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Isotopic discrimination during long-term decomposition in an arid land ecosystem

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Abstract

Discrimination in carbon and nitrogen isotopes of decomposing plant litter in the northern Chihuahuan Desert was determined for a 5-year period. Factors influencing isotopic change were assessed from inter-species comparisons of litter chemistry, mass loss patterns, and isotope values of associated soil. Average $\delta^{15}N_{litter}$ values of buried roots increased 1.2 and 2.6‰ for Big Blue Stem (*Schizachyrium gerardi*, grass) and Varital (*Drypetes glauca*, hardwood) during the study, respectively. Small but inconsistent variations were observed for Slash Pine (*Pinus elliotii*, conifer) roots. Average $\delta^{15}N$ values of wooden dowels from Ramin (*Gonystlylus bancanus*, hardwood) increased ca. 2.0‰ during years 1–4, and then decreased slightly during year 5. Changes in $\delta^{15}N_{litter}$ were independent of N content, and may reflect microbial fractionation or preferential retention of ^{15}N enriched substrates. Surprisingly, there was no clear relationship between litter N dynamics and C/N ratios. There were no discernable changes in $\delta^{13}C_{litter}$ values for *Gonystlylus bancanus* and *Pinus elliotii*. Average $\delta^{13}C_{litter}$ values for *Schizachyrium gerardi* decreased ~2.0‰ during years 0–2 and then increased slightly. In contrast, average $\delta^{13}C_{litter}$ values for *Drypetes glauca* increased ~0.5‰ from years 0–1 then remained relatively constant until decreasing slightly in year 5. $\delta^{13}C_{litter}$ discrimination may have been masked by interfering $\delta^{13}C$ fractionations or feedbacks between decomposers and litter chemistry. Our data indicate that isotopic discrimination is characteristic of early litter decay stages. These results may highlight aspects of isotope discrimination and nutrient cycling unique to arid land environments. Additional studies will be needed to confirm this.

Keywords: Long-term decomposition; Soil organic matter; Carbon isotope; Nitrogen isotope; Chihuahuan Desert

1. Introduction

Discrimination of C and N isotopes in decomposing soil organic matter has been recognized in a variety of ecosystems and can provide important insight into physical and biological processes which mediate C storage, nutrient availability, and trace gas emissions (Evans and Ehleringer, 1993; Hoberg et al., 1995). Nevertheless, specific mechanisms responsible for these isotopic transformations are poorly understood and may depend on environmental factors and site history (Turner et al., 1983; Nadelhoffer and Fry, 1988; Balesdent et al., 1993). These gaps in knowledge are best addressed in long-term studies of litter decay (>1–10 years) where the isotopic chemistry of residues can be evaluated in light of component chemical fractions, mass loss patterns, and the soil environment. Few of such studies have been reported. The extent to which decomposition influences the isotope chemistry of soils is, therefore, poorly constrained.

While $\delta^{15}N$ values of fresh plant litter ($\delta^{15}N_{litter}$) are generally lower than those of the bulk soil (Nadelhoffer and Fry, 1988), profile-level patterns in soil $\delta^{15}N$ values ($\delta^{15}N_{soil}$) vary considerably. In many forest, grassland, and agricultural systems, $\delta^{15}N_{soil}$ increases with depth (up to >12‰), coincident with decreasing concentrations of organic N (Steele et al., 1981; Turner et al., 1983; Nadelhoffer and Fry, 1988) and decreasing organo-mineral size fractions (Tiessen et al., 1984). Such $\delta^{15}N$ profiles may reflect ^{15}N fractionation by microbial decomposers (Silfer et al., 1992) and increasing substrate age (Tiessen et al., 1984). However, patterns of $\delta^{15}N$ enrichment in soil profiles are not consistent for all locations. Shearer et al. (1978) reported higher mean $\delta^{15}N$ values for total N in soil samples collected near the surface as compared to underlying horizons, across a range of cultivated and undisturbed sites. Similar trends have been reported by Riga et al. (1970) for agricultural and forest soils. In other cases, little variation in $\delta^{15}N$ of total N with depth has been observed (Rennie et al., 1975).

Inter-site variations in organic vs. mineral-^{15}N pools probably underlie such discrepancies. For example, ^{15}N enrichment of soil N can result from: (1) adsorption of

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NH_4^- on clay surfaces (Karamanos and Rennie, 1980), (2) uptake or efflux of NO_3^- from plant roots (Kohl and Shearer, 1980), (3) gaseous N losses (Evans and Ehleringer, 1993; Robinson and Conroy, 1999), (4) soil trophic interactions (Minagawa and Wada, 1984), and (5) fractionation of organic-^{15}N during mineralization (Nadelhoffer and Fry, 1988). Only the last is directly linked to the decomposition of organic substrates. In contrast, illuvial N inputs of low ^{15}N content and the export and immobilization of NO_3^- below plant rooting zones can produce low $\delta^{15}N_{soil}$ values in sub-horizons relative to the surface (Nadelhoffer and Fry, 1994). At this time, inadequate understanding of these processes limits the interpretive utility of $\delta^{15}N$ measurements for total soil-N.

Average $\delta^{13}C$ values of C_4 plants ($\sim -12‰$) are distinct from C_3 plants ($\sim -26‰$) (Bender, 1968; Smith and Epstein, 1971) and these differences are maintained in fresh plant litter (Ludlow et al., 1976). However, 1–3‰ increases in the $\delta^{13}C$ values of soil organic matter ($\delta^{13}C_{soil}$) with depth have been reported in ecosystems at steady-state for 100s to >1000s of years with regard to relative C_3/C_4 biomass (Schleser and Bertram, 1981; Nadelhoffer and Fry, 1988). Hypotheses advanced to explain this pattern include: (1) ^{13}C fractionation by microbial decomposers, (2) preferential preservation of biochemical constituents, (3) variations in atmospheric $^{13}CO_2$ over the past century, (4) long-term changes in plant water-use efficiency, (5) variations in species composition within photosynthetic types, and (6) in situ translocation of old organic-C (Nadelhoffer and Fry, 1988; Balesdent et al., 1993). Convergence of $\delta^{13}C_{SOM}$ in deeper soil horizons under tropical forest (C_3) and grassland (C_4) communities has also been observed (Volkoff and Cerri, 1987) and may reflect the relative production and transport of organic acids within these soils (Nissenbaum and Schallinger, 1974). There is no evidence to suggest that any differences in C_3 and C_4 plant physiology influence post-depositional patterns of isotope discrimination in decomposing C_3/C_4 plant litter.

Litter bag experiments offer opportunity to evaluate $\delta^{13}C$ and $\delta^{15}N$ discrimination specific to decomposition. Quantitative relationships between bulk litter chemistry, mass loss rates, and isotope values can be determined by sequential sampling of litter bags (Melillo et al., 1989; Benner et al., 1991; Wedin et al., 1995). Sampling can be stratified to better separate intrinsic properties of litter decay from extrinsic soil properties or faunal characteristics (e.g. Mun and Whitford, 1998). In this way, general patterns of isotopic discrimination can be evaluated across sites and between studies. It must be recognized, however, that changes in litter bag ^{13}C and ^{15}N content may be influenced by microbial colonization and incorporation of new organic-C and N (Wedin et al., 1995) or feedbacks between decomposer growth and efficiency, and changes in litter chemistry (Ågren et al., 1996). Such contributions can be difficult to distinguish in field studies.

Isotopic transformation of plant litter is generally associated with later stages of decay (1 to >10's of years), necessitating a commitment to long-term decomposition studies. Few experiments have been conducted to evaluate mechanisms of isotope discrimination associated with decomposition over >1 year. These are limited to litter bag experiments from a temperate grassland community (Wedin et al., 1995), a mixed hardwood forest (Melillo et al., 1989), and salt-marshes (Benner et al., 1987, 1991). Not surprisingly, data from these investigations have been subject to differing interpretation (e.g. Ågren et al., 1996). Additional studies are needed to understand both the extent and environmental significance of isotopic change during decomposition.

