

Ecosystem response to nutrient enrichment across an urban airshed in the Sonoran Desert

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Abstract. Rates of nitrogen (N) deposition have increased in arid and semiarid ecosystems, but few studies have examined the impacts of long-term N enrichment on ecological processes in deserts. We conducted a multiyear, nutrient-addition study within 15 Sonoran Desert sites across the rapidly growing metropolitan area of Phoenix, Arizona (USA). We hypothesized that desert plants and soils would be sensitive to N enrichment, but that these effects would vary among functional groups that differ in terms of physiological responsiveness, proximity to surface N sources, and magnitude of carbon (C) or water limitation. Inorganic N additions augmented net potential nitrification in soils, more so than net potential N mineralization, highlighting the important role of nitrifying microorganisms in the nitrate economy of drylands. Winter annual plants were also responsive to nutrient additions, exhibiting a climate-driven cascade of resource limitation, from little to no production in seasons of low rainfall (winter 2006 and 2007), to moderate N limitation with average precipitation (winter 2009), to limitation by both N and P in a season of above-normal rainfall (winter 2008). Herbaceous production is a potentially important mechanism of N retention in arid ecosystems, capable of immobilizing an amount equal to or greater than that deposited annually to soils in this urban airshed. However, interannual variability in precipitation and abiotic processes that limit the incorporation of detrital organic matter into soil pools may limit this role over the long term. In contrast, despite large experimental additions of N and P over four years, growth of *Larrea tridentata*, the dominant perennial plant of the Sonoran Desert, was unresponsive to nutrient enrichment, even during wet years. Finally, there did not appear to be strong ecological interactions between nutrient addition and location relative to the city, despite the nearby activity of nearly four million people, perhaps due to loss or transfer pathways that limit long-term N enrichment of ecosystems by the urban atmosphere.

Key words: Ambrosia; arid ecosystem; *Larrea tridentata*; N deposition; nitrogen fertilization; *Pectocarya* spp.; phosphorus; Sonoran Desert, Arizona, USA; urban environments; winter ephemeral annual plants.

INTRODUCTION

Energy use and agricultural practices associated with human activity have increased atmospheric deposition of reactive nitrogen (N) to ecosystems worldwide over the last century (Dentener et al. 2006). Because N limits ecosystem processes in many terrestrial and some aquatic ecosystems (Elser et al. 2007, LeBauer and Treseder 2008), the past two decades have seen intensive research focus on the consequences of enhanced N availability. Most of this research has been conducted in mesic, N-limited ecosystems, including temperate forests, grasslands, and shrublands, among others. In these

systems, N loading generally increases primary production and rates of N cycling (Aber et al. 1997, Magill et al. 2004, de Vries et al. 2009), alters plant and microbial community composition and function (Allison et al. 2007, Clark and Tilman 2008), and may lead to soil acidification (Stevens et al. 2009) and elevated N losses to aquatic systems and the atmosphere when biological sinks become saturated (Emmett et al. 1998, Skiba et al. 2009). Excess N availability from deposition may also shift elemental stoichiometry in N-limited terrestrial and aquatic ecosystems, leading to increased biotic phosphorus (P) demand and P limitation (Menge and Field 2007, Elser et al. 2009).

Rates of N deposition have also increased in arid and semiarid regions, which support some of the fastest urban growth in the United States, and are rapidly

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urbanizing in the developing world (Fenn et al. 2003*b*, UNPD 2007, U.S. Census Bureau 2007). Despite this trend, surprisingly few studies have explored the biogeochemical outcomes of atmospheric N deposition in deserts (Brooks 2003, Báez et al. 2007, Allen et al. 2009, Rao and Allen 2010). Several experiments show that after water, N limits production in dryland plant communities, including herbaceous annual plants (Whitford and Gutierrez 1989, Brooks 2003, Rao and Allen 2010) and perennial shrubs (Ettershank et al. 1978, Fisher et al. 1988, Sharifi et al. 1988, Barker et al. 2006). However, other research suggests that desert plants may have limited ability to respond to N enrichment due to inherent physiological constraints that help them to survive in resource-poor environments (Chapin 1980, Adams et al. 2004). Additionally, although not often explored, P has been shown to limit growth in grasslands and some aridland species (Drenovsky and Richards 2004, Niinemets and Kull 2005, Craine et al. 2008). In arid soils, P may be relatively inaccessible to biota due to sorption of phosphate to fine carbonate particles or calcium-rich secondary minerals (Carreira et al. 2006), and it may become limiting to plant growth under chronic N enrichment. Given strong physiological constraints to growth, coupled with the potential for limitation by water and P, desert plant production may exhibit only a weak response to atmospheric N loading.

The consequences of N enrichment are also unclear for biogeochemical processes in desert soils (Zeglin et al. 2007, Porras-Alfaro et al. 2008). The environmental extremes of arid and semiarid ecosystems favor abiotic biogeochemical transformations and restrict biotic activity to resource-rich patches across space and time. As such, ecosystem properties or processes in mesic regions that promote retention of atmospheric N inputs may be qualitatively different or absent in deserts. For example, low organic matter pools over much of the landscape may restrict mechanisms of N immobilization common to carbon (C)-rich forest and grassland soils (Johnson 1992, Kaye et al. 2002). Enrichment may have limited effects on N mineralization (McNulty et al. 1991) if desert plant growth or chemistry is unresponsive to N, if surface litter is photo-degraded before incorporation into soils (Austin and Vivanco 2006), or if organic matter is oxidized by extracellular enzymes that are stabilized in mineral, alkaline soils (Stursova and Sinsabaugh 2008). Also, intense rainfall events combined with high evapotranspiration and patchy soil permeability can limit water infiltration and promote runoff, which reduces the delivery of N to rooting zones, creates asynchrony in microbial and plant nutrient demand, and concentrates inorganic N pools on soil surfaces where they are susceptible to loss (Peterjohn and Schlesinger 1990, Augustine and McNaughton 2004, Michalski et al. 2004, Welter et al. 2005). In highly permeable soils or in parts of the landscape where runoff collects, pulse rainfall events can leach N

compounds quickly below the rooting zone, where they may be unavailable to biota (Graham et al. 2008, Marion et al. 2008*a*). Alternatively, hot, alkaline surfaces of some deserts may promote abiotic losses of reactive N gases to the atmosphere, punctuated by rapid biogenic gas production following rain events (McCalley and Sparks 2009).

Given the extreme and variable nature of desert environments, it is not surprising that models of ecosystem function in aridlands have been largely organized around precipitation pulses and their effects on plant and microbial activity (Noy-Meir 1973, Ludwig and Tongway 1997, Ogle and Reynolds 2004, Shen et al. 2005, Collins et al. 2008). In the Threshold Delay model, Ogle and Reynolds (2004) built upon the earlier Pulse-Reserve model (Noy-Meir 1973) to show that primary production for a range of North American deserts can be predicted by precipitation timing, soil properties such as antecedent moisture, and functional traits of plants that respond differently to pulse precipitation events. More recently, Collins et al. (2008) expanded this framework in the Threshold Delay Nutrient Dynamics (TDND) conceptual model to emphasize the collective role of soil microorganisms, in addition to water, as modulators of aridland productivity and ecosystem dynamics.

The TDND model predicts that the responsiveness of different microbial functional groups to rainfall pulses, in concert with plant functional types and soil characteristics, will regulate source-sink dynamics of limiting resources such as water, C, and N (Collins et al. 2008). Specifically, this model emphasizes the ability of soil microorganisms to “turn on” at precipitation thresholds too low for vegetation, decoupling biogeochemical transformations from plant production. Moreover, this model builds on recent evidence that fungi play a key role in aridland nutrient cycling through their ability to nitrify, denitrify, and translocate C and N between plants and biological soil crusts through a complex network of hyphae (McLain and Martens 2006, Crenshaw et al. 2008, Green et al. 2008). Despite advances in these ecological models to integrate multiple resources that limit aridland ecosystem dynamics, their ability to predict the consequences of environmental change such as N enrichment has not been explored. Indeed, no conceptual framework or model currently exists to predict how the diverse plant and microbial components of desert ecosystems may respond to elevated N loading, despite the fact that arid and semiarid regions are experiencing rapid environmental change.

In this study, we tested the responsiveness of Sonoran Desert ecosystems to nutrient enrichment by measuring properties and dynamics of plants and soils following N and P addition at sites within and outside the Phoenix, Arizona (USA) metropolitan area. We hypothesized that desert plants and soils are sensitive to N enrichment, but that these effects vary among functional groups that differ in terms of physiological responsive-

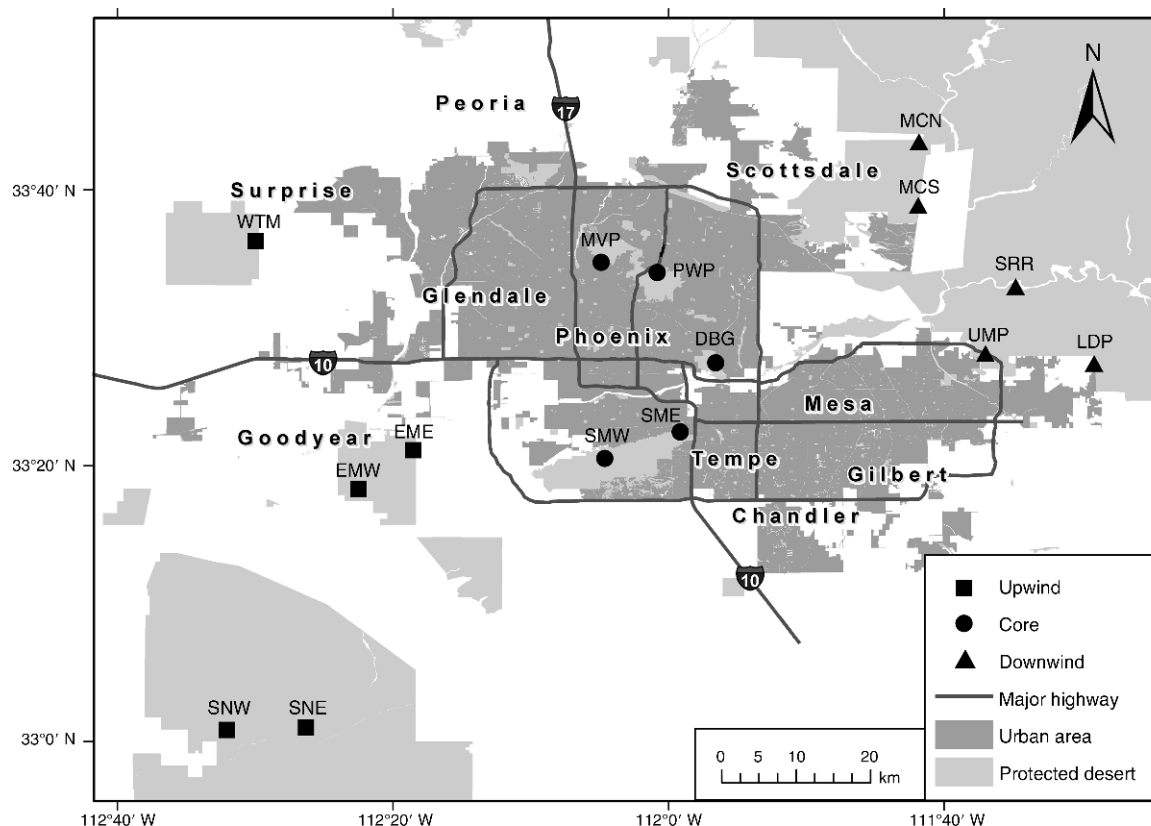


FIG. 1. Map of the 15 Sonoran Desert sites across the Phoenix, Arizona (USA), metropolitan area used in this study, including five each of protected desert sites located upwind (west) and downwind (east) of the urban airshed ("Upwind" and "Downwind," respectively), and five protected remnant desert sites within the city center ("Core"). Expanded site names are in Table 1. Each site contains a 20×20 m plot that was not fertilized ("Control") and three plots of the same size that received fertilizer every six months beginning in December 2005 as N ($60 \text{ kg N} \cdot \text{ha}^{-1} \cdot \text{yr}^{-1}$), P ($120 \text{ kg P} \cdot \text{ha}^{-1} \cdot \text{yr}^{-1}$), or the two in combination (N + P).

