Published in final edited form as:

J Arid Environ. 2007 July ; 70(1): 164–173. doi:10.1016/j.jaridenv.2006.12.005.

CARBON AND NITROGEN STORAGE IN SOIL AND LITTER OF SOUTHERN CALIFORNIAN SEMI-ARID SHRUBLANDS

George L. Vourlitis, Gypsi Zorba, Sarah C. Pasquini, and Robert Mustard

Department of Biological Sciences, California State University, San Marcos, CA 92096

Abstract

Semi-arid shrublands of southern California, including chaparral and coastal sage, are found in widely varying elevation and microclimatic regimes and are subjected to disturbance such as fire and atmospheric N deposition that have the capacity to alter soil and litter C and N storage. Here we present a case study where soil and litter C and N were measured over 19 months in post-fire chaparral and mature coastal sage stands to assess whether differences in soil and litter C and N between these diverse shrublands could be attributed to differences in elevation, stand age, rainfall, and/or estimated N deposition exposure. Our results indicate that atmospheric N deposition exposure, either alone or in conjunction with other environmental variables (elevation, rainfall, and/or stand age), was the most frequent predictor of the spatial pattern in the soil and litter N and C variables observed. These results are consistent with those reported for high-elevation coniferous forests arrayed along an N deposition gradient in southern California, suggesting that N deposition may affect the soil N and C storage of semiarid shrublands and woodlands in a qualitatively similar manner.

Key words and phrases

Adenostoma fasciculatum; *Artemisia californica*; Biogeochemistry; Chaparral; Coastal sage scrub; Global change; *Salvia mellifera*

1. Introduction

Mediterranean-type semi-arid shrublands, including chaparral and coastal sage, are distributed throughout cismontane California, northern Baja California Mexico, and south-central Arizona, inhabiting elevations that vary from sea level to over 2000m, temperature regimes that range from 0–10°C in winter to 15–45°C in summer, and precipitation regimes that vary from 200–1000 mm (Axelrod, 1978; Westman, 1981; Keeley, 2000). These diverse environmental characteristics lead to a concomitant diversity in shrubland associations (Sawyer and Keeler-Wolf, 1995).

Superimposed on these broad environmental characteristics are disturbance regimes (fire and atmospheric N deposition) that affect the structure (species composition, physiognomy, and species diversity) and function (primary production, nutrient cycling) of these shrublands over space and time (Westman, 1981; Keeley, 2000; Fenn et al., 2003a). Fire has

*Corresponding author: George L. Vourlitis, Biological Sciences Department, California State University, San Marcos, CA 92096; Phone (760) 750-4119, Fax (760) 750-3440; georgev@csusm.edu.

Publisher's Disclaimer: This is a PDF file of an unedited manuscript that has been accepted for publication. As a service to our customers we are providing this early version of the manuscript. The manuscript will undergo copyediting, typesetting, and review of the resulting proof before it is published in its final citable form. Please note that during the production process errors may be discovered which could affect the content, and all legal disclaimers that apply to the journal pertain.

an average return interval of every 20–30 years, and the post-fire flora is dominated by herbaceous perennial and annual species that are replaced by shrubs within 4–5 years (Keeley, 2000). The seeds of post-fire herbs, and many of the shrubs that replace them, require heat, smoke, and/or ash to germinate (Keeley, 2000). Fire consumes aboveground biomass, surface litter, and soil organic matter, which depending on intensity, causes losses in ecosystem N storage (DeBano and Conrad, 1978; DeBano *et al.*, 1979). However, ash deposited from the charred remains of shrubs and litter is rapidly mineralized following fire causing a transient increase in available inorganic N (Riggan *et al.* 1985; Stock and Lewis, 1986; Carreira *et al.*, 1994).

Anthropogenic N-deposition represents a significant input of N into urban chaparral and coastal sage shrublands southern California, where fossil fuel combustion and air flow patterns lead to the development of strong gradients of nitrogen oxides (Bytnerowicz and Fenn, 1996; Fenn *et al.*, 2003b). Concentrations of atmospheric N in urban areas are 20 times higher than in remote areas resulting in 20–45 kgN ha⁻¹ to be deposited to heavily polluted southern Californian shrublands annually (Riggan *et al.*, 1985; Bytnerowicz and Fenn, 1996). This deposited N has the potential to enrich the soil and plant N of semi-arid shrublands (Padgett *et al.*, 1999; Egerton-Warburton and Allen, 2000; Vourlitis *et al.*, 2006), which are thought to be N limited (Kummerow *et al.*, 1982; Gray and Schlesinger, 1983; Fenn *et al.*, 2003a).

