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Global patterns in root decomposition: comparisons of climate and litter quality effects

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Abstract Root decomposition represents a significant C flux in terrestrial ecosystems. Roots are exposed to a different decomposition environment than aboveground tissues, and few general principles exist regarding the factors controlling rates of root decay. We use a global dataset to explore the relative importance of climate, environmental variables, and litter quality in regulating rates of root decomposition. The parameters that explained the largest amount of variability in root decay were root Ca concentrations and C:N ratios, with a smaller proportion explained by latitude, mean annual temperature, mean annual precipitation, and actual evapotranspiration (AET). Root chemistry and decay rates varied by plant life form (conifer, broadleaf, or graminoid). Conifer roots had the lowest levels of Ca and N, the highest C:N and lignin:N ratios, and decomposed at the slowest rates. In a stepwise multiple linear regression, AET, root Ca, and C:N ratio accounted for approximately 90% of the variability in root decay rates. Root chemistry appeared to be the primary controller of root decomposition, while climate and environmental factors played secondary roles, in contrast to previously established leaf litter decomposition models.

Keywords Root decay · Carbon:nitrogen ratio · Calcium · Actual evapotranspiration · Q_{10}

Introduction

Decomposition of plant tissues in terrestrial ecosystems regulates the transfer of C and nutrients to the soil, and represents an important source of CO₂ to the atmosphere. For these reasons, litter decomposition can have large impacts on biogeochemical cycling at local, regional,

and global scales. Several authors have summarized patterns in leaf litter decay at large spatial scales (Meentemeyer 1977; 1978; Swift et al. 1979; Anderson and Swift 1983; Aerts 1997). These studies have primarily supported the original findings of Meentemeyer (1977, 1978), who developed a global model for leaf litter decay based on climate and litter chemistry. Much less attention has been given to patterns in root decomposition in terrestrial ecosystems. Fine root mortality and decomposition represent a large C cost to plants, as well as a potential soil C sink. The size of this sink can be significant to global C budgeting, particularly in ecosystems with high belowground allocation such as grasslands (Seastedt 1988), or some tropical forests (Vogt et al. 1986; Nepstad et al. 1994; Silver et al. 2000). Root decay is also an important source of mineral nutrients in the soil (Persson 1978; Fogel and Hunt 1979; Aerts et al. 1992), and thus impacts rates of net primary productivity in nutrient-limited environments.

Estimating rates of root decay is challenging because roots are hidden from view and occur in an environment that must be disturbed as part of the analysis (Bloomfield et al. 1996). Despite these challenges, there is a large and growing database on root decomposition from both temperate and tropical ecosystems. There are few established principles in root decomposition studies as compared to studies of leaf litter decay. Several field methods are available, but few studies have compared methodological approaches, or summarized patterns within and across methods. Both exponential and linear decay models have been used to describe root mass loss over time (Aber et al. 1990; Scheu and Schauer mann 1994; Gijsman et al. 1997). Some models incorporate a two-stage root decomposition process (Fogel and Hunt 1979; McClagherty et al. 1984), where the first stage is characterized by rapid mass loss driven primarily by inorganic chemical composition and water-soluble C loss via microbial utilization or leaching. The second stage is characterized by slower mass loss regulated largely by lignin and other recalcitrant root materials (McClagherty et al. 1984).

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Models of leaf litter decay generally suggest that climate is the single best predictor of decay rates at large spatial scales, with litter quality playing an important, but secondary role (Meentemeyer 1978; Aerts 1997). Similar patterns may or may not occur with root decomposition, which is somewhat buffered from extremes in climate by location in the soil. Substrate quality and its role in decay are also likely to differ for roots than for leaf litter. As with leaf litter, root litter quality indices include mineral nutrient concentrations, the concentrations of secondary compounds, as well as C: nutrient and nutrient:nutrient ratios. However, roots fundamentally differ physiological functions than leaves, which could lead to different chemical compositions. Root litter quality is also defined by root diameter, which integrates both chemical and physical properties (Boot 1990; Andr en et al. 1992). Root decay is likely to be particularly sensitive to soil conditions such as moisture, O₂ concentrations, pH, and direct inorganic nutrient limitations to the decomposer organisms (Swift et al. 1979).

In this paper we use literature data to identify global and regional trends in root decomposition, and determine

generalized patterns in root decay rates with climate, substrate quality, plant life form, and environmental factors. We compare and contrast patterns in root litter decay with those of leaf litter decay, and present a preliminary model of factors controlling root decomposition at a global scale.

Materials and methods

We used data published in peer-reviewed literature that reported first-year mass loss or decay rates, including one review article that reported on a large number of previously published and unpublished studies (Berg et al. 1998). Most studies reported decay constants from multiple treatments, comparisons among life forms, or comparisons across sites. This amounted to a total sample size of 175 rate constants (*k*-values) for analyses (Table 1). Data covered a wide range of latitudes, and allowed for considerable replication within biomes. We divided the data into three diameter classes (<2 mm, 2–5 mm, >5 mm) based on Camir e et al. (1991). Fine roots are thought to be the most ephemeral in terrestrial ecosystems, and more studies have focused on fine root decay. For this reason, we separately report trends in root decomposition for fine roots (<2 mm) and all size classes combined. The data were also roughly organized according to plant life form

Table 1 Summary of root decay studies. Life forms are graminoid (*G*), conifer (*C*), and broadleaf (*B*). Diameter classes are fine (*F*; <2 mm), medium (*M*; 2–5 mm), large (*L*; >5 mm). Several studies

reported multiple rate constants (*k*-values) resulting from multiple treatments, life forms, and sites. *NR* Not reported, *Ex* exponential, *Lin* linear