ness, proximity to surface N sources, and magnitude of C or water limitation. Given this hypothesis, we expected N addition to have little effect on C-limited heterotrophic microbial processes, including nitrification if performed by fungi or other heterotrophic microorganisms as hypothesized by the TDND model. However, if nitrification is primarily autotrophic, we expected this microbial process would be most responsive to N addition, followed by production of shallow-rooted, ephemeral annual plants, and finally deeper-rooted perennial shrubs. Finally, we hypothesized that these responses would vary with proximity to the city, with a large effect of N on ecosystem response variables in deserts outside of the urban core and co-limitation of plant growth by N and P, or limitation by P alone, in Sonoran Desert remnants within the city where atmospheric NO_x and NH_3 concentrations, and likely N deposition, are highest.

METHODS

Site selection and description

We measured ecosystem pools and processes in response to nutrient enrichment at 15 native Sonoran

Desert sites in central Arizona (Fig. 1, Table 1; see Plate 1). Mean daily maximum and minimum temperatures in this region are 30°C and 15°C , respectively (for 1933–2009 [WRCC 2009]). Annual average rainfall is 193 mm, distributed bimodally through the year, with $\sim 35\%$ as convective monsoon storms from June to September and $\sim 65\%$ from Pacific frontal storms between November and March.

Ambient N deposition across the gradient of research sites between 1998 and 2006 ranged from $4 \text{ kg N} \cdot \text{ha}^{-1} \cdot \text{yr}^{-1}$ in upwind and downwind locations to $5\text{--}7 \text{ kg N} \cdot \text{ha}^{-1} \cdot \text{yr}^{-1}$ within the urban core (Lohse et al. 2008). Concentrations of NO_x and especially NH_3 gas are high within the city, estimated at 0.022 ppm and $8.8 \mu\text{g}/\text{m}^3$, respectively (Watson et al. 1994, ADEQ 2009). Properties of surface soils (0–2 cm) vary across the landscape, with predictable resource islands under shrubs (Table 2 [Hall et al. 2009]). SOM content also varies across the urban–rural gradient, with highest concentration in the urban core compared to upwind or downwind locations (Table 2 [Hall et al. 2009]).

To select sites, we first identified all protected land within a 6400-km^2 area defined by the boundaries of the

TABLE 1. Characteristics of the 15 Sonoran Desert sites across the Phoenix, Arizona (USA), metropolitan area used in this study.

Landscape position	Site name	Elevation (m)	MAP (mm)†	MAT (°C)‡	O ₃ (ppb)§	CO ₂ (ppm)¶	Soil classification#
Upwind	EME	331	186	23.3	69.5	400.8	Typic Haplargids
Upwind	EMW	382	164	23.1	68.9	400.8	Typic Haplargids
Upwind	SNE	492	160	22.8	70.0	no data	Typic Camborthids
Upwind	SNW	375	130	22.8	no data	399.3	Typic Camborthids
Upwind	WTM	454	195	22.0	67.1	401.4	Typic Haplargids
Core	DBG	396	172	23.5	77.4	465.0	Typic Paleorthids
Core	MVP	397	190	20.7	79.3	461.3	Typic Haplargids
Core	PWP	456	177	20.7	80.4	406.8	Typic Haplargids
Core	SME	372	194	22.5	75.6	442.7	Typic Haplargids
Core	SMW	458	180	22.4	73.9	400.0	Typic Durorthids
Downwind	LDP	620	203	22.1	80.2	403.5	Typic Haplargids
Downwind	MCN	476	281	22.7	86.0	402.8	Typic Calciargids
Downwind	MCS	539	241	22.7	85.3	402.8	Typic Haplargids
Downwind	SRR	434	197	22.1	81.9	401.0	Typic Calciargid
Downwind	UMP	592	205	22.5	79.6	403.6	Typic Haplargids

Notes: Expanded site names are: EME, Estrella Mountain Regional Park, east side; EMW, Estrella Mountain Regional Park, west side; SNE, Sonoran Desert National Monument, east side; SNW, Sonoran Desert National Monument, west side; WTM, White Tank Mountain Regional Park; DBG, Desert Botanical Garden; MVP, Mountain View Park (North Mountain); PWP, Piestewa Peak (Phoenix Mountains Preserve); SME, South Mountain Park, east side; SMW, South Mountain Park, west side; LDP, Lost Dutchman State Park; MCN, McDowell Mountain Regional Park, north side; MCS, McDowell Mountain Regional Park, south side; SRR, Salt River Recreation Area; UMP, Utery Mountain Regional Park.

† Mean annual precipitation (MAP) values based on 3–18 year average annual rainfall data (excluding first and last data in series; SNW and SRR data are from 2005–2009 only [FCDMC 2009]). Precipitation over the years of this study is shown in Fig. 5.

‡ Mean annual temperature (MAT) values averaged for 2006–2008 based on temperature data from FCDMC [2009] and NCDC (National Climatic Data Center) [2009].

§ Average 8-hour values, 2003–2005 (Buyantuyev 2007).

¶ Average morning (05:00–06:00 hours) CO₂ concentrations, sampled along roadways (Wentz et al. 2007).

Classification from NRCS (2009) except for soil from SRR site, which was classified according to field and laboratory methods described in USDA (1993, 1998).

Central Arizona–Phoenix Long-Term Ecological Research project (CAP LTER), including desert within and surrounding urbanized metro Phoenix. We then stratified potential sites according to their location relative to the city (hereafter referred to as “landscape position”; Fig. 1) as upwind of the urban core (“upwind,” $N = 5$), within the city (“core,” $N = 5$) or downwind of the urban core (“downwind,” $N = 5$). We expected this design to capture differences in N deposition based on model results for this region (Fenn et al. 2003a), although annual rainfall also varies systematically across this gradient (Table 1). Over the

course of our study (October 2005–September 2009), average rainfall was higher in the downwind sites (204 ± 10 mm; mean \pm SE) compared to sites upwind of the city (134 ± 4 mm) or in the urban core (150 ± 3 mm).

Sites were located on alluvial fans with gentle slopes, a common geomorphic setting in deserts, and soils were classified as Aridisols (Table 1) with a sandy loam texture at 0–5 cm depth. McAuliffe (1994) has shown that creosote bush (*Larrea tridentata* (DC.) Coville) and bursage (*Ambrosia* spp.) occur together in the Sonoran Desert on soils that are moderately developed but lack clear argillic horizons that impede water infiltration and

TABLE 2. Soil properties in unfertilized Sonoran Desert plots across the Phoenix metropolitan area; values reported are means with SE in parentheses ($N = 5$ sites per patch type and landscape position).

Variable	Under shrubs†			Interplant space		
	Upwind	Core	Downwind	Upwind	Core	Downwind
SOM (%)‡	2.52 (0.31)	4.45 (0.27)	3.36 (0.42)	1.70 (0.15)	2.44 (0.18)	2.18 (0.34)
Total C (%)	0.85 (0.10)	1.84 (0.21)	1.16 (0.21)	0.35 (0.04)	0.58 (0.06)	0.66 (0.18)
Inorganic C (%)	0.05 (0.02)	0.05 (0.01)	0.05 (0.01)	0.05 (0.02)	0.07 (0.03)	0.14 (0.10)
Organic C (%)§	0.81 (0.11)	1.75 (0.21)	1.11 (0.19)	0.31 (0.04)	0.52 (0.08)	0.53 (0.09)
Total N (%)	0.08 (0.01)	0.18 (0.02)	0.12 (0.02)	0.04 (0.01)	0.06 (<0.01)	0.06 (0.01)
Soil C:N	10.35 (0.20)	10.23 (0.28)	9.90 (0.26)	9.65 (0.75)	9.62 (0.43)	11.10 (1.67)
Extractable NH ₄ ⁺ (µg N/g)	2.83 (0.13)	6.42 (2.70)	4.82 (0.80)	1.89 (0.24)	6.54 (2.77)	2.62 (0.53)
Extractable NO ₃ ⁻ (µg N/g)	11.30 (2.81)	18.44 (2.84)	10.89 (2.45)	3.95 (1.37)	5.39 (0.95)	2.56 (0.48)
Extractable PO ₄ ⁻³ (µg P/g)	20.67 (3.34)	32.78 (1.67)	47.78 (8.53)	14.10 (2.52)	22.70 (7.90)	25.87 (1.77)

† Under-shrub values represent averages of soils collected separately under *Ambrosia* spp. and *Larrea tridentata*.

‡ SOM is total soil C and N, and extractable inorganic N and P values represent averages of soils collected and analyzed separately in spring and fall 2006 ($N = 5$ per landscape position).

§ Organic C estimated by difference (total C – inorganic C) on soils sampled in fall 2006.

availability. Accordingly, to further control for soil properties, we selected sites that included both *L. tridentata* and *Ambrosia* spp., including both white bursage (*Ambrosia dumosa* (A. Gray) Payne; in 2 upwind sites only), and triangle-leaf bursage (*A. deltoidea* (Torr.) Payne; in the 13 remaining sites). Trees with N-fixing microbial associations occur in the Sonoran Desert, but the spatial extent of their canopies is small across the landscape relative to the shrub-interplant space patch types (Schade et al. 2003). Thus we selected plots to avoid inclusion of N-fixing trees. Desert vegetation in our sites also included various cacti, such as saguaro (*Carnegiea gigantea* (Engelm.) Britton and Rose) and cholla (*Cylindropuntia* spp.).

The winter ephemeral plant community across the Sonoran Desert is diverse, including many coexisting species from the Boraginaceae and Brassicaceae families (Pake and Venable 1996, Angert et al. 2009). Fifty-four unique winter herbaceous species were represented across all landscape positions during our study (species richness of 46, 34, 26 in downwind, upwind, and core landscape positions, respectively; C. Clark, unpublished data). Although rare species differed substantially among landscape positions (one-third of the total species were only found in one landscape position), communities across our sites were dominated by the same three species, totaling >50% of cover, including the native species *Pectocarya recurvata* and *Amsinckia menziesii* and the exotic species *Schismus arabicus*. The percentage cover of *S. arabicus* was highest in sites downwind of the city (average $21\% \pm 3\%$) relative to those upwind ($8\% \pm 5\%$) or in the urban core ($7\% \pm 2\%$) (C. Clark, unpublished data). The exotic species *Erodium cicutarium* was also found in our sites, though less frequently (average 0–10% cover in the three landscape positions); other exotic species in the data set were all rare (<1% in all sites).