The widely varying habitat characteristics of semi-arid shrublands, coupled with disturbance from fire and N deposition, have the potential to significantly alter patterns of soil and litter C and N storage (Westman, 1981; Schimel *et al.*, 1985; Hook and Burke, 2000). Here we present a case study where soil and litter C and N properties of chaparral and coastal sage shrublands were measured over 19 months to assess whether variations in C and N storage could be explained by variations in elevation, stand age, rainfall, and estimated N deposition exposure.

2. Materials and methods

Site descriptions

Soil and litter C and N properties were measured over a 19 month period between September 2003 and April 2005 at two post-fire recovering chaparral stands, Sky Oaks Field Station (SOFS) and the San Dimas Experimental Forest (SDEF), and two mature coastal sage stands, Santa Margarita Ecological Reserve (SMER) and the Motte Rimrock Reserve (MRR).

SOFS is located in NE San Diego County, California, USA at an elevation of 1418 m on a 4–10° SE-SW facing slope (Table 1). The stand was approximately 50 years old when it burned in July 2003. Prior to fire the site was a monoculture of the evergreen shrub *Adenostoma fasciculatum* H. & A (nomenclature according to Munz, 1974) and shrub cover was 0.83 m² m⁻² and density was 1.3 shrubs m⁻². Five months post-fire, shrub cover was 0.02 m² m⁻² and density was 0.4 shrubs m⁻². *A. fasciculatum* resprouts were present as soon as 2 months post-fire while herbaceous “fire-followers” and large numbers of *Ceanothus sp.* appeared shortly after the spring rains in 2004. The site receives an average of 53 cm of precipitation annually (mostly rain with occasional snow), and the soil is an Ultic Haploxeroll derived of micaceous schist (Moreno and Oechel, 1992) with a sandy loam texture and a bulk density of 1.34 g cm⁻³.

SDEF (34°10'N:117°44'W) is an *A. fasciculatum*-dominated chaparral located 451 m asl in the San Gabriel Mountains of Los Angeles County, California, USA (Table 1). The site receives on average 68 cm of rainfall annually. The stand was approximately 42 years old

prior to fire in September 2002 (Dunn et al., 1988), and average shrub cover and density was $0.4 \text{ m}^2 \text{ m}^{-2}$ and $2.5 \text{ shrubs m}^{-2}$, respectively 14 months post fire. As with SOFS, *A. fasciculatum* and *Ceanothus sp.* were the dominant post-fire shrubs. Soils are Precambrian complexes of gneiss, schist, and other metamorphic rocks (Dunn et al., 1988) and are sandy loams with a bulk density of 1.26 g cm^{-3} (Table 1).

SMER is located in SW Riverside County, California, USA at an elevation of 338 m and is composed of coastal sage vegetation on a 9–11° S-SW facing slope (Table 1). Soil is a sandy clay loam of the Las Posas Series derived of igneous and weathered Gabbro parent material (Knecht, 1971) with a bulk density of 1.22 g/cm^3 . SMER receives an average of 36 cm of rainfall annually. The site is approximately 35 years old and is dominated almost entirely by mature, drought deciduous shrubs *Artemisia californica* Less. and *Salvia mellifera* Greene. Shrub cover following the spring rains is $2.5 \text{ m}^2 \text{ m}^{-2}$ and density is 6 shrubs m^{-2} .

MRR ($33^\circ 48': 117^\circ 15'$) is a coastal sage site located in Riverside County at an elevation of 485 m. Vegetation is dominated by *A. californica*, *S. mellifera*, and the evergreen shrub *Eriogonum fasciculatum* Benth., and annual rainfall is on average 33 cm (Table 1). The site is approximately 24 years old, and the soil is a sandy clay loam of the Cienega-Fallbrook association derived of granitic rock (Knecht, 1971). Shrub cover and density reach a maximum of $2.2 \text{ m}^2/\text{m}^2$ and 3.0 shrubs/m^2 , respectively by the end of the wet season (June).

Estimates of N deposition from a fine-scale (4-km) model (Tonnesen *unpublished*) indicate that dry atmospheric N deposition inputs are approximately 4 and $6 \text{ kg N ha}^{-1} \text{ y}^{-1}$ at SOFS and SMER, respectively, $10.2 \text{ kg N ha}^{-1} \text{ y}^{-1}$ at MRR, and $23.0 \text{ kg N ha}^{-1} \text{ y}^{-1}$ at SDEF, while wet atmospheric N deposition is responsible for an additional $0.6 \text{ kg N ha}^{-1} \text{ y}^{-1}$ at SOFS and MRR, $0.3 \text{ kg N ha}^{-1} \text{ y}^{-1}$ at SMER, and $3.5 \text{ kg N ha}^{-1} \text{ y}^{-1}$ at SDEF (Table 1). Unfortunately, these estimates have not been validated with independent measures of N deposition (Fenn et al., 2003b); however, this spatial pattern is consistent with measurements of atmospheric N pollution exposure and throughfall (Riggan et al. 1985; Bytnerowicz and Fenn 1996; Padgett et al. 1999).

