 50 to 70 ppb in February and 65 to 95 ppb in July (Fig. 4). Key's View, on the western side of JTNP, was highest in O_3 in February, and Wide Canyon, also on the western side, was highest in July. However, sites on the eastern side of JTNP were also exposed to elevated levels of O_3, with intermediate values at the Lily Preserve and Cadiz Valley sites (Fig.1).

Soil nitrogen

Soils collected in July 2004 on the western side of JTNP (Black Rock and Key's View) and the two sites outside the western boundary (Snow Creek and Dillon Road) had higher levels of extractable soil N than all but three sites on the eastern edge (Fig. 5). The soils in the center of JTNP had low concentrations. The highest values were around 16-20 μg N/g soil, while the lowest values were 4 μg N/g. There was a tendency for ammonium-N (NH_4^+ -N) to be higher than nitrate-N (NO_3^- -N). In general, the sites that had higher reactive atmospheric N also had high extractable soil N concentrations (Black Rock, Key's View, Wide Canyon, Lily Preserve, Cadiz Valley, and Hay Field). Soils collected during the growing season had 1-2 μg N/g (data

not shown), indicating plant uptake and/or leaching of N during the growing season.

Additional edaphic factors were measured at the four N fertilizer sites. Bicarbonate extractable phosphorus (P) ranged from 6-12 µg/g and total P was 650 to 1500 µg/g at the four sites. Total N was 0.040 to 0.078% and total carbon (C) was 0.22 to 0.84%. Soil pH was 6.8 at Covington Flat, 7.1 at Wide Canyon, 7.7 at Pine City and 7.9 at Pinto Wash. Soil texture was sandy loam at all the sites, with varying amounts of gravel and pebble-sized particles. Pinto Wash has the lowest amount of exposed rock on the surface, as it lies in a basin that accumulates surface sand, while the other three sites are a gravelly debris flow (Wide Canyon), rocky alluvial channel (Pine City) and an alluvial fan (Covington Flat).

Extractable N was higher with N fertilizer at the four fertilized sites, with values of 6 to 18 µg/g with 5 kg/ha fertilizer, and 23 to 40 µg/g with 30 kg/ha fertilizer in July 2004 (Fig. 6). Pine City had unexpectedly high soil N in the control plots—as high as the fertilized plots— possibly related to small mammal activity. Covington Flat, on the western side of JTNP, had control soils with low N concentrations (6 µg/g), which were more similar to JTNP interior sites (Figs. 1 and 6). Control plots in Wide Canyon had high soil N concentration, with nearly 15 µg/g, congruent with the high level of atmospheric reactive N. In 2003, total extractable soil N from these sites ranged from a low-control of 11.4 (SE = 2.6) to a high-fertilized (30 kg/ha) of 34.8 (12.6) µg/g, with greater variability than in 2004 (2003 data not shown). The high and low values for 2003 both occurred at Wide Canyon, and other sites were intermediate in both their lowest and highest soil N values.

Response of vegetation to N fertilization

Vegetation changes were related to fertilizer level, initial soil N, and initial vegetation cover. Biomass of non-native grasses increased significantly with N fertilization in three of the

four sites in 2004 (Fig. 7), but percent cover did not increase significantly (Fig. 8) at any site. The lack of change in percent cover with fertilization reflects how difficult it is to visually estimate small increases in grass height (e.g., *Schismus* spp. were only 3-6 cm); percent cover can be determined by calculating the relationships of elevated biomass to cover in fertilized vs. control plots. Percent cover of native vegetation also did not change significantly except at Pine City, where it increased in the higher (30 kg N/ha) fertilization treatment (Fig. 8). Species richness of native vegetation decreased in the 30 kg N/ha fertilization treatment at Pinto Wash (Fig. 9). At Pine City, however, species richness of native vegetation was significantly higher in the 30 kg N/ha treatment (Fig. 9, only data from 2004 are shown). In 2003, there were no significant increases in non-native grasses with N fertilization at any of the sites, although there was an increase in native forb cover with 30 kg N/ha at Pine City as in 2004 (data not shown). As with the soil N data, variability of the plant data was also higher in 2003 than 2004.

The non-native grass species at the two low-elevation sites, Wide Canyon and Pinto Wash, were *Schismus barbatus* and Arabian schismus (*S. arabicus*), with <1% of the latter. *Bromus madritensis* ssp. *rubens* was the dominant non-native grass at the two high-elevation sites, with 1-2% of cheatgrass (*B. tectorum*) and another 1-2% cover of *Schismus barbatus.* The dry mass of non-native grass increased significantly ($P < 0.05$) with 30 kg N/ha in three of the four sites, but not at Covington Flat ($P = 0.101$). There was not a significant increase in non-native grass biomass with 5 kg N/ha fertilizer at any of the sites (Fig. 7). Overall, Pine City had the lowest non-native grass biomass, and Pinto Wash had the highest even in control plots, though it had low extractable soil N and atmospheric reactive N.

