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Influence of soil depth on the decomposition of *Bouteloua gracilis* roots in the shortgrass steppe

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Abstract

The distribution and turnover of plant litter contribute to soil structure, the availability of plant nutrients, and regional budgets of greenhouse gasses. Traditionally, studies of decomposition have focused on the upper soil profile. Other work has shown that temperature, precipitation, and soil texture are important determinates of patterns of decomposition. Since these factors all vary through a soil profile, it has been suggested that decomposition rates may vary with depth in a soil profile. In this work, we examine patterns of root decomposition through a shortgrass steppe soil profile. We buried fresh root litter from *Bouteloua gracilis* plants in litterbags at 10, 40, 70, and 100 cm. Litterbags were retrieved six times between July 1996 and May 1999. We found that the decomposition rate for fresh root litter was approximately 50% slower at 1 m than it was at 10 cm. After 33 months, 55% of the root mass buried at 10 cm remained, while 72% of the root mass buried at 1 m was still present. This corresponds to a 19-year residence time for roots at 10 cm and a 36-year residence time for roots at 1 m. Mass loss rates decreased linearly from 10 cm to 1 m. Patterns of total carbon and cellulose loss rates followed those of mass loss rates. Roots at 1 m tended to accumulate lignin-like compounds over the course of the experiment. Differences in the stabilization of lignin may be a consequence of differences in microbial community through a shortgrass steppe soil profile.

Introduction

Soils in the shortgrass steppe, like most grassland ecosystems, are rich in soil organic matter (SOM), which plays a central role in ecosystem carbon storage and nutrient dynamics (Anderson and Coleman, 1985; Burke et al., 1989; Parton et al., 1993). The distribution and turnover of plant litter and soil organic matter contribute to soil structure, availability of plant nutrients, and regulation of regional budgets of the greenhouse gases CO_2, CH_4, and N_2O (Aerts et al., 1992; Anderson and Coleman, 1985; Angers and Caron, 1998; van Dam et al., 1997). Soil organic matter in grasslands originates primarily from root death and decomposition; therefore understanding processes that control root decomposition is crucial if we are to appreciate one of the principle determinants of soil organic matter dynamics (Dormaar, 1992; Reeder et al., 2001).

Traditionally, soil scientists and ecologists have focused on the upper soil profiles when examining controls over organic matter dynamics (Kelly et al., 1996; Parton et al., 1987), although over 50% of total-profile soil C is stored below 20 cm (Gill et al., 1999; Weaver et al., 1935; Yonker et al., 1988). While the controls over plant litter and soil carbon dynamics are well established for shallow soil layers, the controls over and patterns of decomposition in the lower soil profile remain poorly understood. A few studies, conducted primarily in tropical and temperate forests, have focused attention on SOM dynamics through the soil profile (Elzein and Balesdent, 1995; Jobbágy and

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Jackson, 2000; Nepstad et al., 1994; Trumbore et al., 1995; van Dam et al., 1997). They consistently found that deep soils were an important component of both local and regional C cycling and that decomposition rates decreased with depth in the soil profile.

Regional scale studies have shown that temperature, precipitation, and soil texture are the principal determinants of decomposition rate, and that the relative importance of these factors depends on specific regional characteristics (Burke et al., 1989; Moore et al., 1999; Paruelo et al., 1997; Sala et al., 1988). In humid regions, decomposition responds primarily to increases in temperature, while decomposition in arid and semiarid regions has a greater relative response to precipitation (Jobbágy and Jackson, 2000; Schlesinger, 1977). Regional patterns in soil organic matter and net primary productivity have often been used to infer the controls over decomposition, although the validity of these inferences has been questioned (Gill and Jackson, 2000; Lauenroth and Sala, 1992). Nonetheless, the consensus in the literature is that temperature, moisture, and soil texture are key controls over decomposition rates.

