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Carbon and Nitrogen Mineralization of a Semiarid Shrubland Exposed to Experimental Nitrogen Deposition

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High atmospheric N inputs to southern Californian shrublands can alter organic matter quantity and quality and influence decomposition and N mineralization rates. We conducted a laboratory experiment to test the hypothesis that N addition would increase microbial respiration and net N mineralization. Intact soil cores and litter from *Artemisia californica* Less. were collected from field plots exposed to either ambient or elevated N (50 kg N ha^{-1} yr^{-1}) over a 7-yr period. Microbial respiration was significantly higher in control soil, and litter amendment, regardless of origin, significantly increased respiration. In contrast, net N mineralization was significantly higher in added N soil, and litter addition significantly depressed net N mineralization. Our results suggest that chronic N deposition causes a decline in litter decomposition and microbial N demand. If indicative of the longer-term decomposition kinetics, these results suggest that chronic N inputs may increase soil C storage and N availability in these semiarid shrublands.

Abbreviations: CSS, coastal sage scrub; SMER, Santa Margarita Ecological Reserve.

Polluted urban areas of southern California may receive 20 to 45 kg N ha^{-1} yr^{-1} from atmospheric nitrogen (N) deposition (Fenn et al., 2003a; Meixner and Fenn, 2004). Most of this anthropogenic N (85–95%) is in the form of dry deposition that accumulates on plant and soil surfaces of chaparral and coastal sage scrub (CSS) shrublands during the summer and fall and becomes available as a large and ephemeral pulse after the first winter rainfall event (Padgett et al., 1999; Fenn et al., 2003a).

Nitrogen inputs in these semiarid shrublands have been shown to consistently increase soil N availability, leading to tissue and litter N-enrichment (Padgett et al., 1999; Vourlitis and Zorba, 2007; Vourlitis et al., 2009). In turn, litter N enrichment can reduce C/N and/or lignin/N ratios, which can stimulate N mineralization (Sirulnik et al., 2007; Vourlitis and Zorba, 2007; Vourlitis et al., 2007, 2009) and decomposition (Vitousek and Howarth, 1991; Knorr et al., 2005). However, many studies indicate that while N enrichment may enhance initial rates of litter decomposition, high levels of available N can suppress decomposition over time (Fog, 1988; Carreiro et al., 2000; Knorr et al., 2005). In decomposition experiments of temperate forest leaf litter (Carreiro et al., 2000), added N was found to stimulate cellulase activity but inhibit the synthesis of lignin-degrading enzymes such as phenol oxidase and peroxidase. Elevated N can also reportedly reduce fungal populations (Liu and Crowley, 2009), which are primarily responsible for lignin degradation (Carreiro et al., 2000).

A decline in litter decomposition may lead to an increase in soil C storage in these semiarid shrublands. Given that soil represents the largest C pool in terrestrial ecosystems, and, in particular, semiarid shrublands (Jobbagy and Jackson,

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2000), an increase in soil C storage may lead to an increase in ecosystem C sequestration, although long-term effects are unknown. Similarly, a decline in litter decomposition would also affect N cycling and storage. As with soil C, an increase in the sequestration of N-rich litter would significantly increase soil N storage, which is the largest N pool in semiarid shrublands (Mooney and Rundel, 1979), and would represent a means for semiarid shrublands to sequester large inputs of atmospheric N deposition (Fenn et al., 2003b). However, net N mineralization of N-rich litter may increase N availability, which in turn may lead to higher N losses from leaching and/or gaseous N efflux (Fenn et al., 2003b).

Given the impact of exogenous N on the litter and soil chemistry of southern Californian semiarid shrublands (Vourlitis et al., 2009; Vourlitis and Fernandez, 2012), our goal was to assess the effects of chronic N input on soil microbial C and N processing in a CSS shrubland. We hypothesized that litter produced from shrubs exposed to added N would support a higher rate of microbial respiration and net N mineralization than litter exposed to ambient N because of an increase in litter quality (decline in C/N and/or lignin/N ratios). Furthermore, we hypothesized that an increase in soil N availability would lead to an increase in the rate of microbial respiration and net N mineralization because added N would increase the microbial degradation of labile C in fresh litter.