Percent cover of non-native species did not change significantly with N fertilization at any of the four sites (Fig. 8). Total non-native cover included grasses and stork's bill (*Erodium*

cicutarium), but the latter contributed < 1.5 % cover at each site (Table 1). Cover of native forbs did not change significantly at any of the sites except Pine City, where it increased with elevated N. This was also the site with the lowest non-native grass biomass.

The species richness of native herbaceous species at Pine City increased significantly following N fertilization at the highest rate, from 3.5 to 4.5 species per 0.5 m^2 plot (Fig. 9). Conversely, native species richness declined significantly at Pinto Wash from 1.3 to 0.2 species/plot, and there was not a significant change at the other two sites. Most of the diversity of this desert vegetation is due to annual forbs, which included 57 species at the four sites combined, plus 5 perennial grasses, 15 perennial forbs, and 21 shrub species (Table 2). Very few of these had < 1% cover, and most occurred sporadically with many not occurring at all, so no statistical analyses could be done on individual species.

<div align="center">DISCUSSION</div>

<div align="center">*Reactive atmospheric and soil N*</div>

The relationship between reactive atmospheric N concentrations and soil N were consistent in most sites. The sites with highest extractable soil N (Black Rock, Key's View, Wide Canyon, Hay Field, and Lily Preserve) also had highest atmospheric nitric acid (HNO_3) and/or ammonia (NH_3) concentrations. Cadiz Valley also had high soil N, and had higher-than-expected ozone (O_3) for an eastern site in Joshua Tree National Park (JTNP). Elevated O_3 is an indicator of poor air quality, although we did not observe elevated atmospheric N at Cadiz Valley during the time periods under study. The phenomenon of much greater eastern transport of O_3 compared to N compounds and N deposition has been observed in the adjacent San Bernardino Mountains (Alonso et al. 2003, Fenn et al. 2003b). The sites to the west of JTNP (Snow Creek) also had high soil N, and may be subject to 12 kg ha^{-1} yr^{-1} of N deposition, as

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modeled by Tonnesen et al. (2003, *and unpublished data)*. Studies currently underway will determine the relationship between measured reactive atmospheric N and rates of N deposition to validate air pollution models.

The high levels of O_3 in JTNP are of concern and were the subject of earlier studies on physiological responses of Mojave Desert plants (Thompson et al. 1984, Bytnerowicz et al. 1988). Concentrations of 100 ppb, which occur in JTNP during the summer, affected performance of Mojave Desert plants (Bytnerowicz et al. 1988). A number of species, primarily riparian or deep-rooted species, were observed to have symptoms of O_3 damage in the summer, (Bytnerowicz et al. 1988). The visible damage was mainly in species that are physiologically active in summer.

Unlike O_3, which is easily converted to oxygen (O_2), and no longer has environmental impacts, gaseous HNO_3 and NH_3 remain active and accumulate in the soil during the dry season. Nitrogen-deposition gradients have been detected by sampling soil N in the mixed coniferous forest of the San Bernardino Mountains (Fenn et al. 1998) and in the coastal sage scrub of the Riverside-Perris Plain (Padgett et al. 1999). In both areas, soil N concentrations have been correlated with atmospheric N concentrations. Reactive atmospheric nitrogen accumulates on leaf and soil surfaces during the dry season and moves to the rooting zone via canopy throughfall, stem flow, and leaching (Fenn et al. 1998, 2003b; Padgett et al. 1999). In dry environments, soil N accumulates on the soil surface over time (Padgett et al. 1999, Wood et al. 2006). We measured higher concentrations of N in fertilized soils in 2004, the second year of fertilization, than in 2003, and we also observed significant responses by the vegetation. In contrast, Brooks (2003) measured vegetation response after only one year of 30 kg N/ha fertilization in the Mojave Desert, with only 82 mm precipitation, but noted that there was

higher-than-average precipitation in the month when germination occurred. Likewise, rainfall was greater in our study during 2004 than 2003, and significant effects on invasive grasses were not observed until the second year. Thus it is likely that, in this dry climate where opportunities for leaching are limited to infrequent wet periods, soils exposed to N pollutants and fertilized soils accumulate N over time (Walvoord et al. 2003). Along the N gradient we observed high values of 15-20 μg/g N, but at this time it is not clear whether this is an upper threshold to which N may accumulate under the current air pollution level, or whether higher soil concentrations will be observed over time. Fertilizing with 30 kg N/ha during the rainy season resulted in levels up to 45 μg/g, so if air pollution increases, we expect to observe elevated soil N.

