

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 N in the atmosphere and soils along a N deposition gradient at Joshua Tree National Park, and to examine effects on non-native invasive and on native plant species. Concentrations of atmospheric nitric acid and ozone were elevated in the western Park, but there were some high levels of ammonia in the east that may be related to local sources. The central areas of the Park were lowest in reactive N. Nitric acid was higher in summer than winter, while ammonia concentrations were higher in winter. Extractable soil N was generally higher in sites that had higher atmospheric reactive N. Invasive grasses and forbs, such as *Schismus barbatus*, *Bromus madritensis*, and *Erodium cicutarium* have become more productive and widespread in the last two decades. To test the hypothesis that elevated N may be related to invasive species, N fertilizer experiments were done at four sites in the Park at levels of 5 and 30 kg N/ha for each of two years. Sites with higher and lower 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 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 grass cover. Non-native grass cover was not related to atmospheric reactive N concentrations, but is likely controlled by soil conditions such as texture and soil N supply rate, as well as anthropogenic N inputs. The study provides

evidence that N deposition over time will increase the soil N to levels that may shift the community to a species-poor, non-native grass-dominated vegetation.

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). Both oxidized and reduced forms of nitrogen (N) are of concern because they are deposited on soil and plant surfaces, and fertilize plants with N. Nitrogen deposition may affect plant productivity differentially, with non-native grasses having higher rates of N uptake or production than many native species (Allen et al. 1998, Yoshida and Allen 2001, 2004, Brooks 2003) or similar rates as natives in other studies (Padgett and Allen 1999, Salo et al. 2005). The number of non-native species and their abundance have increased in the desert in the last two decades (Brooks 1999a,b, this volume), and our objectives were to determine whether this is related to elevated N deposition. As non-native grasses increase in productivity, the 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 such as Joshua Tree National Park, which lies within both the Mojave and the Colorado Deserts. The wind patterns create N deposition gradients that have been modeled with highest levels on the west side of the Park (Tonnesen et al. 2003). We selected sites along this modeled anthropogenic N gradient to

make finer-scale measurements of reactive atmospheric as well as soil extractable N, and to determine response of non-native grass cover and native species diversity to elevated soil N.

N deposition in shrublands and forests of the Los Angeles air basin may be as high as 30-50 kg ha⁻¹yr⁻¹ (Bytnerowicz et al. 1987, Fenn et al. 1998, 2003b). Most of this 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 (Bytnerowicz et al. 2000). Relatively few estimates of N deposition have been done in the Mojave or Colorado Deserts, with a value of 8 kg ha⁻¹yr⁻¹ calculated for the Black Rock site in the northwestern Park (Fig. 1, Sullivan et al. 2001), and 12 kg/ ha/yr in the northwestern Coachella Valley (Tonnesen et al. 2003 and unpublished data). Total N deposition reported for the Clean Air Status and Trends Network (CASTNET) monitoring site near Black Rock ranged from 3.2 to 5.9 kg ha⁻¹ yr⁻¹ from 1995 to 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 is a significant fraction of inorganic N deposition (Fenn et al., submitted). Short term measurements at the western Salton Sea, when recalculated on a yearly basis, ranged from 0.4 to 6.6 kg ha⁻¹yr⁻¹ for nitrate-N and 2.6 to 8.7 for ammonium-N (Alonso et al. 2005), but such a calculation is fraught with assumptions about variations in short-term rate and spatial distribution of deposition. The lack of actual measurements of N deposition in the desert 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 coniferous forest in the San Bernardino Mountains (Fenn et al. 2003b), with values for extractable N increasing 5-fold across the gradients. This effect is especially pronounced in seasonally dry soils, where extractable N is highest during the dry season, both from dry deposition and mineralization. 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 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). N fertilizer studies in the Mojave Desert (Brooks 2003) and 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 also performed N fertilization experiments to determine the impacts of N to vegetation and soils using blocked, replicated designs. This was especially critical because the Mojave and Colorado Deserts have low N inputs compared to other studies in mesic climates, that 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, nitric acid, and ammonia. We do not present data on N deposition, only on concentrations of atmospheric pollutants, although research on N deposition rates is underway. Ozone was measured because it co-varies with nitrogen oxides and has been reported at high levels in the Park. Earlier work showed ozone 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 ozone concentrations along N deposition gradients in the Park 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 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 the Park to include areas of potentially higher N deposition (Fig. 1). The Park has approximately 320,000 ha that lie in both 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). The Park has over 700 plant species identified to date. The elevation ranges from 500 to 1650 m. The geologic parent material of the Park consists 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). 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; station locations in 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 the Park (Fig. 1). The locations were chosen to cover the Park, encompass the potential west to east gradient, and be accessible to roads (although not near any well-traveled highways that might contribute to air pollution). They covered the dominant vegetation types (Creosote Bush Scrub, Joshua Tree Woodland, Pinyon Juniper Woodland). Concentrations of ambient gaseous N pollutants (NO, NO₂, NH₃ and O₃) 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 at 2 m above ground level. Nitric acid was collected on three nylon filters placed in double rings hung inside PVC caps protecting them from wind and rain (Bytnerowicz et al., 2001). Two-week long 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.

Soil sampling

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

Fertilization experiment

Fertilization was done at four sites, two on the west end of the Park 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 the Park, and Pinyon-Juniper Woodland in the Mojave Desert. The two vegetation types represent two of the most abundant vegetation types in the Park as well as the extremes in elevation. The relative amounts of N deposition was hypothesized based on the model of Tonnesen et al. (2003), but actual rates of N deposition are not yet known for these sites.

Two levels of fertilizer were used, 5 and 30 kg·ha⁻¹ yr⁻¹, plus unfertilized controls. The higher rate was chosen because 30 kg N/ha increased biomass of *Schismus* spp. (Mediterranean split grass), *Bromus madritensis* ssp. *rubens* (red brome) and *Erodium cicutarium* (stork's bill) in another study within one growing season in the western Mojave Desert (Brooks 2003). However, low productivity vegetation is more sensitive to N inputs, and may experience shifts in composition even with low levels of fertilization (Bowman and Steltzer 1998, Theodose and Bowman 1997). Therefore, the treatments also included a low level of N fertilizer of 5 kg/ha.