These environmental factors all vary with depth in a soil profile, and it has been suggested that this variation in edaphic characteristics causes differences in decomposition rates with depth (Gill et al., 1999; Hunt, 1977; Jobbágy and Jackson, 2000; Weaver et al., 1935). Hunt (1977) proposed that maximum decomposition rates might be eight times slower in the lower soil profile than at the soil surface in semiarid grasslands, while van Dam et al. (1997) determined that decomposition may be as much as six times greater at the soil surface than at 1 m in a humid forest. Gill et al. (1999) found a 2-fold difference in decomposition rates through the soil profile for particulate organic matter (POM) in the shortgrass steppe, with POM at 15–20 cm decomposing at approximate twice the rate as POM at 75–100 cm.

The chemical composition of plant litter is also a contributing factor influencing patterns of decomposition (Meentemeyer, 1978; Olsen, 1963; Reeder et al., 2001). Examining the loss and modification of specific organic constituents is necessary to properly understand the stabilization of organic material into soil organic matter pools with different residence times (McClaugherty et al., 1985; Schlesinger and Hasey, 1981). For example, carbon to nitrogen ratios and lignin to nitrogen ratios have often been employed to explain decomposition rates both locally and globally (Meentemeyer, 1978; Melillo et al., 1982). However, so far as we can determine, nothing has been reported about whether organic constituents such as lignin and cellulose are decomposed differently at various soil depths. Given the importance of composition of decomposer communities on patterns and rates of decomposition, variation in the composition of the community may play a critical role in determining patterns of decomposition. Since the decomposer flora and fauna almost certainly vary with depth, it is possible that the organic constituents of root litter may be lost or modified in different ways depending on soil depth (Lauenroth and Milchunas, 1992; Leetham and Milchunas, 1985). This differential modification of organic constituents, coupled with variation in decomposition rates resulting from differing edaphic environments, could possibly explain the oft-cited difference in organic matter composition through a soil profile (Boutton et al., 1998; Paul et al., 1997; Trumbore et al., 1995).

The specific objectives of this study were to (1) determine rates of mass loss for fresh root material at soil depths ranging from 10 to 100 cm in the shortgrass steppe and (2) establish whether there are differences in the pattern of organic constituent loss or modification with depth. We hypothesized that decomposition rates would be highest in the shallow soil profile and decrease with depth because of variation in edaphic conditions through the soil profile. We tested these hypotheses by conducting a buried litterbag study in the shortgrass steppe of eastern Colorado using fresh root material from *Bouteloua gracilis*, the dominant grass in this region.

Methods

Site description

We conducted this study at the Central Plains Experimental Range (CPER) in northeastern Colorado (Table 1). The U. S. Department of Agriculture manages the CPER, which is a portion of the Shortgrass Steppe Long-Term Ecological Research site. Long-term mean monthly temperatures range between −3 °C in January to 22° C in July, and between 1996 and 1999 the mean annual air temperature was 8.5° C with a mean annual precipitation of 446 mm (Figure 1) (Lauenroth and Milchunas, 1992; Parton and Greenland, 1987). Mean maximum soil temperature between April and September is 22.0° C in the surface 2.5 cm of the soil profile and decreases to 10.7° C at 100 cm (Parton

Table 1. Characteristics of the Central Plains Experimental Range in eastern Colorado, USA

Site characteristics			
Latitude		40° 46′	
Longitude		-104° 46′	
Mean annual precipitation		322 mm	
Mean annual temperature		8.2 °C	
Soil characteristics			
Soil Texture (n=4 sites)			
	Soil depth (cm)	Sand	Clay
	10	0.57	0.20
	40	0.52	0.23
	70	0.52	0.25
	100	0.47	0.29
Bouteloua gracilis root characteristics			
	% Carbon	48.3	
	% Nitrogen	0.8	
	% Cellulose	26.6	
	% Lignin	14.6	
Root biomass distribution			
	Soil depth (cm)	Root biomass (g/m^2)	
	0–5	752	
	5–10	227	
	10–15	158	
	15–20	134	
	20–35	217	
	35–50	194	
	50–75	210	
	75–100	107	

[1]Root biomass data from Gill et al. (1999).

and Lauenroth, 1983). Soil water potential exceeds −1 MPa most frequently in the subsurface soil (5–15 cm) and occurs less frequently in the upper 5-cm of the soil profile and below 15-cm depth (Sala et al., 1992). *Bouteloua gracilis* (H.B.K.) Lag. ex Steud. dominates the principal vegetation community of the shortgrass steppe (Lauenroth and Milchunas, 1992). During the three years of this experiment, precipitation patterns followed the long-term pattern (Sala et al., 1992) with the majority of all precipitation falling during the growing season.