A drawback of the gradient approach is that it fails to detect other reasons that soils may have elevated or variable N concentrations. Soil texture, pH, parent material, moisture, and other factors control the rate of N mineralization and alter the extractable N concentration (Pastor et al. 1984). Soil texture may control growth of non-native grasses, which have fine, shallow root systems. The two rocky/gravelly sites, Wide Canyon and Pine City, had the lowest grass biomass, and Pinto Wash, which lies in a basin that accumulates sand, had the highest grass biomass, even though it had the lowest soil N. Mineralization studies are underway at all of the sites to determine the N supply rate of these soils.

Impacts of elevated N on native and non-native vegetation

Although observations along the N gradient did not reveal a clear relationship between non-native grass cover and soil N concentration, the fertilizer experiments at the four sites did show significant impacts of N on both native and non-native plants. Pinto Wash had the highest grass cover and lowest soil N, but non-native grass biomass was even higher following 30 kg N/ha fertilization. This level of N fertilization also caused increased *Schismus* and *Bromus* spp.

productivity in the western Mojave Desert (Brooks 2003) in an area of low to moderate air pollution (Tonnesen et al., *unpublished data*). This suggests that, if N deposition increases further at any of the sites, the non-native grass biomass may increase, with a potential for loss in productivity and species richness of native herbs. A surface-soil N concentration of 23 and 30 μg/g in the 30 kg N/ha treatment in the two sites with lower air pollution (Pinto Wash and Pine City) resulted in non-native grass growth response. Therefore, 23 μg/g can be conservatively considered the low threshold for significant plant N response based on this fertilization study.

We hypothesize that sites along the gradient that have approximately 23 μg/g soil N are already being affected by elevated N, assuming other edaphic factors are not limiting. It is not yet clear whether elevated soil N is caused by atmospheric N deposition at all of these sites, especially the sites in the eastern edge of JTNP. Furthermore, the two high-deposition N fertilizer sites (Covington Flat and Wide Canyon) had soil concentrations of 18-20 μg/g following fertilization with 5 kg N/ha. Non-native grass productivity is likely also elevated, but there is no longer an unpolluted control plot at these sites to test this statistically. This suggests that even small yearly N increases, such as the 5 kg/ha over two years in this study, will eventually raise the level of soil N to values high enough to cause a significant increase in non-native grass biomass.

The amount of initial non-native grass biomass at each of the sites was critical to the changes that took place in native plant species richness and cover following N fertilization. At Pinto Wash, where non-native grass biomass was the highest, the higher level of N fertilization caused a decrease in native species richness in each plot, while at Pine City, where non-native grass biomass was lowest, the native species richness and cover increased with fertilization. This suggests that the native species are also N-limited, but that the non-native grasses respond to N

more rapidly, assuming the non-natives have already colonized and the site is suitable to their growth. The strong competitive interaction between the non-native and native grasses, as well as non-native forbs, was demonstrated in a grass-removal experiment, where both groups of forbs increased in density and biomass in response to non-native grass thinning (Brooks 2000).

Another study showed that *Bromus madritensis* has a higher rate of ^{15}N uptake than native seedlings of *Artemisia californica* in coastal sage scrub vegetation (Yoshida and Allen 2004). However, in a growth-chamber experiment, native species responded to N fertilization with the same relative percent increase as *B. madritensis* (Salo et al. 2005), a non-native species. Since both native and non-native species respond to N, other factors may also be involved, such as seed production and phenology of germination. The non-native grasses germinate earlier than native species and produce seeds even in dry years when native plants do not germinate, which maintains the non-native seed bank (Brooks 1999b, 2003, *this volume*). Thus it appears that the different responses of native species at Pinto Wash and Pine City may be due to the competitive interactions of natives with high vs. low cover of non-native grasses.

The high grass biomass has been cited, in part, for an increase in fire frequency in the Mojave Desert (Brooks 1999a; Brooks and Esque 2002; Brooks et al. 2004; Brooks and Minnich, *in press*), especially at higher elevations that have higher rainfall and grass productivity. A fire of 5500 ha burned in May 1999 at Covington Flat in blackbrush (*Coleogyne ramosissima*), galleta grass (*Hilaria rigida*) and Joshua tree and pinyon-juniper woodlands (Park staff, *personal communication*). This is the largest fire known in JTNP, and followed the wet spring of 1998, in which there was a high production of *Bromus madritensis* (our N fertilization experiment at Covington Flat was in unburned vegetation). The fuel load for the fire was likely increased due to higher-than-average production of native plus non-native species, although the grass biomass

at that time is not known. The fuel threshold for non-native grass biomass has been estimated at 0.5 to 1.0 T/ha dry matter (Fenn et al. 2003a). This level of biomass was produced in Pinto Wash in quadrats located just beyond the dripline of shrubs (50-70 g/m^2), but a fire would not be expected there because the grass cover is discontinuous in the interspaces.