Individual shrubs or trees were fertilized, encompassing an area beyond the tree canopy. Plot size was determined by the shrub or tree size, with 6 x 6m for creosote bush, 8 x 8m for juniper, and 10 x 10m for pine. Ten replicates of each shrub or tree species were fertilized, and selected across the landscape as 10 replicate blocks, each block containing each of the two N fertilizer levels plus control. Fertilizer levels were chosen to compare with the high level of 30 kg ha⁻¹ yr⁻¹ that has been tested previously in the Mojave Desert and showed a response by non-native grasses (Brooks 2003). The lower levels were chosen to determine if N would accumulate in a dry climate and eventually promote a response by non-native plants. The low level of 5 kg ha⁻¹ yr⁻¹ was similar to the highest known level of 8 kg ha⁻¹ yr⁻¹ calculated by the Environmental Protection Agency at the Black Rock Station (Sullivan et al. 2001). Plots were fertilized in December, 2002, and again in December, 2003, by broadcasting NH₄NO₃ granular fertilizer. The N deposition model of Tonnesen et al. (2003) indicates that more nitrate than ammonium is deposited in southern California, but the relative amount deposited at each of our sites is not known. Prior analyses showed that soil ammonium and nitrate concentrations are high in December due to accumulated dry deposition during the summer/fall dry season and 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 values of soil N that plants have available for uptake at the onset of fall rains.

Vegetation sampling

Vegetation cover was monitored in 1.0 x 0.5 m sampling quadrats placed just outside the dripline 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 of the N fertilizer effect on the two sides, so the mean values for the two sides are shown. Non-native grasses were clipped in 10 replicate, 0.25 x 0.50 m quadrats in each fertilizer level to develop regressions of grass biomass with percent cover. Clippings were dried at 65° to constant mass. Grass biomass was calculated from percent cover data in the 0.5 m² quadrats 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.

RESULTS

Air pollution

Nitric acid had higher atmospheric concentrations across the Park in July than February (Fig. 2), but the reverse was true for ammonia with higher concentrations in winter (Fig. 3). Ozone followed the pattern of nitric acid (Fig. 4). The concentrations of nitric acid ranged from 1.0 to 5.0 µg/m² in February, but were 2.0 to 9.0 µg/m² in July (Fig. 2). The concentrations fell along a gradient of high to low nitric acid from west to east, higher in the west that is closer to the prevailing winds that likely bring air pollutants from the Los Angeles basin. The highest nitric acid value in winter 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 ammonia ranged from 4.0 to 8.5 $\mu\text{g}/\text{m}^2$ in February, with lower values of 2.5 to 7.0 $\mu\text{g}/\text{m}^2$ in July (Fig. 3). The summer concentrations of ammonia followed a west to east gradient as did nitric acid, but the winter pattern was different, with an area of high concentration at the east end of the Park at the Lily Preserve site (Figs. 1, 3). The sites in the Park interior were the lowest in ammonia.

Spatial and temporal patterns of ozone concentrations were similar to nitric acid with 50 to 70 ppb in February and 65 to 95 ppb in July (Fig. 4). Key's View was also the highest in ozone in February, and Wide Canyon in July. However, sites in the eastern side of the Park were also exposed to elevated levels of ozone air pollution, 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 the Park (Black Rock and Key's View) and the two sites outside the western Park boundary (Snow Creek and Dillon Road) had higher levels of extractable N than all but three sites on the eastern edge (Fig. 5). The soils in the center of the Park had low N concentrations. The high values were around 16-20 $\mu\text{g N}/\text{g}$ soil, while the low values were 4 $\mu\text{g}/\text{g}$. There was a tendency for NH_4^+ -N to be higher than 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 $\mu\text{g N/g}$ (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 P ranged from 6-12 $\mu\text{g/g}$ and total P was 650 to 1500 $\mu\text{g/g}$ at the four sites. Total N was 0.040 to 0.078% and total C was 0.22 to 0.84%. 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 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 $\mu\text{g/g}$ with 5 kg/ha fertilizer, and 23 to 40 $\mu\text{g/g}$ 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 control soils had low N concentrations (6 $\mu\text{g/g}$) that were more similar to other Park interior sites (Fig. 6), even though this site lies on the western part of the Park (Fig. 1). Control plots in Wide Canyon had high soil N concentration with nearly 15 $\mu\text{g/g}$, 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 (S.E. = 2.6) to a high fertilized (30 kg/ha) of 34.8 (12.6) $\mu\text{g/g}$, 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 occurred because visual estimation does not perceive small increases in grass height (e.g., *Schismus* spp. were only 3-6 cm) with fertilization that can be determined by the calculated 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 30 kg/ha fertilization treatment (Fig. 8). Richness of native vegetation decreased in the 30 kg/ha fertilization treatment at Pinto Wash. At Pine City, however, both richness and percent cover of native vegetation were significantly higher in the 30 kg/ha treatment (Figs. 8 and 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/ha at Pine City as in 2004 (data not shown). As for 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 *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 *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/ha in three of the four sites, but not at Covington Flat ($p = 0.101$). There was not a significant increase in 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, even 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 *Erodium cicutarium*, but the latter contributed < 1.5 % cover at each site. 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 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 m² quadrat (Fig. 9). Conversely, native species richness declined significantly at Pinto Wash from 1.3 to 0.2 species/quadrat, 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 69 species in sample quadrats at the four sites, plus 1 annual grass, 5 perennial grasses, 16 perennial forbs, and 21 shrub species (Table 2). Very few of these had > 1% cover, and most occurred sporadically with many zero values, so no statistical analyses could be done on individual species.

DISCUSSION

Reactive atmospheric and soil N

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 and/or ammonia concentrations. Cadiz Valley also had high soil N, and had higher than expected ozone for an eastern site in the Park. Elevated ozone 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 ozone 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 the Park (Snow Creek) also had high soil N, and may be subject to $12 \text{ kg ha}^{-1} \text{ yr}^{-1}$ of N deposition as modeled by (Tonnesen et al. 2003 and unpublished data, 2005). 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 ozone in the Park 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 the Park during the summer, affected performance of Mojave Desert plants (Bytnerowicz et al. 1988). A number of species were observed to have symptoms of ozone damage in the summer, primarily riparian or deep rooted species (Bytnerowicz et al. 1988). The visible damage was mainly in species that are physiologically active in summer.