Field sampling and chemical analysis

Soil and litter C and N was measured at each site from four $10 \text{ m} \times 10 \text{ m}$ plots per site. Samples were collected quarterly (January, March, June, and September) from 2–4 randomly-located points in each plot.

Surface (0–2 cm) organic matter (litter pool) was collected within a $25 \text{ cm} \times 12.5 \text{ cm}$ quadrat that was centered on each randomly chosen point per plot. For collection purposes litter was defined as dead plant matter that was $> 1 \text{ mm}$ in size. Following the collection of surface litter, soil samples were obtained from the surface (0–10 cm) and subsurface (30–40 cm) mineral layers using a 4.7 cm diameter $\times$ 10 cm deep bucket auger or a 1.8 cm diameter $\times$ 10 cm deep T-bar. As opposed to litter and surface soil surface samples that were collected seasonally (7 sampling dates in total), subsurface soil samples were obtained twice each year in the spring and fall (4 sampling dates in total).

Mixed anion-cation resin bags ($n = 4$ per plot) were installed in the surface (0–10 cm) mineral soil following soil sampling. Resin bags consisted of 25 g anion (USF-A244B) and 25 g cation (USF-C211) exchange resin (US Filter, Rockford, IL, USA) that was mixed within $6.25 \times 15.0 \text{ cm}$ nylon bags (160 mesh), and resin bags were exchanged on a seasonal (3 month) basis (7 sampling dates in total).

Soil and resin bags were immediately returned to the lab after field collection and stored at 4°C for 1–4 days until chemical analysis. Inorganic N ($\text{NO}_3 + \text{NH}_4$) was extracted from soil

samples by KCl extraction (Mulvaney, 1996), where 10 g fresh soil was added to 40 ml of 2M KCl and continuously agitated on a reciprocating shaker for 1 h. The supernatant was filtered using a 0.2 μ m syringe filter and the NH_4 and NO_3 concentration of the extract was measured colorimetrically as ammonia (Hofer, 2001) and nitrite (Knepel, 2001) using an auto-analyzer (Lachat Quikchem 3000, Lachat Instruments, Milwaukee, WI, USA). Soil extractable N concentration determined from fresh soil was converted to a dry soil weight basis using gravimetric soil moisture data. Accumulated NH_4 and NO_3 from resin bags were extracted in a similar manner except that resin bags were extracted in 100 ml of 2M KCl. Extractable N that accumulated in the resin bags was expressed as a mass of N per bag.

Soil pH was measured in 1:2 (w/v) soil slurries, where 15 g of fresh soil was added to 30 ml DI-water and pH was measured after 30 minutes using a standard pH meter (Model MP 220, Mettler-Toledo, Columbus, OH, USA) that was calibrated using a 2-standard procedure (pH 4 and 10).

Approximately 6.5–7.0 mg of oven dried litter material and 45–50 mg of air dried soil was analyzed for $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ natural abundance and total C and N at the Kansas State University Stable Isotope Mass Spectrometry Laboratory using a mass spectrometer (ThermoFinnigan Delta Plus, Thermo Electron, Corp., Bremen, Germany) coupled to an elemental analysis system (CE 1110, Carlo-Erba, Milan, Italy).

Statistical analysis

Stepwise linear regression was used to determine the best set of predictors for a given soil or litter N or C dependent variable (Sokal and Rohlf, 1995). Independent variables included average annual rainfall, elevation, stand age, and estimated N-deposition (Table 1) because of their potential importance on the spatial distribution of soil and litter N and C (DeBano and Conrad, 1978; Schimel et al., 1985; Körner et al., 1988; Hook and Burke, 2000; Fenn et al., 2003b). These variables were not significantly correlated minimizing the potential for co-linearity (Sokal and Rohlf, 1995), and the lack of correlation was presumably because potentially strong latitudinal trends (rainfall and N deposition) were confounded by strong trends in elevation (rainfall, temperature, and N deposition) and/or stand age (Axelrod, 1978; Westman, 1981; Bytnerowicz and Fenn, 1996; Fenn et al., 2003a). Data were average by plot ($n = 4$ per site) prior to analysis, and stepwise regression was conducted using MINITAB (Release 14.1) where the critical p-value (probability of Type-I) for entering or removing an independent variable from the model was 0.05 and 0.10, respectively.