More recent fires occurred at Snow Creek (450 ha, July 2004) and Morongo Valley (1250 ha, August 2005; Fig. 1) Both sites lie just to the west of the Park in areas of higher air pollution (Tonnesen et al. 2003), and we measured 20 μg/g soil N at Snow Creek—enough to trigger a growth response by non-native grasses. The non-native species that burned at Snow Creek were *Schismus* spp. and *Brassica tournefortii*, while at the higher elevation Morongo Valley, *Bromus madritensis* was the primary non-native species that burned. Typical for burned desert vegetation (Brooks and Minnich, *in press*), recovery of native shrubs at Covington Flat and Snow Creek is slow, and Snow Creek remains densely covered with non-native species (R. Steers, *personal observation*).

CONCLUSIONS

This study has shown that a large pulse of 30 kg N/ha, added over two years, will increase the biomass of non-native grass and either increase or decrease native forb species richness depending on initial non-native grass production. However, estimated annual anthropogenic N inputs in this region are much lower than the 30 kg N/ha fertilization treatment (CASTNET 2005, Sullivan et al. 2001, Tonnesen et al. 2003). In arid environments, these small amounts may build up over time, as leaching rates are low, and N may also accumulate in lower soil horizons within and below the rooting zone (Walvoord et al. 2003, Wood et al. 2006).

The concentrations of soil N in sites along the gradient were as high as fertilized low-deposition sites that had a significant response by non-native grasses. This indicates that long-

term, low-level N inputs on the west end of Joshua Tree National Park may have already accumulated enough N in surface soils (e.g., 23 µg/g) to affect non-native grass productivity. Characteristics intrinsic to local sites will determine to what extent non-native species will invade a site, but anthropogenically elevated N will cause a further imbalance if the invaders are nitrophilous and/or prolific seed producers (Brooks 2003, Yoshida and Allen 2004). Further studies on N mineralization are underway to determine the rate at which N is supplied in soils of different sites along the gradient. These may help to predict which soil types are predisposed to support greater productivity of non-native invaders.

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Table 1. Vegetation, elevation, and hypothesized relative N deposition of four sites at Joshua

Tree National Park chosen for N fertilization study. See Fig. 1 for site locations.

Site	Vegetation Type	Elevation	N deposition
Pinto Wash	Creosote Bush Scrub	750	Low
Wide Canyon	Creosote Bush Scrub	550	High
Pine City	Pinyon-Juniper Woodland	1400	Low
Covington Flat	Pinyon-Juniper Woodland	1500	High

Table 2. Percent cover of the most abundant native species in 0.5 m^2 quadrats at four sites under two N fertilization levels and an unfertilized control in 2004. There were no significant differences for any of these species when analyzed individually, as there were many zero values for each species.

	Pinto Wash			Wide Canyon			Pine City			Covington Flat		
N treatment (kg/ha):	0	5	30	0	5	30	0	5	30	0	5	30
Chaenactis fremontii		1.3		3.7	2.2	1.9						
Chaenactis stevioides							2.6	4.3	3.8		1.7	1.9
Coleogyne ramosissima								2.2				
Cryptantha angustifolia				6.6	4.9	8.2						
Cryptantha pterocarya							1.5	3.2	4.8			2.9
Descurainia pinnata							2.3	3.0	4.0			
Euphorbia polycarpa				1.2								
Gilia stellata							1.5	1.1	1.6			
Malacothrix glabrata				2.5	2.0	2.0						
Mentzelia affinis										1.2	3.3	
Mirabilis californica												1.6
Pectocarya recurvata				1.5	1.5	1.4						
Phacelia distans								2.4	2.9	4.5	4.8	5.8
Poa secunda												1.1
Salvia columbariae	8.3									1.4		

Species with < 1% cover

Shrubs (20 species):

Brickellia californica, Chrysothamnus nauseosus, Echinocereus engelmannii, Ephedra nevadensis, Eriogonum fasciculatum, E. wrightii, Eriophyllum confertiflorum, E. wallacei, Gutierrezia microcephala, G. sarothrae, Hymenoclea salsola, Juniperus californica, Lycium andersonii, Nolina parryi, Opuntia erinacea, Purshia tridentata, Quercus cornelius-muelleri, Salazaria mexicana, Viguiera parishii, Yucca schidigera