MATERIALS AND METHODS

Hypotheses were tested during an 8-wk laboratory incubation experiment using soil and litter collected from a long-term N addition field experiment conducted at the Santa Margarita Ecological Reserve (SMER) located in SW Riverside County, California (details are provided by Vourlitis et al. [2009] and Vourlitis and Pasquini [2009]). SMER is representative of a mature CSS stand that has not experienced fire for over 35 yr. Vegetation is dominated by the deciduous shrubs *Artemisia californica* Less. and *Salvia mellifera* Greene, which make up approximately 95% of the vegetation biomass (Vourlitis and Pasquini, 2009; Vourlitis, 2012). Soil is a sandy clay loam of the Las Posas Series that is derived of igneous and weathered Gabbro material (Knecht, 1971) with a bulk density of 1.22 g cm^{-3}. The soil lacks an organic horizon but has a small surface litter pool that varies over seasonal time scales due to the deciduous nature of the dominant shrubs (Vourlitis et al., 2009).

The experiment has been running since September 2003 with the aim of assessing how ecosystem N and C dynamics respond to large, chronic, dry-season N inputs that are typical of heavily polluted urban shrublands. The experimental layout consists of a randomized design where four 10 by 10 m plots have received 50 kg N ha^{-1} yr^{-1} as granular NH_4NO_3, $(NH_4)_2SO_4$, or urea (added N) and an additional four 10 by 10 m plots served as unmanipulated controls. This fertilization rate is nearly 10 times higher than the estimated ambient rate of N deposition for SMER (Tonnesen et al., 2007) but is comparable to that reported for polluted southern Californian urban shrublands (Fenn et al., 2003a; Meixner and Fenn, 2004). Nitrogen fertilizer has been added annually during a single application in September–October using a handheld spreader (Vourlitis et al., 2009).

Mineral soil core samples (6 subsamples per plot extending 8 cm below the soil surface) were taken from random points in each 10 by 10 m plot in February 2011 using clean microcosms. The microcosm system used for this experiment was similar to that described by Taylor and Parkinson (1988) and consisted of a 10 cm long by 7.4-cm inside diameter polyvinylchloride pipe fitted with two fixed lids (top and bottom) that were sealed to the pipe using silicone. A hole in the top lid allowed gas exchange and the collection of gas samples and a hole in the bottom lid provided drainage and a means for collecting leachate. Soil core samples were dry at the time of sample collection (soil water content < 0.07 kg H_2O kg^{-1} dry soil), and were stored in the laboratory at room temperature for 6 d until incubation experiments were performed.

Fresh litter of *A. californica* was taken from random points in each 10 by 10 m plot in February 2011. *A. californica* accounts for approximately 60% of the total aboveground biomass in control plots and as much as 90% of the total biomass in added N plots (Vourlitis and Pasquini, 2009), and thus, has a proportionally large influence on the surface litter pool in this CSS shrubland. Litter was collected by lightly shaking *A. californica* shrubs and collecting fallen litter on clean tarps deployed under the shrub canopy. Litter collected from control plots was pooled as was litter collected from added N plots.

In the laboratory, the surface litter was removed from each soil core to allow a known mass and origin of litter to be added to the microcosms. Litter was reestablished on four of the six cores taken in each plot. On two of the cores, 0.5 g of litter collected from control plots was added to each core; on another two cores, 0.5 g of litter collected from added N plots was added to each core; while on the remaining two cores, no litter was added. The amount of litter added to each core was based on the average litter pool mass (115 g m^{-2}) observed for this shrubland (Vourlitis et al., 2009). Initial soil and litter total N and C concentration was analyzed using a CHN analyzer (ECS 4010, Costech Analytical Technologies, Inc., Valencia, CA). Initial litter soluble C, holocellulose (polysaccharides and non-lignin hemicelluloses), and lignin content was measured using methods described by Moorhead and Reynolds (1993).

Microcosm soils were remoistened to saturation by addition of 100 mL of deionized water when the experiment commenced (Taylor and Parkinson, 1988). The initial N (NH_4^+ + NO_3^-) concentration of leachate that was collected during the remoistening phase (initial leachate volume was on average 25 mL) was measured using an autoanalyzer (Lachat Quikchem 3000, Lachat Instruments, Milwaukee, WI). Thereafter, net N mineralization was quantified weekly using sequential leaching techniques (Vourlitis and Zorba, 2007; Vourlitis et al., 2007). Each microcosm was incubated in the dark at a constant temperature of 25°C during an 8-wk period. Mean (±1 SD) soil moisture was maintained at 0.35 ± 0.02 kg H_2O kg dry $soil^{-1}$ for the duration

