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Longevity and turnover of roots in the shortgrass steppe: influence of diameter and depth

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Abstract

We used minirhizotrons to determine patterns of root longevity and turnover for the perennial bunchgrass *Bouteloua gracilis* in the shortgrass steppe of eastern Colorado, USA. We hypothesized that root longevity would be partially controlled by root diameter, following previously observed patterns in woody plants. In addition, we hypothesized that root turnover would be greatest in surface soil horizons and decrease with depth due to variation in soil moisture availability and temperature. Root longevity was correlated with root diameter. Median life span of roots > 0.4 mm was approximately 320 days, while roots < 0.2 mm had a median life span of 180 days. There was approximately a 6% decrease in the likelihood of mortality with a 0.10-mm increase in root diameter, controlling for the effect of depth in the soil profile. Root length production and mortality were highest in the upper 20 cm of the soil profile and decreased with depth. However, because root length density also decreased with depth, there were no significant differences in turnover rate of root length among sampling intervals. Turnover was approximately 0.86 yr⁻¹ based on root length production, while turnover was 0.35 yr⁻¹ using root length mortality as a measurement of flux. The imbalance between turnover estimates may be a consequence of the time the minirhizotrons were in place prior to imaging or may result from our lack of over-winter measures of mortality. Our work suggests that *Bouteloua gracilis* roots have complex life history strategies, similar to woody species. Some portion of the root system is highly ephemeral, while slightly larger roots persist much longer. These differences have implications for belowground carbon and nitrogen cycles in the shortgrass steppe.

Introduction

Root turnover accounts for a large proportion of carbon and nutrient cycling in most terrestrial ecosystems (Weaver et al. 1935; Caldwell 1979; Aerts et al. 1992; Gill et al. 1999). The production and maintenance of roots are potentially large sinks for photosynthates, and the death of roots is the primary input of organic carbon to soil carbon pools in many ecosystems (Dormaar 1992; Burke et al. 1997). In addition, root turnover represents an input of nutrient-rich organic substrate to belowground food webs and is a significant loss of nutrients from plants (Nambiar

1987; Dubach and Russelle 1994; Gordon and Jackson 2000). However, accurately determining rates and controls over root turnover continues to be among the most intractable problems in terrestrial ecology, as is evident from the broad range in estimates of root turnover among ecosystems and sampling methods (Eisenstat and Yanai 1997; Lauenroth 2000; Gill and Jackson 2000). Estimates of root turnover range from less than 1% of the root system annually in boreal forest ecosystems (Finér et al. 1997; Steele et al. 1997) to tropical grassland root systems that turn over several times annually (Picard 1979). In addition, estimates of root turnover at a single site may range

over an order of magnitude depending on the method used (Aber et al. 1985; Milchunas and Lauenroth 1992).

In forests, root diameter is perhaps the best-accepted factor related to root longevity, with coarse roots commonly persisting for years while fine roots cycle rapidly (Gholz et al. 1986; Gill and Jackson 2000). While the relationship between root diameter and longevity for tree and shrub roots is nearly axiomatic, it is unclear whether the turnover of the adventitious root system of grasses is tightly coupled with root diameter. There is increasing evidence that there may be a broad array of root longevity, function, and cost to the plant even within the "fine" root category for woody plants (Pregitzer et al. 1997, 1998; Wells and Eissenstat 2002; Gaudinski et al. 1998). However, we know of no studies that have assessed the relationship between root diameter and longevity in the adventitious root systems of grasses.

One possible way to determine the controls over root longevity would be to examine root turnover through a soil profile, where soil microenvironment varies through time and space. Numerous studies have identified controls over root longevity, with soil microenvironment being the dominant factor (Eissenstat and Yanai 1997; Bloomfield et al. 1996; Lauenroth and Gill 2002; Hendrick and Pregitzer 1996a). Potential environmental or physiological controls over root longevity include: (1) nutrient availability (Wiersum 1958; Nadelhoffer et al. 1985), (2) soil moisture (Caldwell 1976; Hook and Lauenroth 1994; Kramer and Boyer 1995), (3) soil temperature (Fitter et al. 1998, 1999), and (4) whole plant carbon balance (Friend et al. 1994; Farrar and Jones 2000). Alternatively, root longevity may be determined during development independently of soil conditions (Marshall and Waring 1985). It is critical to identify what the ultimate controls over root longevity are considering the importance of root turnover for whole-plant carbon budgets and ecosystem element cycling.