Perennial grasses (5):

Achnatherum lettermanii, A. speciosum, Aristida adscenscionis, Elymus elymoides, Erioneuron pulchellum

Annual forbs (57):

Adenophyllum porophylloides, Amsinkia tessellata, Anisocoma acaulis, Arabis pulchra, Arenaria macrademia, Calycoceris parryi, Calyptridium monandrum, Camissonia californica, C. campestris, C. claviformis, C. pallida, Castelleja angustifolia, Caulanthus cooperi, Centrostegia thurberi, Chaenactis macrantha, Chorizanthe brevicornu, Crassula connata, Cryptantha barbigera, C. circumscissa, C. maritima, C. micrantha, C. nevadensis, C. utahensis, Draba cuneifolia, Eriogonum davidsonii, E. maculatum, E. nidularium, E. pusillum, Eriastrum diffusum, Eschscholzia minutiflora, Eucrypta chrysanthemifolia, Euphorbia albomarginata, Filago arizonica, F. depressa, Layia glandulosa, Lepidium lasiocarpum, L. aureus, Linanthus biglovii, L. dichotomous, L. jonesii, Loeseliastrum matthewsii, Lotus strigosus, Lupinus concinnus, Mentzelia sp., Nama demissum, Nemophila menziesii, Pectocarya heterocarpa, P. penicillata, P. platycarpa, P. setosa, Phacelia ciliata, P. cryptantha, Plantago ovata, P. patagonica, Rafinesquia neomexicana, Syntrichopappus fremontii, Thysanocarpus curvipes,

Uropappus lindleyi

Perennial forbs (15):

Allium parishii, Astragalus bernardanus, A. lentiginosus, A. nuttallianus, Calochortus kennedyi,

Delphinium parishii, Dichelostemma capitatum, Dudleya saxosa, Eriogonum inflatum,

Lomatium mohavense, Lotus argophyllus, L. rigidus, Mirablis bigelovii, Sphaeralcea ambigua,

Stephanomeria exigua
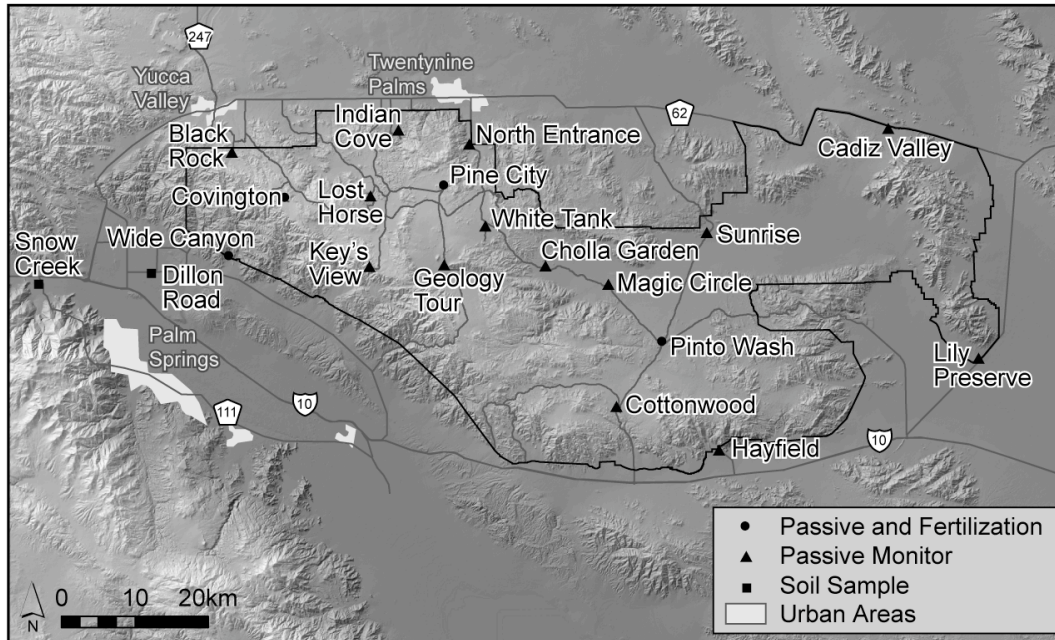
Nomenclature from Hickman (1993).