| Latitude ( N) | Life form | Model and number of <i>k</i> -values | Diameter class(es) | Method | Mesh size(s) (mm) | Study |
|---------------|-----------|--------------------------------------|--------------------|-------------------|-------------------|---------------------------------------|
| 4 | G | Ex (16) | F | Buried pots | – | Gijsman et al. (1997) |
| 8 | G | Ex (6) | F, M | Litterbags | 0.2, 5.0 | Lehmann et al. (1995) |
| 18 | B | Ex (2) | F | Litterbags | 1.5 | Bloomfield et al. (1993) ^a |
| 18 | B | Ex (3) | F | Trench plots | – | Silver and Vogt (1993) |
| 19 | B | Lin (14) | F | Litterbags | 0.3 | Ostertag and Hobbie (1999) |
| 25 | B | Ex (3) | F | Litterbags | 1.0 | Arunachalam et al. (1996) |
| 25 | G | Ex (3) | NR | Litterbags | 1.0 | Singh and Shekhar (1989) |
| 25 | G | Ex (1) | F | Litterbags | 1.0 | Tripathi and Singh (1992) |
| 30 | C | Ex (2) | F, M | Litterbags | 0.2, 1.0 | Gholz et al. (1986) |
| 32 | G | Ex (5) | F | Litterbags | 1.0 | Mun and Whitford (1998) |
| 32 | G | Ex (3) | NR | Litterbags | 1.2 | Parker et al. (1984) |
| 34 | C | Ex (3) | M, L | Litterbags | 1.0 | King et al. (1997) |
| 37 | G, B | Ex (8) | F, M | Litterbags | 1.0 | Conn and Day (1997) |
| 39 | G | Ex (2) ^b | F | Litterbags | 1.0, 3.0 | Seastedt (1988) |
| 39 | G | Ex (1) | F | Litterbags | Pool 1.0, 3.0 | Seastedt et al. (1992) |
| 41 | C | Ex (6) | L | Sequential coring | – | Yavitt and Fahey (1982) |
| 43 | C | Ex (2) | F | Litterbags | 0.1, 2.0 | Aber et al. (1990) |
| 43 | B | Ex (4) | L | Tethered | – | Fahey and Arthur (1994) |
| 43 | B | Ex (12) | F, L | Tethered | – | Fahey et al. (1988) |
| 43 | C, B | 1st Order (4) | F, M | Litterbags | 0.1, 0.4, 3.0 | McClagherty et al. (1982) |
| 44 | B | Ex (6) | F, M | Litterbags | 2.0 | Burke and Raynal (1994) |
| 44 | C | Ex (1) | M | Litterbags | 1.0 | Fogel and Hunt (1979) |
| 46 | B | Ex (6) | F, M, L | Litterbags | 0.1, 1.0, 3.0 | Camir e et al. (1991) |
| 51 | B | Ex (6) | F, M, L | Litterbags | Pool 1.0, 4.0 | Scheu and Schauerermann (1994) |
| 52 | G | Ex (2) | M | Litterbags | 0.1 | Van Vuuren et al. (1993) |
| 54 | G, B | Ex (2) | NR | Litterbags | 1.0 | Heal et al. (1978) |
| 59 | G | Ex (4) | NR | Litterbags | 1.0 | Andr en et al. (1992) |
| 59 | C | Ex (2) | F | Litterbags | 0.1 | Lohmus and Ivask (1995) |
| 60 | C, B | Ex (9) | F, M, L | Litterbags | 1.0 | Berg (1984) |
| 64 | C | Ex (1) ^b | L | Litterbags | 1.0 | B a th et al. (1980) |
| 38, 43, 45 | B | Ex (8) | F, M | Litterbags | 0.1, 0.4, 3.0 | McClagherty et al. (1984) |
| 56–66 | C | Ex (28) | F, M | Litterbags | 1.0 | Berg et al. (1998) |

^a Litterbags were placed on the soil surface

^b Calculated *k*-value

types of graminoid, broadleaf, and conifer. While this categorization is simplistic, we use it here to arrive at a first approximation of the effects of life form on root decay. The broadleaf category included tree and understory broadleaf species. We assumed that the roots were in the <2-mm category when root size class for graminoid species was not given.

Differences in methodology present a challenge for comparisons of root decay rates. Buried litterbags are the most common approach used ($n=152$; 87% of the data). For litterbag studies, mesh size varied from 0.1 to 5 mm, although most studies used a 1- to 2-mm mesh, and mesh size was generally chosen by taking into consideration root diameter (e.g., a larger mesh size for larger roots). Several studies have examined the effects of mesh size on root decay (McClougherty et al. 1982, 1984; Gholz et al. 1986; Seastedt 1988; Camiré et al. 1991; Scheu and Schauermaun 1994). Only one of these studies, Scheu and Schauermaun (1994), found a significant effect of mesh size on root decomposition rates. The authors note that the effect was small and likely to be important only for very large-diameter roots. The lack of an obvious effect of mesh size on root decay may be due to the greater relative importance of microbial decomposers within the soil than on the soil surface where leaf litter is generally decomposed. We report mesh size in Table 1, but do not consider it further in the analyses.

In addition to litterbags, methods used to estimate root decay included trench plots ($n=3$ k -values), tethered roots ($n=4$ k -values), and buried pots ($n=16$ k -values). For the trench plots (2×2 m each), trenches were dug to 60 cm, surrounded with mesh screening of <1-mm openings, back-filled, and continuously weeded, effectively isolating a block of cleared land where roots decomposed in situ (Silver and Vogt 1993). The buried pots were covered with mesh on the ends to allow access to invertebrates and other decomposers and inverted for burial (Gijsman et al. 1997). The tethered root approach was used for fine and coarse woody roots (Fahey et al. 1988; Fahey and Arthur 1994). The effects of differences in methodology on root decay rates are unknown. However, litterbag studies are likely to be the most comparable. Here we separately report results based on litterbag studies only and all methods combined. We also performed a preliminary analysis of the impact of including non-litterbag methods in regional- or global-scale analyses by comparing methods within biomes and life forms. Of course, in situ studies are the best test of differences among techniques. Our purpose here is to determine if large and obvious differences can be discerned among methods at this scale of analysis.

For studies that reported only mass loss or C loss over time without a decay constant, we fit both a linear and an exponential decay function to calculate the root decay constant from tabulated data or graphs. In all cases, the exponential equation provided a fit as good or better than the linear model. Therefore, we used the following exponential equation to estimate rates of root decay:

$$Y = e^{-kt} \quad (1)$$

where Y is the fraction of initial mass or C remaining at time t (years), and k is the root decay constant (year^{-1}) (Weider and Lang 1982). Studies that estimated root turnover from annual root production and mean standing crop were not included in this analysis. These methods do not directly report root decomposition rates and there were no applicable conversion factors available to make valid comparisons with mass loss over time [although see Schlesinger (1997) for a discussion of this under the assumption of steady state conditions]. Laboratory root decomposition studies were also excluded due to the lack of comparable data for climate and environmental factors. We excluded one study where root decay was estimated from a one-time sample of woody tree roots using a density analysis (Yavitt and Fahey 1982), as this method differed dramatically from all other methods reported.