Unlike ozone, which no longer has environmental impacts after it is converted to O_2 , gaseous nitric acid and ammonia are deposited 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 cases soil N has been correlated with atmospheric N concentrations. Reactive nitrogen accumulates on leaf and soil surfaces during the dry season and moves to the rooting zone via canopy throughfall, stem flow, and leaching (Padgett et al. 1999, Fenn et al. 1998, 2003b). 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/ha N 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. Rainfall was greater in our study during 2004 than 2003, but significant effects on invasive grasses were not observed until the second year. Thus it is likely that soils exposed to N pollutants and fertilized soils accumulate N over time in this dry climate where opportunities for leaching are limited to infrequent wet periods (Walvoord et al. 2003). Along the N gradient we observed high values of 15-20 $\mu\text{g/g}$ 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 $\mu\text{g/g}$, so if air pollution increases, we expect to observe elevated soil N.

Soils may have elevated or variable N concentrations for reasons other than atmospheric inputs, a drawback of the gradient approach. 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 with fine, shallow root systems. The two rocky/gravelly sites, Wide Canyon and Pine City, had lowest grass biomass, and Pinto Wash, which lies in a basin that accumulates sand, had the highest grass biomass even though it had 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 experiment at the four sites showed significant impacts of N on native and non-native plants. Pinto Wash had the highest grass cover and low soil N, but non-native grass biomass was even higher following 30kg 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. 2003 and unpublished). This suggests that, if N deposition increases further at any of the sites, the non-native grass biomass may increase with a potential for a loss in productivity and richness of native herbs. A surface soil N concentration of 23 and 30 $\mu\text{g/g}$ in the 30 kg/ha treatment in the two lower air pollution sites (Pinto Wash and Pine City) resulted in non-native grass growth response. Therefore, 23 $\mu\text{g/g}$ 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 $\mu\text{g/g}$ soil N are already being affected by elevated N, assuming other edaphic factors are not limiting. It is yet not clear whether elevated N is caused by N deposition at all of these sites, especially the sites in the eastern edge of the Park. Furthermore, the two high deposition N fertilizer sites (Covington Flat and Wide Canyon) had soil concentrations of 18-20 $\mu\text{g/g}$ following fertilization with 5 kg N/ha. Non-native grass productivity is likely also elevated at these sites, but there is no longer an unpolluted control plot at these sites

to test this statistically. This suggests that even small yearly N increments such as 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 grass biomass at each of the sites was critical to the changes that took place in native richness and cover following N fertilization. At Pinto Wash where grass biomass was the highest, the higher level of N fertilization caused a decrease in native species richness per plot, while at Pine City where non-native grass biomass was lowest, the native species richness and cover increased with N 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 grasses and native as well as non-native forbs was demonstrated in a grass removal experiment, where both groups of forbs responded to competitive release following grass thinning (Brooks 2000). Another study showed that *Bromus madritensis* has a higher rate of ¹⁵N 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 percentage of increase as *B. madritensis* (Salo et al. 2005). 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 seed even in dry years when native plants do not germinate, maintaining 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 interpreted as competitive interactions with high cover of non-native grasses, vs. no competition with low cover.

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 the higher elevations with higher rainfall and grass productivity. A fire of 5500 ha burned in May 1999 at Covington Flat in *Coleogyne ramosissimum* (blackbrush), *Hilaria rigida* (galleta grass) and Joshua Tree and Pinyon-Juniper Woodlands (Park staff, personal communication). This is the largest fire known from the Park, and followed the wet spring of 1998 that had high production of *B. madritensis* at this high elevation (our N fertilization experiment at Covington Flat was in unburned vegetation). The fuel load for the fire was likely a combination of increased 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/m²), 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). 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 the higher elevation Morongo Valley fire was primarily in areas colonized by *Bromus madritensis*. 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 observations, 2005),

CONCLUSIONS

This study has shown that a large pulse of 30 kg/ha N added over two years will increase the biomass of non-native grass and either increase or decrease native forb richness depending on initial non-native grass production. However, estimated annual anthropogenic N inputs in this region are much lower than the 30 kg/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 the Park may have already accumulated enough N in surface soils (e.g., 23 $\mu\text{g/g}$) 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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Literature Cited

- Aber, J., W. McDowell, K. Nadelhoffer, A. Magill, G. Berntson, M. Kamakea, S. McNulty, W. Currie, L. Rustad, and I. Fernandez. 1998. Nitrogen saturation in temperate forest ecosystems - Hypotheses revisited. *Bioscience* **48**:921-934.
- Allen, E. B. 2004. Restoration of *Artemisia* shrublands invaded by exotic annual *Bromus*: A comparison between southern California and the Intermountain Region. Pp. 9-17 in A. L. Hild, N. L. Shaw, S. E. Meyer, E. W. Schupp, and T. Booth, compilers. Seed and Soil Dynamics in Shrubland Ecosystems: Proceedings; August 12-16, 2002, Laramie, Wyoming RMRS-P-31. U.S. Department of Agriculture Forest Service, Rocky Mountain Research Station, Ogden, Utah.
- Allen, E. B., P. E. Padgett, A. Bytnerowicz, and R. A. Minnich. 1998. Nitrogen deposition effects on coastal sage vegetation of southern California. Pages 131-140 in Proceedings of the International Symposium on Air Pollution and Climate Change Effects on Forest Ecosystems. USDA Forest Service, Pacific Southwest Research Station, Riverside, CA. <http://www.rfl.psw.fs.fed.us/pubs/psw-gtr-164/fulltext/allen/allen.html#anchor1473574>
- Alonso, R., A. Bytnerowicz, J. L. Yee, and W. I. Boarman. 2005. Atmospheric dry deposition in the vicinity of the Salton Sea, California - II: Measurement and effects of an enhanced evaporation system. *Atmospheric Environment* **39**:4681-4689.
- Alonso, R., M. J. Arbaugh, A. Bytnerowicz. 2003. Forest health research on a natural air pollution gradient in the San Bernardino Mountains, southern California, *Ekologia* (Bratislava), **22**: 18-23.