Quantifying root decomposition

We assessed decomposition rates of fresh *B. gracilis* litter buried at four soil depths. In May 1996, we excavated 12 *B. gracilis* individuals that grew adjacent to an exposed slope in a sandy loam soil. To provide a nearly homogeneous substrate for decomposition, we used only attached, live roots. The roots were collected from the upper 50-cm of the soil profile. While there may be some chemical differences between deep and shallow roots, we wished to focus on the environmental factors that influence decomposition rates rather than differences caused by plant allocation patterns. After oven-drying the plants at 55° C for 72 h, we shook the roots to remove much of the attached soil. Crowns and shoots were cut from *B. gracilis* roots and discarded.

We constructed litterbags (10 × 10 cm^2) from fiberglass-nylon mesh with a pore size of 1.4 mm^2. This mesh size is a compromise that allows the decomposer communities to access the root litter while minimizing loss of litter from the bags through fragmentation (Beare et al., 1992; Schlesinger and Hasey, 1981). We prepared 288 litterbags by weighing ∼1.5

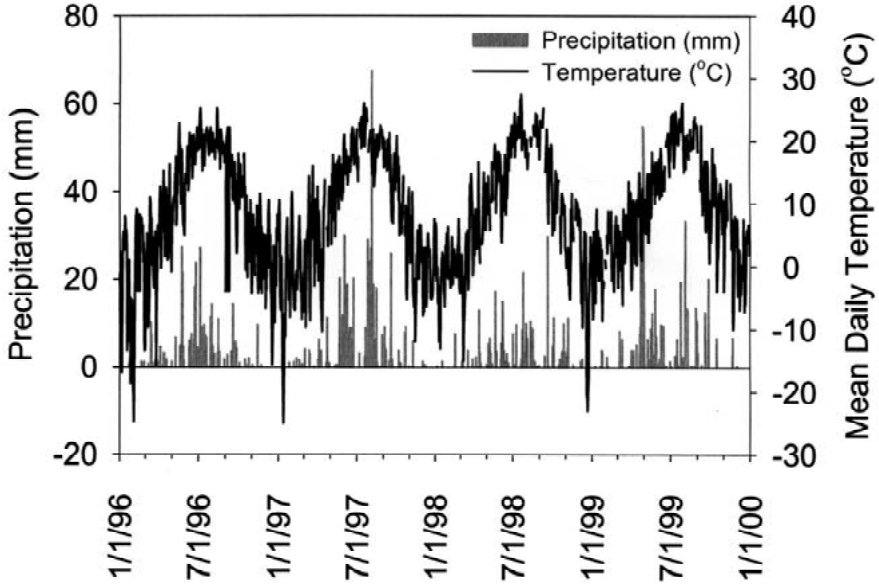

Figure 1. Daily weather for the Central Plains Experimental Range in northeastern Colorado between 1996 and 2000.

g of dried root tissue to the nearest 0.01 g, placing the litter within each bag, sealing the bags, and randomly assigning aluminum numbered tags.

We buried 72 litterbags (n=18 at four depths) at each of four sites at the CPER during the first week of July 1996. The four sites spanned the typical variation in soil texture that is observed in the shortgrass steppe. After extracting 15 intact 1-m deep soil cores from each site, we placed litterbags at 100, 70, 40, and 10 cm, backfilling between litterbags using the soil extracted from that core. Nylon tethers, attached to each bag and extending to the soil surface, marked litterbag locations. During July-96, Sept-96, April-97, Oct-97, May-98, and May-99 we retrieved three samples from each soil depth at each site (n=12 site^{-1} sampling date^{-1}). The three subsamples were processed and then averaged to avoid pseudoreplication. The 15 July 1996 collection was 1 week after burial, and was used to correct for mass loss due to handling and burying, and to determine initial litter chemistry.