FIGURE LEGENDS

FIG. 1. Atmospheric nitrogen (N), extractable soil N, and vegetation sample sites at Joshua Tree National Park (JTNP). The nitrogen fertilization experiments, indicated with triangles, are described in table 1. Passive air samples and soil samples were taken from all sites in JTNP, and soils samples were also taken from two sites to the west of JTNP—Snow Creek and Dillon Road..
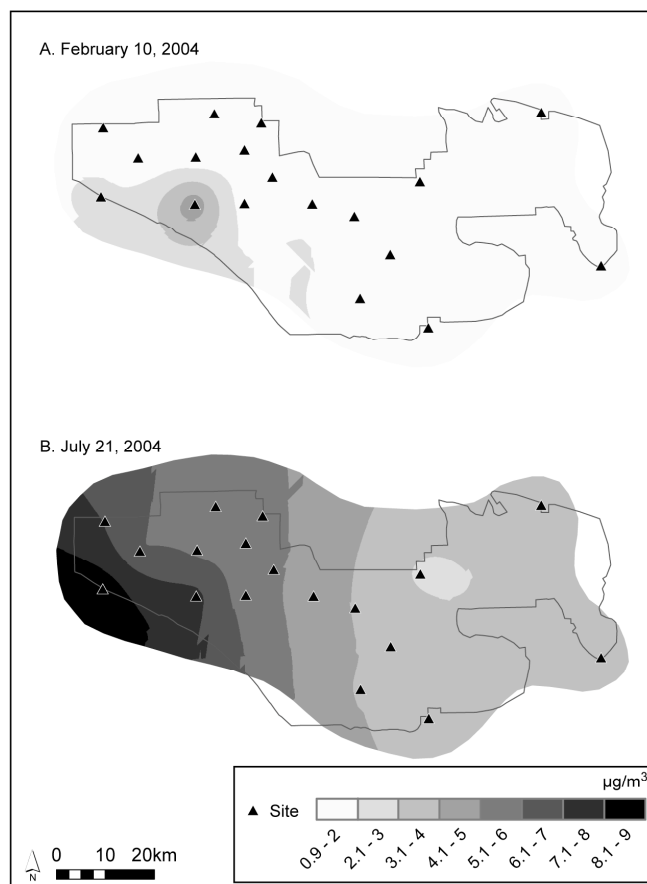
FIG. 2. Two-week-long average nitric acid (HNO$_3$) concentration (μg/m^3) in the atmosphere over Joshua Tree National Park in A) winter and B) summer, 2004 (dates on graph show start of sampling).

FIG. 3. Two-week-long average ammonia (NH$_3$) concentration (μg/m^3) in the atmosphere over Joshua Tree National Park in A) winter and B) summer, 2004 (dates on graph show start of sampling).

FIG. 4. Two-week-long average ozone (O$_3$) concentration (ppb) in the atmosphere over Joshua Tree National Park in A) winter and B) summer, 2004 (dates on graph show start of sampling).

FIG. 5. Extractable soil nitrogen as ammonium (NH$_4^+$) and nitrate (NO$_3^-$) in 14 sites in Joshua Tree National Park (JTNP) and two sites west of JTNP in July 2004 (Fig. 1).

FIG. 6. Extractable soil nitrogen (N) as ammonium (NH$_4^+$) and nitrate (NO$_3^-$) in plots fertilized with ammonium nitrate (NH$_4^+$-NO$_3$) for two years at two levels (5 and 30 kg/ha) at four sites—Covington Flat, Wide Canyon, Pine City, and Pinto Wash (Fig. 1).

FIG. 7. Dry weight of non-native grass in Mar-Apr 2004 following nitrogen fertilization at 5 and 30 kg/ha at four sites. Non-native grasses were primarily Mediterranean split grass *(Schismus barbatus)* at Wide Canyon and Pinto Wash, and red brome (*Bromus madritensis*) at Covington Flat and Pine City. Different letters above bars indicate significantly different at *P* = 0.05.

FIG. 8. Percent cover of non-native species and native herbaceous species in Mar-Apr 2004 following nitrogen fertilization at 5 and 30 kg/ha at four sites. See Table 2 for list of species. Different letters above bars indicate significantly different at $P = 0.05$.

FIG. 9. Species richness (number/0.5 m^2) of native herbaceous species in Mar-Apr 2004 following nitrogen fertilization for two years at 5 and 30 kg/ha at four sites. See Table 2 for list of species. Different letters above bars indicate significantly different at $P = 0.05$.

FIG. 1. Atmospheric nitrogen (N), extractable soil N, and vegetation sample sites at Joshua Tree National Park (JTNP). The nitrogen fertilization experiments, indicated with triangles, are described in table 1. Passive air samples and soil samples were taken from all sites in JTNP, and soils samples were also taken from two sites to the west of JTNP—Snow Creek and Dillon Road..

