

Nitrogen mineralization across an atmospheric nitrogen deposition gradient in Southern California deserts

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ABSTRACT

Dry nitrogen deposition is common in arid ecosystems near urban and agricultural centers, yet its impacts on natural environments are relatively understudied. We examined the effects of N deposition on soil N mineralization across a depositional gradient at Joshua Tree National Park. We hypothesized that N deposition affects N mineralization by promoting exotic grass invasion and increasing soil carbon and nitrogen. These relationships were tested through a laboratory incubation on soils collected from sixteen sites where atmospheric N, soil characteristics, and annual vegetation were measured. Mineralization parameters modeled using the Gompertz model were compared to soil C, soil N, estimated soil N from deposition, and percent cover of exotic and native annuals. Calculated soil N from deposition was directly correlated with measured soil C and N and decreasing C:N ratios, which were associated with increased total amounts of mineralized N. However, no effects of soil C or N, and thus N deposition, were observed on mineralization rates. Exotic grasses, but not native forbs or total annual cover, increased with soil C, soil N, and total mineralized N, suggesting that exotic grasses and N deposition are correlated and associated with increasing total C and N in the interspace soils at polluted locations.

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1. Introduction

Nitrogen inputs to ecosystems around the world have increased dramatically over the last four decades and have had well documented impacts on natural systems (Devitt and Smith, 2002; Egerton-Warburton and Allen, 2000; Fenn et al., 1998; Holland et al., 1999; Krupa, 2003). Urban areas such as Los Angeles may receive as much as 30 kg-N ha⁻¹ yr⁻¹, with natural areas as far as 225 km downwind receiving up to 12 kg ha⁻¹ yr⁻¹ (Fenn et al., 2003b; Sullivan et al., 2001; Tonnesen et al., 2007). Due to seasonal and infrequent precipitation in the arid and semi-arid southwest, most N deposition occurs as dry deposition and accumulates on the soil surfaces during the summer (Padgett et al., 1999). With the first rains of the fall season, a pulse of N moves into the soil providing a fertilization effect for the plant species that are first to germinate. Because production in arid systems is considered precipitation limited and N regulated (Gutierrez, 1992; Gutierrez and Whitford, 1987; Ludwig, 1987), this fertilization effect can have dramatic impacts on plant communities and soil processes (Allen et al., 2009;

Fenn et al., 2003a; Hooper and Johnson, 1999). However, the effects of N deposition on mineralization and consequently the N supply to plants are not straightforward, with studies showing increased or even decreased rates of litter decomposition (Knorr et al., 2005).

Nitrogen mineralization, the microbially mediated release of inorganic N from soil organic matter, is primarily influenced by soil moisture, temperature, and organic matter quality (Fisher et al., 1987; Nunez et al., 2001; Sierra, 1997). In arid systems microbial activity is often limited by moisture (Austin et al., 2004), followed by available carbon and nitrogen (Schaeffer et al., 2003). However, assuming adequate moisture and temperature, it is the soil organic matter quantity and quality (i.e., C:N and lignin:N) that regulates the amount and rapidity of N mineralization such that organic matter that is high in N content has greater N mineralization than organic matter that is low in N content (Burke, 1989; Charley and West, 1977; Lajtha and Schlesinger, 1986). Because many arid land annual plants have been shown to increase tissue %N under N fertilization (Brooks, 2003; DeFalco et al., 2003; Romney et al., 1974; Yoshida and Allen, 2001), it is likely that N deposition will increase mineralization rates by increasing N content in plant tissues and soil organic matter over time.

Exotic annual grasses have spread across the Mojave and Sonoran Deserts (Brooks, 2000a,b) and are associated with increased fire

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frequency and decreased success of native annuals (Allen et al., 2009; Brooks, 1999; DeFalco et al., 2003). These grasses may also be promoted by N deposition as demonstrated by greenhouse N fertilization studies with *Bromus madritensis*, which show that this exotic grass takes up N more rapidly than native species and produces greater biomass (DeFalco et al., 2003; Yoshida and Allen, 2004). Field N fertilization experiments show that under some conditions both exotic grasses *B. madritensis* and *Schismus barbatus* increased biomass production (Allen et al., 2009; Gutierrez et al., 1992). Studies on *Bromus tectorum*, which has invaded the northern Mojave, have shown that N mineralization rates are affected by *B. tectorum* invasion due to their production of large amounts of litter (Booth et al., 2003) and higher C:N and lignin:N ratios when compared to native grasses (Evans et al., 2001). By promoting exotic grasses, N deposition may thus be having a secondary effect on N mineralization beyond increasing tissue N concentrations.

An N deposition gradient exists across Joshua Tree National Park, which spans the southwestern Mojave and western Sonoran Deserts (Allen et al., 2009). The existence of this gradient across a region with different soils, precipitation, and degree of exotic grass invasion, makes it ideal for evaluating the complex interactions that affect N mineralization. The objectives of this study are to: (1) examine potential N mineralization across an N gradient to determine effects of increased N inputs on N dynamics, and (2) determine the extent to which N supply through mineralization is correlated with exotic annual grass cover. These objectives were accomplished through a 14-week laboratory incubation of soils collected from sixteen sites in and around Joshua Tree N.P. where atmospheric N concentrations, vegetation cover, and soil properties were measured. Because microbial processes in arid systems are often limited in both C and N (Schaeffer et al., 2003) we hypothesize that long-term N deposition will increase N mineralization by increasing organic C and N content of the soils through greater production of herbaceous annuals (Allen et al., 2009) and higher N content of the annuals (Sirulnik et al., 2007).

While laboratory incubations are useful when examining soils from a large number of distant sites because they are standardized with respect to water content and temperature (Barrett and Burke, 2000), distant sites may have different mineralization dynamics due to varied soil textures (Austin et al., 2004; Bechtold and

Naiman, 2006). Different dynamics can be difficult to compare if the mineralization curves cannot be modeled with the same set of parameters. Thus, a third objective of this study is to determine the best model for evaluating the mineralization dynamics from the soils collected across the N deposition gradient.

2. Methods

2.1. Study area

Sixteen sites in the Joshua Tree National Park region of Southern California were chosen for this study (Fig. 1). The 321 000 ha Park is located approximately 225 km east of Los Angeles, CA and 350 km southwest of Las Vegas, NV and spans the low elevation Sonoran Desert to the high elevation Mojave Desert. The sites selected for this study are spread throughout both deserts and lie on a west to east gradient of precipitation and nitrogen deposition (Allen et al., 2009). Selected site characteristics are presented in Table 1.

Exotic grasses have invaded the entire study area to varying degrees. *B. madritensis* is most prevalent in the high elevation portions of the Park due to the requirement of this grass for higher nutrient and water supplies (Brooks, 2000a). *S. barbatus* and *Schismus arabicus* are found in all but the highest elevations of the Park and are the dominant winter season grasses in the low elevation regions.