Laboratory analyses

Litterbags were dried for 24 h at 55° C, contents were removed and weighed, and samples were ground using a ball grinder. Ground material was subsampled for three analyses: a 0.2-g subsample was used for ash determination, a 0.3-g subsample was used for organic constituent analyses, and the remaining sample was used for C and N determination. The first subsample was combusted in a muffle furnace at 500° C for 4 h. Values presented are ash corrected for soil contamination. To determine the amount of soluble organics and hemicellulose, cellulose, and lignin in litter, we used a repeated washing method (Van Soest, 1967, Goering & Van Soest 1970). The second subsample of ground litterbag material (0.3 g) was heated at 110° C for 1 h in a solution of 1 N H_2SO_4 + hexadecyltrimethyl ammonium bromide, thereby solubilizing all organic compounds other than cellulose and lignin. This solution was rinsed through a fritted glass crucible, dried and weighed. The unsolubilized material (cellulose + lignin + ash) remaining on the fritted glass was then rinsed for 3 h in 73% H_2SO_4, dried, and weighed. Finally, the remaining material (lignin + ash) was ashed for 4 h at 500° C in a muffle furnace. The only material remaining following combustion was residual ash. By calculating mass differences between washings, we determined the mass of ash, lignin, cellulose, and soluble organics plus hemicellulose. We report only the values from the lignin and cellulose fractions because the organic constituents in the first washing are diverse enough that it is difficult to distinguish loss rates of the first washing independently from the cellulose fraction. Finally, with the last subsample, we determined percent organic C and N content using automated combustion analysis (LECO CHN-1000 Element Analyzer, St. Joseph, MI, USA). Repeated washing does not necessarily identify specific chemical constituents — rather, this approach identifies the proportion of

organic molecules that resists oxidation in ways consistent with either cellulose or lignin. This designation is particularly important for the lignin fraction of litter, which may be modified into soil humus but still retains many of the chemical characteristics of the original lignin.

Statistical analyses

The objective of this litterbag study was to determine how depth influenced changes in litter mass, C, and organic constituents over 33 months of decomposition. We used a three-way factorial, mixed model analysis of variance with the proportion of each constituent remaining at time t as the response variable (SAS Institute Inc., Cary, NC). The two fixed effects were depth and time, while location was a random effect. The subsamples were nested within location and were considered an additional random effect. We used a saturated model with both main effects and all interactions. As a second way to evaluate the influence of depth on decomposition we calculated a decay rate constant (k) for each response variable for the entire study period, using the formula:

$$\ln(\frac{X_t}{X_0}) = -kt,$$

where X_t and X_0 are the amount of each constituent at time t and time 0 (Olsen, 1963; Schlesinger, 1985). We used the mean values of all subsamples at a site for a specific depth in producing these regressions and used an analysis of covariance to test for significant differences in k among depths. Many studies use $1/k$ to calculate mean residence time, which is the time required to lose roughly 37% of the original material (Olsen, 1963). We chose to calculate mean residence time as $5/k$, which corresponds to the time necessary to lose 99% of the original material, assuming first-order decomposition kinetics (King et al., 1997; Olsen, 1963).

Results

Mass loss and decay rate

The decomposition rate of fresh *Bouteloua gracilis* root material decreases by approximately 50% from 10 to 100 cm in a soil profile. This is reflected in both the mass remaining at the conclusion of the experiment and in the decomposition rate constant. After 33 months of incubation, 55% of the roots buried in litterbags at 10 cm remained, while 72% of the roots buried at 100 cm persisted (Figure 2a). Roots incubated at 40 and 70 cm had intermediate mass-loss, with 63% of the original roots persisting at 40 cm and 68% of root mass remaining at 70 cm (Figure 2a). The decomposition rate constant (k_{mass}) was significantly higher for roots at 10 cm than for roots at 100 cm (Table 2). At 10 cm k_{mass} was 0.26 year^{-1}, while at 100 cm, k_{mass} was 0.14 year^{-1}. Based on first-order decomposition kinetics, 99% of root mass would be lost in 19 years for roots at 10 cm while it would take 36 years for the same roots to decompose at 100 cm. Mass loss rates decreased essentially linearly from 10 to 100 cm (Table 2). The instantaneous decay rate was greatest in the first 2 months of incubation and then decreased through the course of the experiment (Figure 2b). This supports our use of a first-order decomposition model, where the most labile material is lost quickly and the remaining, more recalcitrant material decays at a relatively constant rate.