3. Results and Discussion

The N concentration of litter varied between 0.65% (SMER) and 1.07% (SDEF), and estimated atmospheric N deposition alone explained 54% of the variability in litter N concentration ($p < 0.01$; Table 2 and 3). The N concentration of mineral soil varied between 0.05% (SOFS) and 0.11% (SDEF) for the surface (0–10 cm) and 0.02% (SOFS) and 0.05% (SDEF) for the subsurface (30–40) soil layers (Table 2), and estimated N deposition alone explained 53% ($p < 0.01$) and 35% ($p < 0.05$) of the variance in the surface and subsurface mineral soil N concentration, respectively (Table 3). These data are consistent with those from coniferous forests of southern California where N deposition exposure caused soil and tissue N enrichment (Fenn et al., 1996; Korontzi et al., 2000). In contrast, the subsurface soil C concentration declined with stand age ($p < 0.05$) while the C concentration of litter and surface mineral soil was not adequately described by any of the independent variables (Table 3).

The C:N ratio of surface litter varied between 41 (SDEF) and 71 (SMER) and increased significantly with stand age ($p < 0.05$; Table 2 and 3). Previous studies in post-fire

coniferous forest and chaparral suggest that the C:N ratio of tissue and litter may decline following fire because of a transient increase in available N (Kutiel and Naveh, 1987; Stock and Lewis, 1986; Carreira et al., 1994), luxury consumption of N by regenerating shrubs (Gillon *et al.*, 1999), or N inputs from N-fixing “fire following” species (Keeley, 2000) that were common at both post-fire (SOFS and SDEF) study sites. Unfortunately neither of these mechanisms can be ruled out with the data provided. In contrast, the C:N ratio of the surface and subsurface mineral soil increased with elevation ($p < 0.001$; Table 3) presumably because high elevation sites generally have a higher proportion of evergreen shrubs that have a higher lignin content and/or C:N ratio than low-elevation, drought deciduous shrubs (Westman, 1981; Schlesinger and Hasey, 1981).

The $\delta^{15}\text{N}$ natural abundance of litter varied between -0.51‰ (MRR) and -4.14‰ (SMER) and increased significantly as a function of estimated N deposition (Table 2 and 3), which is consistent with results from coniferous forest where litter and soil exposed to high N deposition were significantly enriched in ^{15}N (Korontzi et al., 2000). Litter $\delta^{15}\text{N}$ also was significantly affected by rainfall and stand age ($p < 0.001$; Table 3); however, the mineral soil $\delta^{15}\text{N}$ natural abundance was not significantly related to any of the selected independent variables (Table 3).

The $\delta^{13}\text{C}$ natural abundance of litter and subsurface mineral soil declined significantly as a function of estimated N deposition (Table 2 and 3), and similar patterns have been observed in high-elevation coniferous forests arrayed along a N deposition gradient (Grulke et al., 2001; Korontzi et al., 2000). The $\delta^{13}\text{C}$ natural abundance of surface and subsurface mineral soil also increased significantly as a function of elevation (Table 2 and 3), which is consistent with patterns of C isotope discrimination by plants across elevation gradients (Körner et al., 1988).

Soil N availability, expressed as the concentration of extractable NH_4 in mineral soil and ion exchange resins, increased significantly with N deposition (Table 2 and 3), and N deposition has been shown to increase soil N availability from direct atmospheric input of oxidized N compounds (Bytnerowicz and Fenn, 1996; Padgett et al., 1999) and stimulation of net N mineralization (Fenn et al., 1996; Korontzi et al., 2000; Vourlitis and Zorba, 2006). In contrast, soil NO_3 availability was significantly correlated with estimated N deposition (surface mineral soil; $p < 0.001$), stand age (subsurface mineral soil; $p < 0.05$), and rainfall (ion exchange resins; $p < 0.01$), suggesting a more complex spatial pattern on NO_3 availability and nitrification.

Surface soil pH ranged between 6.57 (SOFS) and 5.96 (SDEF) and declined significantly as a function of estimated N deposition (Table 2 and 3), a pattern that is similar to that reported for high-elevation coniferous forests where N deposition has stimulated the leaching of base cations causing a decrease in soil pH (Fenn et al., 1996). The pH of subsurface mineral soil ranged between 6.07 (SDEF) and 6.95 (SMER) and declined significantly as a function of rainfall.