- Baumgardner, R. E., T. F. Lavery, C. M. Rogers, and S. S. Isil. 2002. Estimates of the atmospheric deposition of sulfur and nitrogen species: Clean air status and trends network, 1990-2000. *Environmental Science & Technology* **36**:2614-2629.
- Bobbink, R., M. Hornung, and J. G. M. Roelofs. 1998. The effects of air-borne nitrogen pollutants on species diversity in natural and semi-natural European vegetation. *Journal of Ecology* **86**:717-738.
- Bowman, W. D., and H. Steltzer. 1998. Positive feedbacks to anthropogenic nitrogen deposition in Rocky Mountain Alpine tundra. *Ambio* **27**:514-517.
- Brooks, M. L. 1999a. Alien annual grasses and fire in the Mojave Desert. *Madroño* **46**:13-19.
- Brooks, M. L. 1999b. Habitat invasibility and dominance by alien annual plants in the western Mojave Desert. *Biological Invasions* **1**:325-337.
- Brooks, M. L. 2000. Competition between alien annual grasses and native annual plants in the Mojave Desert. *American Midland Naturalist* **144**:92-108.
- Brooks, M. L. 2003. Effects of increased soil nitrogen on the dominance of alien annual plants in the Mojave Desert. *Journal of Applied Ecology* **40**:344-353.
- Brooks, M. L. 2006. Spatial and Temporal Distribution of Non-native Plants in the Mojave Desert. *In* R.H. Webb, L.F. Fenstermaker, J.S. Heaton, D.L. Hughson, E.V. McDonald, and D.M. Miller, eds. *The Mojave Desert: Ecosystem Processes and Sustainability*. University of Arizona Press, Tucson.
- Brooks, M. L., C. M. D'Antonio, D. M. Richardson, J. B. Grace, J. E. Keeley, J. M. DiTomaso, R. J. Hobbs, M. Pellant, and D. Pyke. 2004. Effects of invasive alien plants on fire regimes. *Bioscience* **54**:677-688.

- Brooks, M. L. and T. C. Esque. 2002. Alien annual plants and wildfire in desert tortoise habitat: status, ecological effects, and management. *Chelonian Conservation Biology* **4**:330-340.
- Brooks, M. L. and R. A. Minnich. In press. Fire in the Southeastern Desert Bioregion. Chapter 16 *in*: Sugihara, N. G., J. W. van Wagendonk, J. Fites-Kaufman, K. E. Shaffer, and A. E. Thode (eds.). *Fire in California ecosystems*. University of California Press, Berkeley.
- Bytnerowicz, A., J. J. Carroll, B. Takemoto, P. R. Miller, M. E. Fenn, and R. C. Musselman. 2000. Distribution and transport of air pollutants to vulnerable California ecosystems. Pages 93-118 *in* K. M. Scow, G. E. Fogg, D. E. Hinton, and M. J. Johnson, editors. *Integrated Assessment of Ecosystem Health*. Lewis Publishers, Boca Raton, FL.
- Bytnerowicz, A., P. R. Miller, and D. M. Olszyk. 1987. Dry deposition of nitrate, ammonium and sulfate to a *Ceanothus crassifolius* canopy and surrogate surfaces. *Atmospheric Environment* **21**:1749-1757.
- Bytnerowicz, A., D. M. Olszyk, C. A. Fox, P. J. Dawson, G. Kats, C. L. Morrison, and J. Wolf. 1988. Responses of desert annual plants to ozone and water stress in an in situ experiment. *Journal of Air Pollution Control Association*, **38**:1145-1151.
- Bytnerowicz, A., P. E. Padgett, M. J. Arbaugh, D. R. Parker, and D. P. Jones. 2001. Passive sampler for measurement of atmospheric nitric acid vapor (HNO₃) concentrations. *TheScientificWorld* **1** (S2): 433-439.
- CASTNET (Clean Air Status and Trends Network). 2005.
<http://www.epa.gov/castnet/sites/jot403.html>

- DeFalco, L. A., J. K. Detling, C. R. Tracy, and S. D. Warren. 2001. Physiological variation among native and exotic winter annual plants associated with microbiotic crusts in the Mojave Desert. *Plant and Soil* **234**:1-14.
- Edinger, J. G., M. H. McCutchan, P. R. Miller, B. C. Ryan, M. Schroeder, and J. V. Behar. 1972. Penetration and duration of oxidant air pollution in the South Coast Air Basin of California. *Journal of the Air Pollution Control Association* **22**:881-886.
- Fenn, M. E., J. S. Baron, E. B. Allen, H. M. Rueth, K. R. Nydick, L. Geiser, W. D. Bowman, J. O. Sickman, T. Meixner, D. W. Johnson, and P. Neitlich. 2003a. Ecological effects of nitrogen deposition in the western United States. *Bioscience* **53**:404-420.
- Fenn, M. E., G. S. Haeuber, J. S. Tonnesen, J. S. Baron, S. Grossman-Clarke, D. Hope, D. A. Jaffe, S. Copeland, L. Geiser, H. M. Rueth, and J. O. Sickman. 2003b. Nitrogen emissions, deposition and monitoring in the western United States. *Bioscience* **53**:391-403.
- Fenn, M. E., M. A. Poth, J. D. Aber, J. S. Baron, B. T. Bormann, D. W. Johnson, A. D. Lemly, S. G. McNulty, D. E. Ryan, and R. Stottlemyer. 1998. Nitrogen excess in North American ecosystems: Predisposing factors, ecosystem responses, and management strategies. *Ecological Applications* **8**:706-733.
- Fenn, M. E., J. O. Sickman, A. Bytnerowicz, D. W. Clow, N. P. Molotch, J. E. Pleim, G. S. Tonnesen, K. C. Weathers, P. E. Padgett, and D. H. Campbell. submitted. Methods for measuring atmospheric nitrogen deposition inputs in arid and montane ecosystems of western North America. *in* A. H. Legge, editor. *Developments in Environmental*

Science: Relating Atmospheric Source Apportionment to Vegetation Effects:
Establishing Cause Effect Relationships. Elsevier, Amsterdam.