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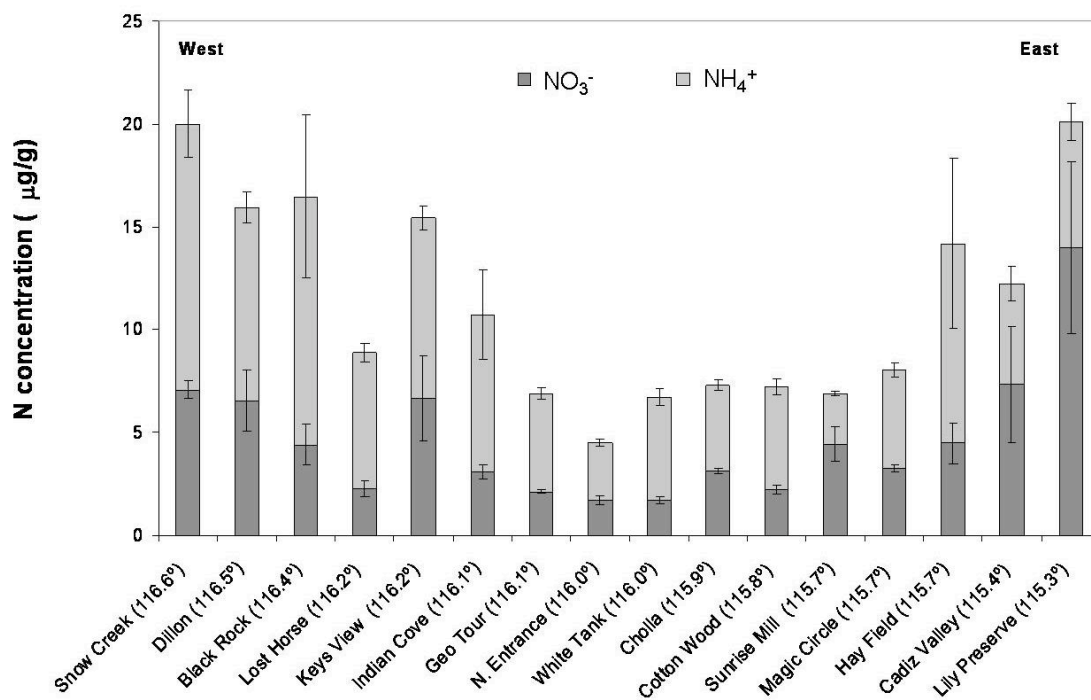
FIG. 3. Two-week-long average ammonia (NH₃) concentration ($\mu g/m^3$) in the atmosphere over Joshua Tree National Park in A) winter and B) summer, 2004 (dates on graph show start of sampling).