In this study, we compare mass loss patterns, bulk chemistry, and isotope values of buried root litter in a northern Chihuahuan Desert ecosystem. Our goal was to identify relationships between long-term decomposition and isotopic discrimination in plant litter as characteristic of this environment. We hypothesized that patterns of N immobilization and mineralization control changes in $\delta^{15}N_{litter}$ values, while $\delta^{13}C$ values are determined by changes in lignin concentration.

2. Materials and methods

2.1. Project history and site location

Plant litter from a 5-year decomposition sequence was obtained from LIDET (Long-Term Intersite Decomposition Team) at Oregon State University, Forestry Sciences Laboratory. LIDET was initiated by the Long Term Ecological Research (LTER) site network to determine effects of litter quality and climate on long-term decomposition processes (LIDET, 1995). The program included 21 sites representing a variety of temperature and moisture conditions. Decomposition dynamics were studied for 10 litter types at each site. These included 3 types of fine roots (grass, hardwood, and conifer), 6 types of leaf litter (over a range of lignin/N ratios), and wooden dowels. Our analyses were restricted to fine roots (<2 mm diam.) and dowels.

Samples used for this investigation were taken from the Jornada LTER site, 40 km NNE of Las Cruces, NM (32°30′N 106°45′W) during 1990–1995. The study area is located on an east-facing alluvial piedmont surface comprised of monzonitic parent material. Soils consist of fine- and coarse loamy Typic Haplargids and support a *Larrea tridentata* dominated shrub community (Gile and Grossman, 1979). Accumulations of pedogenic carbonate are common at this location. The mean annual precipitation is 211 mm with 53% falling between July and September; the mean annual temperature is 15.6°C (Conley et al., 1992).

2.2. LIDET materials and protocal

Fine roots of Varital (*Drypetes glauca*), a C_3 tropical

hardwood, Slash Pine (*Pinus elliotii*), a C_3 conifer, and Big Blue Stem (*Schizachyrium gerardi*), a C_4 grass, were collected by LIDET members from the Luquillo LTER in Puerto Rico, Florida, and Konza LTER (respectively). Root samples were washed with deionized water, and air-dried (*D. glauca* was oven dried at 40°C). Approximately 5–7 g of roots of each species were placed in $20 \times 20\ cm^2$ fiberglass mesh bags (mesh size = 55 μm). Bag openings were sealed with 6 monel staples. Wooden dowels (13 mm × 61 cm) were constructed from Ramin (*Gonystylus bancanus*), a C_3 tropical hardwood. While *G. bancanus* grows in Indonesia and Malaysia, the dowels are a commercially available in the United States. The LIDET experiment did not include root litter from species native to the Jornada LTER.

The LIDET study was designed for the annual retrieval of 1 litter-bag of each species from 4 replicate plots over a 10 year period. Sample placement was initiated during Fall 1990. Root litter was buried within the top 20 cm of the soil surface and wooden dowels were inserted to ~30 cm depth. Among sites, litter-bags for each collection period were randomly connected (by species) along a cord. Upon retrieval, samples were rinsed with distilled water to remove adhering soil, oven dried at 55°C, ground to <2 mm, and stored in plastic vials. Initial and final air-dry weights and oven-dry weights were recorded. Subsamples of initial and final material were ashed at 550°C for 5 h to obtain organic-C content. Percent mass remaining was corrected for contamination (by the authors) using a modified equation of (MacKay et al., 1987):

$$R(\%) = \frac{F - ((A - C)/S_i)}{I} \times 100$$

where R is the percent mass remaining; I, the initial dry weight; F, the final dry weight; A, the ash weight of final sample; C, the ash weight of initial sample; and S_i, the ash content of mineral soil under a litter-bag. Soil samples were collected from each study plot for the determination of ash content and isotope chemistry. In a subset of litter-bags ($n = 3$), the correction equation failed to account for all contamination ($R > 100\%$). These samples were excluded from further analyses.

2.3. Analytical measurements

Elemental C and N concentrations ([C] and [N], respectively) and isotope values of soils, litter, and belowground portions of wooden dowels, were measured by dry combustion on a Carlo Erba 1108 Elemental Analyzer coupled with a Finnigan MAT 252 Isotope Ratio Mass Spectrometer at the Dartmouth College D-LITE laboratory. Litter and dowel samples were ground through a #40 mesh prior to isotope analysis. The C and N isotope results are expressed in delta (δ) notation where: $\delta(‰) = [(R_{sample}/R_{standard}) - 1 \times 1000$ and R_{sample} and $R_{standard}$ refer to the $^{13}C/^{12}C$ or $^{15}N/^{14}N$ ratios of sample and standard, respectively. $\delta^{13}C$ values are reported in parts per thousand (‰) relative to the Vienna Pee Dee Belemnite (VPDB) standard; $\delta^{15}N$ values are reported relative to atmospheric N (AIR) (Coplen, 1994). Repeated measurements ($n = 14$) of a plant standard (*Prosopis glandulosa*) over time yielded a precision (1 standard deviation, SD) of ±0.22‰ ($\delta^{15}N$), ±0.08‰ ($\delta^{13}C$), ±0.74 [N], and ±0.75 [C]. Precision for isotope measurements of a chemical standard (acetanilide) within sample runs was ±0.22 and 0.17‰ for $\delta^{15}N$ and $\delta^{13}C$, respectively.

Lignin concentrations ([Lignin]) were measured using near infrared reflectance spectroscopy (NIR) at Oregon State University, Department of Forest Science (see McLellan et al., 1991). The NIR technique accurately estimated [lignin] in senescent roots ($r^2 > 0.99$) and wood ($r^2 > 0.98$) from a calibration data set obtained by wet chemistry (Jay Sexton, personal communication, 1998). In the latter case, C fractions were determined by forest product techniques (e.g. Melillo et al., 1989). Unfortunately, initial [lignin] (t_0) was not determined for roots or dowels. In addition, NIR measurements were sometimes restricted to pooled samples (across replicates) due to cost restrictions or inadequate sample amounts. The LIDET program intended NIR measurements of total cellulose and hemicellulose in litter samples, as well as chemical determination of other C fractions. These measurements were not available for our study.

2.4. Decomposition models and statistical treatment

A single exponential decay model was used to estimate turnover rates (τ) for root litter between years: $X = X_o\, e^{-kt}$ and $\tau = 1/k$; where k, the decomposition constant; t, the time elapsed since burial (year); X_o, fraction of ash free mass at t_0 (100%), and X, fraction of ash-free mass at time t. The model assumes that a single constant, k, characterizes the mass loss of decomposing substrates and that the relative rate of decomposition is constant (Wieder and Lang, 1982). In this context, a single exponential model describes the basic attributes of organic decomposition — rapid loss of easily degradable compounds (sugars, starches, and proteins) and slower loss of recalcitrant materials (cellulose, fat, tannins, lignins) (e.g. McClaugherty et al., 1985; Schlesinger, 1985).