At each site, we established four 20×20 m plots with a 5-m buffer, each of which included at least five individuals of *L. tridentata* and five individuals of *A. deltoidea* or *A. dumosa*. Nutrient treatments of ambient (no fertilizer, i.e., Control), N, P, and both N and P (N + P) were assigned randomly to plots, taking care to ensure that potential runoff would not contaminate other treatments. Fertilization began in December 2005, broadcast as solids by hand at $60 \text{ kg N} \cdot \text{ha}^{-1} \cdot \text{yr}^{-1}$ as NH_4NO_3 (double the hypothesized rate of N deposition near urban centers in the western United States (Fenn et al. 2003a); fertilization took the form of P as triple superphosphate at $120 \text{ kg P} \cdot \text{ha}^{-1} \cdot \text{yr}^{-1}$, and both N and P at the same rates in combination. Calcium-rich aridisols are known to bind P into insoluble forms (Lajtha and Bloomer 1988); accordingly, P was applied in excess at $120 \text{ kg P} \cdot \text{ha}^{-1} \cdot \text{yr}^{-1}$ to enhance the probability of soluble P enrichment to deeper-rooted shrubs. Half of the fertilizer was applied after the first rainfall of the winter season (typically in January), and the other half at the onset of the summer monsoon rains (July). In each plot,

we measured plant growth and/or soil properties twice per year over four years (spring 2006–fall 2009), once in late spring (March–May), hereafter referred to as spring) and once in fall after the summer monsoon storms (October; hereafter referred to as fall).

Growth of annual and perennial plants

Seasonal growth of the perennial shrubs *L. tridentata* and *Ambrosia* spp. was estimated by measuring elongation of stems in April (growth from October–April; winter/spring) and in October (growth from April–October; summer/fall) (Chew and Chew 1965, Fisher et al. 1988). One apical stem was selected from each of four cardinal directions on each of five individual plants per plot. Each stem was marked with tape several centimeters from the tip and measured at the beginning of the growth interval. Stem elongation was calculated as the difference in stem length from the beginning to the end of the measurement interval. Drought conditions prior to our study resulted in decline and mortality of many of the *Ambrosia* shrubs within our experimental plots during 2006–2007. (This pattern occurred throughout the Southwest [Miriti et al. 2007].) Consequently, we measured stem elongation in *Ambrosia* only until fall 2007. In February 2010 (five years after the initiation of fertilization), we assessed the effects of nutrient additions on leaf density of *L. tridentata*. Two 10-cm branches were harvested from the east and west sides of *L. tridentata* shrubs within each plot (five shrubs per plot). In the laboratory, leaf number, stem length, and empty nodes were recorded for a 5-cm section of an apical stem and a lateral stem. Each bifid leaf pair was counted as one leaf. Leaf densities were averaged from two branches per stem and the two stems per shrub, then averaged across shrubs within each plot.

Growth of spring annual plants was estimated by harvesting total herbaceous aboveground biomass at peak production. Four 1-m^2 quadrats were identified and permanently marked within each plot, two under *L. tridentata* shrubs and two in interplant spaces (hereafter, “under *L. tridentata*” and “interplant” locations are referred to as “patch types”). In March 2008, total herbaceous biomass was harvested from one quarter of each 1-m^2 quadrat (0.25-m^2 subplot). In March 2009, the location of the 0.25-m^2 subplot was rotated within the permanent 1-m^2 quadrat to avoid the area harvested the previous year. Biomass from each of the subplots was dried at 60°C and averaged (two 0.25-m^2 subplots per 1-m^2 quadrat; two quadrats per patch type; two patch types per plot).

Surface soil collection

We stratified soil sampling by patch type. Three 8 cm (diameter) \times 2 cm (depth) soil cores per patch type were taken and homogenized per plot. Relatively shallow depths were sampled for biogeochemical variables because microbial activity in arid ecosystems attenuates quickly below the first several millimeters of soil (Belnap

et al. 2003). For all soils in every season, we measured soil moisture, water-holding capacity, inorganic N and P concentration, soil organic matter [SOM] content, and potential rates of net N mineralization and nitrification. For total C and N, soils from control plots were sampled in March 2006, while samples from all treatments were collected in October 2006. Soil pH from all treatments was measured in spring 2008 and spring 2009. Soils were stored on ice for up to 48 hours after collection (10–12°C), after which they were sieved (2 mm) and processed immediately for time-sensitive microbial properties and processes (inorganic N and P concentration, net potential N transformations, and soil moisture). Soil pH was measured on air-dried soils. Other soil properties were measured on oven-dried soils (total soil C and N, inorganic C, SOM, and texture).

Net potential N transformations and inorganic N and P concentration

We measured net potential N mineralization (written hereafter as “net $N_{min_{pot}}$ ”) and net potential nitrification (“net Nit_{pot} ”) in soils incubated at 60% water-holding capacity over 30 days in order to assess relative differences in C and N demand by microorganisms between nutrient treatments and across similar soils in locations differentially exposed to the urban atmosphere (Robertson and Paul 2000). Microbial community structure is known to shift in response to short-term changes in water potential, particularly those communities from arid and semiarid soils that are acclimated to pulsed rainfall (Gleeson et al. 2008). For this reason, the laboratory incubations used in this assay were not intended to assess actual N mineralization or nitrification rates experienced in the field, but were instead intended to identify relative differences in microbial N transformation potential. One 10-g subsample of soil was immediately shaken for 1 hour in 50 mL of 2 mol/L KCl, filtered through pre-leached Whatman No. 42 filters (Whatman, Florham Park, New Jersey, USA), and then frozen for later analysis. Another 10-g subsample was placed in a small, capped cup, its water content raised to 60% water-holding capacity with deionized water, and incubated in the dark for 30 days at 24°C (Robertson and Paul 2000). After the incubation, soils were extracted as described above. All KCl extracts were analyzed colorimetrically for NH_4^+ -N and $NO_2^- + NO_3^-$ -N (hereafter, referred to as “ NO_3^- -N”) using a Lachat Quikchem 8000 autoanalyzer (Lachat, Loveland, Colorado, USA). Net $N_{min_{pot}}$ was calculated as the difference between the sum of NH_4^+ -N and NO_3^- -N concentration before and after each incubation. Net Nit_{pot} was calculated as the difference between NO_3^- -N concentration before and after each incubation. Bicarbonate extractable soil P pools were measured by shaking 2 g of soil in a 0.5 mol/L bicarbonate solution for one hour. Soils were filtered as above and extracts were frozen until analysis on a Bran-Luebbe (now Seal

Analytical) TRAACS 800 autoanalyzer (Mequon, Wisconsin, USA).

Other soil properties

Gravimetric soil water was determined by drying soil subsamples for 24 hours at 105°C. Water-holding capacity was estimated as the gravimetric water content 24 hours after soils were saturated and allowed to drain. SOM was estimated gravimetrically as mass lost following combustion for 4 hours at 550°C. Inorganic C was determined on a 1-g sample of ball-milled soil using the modified calcimeter method (Sherrod et al. 2002). Soil pH was determined by adding one 15-g subsample to 30 mL of deionized water (in 2008) or 0.01 mol/L $CaCl_2$ (in 2009). Samples were gently stirred and allowed to stand for 30 minutes before analyses. To compare soil pH between years, a subset of 12 soils (interplant patches from four treatments within three sites, one in each landscape position) was tested for pH using both deionized water and $CaCl_2$, and pH($CaCl_2$) data were corrected to pH(water) using the following linear relationship: $pH(water) = 0.86 \times pH(CaCl_2) + 1.56$ ($r^2 = 0.85$).

Plant tissue chemistry

Leaves from the perennial shrubs *L. tridentata*, *Ambrosia* spp., and aboveground leaves and stems from the dominant annual forbs *Pectocarya recurvata* and *P. platycarpa* were collected in the field and analyzed for foliar C, N, and P. *P. platycarpa* was present across our sites at low abundance (C. Clark, unpublished data) and was not differentiated from *P. recurvata* for tissue nutrient analysis. For the shrubs, two mature, undamaged leaves from the most recent growing season were sampled on each individual from each of four cardinal directions. For *Pectocarya* spp., both green stems and leaves from at least five individuals were sampled after air-drying. Plant tissue from all species was dried at 60°C, ground on a ball mill, and analyzed for C and N on a Perkin-Elmer 2400 Series II CHNS/O elemental analyzer (Waltham, Massachusetts, USA). Tissue P was measured using persulfate/sulfuric acid digestion followed by colorimetric analysis (ascorbic acid analysis method [APHA 1998]). One 2-mg subsample from each foliar sample was placed in a 5% potassium peroxodisulfate and 30% sulfuric acid solution and digested in an autoclave for 90 minutes. Digests were analyzed using a modified ascorbic acid colorimetric method using a Thermo Scientific Genesys Bio spectrophotometer set to 880 nm.

Data analysis

Statistical tests were conducted using SPSS 17.0.1 for Mac (SPSS 2008). All data with nonnormal distributions were transformed prior to parametric analyses to satisfy linear model assumptions. When data were nonnormal even after transformation (net $N_{min_{pot}}$ and net Nit_{pot}), nonparametric Mann-Whitney *U* tests were performed

within patch types and season. Data were then combined across all landscape positions to test the effects of N addition (N and N + P plots combined) and P addition (P and N + P plots combined). Alpha values were Bonferroni-corrected when assessing significance. For variables that were measured over multiple seasons, we used a repeated-measures full-factorial ANOVA model with sampling dates as within-subject factors and landscape position, N addition (N and N + P plots), P addition (P and N + P plots), and all interactions as between subject factors. Removal of nonsignificant higher order interactions was performed with stepwise backward elimination, retaining the main effects and the N \times P interaction at the minimum in the final model. Analyses were run separately by patch type. When the effect of treatment was significant, three-way post hoc ANOVA tests were performed by season, using Bonferroni corrections. Annual herbaceous biomass data and foliar nutrients of *Pectocarya* spp. were analyzed separately within each patch type and year (2008 and 2009). Multiple stepwise regression analysis was conducted to determine the relationship between winter ephemeral plant growth and noncorrelated soil and climatic factors (independent variables: rainfall, soil pH, extractable soil N and P, net N_{min}_{pot}). Independent variables were checked for collinearity in SPSS by running a full model and eliminating variables (a) if they had a tolerance <0.2, and (b) if two variables had a variance proportion of 0.50 or higher with a condition index >30 (Weiner et al. 2003).

RESULTS

Soil properties and processes

Experimental nutrient additions had variable consequences for soil resource pools. Neither N nor P additions significantly altered SOM over the course of this study in either patch type (Appendix A; three-way repeated-measures ANOVA within patch types). Additionally, although the power to detect differences in the interaction of landscape position and nutrient addition was relatively low, the effect of nutrient additions on SOM content did not vary with landscape position in this study (Appendix A). In contrast, P additions significantly decreased average soil pH in the springs of 2008 and 2009, from 7.3 to 7.0 (Appendix B). The pH of soil under shrubs was also significantly lower in the urban core (average pH 7.3) compared to upwind and downwind sites (average pH 6.8) (three-way repeated-measures ANOVA: landscape position, $P < 0.001$ with post hoc Tukey test). Soil moisture was low during sample collection, ranging from 0.6% average gravimetric water content in interplant spaces (spring 2006, fall 2007) to 1.4% under *L. tridentata* (spring 2007 and 2008).