No soil survey has been conducted for the entirety of the Park, but soils are largely granitic in origin with some basaltic parent material present at a few locations. July was chosen as the sampling time because maximum N concentrations at the surface are found during the summer in arid and semi-arid environments where atmospheric N deposition is primarily in the dry form, accumulating at the soil surface until the first rains (Fenn et al., 2003b; Padgett et al., 1999). Because this region of the Sonoran and Mojave Deserts can receive summer monsoonal precipitation beginning in mid-July, collecting soils in prior to the onset of summer rainfall provides the best opportunity for linking N deposition with mineralization.

2.2. Atmospheric nitrogen

Atmospheric N (NO, NO₂, NH₃, and HNO₃) was measured seasonally with passive samplers during 2004 and 2005 (Allen

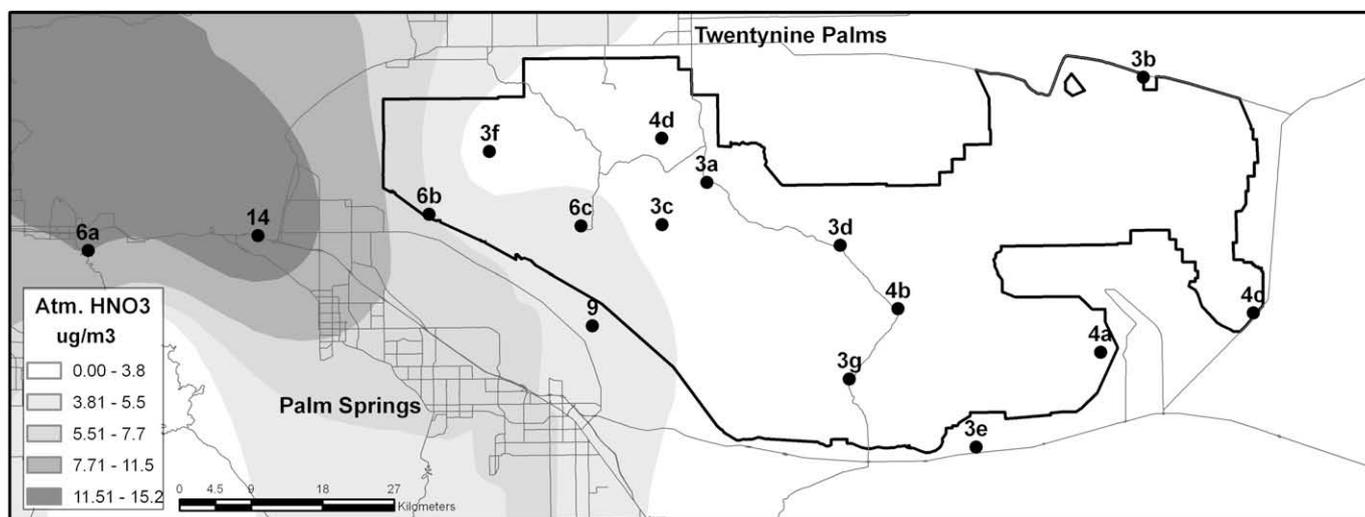


Fig. 1. Locations sampled within and around Joshua Tree National Park during July 2005. The dark line indicates the Park boundary and the thinner lines the major roads and highways in and around the Park. The cities of Palm Springs and Twenty nine Palms are noted for reference. Average atmospheric HNO₃ concentrations ($\mu\text{g m}^{-3}$) for July 2005 indicate a strong west to east gradient of the concentrations of nitrogen in the air, and thus nitrogen deposition to the soil surface. Sampling sites are labeled by the calculated annual dry N deposition values (kg-N ha^{-1}) using the inferential method, which overestimates dry deposition. Contours generated using an original kriging method with 29 data points in ArcMap.

Table 1
Selected characteristics for sites listed across the N deposition gradient from highest to lowest N deposition.

Site	Landform ^a	Bulk density (g/cm ³)	% Sand–silt–clay	pH	Vegetation type ^b	Soil rock content by mass (g g ⁻¹) ^c	Ave. precip. (cm) ^d
14	erosional highland	1.43	89–11–1	7.54	creosote bush scrub	0.01	29.95
9	erosional highland	2.08	82–15–3	7.79	creosote bush scrub	0.62	9.6
6a	erosional highland	1.21	81–18–1	6.73	transitional desert scrub	0.17	32.84
6b	bajada	1.61	88–10–2	7.1	creosote bush scrub	0.25	14.2
6c	erosional highland	1.58	83–16–2	7.12	joshua tree woodland	0.21	10.82
4a	older alluvial deposit	1.58	37–55–8	9.18	creosote bush scrub	0.4	9.7
4b	intramontane undifferentiated deposit	1.63	81–18–1	7.92	creosote bush scrub	0.29	9.58
4c	bajada	1.79	79–19–2	8.97	creosote bush scrub	0.54	9.19
4d	erosional highland	1.76	75–22–3	7.7	piñon-juniper	0.36	10.62
3a	intramontane alluvial plain	1.51	82–16–2	7.23	creosote bush scrub	0.4	10.11
3b	bajada	1.76	90–10–0	8.54	creosote bush scrub	0.12	9.35
3c	active alluvial plain	1.82	90–10–0	7.02	joshua tree woodland	0.25	9.93
3d	bajada	1.56	87–12–0	8.34	creosote bush scrub	0.09	9.93
3e	bajada/wash	1.71	85–14–1	8.45	creosote bush scrub	0.4	9.68
3f	intramontane undifferentiated deposit	1.39	88–11–1	6.81	piñon-juniper	0.17	13.87
3g	older alluvial deposit	1.77	68–28–4	8.67	creosote bush scrub	0.39	9.78

^a Landform information for each site determined from a GIS coverage based on information from the U.S. Army Topographic Engineering Center, Alexandria, VA (<http://www.mojavedata.gov>).

^b Vegetation classification from a GIS coverage of the Mojave Desert available from the Mojave Desert Ecosystem Program (<http://www.mojavedata.gov>).

^c Rock content by mass of the soil to 5 cm depth (g-rock g-total soil⁻¹).

^d Average precipitation based on a GIS coverage in which 30 years of average precipitation from weather stations in the Mojave Desert were used to estimate a continuous coverage through interpolation (<http://www.mojavedata.gov>).

et al., 2009). Atmospheric nitric acid (HNO₃) was collected on three nylon filters placed in double rings hung inside PVC caps protecting them from wind and rain (Bytnerowicz et al., 2001). Concentrations of ambient gaseous nitrogen oxides (NO and NO₂) and ammonia (NH₃) were determined with Ogawa passive samplers (Ogawa & Company USA, Inc., Pompano Beach FL). Samplers were deployed for three consecutive 2-week periods in the winter growing season and summer dry season.