4. Conclusions

Our results indicate that estimated atmospheric N deposition exposure, either alone or in conjunction with other environmental variables, was the most frequent predictor of the soil and litter N and C variables measured from these semi-arid shrublands (Table 3). These results are consistent with those reported for coniferous forests (Fenn et al., 1996, 2003a; Korontzi et al., 2000), suggesting that N deposition affects the soil N and C dynamics of semi-arid shrublands and woodlands in a qualitatively similar manner. Admittedly, this case study suffers from a variety of limitations that preclude a complete

understanding of how N deposition alters C and N cycling in semi-arid shrublands. First, this study had a limited spatial ($n = 4$ sites) and temporal (19 months) perspective, which constrains the ability to generalize results over larger spatial and longer temporal scales. Secondly, both of the youngest stands were post-fire chaparral, which potentially confounds the interpretation of how stand age affected soil and litter N and C. Finally, this was a correlative study, and thus, the underlying mechanisms for the observed patterns cannot be determined with the data provided. Despite these possible limitations, this research highlights how long-term atmospheric N deposition interacts with other environmental variables to alter the N and C storage of southern Californian semi-arid shrublands.

Acknowledgments

This research was supported in part by the NSF-CAREER (DEB-0133259) and NIN-NIGMS-SCORE (S06 GM 59833) programs. The authors thank David Faber for elemental analysis, R. Fagan of the Kansas State University-Stable Isotope Mass Spectrometry Laboratory (SIMSL) for the stable isotope analyses, and the over 25 graduate and undergraduate student assistants whose effort made this research possible. Permission to use the SOFS and SMER (SDSU Field Station Programs), SDEF (M. Oxford, US Forest Service), and the MRR (B. Carlson, UC Riverside) field sites is gratefully appreciated.

Literature cited

- Axelrod DI. The origin of coastal sage vegetation, Alta and Baja California. *Am Jour Bot.* 1978; 65:1117–1131.
- Bytnerowicz A, Fenn ME. Nitrogen deposition in California forests: A review. *Environ Poll.* 1996; 92:127–146.
- Carreira JA, Niell FX, Lajtha K. Soil nitrogen availability and nitrification in Mediterranean shrublands of varying fire history and successional stage. *Biogeochem.* 1994; 26:189–209.
- DeBano LF, Conrad CE. The effect of fire on nutrients in a chaparral ecosystem. *Ecology.* 1978; 59:489–497.
- DeBano LF, Eberlein GE, Dunn PH. Effects of burning on chaparral soils: I. Soil nitrogen. *Soil Sci Soc Am J.* 1979; 43:504–509.
- Dunn, PH.; Barro, SV.; Wells, WG., II; Poth, MA.; Wohlgemuth, PM.; Colver, CG. United States Department of Agriculture, Forest Service, General Technical Report PSW-104. Pacific Southwest Forest and Range Experiment Station; Berkeley, CA: 1988. The San Dimas Experimental Forest: 50 Years of Research; p. 49
- Egerton-Warburton LM, Allen EB. Shifts in arbuscular mycorrhizal communities along an anthropogenic nitrogen deposition gradient. *Ecol Appl.* 2000; 10:484–496.
- Fenn ME, Poth MA, Johnson DW. Evidence for nitrogen saturation in the San Bernardino Mountains in southern California. *For Ecol Man.* 1996; 82:211–230.
- Fenn ME, Haeuber R, Tonnesen GS, Baron JS, Grossman-Clarke S, Hope D, Jaffe DA, Copeland S, Geiser L, Rueth HN, Sickman JO. Nitrogen emissions, deposition, and monitoring in the western United States. *Bioscience.* 2003a; 53:391–403.
- Fenn ME, Baron JS, Allen EB, Rueth HN, Nydick KP, Geiser L, Bowman WD, Sickman JO, Meixner T, Johnson DW, Neitlich P. Ecological effects of nitrogen deposition in the western United States. *Bioscience.* 2003b; 53:404–420.
- Gillon D, Houssard C, Valette JC, Rigolot E. Nitrogen and phosphorus cycling following prescribed burning in natural and managed Aleppo pine forests. *Can Jour For Res.* 1999; 29:1237–1247.
- Gray JT, Schlesinger WH. Nutrient use by evergreen and deciduous shrubs in Southern California. II Experimental investigations of the relationship between growth, nitrogen uptake, and nitrogen availability. *J Ecol.* 1983; 71:43–56.
- Gurlke NE, Andersen CP, Hogsett WE. Seasonal changes in above- and belowground carbohydrate concentrations of ponderosa pine along a pollution gradient. *Tree Physiology.* 2001; 21:173–181. [PubMed: 11303648]
- Hofer, S. Lachat QuikChem Method 12-107-06-2-A. Lachat Instruments, Inc; Milwaukee, WI, USA: 2001. Ammonia (Salicylate) in 2M KCl soil extracts.