This study focuses on patterns of root turnover in the shortgrass steppe of northeastern Colorado, particularly concentrating on root turnover among various root diameter classes and patterns of root turnover with depth. Our first hypothesis was that small diameter roots in grasslands have a shorter lifespan and are replaced more frequently than are large diameter roots because of the larger investment of carbon in constructing large diameter roots. Our second hypothesis was that all size classes of roots in surface soils would turn over more quickly than roots lower

in the soil profile because both temperature and moisture availability decrease with depth during the growing season in the shortgrass steppe, as well as because of the high temporal variability in temperature and water in the surface soil horizon (Sala et al. 1992). In theory, respiration rates would be lowest in regions of the soil profile with the lowest temperature and mineral nutrient concentrations, and therefore root life span may increase with depth in the soil profile. We evaluated these hypotheses by monitoring root growth and loss at eight minirhizotrons in the shortgrass steppe during the 1997 growing season.

Methods

Site description

We conducted this study at the Central Plains Experimental Range (CPER) in northeastern Colorado. The U.S.D.A. Agricultural Research Service manages the CPER, which is part of the Shortgrass Steppe Long-Term Ecological Research site (Franklin et al. 1990). Mean monthly temperatures range between -2.3°C in January to 22°C in July, with a long-term mean annual air temperature of 8.2°C . Mean annual precipitation is 322 mm (Parton and Greenland 1987; Lauenroth and Milchunas 1992). Temperatures during 1997 were very close to the long-term average, while annual precipitation exceeded the long-term average by 225 mm. 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 (Lauenroth, W.K. unpublished data). *Bouteloua gracilis* (H. B. K.) Lag. ex Steud. dominates the principal plant community of the shortgrass steppe (Lauenroth and Milchunas 1992).

Root turnover

We installed four clear polybutyrate minirhizotron observation tubes (with an inside diameter of 4.4 cm and a length of 183 cm) under uniform *B. gracilis* stands at two sites with similar plant communities in May 1996 ($n = 8$). All eight minirhizotrons are within two areas where grazing is restricted, limiting the realm of inference for this study. These results were not intended to be representative of the entire shortgrass steppe. The minirhizotron tubes were installed at a 45° angle to the soil surface, extending into the soil 1.45 meters along their length (~ 1 meter verti-

cal depth) (Hendrick and Pregitzer 1997; Hook and Lauenroth 1994). The lower ends of the tubes were sealed to prevent the movement of water from the soil into the tube. The aboveground portion of the tubes was covered with fiberglass insulation, wrapped in reflective duct tape and sealed with rubber lab stoppers to minimize absorption or loss of heat to the atmosphere and to prevent light from entering (Hendrick and Pregitzer 1996b; Hansson et al. 1995). The minirhizotron tubes were in place for 10 months before the first imaging date to allow the root system to recover following the disturbance caused by minirhizotron installation and to allow them to equilibrate with the surrounding soil. Several studies have shown that a single growing season may be sufficient to equilibrate minirhizotron tubes with native vegetation (Aerts et al. 1989; Hansson et al. 1995; Hendrick and Pregitzer 1996b). Images were recorded on Sony Hi-8 videotapes using a high magnification video camera attached to a ratcheting handle (Bartz Technology Co., Santa Barbara, CA). We drilled a hole in the tube on the top face just below the upper end, fixing the camera in an upward position during imaging. Minirhizotron tube and frame number were recorded directly on the video image during recording using an on screen display. We collected images during the 1997-growing season on 4/1, 6/5, 7/11, 9/1, and 10/3.

We used a Macintosh-based video processing system to digitize videotaped images. Images were processed using RooTracker (Dave Tremmel, Duke University Phytotron, Durham, NC, USA). This program allowed us to trace root length and width, and to classify roots based on apparent branching order and condition. The initial tracings were saved in a Macintosh hypercard stack, which were then superimposed on images taken from the same frame on subsequent sampling days. We monitored changes in root length of previously existing roots, measured new root growth, and recognized roots lost since the previous imaging. We assigned a condition code to each root, identifying it as a *live root*, a *live root with root hairs*, or an apparently *dead root*. Roots were classified as dead when they appeared dark or disappeared, following the convention of previous minirhizotron studies (Cheng et al. 1991; Hendrick and Pregitzer 1993).