The inferential method was used to calculate annual N deposition by multiplying the atmospheric concentration by the deposition velocity. Average monthly deposition velocities for the 2004–2005 growing season were obtained for the Park from the Clean Air Status and Trends Network (CASTNet) website (U.S. EPA, 2005). The National Park Service operates a CASTNet site in the northwestern portion of Joshua Tree N.P. (34.0714°N, –116.3906°W, 1244 m elevation). Although this site is high elevation piñon-juniper woodland while the majority of sampling sites are low elevation creosote bush scrub, the deposition velocities calculated for this site were applied uniformly to provide a rough estimate of dry deposition for all sites.

The average measured concentration of HNO₃ and NH₃ from the winter sampling period (March 2005) and summer sampling period (July 2005) were used to obtain an estimate of the annual dry N depositional flux. Only HNO₃ and NH₃ were used because these two pollutants dominate deposition, with HNO₃ alone comprising nearly 70% of the dry N deposition in this region (U.S. EPA, 2005). Estimated annual N deposition was converted into an estimated aerial soil concentration using measured rock content. Although deposited N from one year would not accumulate at the surface in its entirety, adjusting estimated annual deposition to an aerial fine earth fraction basis allowed for direct comparison of deposited N to other soil parameters.

2.3. Soils and vegetation

Half hectare plots (50 m × 100 m) were established at each site using the air sampler as the center of the plot. In July 2005, five soil samples from each plot were collected to a 5 cm depth from the interspace areas between shrubs or trees and bulked for use in the mineralization incubation, soil chemistry analyses, and particle size analysis. Interspace soils are used because these soils are nutrient poor and should elicit the greatest winter annual response with N

fertilization. Bulk soil samples were used in order to generally characterize the interspaces soils at each site, where each site was used as an individual data point in subsequent analyses.

Soil samples were analyzed for total percent N and C by combustion (Thermo-Finnigan, Bremen, Germany), soil pH, and particle size analysis by hydrometer (Day, 1965). A small number of sites (4) were later found to contain minor amounts of carbonates, and so post-hoc inorganic C content was determined by mass loss after treatment with 2 N HCl (Allison and Moodie, 1965) to allow for subtraction of carbonate-C from the total C values providing an estimate of organic C in the soil.

The sixteen sites were sampled for percentage of rock in the soil by mass and volume, and bulk density. At four locations along a 50 m transect in the center of the plot a 25 cm diameter hole was dug to a depth of 5 cm, the volume of the hole measured, and the material from the hole transported to the lab for rock and soil density determination (Poesen and Lavee, 1994).

Percent cover of exotic annual grass and native annual forbs in interspaces was estimated in July from the dry material present in the 0.5 ha plot using the relevé method (Knapp, 1984). Because sampling was conducted prior to the onset of the summer monsoons, the dried annual plants had not yet degraded and percent cover values compared well with data collected in May when the annuals were still green (Allen et al., 2009). Both exotic grasses and native forbs were measured to determine the total cover of annual plants in the interspaces at each site because the amount of total plant cover influences the amount of soil carbon and thus available substrate for N mineralization (Fisher et al., 1987; Nunez et al., 2001). Native annual grasses are extremely sparse and exotic forbs (primarily *Erodium cicutarium*) were infrequent and low in cover and not included in the analysis. The percent cover estimate from each site was treated as an individual point sample in the statistical analyses.

2.4. Nitrogen mineralization

2.4.1. Laboratory incubation

Methods for the mineralization incubation were based on those used by the Long-Term Ecological Research program (Robertson et al., 1999). Field dry composite soil samples were stored at 4 °C until analysis. After sieving to remove rock fragments >2 mm, the

moisture content of the soils was brought up to 60% water filled pore space (WFPS) with deionized water. Despite the sandy nature of these soils, 60% WFPS was found to be sufficient to wet the soils thoroughly without resulting in excess standing water. Three replicate samples were extracted immediately for initial inorganic N determination and the remaining samples covered with air-permeable polyethylene film and incubated at 25 °C for 98 days. Eight times during the incubation, three replicate samples were extracted for inorganic N. Extractable NH_4^+ and NO_3^- were determined colorimetrically (Technicon Instruments Corp., Tarrytown, NY).

2.4.2. Mineralization models

The amount of N mineralized at time t (N_{\min}) was calculated by subtracting the average initial extractable N concentration from the average amount of NH_4^+ + NO_3^- measured at time t from each site's soils. Common mineralization models (first order and double exponential or two pool model) were initially employed to model the nitrogen mineralized in the soils from each site. However, eleven of the sixteen soils exhibited a pronounced lag phase lasting up to several weeks and so were not capable of being fit with either of the common models. Thus, three mineralization models capable of modeling lagged data were chosen for further evaluation and were compared to the first order model. The four models examined were:

- 1) First order $N_{\min} = N_0(1 - e^{-kt})$ (Stanford and Smith, 1972)
- 2) Consecutive reaction $N_{\min} = N_0 - N_0e^{-kt}(kt + 1)$ (Ellert and Bettany, 1988)
- 3) Mixed order $N_{\min} = N_0(1 - e^{-k_1t - 0.5k_2t^2})$ (Brunner and Focht, 1984)
- 4) Gompertz $N_{\min} = N_0e^{-he^{-kt}} - N_0e^{-h}$ (France and Thornley, 1984)

In these models, N_0 is the mineralization potential, k is the mineralization rate constant, and h is the proportionality constant.

The models were run using the SAS nonlinear modeling procedure, method Marquardt for correlated coefficients (SAS Institute Inc., Cary, NC 1999). The goodness-of-fit of the models was compared using a calculated R^2 and an F_{extra} statistic. R^2 was calculated by dividing the model's residual sums of squares by the corrected total sums of squares and subtracting the quotient from one. F_{extra} was used to determine if a model was significantly improved by adding an additional parameter and was calculated according to Draper and Smith (1981) and in the manner applied by Ellert and Bettany (1992). Here, the F_{extra} was used to compare the three parameter models (mixed order and Gompertz) to the two parameter models (single exponential and consecutive reaction). The model with the best fit across both lagged and unlagged data was used in all subsequent comparisons to site-specific soil, vegetation, and atmospheric data.

2.5. Statistical analyses

Prior to statistical analyses, the soil N, C, and mineralized N were converted to an aerial fine earth basis using the average percent rock content by mass, bulk density, and sampling depth from each site. Given that the annual plants only have access to the biologically active fine earth fraction of the soil, accounting for variations in rock content allows for site-specific comparisons of plant-available nutrients.

All statistical analyses were conducted using the JMP 6.0 statistical software package (SAS Institute Inc., Cary, NC 2006). Parameters were transformed prior to analysis to meet assumptions of the statistical tests employed. Percent data were arcsine transformed and most other data were natural log or negative inverse transformed. Parameters were compared using Pearson product-moment correlation

(parametric), Kendall's τ rank correlation (nonparametric), and linear regression. Results were deemed significant at an α -level of 0.05.