Extractable soil inorganic N and P concentrations varied significantly by landscape position and were elevated in plots that received N and P additions, respectively (Fig. 2, only interplant spaces shown;

Appendix C). In interplant spaces, inorganic N concentration was highest in the urban core compared to soils in upwind or downwind locations. Soil inorganic N did not vary by landscape position under shrubs. P addition increased extractable PO_4^{3-} across all landscape positions in interplant spaces, but under shrubs, the effect of P additions on soil PO_4^{3-} was highest upwind; landscape position \times P interaction, $P = 0.03$). Under shrubs, N added in combination with P decreased soil PO_4^{3-} concentration (N \times P interaction, $P = 0.03$; Appendix C).

Despite receiving equal molar ratios of N as NH_4 and NO_3 (N added as granular NH_4NO_3), the ratio of $\text{NH}_4^+/\text{NO}_3^-$ in both patch types was significantly greater following both N and P addition ($P \leq 0.001$). Under shrubs, the effect of N on the ratio of $\text{NH}_4^+/\text{NO}_3^-$ depended on landscape position (lowest effect of N on $\text{NH}_4^+/\text{NO}_3^-$ in the downwind sites; landscape position \times N interaction, $P = 0.03$). No other higher-order interactions were significant (under *L. tridentata*, $P = 0.08$ for N \times P interaction; all others $P > 0.24$ in both patch types). Combining all dates, soils in N and N + P plots contained an average $\text{NH}_4^+/\text{NO}_3^-$ ratio of 4.4 ± 1.0 under *L. tridentata* and 15.5 ± 1.6 in interplant spaces ($n = 149$ and 150 , respectively). In comparison, $\text{NH}_4^+/\text{NO}_3^-$ ratios for control plots during the same time period averaged 1.2 ± 0.2 (mean \pm SE) under *L. tridentata* and 2.1 ± 0.3 in interplant spaces ($n = 75$ for both patches), with the highest values occurring during the wet spring of 2008 (3.7 ± 0.6 under *L. tridentata* and 5.1 ± 0.9 in interplant spaces; $N = 15$ for both patches).

Rates of net N_{min}_{pot} were affected variably in soils receiving N addition compared to those that did not, while rates of net Nit_{pot} were elevated under enrichment across patch types and most seasons. Under *L. tridentata*, N addition significantly decreased net N_{min}_{pot} compared to soils that did not receive N during the fall of 2006, but rates were not significantly altered in the other four of five seasons sampled (Table 3; Appendix D). In interplant spaces, N addition altered net N_{min}_{pot} in 3 of 5 seasons, increasing rates of net N_{min}_{pot} in the spring of 2007 but again decreasing rates to near zero compared to plots not receiving N in the fall seasons of 2006 and 2007 (Fig. 3a, Table 3, Appendix D). In contrast, rates of net Nit_{pot} were highly sensitive to N addition, increasing in both patch types across most seasons (Fig. 3b; Table 3, Appendix D). Across all landscape positions, rates of net Nit_{pot} were equal to net N_{min}_{pot} in soils not receiving N additions (Fig. 3, Appendix D; ratio of net Nit_{pot}/net N_{min}_{pot} = 1.2 ± 0.3 [mean \pm SE, $N = 147$] under *L. tridentata*; 1.1 ± 0.1 [$N = 149$] in interplant spaces). However, N addition on average doubled the ratio of net Nit_{pot}:net N_{min}_{pot} in both patch types across most seasons (interplant, 2.4 ± 1.0 ; *L. tridentata*, 2.8 ± 1.1 ; Table 3).

Growth of annual herbaceous plants and perennial shrubs

Annual herbaceous plants emerged following winter rainfall in spring 2008 and 2009 but were rare in the low-

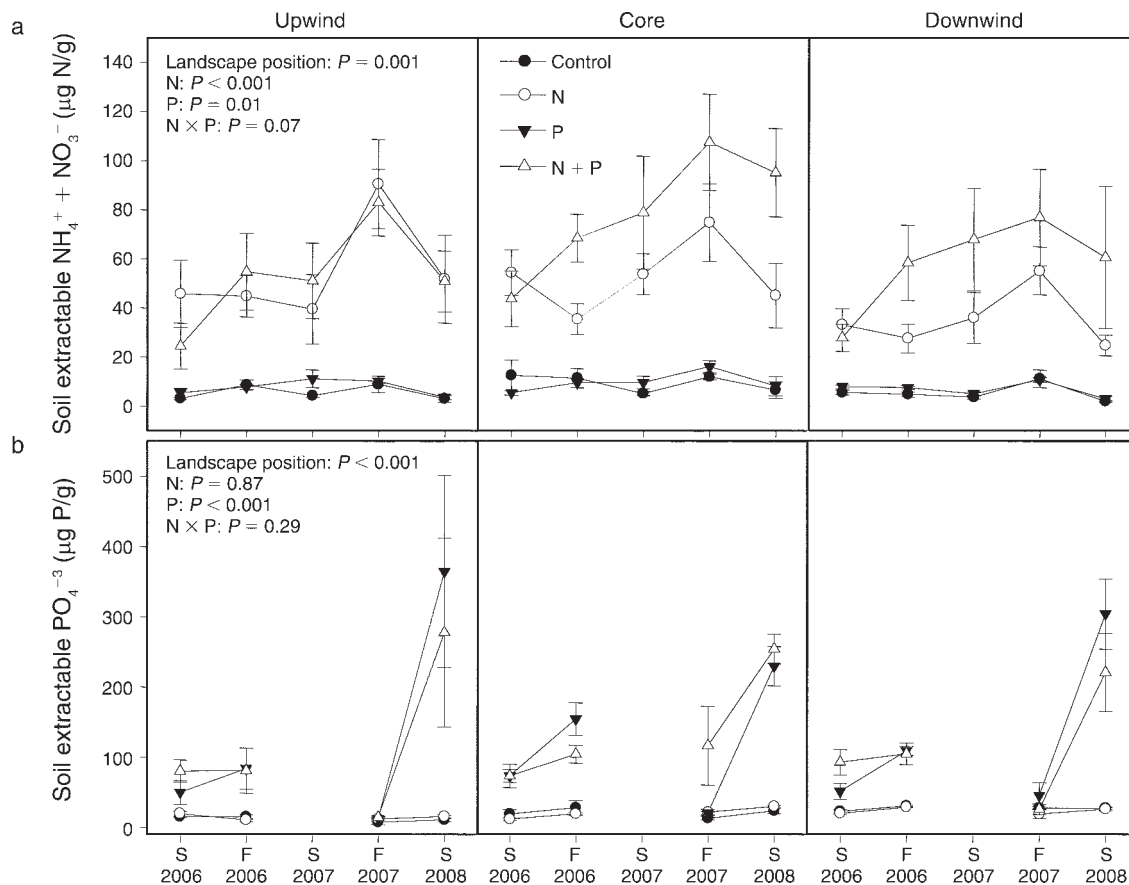


FIG. 2. Extractable inorganic N (sum of NO_3^- and NH_4^+) and PO_4^{3-} concentrations (mean \pm SE; $N = 5$) in soils from experimental plots across the Phoenix metropolitan area. Statistical results are from three-way repeated-measures ANOVA with landscape position, N addition, and P addition as between-subjects factors, following removal of nonsignificant higher-order interactions (retaining the N \times P interaction at the minimum). Data are from interplant spaces only. S stands for spring soil collection; F stands for fall soil collection.

precipitation winters of 2006 and 2007 (not measured). In spring 2008, when winter precipitation exceeded 100 mm across the city, annual herbaceous production increased with N and P addition both under shrubs and in interplant spaces (Fig. 4). There appeared to be a larger effect of P addition under *L. tridentata* in downwind locations compared with other regions that

had less rainfall (Fig. 5a), and a weaker overall P effect in interplant spaces, but interactions between landscape position and nutrient additions were not statistically significant (landscape position \times P: $P = 0.39$ under *L. tridentata*, $P = 0.84$ in interplant space). Production of annuals in spring 2009 was lower than in 2008 following winter rainfall ranging from 69 mm in upwind sites to

TABLE 3. Significance (P values) of N addition on net potential N transformations in soils.

Effects of N addition	Spring 2006	Fall 2006	Spring 2007	Fall 2007	Spring 2008
Net potential N mineralization					
Under <i>L. tridentata</i>	0.19	0.008	0.89	0.23	0.16
Interplant	0.36	<0.001	0.007	<0.001	0.34
Net potential nitrification					
Under <i>L. tridentata</i>	<0.001	0.99	0.011	<0.001	<0.001
Interplant	<0.001	<0.001	<0.001	<0.001	<0.001
Ratio net Nnit_{pot} : Net min_{pot}					
Under <i>L. tridentata</i>	<0.001	0.07	<0.001	0.06	<0.001
Interplant	<0.001	0.001	<0.001	0.02	0.009

Notes: Data represent P values from Mann-Whitney U tests by season and patch type, combining all landscape positions ($N = 30$ per patch type, $\alpha = 0.01$). N addition = N and N + P plots; no N addition = C and P plots.

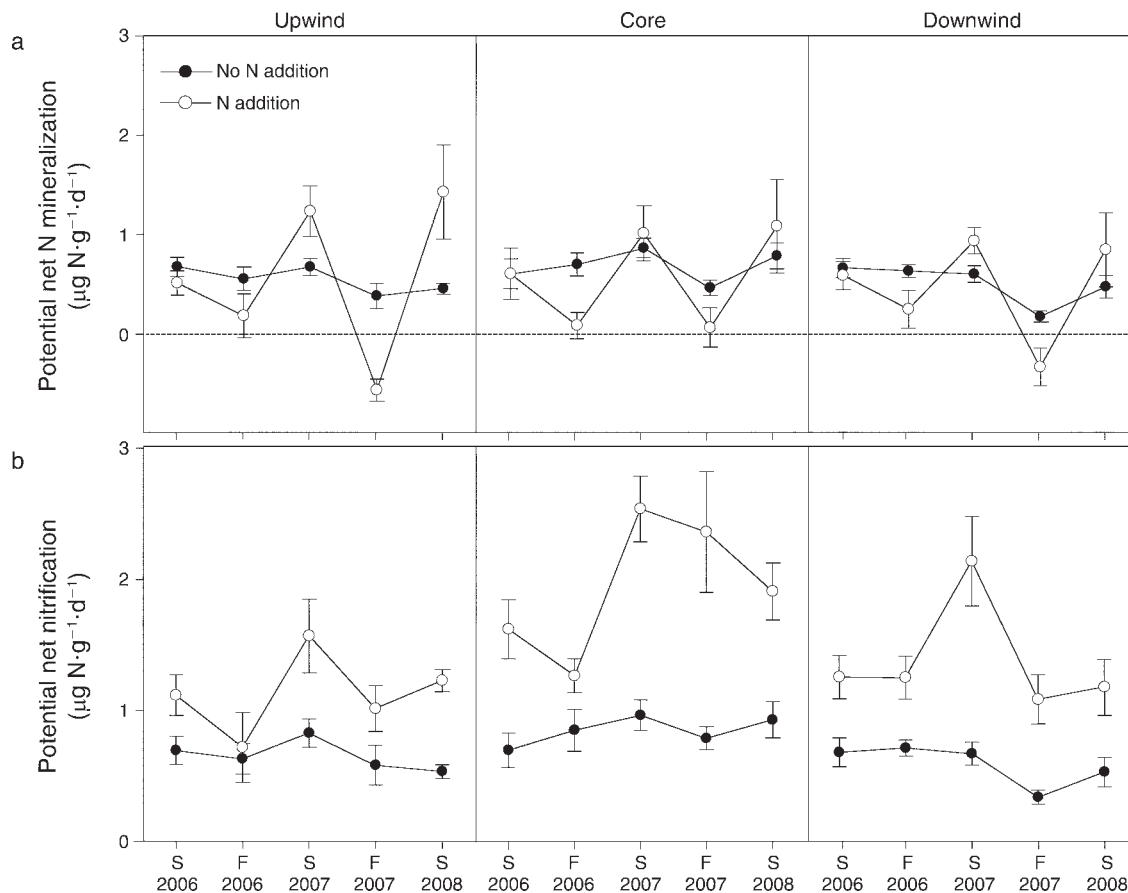


FIG. 3. Potential rates of net N mineralization and nitrification (mean \pm SE; $N = 10$) in soils with N amendments (N and N + P) and without N amendments (C and P). Data are from interplant spaces only.