of the laboratory incubation. Microcosms were leached weekly by adding 50 mL of deionized water. Soil saturated with deionized water was left to stand for 1 h, and approximately 35 mL of leachate was removed using a 0.06-MPa vacuum pump. Leachate was immediately frozen until analysis for extractable NH_4^+ and NO_3^- using an autoanalyzer (Lachat Quikchem 3000, Lachat Instruments, Milwaukee, WI). The amount of inorganic N from each microcosm ($\mu g\ N\ g^{-1}$ dry mass) was calculated as the concentration of NH_4^+ and NO_3^- times the volume of leachate divided by the weight of dry soil of each microcosm. Inorganic N per unit mass of dry soil was multiplied by the soil bulk density measured for each plot (Vourlitis et al., 2009) and the height of the soil core to express net NH_4^+ and NO_3^- production per unit area ($g\ N\ m^{-2}$).

Soil microbial respiration was determined by measuring the change in CO_2 concentration in the microcosm head space (Nadelhoffer, 1990). Carbon dioxide evolution was measured weekly, a day after leaching with deionized water. Microcosms were purged of CO_2 by flowing 1.5 L min^{-1} of N_2 through the bottom of the microcosm for 20 s and immediately sealed thereafter. Gas samples were obtained using a 10-mL syringe at 0, 5, and 10 min after purging, and the sample volume was replaced by N_2 after each gas sample was collected to minimize the development of a vacuum inside the microcosm. The CO_2 concentration of the microcosm head space was measured using an infrared gas analyzer (LI-6200, LI-COR Inc., Lincoln, NE) equipped to integrate the CO_2 concentration of the injected air sample (LI-COR, 1998). Microbial respiration was determined by the rate of increase of CO_2 concentration over the 10 min measurement period.

Initial differences in the litter and soil N and C concentration and C/ N ratio, extractable soil N ($NH_4^+ + NO_3^-$), and litter structural chemistry (soluble C, holocellulose, lignin, and the lignin:N ratio) between control and added N plots were assessed using a two-tailed *t* test. Repeated-measures ANOVA was used to assess whether soil and litter treatments affected C and net N mineralization over time, and a two-way ANOVA was performed to assess whether soil and litter treatments affected total C and N mineralized over the 8-wk experiment. For all analyses, litter (added N, control, and no litter) and soil (control and added N) were treated as fixed-effects. Data were tested for normality and heteroscedasticity on residuals after parametric analysis and data violating assumptions of ANOVA were transformed to fulfill assumptions.

RESULTS AND DISCUSSION

We initially hypothesized that litter produced from shrubs exposed to added N would support a higher rate of microbial respiration and N mineralization than litter exposed to ambient N because of an increase in litter quality (i.e., decline in C/N and/or lignin/N ratios). However, our data do not support this hypothesis as litter origin (i.e., added N vs. control) had no effect on soil respiration or net N-mineralization. Rather, litter addition, regardless of origin, caused an increase in microbial respiration (Fig. 1) and a decline in net N mineralization (Fig. 2) that varied in magnitude over time (Table 1). This result is surprising given that litter exposed to added N had a significantly higher N concentration, lower C concentration, and a lower C to N ratio than litter collected from control plots (Table 2). However, control litter had a significantly higher concentration of soluble C, and differences in the holocellulose and lignin concentrations and the lignin:N ratio were minimal between control and added N litter (Table 2). These structural attributes, particularly lignin concentration and the lignin/N ratio, are known to exert a stronger control on the decomposition of CSS shrub litter than bulk chemical indices such as the litter N concentration and the C/N ratio (Schlesinger and Hasey, 1981).

Over the 8-wk incubation, total C mineralization from treatments that received added litter was approximately 20 to 25 g C m^{-2} higher than treatments receiving no litter input (Fig. 2a). However, temporal variations in soil microbial respiration were large and were significantly affected by soil N enrichment and litter input, and there were significant soil × time and litter × time interactions highlighting the complexity in the litter decomposition kinetics (Fig. 1 and Table 1). Initial rates of soil respiration were significantly higher in the litter treatments until Day 28, but thereafter respiration rates were similar regardless of litter input (Table 1 and Fig. 1). Labile C compounds, including soluble sugars and holocellulose (hemicellulose and polysaccha-