3. Results

3.1. Model selection

The R^2 and F_{extra} values calculated for each site and model were compared to determine the best model for all sites (see Appendix A for details on model parameterizations and fits). Briefly, the R^2 values indicate that the Gompertz model fits the lagged data as well as or better than the consecutive reaction model and also fits the unlagged data as well as or better than the first order model (Fig. 2). The F_{extra} statistics show that the Gompertz model is better than the first order model in the eleven soils where the data is lagged and better than the consecutive reaction model for the five sites where the data is not lagged. Given these results, the Gompertz model was deemed the most appropriate model for these data and the parameterization from this model used in subsequent analyses.

The Gompertz proportionality constant h , which governs the shape of the curve, and the rate parameter k are highly correlated ($r = 0.79$, $P = 0.0003$). Because of this correlation it is not possible to compare k alone to the soil and vegetation characteristics at the sixteen sites. Instead, a parameter that is a function of both h and k , such as the time needed to produce 50% of the mineralized N (mineralization half-life), is more appropriate. The mineralization half-life, $t_{0.5}$, is directly calculated from both h and k . The approximate standard error for $t_{0.5}$ was calculated using the SE values estimated for h and k (Table 2).

The model results indicate a large variation in the N mineralization potential (N_0) among the sixteen sites with a coefficient of variation (CV) of 55.0% (Table 2). In over a third of the sites the modeled N_0 was between 20 and 70% greater than the actual amounts of N mineralized during the 14-week incubation ($N_{\min(t)}$). In these cases the estimated standard error around N_0 is also large and so given this uncertainty, the actual $N_{\min(t)}$ was used instead of N_0 for comparison to environmental parameters in all subsequent analyses. There are few differences between the sites in $t_{0.5}$ (mean = 4.66 weeks, SE = 0.17, CV $t_{0.5}$ = 14.88%).

3.2. Nitrogen deposition and mineralization

Predicted annual dry N deposition ranged from 2.8 to 14.4 $\text{kg-N ha}^{-1} \text{yr}^{-1}$ (Table 3), and was not correlated with average annual precipitation (Kendall's $\tau = 0.24$, $P = 0.19$). The amount of inorganic N extracted from the soils prior to the mineralization incubation (Table 3) was correlated with the amount of N in the soil predicted from dry N deposition ($r = 0.67$, $P = 0.004$), although the July extractable soil N concentrations were approximately 25% smaller (Fig. 3). There is a highly significant positive relationship between $N_{\min(t)}$ and July extractable N ($R^2 = 0.82$, $P < 0.0001$), indicating a strong relationship between the dry N deposition proxy of summer extractable soil N and N mineralization (Fig. 3).

Regression of measured total N against the predicted content of N in the soil from one year of dry deposition shows that deposition is directly related to the observed total soil N content (Fig. 4; $R^2 = 0.35$, $P = 0.015$). The total amount of C also increases with increasing deposition ($R^2 = 0.32$, $P = 0.023$) at a rate similar to that of total N, leading to a slight, but non-significant, decrease in the C:N ratio with increasing deposition ($R^2 = 0.22$, $P = 0.070$). As the C:N ratio decreases $N_{\min(t)}$ increases ($R^2 = 0.31$, $P = 0.024$) although there is no effect of the decreasing C:N ratio on $t_{0.5}$ ($R^2 = 0.18$, $P = 0.10$). Examining the effects of C and N alone on mineralization we find an increase in $N_{\min(t)}$ with increasing C ($R^2 = 0.63$,

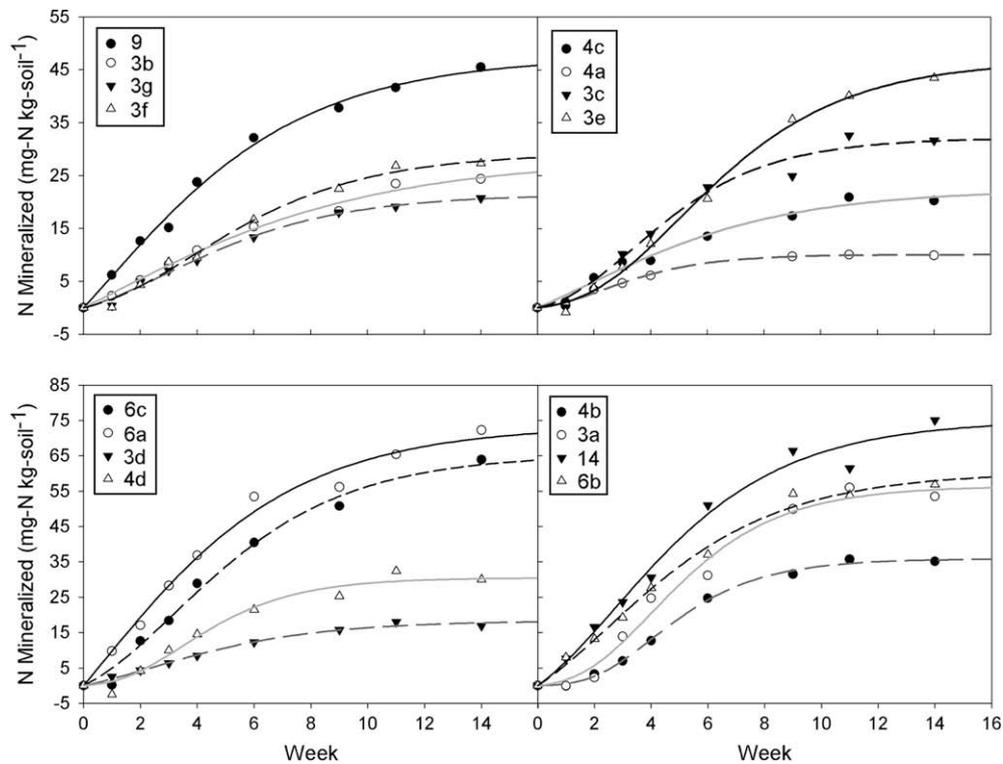


Fig. 2. Results from the mineralization incubation from the soils collected at sixteen sites across an N deposition gradient around Joshua Tree National Park. Each point represents an average of three replicates sampled at each time interval. Lines through each set of points are the results from the Gompertz modeling runs. The shapes of the mineralization curves ranged from first order exponential (e.g., 6a) to sigmoidal (e.g., 4b) in nature. Only the Gompertz model was able to adequately capture this range of curve shapes (Appendix A).

$P=0.0003$) and increasing N ($R^2=0.67$, $P<0.0001$), but no significant effects either on $t_{0.5}$ (Fig. 5).

3.3. N mineralization and cover of annuals

There is no relationship between annual vegetation cover and the mineralization half-life, but a positive correlation is observed between the Gompertz model shape parameter, h , and exotic grass cover ($r=0.50$, $P=0.050$). Exotic grass cover is positively correlated

with $N_{\min(f)}$ (Fig. 6; $r=0.61$, $P=0.012$). While regression lines are presented in Fig. 6, it is impossible to determine if changes in mineralization are due to an increase in exotic grass cover or if exotic grasses are increasing in response to greater soil N supply and so only correlations are considered appropriate. There appears to be a negative association between $N_{\min(f)}$ and native forb cover (Fig. 6; $r=-0.30$, $P=0.26$) although this relationship is not significant. Cover of exotic grasses and native forbs are significantly negatively correlated ($r=-0.53$, $P=0.034$) and exotic grass cover is

Table 2
Gompertz model parameterization from the mineralization incubation data.