Effects of litter quality on τ and isotope values of root litter and wooden dowels were evaluated using multiple step-wise regression. Parameter selection was based on a significance level of $P < 0.05$. Parameters included [N] and [lignin], N content, and C/N ratio. A two-way ANOVA was used to test the main effect of species and time on litter mass loss. The data were log-transformed prior to analyses to meet assumptions of normality. Initial values (t_0) were also excluded from ANOVA analyses (Wieder and Lang, 1982). For a posteriori testing of intra-specific differences in litter τ with time we used one-way ANOVAs. When significance was observed at the $P < 0.05$ level, paired comparisons were used to distinguish the least

Table 1
Concentrations of elements, organic fractions, parameters of mass loss, and isotope values for remaining plant litter. Values in parenthesis indicate 1SD from the mean of replicate samples. For turnover rate (τ), means with the same superscript within species are not significantly different ($P < 0.05$) for years 1–5 (ND, not determined; NA, not applicable; P, samples pooled within replicates)

Species	Time (years)	N (%)	C/N	Lignin (%)	Mass loss (% of initial)	k (years^{-1})	Turnover rate (years)
S. gerardi	0	0.53	52.0	ND	0.0	NA	NA
	1	0.55 (0.09)	36.7 (6.9)	80.6 (7.5)	10.0 (2.5) [a]	−0.11 (0.03)	10.0 (2.8)[ab]
	2	0.66 (0.08)	24.9 (3.1)	80.7 (P)	21.2 (3.0)[b]	−0.12(0.02)	8.5 (1.3)[a]
	3	0.73 (0.11)	23.9 (3.3)	88.7 (P)	22.5 (5.7)[b]	−0.09 (0.02)	12.3 (3.4)[bc]
	4	0.72 (0.10)	22.1 (3.6)	82.7 (6.7)	29.2 (1.5)[c]	−0.09 (0.01)	11.5 (0.6)[abc]
	5	0.71 (0.12)	23.5 (4.6)	37.7 (34.5)	29.5 (4.4)[c]	−0.01 (0.02)	14.8 (2.5)[c]
D. glauca	0	0.61	65.4	ND	0.0	NA	NA
	1	0.94 (0.12)	40.5 (5.3)	46.3 (2.6)	22.2 (4.3)[a]	−0.25 (0.06)	4.3 (1.0)[a]
	2	1.28 (0.03)	27.9 (3.2)	41.3	37.3 (8.0)[b]	−0.02 (0.07)	4.3 (1.5)[a]
	3	1.17 (0.07)	32.7 (2.2)	42.8 (P)	43.2 (5.4)[bc]	−0.19 (0.03)	5.3 (1.3)[a]
	4	1.53 (0.28)	23.8 (3.8)	30.6 (6.4)	46.2 (15.3)[c]	−0.16 (0.08)	7.3 (3.4)[a]
	5	1.53 (0.22)	25.3 (4.3)	73.0	68.7 (7.7)[d]	−0.24 (0.05)	4.5 (1.3)[a]
G. bancanus	0	0.20 (P)	204.5 (P)	ND	0.0	NA	NA
	1	0.17 (P)	238.5 (P)	11.9	10.7 (1.5)[a]	−0.11 (0.02)	9.0 (1.4)[ab]
	2	0.21 (P)	197.7 (P)	73.0	32.5 (15.4)[ab]−0.21 (0.12)	6.3 (3.4)[a]	
	3	0.20 (P)	199.32 (P)	59.7	17.7 (4.1)[ab]	−0.07 (0.02)	15.8 (4.1)[bc]
	4	0.23 (P)	174.5 (P)	79.5	21.0 (2.8)[b]	−0.06 (0.01)	17.5 (3.1)[c]
	5	0.23 (P)	175.0 (P)	ND	22.0 (8.6)[b]	−0.05 (0.02)	23.0 (9.3)[c]
P. elliotii	0	0.62	65.5	ND	0.0	NA	NA
	1	0.78 (0.08)	47.6 (1.2)	31.3 (2.5)	13.5 (0.58)[a]	−0.15 (0.01)	7.0 (0.0)[a]
	2	0.81 (0.05)	51.3 (4.3)	29.8 (0.83)	21.2 (7.4)[ab]	−0.12 (0.04)	9.3 (4.0)[ab]
	3	0.82 (0.07)	47.3 (4.6)	36.0 (P)	33.0 (18.8)[ab]−0.13 (0.07)	9.0 (3.5)[a]	
	4	0.71 (0.39)	44.2 (4.9)	33.9 (7.9)	20.5 (2.1)[ab]	−0.06 (0.01)	17.5 (2.1)[bc]
	5	0.93 (0.05)	43.0 (1.9)	23.5 (4.4)	26.2 (9.6)[b]	−0.06 (0.02)	19.0 (8.1)[c]

square means (Sokal and Rohlf, 1969). A posteriori tests for τ were conducted to evaluate the potential patterns of litter decomposition, undetected in litter chemistry parameters, which might influence isotope discrimination.

We tested effects of collection time on $\delta^{15}N_{litter}$ values in a similar manner. Isotope values for *G. bancanus* were only obtainable from pooled samples. Consequently, ANOVAs for isotope data were restricted to root litter. Analysis of variance was not used to evaluate the $\delta^{13}C$ data due to dependence between treatment and error terms. All statistical procedures were conducted using SAS-version 6.12 (SAS, 1997).

3. Results

3.1. Mass loss patterns

Total mass loss was greatest for *D. glauca*, with approximately 69% of the ash-free mass removed after 5 years (Table 1). Total mass loss of *P. elliotii* (~26%) and *S. gerardi* (~29%) litter was substantially less, but was similar to the *G. bancanus* dowel (~22%). Turnover rates varied significantly among species ($P < 0.0001$, df $= 2$, $F = 42.29$) and collection times ($P < 0.0001$, df $= 4$, $F = 13.31$), with values ranging from 4.3 ± 1.0 years in *D. glauca* litter (year 1) to 23 ± 9.3 for *G. bancanus* (year 5). However, the species–year interaction was significant ($P < 0.0105$, df $= 4$, $F = 2.50$), owing to greater mass loss for *G. bancanus* at year 2 and *P. elliotii* at year 3, than during subsequent collection times.

One-way ANOVAs indicated that significant differences in the annual τ of root litter were most apparent between years 1–2 and 3–5 for *S. gerardi* ($P < 0.0230$, df $= 4$, $F = 3.9$) and years 1–3 and 4–5 for *P. elliotii* ($P < 0.0174$, df $= 4$, $F = 4.46$) (Table 1). Mass loss of *G. bancanus* dowels was greater in years 1–2 than years 3–5 ($P < 0.0006$, df $= 4$, $F = 9.27$). There was no significant difference in annual τ of *D. glauca* litter ($P < 0.2463$, df $= 4$, $F = 1.53$).

3.2. Litter quality indicators

Initial [N] in root litter was similar across species, ranging from 0.53% *(S. gerardi.)* to 0.62% *(P. elliotii)*. Initial [N] of *G. bancanus* wood was substantially less, 0.20% (Table 1). Similar patterns in initial C/N ratios were evident, although the C/N ratio of *G. bancanus* (205) was the highest among species (Table 1). [N] increased over time in the litter-bags but remained relatively constant for the dowels. The greatest total increase in [N] was measured in *D. glauca* litter, approximately 106%. C/N ratios of root litter and the wooden dowel decreased through time. The greatest total

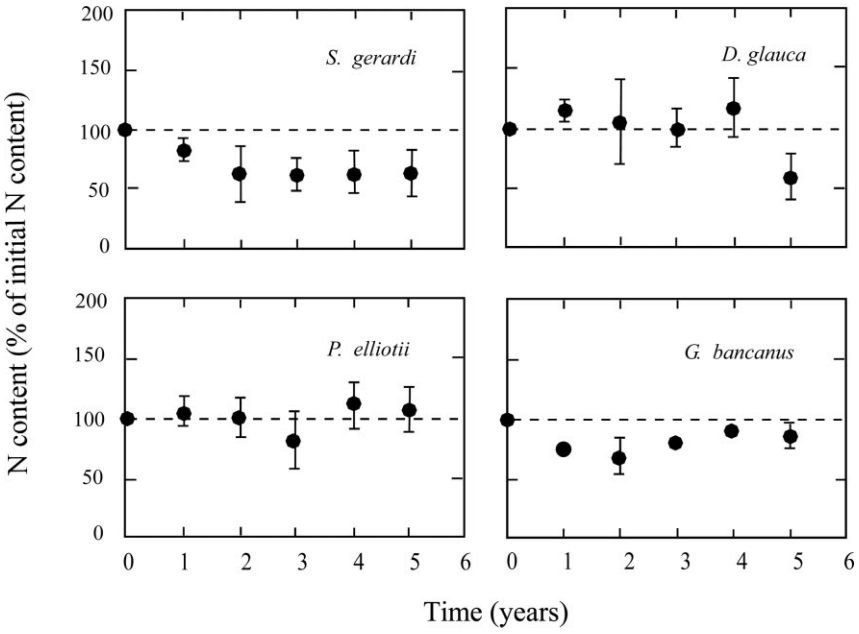

Fig. 1. Nitrogen content for remaining plant litter. Error bars indicate 1SD from the mean of replicate samples.

decrease in C/N occurred in *P. elliotii* litter, 34% of the initial value.