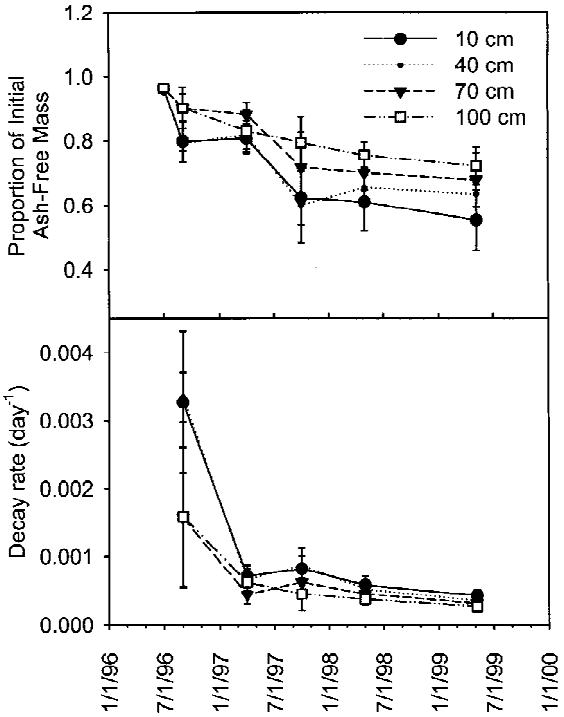

Figure 2. (a) Mass loss of *Bouteloua gracilis* root litter at four depths in the shortgrass steppe of eastern Colorado. Values are means (n=4) and bars are 1 SE. (b) Daily mass loss rate constants for the same root litter, showing the two-phase decomposition pattern indicative of first-order decay kinetics.

Table 2. Decay rates (n=4) for mass and organic constituents of *Bouteloua gracilis* roots buried at four soil depths during a 33-month study conducted at the Central Plains Experimental Range in eastern Colorado. We calculated the decomposition rate constant (k_0) using the first-order decay equation $\ln(\frac{X_t}{X_0}) = -kt$ and calculated the mean residence time as 5/k. X_t is the mass of the constituent at the time of collection, X_0 is the original mass, and t is time. For lignin at 10 and 40 cm the regressions were not significant ($P>0.05$). k-values for each constituent that share the same letter are not significantly different ($P<0.05$).

	Constituent	k (year^{-1})	r^2	P	Mean residence time (years)
10 cm					
	Ash-free mass	0.26^{a}	0.75	0.001	19.2
	Total C	0.29^{a}	0.80	0.001	17.2
	Cellulose	0.41^{a}	0.81	0.001	12.2
	Lignin	N S	N S	N S	
40 cm					
	Ash-free mass	$0.22^{a,b}$	0.69	0.001	22.7
	Total C	$0.22^{a,b}$	0.74	0.001	22.7
	Cellulose	$0.30^{a,b}$	0.70	0.001	16.7
	Lignin	N S	N S	N S	
70 cm					
	Ash-free mass	$0.17^{b,c}$	0.71	0.001	29.4
	Total C	$0.18^{a,b}$	0.65	0.001	27.8
	Cellulose	0.26^{b}	0.66	0.001	19.2
	Lignin	-0.12^{a}	0.47	0.005	
100 cm					
	Ash-free mass	0.14^{c}	0.74	0.001	35.7
	Total C	0.17^{b}	0.75	0.001	29.4
	Cellulose	0.21^{b}	0.70	0.001	23.8
	Lignin	-0.17^{a}	0.66	0.001	