The role of climatic and environmental variables in predicting rates of root decay were examined by using mean annual temperature (MAT), mean annual precipitation (MAP), latitude, elevation, actual evapotranspiration (AET), and soil texture. Data spanned a wide range of MAP (211–4,000 mm/year), MAT (-2°C – 30°C), and latitude (4 – 60°N). AET (mm/year) was estimated using the

method described by Thornwaite and Mather (1955) when AET was not reported. Few papers contained suitable monthly climatic data needed to calculate AET. Therefore, average monthly climate data (temperature and precipitation) were obtained from LTER websites (<http://lternet.edu>) when applicable, or from the worldclimate.com website (<http://www.worldclimate.com>) using data collected from nearby weather stations with similar latitude, longitude, and elevation as described by each paper. Elevation was available for all sites except The Netherlands; for these data we estimated an elevation of 10 m. Soil texture data were available for most studies.

We also used the initial litter quality parameters of root diameter (mm), N (%), P (%), Ca (mg/g), lignin (%), and the ratios of C:N, lignin:N, and lignin:P. Not all litter chemistry variables were available for all studies.

We used Systat 7.0 (Wilkinson 1996) for statistical analyses. When variables were not normally distributed, they were logarithmically transformed in order to meet the assumptions for ANOVA. One-way and two-way ANOVAs were used to test for differences in k -values and litter quality parameters among root-diameter classes, plant life forms, and soil texture classifications. Means were compared using Tukey-Kramer LSD multiple comparison tests. Simple and stepwise multiple linear regressions were conducted to determine if initial root quality indices and/or environmental variables were correlated with root decay constants. When reported in the text, mean values are followed by Standard Errors (SE). Significance was defined as $P < 0.05$ unless otherwise noted.

Results

Patterns in root decomposition by latitude and size class

There was a relatively even distribution of root decay studies latitudinally, ranging from 4 to 66°N . There was a wider global distribution of studies using small- and medium-diameter roots, while the decay of large-diameter roots has primarily been studied in the temperate zone (Fig. 1a). Studies of graminoid and broadleaf root decomposition were also widely distributed globally, while most studies of coniferous root decay have been conducted in northern latitudes (Fig. 1b). Latitude alone explained 28% and 20% of the variability in root decomposition for all size classes, and 48–45% for fine roots only, when considering all methods and root litterbags, respectively (Table 2). Latitude explained 44% of the variability in graminoid decay ($r = -0.66$), but only 18% ($r = -0.43$) and 26% ($r = -0.51$) for broadleaf and conifer life forms (Table 3). For litterbag studies, the correlation of graminoid root decay with latitude was even stronger ($r = -0.80$). More studies focused on fine root decomposition (<2 mm diameter, $n=88$), than larger size classes (2–5 mm, $n=62$; >5 mm, $n=20$). Fewer studies looked at graminoids ($n=46$), than at broadleaf ($n=71$), and conifer roots ($n=58$).

Single climatic and environmental variables

Individual climatic and environmental variables significantly influenced rates of root decomposition (Table 2). MAT was positively correlated with root decay rates globally, and the relationship was strongest when only fine roots were considered. We found a weak positive

linear relationship between MAP and root decay for fine roots, and no significant relationship when all root size classes were considered. Both temperature and precipitation were negatively correlated with latitude ($r^2=0.73$ for MAT, $r^2=0.54$ for MAP), and probably contribute to the observed increase in root decomposition with decreasing

latitude. AET explained between 26% and 34% of the variability in decay rates for fine roots in litterbags, and all methods, respectively, and 25% of the variability in root decay for the whole data set (Table 2). There were weak positive correlations between AET and MAT ($r^2=0.39$) and AET and MAP ($r^2=0.53$), and a stronger negative relationship between AET and latitude ($r^2=0.73$).

Examinations of trends with plant life form yielded some interesting relationships between root decay and climate (Table 3). Root decay of broadleaf species was weakly positively correlated with MAT and MAP for all categories examined, with the exception of MAP and lit-

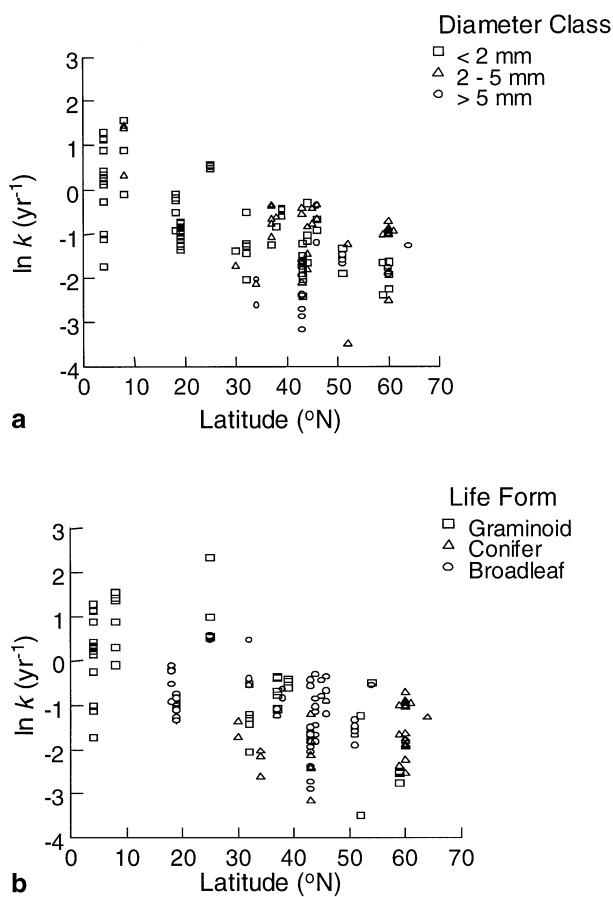


Fig. 1 Root decomposition rates [natural log of root decay constant (k) in years (yr^{-1})] by latitude and **a** root-diameter class, and **b** by plant life form. Data are from studies given in Table 1

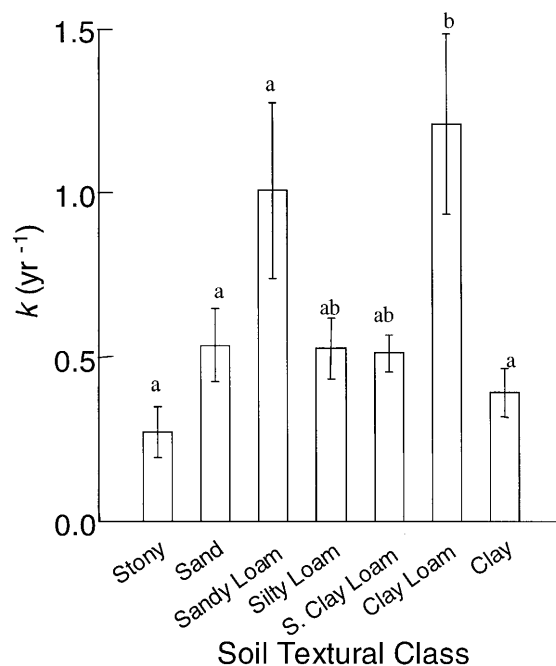


Fig. 2 Root decomposition constants (k) by soil textural class. Bars are means \pm SE; different lower case letters identify groups that are significantly different ($P < 0.05$). Data are from studies given in Table 1