Patterns in total N content varied across species and through time (Fig. 1). Total N in *S. gerardi* litter decreased during years 1–2 and then remained relatively constant. Total N in *G. bancanus* dowels also decreased during years 1–2 but then increased. N accumulated in *D. glauca* and *P. elliotii* litter, excepting years 5 and 3, respectively.

[Lignin] in root litter varied irregularly across species and through time (Table 1). [Lignin] in *S. gerardi* litter was similar during years 1–4 but decreased substantially in year 5. In contrast, [lignin] in *D. glauca* litter was similar during years 1–4 but increased in year 5. [Lignin] increased through time in *G. bancanus* dowels (except year 3); smaller increases were observed in *P. elliotii* litter. These patterns should be interpreted cautiously given that replicate measurements were often unavailable. In most cases variation within replicates was <8%.

3.3. ^{13}C and ^{15}N isotope dynamics

$\delta^{13}C_{litter}$ values ranged from −25.3 to −30.2‰ among C_3 species (*G. bancanus, D. glauca*, and *P. elliotii*) and −12.7 to −14.8‰ for *S. gerardi*, a C_4 species (Fig. 2 and Table 2). In comparison, $\delta^{13}C$ and $\delta^{15}N$ values of surrounding soils ($n = 4$; pooled within replicate plots) were -21.98 ± 0.75 and 2.03 ± 1.05‰, respectively. Temporal changes in $\delta^{13}C_{litter}$ values compared both within and among species were inconsistent. For example, average $\delta^{13}C_{litter}$ values of *S. gerardi* decreased ~1.1–2.0‰ from years 0 to 3, and then increased slightly during years 4–5. Average $\delta^{13}C_{litter}$ values of *D. glauca* increased by ~0.5‰ during years 0–5. In contrast, changes in the $\delta^{13}C_{litter}$ values of *G. bancanus* dowels and *P. elliotii* litter were negligible. Variation in $\delta^{13}C$ values across replicates and within years was least for these latter two species.

Initial $\delta^{15}N_{litter}$ values ranged from −1.9 (*G. bancanus*) to 1.2‰ (*S. gerardi*.). $\delta^{15}N_{litter}$ values of *S. gerardi* and *D. glauca* increased by approximately 1.2 and 2.6‰, respectively, over 5 years of decomposition (Fig. 2 and Table 2). However, there were no significant differences ($P < 0.05$) between collection years for these species. While clear increases in $\delta^{15}N_{litter}$ values from these species occurred between years 1–2, year 1 was excluded from ANOVAs due to lack of replication. This, and large standard deviations for *D. glauca*, may explain the absence of a significant treatment effect. Small but inconsistent variations were observed in $\delta^{15}N_{litter}$ values of *P. elliotii*. In this context, it was surprising to find a significant effect for collection time in *P. elliotii* ($P < 0.0270$, $df = 4$, $F = 3.72$). $\delta^{15}N_{litter}$ values of *G. bancanus* dowels increased by nearly 2.0‰ during years 1–4, and then decreased slightly during year 5.

3.4. Factors influencing decomposition rates and isotope values of litter

[N] was the only component of litter quality to explain a significant proportion ($P < 0.05$) of variability in the mass loss data (Table 3). However, we could not examine the importance of initial [N] as a predictor of mass loss, owing to the lack of sample replication. Similarly, initial [lignin] was not available at the time of this study. This is unfortunate since initial [lignin] or initial lignin:N ratios of litter are often the best predictors of

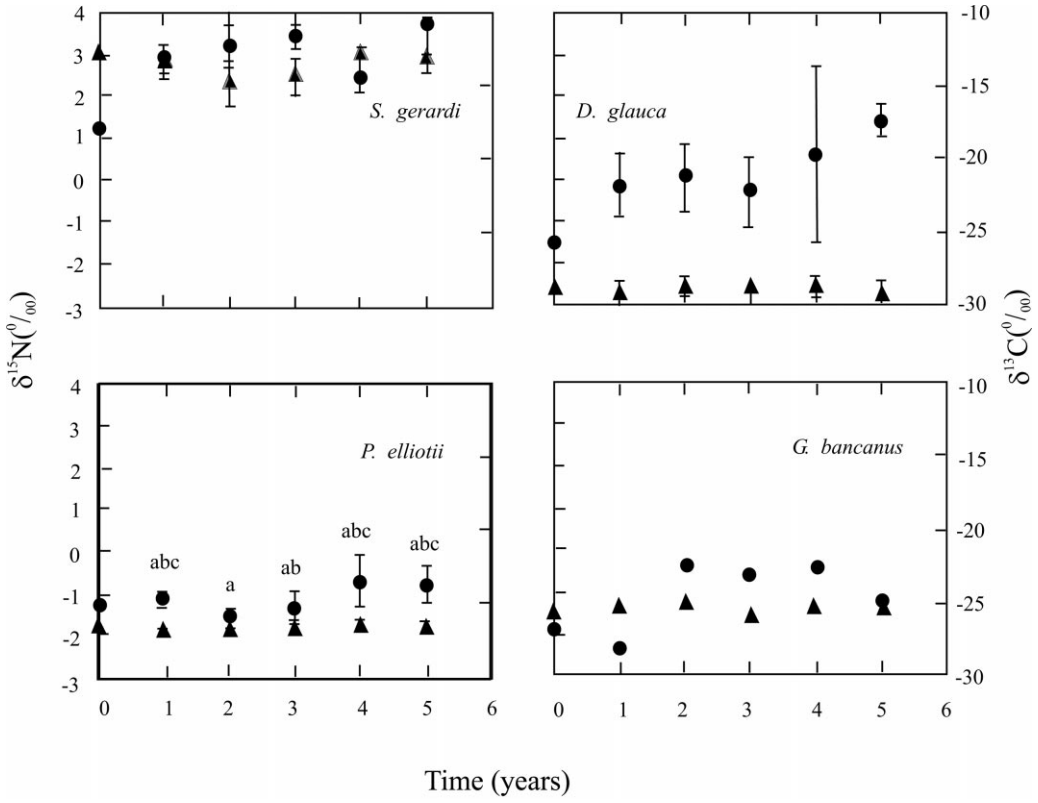

Fig. 2. $\delta^{15}N$ (circles) and $\delta^{13}C$ (triangles) values for remaining plant litter. Error bars indicate 1SD from the mean of replicate samples. Samples were pooled for *G. bancanus*. Means with the same superscript are not significantly different between years ($P < 0.05$).

mass loss (Melillo et al., 1982; Taylor et al., 1991; Mun and Whitford, 1998) and the former is correlated with N-use efficiency by microbial decomposers (Melillo et al., 1989).