- Hook PB, Burke IC. Biogeochemistry in a shortgrass landscape: Control by topography, soil texture, and microclimate. *Ecology*. 2000; 81:2686–2703.
- Keeley, JE. Chaparral. In: Barbour, MG.; Billings, WD., editors. *North American Terrestrial Vegetation*. 2. Cambridge University Press; Cambridge, UK: 2000. p. 203–254.
- Knecht, AA. Soil Survey for Western Riverside Area California. United States Department of Agriculture, Soil Conservation Service; Washington, DC: 1971.
- Knepel, K. Lachat QuikChem Method 12-107-04-1-B. Lachat Instruments, Inc; Milwaukee, WI, USA: 2001. Nitrate in 2M KCl soil extracts.
- Korontzi S, Macko SA, Anderson IC, Poth MA. A stable isotopic study to determine carbon and nitrogen cycling in a disturbed southern California forest ecosystem. *Glob Biogeochem Cyc*. 2000; 14:177–188.
- Körner C, Farquhar GD, Roksandic Z. A global survey of carbon isotope discrimination in plants from high altitude. *Oecologia*. 1988; 74:623–632.
- Kummerow J, Avila G, Aljaro ME, Araya S, Montenegro G. Effect of fertilizer on fine root density and shoot growth in Chilean matorral. *Bot Gazette*. 1982; 143:498–504.
- Kutiel J, Naveh Z. The effects of fire on nutrients in a pine forest soil. *Plant and Soil*. 1987; 104:269–274.
- Moreno JM, Oechel WC. Factors controlling postfire seedling establishment in southern California chaparral. *Oecologia*. 1992; 90:50–60.
- Mulvaney, RL. Nitrogen-inorganic forms. In: Sparks, DL.; Page, AL.; Helmke, PA.; Loeppert, RH.; Soltanpour, PN.; Tabatabai, A.; Johnson, CT.; Sumner, ME., editors. *Methods of soil analysis: Part 3. Chemical Methods*, Soil Science Society of America Book Series No. 5. Soil Science Society of America, Inc; Madison, WI: 1996. p. 1123–1184.
- Munz, PA. *A Flora of Southern California*. University of California Press; Berkeley, CA, USA: 1974.
- Padgett PE, Allen EB, Bytnerowicz A, Minich RA. Changes in soil inorganic nitrogen as related to atmospheric nitrogenous pollutants in southern California. *Atm Environ*. 1999; 33:769–781.
- Riggan PF, Lockwood RN, Lopez EN. Deposition and processing of airborne nitrogen pollutants in Mediterranean-type ecosystems of southern California. *Environ Sci Tech*. 1985; 19:781–789.
- Sawyer, JO.; Keeler-Wolf, T. *A Manual of California Vegetation*. California Native Plant Society; Sacramento, CA, USA: 1995. p. 471
- Schimel D, Stillwell MA, Woodmansee RG. Biogeochemistry of C, N, and P in a soil catena of the shortgrass steppe. *Ecology*. 1985; 66:276–282.
- Schlesinger WH, Hasey MM. Decomposition of chaparral shrub foliage: Losses of organic and inorganic constituents from deciduous and evergreen leaves. *Ecology*. 1981; 62:762–774.
- Sokal, RR.; Rohlf, FL. *Biometry*. 3. W. H. Freeman and Company; San Francisco: 1995.
- Stock WD, Lewis OAM. Soil nitrogen and the role of fire as a mineralizing agent in a South African coastal fynbos ecosystem. *Jour Ecol*. 1986; 74:317–328.
- Vourlitis GL, Pasquini S, Zorba G. Plant and soil N response of southern Californian semi-arid shrublands after one year of experimental N deposition. *Ecosystems*. 2006 in press.
- Vourlitis GL, Zorba G. Nitrogen and carbon mineralization of semi-arid shrubland soil exposed to long-term atmospheric nitrogen deposition. *Biol Fert Soils*. 2006 in press.
- Westman WE. Factors influencing the distribution of species of Californian coastal sage scrub. *Ecology*. 1981; 62:439–455.