Hickman, J.C., editor. 1993. The Jepson manual: higher plants of California. University
of California Press, Berkeley.

Joshua Tree National Park 2004. Strategic Plan.

<http://www.nps.gov/jotr/manage/strategic/externals.html>

Koutrakis, P., J. M. Wolfson, A. Bunyaviroch, S. E. Froehlich, K. Hirano, and J. D.

Mulik. 1993. Measurement of ambient ozone using a nitrite-coated filter. *Analytical
Chemistry* **65**:209-214.

Padgett, P. E., and E. B. Allen. 1999. Differential responses to nitrogen fertilization in
native shrubs and exotic annuals common to Mediterranean coastal sage scrub of
California. *Plant Ecology* **144**:93-101.

Padgett, P. E., E. B. Allen, A. Bytnerowicz, and R. A. Minich. 1999. Changes in soil
inorganic nitrogen as related to atmospheric nitrogenous pollutants in southern
California. *Atmospheric Environment* **33**:769-781.

Pastor, J., J. D. Aber, C. A. Mcclaugherty, and J. M. Melillo. 1984. Above-ground
production and N and P cycling along a nitrogen mineralization gradient on
Blackhawk Island, Wisconsin. *Ecology* **65**:256-268.

Salo, L. F., G. R. McPherson, and D. G. Williams. 2005. Sonoran desert winter annuals
affected by density of red brome and soil nitrogen. *American Midland Naturalist*
153:95-109.

Sawyer, J. O. and T. Keeler-Wolf. 1995. A manual of California vegetation. California
Native Plant Society, Sacramento, California.

- Stevens, C. J., N. B. Dise, J. O. Mountford, and D. J. Gowing. 2004. Impact of nitrogen deposition on the species richness of grasslands. *Science* **303**:1876-1879.
- Sullivan, T. J., C. L. Peterson, C. L. Blanchard, and S. J. Tanenbaum. 2001. Assessment of quality and air pollutant impacts in class I national parks of California. Unpublished report. National Park Service-Air Resources Division.
- Theodose, T. A., and W. D. Bowman. 1997. Nutrient availability, plant abundance, and species diversity in two alpine tundra communities. *Ecology* **78**:1861-1872.
- Thompson, C. R., D. M. Olszyk, G. Kats, A. Bytnerowicz, P. J. Dawson, and J. W. Wolf. 1984. Effects of ozone or sulfur-dioxide on annual plants of the Mojave Desert. *Journal of the Air Pollution Control Association* **34**:1017-1022.
- Tonnesen, G. S., Z. Wang, M. Omary, and C. J. Chien. 2003. Formulation and application of regional air quality modeling for integrated assessments of urban and wildland pollution. Pages 285-298 in A. Bytnerowicz, M. J. Arbaugh, and R. Alonso, editors. *Ozone air pollution in the Sierra Nevada: distribution and effects on forests*. Elsevier Press, Amsterdam.
- Trent, D. D. 1984. Geology of the Joshua Tree National Monument. *California Geology* **37**: 75-86.
- Walvoord, M. A., F. M. Phillips, D. A. Stonestrom, R. D. Evans, P. C. Hartsough, B. D. Newman, and R. G. Striegl. 2003. A reservoir of nitrate beneath desert soils. *Science* **302**:1021-1024.
- Wood, Y.A., T. Meixner, P.J. Shouse, and E.B. Allen. 2006. Altered ecohydrologic response drives native shrub loss under conditions of elevated N-deposition. *Journal of Environmental Quality* **35**: 76-92.

- Yoshida, L. C., and E. B. Allen. 2001. Response to ammonium and nitrate by a mycorrhizal annual invasive grass and native shrub in southern California. *American Journal of Botany* **88**:1430-1436.
- Yoshida, L. C., and E. B. Allen. 2004. N-15 uptake by mycorrhizal native and invasive plants from a N-enriched shrubland: a greenhouse experiment. *Biology and Fertility of Soils* **39**:243-248.

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 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 m² quadrats at four sites under two N fertilization levels and an unfertilized control in 2004. All are annual forbs except *C. ramossisimum* (shrub) and *P. secunda* (perennial grass). 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
<i>Chaenactis fremontii</i>		1.3		3.7	2.2	1.9						
<i>Chaenactis stevioides</i>							2.6	4.3	3.8		1.7	1.9
<i>Chamaesyce polycarpa</i>				1.2								
<i>Coleogyne ramosissima</i>								2.2				
<i>Cryptantha angustifolia</i>				6.6	4.9	8.2						
<i>Cryptantha pterocarya</i>							1.5	3.2	4.8			2.9
<i>Descurainia pinnata</i>							2.3	3.0	4.0			
<i>Gilia stellata</i>							1.5	1.1	1.6			
<i>Malacothrix glabrata</i>				2.5	2.0	2.0						
<i>Mentzelia affinis</i>										1.2	3.3	
<i>Mirabilis californica</i>												1.6
<i>Pectocarya recurvata</i>				1.5	1.5	1.4						
<i>Phacelia distans</i>								2.4	2.9	4.5	4.8	5.8
<i>Poa secunda</i>												1.1
<i>Salvia columbariae</i>	8.3										1.4	

Native species with < 1% cover

Shrubs (20 species): *Adenophyllum porophylloides*, *Brickellia californica*,
Chrysothamnus nauseosus, *Echinocereus engelmannii*, *Ephedra nevadensis*, *Eriogonum fasciculatum*, *E. wrightii*, *Eriophyllum confertiflorum*, *Gutierrezia microcephala*, *G. sarothrae*, *Hymenoclea salsola*, *Juniperus californica*, *Lycium andersonii*, *Nolina parryi*, *Opuntia erinacea*, *Purshia tridentata*, *Quercus cornelius-mulleri*, *Salazaria mexicana*, *Viguiera parishii*, *Yucca schidigera*

Perennial grasses (4): *Achnatherum lettermanii*, *A. speciosum*, *Elymus elymoides*,
Erioneuron pulchellum