When all images for a sampling date had been traced, we compiled root length, width, and condition classifications for each root on each image into a database. Root length density (RLD, mm cm^{-2}) was determined by summing the total live root length found in a 20-cm soil increment and dividing by surface

area of the observed images (Hendrick and Pregitzer 1997). At the conclusion of the growing season, the data for each minirhizotron were composited. We used a relational database manager (Access, Microsoft, Seattle, WA) to determine total root length production (RLP, $\text{mm cm}^{-2} \text{ yr}^{-1}$) and root length mortality (RLM, $\text{mm cm}^{-2} \text{ yr}^{-1}$) for the 1997 growing season for each 20-cm depth increment for each minirhizotron. This was done by comparing root length for each root in each frame between sequential dates.

Root turnover represents the fraction of the root system that is produced or dies annually and can be determined using a systems-based approach by dividing the flux into or out of the root pool by root standing crop. We modified the Dahlman and Kucera (1965) turnover definition to reflect our use of root length rather than biomass in calculating root flux and standing crop. We defined root turnover as:

$$\text{Turnover} = \frac{\text{RLP}}{\text{MRLD}} \text{ or } \frac{\text{RLM}}{\text{MRLD}} \quad (1)$$

where RLP is root length production ($\text{mm cm}^{-2} \text{ yr}^{-1}$), RLM is root length mortality ($\text{mm cm}^{-2} \text{ yr}^{-1}$), and MRLD is maximum root length density (mm cm^{-2}). We calculated root turnover (yr^{-1}) for each 20-cm depth increment for each minirhizotron (Hendrick and Pregitzer 1993; Aerts et al. 1989).

Statistical analyses

We used two alternative methods for determining the role of root diameter on root survival. The first method was an analysis of covariance, using diameter intervals as class variables and time as a covariate, and using the percent survivorship of an individual cohort as the response variable. We calculated the percent of the initial roots that survived at subsequent observation dates for three size classes (≤ 0.2 mm, $0.2\text{--}0.4$ mm, ≥ 0.4 mm) (Figure 1). After testing for, and finding no significant differences in survivorship between cohorts, we composited the data and evaluated the influence of diameter on survivorship for all roots observed during the growing season. We then tested for differences in survivorship among the three size classes using an analysis of covariance and a post-hoc Tukey's HSD test for determining significant differences among means (SAS, Cary, NC). We used

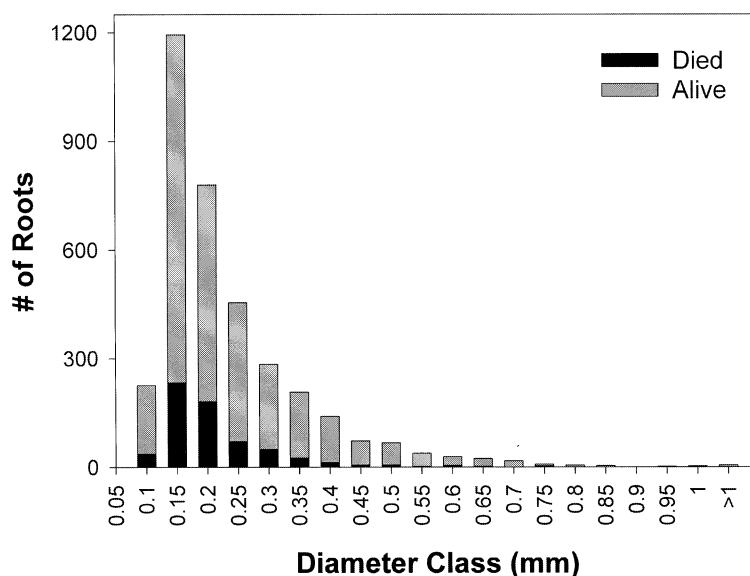


Figure 1. The distribution of the 3,566 roots among 0.05-cm diameter classes for *Bouteloua gracilis* measured using minirhizotrons in the shortgrass steppe of northeastern Colorado. The black portion of the bar represents roots that died over the course of our observations, while the gray portion of the bar are roots that persisted from our first observation of them until October 1997.

the estimated linear regression to calculate the mean residence time, where the proportion of roots remaining is 0.5, for the three size classes.