Table 1

Location and selected characteristics of the research sites. Data for soil bulk density and texture are for the upper 0–10 cm soil layer. N-deposition estimates were derived from a high-resolution (4 km) model (Tonneson, *unpublished*). Rainfall data are from the Santa Margarita Ecological Reserve web site (<http://fs.sdsu.edu/kf/reserves/smer/>), Motte Rimrock Reserve (J. Messin, UCR, *unpubl. data*), Sky Oaks Field Station (<http://www.sci.sdsu.edu/GCRG/>), and San Dimas Experimental Forest (Dunn *et al.*, 1988).

Variable	Chaparral		Coastal sage scrub	
	Sky Oaks Field Station	San Dimas Experimental Forest	Santa Margarita Ecological Reserve	Motte Rimrock Reserve
Lat.:Long. (N:W)	33°21':116°34'	34°10':117°44'	33°29':117°09'	33°48':117°15'
California County	San Diego	Los Angeles	Riverside	Riverside
Elevation (m)	1418	451	338	485
Annual rainfall (cm)	53	68	36	33
Dry deposition (kgN ha ⁻¹ y ⁻¹)	4.0	23.0	6.0	10.2
Wet deposition (kgN ha ⁻¹ y ⁻¹)	0.6	3.5	0.3	0.6
Sand, silt, clay (%)	78, 14, 8	70, 14, 16	68, 19, 13	72, 22, 6
Bulk density (g/cm ³)	1.34	1.26	1.22	1.35
Dominant species [†]	<i>Af</i> , <i>C. sp.</i> , <i>As</i>	<i>Af</i> , <i>C. sp.</i>	<i>Ac</i> , <i>Sm</i>	<i>Ef</i> , <i>Ac</i> , <i>Sm</i>
Stand Age (years)	2	2.75	35	24

[†] *Af* = *Adenostoma fasciculatum*; *As* = *A. sparsifolium*; *C. Sp.* = *Ceanothus sp.*; *Ef* = *Eriogonum fasciculatum*; *Sm* = *Salvia mellifera*.

Mean ($\pm$ se; $n = 4$) litter and soil C and N properties for the chaparral sites Sky Oaks Field Station (SOFS) and San Dimas Experimental Forest (SDEF) and the coastal sage scrub sites Santa Margarita Experimental Reserve (SMER) and Motte Rimrock Reserve (MRR) along the N deposition gradient. N deposition depicts the total estimated wet + dry deposition calculated from table 1.

Table 2

Variable	Units	Research site			
		SOFS	SMER	MRR	SDEF
N deposition	kg/h* $\bar{y}$	4.6	6.3	10.8	26.5
Litter $\delta^{15}\text{N}$	‰	-3.62 $\pm$ 0.28	-4.14 $\pm$ 0.30	-0.51 $\pm$ 0.14	-0.97 $\pm$ 0.16
Litter N	%	0.83 $\pm$ 0.08	0.65 $\pm$ 0.04	0.88 $\pm$ 0.01	1.07 $\pm$ 0.05
Litter $\delta^{13}\text{C}$	‰	-26.92 $\pm$ 0.07	-26.98 $\pm$ 0.18	-26.98 $\pm$ 0.22	-27.51 $\pm$ 0.24
Litter C	%	40.57 $\pm$ 1.61	42.96 $\pm$ 1.11	43.34 $\pm$ 0.68	40.50 $\pm$ 1.63
Litter C:N	gC/gN	54.27 $\pm$ 5.39	70.49 $\pm$ 6.11	51.54 $\pm$ 1.45	41.06 $\pm$ 3.26
Surface $\delta^{15}\text{N}$	‰	1.69 $\pm$ 0.14	0.93 $\pm$ 0.10	2.85 $\pm$ 0.17	1.14 $\pm$ 0.22
Surface N	%	0.05 $\pm$ 0.01	0.07 $\pm$ 0.01	0.08 $\pm$ 0.01	0.11 $\pm$ 0.02
Surface $\delta^{13}\text{C}$	‰	-24.60 $\pm$ 0.16	-26.36 $\pm$ 0.08	-26.18 $\pm$ 0.04	-26.48 $\pm$ 0.26
Surface C	%	1.18 $\pm$ 0.09	1.04 $\pm$ 0.06	1.08 $\pm$ 0.10	1.36 $\pm$ 0.26
Surface C:N	gC/gN	25.45 $\pm$ 1.59	15.42 $\pm$ 0.20	12.99 $\pm$ 0.37	13.00 $\pm$ 0.60
Surface NO_3	$\mu\text{gN/g}$	5.77 $\pm$ 0.89	2.47 $\pm$ 0.16	8.62 $\pm$ 1.46	29.17 $\pm$ 6.43
Surface NH_4	$\mu\text{gN/g}$	2.47 $\pm$ 0.60	1.88 $\pm$ 0.18	4.80 $\pm$ 0.94	25.78 $\pm$ 6.59
Surface resin NO_3	mgN/bag	8.16 $\pm$ 2.53	1.77 $\pm$ 0.31	4.35 $\pm$ 0.86	11.42 $\pm$ 2.81
Surface resin NH_4	mgN/bag	0.83 $\pm$ 0.20	0.65 $\pm$ 0.16	0.86 $\pm$ 0.15	2.20 $\pm$ 0.29
Surface pH		6.57 $\pm$ 0.04	6.54 $\pm$ 0.04	6.39 $\pm$ 0.09	5.96 $\pm$ 0.02
Subsurface $\delta^{15}\text{N}$	‰	3.73 $\pm$ 0.43	2.66 $\pm$ 0.18	3.65 $\pm$ 0.16	2.82 $\pm$ 0.22
Subsurface N	%	0.02 $\pm$ 0.01	0.03 $\pm$ 0.01	0.03 $\pm$ 0.01	0.05 $\pm$ 0.01
Subsurface $\delta^{13}\text{C}$	‰	-23.91 $\pm$ 0.11	-25.43 $\pm$ 0.05	-25.44 $\pm$ 0.07	-25.78 $\pm$ 0.31
Subsurface C	%	0.74 $\pm$ 0.13	0.46 $\pm$ 0.02	0.43 $\pm$ 0.04	0.68 $\pm$ 0.19
Subsurface C:N	gC/gN	32.07 $\pm$ 2.58	14.49 $\pm$ 0.44	13.31 $\pm$ 0.54	13.96 $\pm$ 0.84
Subsurface NO_3	$\mu\text{gN/g}$	4.38 $\pm$ 0.70	0.79 $\pm$ 0.05	4.04 $\pm$ 1.45	4.59 $\pm$ 0.73
Subsurface NH_4	$\mu\text{gN/g}$	1.41 $\pm$ 0.37	0.64 $\pm$ 0.09	1.48 $\pm$ 0.68	3.47 $\pm$ 0.39