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FIG. 6. Extractable soil nitrogen (N) as ammonium (NH_4^+) and nitrate (NO_3^-) in plots fertilized with ammonium nitrate (NH_4^+-NO_3) for two years at two levels (5 and 30 kg/ha) at four sites—Covington Flat, Wide Canyon, Pine City, and Pinto Wash (Fig. 1).
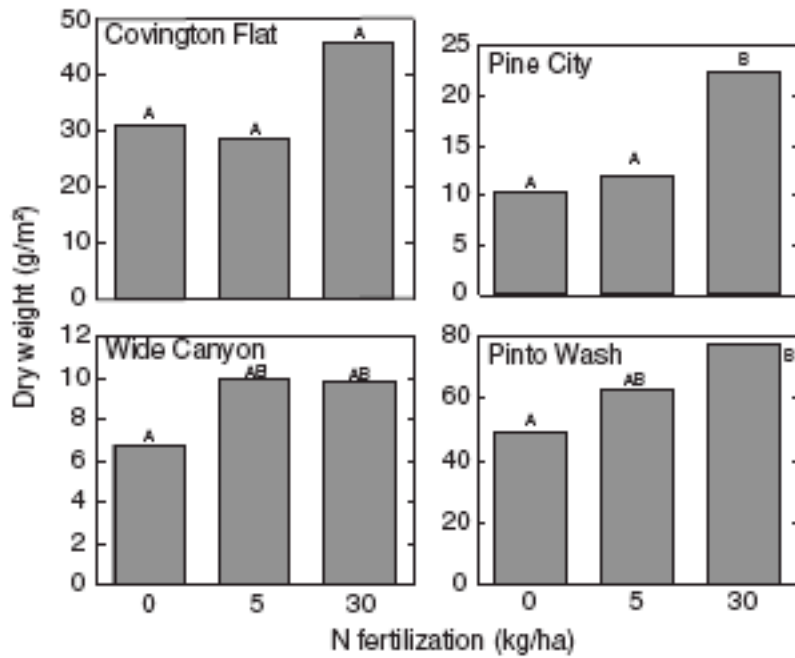
F<small>IG</small>. 7. Dry weight of non-native grass in Mar-Apr 2004 following nitrogen fertilization at 5 and 30 kg/ha at four sites. Non-native grasses were primarily Mediterranean split grass *(Schismus barbatus)* at Wide Canyon and Pinto Wash, and red brome (*Bromus madritensis*) at Covington Flat and Pine City. Different letters above bars indicate significantly different at $P = 0.05$.
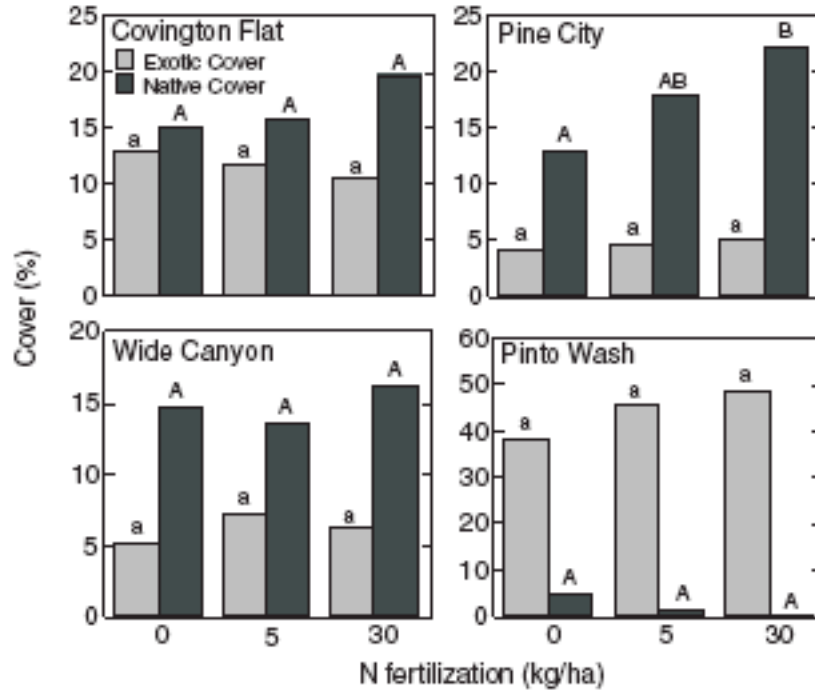
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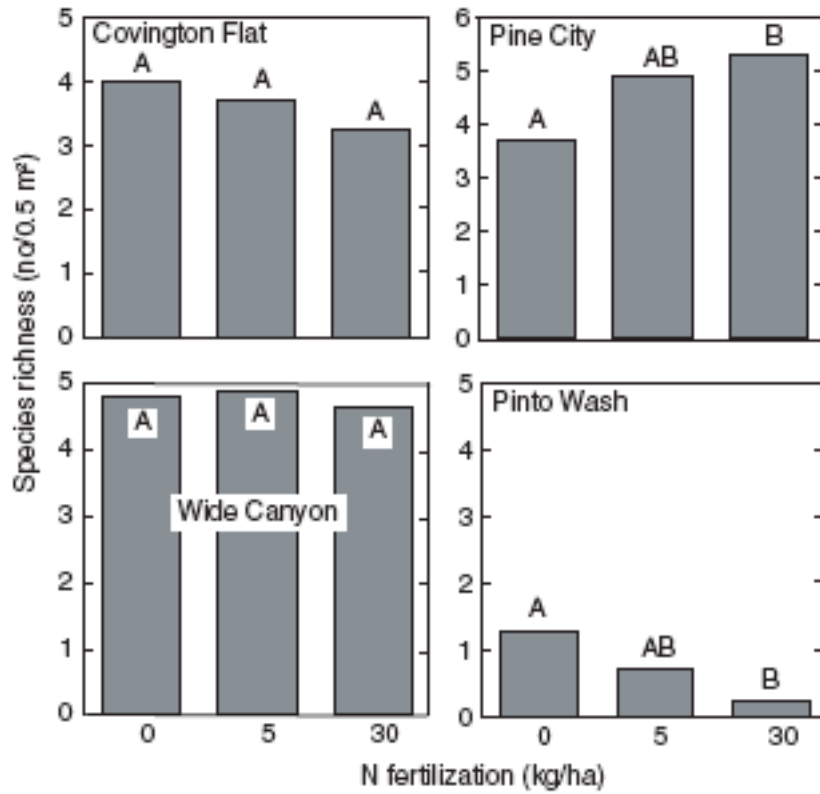
FIG. 9. Species richness (number/0.5m^2) of native herbaceous species in Mar-Apr 2004 following nitrogen fertilization for two years at 5 and 30 kg/ha at four sites. See Table 2 for list of species. Different letters above bars indicate significantly different at $P = 0.05$.