The second analysis that we conducted allowed us to use diameter as a continuous variable rather than using size class intervals for evaluating the role of root diameter on survivorship. We used a stratified Cox proportional hazards regression (SAS, PROC PHREG) to estimate the effects of root diameter and depth on root life span. In our study, “hazard” is considered the instantaneous risk of disappearance at time t if it has survived until then. In the Cox proportional hazards regression, the hazard for an individual at time t is the product of an unspecified baseline hazard function (h_0) and an exponential function of k covariates:

$$h_i(t) = h_0(t)e^{(\beta_1 x_{i1} + \dots + \beta_k x_{ik})} \quad (2)$$

The Cox model estimates a β coefficient for each model covariate and tests the null hypothesis that $\beta=0$ using a chi-square statistic. A negative β coefficient corresponds to a decreased risk of mortality as the parameter increases. A risk ratio (e^β) was also calculated, which can be used to calculate the percent change in the risk of mortality with a one unit change in the covariate, controlling for all other covariates (Allison 1995; Wells and Eissenstat 2002). For the variables we considered, the percent change in the

likelihood of death for a one-unit change in either diameter or soil depth can be calculated by subtracting one from the risk ratio and multiplying by 100.

To determine how depth influenced the distribution of RLD and RLP, we used a repeated measures analysis of variance to test for significant differences in RLD and RLP among soil depths. Since minirhizotrons monitor the same plane of soil throughout the growing season, we considered a 20-cm depth increment within a minirhizotron as an experimental unit, with RLD as a repeated measure with time. The assumption of a common covariance matrix of the tube \times depth effect was met, and the data satisfied the Huynh-Feld conditions (SAS Institute, Cary, NC). We used the Type III MSE in the F test to determine significance. In cases where depth and time were significant main effects, we performed a Tukey’s HSD pairwise test to determine significant differences. Since RLP were nonrepeated measures, we used a standard analysis of variance with a Type III MSE used in the F-test for significance.

Results

Root size classes

We hypothesized that small diameter roots would cycle more quickly than large diameter roots. Both the

analysis of covariance and hazard model supported this hypothesis (Table 1). There were significant differences among size classes ($p < 0.01$) showing that roots > 0.4 mm diameter persisted significantly longer than roots < 0.4 mm, while there were no significant differences between roots ≤ 0.2 mm and 0.2–0.4 mm. Using a linear regression approach, 50% disappearance of roots > 0.4 mm was predicted to occur by 320 days, while 50% disappearance of roots < 0.2 mm was predicted to happen by 187 days (Figure 2). However, our ability to predict the life span for roots of different diameter is restricted because of the length of this study. Root diameter was significantly related to the risk of root mortality (Table 1). Root diameter had a risk ratio of 0.424, which corresponds to approximately a 6% decrease in the likelihood of mortality with a 0.10-mm increase in root diameter, controlling for the effect of depth in the soil profile.

Patterns with depth

We hypothesized that root turnover would be highest in the surface soil horizons, and decrease with depth through the soil profile because of variation in edaphic factors. This hypothesis was not supported. Depth was not a significant factor in explaining variation in turnover, regardless of whether it was calculated using production or mortality as the flux measurement (Figure 3). Mean turnover for the entire soil profile, using RLP as the numerator, was 0.86 yr^{-1} . Estimates of turnover based on RLM were lower than the RLP estimate, and averaged 0.35 yr^{-1} . However, depth was a significant, although minor component of the hazard models (Table 1). The risk ratio for depth was 0.995, which corresponds to a 0.5% decreased risk of mortality for each cm from the soil surface to 1 meter.

Both time and depth were significant main effects in explaining variation in RLD (Figure 4, $p < 0.001$). The interaction between depth and time was not significant. During the growing season, maximum RLD occurred during the September and October sampling dates. Mean RLD increased over the growing season from 4.3 mm cm^{-2} in April to 11.2 mm cm^{-2} in October. Through the soil profile, maximum RLD was observed in the 0–40 cm depths, with no significant differences among depths below 40 cm ($p < 0.05$).