Table 2 Regressions of individual environmental and climate parameters with root decay rates (k). Results are divided by method [all methods (*All*) or litterbag studies only (*Litterbags*)]. All plant life forms were combined for analyses. Only statistically significant regressions ($P < 0.05$) where one or both values (by method) have $r^2 > 0.10$ are reported. n Sample size, *MAT* mean annual temperature, *MAP* mean annual precipitation, *AET* actual evapotranspiration, *NS* not significant

| Parameter | Method | n | Regression equation | r^2 | Significance |
|----------------------|------------|-----|---|-------|--------------|
| Fine roots | | | | | |
| Latitude | All | 88 | $\ln(k)=0.37-0.04 \times \text{latitude}$ | 0.48 | $P < 0.001$ |
| | Litterbags | 69 | $\ln(k)=0.57-0.05 \times \text{latitude}$ | 0.45 | $P < 0.001$ |
| MAT | All | 88 | $\ln(k)=-2.00+0.07 \times \text{MAT}$ | 0.37 | $P < 0.001$ |
| | Litterbags | 69 | $\ln(k)=-1.94+0.07 \times \text{MAT}$ | 0.29 | $P < 0.001$ |
| MAP | All | 88 | $\ln(k)=-1.52+\text{MAP}$ | 0.13 | $P < 0.001$ |
| | Litterbags | 69 | NS | | |
| AET | All | 88 | $\ln(k)=-2.21+0.002 \times \text{AET}$ | 0.34 | $P < 0.001$ |
| | Litterbags | 69 | $\ln(k)=-2.16+0.001 \times \text{AET}$ | 0.26 | $P < 0.001$ |
| All diameters | | | | | |
| Latitude | All | 175 | $\ln(k)=0.09-0.03 \times \text{latitude}$ | 0.28 | $P < 0.001$ |
| | Litterbags | 152 | $\ln(k)=0.04-0.03 \times \text{latitude}$ | 0.20 | $P < 0.001$ |
| MAT | All | 175 | $\ln(k)=-1.64+0.06 \times \text{MAT}$ | 0.27 | $P < 0.001$ |
| | Litterbags | 152 | $\ln(k)=-1.56+0.05 \times \text{MAT}$ | 0.18 | $P < 0.001$ |
| AET | All | 175 | $\ln(k)=-1.96+0.001 \times \text{AET}$ | 0.25 | $P < 0.001$ |
| | Litterbags | 152 | $\ln(k)=-1.85+0.001 \times \text{AET}$ | 0.15 | $P < 0.001$ |

Table 3 Correlation coefficients for root decomposition with latitude, elevation, and climate by life form, methodology, and diameter class. MAP Mean annual precipitation, *m.a.s.l.* meters above sea level; for other abbreviations, see Table 2

| | All | | | Litterbags | | |
|----------------------|-----------|---------|-----------|------------|---------|-----------|
| | Broadleaf | Conifer | Graminoid | Broadleaf | Conifer | Graminoid |
| Fine roots | | | | | | |
| <i>n</i> | 43 | 10 | 35 | 40 | 10 | 19 |
| Latitude (°N) | -0.55* | -0.42 | -0.64* | -0.52* | -0.42 | -0.80* |
| Elevation (m.a.s.l.) | 0.44 | -0.03 | -0.25 | 0.54* | -0.03 | -0.19 |
| MAP (mm) | 0.50* | 0.19 | 0.46* | 0.44* | 0.19 | 0.67* |
| MAT (°C) | 0.58* | 0.39 | 0.44* | 0.54* | 0.39 | 0.44 |
| AET | 0.26 | 0.42 | 0.63* | 0.28 | 0.42 | 0.78* |
| All size classes | | | | | | |
| <i>n</i> | 71 | 58 | 46 | 65 | 57 | 30 |
| Latitude (°N) | -0.43* | 0.51* | -0.66* | -0.39* | 0.49* | -0.80* |
| Elevation (m.a.s.l.) | 0.33* | -0.29* | -0.13 | 0.38* | -0.23 | -0.08 |
| MAP (mm) | 0.26* | -0.58* | 0.45* | 0.19 | -0.55* | 0.58* |
| MAT (°C) | 0.53* | -0.29* | 0.49* | 0.49* | -0.30* | 0.48* |
| AET | 0.16 | -0.31* | 0.64* | 0.13 | -0.32* | 0.76* |

* Significant at the 95% level

Table 4 Root decomposition and initial litter quality by root diameter classes. Values are means±SE. *n* given in parentheses. Different letters indicate statistically significant differences among

root-diameter size classes ($P<0.05$). Data are from studies listed in Table 1. For abbreviations, see Table 2

| Variable | | <2 mm | | 2–5 mm | | >5 mm | |
|------------------|------------|--------------|------|--------------|------|--------------|------|
| <i>k</i> -Values | All | 0.83±0.15 a | (88) | 0.52±0.09 a | (62) | 0.18±0.03 b | (20) |
| | Litterbags | 0.69±0.17 a | (69) | 0.52±0.09 a | (62) | 0.19±0.04 b | (16) |
| C:N | All | 67±6 a | (39) | 104±25 a | (9) | 156±19 b | (10) |
| | Litterbags | 62±6 a | (23) | 104±25 a | (9) | 156±19 b | (10) |
| Ca (mg/g) | All | 2.32±0.43 a | (24) | 2.91±0.25 b | (37) | 0.87±0.22 c | (11) |
| | Litterbags | 2.07±0.46 a | (21) | 2.91±0.25 b | (37) | 1.31±0.19 a | (7) |
| N (%) | All | 0.94±0.05 a | (84) | 0.59±0.05 b | (51) | 0.45±0.06 b | (18) |
| | Litterbags | 0.88±0.05 a | (65) | 0.59±0.05 b | (51) | 0.41±0.05 c | (14) |
| P (%) | All | 0.05±0.003 a | (61) | 0.07±0.004 b | (46) | 0.05±0.003 a | (11) |
| | Litterbags | 0.06±0.004 a | (42) | 0.07±0.004 b | (46) | 0.04±0.006 a | (7) |
| Lignin (%) | All | 23.6±0.8 | (66) | 22.4±0.8 | (51) | 22.7±1.0 | (10) |
| | Litterbags | 26.0±0.8 a | (50) | 22.4±0.8 b | (51) | 22.7±1.0 ab | (10) |
| Lignin:N | All | 37±3 a | (66) | 53±5 b | (47) | 73±11 b | (10) |
| | Litterbags | 40±4 a | (50) | 53±5 b | (47) | 73±11 b | (10) |
| Lignin:P | All | 565±48 a | (52) | 380±48 b | (42) | 720±157 a | (7) |
| | Litterbags | 610±67 a | (36) | 380±48 b | (42) | 720±157 a | (7) |