There were no clear relationships between litter quality, mass loss, and corresponding isotopic data among the species examined in this study (Table 3). [Lignin] accounted for 78% of the variability in $\delta^{15}N_{litter}$ values of *S. gerardi*; the model improved slightly when [N] was included. In comparison, [N] accounted for 17% of the variability in *D. glauca* and C/N ratios accounted for 41% of the variability in *P. elliotii*. No other variable were significant at $P < 0.05$. Similarly, C/N ratios accounted for 80% of the variability in $\delta^{13}C_{litter}$ values of *S. gerardi*, while [N] accounted for only 25% of the variability in $\delta^{13}C_{litter}$ values of *S. gerardi*. No other variables were significant. $\delta^{13}C_{litter}$ values of *P. elliotii* were not explained by any of the litter quality parameters used in this study.

4. Discussion

Variations in the C and N isotope values of decomposing root litter from this study contrast to patterns reported in prior decomposition experiments. Specifically, $\delta^{15}N_{litter}$ did not reflect changes in N content and $\delta^{13}C_{litter}$ did not vary with [lignin]. Similar isotopic patterns were observed for wooden dowels. $\delta^{15}N$ values increased among species over time, which may be explained by microbially mediated fractionation or the preferential retention of ^{15}N enriched substrates. In contrast, $\delta^{13}C_{litter}$ values varied irregularly among C_3 and C_4 species. These patterns were not explained by mass loss patterns, changes in other litter quality parameters, or the incorporation of exogenous biomass. Additionally, there was no clear relationship between litter N dynamics and C/N ratios.

4.1. Theoretical framework

Factors thought to underlie isotopic discrimination in organic substrates during decomposition include preferential retention of component tissue fractions, respiratory fractionation by microbes, incorporation of exogenous substrate, and continuous cycling of C between litter and decomposers (Nadelhoffer and Fry, 1988; Balesdent et al., 1993; Ågren et al., 1996). The relative extent to which each process occurs determines the bulk isotopic signal of residue litter. In this context, competing factors can produce either negative or positive feedbacks on substrate chemistry depending on their overall mass-balance and the direction and magnitude of isotopic change. While positive

Table 2
$\delta^{13}C$ and $\delta^{15}N$ values of remaining plant litter. A capitalized P refers to a measurement taken from a sample pooled across replicates (all measurements for *G. bancanus* are from pooled samples). Superscripts indicate year of measurement

Collection Time (year)	Replicate	*S. gerardi*		*D. glauca*		*P. elliotii*		*G. bancanus*	
		$\delta^{13}C$ (‰)	$\delta^{15}N$ (‰)	$\delta^{13}C$ (‰)	$\delta^{15}N$ (‰)	$\delta^{13}C$ (‰)	$\delta^{15}N$ (‰)	$\delta^{13}C$ (‰)	$\delta^{15}N$ (‰)
0	P	−12.89	1.22	−29.22	−1.47	−26.63	−1.30	−25.74	-1.90^{0}
1	1	−13.58	2.57	−28.60	−0.88	−26.98	−1.08	−25.37	-2.31^{1}
	2	−13.76	3.21	−28.09	0.58	−26.79	−1.05		
	3	−14.79	3.11	−28.95	0.42	−26.96	−0.98		
	4	−13.70	2.85	−29.30	−0.62	−26.71	−1.39		
2	1	−15.93	3.15	−29.02	0.29	−26.95	−1.68	−25.32	-0.34^{2}
	2	−16.10	2.48	−27.63	0.81	−26.69	−1.84		
	3	−14.73	3.45	−29.32	0.30	−27.19	−1.70		
	4	−12.68	3.63	−28.92	−1.06	−26.95	−1.30		
3	1	−13.13	3.74	−28.86	−1.29	−26.30	−1.59	−25.93	-0.54^{3}
	2	−13.56	3.45	−28.83	−0.50	−26.72	−1.75		
	3	−15.67	3.04	−28.55	0.76	−26.89	−1.41		
	4	−14.95	3.51	−28.99	−0.33	−27.12	−0.78		
4	1	−12.66	2.59	−29.64	−1.07	−26.48	0.15	−25.39	-0.41^{4}
	2	−13.12	2.04	−28.70	0.50	−26.66	−1.03		
	3	−12.75	2.39	−27.88	3.57	−26.64	−1.22		
	4	−12.73	2.89	−28.76	−0.55	−26.90	−0.75		
5	1	−13.12	4.58	−30.21	1.84	−26.64	−0.80	−25.48	-1.22^{5}
	2	−13.36	2.63	−28.48	1.18	−26.72	−0.79		
	3	−12.84	5.02	−29.72	1.57	−26.55	−0.27		
	4	−13.09	2.92	−28.59	1.00	−26.81	−1.30		

identification of the process(s) actually responsible for isotope discrimination is difficult, if not impossible, others can be eliminated.

4.2. Controls on litter $\delta^{15}N$ values during decomposition

Previous litter-bag studies indicate that $\delta^{15}N_{litter}$ is determined primarily by the incorporation or loss of exogenous biomass during N_{immob} and N_{min}, respectively. In this context, N contents >100% indicate net N accumulation through immobilization (N_{immob}), while N contents <100% indicate N loss through mineralization (N_{min}) (Aber and Melillo, 1980; Benner et al., 1991). It also follows that an increase (decrease) in litter N content between years indicates net N_{immob} (N_{min}) during that time.

During a 77-month decomposition study of red pine (*Pinus resinosa*) needles, Melillo et al. (1989) noted an initial 2–3‰ decrease in whole tissue $\delta^{15}N_{litter}$ values that coincided with net N_{immob}. The $\delta^{15}N$ values increased by ca. 0.5‰ during subsequent N_{min} despite large N losses. Similar results were reported in an 18-month study of anaerobic decomposition of *Spartina alterniflora* roots in salt-marsh sediments (Benner et al., 1991). During the first 120 days, N_{litter} contents decreased 60% while $\delta^{15}N_{litter}$ values varied by <0.4‰ of initial values. Later stages of decomposition were characterized by net N_{immob} and a marked decrease in $^{15}N_{litter}$. These patterns were attributed to the incorporation and subsequent release of immobilized-N with lower ^{15}N content than the original plant material, either from soil pore waters or heterotrophic bacteria (Benner et al., 1991).

Interestingly, Fogel and Tuross (1995) reported that N_{immob} covaried with the $\delta^{15}N_{litter}$ of decomposing *Nuphar advena* (Spatterdock) roots and rhizomes. Part of the newly immobilized-N consisted of amino acids, perhaps from decomposing material in pore waters or microbial colonizers (Fogel and Tuross, 1995). From mass balance of ^{15}N, it follows that the $\delta^{15}N$ of immobilized-N was greater than that of *N advena* litter. It is important to point out, however, that the actual source and isotopic composition of immobilized-N was not uniquely determined.

Discrimination of $^{15}N_{litter}$ was not caused by incorporation of exogenous biomass from surrounding soils in our study. From results of previous studies, we hypothesized that changes in $\delta^{15}N_{litter}$ values would correlate with N_{immob} and the extent and direction of isotopic change would be determined by differences between initial $\delta^{15}N_{litter}$ and $\delta^{15}N_{soil}$ values. Since the surrounding $\delta^{15}N_{soil}$ was ca. 2.03‰, it follows that $\delta^{15}N_{litter}$ values should converge on this value during periods of net N_{immob} (Wedin et al., 1995). However, $\delta^{15}N_{litter}$ values increased during both N_{min} and N_{immob} and in *S. gerardi*, were as high as 5.02‰. These observations imply that $\delta^{15}N_{litter}$ values were not determined by additions of microbial or soil-N. The lack of consistent discrimination in $\delta^{13}C_{litter}$ values (discussed later) and the absence of a statistical relationship between N content and $\delta^{15}N_{litter}$ values lends further support to this conclusion.