Depth was significant in explaining variation in RLP and RLM (Table 2, $p < 0.01$). We observed the highest RLP in the 0–20 cm depth increment ($15.1 \text{ mm cm}^{-2} \text{ yr}^{-1}$), while the lowest mean RLP was 3.0

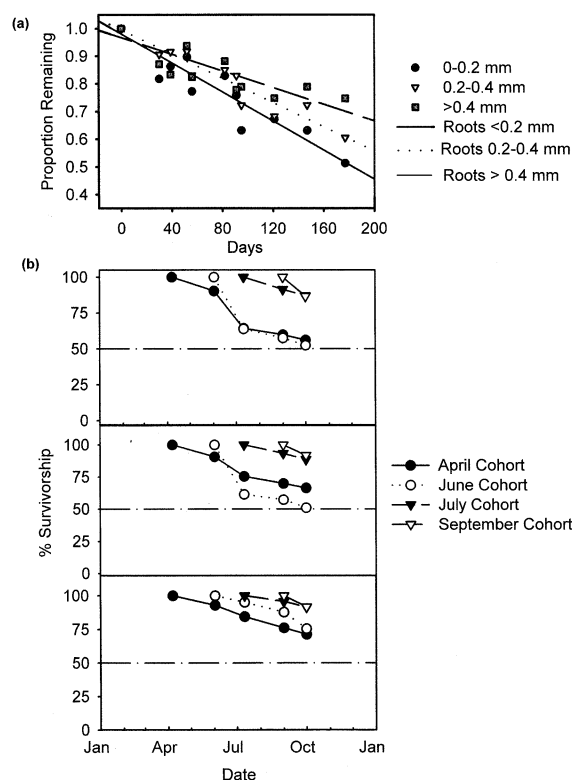


Figure 2. (a) The relationship between time since first observation and the proportion of roots remaining for three diameter classes (≤ 0.2 mm, 0.2 mm–0.4 mm, ≥ 0.4 mm) in the shortgrass steppe of northeastern Colorado during the 1997 growing season. The linear regression for roots ≤ 0.2 mm is $\text{Proportion Remaining} = 0.980 - 2.62 \times \text{day}$ ($R^2 = 0.906$); the linear regression for roots 0.2–0.4 mm is $\text{Proportion Remaining} = 0.990 - 2.19 \times \text{day}$ ($R^2 = 0.934$); the linear regression for roots ≥ 0.4 mm is $\text{Proportion Remaining} = 0.980 - 1.51 \times \text{day}$ ($R^2 = 0.770$). (b) The survivorship of roots by the date that they were first observed and by size class. The upper panel is for roots ≤ 0.2 mm, the center panel is roots 0.2–0.4 mm, and the lower panel is for roots ≥ 0.4 mm. The 50% line indicates the time at which a cohort has lost 50% of the roots.

$\text{mm cm}^{-2} \text{ yr}^{-1}$ in the 80–100 cm depth increment (Table 2). There were no significant differences in RLP between the 0–20 and 20–40 cm depth increments ($p > 0.05$), although production was significantly higher in the upper 40 cm of the soil profile than in the lower 60 cm. The highest RLM ($4.46 \text{ mm cm}^{-2} \text{ yr}^{-1}$) was likewise in the 0–20 cm depth increment, with the lowest RLM in the 80–100 cm depth increment. Root length mortality was significantly higher in the upper 40 cm of the soil profile than below 60-cm.

Table 1. Output for the analysis of covariance and Cox proportional hazard model showing that root diameter is a significant determinant of root lifespan.

Analysis of Covariance						
Source	DF	Sum of Squares	Mean Square	F Value	Pr > F	
Model	3	0.742	0.247	27.2	0.0001	
Error	38	0.346	0.009			
Corrected Total	41	1.088				
		R ²	C.V.	Root MSE		
		0.682	11.387	0.095		
Source	DF	Type III SS	Mean Square	F Value	Pr > F	
Time	1	0.651	0.651	71.6	0.001	
Size Class	2	0.091	0.046	5.0	0.012	
Hazards Dataset						
Testing Global Null Hypothesis $\beta = 0$						
Criterion	Without covariates		With covariates		Model Chi-Square	
–2 Log L	9944		6176		3768 with 3 DF (p = 0.0001)	
Score	*		*		2529 with 3 DF (p = 0.001)	
Wald	*		*		715 with 3 DF (p = 0.001)	
Variable	DF	Parameter Estimate	Standard Error	Wald Chi-Square	Pr > Chi-Square	Risk Ratio
Depth	1	–0.005	0.001	20.061	0.0001	0.995
Diameter	1	–0.858	0.175	24.154	0.0001	0.424