Carbon, cellulose, and lignin

Patterns of total carbon and cellulose loss followed the pattern of total mass loss. Rates of total carbon loss occurred at rates similar to total mass, while cellulose loss occurred more quickly than total mass (Figure 3a, b and Table 2). Depth was a significant factor in explaining variation in loss rates for total C and cellulose, with fractional loss at 10 cm occurring at twice the rate as at 100 cm. The loss rate constant for total C was significantly higher for shallow roots, compared with roots at 100 cm. The mean values of k_C for total C at 10 cm was 0.29 year^{-1} and was 0.17 year^{-1} at 100 cm ($P<0.01$, Table 2). For cellulose, $k_{Cellulose}$ was 0.41 year^{-1} at 10 cm and 0.21 year^{-1} at 100 cm, and these differences between depths were statistically significant ($P<0.01$, Table 2). While cellulose and total carbon decreased over the 33 months of the experiment, the concentration of what we analyzed as lignin increased in the root litter, and total lignin increased for the litter decomposed at 100 cm (Figure 3). Depth was a significant factor in explaining differences in lignin concentration through time, with deep roots increasing in lignin concentration at a faster rate than shallow roots ($P<0.01$). At the conclusion of the experiment, litter bags at 100 cm had increased by 62% of what we originally estimated as lignin content, while the lignin-like content in roots at 10 cm was not significantly different from the initial amount (Figure 3c).

C:N and lignin:N

Decomposition decreased the C:N ratios of all roots, but the decrease in C:N was most pronounced in roots incubated at 10 cm (Figure 4a). For roots decomposed at 10 cm, C:N ratios decreased from an initial value of 60.6 to 29.6 after 33 months. This 50% decrease in C:N ratio is driven primarily by carbon loss, since there are no significant changes in the nitrogen content of the decomposing litter. There were no significant differences among depths for final C:N for roots decomposing at 40, 70, and 100 cm ($P>0.05$). Lignin:N

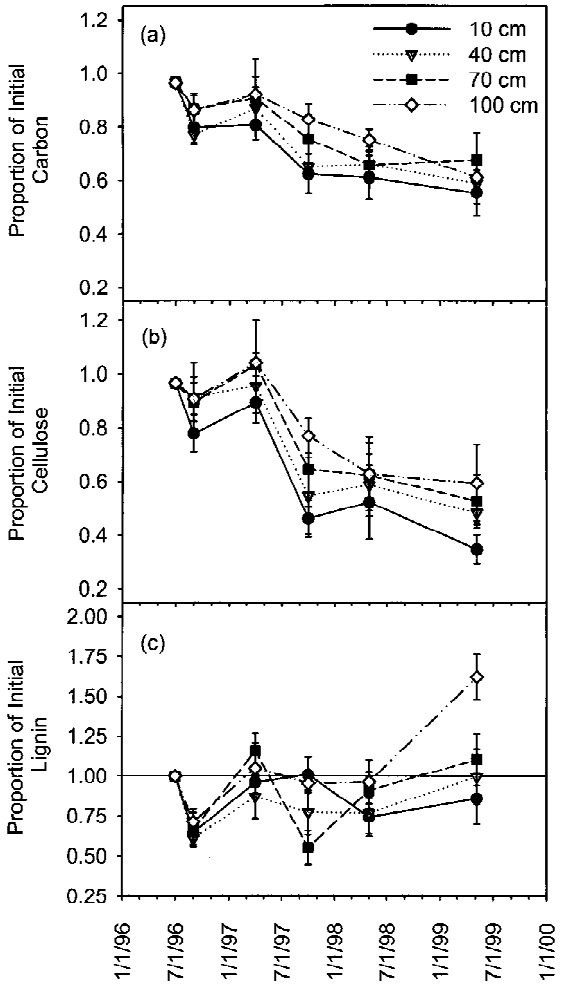

Figure 3. Proportion of the original content of (a) carbon, (b) cellulose, and (c) lignin in roots decomposed at 10, 40, 70, and 100 cm. Values are means (n=4) and bars are 1 ± SE.