Annual grass (1): *Aristida adscensionis*

Annual forbs (56): *Amsinckia tessellata*, *Anisocoma acaulis*, *Calycocercis parryi*,
Calyptridium monandrum, *Camissonia californica*, *C. campestris*, *C. claviformis*, *C. pallida*, *Castilleja angustifolia*, *Caulanthus cooperi*, *Centrostegia thurberi*, *Chaenactis macrantha*, *Chorizanthe brevicornu*, *Crassula connata*, *Cryptantha barbiger*, *C. circumscissa*, *C. maritima*, *C. micrantha*, *C. nevadensis*, *C. utahensis*, *Draba cuneifolia*,
Eriastrum diffusum, *Eriogonum davidsonii*, *E. maculatum*, *E. nidularium*, *E. pusillum*,
Eriophyllum wallacei, *Eschscholzia minutiflora*, *Eucrypta chrysanthemifolia*, *Filago arizonica*, *F. depressa*, *Layia glandulosa*, *Lepidium lasiocarpum*, *Linanthus aureus*, *L. 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*, *Stephanomeria exigua*,
Syntrichopappus fremontii, *Thysanocarpus curvipes*, *Uropappus lindleyi*

Perennial forbs (16): *Allium parishii*, *Arabis pulchra*, *Arenaria macradenia*, *Astragalus bernardianus*, *A. lentiginosus*, *A. nuttallianus*, *Calochortus kennedyi*, *Chamaesyce albomarginata*, *Delphinium parishii*, *Dichelostemma capitatum*, *Dudleya saxosa*, *Eriogonum inflatum*, *Lomatium mohavense*, *Lotus argophyllus*, *L. rigidus*, *Sphaeralcea ambigua*

Nomenclature from Hickman (1993).

Figure captions

Figure 1. Map of air, soil, and vegetation sample sites at Joshua Tree National Park. The N fertilization experiments were carried out at the sites indicated with triangles (Table 1). Passive air samplers and soil samples were taken from all sites in the Park, and soils samples were also taken from two sites outside the Park to the west.

Figure 2. Two week-long average nitric acid concentration ($\mu\text{g}/\text{m}^3$) in the atmosphere over Joshua Tree National Park in A) winter and B) summer, 2004 (dates on graphs show start of sampling).

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

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

Figure 5. Extractable soil N as NH_4^+ and NO_3^- in 14 sites in Joshua Tree National Park and two sites west of the Park in July 2004 (map, Fig. 1).

Figure 6. Extractable soil N as NH_4^+ and NO_3^- in plots fertilized with NH_4NO_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).

Figure 7. Dry weight of exotic grass in Mar-Apr 2004 following N fertilization at 5 and 30 kg/ha at four sites. Exotic grasses were primarily *Schismus barbatus* at Wide Canyon and Pinto Wash, and *Bromus madritensis* at Covington Flat and Pine City. Different letters above bars indicate significantly different at $p = 0.05$.

Figure 8. Percent cover of exotic species and native herbaceous species in Mar-Apr 2004 following N 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 $p = 0.05$.

Figure 9. Richness (number/0.5m²) of native herbaceous species in Mar-Apr 2004 following N 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 $p = 0.05$.