Discussion

Root Diameter

Our data suggest that root diameter is correlated with longevity in grass roots. Contrary to the common view that the adventitious roots of grasses are homogenous with respect to life history traits, grass roots that differ by only tenths of a millimeter have different patterns of persistence. A few of the roots – primarily those of small diameter – appeared in only a single observation date, while many others persisted throughout the growing season and presumably much longer. This study showed that small differences in root diameter could result in a significant change in individual root survival.

Several forest studies have shown differences in physiology and demography among roots of different

diameter. However, we know of no similar studies that explore the functional differences of grass roots of different diameter. The tree literature shows that small differences in diameter influence root nitrogen content (McClaugherty et al. 1984; Pregitzer et al. 1997; Gordon and Jackson 2000), turnover and longevity (Gaudinski et al. 1998; Gill and Jackson 2000; Wells and Eissenstat 2002), root respiration rates (Pregitzer et al. 1998) and decomposition kinetics (McClaugherty et al. 1984; Scheu and Schauermaun 1994).

Our observation that there are differences in longevity among grass roots raises several questions about the role of root demography on carbon and nitrogen cycling in grasslands. Most ecosystem models assume that grass root systems are homogenous and can be described by a single turnover function (e.g. Parton and Greenland (1987)). If the small diameter

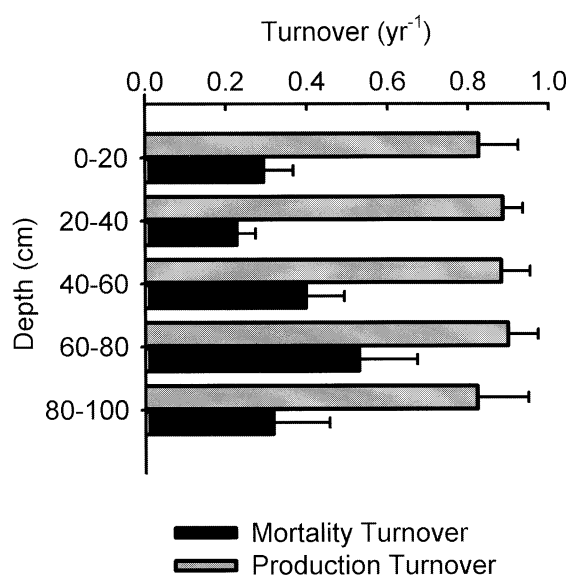


Figure 3. The turnover of roots through the soil profile in a short-grass steppe ecosystem during 1997. The dark, hatched bars are turnover calculated as Root Length Production/Maximum Root Length Density. The solid, gray bars are turnover calculated as Root Length Mortality/Maximum Root Length Density. There are no significant differences in turnover among depths for either measure of turnover.

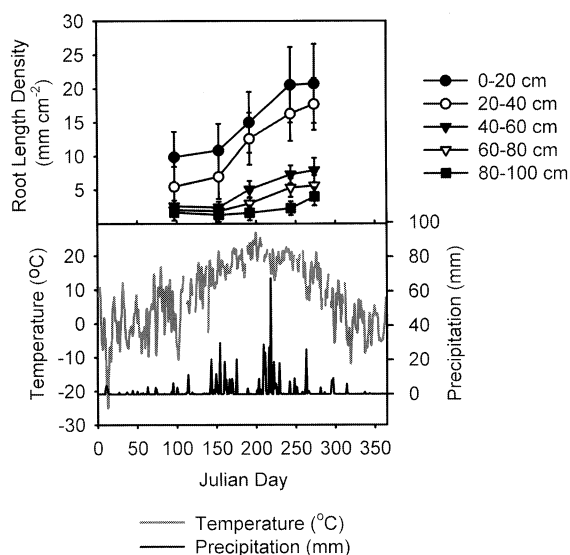


Figure 4. Root length density at five depth increments in the soil profile. The lower panel includes the mean daily temperature and precipitation for 1997 at the Central Plains Experimental Range.