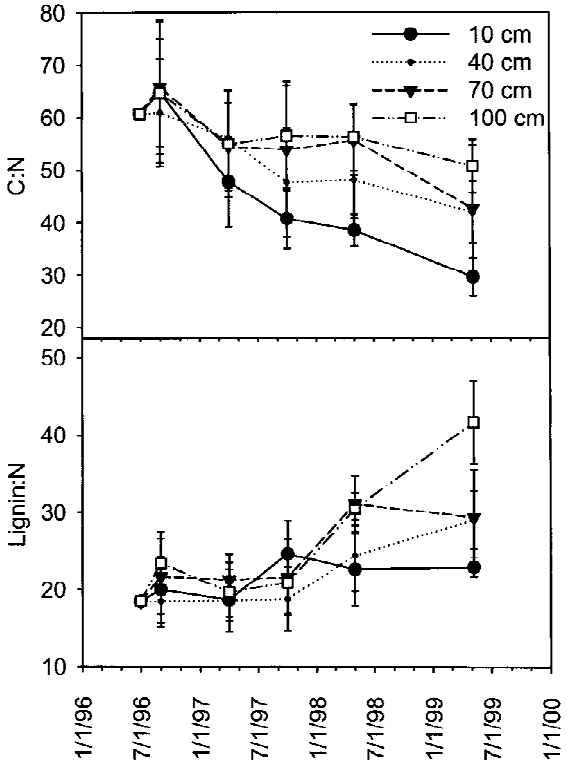

Figure 4. Ratios of (a) carbon to nitrogen and (b) lignin to nitrogen for *Bouteloua gracilis* roots incubated at 10, 40, 70, and 100 cm in the 33-month decomposition experiment conducted at the Central Plains Experimental Range in eastern Colorado.

ratios did not change significantly in roots incubated at 10 cm, but there were significant increases in the lignin:N ratio for the root litter incubated at 40, 70, and 100 cm. The change in lignin:N was most pronounced in roots decomposed at 100 cm, increasing from an initial value of 18.5 to 41.6 after 33 months.

Discussion

Weaver et al. (1935) were the first to propose that decomposition rates would be highest in the upper soil profile and decrease with depth because temperature and moisture availability decline through a soil profile. In the shortgrass steppe, both temperature and soil moisture vary throughout the soil profile. Sala et al. (1992) showed that in the shortgrass steppe, water potentials > -1 MPa occur most frequently in soils between 5 and 15 cm, with the lowest frequency of plant-available soil water in the deepest soil layers. Maximum temperatures during the growing season are highest at the soil surface and diminish with depth (Parton, 1984). Given the strong overlap between temperature and soil water potential, we anticipated finding a strong correlation between depth and decomposition rates. We found that mass, carbon, and cellulose loss from fresh root litter varied by a factor of 2 from 10 to 100 cm, with decomposition rates of roots in shallow soils approximately double those of roots at 1 m. In an experiment that evaluated the effect of temperature, moisture, and nitrogen on decomposition rates of *Bouteloua gracilis*, (I.C. Burke, unpublished data) it was determined that decomposition rates increased with water additions and were unaffected by increases in temperatures.

Several studies have suggested that decreasing decomposition rates with depth explains why root distri-

butions are more weighted toward the surface of soil profiles than is soil organic matter (Gill et al., 1999; Jobbágy and Jackson, 2000; Weaver et al., 1935; van Dam et al., 1997). If decomposition is much slower in the lower soil profile, a larger proportion of root biomass would be stabilized as soil organic matter at depth than the upper soil layers. While the differences in decomposition rates among depths that we measured are significant, the influence of depth on decomposition is not as extreme as was considered necessary to explain the disparity between root biomass and soil organic matter distributions (Hunt, 1977; van Dam et al., 1997). Hunt (1977) used the ELM model to simulate the accumulation of soil organic matter with depth for soils in the shortgrass steppe. After accounting for the influence of temperature and soil moisture on decomposition rates, he needed to vary maximum decomposition rates by a factor of eight from 0–4 to 15–60 cm to explain patterns of soil carbon accumulation. Paul et al. (1997) used radiocarbon dating to show that the age of soil carbon in the shortgrass steppe increases with depth. Using first order decomposition kinetics, they calculated that k for total soil organic carbon would decrease by a factor of approximately 7 from the upper soil profile to 1 m, although the k for non-hydrolysable C varied by a factor of only 1.5 over the same soil depths. In contrast to the hypothesis that decomposition varies by a large amount through a soil profile, Trumbore et al. (1995) showed that the residence time of slowly cycling soil organic matter in eastern Amazonian soils was approximately the same for surface soil layers and soils 5 m deep. In the earliest work that we know of that examined decomposition rates with depth, Weaver (1947) concluded that decomposition was nearly uniform through a prairie soil profile, with the exception of slightly higher decomposition rates between 15 and 30 cm than above or below this depth.