Site	$N_{\min(f)}$ (mg kg ⁻¹) ^a	N_0 (mg kg ⁻¹) ^b	h^c	k^d	$t_{0.5}^e$	Lower bound	Upper bound	Approx. SE
14	75.13	83.666 (13.098)	2.277 (0.888)	0.298 (0.078)	4.498	2.876	7.183	2.154
9	45.454	67.303 (19.580)	1.223 (0.588)	0.243 (0.057)	4.249	2.873	6.485	1.806
6a	72.262	105.600 (45.431)	1.195 (0.852)	0.252 (0.084)	4.076	2.333	7.61	2.638
6b	56.862	69.217 (9.080)	2.058 (0.623)	0.289 (0.057)	4.431	3.176	6.263	1.544
6c	63.943	70.730 (8.444)	2.591 (0.805)	0.294 (0.066)	4.859	3.335	7.174	1.919
4a	9.899	10.490 (0.647)	3.178 (0.990)	0.497 (0.093)	3.184	2.23	4.49	1.13
4b	35.14	35.927 (0.706)	6.637 (0.862)	0.471 (0.035)	4.801	4.203	5.457	0.627
4c	20.288	28.470 (9.847)	1.539 (0.968)	0.244 (0.091)	4.618	2.524	9.169	3.323
4d	30.022	30.754 (2.234)	4.817 (1.995)	0.454 (0.117)	4.299	2.615	6.781	2.083
3a	53.514	56.863 (3.810)	4.949 (1.595)	0.399 (0.084)	4.949	3.365	7.136	1.886
3b	24.366	41.341 (19.119)	1.152 (0.767)	0.180 (0.069)	5.628	3.193	11.137	3.972
3c	31.645	33.044 (2.812)	3.591 (1.223)	0.377 (0.088)	4.473	2.944	6.742	1.899
3d	16.883	21.088 (2.843)	2.059 (0.661)	0.302 (0.061)	4.229	2.985	6.066	1.54
3e	40.688	47.250 (2.049)	4.687 (0.617)	0.307 (0.031)	6.263	5.306	7.391	1.042
3f	27.289	30.637 (2.377)	3.094 (0.750)	0.293 (0.055)	5.324	3.905	7.312	1.703
3g	20.684	23.651 (2.713)	2.386 (0.604)	0.294 (0.052)	4.661	3.462	6.331	1.434

^a $N_{\min(f)}$, final amount of nitrogen mineralized during the 14-week incubation, mg-N kg-soil⁻¹ 14 week⁻¹.

^b N_0 , nitrogen mineralization potential as estimated from the Gompertz equation in mg-N kg-soil⁻¹.

^c h , Gompertz proportionality constant (dimensionless) with SE as calculated by SAS in parentheses.

^d k , Gompertz rate constant in mg-N kg-soil⁻¹ week⁻¹ with SE as calculated by SAS in parentheses.

^e $t_{0.5}$, half-life or time necessary for half of the nitrogen to mineralize as calculated by: $-k^{-1}(\ln(-h^{-1} \ln 0.5(1 + e^{-h})))$.

Table 3

Atmospheric and soil N values for each site. Presented N values include N mineralized on an aerial fine earth basis (g-N m^{-2}), calculated annual dry N deposition ($\text{kg ha}^{-1} \text{yr}^{-1}$), predicted soil N from one year of dry deposition (g-N m^{-2}), and for comparison, inorganic N concentration (mg-N kg-soil^{-1}) from soils collected in July 2005.

Site	N_{min} (g-N m^{-2})	Calculated dry deposition ($\text{kg-N ha}^{-1} \text{yr}^{-1}$)	Predicted soil N from deposition (g-N m^{-2})	July 2005 inorganic N (mg-N kg-soil^{-1})
14	5.3	14.4	1.43	11.1
9	1.8	8.8	0.34	5.6
6a	3.6	6.4	0.53	11.3
6b	3.4	6.2	0.47	5.5
6c	4.0	6.0	0.47	7.0
4a	0.5	4.1	0.25	4.2
4b	2.0	3.6	0.25	2.4
4c	0.8	3.5	0.16	2.7
4d	1.7	3.5	0.22	3.2
3a	2.4	3.5	0.21	5.3
3b	1.9	3.4	0.30	2.1
3c	2.2	3.4	0.26	2.2
3d	1.2	3.2	0.29	1.8
3e	2.1	3.0	0.18	3.5
3f	1.6	2.8	0.23	2.5
3g	1.1	2.7	0.16	2.1

positively correlated with soil C ($r=0.53$, $P=0.034$) and total N ($r=0.62$, $P=0.011$), but not the C:N ratio ($r=-0.42$, $P=0.10$). There are no significant correlations between total annual cover and soil N from deposition ($r=0.23$, $P=0.40$), $N_{\text{min(f)}}$ ($r=0.45$, $P=0.079$), or soil C ($r=0.37$, $P=0.16$).

4. Discussion

4.1. Mineralization and deposition

The sixteen sites across Joshua Tree N.P. span an N deposition and precipitation gradient, with the greatest amount of N mineralized observed from the site with the most N deposition and second largest annual precipitation. However, the effect of precipitation on N mineralization across our study area is probably small

given that studies linking precipitation to N mineralization in arid and semi-arid systems have had differing results, with a few finding increased (Mazzarino et al., 1998) or decreased (Fisher et al., 1987) mineralization in wet years, but most finding either no effect of mean annual precipitation on N mineralization (Barrett et al., 2002; Yahdjian and Sala, 2008; Yahdjian et al., 2006) or only an effect of drought and not increased soil moisture (Fisher and Whitford, 1995; Whitford et al., 1995). Given that winter precipitation was between 285 and 343% above normal for the winter of 2004–2005 across our gradient, the effect of current year precipitation on mineralization across these sites is likely small. Such high precipitation amounts will increase the soil organic active pools in all samples (Bates et al., 2002), reducing the precipitation gradient effects as well as possibly accounting for the lack of difference in the mineralization rates observed. Similarly, while there are differences in the soil properties at the sixteen sites, the soils are generally sandy and rocky with percent clay ranging between 0 and 8%. Since it has been suggested that N storage in partially decomposed roots and associated microbial biomass influences mineralization rates in very sandy soils more than SOM protection by adsorption and aggregation associated with clays (Hook and Burke, 2000), it is unlikely that differences in soil texture are greatly influencing N mineralization across the N deposition gradient.