Figure 1

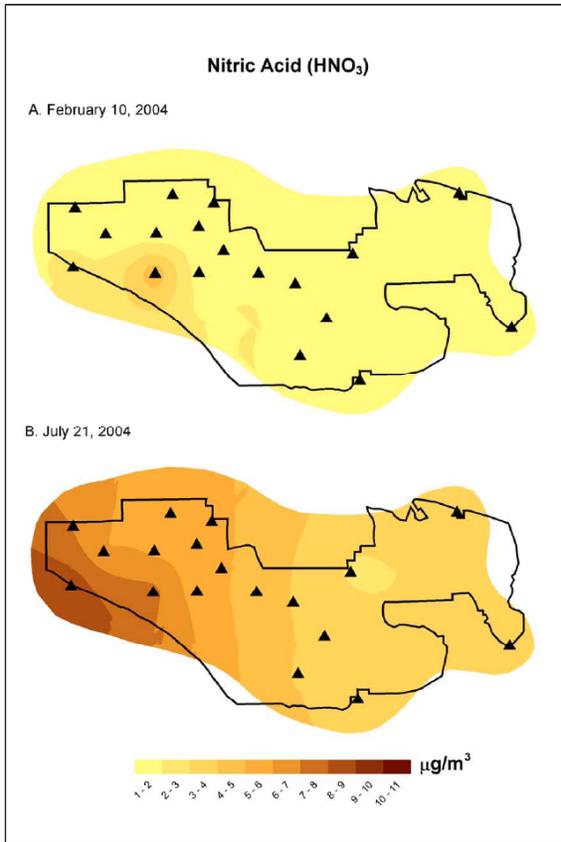


Figure 2

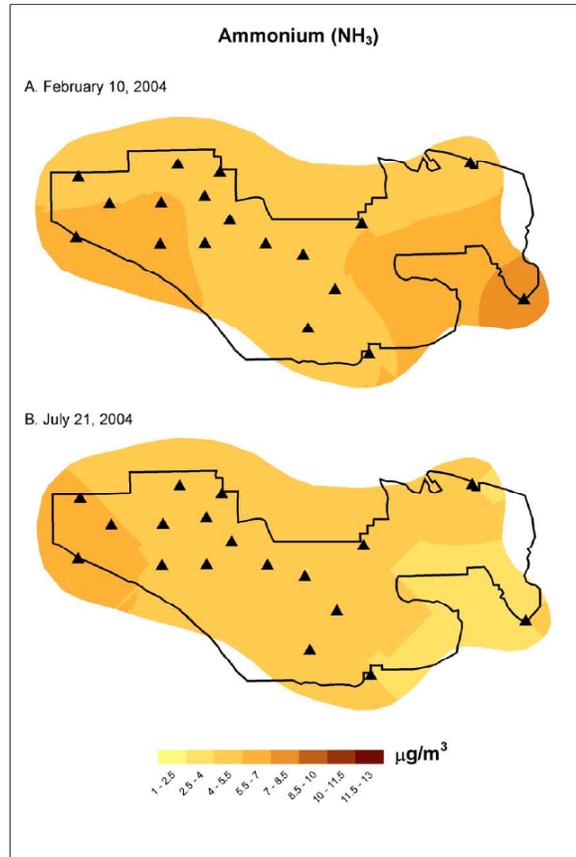


Figure 3

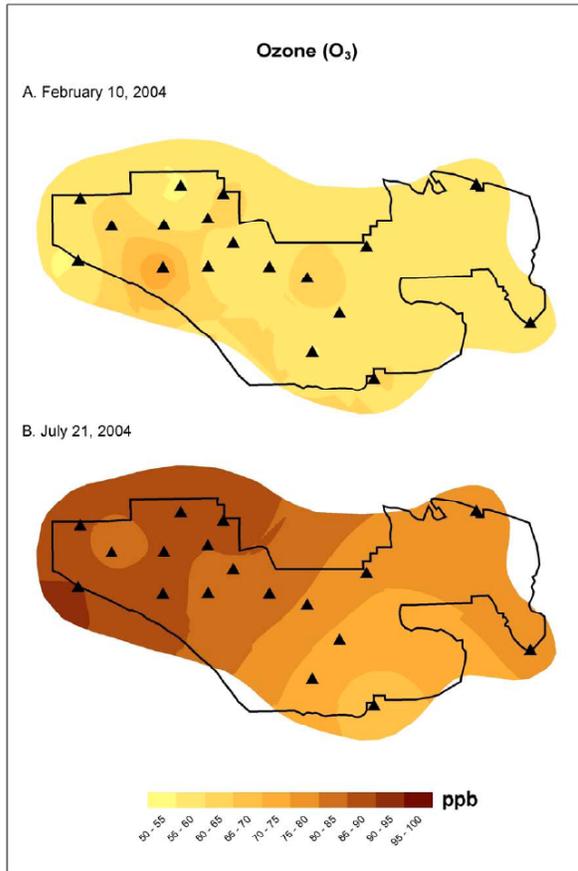


Figure 4

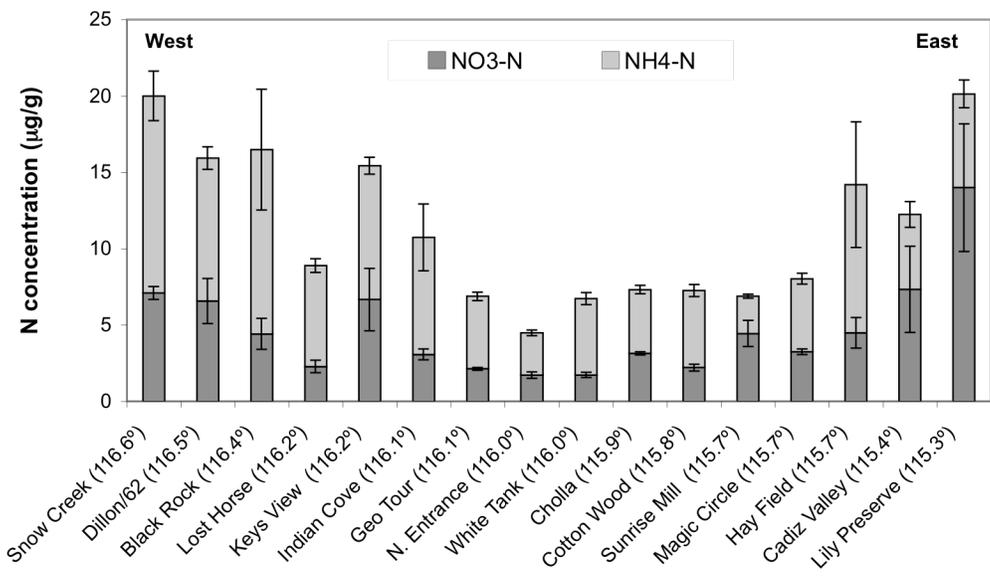