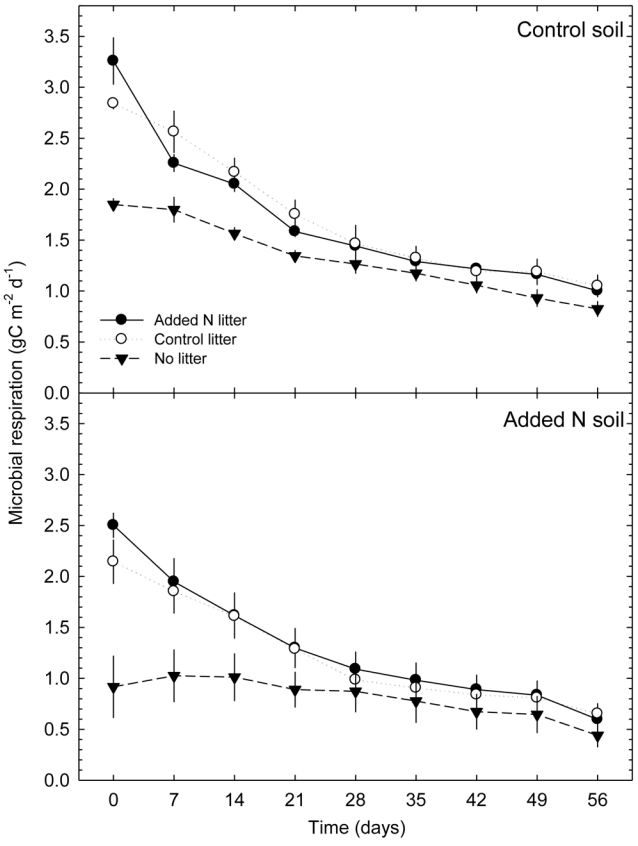

Fig. 1. Mean (±1 SE, *n* = 4) microbial respiration, measured as soil CO_2 efflux, during the 8-wk experiment from microcosms of soil collected from control (top panel) and added N plots (bottom panel) that were treated with either no added litter (black inverted triangles) or with *Artemisia californica* litter collected from added N (black circles) or control plots (white circles).

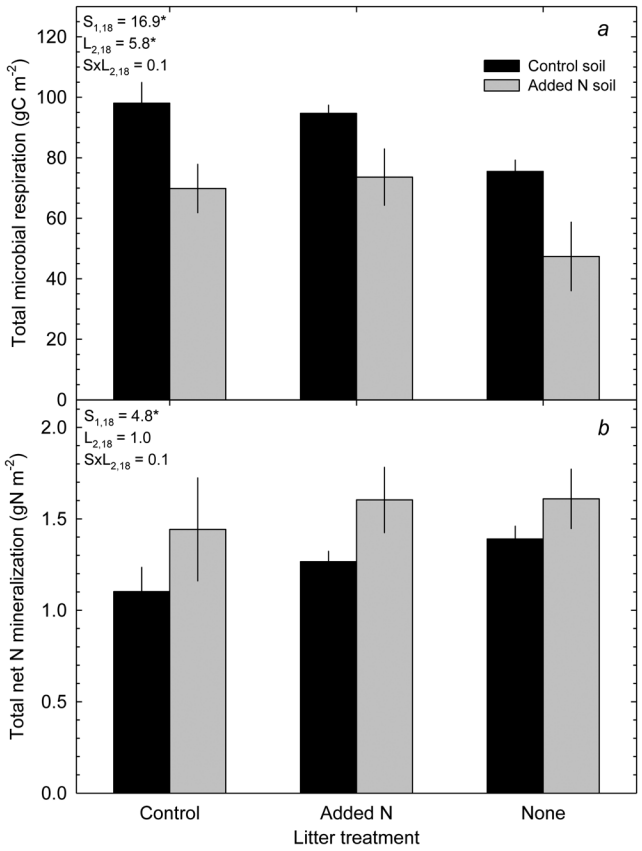

Fig. 2. Mean (±1 SE, *n* = 4) total microbial respiration (a) and net N mineralization ($NH_4^+ + NO_3^-$) (b) calculated over the 8 wk laboratory experiment from microcosms of soil collected from control (black bars) and added N plots (gray bars) that were treated with either no added litter or with *Artemisia californica* litter collected from added N or control plots. Also shown are the results (*F*-statistics and degrees of freedom) from ANOVA for differences between soil treatment (S), litter treatment (L), and soil x litter interaction (S x L). *, *P* < 0.05.