Calculated dry N deposition is correlated with the initial extractable N from the incubation soils that were collected in July, indicating that dry season extractable N in these ecosystems is a viable proxy for dry N deposition, which is difficult to measure and often overestimated when calculated using the inferential method as opposed to direct measurement by throughfall collection or branch washing (Bytnerowicz et al., 2005; Cooter and Schwede, 2000; Schmitt et al., 2005). The N deposition values calculated via the inferential method for our sites are likely overestimates due to several factors including uncertainties in the input data used in the multilayer model that calculates deposition velocities (NOAA-MLM) (Cooter and Schwede, 2000), the fact that the Joshua Tree N.P. CASTNet site does not conform to assumptions of NOAA-MLM (U.S. EPA, 2005), the use of highly averaged atmospheric N concentrations and deposition velocities, and because the climate and vegetation data used by NOAA-MLM were from a site with different characteristics than many of the sampling locations (high elevation piñon-juniper versus low elevation creosote bush scrub). Measurements of

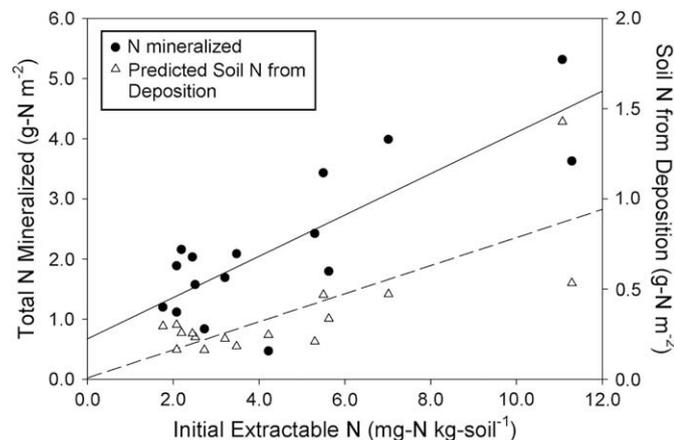


Fig. 3. Relationship between the concentration of inorganic N present in the soil at the beginning of the incubation and the N mineralized during the incubation (solid circles; $R^2=0.82$, $P<0.0001$). Given that the initial extractable N is also highly correlated to the amount of N predicted to be in the soil from atmospheric dry deposition (open triangles; $r=0.67$, $P=0.004$), we suggest that extractable N is a good proxy for dry N deposition in these arid systems as long as the soils are sampled during the high air pollution, dry season.

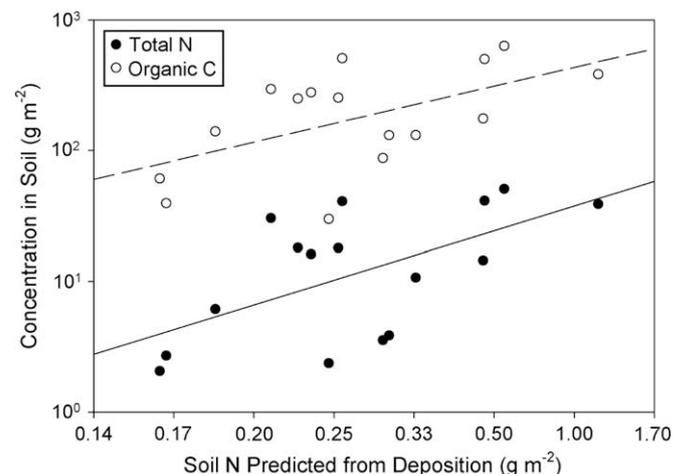


Fig. 4. Regressions of the calculated inorganic N in the surface 5 cm of the soil due to one year of dry N deposition versus the amount of total N and organic C in the soil. Regressions were performed on transformed data, and transformed data are presented in the graph with back-transformed axis labels for ease of interpretation.

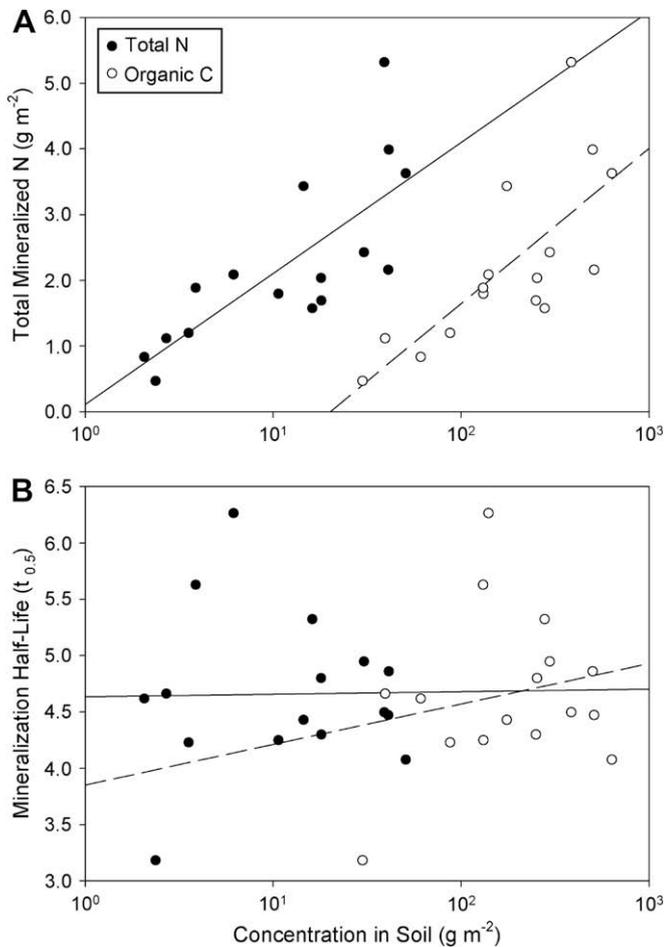


Fig. 5. Regressions between the concentration of C and N in the soil and the total amount of mineralized nitrogen (A). These regressions indicate that as C and N increase with increasing deposition the total amount of mineralized N increases (C: $R^2 = 0.63$, $P = 0.0003$; N: $R^2 = 0.67$, $P < 0.0001$). However, there are no significant relationships between C or N and the mineralization half-life (B).

total wet plus dry deposition from two of the creosote bush scrub sites ($6.6 \text{ kg ha}^{-1} \text{ yr}^{-1}$ at 6b and $3.8 \text{ kg ha}^{-1} \text{ yr}^{-1}$ at 4b) indicate the inferential method overestimated dry deposition, which was likely only a small component of total deposition in the wet 2004–2005