Table 3
Results of stepwise regression comparing mass loss of root litter with N and concentration, C/N ratio, and lignin concentration. C and N isotope values of root litter were compared with N and lignin concentration, C/N ratio, and N content. Variables were included in the regression model when $P < 0.05$. Pooled measurements were excluded from the analyses

Litter quality parameters by Species	Slope	Partial r^2	P
Biomass remaining			
S. gerardi (df = 11)			
N concentration(%)	−69.0	0.60	0.0033
D. glauca (df = 12)			
N concentration (%)	−19.0	0.70	0.0004
P. elliotii (df = 12)			
N concentration (%)	−88.6	0.68	0.0001
δ^{15}N of Litter			
S. gerardi (df = 11)			
N concentration (%)	−2.11	0.10	0.0001
Lignin (%)	−0.03	0.78	0.0235
D. glauca (df = 12)			
N concentration (%)	1.71	0.17	0.0082
N content (% initial)	−0.02	0.48	0.0501
P. elliotii (df = 12)			
C/N	−0.09	0.41	0.0185
N content (% initial)	−0.01	0.17	0.0643
δ^{13}C of Litter			
S. gerardi (df = 11)			
C/N	−0.08	0.80	0.0001
D. glauca (df = 12)			
No significant predictors			
P. elliotii (df = 12)			
N concentration (%)	1.02	0.25	0.0275
N content (% initial)	−0.01	0.35	0.0326

Microbially mediated fractionations or preferential retention of ^{15}N-enriched refractory compounds could explain enrichment of ^{15}N in decomposing litter from our study. The latter is uncertain given that δ^{15}N values of component litter fractions vary little from whole tissue N (Nadelhoffer and Fry, 1988). However, DeNiro and Hastore (1985) did observe large differences in $\delta^{15}N_{litter}$ values (up to 21‰) of different fractions of uncarbonized prehistoric plant remains that were not apparent in their modern counterparts, and could not be attributed to adsorption of exogenous N. The authors indicated that isotopic fractionation during microbial decomposition was an unlikely source of δ^{15}N variation due to the excellent state of sample preservation.

There is evidence for discrimination against ^{15}N by microbial decomposers that is consistent with our data. For example, changes in $\delta^{15}N_{soil}$ values of +0.3–0.7‰ were measured during 600-day aerobic incubations of mineral soil (Nadelhoffer and Fry, 1988), although δ^{15}N fractionations specific to biodegradation were not resolved. In contrast, Macko and Estep (1984) demonstrated ^{15}N discrimination in aerobic, heterotrophic, bacterium cultured on amino acids. Bacterial ^{15}N was enriched (up to +22‰) when grown on glutamic or aspartic acid, but was depleted (up to −12‰) when grown on alanine and serine. Differences in isotope fractionation among the treatments were related to initial substrate chemistry.

$\delta^{15}N_{litter}$ discrimination in our study was 1–4‰ greater than previously inferred for decomposition (Macko and Estep, 1984). This discrepancy may owe to the local environmental controls on microbial processes or the additive effects of other discriminatory processes on $^{15}N_{litter}$ content. Preferential retention of ^{15}N enriched substrates may be important in this case, although there was no clear relationship between $\delta^{15}N_{litter}$ and N content. A linear association between these variables should result if isotope discrimination followed from a directional loss of substrate (e.g. Robinson and Conroy, 1999).

4.3. Controls on litter δ^{13}C values during decomposition

As mentioned, factors effecting discrimination of C isotopes in litter-bag residues during biodegradation may include: (1) preferential retention of recalcitrant compounds depleted in ^{13}C such as lignin; (2) preferential use of ^{12}C for respiration by decomposers; (3) incorporation of exogenous biomass; and (4) feedback between litter quality and decomposers (Nadelhoffer and Fry, 1988; Balesdent et al., 1993; Ågren et al., 1996). In isolation, factors 1 and 2 produce a decrease or increase in $\delta^{13}C_{litter}$ values, respectively. Factors 3 and 4 can have variable effects depending on the difference in ^{13}C content between litter and surrounding soil (factor 3) or feedbacks between litter quality and microbial dynamics (factor 4). We will evaluate each possibility in the context of our data.

There was no discernable discrimination in $\delta^{13}C_{litter}$ from our study that could be attributed to selective preservation. As biodegradation progresses the relative proportion of lignin in residues generally increase, biasing the $\delta^{13}C_{litter}$ signal toward more negative values (Melillo et al., 1982, 1989). This owes to the fact that lignin is depleted in ^{13}C relative to less refractory C fractions (Benner et al., 1987, 1991). For example, a decrease in $\delta^{13}C_{litter}$ values of *S. alterniflora* during aerobic decomposition was attributed to proportional losses of polysaccharide relative to lignin-C (Benner et al., 1987, 1991). Similar variations in δ^{13}C values of decomposing *P. resinosa* needles were explained by relative losses of ^{13}C-enriched or depleted C fractions (Melillo et al., 1989).

$\delta^{13}C_{litter}$ values did not decrease regularly through time in our study, nor did $\delta^{13}C_{litter}$ values and [lignin] covary within species. In fact, $\delta^{13}C_{litter}$ values of *G. bancanus* and *P. elliottii* remained relatively constant throughout the five years and, while average $\delta^{13}C_{litter}$ values of *S. gerardi* decreased during years 0–2, they increased again during years 3–5. Additionally, [lignin] did not increase regularly in all species during decomposition. This may be an artifact of our data given the absence of initial [lignin] measurements and the fact that samples were sometimes pooled within years. A pattern of increasing [lignin] in buried litter was

reported in an earlier long-term decomposition study from the Jornada LTER (Mun and Whitford, 1998). The absence of a consistent isotopic pattern across species and time does suggest that edaphic factors had little direct or indirect influence on isotope discrimination.

Respiratory fractionation of $^{13}C/^{12}C$ by microbial decomposers was not obvious from $\delta^{13}C_{litter}$ values in our study. As previously mentioned, microbial fractionation should produce increased $\delta^{13}C_{litter}$ values in remaining substrates. The only apparent increase in average $\delta^{13}C_{litter}$ values occurred in *D. glauca* between years 0–1. During subsequent years litter variations were either invarient (years 1–4) or decreased (year 5) relative to the previous year.

Direct evidence for $\delta^{13}C$ fractionation with microbial growth stems from in vitro culture experiments. Macko and Estep (1984) demonstrated a $+0.1$–$11.1‰$ enrichment of ^{13}C in bacteria grown on amino acids (excepting tyrosine and arginine), which they attributed to proportionate losses of ^{12}C during respiration. In two oak forests (*Quercus* spp.) of Wisconsin, $\delta^{13}C_{soil}$ values varied with litter inputs and organic-C mineralization (Nadelhoffer and Fry, 1988). The former lowered $\delta^{13}C_{soil}$ values while the latter increased them. Field soils and laboratory incubations indicated an inverse relationship between the $\delta^{13}C_{soil}$ and [C], although isotopic enrichment was generally $<0.5‰$. It is not surprising, therefore, that ^{13}C enrichment of decomposing litter has not been detected in other forests (Balesdent et al., 1993) or in our study.