terbag studies of all root size classes combined. Graminoid root decay was positively correlated with MAP and AET. Graminoid root decay was also positively correlated with MAT when all methods were considered, and for litterbag studies with all root size classes combined. The sample size for coniferous fine roots was relatively small ($n=10$), and there were no significant correlations with climatic or other environmental variables. When all root size classes were combined, coniferous root decomposition was negatively correlated with MAP, MAT, and AET (Table 3).

Classification of soil texture was available for 147 *k*-values. We categorized soil texture data into seven classifications based on the descriptions given by the original authors. These included stony material ($n=8$), sands ($n=43$), sandy loams ($n=46$), silt loams ($n=15$), silty clay loams ($n=11$), clay loams ($n=11$) and clays ($n=13$). Roots decayed significantly faster (Fig. 2) in

clay loam soils than in other soil texture types ($P<0.05$). Roots in litterbags (both fine roots and all size classes) decayed faster in sandy loams and clay loam soils than in other textural classes (data not shown) ($P<0.05$).

Single root physical and chemical parameters

Secondary thickening in woody species results in changes in the amount of wood versus more ephemeral tissues, and thus root diameter can be thought of as one index of litter quality. There were no statistically significant differences in decomposition rates between small- (<2 mm) and medium- (2–5 mm) diameter roots, but large-diameter roots (>5 mm) decomposed significantly more slowly than the smaller size classes (Table 4). The initial chemistry of roots varied by size class. The C:N ratio of roots ranged from 62 (±6) to 156 (±19) among size classes and

followed the same trend as decay rates. Lignin concentrations were remarkably similar among root-diameter classes ($23.3 \pm 0.6\%$, $n=129$), and were slightly higher in fine roots that were used in litterbag studies. In contrast, the lignin:N ratio was highest in medium- and large-diameter roots, reflecting the generally lower N concentrations in these diameter classes. The lignin:P ratio was lowest and root P was greatest in medium-diameter roots. Root Ca concentrations were also greatest in the intermediate size class (Table 4).

Root Ca was the single best predictor of decomposition rates for fine roots ($r^2=0.55$), and explained approximately one-third of the variability in root decay when all diameter classes were combined (Fig. 3a, Table 5). Root C:N ratios were significantly negatively correlated with decay (Fig. 3b, Table 5). Lignin, and the lignin:N and lignin:P ratios were also significantly negatively correlated with root decay rates, although these parameters explained a smaller proportion of the patterns observed. Initial root P concentrations were weakly positively correlated with root decay when all diameter classes were combined, but no relationship was found when only fine roots were considered (Table 5). Root N was very weakly positively correlated with root decomposition for all diameters and methods combined ($r^2=0.05$, $n=155$), and not significantly correlated with fine root decay regardless of method, or all diameter classes combined for litterbags studies (data not shown). Of course, there is some degree of colinearity among certain variables. Root C:N was negatively correlated with root N ($r^2=0.70$) and positively correlated with lignin:N ($r^2=0.84$), although these parameters affected root decay differently.

Root decay rates and litter chemistry also varied significantly by plant life form (Table 6). Graminoid species decayed the fastest followed by broadleaf roots, and then coniferous species. Conifer roots had significantly higher C:N ratios for all categories except fine roots with methods combined, and broadleaf and graminoid roots were not statistically different. The N concentrations of fine roots did not differ significantly by life form, but the Ca concentrations of graminoid fine roots were 2–3 times greater than those of broadleaf roots, and 5 times greater than those of conifer roots on average (Table 6). When all diameter classes were combined, conifers had lower root N, and broadleaf species had lower root Ca than other plant life forms. Lignin concentrations were lower in fine roots of graminoid species, and followed a pattern of broadleaf>conifer>graminoid when all diameter classes were combined. Lignin:N ratios followed a pattern of conifer>broadleaf>graminoid, and broadleaf roots had greater lignin:P ratios than other life forms (Table 6).

All plant life forms showed strong positive correlations of root decay with initial Ca concentrations when all root size classes were included in the analysis (Table 7). For fine roots, only broadleaf species were correlated with Ca. Root decay of broadleaf species was strongly negatively correlated with tissue C:N ratios. The decomposition of fine graminoid roots decreased with increasing lignin:N.

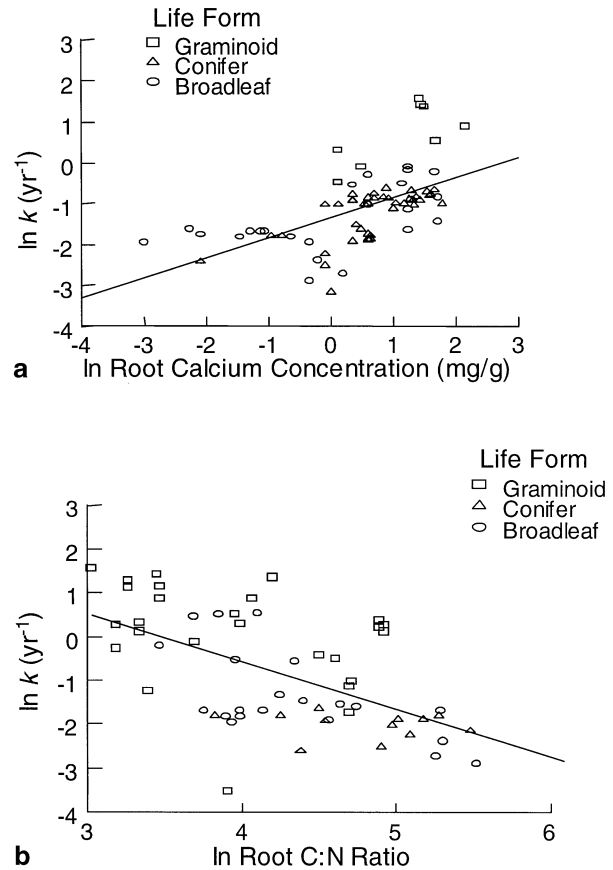


Fig. 3 Root decomposition constants (k) (natural log of k in year⁻¹) of initial root Ca concentrations (a). All root diameters and methods are included. Different symbols refer to different plant life forms. The equation for the line given is: $\ln(k) = -1.33 + [0.49 \times \ln(\text{Ca})]$. Root k s (natural log of k in year⁻¹) of initial root C:N ratios (b). All root diameters and methods are included. Different symbols refer to different plant life forms. The equation for the line given is $\ln(k) = 3.92 + [1.12 \times \ln(\text{C:N})]$. Data are from studies listed in Table 1