Variable	Units	Research site			
		SOFS	SMER	MRR	SDEF
Subsurface pH		6.40±0.06	6.95±0.04	6.69±0.09	6.07±0.05

Table 3

Summary statistics of a stepwise multiple linear regression between soil and litter N and C variables (dependent variable) and rainfall, elevation, stand age, and estimated N deposition (independent variables) for chaparral and coastal sage scrub ecosystems arrayed along an N-deposition gradient in southern California (n = 4 sites with 4 plots per site). C = y-intercept.

Dependent variable	Independent variables					R ²
	C	Rainfall	Elevation	Stand age	N-deposition	
Litter $\delta^{15}\text{N}$	7.69	-0.233	—	-0.150	0.286	0.94***
Litter N	0.68	—	—	—	0.015	0.54**
Litter $\delta^{13}\text{C}$	-26.77	—	—	—	-0.027	0.33*
Litter C	—	—	—	—	—	NS
Litter C:N	45.10	—	—	-0.579	—	0.35*
Surface $\delta^{15}\text{N}$	—	—	—	—	—	NS
Surface N	0.05	—	—	—	0.002	0.53**
Surface $\delta^{13}\text{C}$	-27.07	—	0.002	—	—	0.87***
Surface C	—	—	—	—	—	NS
Surface C:N	9.14	—	0.001	—	—	0.83***
Surface NO_3	-2.75	—	—	—	1.176	0.74***
Surface NH_4	-4.87	—	—	—	1.129	0.72***
Surface resin NO_3	-5.29	0.246	—	—	—	0.48**
Surface resin NH_4	0.29	—	—	—	0.069	0.71***
Surface pH	6.69	—	—	—	-0.028	0.87***
Subsurface $\delta^{15}\text{N}$	—	—	—	—	—	NS
Subsurface N	0.02	—	—	—	0.001	0.35*
Subsurface $\delta^{13}\text{C}$	-25.80	—	0.001	—	-0.024	0.86***
Subsurface C	0.72	—	—	-0.009	—	0.26*
Subsurface C:N	6.43	—	0.018	—	—	0.89***
Subsurface NO_3	4.93	—	—	-0.093	—	0.36*

Dependent variable	Independent variables					R ²
	C	Rainfall	Elevation	Stand age	N-deposition	
Subsurface NH ₄	0.37	—	—	—	0.114	0.58**
Subsurface pH	7.52	-0.022	—	—	—	0.80***

* p ≤ 0.05;
** p ≤ 0.01;
*** p ≤ 0.001.
—; variable not added to model (p > 0.05). NS; model not statistically significant (p > 0.05).