It is clear that any import of exogenous C into our litterbag had little influence on $^{13}C_{litter}$ contents overall. This follows from Wedin et al. (1995), who attributed opposite shifts in the $\delta^{13}C_{litter}$ values of C_3 and C_4 grasses to incorporation of new C from surrounding soils. In our study, there was no directional increase in C_3 litter toward that of surrounding SOM (ca. $-21.98‰$), excepting *D. glauca* during years 0–1. *S. gerardi*, a C_4 species, did exhibit a tendency toward more negative $\delta^{13}C_{litter}$ values during years 0–2, as would be expected from such contamination. However, average $\delta^{13}C_{litter}$ values for this species increased slightly during subsequent years. The lack of an obvious contaminant effect is consistent with the similar lack of correlation between N_{immob} patterns and $\delta^{15}N_{litter}$ values.

Feedbacks between litter quality and microbial decomposers could be invoked to explain the $\delta^{13}C_{litter}$ patterns observed in our study. Ågren et al. (1996) propose a continuous quality theory in which temporal trends in $\delta^{13}C$ values of decomposing substrates are controlled by the partitioning of ^{13}C and ^{12}C among chemical fractions of varying quality and decomposer properties (C assimilation efficiency and growth rate). Isotope effects due to litter quality would lead to decreasing $^{13}C_{litter}$ through time, while those due to decomposers would lead to an increase. Combinations of these effects could produce variable patterns $\delta^{13}C$ discrimination as a function of the degree of decomposition. The authors do indicate that initial litter quality is the strongest determinant of $\delta^{13}C$ discrimination. Unfortunately, this relationship could not be evaluated in our study due to the lack of initial [lignin].

4.4. Comparison of decomposition patterns and N dynamics

Mass loss of buried root-litter in our study was generally less than values typical for the Jornada LTER. Whitford et al. (1988) reported a total mass loss for woody and herbaceous annual roots at the Jornada of 40 and 85–90% (respectively) after 1 year. More recently, Mun and Whitford (1998) measured rates of root decomposition across a topographic gradient at the Jornada. Total mass loss for *Bouteloua eriopoda* (perennial grass; upper piedmont) and *Baileya multiradiata* (herbaceous annual; basin slope) roots after 3.5 years were ca. 60 and 80%, respectively. Total mass loss was significantly lower only for *Panicum obtusum* (perennial grass; dry lake), ca. 80%.

Total mass loss for *P. elliotii* and *S. gerardi* roots in our study was ca. 20–30% after 5 years, while that of *D. glauca* was ca. 69%. Slower litter turnover may owe to dry conditions at the Jornada during the sampling period or perhaps to lower affinities of native decomposers to exogenous plant litter. The latter case is unlikely; previous studies indicate that litter chemistry, rather than source, is the primary factor controlling decomposition rates (Coleman et al., 1990). Regardless, the lack of correlation between mass loss and isotope values implies that mass loss was not a determinant of isotopic discrimination in decomposing root litter in our study.

Dynamics of N_{litter} observed in our study are generally consistent with previous decomposition studies in that [N] increased and C/N ratios decreased through time. However, the patterns of N accumulation and loss were unusual. For example, net N_{min} typically occurs at C/N values of <30 (Lutz and Chandler, 1946). Our data indicate that N_{min} occurred at C/N values as high as 238 (*G. bancanus*) and that N_{immob} was common at C/N <30. Several studies in the Chihuahuan Desert indicate little or no N_{immob} by decomposing litter with C/N ratios ca. 60 (Schaefer et al., 1985; Montana et al., 1988). However, herbaceous plant roots often produce high C/N litter resulting in substantial N_{immob} in desert soils (Parker et al., 1984; Fisher et al., 1990). Given that N limitation is an important control on net primary production in aridlands (Schlesinger et al., 1990), the role of litter quality in desert N cycling deserves further study.

Results of this study contrast to prior long-term decomposition experiments in that: (1) $\delta^{15}N_{litter}$ values did not reflect changes in N content; (2) $\delta^{13}C_{litter}$ values did not vary with [lignin]; (3) and the isotopic patterns of litter were not explained by mass loss, litter quality, or the incorporation of exogenous biomass. Temporal enrichment of $\delta^{15}N_{litter}$ may be explained by microbially mediated fractionation or the preferential retention of ^{15}N enriched substrates. The absence of any regular pattern in $\delta^{13}C$ discrimination across time may reflect the interference of distinct $\delta^{13}C$ fractionations during decomposition (Macko

and Estep, 1984) or feedbacks between decomposers and litter quality. In this context, factors responsible for isotope discrimination may vary in their importance as biodegradation proceeds. Significant changes in $\delta^{13}C_{litter}$ and $\delta^{15}N_{litter}$ values were also observed by year 2. This suggests that mechanisms responsible for isotopic discrimination are, in part, characteristic of earlier decay stages. Additional studies from other ecosystems are needed to determine the prevalence of these patterns and to better identify factors controlling the isotopic chemistry of decomposing litter.

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References

Aber, J.D., Melillo, J.M., 1980. Litter decomposition: measuring relative contributions of organic matter and nitrogen to forest soils. Canadian Journal of Botany 58, 416–421.

Ågren, G.I., Bossatta, E., Balesdent, J., 1996. Isotope discrimination during decomposition of organic matter: a theoretical analysis. Soil Science Society of America Journal 60, 1121–1126.

Balesdent, J., Girardin, C., Mariotti, A., 1993. Site-related (^{13}C of tree leaves and soil organic matter in a temperate forest. Ecology 74, 1713–1721.

Bender, M.M., 1968. Mass spectrometric studies of carbon-13 variations in corn and other grasses. Radiocarbon 10, 468–472.

Benner, R., Fogel, M.L., Sprague, E.K., 1991. Diagenesis of belowground biomass of *Spartina alternaflora* in salt marsh sediments. Limnology and Oceanography 36, 1358–1374.

Benner, R., Fogel, M.L., Sprague, E.K., Hodson, R.E., 1987. Depletion of ^{13}C in lignin and its implications for stable carbon isotope studies. Nature 329, 708–710.

Coleman, D.C., Ingham, E.R., Hunt, H.W., Elliot, E.T., Reid, C.P.P., Moore, J.J., 1990. Seasonal and faunal effects on decomposition in semiarid prairie, meadow and lodgepole pine forest. Pedobiologia 34, 207–219.

Conley, W., Conley, M.R., Karl, T.R., 1992. A computational study of episodic events and historical context in long-term ecological processes: climate and grazing in the northern Chihuahuan desert. Coenoses 7, 55–60.

Coplen, T.B., 1994. Reporting of stable hydrogen, carbon, and oxygen isotopic abundances. Pure and Applied Chemistry 66, 272–276.

DeNiro, M.J., Hastore, C.A., 1985. Alteration of $^{15}N/^{14}N$ and $^{13}C/^{12}C$ ratios of plant matter during the initial stages of diagenesis: studies utilizing archaeological specimens from Peru. Geochimica et Cosmochimica Acta 49, 97–115.

Evans, R.D., Ehleringer, J.R., 1993. A break in the nitrogen cycle in aridlands? Evidence from $\delta^{15}N$ of soils. Oecologia 94, 314–317.

Fisher, F.M., Freckman, D.W., Whitford, W.G., 1990. Decomposition and soil nitrogen availability in Chihuahuan Desert field microcosms. Soil Biology and Biochemistry 22, 241–249.

Fogel, M.L., Tuross, N., 1995. Transformation of biochemical macromolecules into geological polymers during early diagenesis. In: Organic Geochemistry: Developments and Applications to Energy, Climate, Environment and Human History. 17th Meeting on Organic Geochemistry. AIOGOA, Spain.

Gile, L.H., Grossman, T.R., 1979. The desert soil mongraph. Soil Conservation Service, United States Department of Agriculture, Washington.

Hoberg, P., Johannisson, C., Hoberg, M., Hogbom, L., Nasholm, T., Hallgren, J.E., 1995. Measurements of abundances of ^{15}N and ^{13}C as tools in retrospective studies of N balances and water stress in forests: a discussion of preliminary results. Plant and Soil 168, 125–133.

