Short communication

Carbon and nitrogen storage in soil and litter of southern Californian semi-arid shrublands


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

Received 5 April 2006; received in revised form 20 September 2006; accepted 5 December 2006
Available online 5 February 2007

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.

© 2007 Elsevier Ltd. All rights reserved.

Keywords: Adenostoma fasciculatum; Artemisia californica; Biogeochemistry; Chaparral; Coastal sage scrub; Global change; Nitrogen deposition; 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 2000 m, temperature regimes that range from 0–10 °C in winter to 15–45 °C in summer, and precipitation regimes that vary from 200 to 1000 mm (Axelrod, 1978; Keeley, 2000; Westman, 1981). 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 (Fenn et al., 2003a; Keeley, 2000; Westman, 1981). Fire has 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 (Carreira et al., 1994; Riggan et al., 1985; Stock and Lewis, 1986).

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 kg N/ha to be deposited to heavily polluted southern Californian shrublands annually (Bytnerowicz and Fenn, 1996; Riggan et al., 1985). This deposited N has the potential to enrich the soil and plant N of semi-arid shrublands (Egerton-Warburton and Allen, 2000; Padgett et al., 1999; Vourlitis et al., 2007), which are thought to be N limited (Fenn et al., 2003a; Gray and Schlesinger, 1983; Kummerow et al., 1982).

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 (Hook and Burke, 2000; Schimel et al., 1985; Westman, 1981). 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

2.1. 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, CA, 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 m$^2$/m$^2$ and density was 1.3 shrubs/m$^2$. Five months post-fire, shrub cover was 0.02 m$^2$/m$^2$ and density was 0.4 shrubs/m$^3$. *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 is an *A. fasciculatum*-dominated chaparral located 451 m asl in the San Gabriel Mountains of Los Angeles County, CA, 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 m$^2$/m$^2$ and 2.5 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 1.34 g/cm$^3$ (Table 1).

SMER is located in SW Riverside County, CA, 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

### Table 1: Location and selected characteristics of the research sites

<table>
<thead>
<tr>
<th>Variable</th>
<th>Chaparral</th>
<th>Coastal sage scrub</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Sky Oaks Field Station</td>
<td>Santa Margarita Ecological Reserve</td>
</tr>
<tr>
<td>Lat.:Long. (N:W)</td>
<td>33°21′116′34″</td>
<td>34°10′117′44″</td>
</tr>
<tr>
<td>California county</td>
<td>San Diego</td>
<td>Los Angeles</td>
</tr>
<tr>
<td>Elevation (m)</td>
<td>1418</td>
<td>451</td>
</tr>
<tr>
<td>Annual rainfall (cm)</td>
<td>53</td>
<td>68</td>
</tr>
<tr>
<td>Dry deposition (kgN ha$^{-1}$/y$^{-1}$)</td>
<td>4.0</td>
<td>23.0</td>
</tr>
<tr>
<td>Wet deposition (kgN ha$^{-1}$/y$^{-1}$)</td>
<td>0.6</td>
<td>3.5</td>
</tr>
<tr>
<td>Sand, silt, clay (%)</td>
<td>78, 14, 8</td>
<td>70, 14, 16</td>
</tr>
<tr>
<td>Bulk density (g/cm$^3$)</td>
<td>1.34</td>
<td>1.26</td>
</tr>
<tr>
<td>Dominant species*</td>
<td><em>Af, C.sp., As</em></td>
<td><em>Af, C.sp.</em></td>
</tr>
<tr>
<td>Stand age (years)</td>
<td>2</td>
<td>2.75</td>
</tr>
</tbody>
</table>

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).

*Af = Adenostoma fasciculatum; As = A. sparsifolium; C.sp. = Ceanothus sp.; Ef = Eriogonum fasciculatum; Sm = Salvia mellifera.*
almost entirely by mature, drought deciduous shrubs *Artemisia californica* Less. and *Salvia mellifera* Greene. Shrub cover following the spring rains is 2.5 m$^2$/m$^2$ and density is 6 shrubs/m$^2$.

MRR 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 Cieneba–Fallbrook association derived of granitic rock (Knecht, 1971). Shrub cover and density reach a maximum of 2.2 m$^2$/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 kg N ha$^{-1}$ y$^{-1}$ at SOFS and SMER, respectively, 10.2 kg N ha$^{-1}$ y$^{-1}$ at MRR, and 23.0 kg N ha$^{-1}$ y$^{-1}$ at SDEF, while wet atmospheric N deposition is responsible for an additional 0.6 kg N ha$^{-1}$ y$^{-1}$ at SOFS and MRR, 0.3 kg N ha$^{-1}$ y$^{-1}$ at SMER, and 3.5 kg N ha$^{-1}$ 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 (Bytnerowicz and Fenn, 1996; Padgett et al., 1999; Riggan et al., 1985).

2.2. Field sampling and chemical analysis

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

Surface (0–2 cm) organic matter (litter pool) was collected within a 25 cm × 12.5 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 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 × 10 cm deep bucket auger or a 1.8 cm diameter × 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 15 g anion (USF-A244B) and 15 g cation (USF-C211) exchange resin (US Filter, Rockford, IL, USA) that was mixed within 6.25 × 15.0 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 (NO$_3$ + NH$_4$) was extracted from soil samples by KCl extraction (Mulvaney, 1996), where 10 g fresh soil was added to 40 ml of 2 M KCl and continuously agitated on a reciprocating shaker for 1 h. The supernatant was filtered using a 0.45 µm syringe filter and the NH$_4$ and NO$_3$ concentration of the extract was measured colorimetrically as ammonia (Hofer, 2001) and nitrite (Knapel, 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 2 M 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 min 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 δ13C and δ15N 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).

2.3. 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; Fenn et al., 2003b; Hook and Burke, 2000; Körner et al., 1988; Schimel et al., 1985). 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; Bytnerowicz and Fenn, 1996; Fenn et al., 2003a; Westman, 1981). 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 error) 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; Tables 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; Tables 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 (Carreira et al., 1994; Kutiel and Naveh, 1987; Stock and Lewis, 1986), 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 (Schlesinger and Hasey, 1981; Westman, 1981).

The δ15N natural abundance of litter varied between −0.51‰ (MRR) and −4.14‰ (SMER) and increased significantly as a function of estimated N deposition (Tables 2 and 3), which is consistent with results from coniferous forest where litter and soil exposed to high N deposition were significantly enriched in 15N (Korontzi et al., 2000). Litter δ15N also was significantly affected by rainfall and stand age (p < 0.001; Table 3); however, the
mineral soil $\delta^{15}N$ natural abundance was not significantly related to any of the selected independent variables (Table 3).

The $\delta^{13}C$ natural abundance of litter and subsurface mineral soil declined significantly as a function of estimated N deposition (Tables 2 and 3), and similar patterns have been observed in high-elevation coniferous forests arrayed along a N deposition gradient (Gurlke et al., 2001; Korontzi et al., 2000). The $\delta^{13}C$ natural abundance of surface and subsurface mineral soil also increased significantly as a function of elevation (Tables 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 (Tables 2 and 3), and N deposition has been shown to increase soil N availability from direct atmospheric input (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 for soil NO\(_3\) content and availability.

Surface soil pH ranged between 6.57 (SOFS) and 5.96 (SDEF) and declined significantly as a function of estimated N deposition (Tables 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.

Acknowledgements

This research was supported in part by the NSF-CAREER (DEB-0133259) and NIH-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.

References