128 mm in sites downwind of the city (Fig. 4). In contrast to spring 2008, production in spring 2009 was not significantly responsive to N or P under shrubs, but increased in response to N in interplant spaces (Fig. 4). There appeared to be an $N \times P$ effect in interplant spaces in 2009, particularly downwind, but this interaction was not significant ($P = 0.15$). No interactions between nutrient additions and landscape position were significant in 2009; $P > 0.46$ for both patch types).

In both springs of 2008 and 2009, rainfall was higher downwind compared to the core and upwind sites, which received similar rates of precipitation (Fig. 5a; one-way ANOVA rainfall \times landscape position within years; $N = 5$ plots per landscape position). Heterogeneity of regression coefficients across landscape positions prevented use of rainfall as a covariate in an ANCOVA to explore the relationship of nutrient additions to growth of winter ephemeral plants. However, across all treatments, herbaceous biomass was significantly related to rainfall only under shrubs in 2008 (under shrubs, $r^2 = 0.13$, $P = 0.005$; interplant space not significant, $r^2 = 0.01$, $P = 0.42$) and in both patch types in 2009 (under shrubs, $r^2 = 0.49$, $P < 0.001$;

interplant space, $r^2 = 0.31$, $P < 0.001$). Changes in soil acidity resulting from fertilization could also confound the effects of nutrient availability in our sites. However, in a stepwise multiple regression with seasonal rainfall and soil properties/processes as independent variables (pH, inorganic N, net N mineralization; all variables measured only in spring 2008), soil pH in unfertilized plots was not significantly related to herbaceous plant growth within either patch type, despite a pH range of 6.6 to 8.2 in interplant spaces and 6.1 to 8.0 under *L. tridentata* across the three landscape positions studied ($N = 15$ per patch type).

In contrast to annual plants, perennial desert shrubs showed no responses to nutrient enrichment, even in the wet year of 2007–2008 (October to October) in which rainfall was $>30\%$ higher than long-term average (20-year average, 198 mm; Fig. 5a [FCDMC 2009]). Stem elongation of *L. tridentata* averaged 56 ± 2 mm/season over the winter/spring and 132 ± 13 mm/season (mean \pm SE) during the summer and fall ($N = 240$, 239, respectively; Fig. 5b). Growth was not affected by nutrient addition (between-subjects tests of repeated-measures ANOVA over eight seasons [spring 2006–

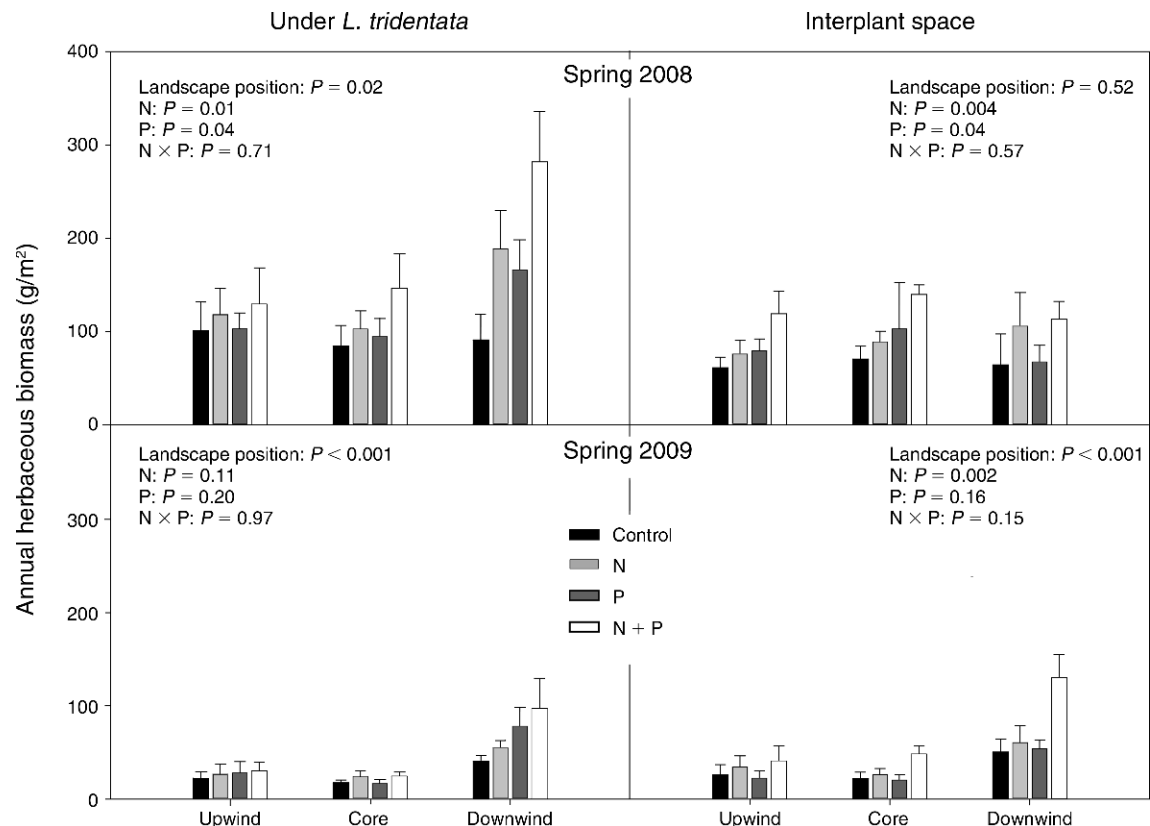


FIG. 4. Annual herbaceous biomass (mean \pm SE; $N = 5$) harvested in March of each year following winter rains in 2008 and 2009. Statistical results are from three-way ANOVA performed separately for each patch type within each year. $N = 5$; error bars indicate \pm SE.

spring 2009]; $P = 0.81, 0.96, 0.98$, for N, P, and N \times P, respectively; Fig. 5b). Interactions between landscape position and nutrient additions were not significant, although the power to detect small differences in stem elongation was low. In contrast, stem elongation was significantly different among landscape positions ($P < 0.001$; upwind < core = downwind). Density of leaves on *L. tridentata* stems averaged 1.6 ± 0.03 leaves/cm (mean \pm SE) and was also unrelated to nutrient additions (three-way ANOVA, landscape position, N, and P; $P = 0.95, 0.32$, and 0.90 , respectively; no significant higher-order interactions). Elongation of *Ambrosia* stems declined from 78 ± 8 mm between October and March of 2006 to 27 ± 4 mm over the same time period in winter 2007. (Growth was not significantly different from zero during the summer seasons.) During the springs of 2006 and 2007, *Ambrosia* stem elongation was higher in core and downwind locations compared to sites upwind (landscape position, $P < 0.001$), but, like *L. tridentata*, was not affected by N or P addition (for N, $P = 0.58$; for P, $P = 0.76$; N \times P interaction, $P = 0.39$; data not shown). Similarly, there were no significant interactions between landscape position and nutrient additions on *Ambrosia* stem elongation.

Plant tissue chemistry

Nutrient additions altered foliar chemistry of all plant functional groups sampled in this study, but the strength of this effect was larger for winter herbaceous annual plants compared to perennial shrubs (Fig. 6). Foliar N concentration of *L. tridentata* increased with N addition, but the effects of landscape position, P addition, or the interaction between N and P were not significant (Fig. 6a: $P < 0.001, 0.07, 0.09$, and 0.40 , respectively). Although there appeared to be an interaction between N additions and landscape position (larger effect of N in upwind and downwind regions), this relationship was not statistically significant within our experimental design (landscape position \times N, $P = 0.07$; Fig. 6a). Post hoc ANOVA tests showed that N addition increased *L. tridentata* foliar N concentration only after winter rainfall (spring 2006, 2007, 2008; $P = 0.01, 0.001$, and 0.001 , respectively), and then only modestly, by 8% on average. Foliar P varied by landscape position ($P < 0.001$; upwind > core, core = downwind, upwind = downwind), but P concentration of *L. tridentata* foliage was not significantly affected by N or P addition, or their interaction ($P = 0.43, 0.07, 0.85$, respectively; Fig. 6b). Lack of a significant P fertilization effect on *L. tridentata* foliar P concentration was confirmed in post

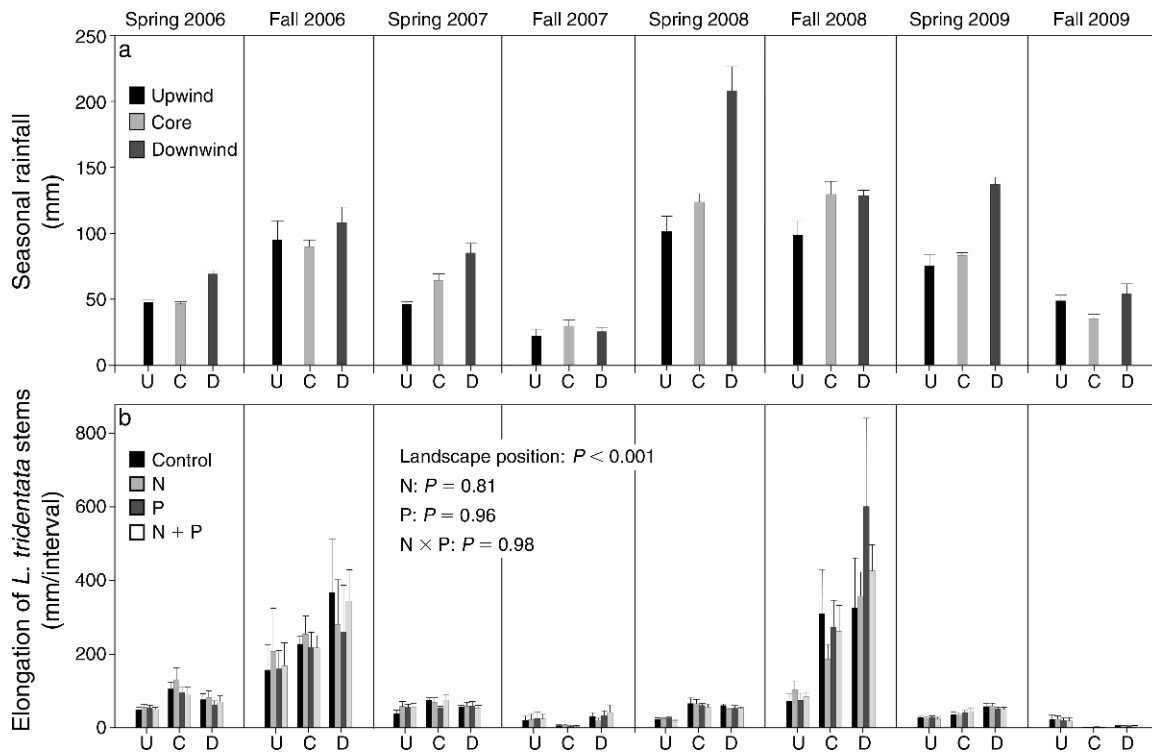


FIG. 5. (a) Seasonal rainfall in sites across the city and (b) stem elongation of *Larrea tridentata* in experimental plots across eight seasons from 2006 through 2009 in relation to landscape position relative to the urban airshed. Key to abbreviations: U, upwind; C, core; D, downwind. Data are mean \pm SE; $N = 5$. Statistical results are from repeated-measures ANOVA.