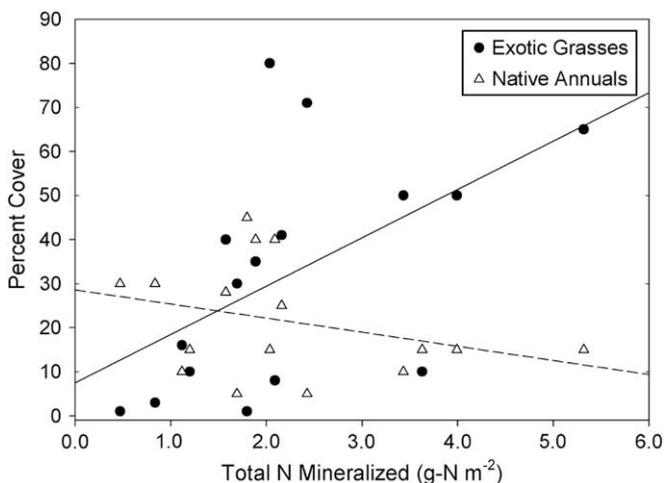


Fig. 6. Correlations between mineralized N ($N_{\text{min}(t)}$) and increased exotic grass cover ($r = 0.61$, $P = 0.012$) and decreased native forb cover ($r = -0.30$, $P = 0.26$).

rain year (A. Bytnerowicz and M. Fenn, personal communication). However, the calculation of N deposition via the inferential method is useful for converting measured atmospheric N concentrations to a soil basis for comparison to other soil parameters. Additionally we observe a significant increase in the amount of mineralized N across the deposition gradient as measured by extractable soil N suggesting that there is an effect of N deposition on mineralization dynamics.

We hypothesized that N deposition would affect N mineralization by increasing the amount of C and N in the soil. Mineralization rates appear unrelated to deposition possibly due to the high precipitation preceding sample collection or because of the low soil N content. Studies have found a threshold of 1.1–1.4% N above which mineralization rates increase linearly (Baron et al., 2000; McNulty et al., 1991), while the maximum soil N at our sites was 0.101%. Total mineralized N did demonstrate marked trends with increasing soil C and N content, which in turn were directly correlated with increasing soil N from dry deposition. Results from other studies indicate N deposition may increase or decrease soil C depending on the ecosystem and type of litter production stimulated by deposition (Dijkstra et al., 2004; Manning et al., 2006; Throop et al., 2004; Vourlitis et al., 2007; Waldrop et al., 2004). The positive relationship between N deposition and soil C observed here suggests that in this arid ecosystem N deposition may be increasing production and/or altering litter C:N ratios resulting in an increase in soil C.

The trend of increasing total mineralization with increasing C and N contents has been widely observed (Barrett and Burke, 2000; Burke, 1989; Haque and Walmsley, 1972; Simard and Ndayegamiye, 1993; Wang et al., 2004), although the relationship between potential N mineralization and the C:N ratio is varied (Marion et al., 1981). Although we observed an inverse relationship between the C:N ratio and total N mineralized, organic C and total N both have a positive correlation with mineralization. These results appear to support the hypothesis by Schaeffer et al. (2003) that microbial activity in low productivity arid land soils is primarily limited by C and secondarily limited by N.

4.2. N deposition and exotic grass invasion

The percent cover of exotic grasses, but not native forbs, is correlated with increasing total N mineralized, although only 38% of the variation in exotic grass cover is explainable by mineralized N indicating that additional factors are important in controlling grass production. One factor that may be influencing exotic grass cover at these sites is precipitation. However, because the winter growing season prior to sample collection was >250% above average across the gradient, production of all winter annuals was very high and water was not likely the most limiting factor that year. Another factor that may be influencing grass cover is the presence of desert pavement. Four of the sixteen sites contained well developed desert pavement, which has been shown to reduce herbaceous annual growth through reduced water infiltration and physical restrictions (Wood et al., 2005). These paved sites spanned the deposition gradient, but generally had low percent cover of exotic grasses (8.8%) and average cover of native forbs (27.5%). However, a full analysis of the interactions between rock cover, N mineralization, and exotic grass production would require a larger sample size and should be the focus of additional research.

While it cannot be determined from these data whether or not exotic grasses are causing the increase in mineralized N, examination of soil C and N in relation to annual cover can help in understanding some of the complex interrelationships at play. Soil C significantly increased with increased soil N from deposition and is associated with an increase in exotic grasses, but

not native forbs or total winter annual cover. These results suggest that it is the exotic grasses themselves, and not simply an increase in total vegetative cover that may be involved in increasing the soil C at these sites. In the Great Basin, it has been observed that exotic grasses increase the litter input into the system, and because the exotic litter has higher C:N and lignin:N ratios than native litter results in a decrease in N mineralization (Evans et al., 2001).

Tissue C:N ratios for all sixteen sites are not available, but the C:N ratios from exotic grasses and native forbs collected at two sites, 4b and 3f, in 2005 indicate that the exotic grasses at these sites have greater C:N ratios than the native forbs (Rao, 2008). The increased grass C:N ratios at sites with greater grass cover should have lowered N mineralization rates (Parker et al., 1984). While we did not observe a decrease in mineralization rates, there is a correlation between the shape parameter, h , and exotic grass cover indicating that sites with greater grass cover are prone to larger initial lags in mineralization. Additionally, we observe an increase in total N mineralized with exotic grass cover, suggesting that the fertilization effect of N deposition is overriding the effect of high C:N ratio litter being added to the system in invaded areas over the total time of the incubation.

Many studies have shown that exotic grasses will increase in tissue N content with increasing N fertilization (DeFalco et al., 2003; Padgett and Allen, 1999; Yoshida and Allen, 2001). However, the studies with native annual forbs have been mixed, with some species showing increased N uptake and others not (DeFalco et al., 2003; Gutierrez and Whitford, 1987; Romney et al., 1978). Additionally, studies have shown that the microbial communities themselves may be stimulated by N fertilization in these low N environments (Gallardo and Schlesinger, 1992; Schaeffer et al., 2003). Thus, it is not immediately clear as to whether N deposition is increasing mineralized N by improving litter quality through an increase in the N content of rapidly growing winter annuals, or by another mechanism such as directly reducing N limitation of microbial communities. What is clear is that positive relationships exist between N deposition, soil N, soil C, and exotic grass cover in this region.

4.3. Mineralization incubations

The third objective of this study was to determine the best model for fitting mineralization curves from these sixteen sites with different soil characteristics. A majority of the incubated soils exhibited lag patterns, most likely due to the combination of high C:N ratio litter input from exotic grasses and the fact that the soils were collected during July, after the soils had been dry for several months. Microbial communities that survive the heat and lack of water require a period of time to grow once wetted and not until the communities reach sufficient size does mineralization proceed rapidly (Cabrera, 1993; Ellert and Bettany, 1988; Grierson et al., 1998). While a number of N mineralization incubation studies have found that at least some portion of the data exhibited marked lags, few models have been shown to handle both the lagged and unlagged data (Ellert and Bettany, 1988; Simard and Ndayegamiye, 1993; Stanford and Smith, 1972). The Gompertz model is recommended here for its flexibility and ability to fit the data statistically better than models with equal or lesser numbers of parameters.