grass roots that we observed to have short life spans are similar to the analogous roots in forests, they would be higher in nitrogen content and decompose more easily than larger, more persistent roots. Following the example of soil organic matter models, a mul-

tle pool model could potentially be applied to grass root systems, with an active fraction of the root system having short life spans, while other roots persist year to year. The rapid disappearance of the very small roots from the surface of the minirhizotrons indicates that decomposition of very fine roots occurs much more quickly than the estimates obtained from buried bag techniques, which are likely biased toward the decomposition of larger, more recalcitrant roots (Gill and Burke, unpublished data).

Root Turnover

We were surprised to find there were no significant differences in turnover with depth in the soil profile. We hypothesized that the differences in soil temperature (Lauenroth, W.K. unpublished data), moisture (Sala et al. 1992), and nitrogen availability (Dodd et al. 2000) would result in much higher root turnover rates in surface soil horizons than at depth. There are at least three possible mechanisms that would result in a constant proportion of the root system turning over, without regard to soil environment. First, it is possible, but not likely, that root longevity is determined primarily during root development, and therefore would not be influenced by the soil environment that the root grows in (Marshall and Waring 1985). However, several studies have shown that root turnover is sensitive to changes in water or nitrogen availability and temperature, and therefore is not universally controlled by initial root development (Jackson and Caldwell 1989; Hendrick and Pregitzer 1992; Pregitzer et al. 1997; Fitter et al. 1999). Furthermore, the change in environment with depth would likely alter patterns of root development and may influence the initial amount of carbohydrate allocated to individual roots. Second, turnover may be primarily controlled by soil herbivores, which may be distributed through the soil profile in a constant proportion to root biomass (Leetham and Milchunas 1985). This mechanism is consistent with our observation of root mortality, but fails to explain the constant turnover observed using root length production estimates. Finally, the constant turnover estimates that we observed with depth may be an artifact of the minirhizotrons themselves. If root turnover is controlled by local soil microenvironment, it is possible that the differences in temperature and moisture with depth are ameliorated at the surface of the minirhizotron (Levan et al. 1987; Cheng et al. 1991; Pagès and Bengough 1997; Majdi 1996; Joslin and

Table 2. Root length production and mortality for the 1997 growing season in the Shortgrass Steppe for five depth intervals (Coefficient of variance in parentheses).

Depth	Root Length Production (mm cm ⁻² yr ⁻¹)	Root Length Mortality (mm cm ⁻² yr ⁻¹)	Average
0–20	15.058 (3.632)	4.464 (0.977)	9.761
20–40	14.857 (2.489)	4.151 (1.370)	9.504
40–60	7.743 (1.819)	2.829 (0.615)	5.286
60–80	5.289 (1.315)	2.112 (0.453)	3.701
80–100	2.982 (1.008)	1.027 (0.407)	2.005

Wolfe 1999). Therefore, it is possible that the patterns that we observed are a consequence of a constant temperature along the length of the minirhizotron rather than inherent similarities in root demography with depth.

The turnover coefficient that we derived was higher than had previously been reported for the shortgrass steppe (Table 3). Estimates of turnover using traditional coring techniques have ranged from 0.0 yr⁻¹ (Milchunas and Lauenroth 1992) to 0.65 yr⁻¹ (Sims and Singh 1978), with a mean of 0.236 yr⁻¹. Turnover estimates based on ¹⁴C turnover average 0.185 yr⁻¹ and have a very narrow interannual variability (Milchunas and Lauenroth 1992). A potential explanation for the differences in turnover coefficient in the shortgrass steppe could relate to the size class of roots being accounted for in each method. The methods of root biomass collection in the ¹⁴C-dilution study and the sequential harvesting methods may have been biased toward larger roots, since they relied on physical retrieval of roots (Sims and Singh 1978; Milchunas and Lauenroth 1992). Minirhizotrons may be more sensitive than destructive sampling at monitoring root length changes in small size classes (Hendrick and Pregitzer 1996b). Ares (1976) work using vertical-window rhizotrons at the CPER showed that small roots are more dynamic in production and decomposition than mature roots. The higher production calculated using minirhizotrons rather than sequential coring may be accounted for by differences in methodology, particularly since the calculations used by Sims and Singh (1978); Milchunas and Lauenroth (1992) did not correct for concurrent losses and production. A key issue is that, while the minirhizotrons result in large estimates of root turnover because they do a better job with small roots, this may not tell us much about root production. Since production may be controlled by the portion of the root system that accounts for most of the biomass, the fast turnover of the smallest roots may have a very small influence on production and

carbon cycling because they account for such a small amount of material.