hoc three-way ANOVA tests by season ($\alpha = 0.016$; spring 2006, $P = 0.51$; fall 2006, $P = 0.02$; spring 2008, $P = 0.06$). There were no significant interactions between nutrient additions and landscape position (Fig. 6b). For *Ambrosia* spp. (only *A. deltoidea* used, all landscape positions averaged), N addition had no effect on N concentration in spring foliage (two-way repeated measures ANOVA, $P = 0.95$), which ranged from 3.0% to 3.2% N. P addition, however, did increase foliar N of *A. deltoidea* ($P = 0.03$), and post hoc ANOVA tests showed that this was observed only in spring 2007 (by 11%) but not spring 2006. The interaction between N and P was not significant, nor were there significant interactions between landscape position and nutrient addition. Measured in spring 2006 only, foliar P of *A. deltoidea* ranged from 0.12% to 0.23% and was not significantly affected by N addition ($P = 0.78$), P addition ($P = 0.24$) or interaction of the two ($N \times P$; $P = 0.47$).

In contrast to the subtle effect of nutrient enrichment on foliar chemistry of perennial shrubs, both N and P addition dramatically altered tissue nutrient concentration of *Pectocarya* spp. In spring 2008, foliar N concentration of *Pectocarya* spp. was similar across both patch types (Appendix E; four-way ANOVA, patch, $P = 0.97$; no significant patch \times landscape position, N, or P interactions). Combining patch types, foliar N varied by landscape position ($P = 0.04$), but

post hoc Tukey analyses failed to distinguish differences between upwind, core, and downwind locations. In 2008, N addition increased foliar N concentration of *Pectocarya* spp. by 50% on average ($P < 0.001$; Fig. 6c). Neither P nor the interaction between N and P were significant ($P = 0.77$, 0.09 , respectively), nor were there any significant landscape \times nutrient interactions ($P > 0.14$). In spring 2009, the effect of patch type on foliar N concentration depended on landscape position, so patches were analyzed separately. Foliar N of *Pectocarya* varied by landscape position under shrubs but not in interplant spaces (shrubs: $P < 0.001$, upwind $>$ core and downwind, core = downwind; interplant space: $P = 0.12$). Both under *L. tridentata* and in interplant spaces, N addition increased tissue N concentration of *Pectocarya* on average by 98% across all landscape positions ($P < 0.001$ for both patch types). Foliar N of *Pectocarya* spp. in 2009 was not affected by P addition ($P = 0.96$), the interaction between N and P ($P = 0.32$), or interactions between landscape position and nutrient additions (Fig. 6c).

The effect of nutrient enrichment on foliar P concentration of *Pectocarya* was larger than the response of foliar N. Under *L. tridentata* canopies, N addition and P addition significantly increased foliar P concentration in *Pectocarya* spp. on average by 30% and $>100\%$, respectively (mean across 2008 and 2009; N, $P = 0.04$ for both years; P, $P < 0.001$ for both years;

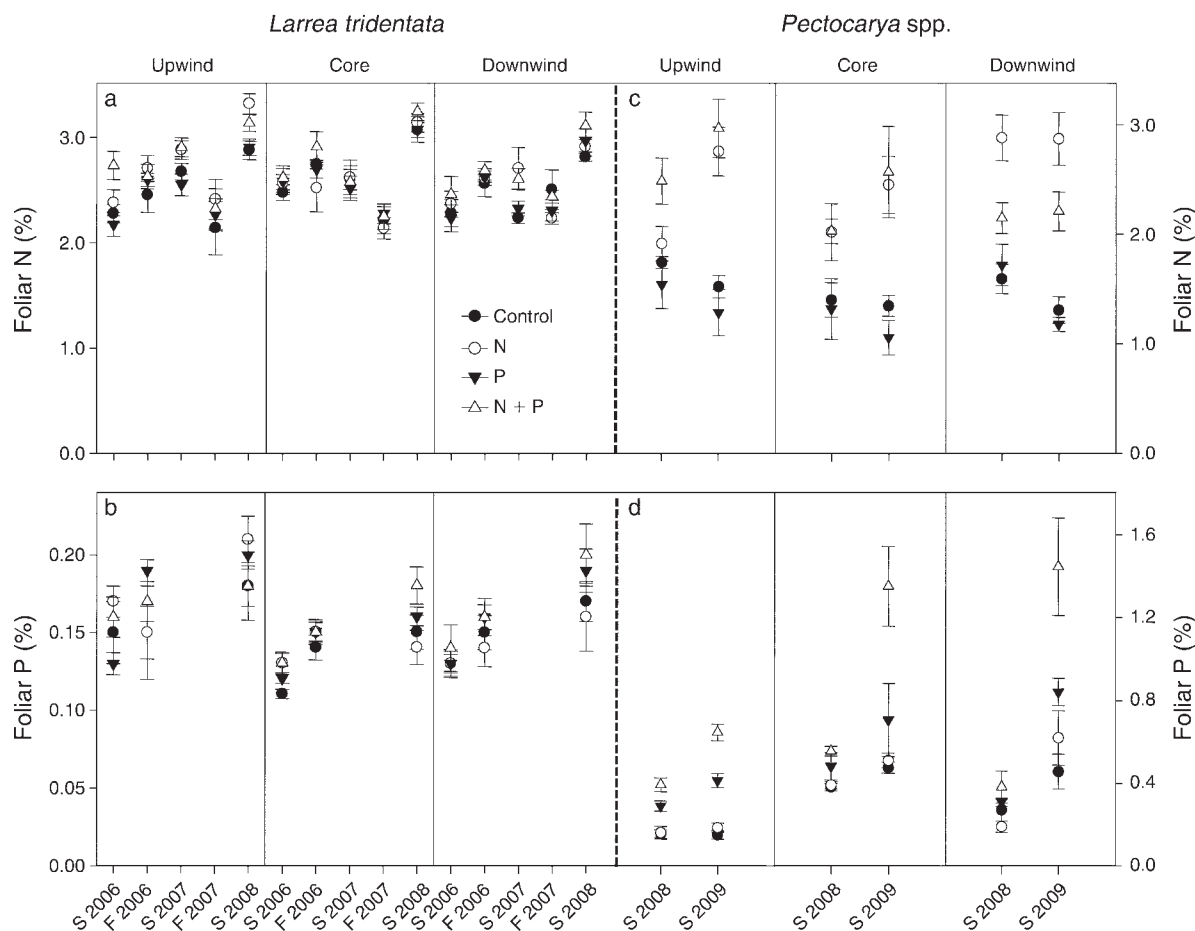


FIG. 6. Foliar N and P concentrations in response to factorial nutrient enrichment in individuals of the perennial evergreen shrub *Larrea tridentata* (a, b; left-hand scale), and *Pectocarya* spp., spring herbaceous annual species growing in interplant spaces (c, d; right-hand scale); note the difference in scale for foliar P of *Pectocarya* compared to *L. tridentata*. Data are means \pm SE; $N = 4-5$ (*Pectocarya* was absent from one site in the urban core).

Appendix E). In interplant spaces, the effect of P addition on foliar P concentration depended on N, with tissue concentration highest under combined N and P fertilization ($N \times P$ interaction, $P = 0.03$, 0.05 for 2008 and 2009, respectively). In interplant spaces, P and N + P additions increased foliar P of *Pectocarya* by 53% and 101% above that in unfertilized plots in 2008 and by 112% and 299%, respectively, in 2009 (Fig. 6d). Foliar P also varied by landscape position in both years (2008 foliar P highest downwind; 2009 foliar P lowest in core), but interactions between landscape position and nutrient addition were not significant in either patch type or year ($P > 0.15$; Appendix E).

DISCUSSION

Sonoran Desert ecosystems within and outside the Phoenix metropolitan area were both resistant and sensitive to N enrichment, depending on the functional groups considered and the extent to which they were limited by factors other than N, including water, C, or P.

Impacts of nutrient additions on potential microbial N transformations in soils

Soil microorganisms in deserts are most abundant within the top few centimeters of the surface, where they are readily exposed to exogenous N sources from atmospheric deposition, overland hydrologic transfers, and NH_4^+ fixed by biological soil crust communities (Belnap et al. 2003, Welter et al. 2005). The relative availability of surface N, combined with abiotic photo-degradative losses of litter C and low organic matter pools, leads to persistent C limitation of microbial biomass (Gallardo and Schlesinger 1995, Austin and Vivanco 2006). Given C limitation, we hypothesized that heterotrophic processes such as N mineralization would respond less consistently to inorganic N addition than would nitrification, assuming that nitrification is performed by chemoautotrophic microorganisms. Recent data from the Chihuahuan and Sonoran Deserts suggest that fungi are the dominant nitrifiers and denitrifiers in arid ecosystems (McLain and Martens 2006, Crenshaw

et al. 2008), a link that is explicitly incorporated in the Threshold-Delay Nutrient Dynamics model (Collins et al. 2008). However, preliminary data from laboratory incubations of soils from our sites show that nitrification is performed by nonfungal, primarily autotrophic organisms (S. Hall, *unpublished data*). Consistent with our expectations, we found that N enrichment of desert soils increased the ratio of net $\text{nit}_{\text{pot}}:\text{net N}_{\text{min}_{\text{pot}}}$ immediately after the onset of N additions, similar to patterns found in N-rich ecosystems such as N-saturated temperate and P-limited tropical forests (Johnson 1992, Aber et al. 1997, Hall and Matson 2003).