Table 1. Repeated measures analysis of variance results for microbial respiration and net N mineralization over the experimental period. Shown are the source terms of the model, source and error degrees of freedom (DF), sum of squares (SS), mean square (MS), *F*-ratio, and *p*-value.

Source term	DF	SS	MS	*F*-ratio	*p*-value
		Microbial respiration			
Soil (S)	1,18	12.32	12.32	19.06	0.0004
Litter (L)	2,18	9.51	4.76	7.36	0.005
S x L	2,18	0.16	0.08	0.12	NS
Time (T)	8144	50.66	6.33	239.14	<0.0001
S x T	8144	1.13	0.14	5.35	<0.0001
L x T	16,144	7.52	0.47	17.75	<0.0001
S x L x T	16,144	0.29	0.01	0.67	NS
		Net N mineralization			
Soil (S)	1,18	0.06	0.06	4.84	0.041
Litter (L)	2,18	0.02	0.01	0.99	NS
S x L	2,18	0.002	0.001	0.09	NS
Time (T)	8144	0.65	0.08	104.57	<0.0001
S x T	8144	0.006	0.001	1.04	NS
L x T	16,144	0.05	0.003	3.77	<0.0001
S x L x T	16,144	0.006	0.003	0.48	NS

rides) made up nearly three quarters of the litter C (Table 2), and typically, soluble C and non-lignified carbohydrates are consumed during the initial phase of litter decomposition (Staaf and Berg, 1982; Berg and Matzner, 1997) when labile C associated with fresh litter is a preferred source of C for soil microbes than the more recalcitrant soil organic matter (Blagodatskaya and Kuzyakov, 2008). Presumably, when the labile compounds were consumed the overall C quality of the litter became qualitatively similar to the soil organic matter in the microcosms.

Net N mineralization ($NO_3^- + NH_4^+$) was significantly affected by soil N addition but not litter addition; however, there was a significant litter × time interaction that was caused by lower rates of net N mineralization in the added litter treatments during the early stages of litter decomposition (Table 1 and Fig. 3). These results suggest that relatively more N was immobilized in the added litter treatments to support the initial increase in microbial growth (Blagodatskaya and Kuzyakov, 2008). After an initial peak (Day 21), net N mineralization declined and differences between litter treatments were negligible (Fig. 3), and over the 8-wk incubation, total net N mineralization was similar for all litter treatments (Fig. 2b).

We also hypothesized that an increase in soil N availability would lead to an increase in the initial rate of litter decomposition because N would increase the microbial degradation of labile C in fresh litter. Indeed soil exposed to added N had significantly higher extractable N, although total N and C concentrations were comparable for control and added N soils (Table 2). However, contrary to our hypothesis total microbial respiration in the control soil treatment was approximately 20 to 30 g C m^{-2} higher than in the added N soil treatment (Fig. 2a), indicating that soil N enrichment significantly reduced microbial activity on both old (soil) and new (litter) C substrates. Similar results have been reported for a temperate deciduous forest exposed to long-term (13 yr) N deposition exposure (Bowden et al., 2004), suggesting that a decline in microbial C mineralization may be

Table 2. Initial mean (±SE; *n* = 4 observations per treatment) litter and surface soil (0–10 cm) properties from control and added N plots in the field experiment at the Santa Margarita Experimental Reserve. Also shown is the *t*-statistic from a two-sample *t* test (degrees of freedom), and *p*-value.

Variable	Control (±SE)	Added N (±SE)	*t*-value (3)	*p*-value
Extractable $NH_4^+ + NO_3^-$ (μg/g)	0.11 ± 0.04	0.52 ± 0.20	−2.4	0.05
Soil N (%)	0.06 ± 0.01	0.08 ± 0.02	−1.2	NS†
Soil C (%)	0.69 ± 0.08	1.06 ± 0.27	−1.3	NS
Litter N (%)	0.88 ± 0.04	1.01 ± 0.05	−2.9	0.03
Litter C (%)	47.1 ± 1.5	42.5 ± 0.6	4.7	0.003
Litter C:N	53.5 ± 2.4	42.7 ± 2.0	4.3	0.005
Litter soluble C (%)	42.5 ± 0.3	39.0 ± 1.0	5.1	0.002
Litter holocellulose (%)	31.7 ± 1.8	33.6 ± 1.5	−0.7	NS
Litter lignin (%)	25.7 ± 1.9	27.3 ± 1.7	−0.6	NS
Litter lignin:N	29.1 ± 2.2	27.1 ± 1.7	0.5	NS