Climatic, environmental, and substrate quality factors combined

Litter decay models with the strongest predictive power generally incorporate multiple variables of climate and/or initial substrate quality (Meentemeyer 1978; Aerts 1997). The use of multiple variables must also be treated with caution, however, because of autocorrelation of climatic variables such as MAT, MAP, AET (AET is a function of temperature and precipitation), and latitude, or litter quality variables such as C:N, N, and lignin:N ratios as mentioned above.

The multiple regressions that best fit patterns in root decomposition when considering all climatic and environmental variables are MAP and latitude for fine roots, with the addition of elevation for fine root litterbag studies (Table 8). A much smaller proportion of the variability is explained when all methods and size classes are considered.

Multiple root chemistry parameters were much better at describing patterns observed. Ca concentrations and

Table 5 Regressions of individual root chemistry parameters with root *k*s. Results are divided by method (All or Litterbag). All plant life forms were combined for analyses. Only statistically significant regressions ($P < 0.05$) where one or both values (by method) have $r^2 > 0.10$ are reported. For abbreviations, see Table 2

| Parameter | Method | <i>n</i> | Regression equation | r^2 | Significance |
|---------------|------------|----------|--|-------|--------------|
| Fine roots | | | | | |
| C:N | All | 39 | $\ln(k) = 3.16 - 0.90 \times \ln(\text{C:N})$ | 0.21 | $P < 0.05$ |
| | Litterbags | 23 | $\ln(k) = 5.36 - 1.54 \times \ln(\text{C:N})$ | 0.32 | $P = 0.005$ |
| Ca mg/g | All | 24 | $\ln(k) = -1.22 + 0.70 \times \ln(\text{Ca})$ | 0.55 | $P < 0.001$ |
| | Litterbags | 21 | $\ln(k) = -1.21 + 0.72 \times \ln(\text{Ca})$ | 0.55 | $P < 0.001$ |
| Lignin % | All | 66 | $\ln(k) = 4.61 - 1.72 \times \ln(\text{lignin})$ | 0.26 | $P < 0.001$ |
| | Litterbags | 50 | $\ln(k) = 3.59 - 1.43 \times \ln(\text{lignin})$ | 0.16 | $P < 0.005$ |
| Lignin:N | All | 66 | $\ln(k) = 1.47 - 0.66 \times \ln(\text{lignin:N})$ | 0.20 | $P < 0.001$ |
| | Litterbags | 43 | NS | | |
| Lignin:P | All | 52 | $\ln(k) = 2.99 - 0.58 \times \ln(\text{lignin:P})$ | 0.10 | $P < 0.05$ |
| | Litterbags | 36 | $\ln(k) = 225 - 0.51 \times \ln(\text{lignin:P})$ | 0.12 | $P < 0.05$ |
| All diameters | | | | | |
| C:N | All | 60 | $\ln(k) = 3.92 - 1.12 \times \ln(\text{C:N})$ | 0.34 | $P < 0.001$ |
| | Litterbags | 44 | $\ln(k) = 4.00 - 1.19 \times \ln(\text{C:N})$ | 0.35 | $P < 0.001$ |
| Ca mg/g | All | 74 | $\ln(k) = -1.33 + 0.49 \times \ln(\text{Ca})$ | 0.31 | $P < 0.001$ |
| | Litterbags | 67 | $\ln(k) = -1.46 + 0.63 \times \ln(\text{Ca})$ | 0.31 | $P < 0.001$ |
| P % | All | 120 | $\ln(k) = 0.19 + 0.37 \times \ln(\text{P})$ | 0.03 | $P < 0.05$ |
| | Litterbags | 97 | $\ln(k) = 1.08 + 0.74 \times \ln(\text{P})$ | 0.16 | $P < 0.001$ |
| Lignin % | All | 129 | $\ln(k) = 3.47 - 1.40 \times \ln(\text{lignin})$ | 0.18 | $P < 0.001$ |
| | Litterbags | 113 | $\ln(k) = 2.47 - 1.11 \times \ln(\text{lignin})$ | 0.12 | $P < 0.01$ |
| Lignin:N | All | 125 | $\ln(k) = 1.27 - 0.60 \times \ln(\text{lignin:N})$ | 0.20 | $P < 0.001$ |
| | Litterbags | 109 | $\ln(k) = 0.61 - 0.45 \times \ln(\text{lignin:N})$ | 0.11 | $P < 0.001$ |
| Lignin:P | All | 103 | $\ln(k) = 2.36 - 0.53 \times \ln(\text{lignin:P})$ | 0.12 | $P < 0.001$ |
| | Litterbags | 87 | $\ln(k) = 2.41 - 0.57 \times \ln(\text{lignin:P})$ | 0.19 | $P < 0.001$ |