Microbial N cycling in N-limited mesic ecosystems is often tightly linked to plant demand, such that nitrification (and the NO_3^- pool) is low relative to N mineralization due to competition for NH_4^+ between nitrifiers, plants, and other microbes (Schimel and Bennett 2004). In arid ecosystems, including the ones studied here, rates of net nitrification are often similar to net N mineralization ($\sim 1:1$), highlighting the important role of nitrifying microorganisms in the nitrate economy of drylands (Davidson et al. 1993, Fenn et al. 2003b), and the close linkage between these two processes. The TDND model highlights the low activation thresholds of soil microbial communities, which can be stimulated by even trace precipitation in amounts too low to trigger plant responses (Collins et al. 2008). Combined with a patchy plant distribution, this differential response to precipitation can lead to spatial and temporal decoupling of microbial N turnover and plant N uptake (Augustine and McNaughton 2004), which can leave NH_4^+ susceptible to nitrification and subsequent hydrologic and gaseous losses. Our results are consistent with this model but further suggest that the ecological consequences of N enrichment will depend in part on the relative importance of chemoautotrophic and heterotrophic nitrification in desert soils. If nitrification is linked to organic C degradation in fungal metabolism, supplemental NH_4^+ alone would have a limited effect on this process, unless long-term N enrichment significantly increases C availability to microorganisms. We propose that in situations where chemoautotrophic nitrifiers dominate, N deposition is likely to uncouple interactions between heterotrophic and chemoautotrophic microbial communities.

Multiple resource limitation in desert plant communities

In a recent global meta-analysis, Le Bauer and Treseder (2008) found that N limitation of net primary production is widespread across latitude and climate in all the biomes they considered, with a notable exception of deserts. Indeed, few experimental studies have evaluated nutrient limitation in arid plant communities, particularly over the long term (see Adams [2003] for a global review). Our results provide evidence for N limitation, but only for seasonal herbaceous plants, which are important components of arid ecosystems. Desert annuals are valued for their diverse wildflower

displays and as forage for arthropods and other animal consumers (Davidson et al. 1984). As shallow-rooted drought-avoiders, their germination and subsequent growth ultimately depend on the timing and abundance of rainfall (Whitford 2002). However, during seasons when water is available, production of these communities has been shown to be N-limited (Gutierrez et al. 1988, Ludwig et al. 1989, Brooks 2003, Allen et al. 2009, Rao and Allen 2010), although few studies have explored growth over multiple years (see Xia et al. 2010) or investigated the joint importance of P (McMaster et al. 1982, Drenovsky and Richards 2004).

In this study, production of winter annual plants in the Sonoran Desert responded to additions of both N and P in the wet winter of 2008 (>100 mm average rainfall) but only to N, and only in some parts of the landscape, during the drier winter of 2009. Specifically, N availability in more fertile plant islands appeared to be sufficient to support moderate rates of annual herbaceous production induced by low rainfall in 2009, but N limitation was more prominent in less-fertile interplant patches. Alternatively, annual plants growing under *L. tridentata* may have been more water limited than those in interplant patches, as species interactions under shrub canopies can switch from facilitation to competition in dry years (Báez and Collins 2008). Together, these results underscore the secondary role of nutrients relative to water, even in seasonal herbaceous plant communities (Rao and Allen 2010). Specifically, over the four years studied here, winter annual plants exhibited a climate-driven cascade of resource limitation, from very low production in seasons of low rainfall (winter 2006 and 2007), to moderate and patchy N limitation with average precipitation (winter 2009), to limitation by both N and P in a season of above-normal rainfall (winter 2008). Both the TDND model and the Threshold-Delay model of aridland plant productivity predict sequential limitation by water and N, but neither explicitly considers the role of available P in ecosystem dynamics, despite its possible importance to biota under conditions of elevated N deposition, particularly in wet years, seasons, or parts of the landscape.

The responsiveness of annual herbaceous growth and foliar chemistry also highlights the important role these communities play in regulating N dynamics of desert ecosystems. Additions of N increased production by 50% in both 2008 and 2009, despite substantial differences in absolute growth between years. Additionally, nutrient content of herbaceous plants was highly plastic. Tissue N concentration of the dominant annual forb, *Pectocarya* spp., increased by 50% in a wet year and up to 98% the following drier year in N-fertilized plots compared to controls, with the difference between years likely reflecting a dilution effect of higher production in 2008. If the tissue nutrient concentration of *Pectocarya* is representative of the total herbaceous plant biomass, production of spring annual

plants in unfertilized plots would take up 13 kg N/ha in a wet year (average 79 g dry mass/m², 1.6% N) and 4.2 kg N/ha in a drier year (average 30 g dry mass/m², 1.4% N), which is within the range of modeled and measured annual N deposition within the Phoenix metropolitan area (7.5–15 kg N·ha⁻¹·yr⁻¹ modeled [Fenn et al. 2003a]; 4–7 kg N·ha⁻¹·yr⁻¹ measured [Lohse et al. 2008]). The rate, timing, and form of N addition in this experiment is far different than what is likely to be experienced naturally from N deposition and was used to test the plasticity and limitation of the system under substantial perturbations of nutrient supply. However, the apparent sensitivity of biomass and tissue N concentration of *P. recurvata* to N enrichment support the idea that these ephemeral communities may act as a “vernal dam” for nutrients, comparable in function to spring herbaceous plants that reduce N losses within northern hardwood forests (Muller and Bormann 1976, Chen et al. 2009). Microorganisms in forest soils also play a large role in nutrient retention, immobilizing larger quantities of N in spring runoff than understory herbs (Zak et al. 1990, Rothstein 2000). Although this hypothesis must be tested directly, growth of seasonal annual plants may be particularly important for nutrient retention in deserts due to C limitation of microbial biomass that may limit microbial N immobilization. Our results suggest that changes in climate that reduce or enhance winter rainfall in arid ecosystems are likely to have major implications for nutrient cycling through the dynamics of ephemeral plant assemblages.

Although they showed considerable plasticity in their response to N additions in the short term, the ability of spring annuals to retain N deposition within desert ecosystems over the long term is unclear. If N additions increase the supply of labile C to arid soils through enhanced plant growth, litter quality, and decay, herbaceous production could represent an important mechanism of N retention through a reinforcing cycle of fertility due to plant and microbial growth, higher SOM pools, increased water-holding capacity, and increased soil moisture. However, prominent abiotic forces in deserts such as aeolian or hydrologic redistribution of litter (Belnap et al. 2005) or photodegradation (Austin and Vivanco 2006) may ultimately limit incorporation of C from annual herbaceous biomass into soils and biotic pools. Moreover, years with high growth of herbaceous annuals in the Mojave and Sonoran Deserts are infrequent, occurring on average every 5–7 years, associated with El Niño Southern Oscillation (ENSO) episodes (Bowers 2005). Thus, while N is retained temporarily through uptake into herbaceous plant communities, high-production years are unpredictable and abiotic processes during the subsequent hot and dry seasons may recycle N back to surface soils, where it is susceptible to loss.

In contrast to the responsiveness of annual plants, production of perennial shrubs in the northern Sonoran Desert was not affected by N or P after four years of

fertilizer addition. Growth of desert shrubs is expected to be primarily N limited in wet years or seasons, or in parts of the landscape where water accumulates (Smith et al. 1997). Indeed, several studies in the Chihuahuan Desert found that N fertilization increased production of *L. tridentata*, even without supplemental water additions (Ettershank et al. 1978, Lightfoot and Whitford 1987, Fisher et al. 1988, Lajtha and Whitford 1989). However, in the Sonoran and Mojave Deserts, both of which receive less summer rain on average than the Chihuahuan Desert (Reynolds et al. 2004), N fertilization had a weak effect on *L. tridentata* growth or N uptake, and only in some years (Romney et al. 1978, Sharifi et al. 1988, Barker et al. 2006). *L. tridentata* is a drought-resistant evergreen shrub that is thought to maintain metabolic activity in dry periods through both deep root systems that can access subsurface water from prior seasons or years, as well as shallow “rain” roots that can proliferate quickly when soil moisture becomes available (Smith et al. 1997, BassiriRad et al. 1999, Ogle and Reynolds 2004). Consequently, like many drought-adapted plants, *L. tridentata* is thought to be capable of responding rapidly to pulsed nutrient availability through increased N uptake and storage (BassiriRad et al. 1999).

Despite this potential for nutrient response, growth of shrubs for all treatments in this study was greatest following summer monsoon rainfall and modulated by rates of water infiltration across all four years that span a range of precipitation inputs (summer rainfall 26–121 mm; R. Sponseller, *unpublished data*). Furthermore, although slight in comparison to the responsiveness of annual plants, foliar N concentration of *L. tridentata* was augmented by N addition during the winter and spring, which suggests that nutrient treatments were effective in reaching plant roots. Overall, these results are similar to those recently reported in a multiyear, nutrient-addition experiment in a seasonally dry mediterranean ecosystem in southern California, which also showed no N limitation of shrub growth (Vourlitis et al. 2009). Slow-growing plants in environments where resources are unpredictable are known to consume limiting nutrients beyond their immediate growth requirements; for example, absorbing and storing N to support production at a later time (Chapin 1980). However, additional N taken up by *L. tridentata* did not translate into an aboveground growth response during any season, even during a wet year, over this four-year study.

The current paradigm of desert primary production dynamics, reflected in the TDND and other models, predicts that growth of shrubs such as *L. tridentata* will be limited by N availability during above-normal rainfall years, when soil moisture is sufficient. Thus, one hypothesis is that *L. tridentata* in this part of the Sonoran Desert are more shallow rooted than in other similar systems, and thus receive pulses of N following storms, but ultimately experience stronger water limita-

tion from soil drying than nutrient availability for most, if not all, of the year. This idea is consistent with observations made in the Colorado Plateau, where N addition increased production of a deeper-rooted perennial C3 grass but did not affect growth of a more shallow-rooted, C4 species that may have experienced water stress (Schwinning et al. 2005). An alternative explanation for a lack of nutrient effects on shrubs is that deeper roots of *L. tridentata* are tapping into subsurface nitrate pools (Walvoord et al. 2003), or that high ambient N concentration in spring *L. tridentata* leaves (average $2.6\% \pm 0.3\%$ N unfertilized) is sufficient to support temporary pulses of production associated with summer monsoon storms. Regardless of mechanism, our results suggest that different plant functional groups are likely to respond in very different ways to environmental change in desert ecosystems.

Urbanization and nutrient limitation of plant growth in the Sonoran Desert

We hypothesized that primary production in the urban core would be less N limited and more limited by P than in locations upwind or downwind of the Phoenix metropolitan area due to long-term N enrichment from the urban atmosphere. In our design the power to detect significant landscape \times nutrient interactions was low when effect sizes were small (five replicate plots per landscape position and nutrient additions over multiple seasons). Moreover, a gradient of rainfall across our sites was more important than nutrient additions for shrub growth, even during a wet year, suggesting persistent water limitation across the year. However, we were particularly surprised to find limited interaction between nutrient additions and landscape position for annual herbaceous plants that show considerable plasticity in nutrient uptake and growth and experienced P limitation during the wet winter of 2008. Rates of N deposition in the Phoenix area are relatively low, and recent research suggests that aerosol nitric acid (HNO_3), a large component of dry deposition near cities (Bytnerowicz et al. 2007), may accumulate abiotically on leaf surfaces in insoluble form, effectively decreasing atmospheric N entry into arid soils until leaf abscission (Padgett et al. 2009). Nevertheless, N deposition is higher in the urban core compared to upwind and downwind locations (Lohse et al. 2008), and soil inorganic N concentration is elevated in unamended desert remnant sites within the city over most seasons (Hall et al. 2009, Koerner and Klopatek 2010). Upon soil wetting, it is possible that deposited NH_4^+ and NO_3^- are rapidly transformed through biotic and abiotic processes (Davidson et al. 1993, Schaeffer and Evans 2005, McCalley and Sparks 2009), leached below the rooting zone (Marion et al. 2008a), or redistributed and concentrated to low points of the landscape in surface runoff (Belnap et al. 2005), leading to losses or transfers that limit long-term N enrichment of desert ecosystems exposed to the urban atmosphere.