Since the decomposition rates necessary to explain the divergence between root and soil organic matter profiles apparently do not occur, we should further evaluate alternative mechanisms for this divergence. Alternative explanations include the leaching of soil carbon from shallow to deep soil layers or the vertical mixing of soils by soil organisms. Our results suggest another option. Conceivably, soil fauna in the lower soil profile may modify lignin into more recalcitrant forms of humus than the fauna in shallow soil profiles. As a result, a larger proportion of root detritus will be stabilized into soil organic matter pools with long residence times in the lower soil profile than in the upper soil profile.

We propose that the patterns of lignin accumulation in litter that we observed may be a consequence of differences in microbial community composition with depth. Lignin-like compounds accumulate in decomposing litter through the complexation of phenolic compounds and proteins in the litter (King and Heath, 1967; Schlesinger and Hasey, 1981). Schlesinger and Hasey (1981) presume that the accumulation of lignin, or lignin-like compounds, in litter during decomposition may occur through the microbial synthesis of resistant compounds. Zak et al. (1996) proposed that the composition of soil microbial communities is sensitive to both the quality and amount of available carbon substrate. Microbial community composition in the shortgrass steppe varies through the soil profile and is reflected in the relatively shallow distribution of fungal biomass, with 53% of the profile total occurring in the upper 3 cm, in contrast to bacteria which have only 25% of their biomass in this same soil layer (Lauenroth and Milchunas, 1992; Doxtader, 1969). Patterns of microbial community structure, and consequently litter modification, may be sensitive to the depth because of the differences in substrate availability and soil environment. The cooler, drier environment in the lower soil profile, relative to the subsurface soils, may promote bacteria or fungi that degrade only simple molecules, leaving a higher proportion of complex carbohydrates and proteins available for incorporation into heterocyclic molecules which are included in the lignin fraction of our analysis.

We chose to use fresh root material so that we would have a uniform initial substrate for decomposition (Berg, 1984). The litter chemistry of live roots may differ from abscised roots, and this may influence the mass loss of roots that die and detach naturally. However, there is little evidence for nutrient retranslocation in roots prior to senescence (Gordon and Jackson, 2000; Nambiar and Fife, 1991), so presumably the initial litter chemistry should be similar between the fresh material that we used and naturally detaching roots. Gill et al. (in press) showed that there are differences in root life span associated with root diameter for *Bouteloua gracilis*. Because of this, the tissue chemistry of the roots that die annually may not be the same as a bulk tissue sample of roots. Furthermore, it has been proposed that shallow and deep roots may differ in their chemical composition, reflecting the localization of metabolically expensive tasks that occur in shallow soils, such as nutrient acquisition,

compared to the metabolically inexpensive task of water uptake that occurs in deeper soils (Jobbágy and Jackson, 2000; Pregitzer et al., 1998). However, Gill et al. (in press) found no differences in root turnover rates through a shortgrass steppe soil profile, which may suggest that there are not major functional differences, with associated changes in tissue chemistry, within a *B. gracilis* root system.

Our results provide an interesting insight into some potential consequences of land cover change in arid and semi-arid ecosystems (Gill and Burke, 1999). The introduction of deeply rooted life forms, as occurs when shrubs encroach into grasslands or during the afforestation of croplands, may result in higher inputs of carbon into regions of the soil profile that have slow decomposition rates, leading to long-term ecosystem C storage (Jobbágy and Jackson, 2000). However, we do not entirely understand the feedback between changes in vegetation and soil C storage in the lower soil profile. The fate of root litter in the lower soil profile is complex, particularly given the interaction between soil environment, root tissue chemistry, and soil fauna.

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