Table 6 Root decomposition and initial litter quality by plant life form. Values are means \pm SE. *n* given in parentheses. Different letters indicate statistical difference among life forms ($P < 0.05$). Data are from studies listed in Table 1. For abbreviations, see Table 2

| Variable | Method | Broadleaf | Conifer | Graminoid |
|------------------|------------|-------------------------|--------------------------|------------------------|
| Fine roots only | | | | |
| <i>k</i> -values | All | 0.46 \pm 0.06 a (43) | 0.17 \pm 0.02 b (10) | 1.48 \pm 0.33 c (35) |
| | Litterbags | 0.44 \pm 0.06 a (40) | 0.17 \pm 0.02 b (10) | 1.49 \pm 0.57 a (19) |
| C:N | All | 55 \pm 4 (13) | 93 \pm 20 (5) | 70 \pm 10 (21) |
| | Litterbags | 55 \pm 4 a (13) | 93 \pm 20 b (5) | 52 \pm 11 a (5) |
| Ca (mg/g) | All | 2.10 \pm 0.42 ab (15) | 0.95 \pm 0.24 a (5) | 4.88 \pm 1.43 b (4) |
| | Litterbags | 1.61 \pm 0.40 a (12) | 0.95 \pm 0.24 a (5) | 4.88 \pm 1.43 b (4) |
| N (%) | All | 0.93 \pm 0.07 (43) | 0.82 \pm 0.10 (9) | 0.98 \pm 0.10 (32) |
| | Litterbags | 0.87 \pm 0.06 (40) | 0.82 \pm 0.10 (9) | 0.93 \pm 0.11 (16) |
| P (%) | All | 0.06 \pm 0.004 (34) | 0.05 \pm 0.008 (5) | 0.05 \pm 0.005 (22) |
| | Litterbags | 0.06 \pm 0.005 (31) | 0.05 \pm 0.008 (5) | 0.07 \pm 0.01 (6) |
| Lignin (%) | All | 27.6 \pm 0.7 a (33) | 26.1 \pm 1.2 a (7) | 17.9 \pm 0.9 b (26) |
| | Litterbags | 27.6 \pm 0.7 a (33) | 26.1 \pm 1.2 a (7) | 20.5 \pm 2.1 b (10) |
| Lignin:N | All | 44 \pm 5 a (33) | 41 \pm 9 ab (7) | 26 \pm 3 b (26) |
| | Litterbags | 44 \pm 5 (33) | 41 \pm 9 (7) | 27 \pm 4 (10) |
| Lignin:P | All | 646 \pm 82 (27) | 628 \pm 161 (5) | 439 \pm 36 (20) |
| | Litterbags | 646 \pm 82 a (27) | 628 \pm 161 a (5) | 340 \pm 163 b (4) |
| All size classes | | | | |
| <i>k</i> -values | All | 0.44 \pm 0.04 a (71) | 0.30 \pm 0.02 a (58) | 1.41 \pm 0.27 b (46) |
| | Litterbags | 0.44 \pm 0.05 a (65) | 0.30 \pm 0.02 a (57) | 1.38 \pm 0.39 b (30) |
| C:N | All | 92 \pm 14 a (21) | 132 \pm 17 b (12) | 66 \pm 8 a (27) |
| | Litterbags | 92 \pm 14 a (21) | 132 \pm 17 b (12) | 54 \pm 7 a (11) |
| Ca (mg/g) | All | 1.95 \pm 0.37 a (24) | 2.34 \pm 0.22 b (42) | 3.79 \pm 0.89 b (8) |
| | Litterbags | 1.91 \pm 0.41 a (18) | 2.39 \pm 0.22 b (41) | 3.79 \pm 0.89 b (8) |
| N (%) | All | 0.84 \pm 0.05 a (67) | 0.47 \pm 0.04 b (45) | 0.90 \pm 0.08 a (43) |
| | Litterbags | 0.82 \pm 0.05 a (61) | 0.46 \pm 0.04 b (44) | 0.94 \pm 0.08 a (27) |
| P (%) | All | 0.06 \pm 0.004 (44) | 0.06 \pm 0.003 (43) | 0.06 \pm 0.005 (33) |
| | Litterbags | 0.06 \pm 0.005 a (38) | 0.06 \pm 0.003 ab (42) | 0.08 \pm 0.01 b (17) |
| Lignin (%) | All | 26.8 \pm 0.9 a (47) | 24.0 \pm 0.5 b (45) | 18.2 \pm 1.0 c (37) |
| | Litterbags | 26.8 \pm 0.9 a (47) | 24.0 \pm 0.5 b (45) | 19.6 \pm 1.7 c (21) |
| Lignin:N | All | 44 \pm 4 a (47) | 67 \pm 4 b (41) | 26 \pm 3 c (37) |
| | Litterbags | 44 \pm 4 a (47) | 67 \pm 4 b (41) | 27 \pm 3 c (21) |
| Lignin:P | All | 698 \pm 80 a (32) | 431 \pm 36 b (40) | 414 \pm 56 b (31) |
| | Litterbags | 698 \pm 80 a (32) | 431 \pm 36 b (40) | 362 \pm 114 b (15) |

Table 7 Correlation coefficients of the relationships among root decomposition and plant litter chemistry by life form, methodology, and size class. All root chemistry data and decay constants (k)

| | All methods | | | | | | Litterbags | | | | | |
|------------------|-------------|-----|---------|-----|-----------|-----|------------|-----|---------|-----|-----------|-----|
| | Broadleaf | | Conifer | | Graminoid | | Broadleaf | | Conifer | | Graminoid | |
| | k | n | k | n | k | n | k | n | k | n | k | n |
| Fine roots | | | | | | | | | | | | |
| C:N | -0.41 | 13 | -0.68 | 5 | -0.59* | 21 | -0.41 | 13 | -0.68 | 5 | -0.76 | 5 |
| N % | 0.06 | 43 | -0.04 | 9 | 0.20 | 32 | -0.04 | 40 | -0.04 | 9 | -0.05 | 16 |
| P % | 0.06 | 34 | 0.67 | 5 | 0.32 | 22 | 0.05 | 31 | 0.67 | 5 | 0.43 | 6 |
| Ca mg/g | 0.76* | 15 | 0.00 | 5 | 0.57 | 4 | 0.70 * | 12 | 0.00 | 5 | 0.57 | 4 |
| Lignin % | -0.07 | 33 | -0.33 | 7 | -0.31 | 26 | -0.07 | 33 | -0.33 | 7 | -0.55 | 10 |
| Lignin:N | 0.08 | 33 | -0.27 | 7 | 0.64* | 26 | 0.08 | 33 | -0.27 | 7 | -0.86 * | 10 |
| Lignin:P | -0.10 | 27 | -0.84 | 5 | -0.29 | 20 | -0.10 | 27 | -0.84 | 5 | -0.34 | 4 |
| All size classes | | | | | | | | | | | | |
| C:N | -0.64* | 21 | -0.14 | 12 | -0.36 | 27 | -0.64* | 21 | -0.14 | 12 | -0.19 | 11 |
| N % | 0.35 * | 67 | -0.44* | 45 | 0.15 | 43 | 0.32* | 61 | -0.41* | 44 | -0.06 | 27 |
| P % | 0.27 | 44 | 0.45* | 43 | 0.24 | 33 | 0.26 | 38 | 0.48* | 42 | 0.47 | 17 |
| Ca mg/g | 0.56* | 24 | 0.63* | 42 | 0.72* | 8 | 0.52* | 18 | 0.59* | 41 | 0.72* | 8 |
| Lignin % | -0.07 | 47 | -0.24 | 45 | -0.33* | 37 | -0.07 | 47 | -0.24 | 45 | -0.42 | 21 |
| Lignin:N | -0.25 | 47 | 0.28 | 41 | -0.51* | 37 | -0.25 | 47 | 0.28 | 41 | -0.51* | 21 |
| Lignin:P | -0.21 | 32 | -0.50* | 40 | -0.26 | 31 | -0.21 | 32 | -0.50* | 40 | -0.43 | 15 |