Toward a conceptual understanding of the fate of N deposition in arid ecosystems

Synthesized with evidence from recent studies and predictions from the TDND model, our research suggests that desert ecosystems may have limited ability to retain atmospheric N deposition due to water or C limitation of plant and microbial production, the prevalence of abiotic biogeochemical processes, and the temporal/spatial separation of N availability and biotic N demand that allows N losses or transfers to occur (Fig. 7). We hypothesize that in dry periods (Fig. 7a), abiotic processes dictate the fate of N deposition, including accumulation of insoluble, dry-deposited N compounds on shrub foliage (Padgett et al. 2009), accumulation of dry-deposited inorganic N on soil surfaces (Michalski et al. 2004), photodegradation and aeolian transfer of plant material that may have assimilated N from deposition during previous wet periods (Austin and Vivanco 2006, Peters and Havstad 2006), and, in some cases, trace N gas emissions from organic or inorganic N compounds on hot or alkaline soil surfaces (McCalley and Sparks 2009). When pulsed precipitation events punctuate hot, dry summer periods (Fig. 7b), biotic activity quickly processes deposited N through nitrification of deposited, newly fixed, or mineralized NH_4^+ (or organic N, if fungi are dominant nitrifiers), leading to NO_3^- and NO_x gas losses (Hall et al. 2008), and denitrification of deposited or transferred NO_3^- in low spots on the landscape that receive runoff (also leading to gas losses [Belnap et al. 2005]). Uptake of N into vegetation may be minimal due to rapid evaporation and runoff from pulsed rainfall events that limit infiltration. Alternatively, in permeable soils or parts of the landscape that support rapid infiltration, such as under shrubs, NO_3^- in runoff may be leached quickly below the rooting zone before plant uptake can occur (Graham et al. 2008, Marion et al. 2008a).

We hypothesize that the fate of N deposition in warm, arid ecosystems will be most similar to mesic ecosystems during winter and spring (Fig. 7c) when cooler temperatures and less intense, longer-duration precipitation events limit the magnitude of evaporation and runoff (Schwinning and Sala 2004), promoting infiltration of deposited N to surface or subsurface soils. Accumulated N may be taken up into ephemeral annual plants, but only if the timing and magnitude of winter rainfall is appropriate for germination and growth of herbaceous flora. N that is assimilated by winter ephemeral plants may be remobilized during the subsequent warm, dry spring and summer through abiotic processes (Fig. 7a, b).

Because ecosystem nutrient dynamics depend ultimately on climate, the fate of N deposition in deserts will depend on current and future temperature and precipitation regimes. In deserts that experience higher summer rainfall (e.g., Chihuahuan Desert), growth of summer herbaceous vegetation may act as an additional nutrient "dam," reducing N losses. Indeed, the extent of

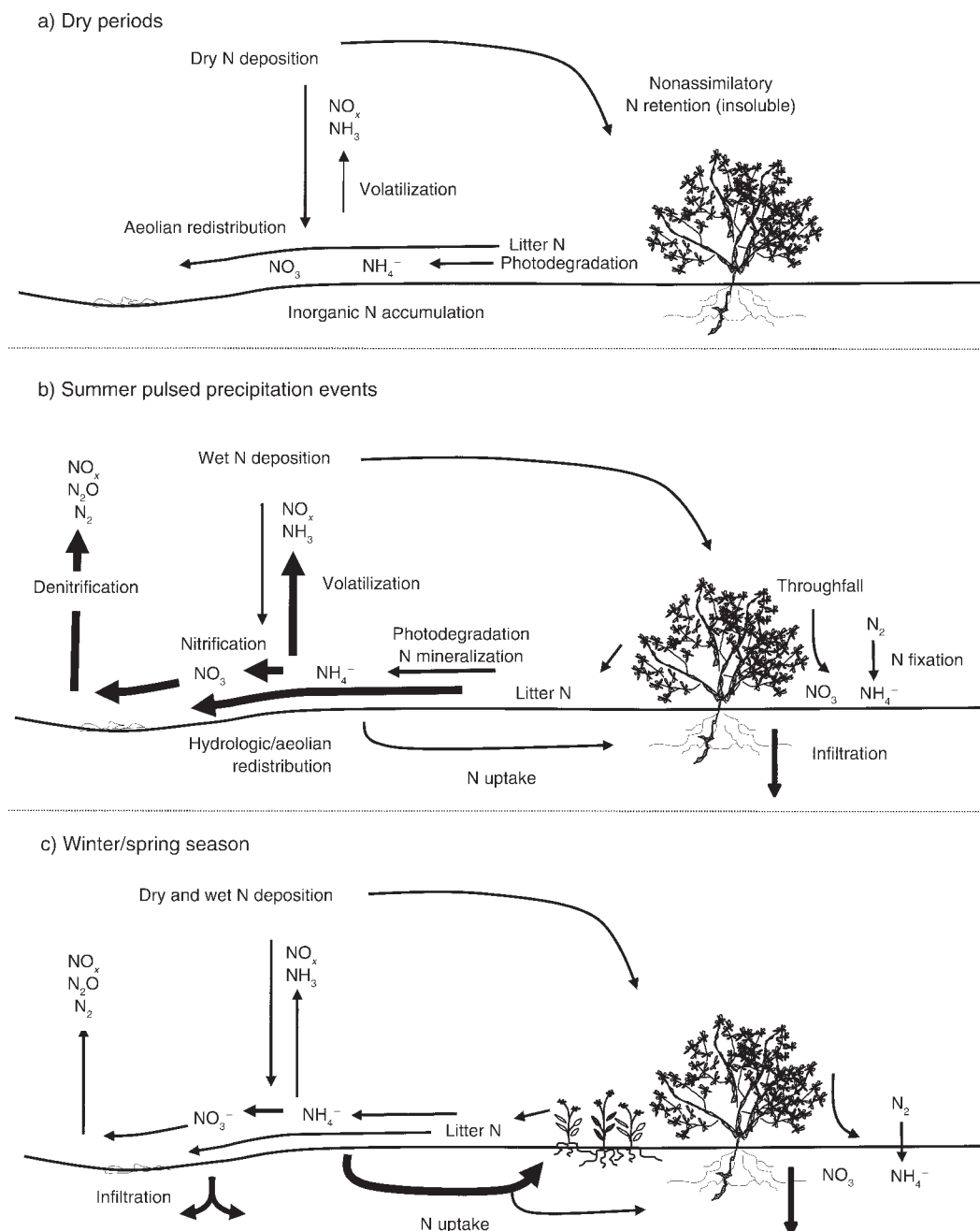


FIG. 7. Conceptual framework describing the fate of N deposition in deserts. Arrows highlight hypothesized pathways of N deposition, uptake, transfer, or loss. The width of the arrows signifies the relative strength of each process. Further research to clarify the mechanisms and importance of these pathways is necessary for a more complete understanding of N cycling and retention in arid ecosystems. For additional explanation, see *Discussion: Toward a conceptual understanding of the fate of N deposition in arid ecosystems*.

N retention in arid ecosystems is likely regulated by the spatial and temporal continuity of plant and microbial biomass across the landscape. For example, in semiarid ecosystems of New Mexico, biological soil crusts and perennial grasses are functionally linked by networks of fungal hyphae (Green et al. 2008), which integrate distinct patches and thus reduce the probability of N

losses. N deposition may stimulate invasion of exotic grasses, as in the Mojave and Sonoran Deserts (Brooks 2003, Allen et al. 2009), which could lead to higher N retention, at least in the short term. However, N losses would occur if grass invasion promotes fire, along with a fundamental change in ecosystem functioning (D'Antonio and Vitousek 1992, Brooks and Pyke 2001).



PLATE 1. Graduate students harvesting herbaceous annual biomass in the N + P fertilized plots at the White Tank Mountains (Arizona, USA) in spring 2010. Note the relatively low biomass on the other side of the plot boundary in the upper left corner of the photo. Photo credit: D. Huber.

CONCLUSIONS

Ecosystems in the Sonoran Desert across the Phoenix metropolitan area exhibited variable responses to N enrichment, depending on the functional groups considered and the extent to which these organisms were limited by water, P, or C. Results from this study highlight the importance of using long-term experiments and testing multiple resource limitation to understand the mechanisms of plant and microbial community responses in temporally heterogeneous arid systems. Furthermore, our results advance current understanding of aridland ecosystem functioning as articulated by the Threshold-Delay Nutrient Dynamics paradigm, and they provide empirical evidence for modifications that will enhance its utility in predicting the ecosystem consequences of human-induced environmental change. Numerous lines of evidence suggest that aridland N cycling is more “open” than that of mesic systems (Austin and Vitousek 1998, Swap et al. 2004, McCulley et al. 2009) due to high N gas losses from soils and hydrologic redistribution of NO_3^- (Walvoord et al. 2003, Ewing et al. 2007). These findings have led to the suggestion that surface soils in aridlands are functionally “N saturated” (Marion et al. 2008b). Extended to the ecosystem scale, some of our results support this premise, particularly the lack of shrub growth in response to N additions and limited effects of N on potential heterotrophic microbial activity. However, across the year, and over multiple years, we show that

deserts are not N saturated as originally defined for forests, where N availability exceeds biological demand, leading to decreased N retention capacity (Fenn et al. 1998). Rather, some aridland plants experience N limitation, potentially due to high N losses that result from the spatial and temporal decoupling of N supply and demand, and abiotic forces that persist through dry seasons and spatially redistribute N inputs (Vitousek et al. 1998). Indeed, seasonal herbaceous communities are highly responsive to N additions and have the capacity to retain significant quantities of exogenous N, at least temporarily. However, the capacity of ephemeral annual plants to facilitate long-term N retention ultimately depends on the timing and amount of precipitation. In other words, intra- and interannual climate variability will mediate biotic N use within the broader constraints on N availability regulated by transfer and loss pathways. Climate change in the 21st century is expected both to reduce winter–spring precipitation across the Southwest and to potentially change the periodicity of the ENSO (Seager et al. 2007, Karl et al. 2009). These trends suggest that the potential for retention of N deposition in biotic reservoirs is likely to vary from year to year, but ultimately may be limited in desert ecosystems, even as N loading continues to increase.

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APPENDIX A

Effect of nutrient additions on soil organic matter concentration (*Ecological Archives* A021-035-A1).

APPENDIX B

Effect of nutrient additions on soil pH (*Ecological Archives* A021-035-A2).

APPENDIX C

Effect of nutrient additions on soil extractable inorganic N and P concentrations from inter-plant spaces and from under *Larrea tridentata* (*Ecological Archives* A021-035-A3).

APPENDIX D

Effect of nutrient additions on net potential N mineralization and nitrification (*Ecological Archives* A021-035-A4).

APPENDIX E

Effect of nutrient additions on foliar N and P concentrations of *Pectocarya* spp. (*Ecological Archives* A021-035-A5).