† NS, not significant ($p > 0.05$).

typical in soils exposed to chronic and/or high N inputs. Litter decomposition can be inhibited by N enrichment when the initial lignin concentration or lignin:N ratio is high (Fog, 1988; Carreiro et al., 2000; Knorr et al., 2005). For example, Carreiro et al. (2000) found that an increase in soil N availability stimulated initial rates of decomposition in low lignin litter (lignin:N = 9–12) but inhibited litter decomposition with more recalcitrant litter (lignin/N ratio = 29), which is similar to the *A. californica* litter used here (Table 2). Soil N enrichment has been linked to a decline in lignin-degrading enzyme activity and/or fungal population densities, which are primarily responsible for lignin degradation (Carreiro et al., 2000; Liu and Crowley, 2009).

Total net N mineralization over the 8 wk incubation was significantly affected by soil N addition but not litter, nor was there a significant interaction soil x litter (Fig. 2b). Soil exposed to added N accumulated on average (±SE) 1.55 ± 0.19 g N m^{-2} during the incubation period while net N-mineralization for control plots was 1.25 ± 0.10 g N m^{-2} (Fig. 2b). Again, the lower net N mineralization, coupled with higher microbial respiration, observed in the control soil presumably reflects a higher microbial demand for N (Blagodatskaya and Kuzyakov, 2008).

In conclusion, our results indicate that litter amendment, regardless litter origin, significantly increased respiration but reduced net N mineralization, presumably because greater microbial growth on litter substrates increased microbial demand for N. Microbial respiration was significantly higher in control soil, even with the addition of litter, suggesting that an increase in N availability reduced microbial activity but increased net N mineralization. Our results support the observation that chronic N deposition causes a decline in litter decomposition, presumably because soil N enrichment inhibits lignin degrading enzyme function when the initial litter lignin concentration and/or lignin:N ratio is high. Such a decline in microbial respiration and N demand in soil exposed to chronic N inputs, if indicative of the longer-term decomposition kinetics, could act to increase soil C and N sequestration and N availability in these semiarid ecosystems. Longer term field and laboratory decomposition experiments are needed in semiarid regions to determine how the soil C and N dynamics of semiarid shrublands are affected by chronic N deposition.

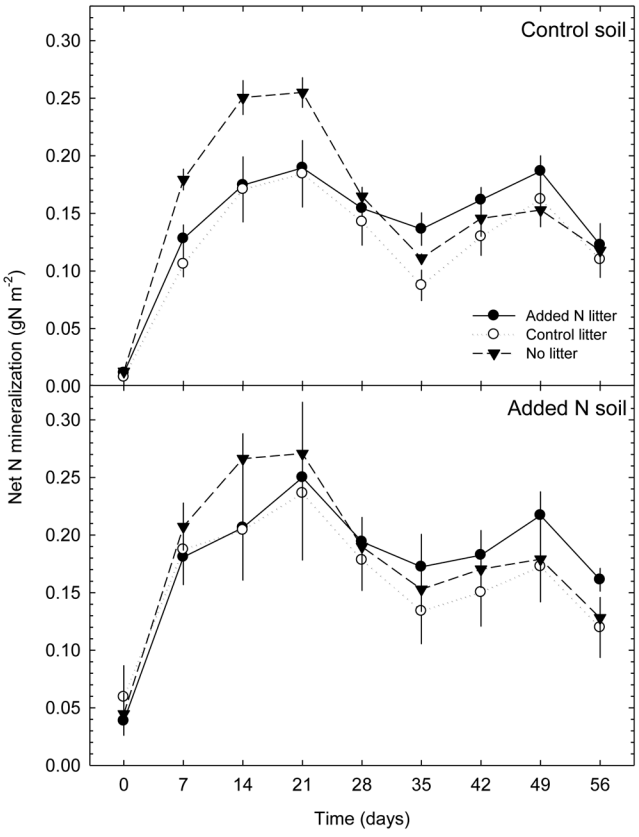

Fig. 3. Mean (±1 SE, n = 4) net N-mineralization ($NH_4^+ + NO_3^-$) during the 8-wk laboratory experiment from microcosms of soil collected from control (top panel) and added N plots (bottom panel) that were treated with either no added litter (black inverted triangles) or with *Artemisia californica* litter collected from added N (black circles) or control plots (white circles).

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