An alternative explanation for the high turnover estimates in this study is that the *B. gracilis* root system was not yet in equilibrium with the minirhizotron tubes. Several studies have shown that a single growing season is adequate to equilibrate tubes in forested systems, although very little work has previously been done in arid grasslands where production and decomposition rates are much lower (Hansson et al. 1995; Hendrick and Pregitzer 1996b; Burton et al. 2000). If actual turnover rates are close to those that were measured by (Milchunas and Lauenroth (1992-¹⁴C Method)), it may take several years before a root system equilibrates around the minirhizotrons. Perhaps the turnover estimate derived by production overestimated turnover because the root standing crop is smaller than would be expected, while the turnover estimate derived from mortality would be low due to the relatively young age of the roots observed. We suggest that perhaps average of the two estimates derived using minirhizotron data is a more robust estimate of turnover (0.57 yr⁻¹).

Grass root dynamics

The variation in root longevity that we observed shows the complexity of grass root systems and the value of methods involving direct observation of root dynamics. Further work needs to be conducted to evaluate the functional characteristics of different grass roots and evaluate the appropriateness of using single parameters to describe grass root dynamics. Furthermore, it would be valuable to evaluate the role of root architecture on root turnover by evaluating the role of root order on turnover dynamics. In addition, work needs to be done to determine the appropriate time interval necessary to observe the production and loss of the most quickly cycling roots. While processing minirhizotron images is very time consuming and may not be appropriate for every study, we believe

Table 3. Comparison of root turnover at the Shortgrass Steppe Long-term Ecological Research site determined by various methods for seven years.

Study	Sampling Method	Calculation Method	Year	Turnover (yr ⁻¹)	Mean Annual Temperature (°C)	Annual Precipitation (mm)
This Study (0–20 cm)	Minirizotron	RLP/MRLD	1997	0.83	8.3	557
		RLM/MRLD	1997	0.30	8.3	557
		Average	1997	0.57	8.3	557
Milchunas and Lauenroth (Unpublished data)	Sequential Coring: Maxima-Minima	BNPP/Maximum Root	1997	0.28 [*] , 0.36 [*]	8.3	557
		Biomass				
Milchunas and Lauenroth 1992 Roots (0–20 cm)	Sequential Coring: Maxima-Minima	BNPP/Maximum Root	1985	0.16 [*] , 0.1 [‡]	9.0	321
		Biomass				
			1986	0.0 [†] ; 0.13 [‡] ; 0.20 [§]	10.9	264
			1987	0.0 [*] ; 0.13 ^{†,‡}	10.5	332
			1988	0.23 [*] , 0.1 [‡]	10.2	335
¹⁴ C Turnover		BNPP/Maximum Root	1985	0.18	9.0	321
		Biomass				
			1986	0.20	10.9	264
			1987	0.19	10.5	332
			1988	0.17	10.2	335
Sims and Singh 1972 Roots (0–20 cm)	Sequential Coring	BNPP/Maximum Root	1971	0.65 ^{**} ; 0.37 ^{†‡}	7.5	311
		Biomass	1972	0.29 ^{**} ; 0.48 ^{†‡}	8.5	294

* BNPP calculated by summing all positive increases in mean root biomass

† BNPP calculated by summing all significant differences in mean root biomass; ANOVA used to determine statistically significant differences between sampling times

‡ BNPP calculated by summing all significant differences in mean root biomass; t-test used to determine statistically significant differences between sampling times

§ BNPP calculated by summing all significant differences in mean root biomass; 1 Standard Deviation used to determine statistically significant differences between sampling times

** Ungrazed

†† Grazed

that there are insights that can be gained by using this technique that are not possible using other methods.

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