Figure 5

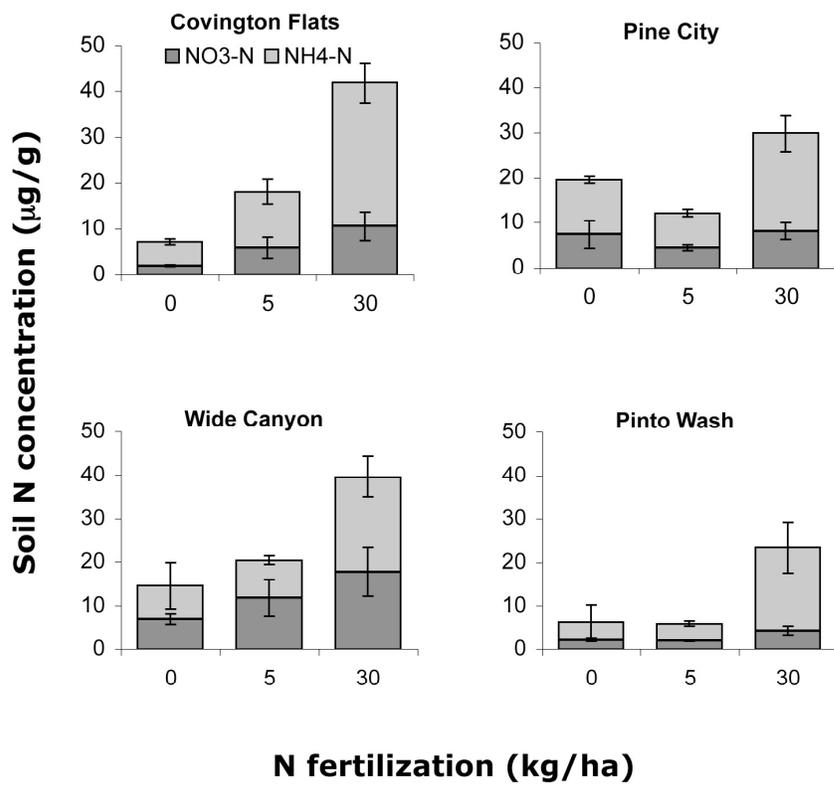


Figure 6

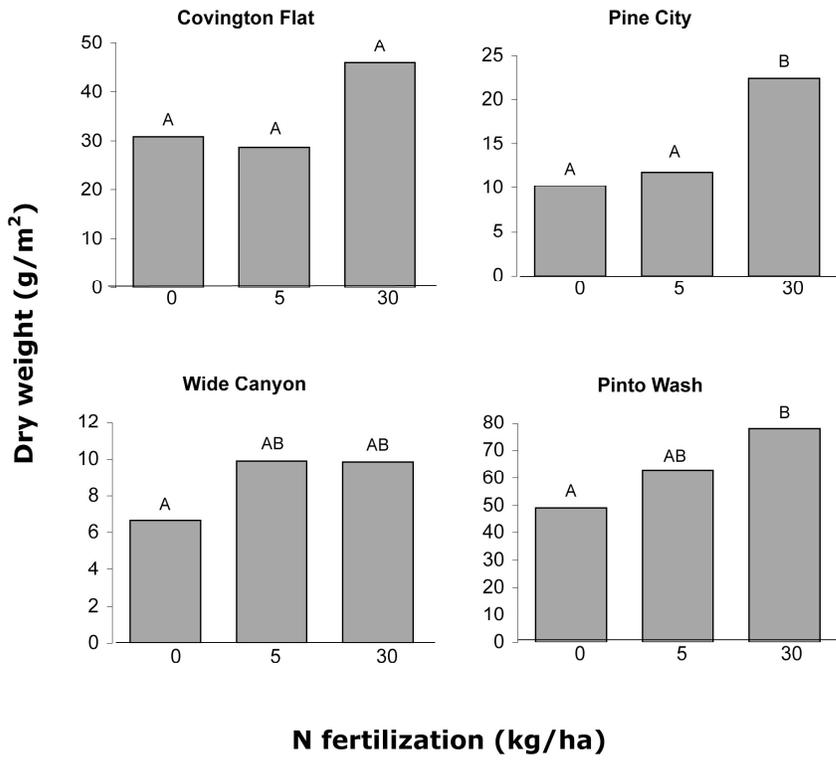


Figure 7

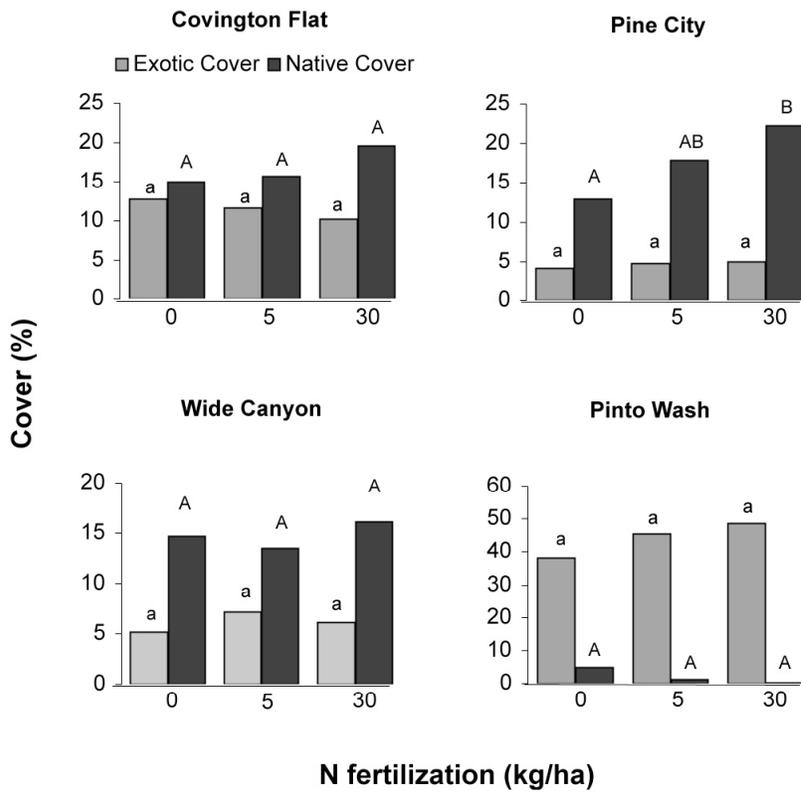


Figure 8

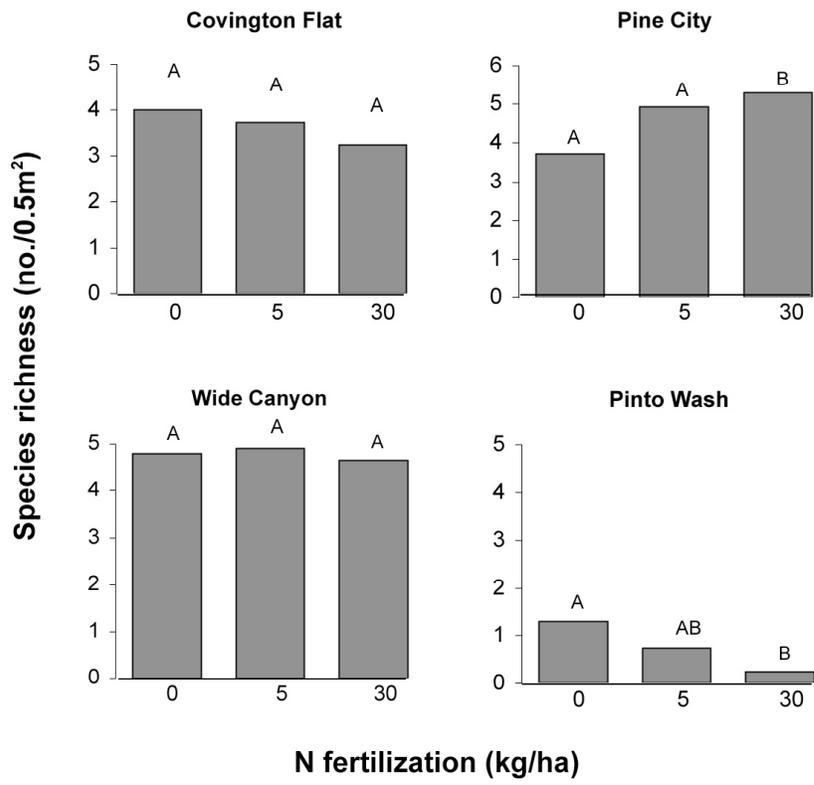


Figure 9