Karamanos, R.E., Rennie, D.A., 1980. Variations in natural nitrogen-15 abundances as an aid in tracing fertilizer nitrogen transformations. Soil Science Society of America Journal 44, 52.

Kohl, D.H., Shearer, G., 1980. Isotopic fractionation associated with symbiotic N_2 fixation and uptake of NO_3^- by plants. Plant Physiology 66, 51–66.

Long-term Intersite Decomposition Experiment Team (LIDET), 1995. Meeting the challenge of long-term, broad-scale ecological experiments. Publication no. 19. US. LTER Network Office: Seattle, WA, USA. 23 p.

Ludlow, M., Troughton, J., Jones, R., 1976. A technique for determining the proportion of C_3 and C_4 species in plant samples using stable natural isotopes of carbon. Journal of Agricultural Science 87, 625–632.

Lutz, H.J., Chandler, R.F., 1946. Forest Soils, Wiley, New York.

MacKay, W.P., Fisher, F.M., Silva, S., Whitford, W.G., 1987. The effects of nitrogen, water, and sulfur amendments on surface litter decomposition in the Chihuahuan Desert. Journal of Arid Environments 12, 223–232.

Macko, S.A., Estep, M.L.F., 1984. Microbial alteration of stable nitrogen and carbon isotopic compositions of organic matter. Organic Geochemistry 6, 787–790.

McClaugherty, C.A., Pastor, J., Aber, J.D., Melillo, J.M., 1985. Forest litter decomposition in relation to soil nitrogen dynamics and litter quality. Ecology 66, 266–275.

McLellan, T.M., Martin, M.E., Aber, J.D., Melillo, J.M., Nadelhoffer, K.J., 1991. Comparison of wet chemistry and near infrared reflectance measurements of carbon-fraction chemistry and nitrogen concentration of forest foliage. Canadian Journal of Forest Research 21, 1689–1693.

Melillo, J., Aber, J.D., Muratore, J.F., 1982. Nitrogen and lignin control of hardwood leaf litter decomposition dynamics. Ecology 63, 621–626.

Melillo, J.M., Aber, J.D., Linkins, A.E., Ricca, A., Fry, B., Nadelhoffer, K.J., 1989. Carbon and nitrogen dynamics along the decay continuum: plant litter to soil organic matter. Plant and Soil 115, 189–198.

Minagawa, M., Wada, E., 1984. Stepwise enrichment of ^{15}N along food chains: further evidence and relation between $\delta^{15}N$ and animal age. Geochimica Cosmochimca Acta 48, 1135.

Montana, C., Ezcurra, E., Carillo, A., Delhoume, J.P., 1988. The decomposition of litter in grasslands of northern Mexico: a comparison between arid and non-arid environments. Journal of Arid Environments 14, 55–60.

Mun, H.T., Whitford, W.G., 1998. Changes in mass and chemistry of plant roots during long-term decomposition on a Chihuahuan Desert watershed. Biology and Fertility of Soils 26, 16–22.

Nadelhoffer, K.J., Fry, B., 1988. Controls on natural nitrogen-15 and carbon-13 abundances in forest soil organic matter. Soil Science Society of America Journal 52, 1633–1640.

Nadelhoffer, K.J., Fry, B., 1994. Nitrogen isotope studies in forest ecosystems. In: Lajtha, K., Michener, R.H. (Eds.). Stable Isotopes in Ecology and Environmental Science, Blackwell Scientific, London, pp. 22–44.

Nissenbaum, A., Schallinger, K.M., 1974. The distribution of the stable carbon isotope ($^{13}C/^{12}C$) in fractions of soil organic matter. Geoderma 11, 137–145.

Parker, L.W., Santos, P.F., Phillips, J., Whitford, W.G., 1984. Carbon and

nitrogen dynamics during the decomposition of litter and roots of a Chihuahuan desert annual *Lepidium lasiocarpum*. Ecological Monographs 54, 339–360.

Rennie, D.A., Paul, E.A., Johns, L.E., 1975. Natural nitrogen-15 abundance of soil and plant samples. Canadian Journal of Soil Science 56, 43–50.

Riga, A., van Praag, H.J., Brigode, N., 1970. Natural abundance of nitrogen isotopes in certain Belgium forest and agricultural soils. Geoderma 6, 213–222.

Robinson, D., Conroy, J.P., 1999. A possible plant-mediated feedback between elevated CO_2, denitrification and the enhanced greenhouse effect. Soil Biology and Biochemistry 31, 43–53.

SAS, 1997 Guide for Personal Computers, Version 6.1.2. SAS Institute, Cary.

Schaefer, D., Steinberger, Y., Whitford, W.G., 1985. The failure of nitrogen and lignin control of decomposition in a North American desert. Oecologia 65, 382–386.

Schleser, G.H., Bertram, H.G., 1981. Investigation of the organic and $\delta^{13}C$ profile in a forest soil. In: Frigerio, A. (Ed.). Recent Developments in Mass Spectrometry in Biochemistry, Medicine and Environmental Research, Elsevier, Amsterdam, pp. 201–204.

Schlesinger, W.H., 1985. Decomposition of chaparral shrub foliage. Ecology 66, 1353–1359.

Schlesinger, W.H., Reynolds, J.F., Cunningham, G.L., Huenneke, L.F., Jarrell, W.M., Virginia, R.A., Whitford, W.G., 1990. Biological feedbacks in global desertification. Science 247, 1043–1048.

Shearer, G., Kohl, D.H., Sen-Hsiung, C., 1978. The nitrogen-15 abundance in a wide variety of soils. Soil Science Society of America 42, 899–902.

Silfer, J.A., Engel, M.H., Macko, S.A., 1992. Kinetic fractionations of stable carbon and nitrogen isotopes during peptide bond hydrolysis: experimental evidence and geochemical implications. Chemical Geology 101, 211–221.

Smith, B.N., Epstein, S., 1971. Two categories of $^{13}C/^{12}C$ ratios for higher plants. Plant Physiology 47, 380–384.

Sokal, R.R., Rohlf, F.J., 1981. Biometery, Freeman, New York.

Steele, K.W., Wilson, A.T., Saunders, W.M.H., 1981. Nitrogen isotope ratios in surface and sub-surface horizons of New Zealand improved grassland soils. New Zealand Journal of Agricultural Research 24, 167–170.

Taylor, B.R., Prescott, C.E., Parsons, W.J.F., Parkinson, D., 1991. Substrate control of litter decomposition in four Rocky Mountain coniferous forests. Canadian Journal of Botany 69, 2243–2250.

Tiessen, H., Karamanos, R.E., Stewart, J.W.B., Selles, F., 1984. Natural nitrogen-15 abundance as an indicator of soil organic matter transformations in native and cultivated soils. Soil Science Society of America Journal 48, 312–315.

Turner, G.L., Bergersen, F.J., Tantala, H., 1983. Natural enrichment of ^{15}N during decomposition of plant material in soil. Soil Biology and Biochemistry 15, 495–497.

Volkoff, B., Cerri, C.C., 1987. Carbon isotopic fractionation in subtropical Brazilian grassland soils. Comparison with tropical forest soils. Plant and Soil 102, 27–31.

Wedin, D.A., Tieszen, L.L., Dewey, B., Pastor, J., 1995. Carbon isotope dynamics during grass decomposition and soil organic matter formation. Ecology 76, 1383–1392.

Whitford, W.G., Stinnet, K., Anderson, J., 1988. Decomposition of roots in a Chihuahuan Desert ecosystem. Oecologia 75, 8–11.

Wieder, R.K., Lang, G.E., 1982. A critique of the analytical methods used in examining decomposition data obtained from litter bags. Ecology 63, 1636–1642.