The Gompertz model contains a unitless h parameter, which governs the shape of the curve and allows us to examine possible causes for the observed lags. However, because of the combined effect of h and k on the mineralization rate, comparison of rate parameter k alone between the different sites is not recommended. The development of the half-life parameter gets around not only

this difficulty, but also allows comparison of the mineralization rates observed in this study with others. The rate parameters obtained from different models are not immediately comparable because in different models the rates have different meanings (Ellert and Bettany, 1988). However, given the incubation temperature and the parameter estimates, half-lives can be computed for any study.

Here, the half-lives were generally low and did not vary significantly between sites (4.66 ± 0.17 weeks), suggesting that the mineralizable substrate at these sites was not particularly recalcitrant. The half-lives observed here are within the range observed from incubation studies on arid soils collected in Morocco, which ranged from 3.6 to 8.4 weeks (White and Marinakis, 1991), and to half-lives calculated for loamy sand (4.93 weeks) and sandy loam (8.53 weeks) soils collected in a granitic sandy alluvial plain in South Africa (Bechtold and Naiman, 2006). However, the half-lives from this study are much lower than those observed in soils from the Chihuahuan desert of between 13.2 and 16.4 weeks (Fisher et al., 1987) and are also lower than those for chaparral soils, 7.5–19.2 weeks (Marion et al., 1981). The difference in half-lives is likely due to differences in the amounts and quality of organic matter at the Chihuahuan and chaparral sites, which are wetter and thus have greater organic inputs to the soils (Huxman et al., 2004; Marion et al., 1981).

5. Conclusions

Nitrogen deposition affects virtually every ecosystem, but N-limited arid environments may be particularly susceptible to damage because of the strong fertilization effect on systems with low productivity (Fenn et al., 2003a). This study demonstrates that N deposition to coarse-textured soils is directly related to an increase in the total amount of N mineralized, but no relationship between deposition and mineralization rates was observed. We observed an increase in total N mineralized with the N deposition proxy of summer extractable N as well as with increases in soil C and N, which themselves increased with deposition. Soil C was also directly correlated with exotic grass cover, but not native forb or total annual cover, suggesting that it is the exotic grasses, and not just an increase in winter annual production with increasing precipitation or N deposition, that is contributing to an increase in soil C. While total N mineralized increased with exotic grass cover, what role N deposition is playing in increasing exotic grass cover is not immediately apparent and further studies on additional factors that may interact with N, including soil rockiness and precipitation, are underway. Although the effect of N deposition on exotic grass cover is unclear from this study, because N fertilization has been shown to increase biomass production of the exotic grasses in this area (Allen et al., 2009; Brooks, 2003), increased available N with deposition may additionally impact this ecosystem through the effect exotic grasses have on lowering cover and diversity of native species (Allen et al., 2009) and altering fire regimes (Brooks et al., 2004).

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Appendix A. Comparison of mineralization model results.

Site	First order model: $N_{\min} = N_0(1 - e^{-kt})$			Consecutive reaction model: $N_{\min} = N_0 - N_0(e^{-kt})(kt + 1)^{-1}$			Mixed order model: $N_{\min} = N_0(1 - e^{-k_1t - 0.5k_2t^2})$					Gompertz Model: $N_{\min} = N_0(e^{-he^{-kt}}) - N_0(e^{-h})$				
	N_0	ak	R^2	N_0	k	R^2	N_0	k_1	k_2	R^2	$^bF_{\text{extra}}$ (FO, CR)	N_0	h	k	R^2	F_{extra} (FO, CR)
14	97.798	0.105	0.979	73.509	0.389	0.984	72.573	0.089	0.032	0.986	2.97, 0.18	83.666	2.277	0.298	0.986	3.35, 1.21
9	53.819	0.136	0.993	43.904	0.443	0.986	46.467	0.136	0.015	0.995	1.51, 3.12	67.303	1.223	0.243	0.995	2.02, 9.68
6a	82.817	0.143	0.988	68.2	0.462	0.983	74.148	0.147	0.01	0.989	0.25, 0.54	105.6	1.195	0.252	0.989	0.71, 3.48
6b	74.477	0.116	0.985	58.541	0.399	0.988	58.203	0.096	0.03	0.994	9.85, 1.56	69.217	2.058	0.289	0.993	7.22, 4.40
6c	81.039	0.097	0.945	64.773	0.356	0.992	64.235	0.11	0.01	0.945	0.02, -0.89	70.73	2.591	0.294	0.989	22.72, -1.31
4a	11.467	0.177	0.975	10.127	0.527	0.994	9.937	0.077	0.088	0.992	9.57, 0.06	10.49	3.178	0.497	0.992	10.45, -6.22
4b	71.949	0.056	0.943	40.322	0.306	0.984	35.299	-0.033	0.074	0.998	141.33, -14.32	35.927	6.637	0.471	0.998	151.70, 35.63
4c	26.779	0.116	0.981	20.832	0.405	0.979	21.548	0.112	0.019	0.985	1.72, 2.62	28.47	1.539	0.244	0.985	1.52, 1.50
4d	47.499	0.085	0.94	32.691	0.36	0.975	29.923	-0.004	0.077	0.974	8.00, -0.03	30.754	4.817	0.454	0.976	8.80, 0.01
3a	108.4	0.057	0.942	61.748	0.308	0.979	55.193	-0.004	0.058	0.985	17.08, 0.42	56.863	4.949	0.399	0.984	15.52, 1.65
3b	34.581	0.092	0.992	24.447	0.369	0.984	27.148	0.103	0.009	0.993	0.86, -4.38	41.341	1.152	0.18	0.993	0.94, 6.21
3c	48.059	0.087	0.963	33.369	0.362	0.985	31.498	0.045	0.049	0.981	5.84, -0.26	33.044	3.591	0.377	0.983	7.20, -0.88
3d	22.036	0.128	0.983	17.903	0.415	0.987	17.814	0.101	0.032	0.994	10.69, -0.64	21.088	2.059	0.302	0.992	7.23, 1.99
3e	487.2	0.007	0.966	54.188	0.231	0.993	44.828	0	0.037	0.998	78.43, 200.27	47.25	4.687	0.307	0.997	59.29, 5.81
3f	51.436	0.06	0.976	29.845	0.313	0.992	28.137	0.047	0.033	0.992	12.05, -0.37	30.637	3.094	0.293	0.992	11.66, -1.37
3g	28.994	0.097	0.985	21.064	0.376	0.994	20.803	0.082	0.03	0.994	8.38, 0.07	23.651	2.386	0.294	0.994	9.24, -1.96

^a The rate parameters, k , are specific to each model type and cannot be compared between models.

^b F_{extra} was calculated to compare the three parameter models with the first order (FO) and consecutive reaction (CR) models with 2 parameters. Additional parameters are warranted if calculated $F_{\text{extra}} > \text{tabulated } F_{\alpha((p_2-p_1)/(n-p_2))}$, (typically $F < 6$ for $\alpha = 0.05$, $p_2 - p_1 = 1$, and $n - p_2 = 6$).

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