* Significant at the 95% level

Table 8 Best-fit multiple regressions of root decomposition with environmental, climatic, and chemical parameters across all life forms. Regressions are significant at $P < 0.01$. Equations followed by the same lower case letter used the same dataset for analysis

| Model equation | Size | Method | n | r^2 |
|---|------|--------------|-----|-------|
| Environmental climatic variables only | | | | |
| $\ln(k) = 1.05 - 0.00 \times \text{MAP} - 0.05 \times \text{latitude}$ | Fine | All | 88 | 0.51 |
| $\ln(k) = 2.08 - 0.00 \times \text{MAP} - 0.07 \times \text{latitude} - 0.00 \times \text{elevation}$ | Fine | Litterbags | 69 | 0.54 |
| $\ln(k) = -1.97 + 0.04 \times \text{MAT} + 0.001 \times \text{AET}$ | All | All | 175 | 0.32 |
| $\ln(k) = -0.02 - 0.00 \times \text{MAP} + 0.001 \times \text{AET} - 0.03 \times \text{latitude}$ | All | Litterbags | 152 | 0.26 |
| Root chemistry variables only | | | | |
| $\ln(k) = 3.79 + 0.74 \times \ln(\text{Ca}) - 1.22 \times \ln(\text{C:N})$ | Fine | Litterbags a | 17 | 0.89 |
| $\ln(k) = 31.25 + 0.55 \times \ln(\text{Ca}) - 8.22 \times \ln(\text{C:N}) + 7.34 \times \ln(\text{lignin:N}) - 7.32 \times \ln(\text{lignin})$ | All | Litterbags b | 29 | 0.83 |
| Combined root chemistry and environmental variables | | | | |
| $\ln(k) = 1.83 + 0.07 \times \text{MAT} - 0.00 \times \text{MAP} - 0.83 \times \ln(\text{C:N}) + 0.35 \times \ln(\text{Ca})$ | Fine | Litterbags a | 17 | 0.96 |
| $\ln(k) = 0.64 + 0.002 \times \text{AET} - 0.73 \times \ln(\text{C:N}) + 0.50 \times \ln(\text{Ca})$ | All | Litterbags b | 29 | 0.90 |

C:N ratios together explained between 83% and 87% of the variability in root decomposition rates (Table 8). When all root size classes were considered, lignin and the lignin:N ratio also contributed to the variability in decay. However, Ca and C:N together accounted for the majority of the variability in root decay (Table 8). It is important to note that the sample sizes for these analyses were smaller than for climate because fewer studies reported multiple litter chemistry values.

The combination of climatic, environmental, and chemical factors produced the strongest relationships with root decomposition rates (Table 8). The predictive power for fine roots was greatest ($r^2 = 0.96$) when the effects of MAP, MAT, C:N, and Ca were combined

were log-transformed to meet assumptions of ANOVA. Data are from studies listed in Table 1

and only included litterbag studies. Studies were excluded if they lacked litter chemistry data used in the analysis. For abbreviations, see Tables 2 and 3

($n = 17$). Ca concentrations alone contributed to over 26% of the variability in fine root decay, and Ca concentration together with the C:N ratio were the two most important variables in the model. When all root diameters were considered, AET, Ca, and C:N ratio accounted for 90% of the variability in root decay (Table 8).

Effects of methodology on patterns in root decomposition

Litterbags have been criticized for decreasing access by larger decomposer organisms such as soil vertebrates and invertebrates (Wachendorf et al. 1997), while methods

that do not enclose roots may result in loss of fine root material during decay. It could be hypothesized that tethering roots or trenching land to allow roots to decay in situ would lead to faster decay rates. The trench plot study included here was conducted in Puerto Rico (Silver and Vogt 1993), and reported very similar root decomposition rates ($k=0.70\pm 0.15$, $n=3$) as a litterbag study ($k=0.72\pm 0.12$, $n=2$) conducted simultaneously in the same forest and using the same diameter class of roots (Bloomfield et al. 1993).

We compared root decay rates for buried pots (tropical graminoid only) and tethered roots (north-temperate broadleaf and conifer only) with litterbag studies for the same biome and life form. The buried pots yielded decay constants ($k=1.47\pm 0.27$, $n=16$) that were significantly lower (slower decay) ($P=0.05$) than litterbags ($k=2.93\pm 0.65$, $n=6$) for tropical grasslands (defined as $<23^\circ\text{N}$ latitude). There were no effects of tethering roots when compared to litterbag studies of conifer species, or large-diameter roots. Fine tethered broadleaf roots ($n=6$) had significantly lower k -values ($P<0.05$) than broadleaf roots decaying in litterbags at similar latitudes ($35\text{--}60^\circ\text{N}$; $n=15$).

Discussion

Climate and environmental variables

Several climate and environmental variables were significantly correlated with rates of root decomposition using the global dataset, but for the most part, the predictive power of these parameters was low. Models of leaf litter decay have generally suggested that climate, and particularly temperature (Jenny et al. 1949), exerts a stronger influence on decomposition than substrate quality at both local (Singh and Shekhar 1989; Ruark 1993; Arunachalam et al. 1996; Hobbie 1996) and global scales (Meetenmeyer 1978; Aerts 1997). Root decomposition was weakly positively correlated with MAT. Other indices of temperature, such as mean monthly values or monthly minimum or maximum temperatures may provide better predictors of belowground processes. For example, Vogt et al. (1986) reported an inverse relationship between live fine root mass and maximum mean monthly temperatures in broadleaf and conifer forests, and suggested that the sites with higher maximum monthly temperatures had faster decomposition rates and greater nutrient availability.

We calculated Q_{10} values for decomposition according to Kirschbaum (1995) as a rough estimate of the temperature sensitivity of root decay using the global dataset. The Q_{10} for root decay was 1.7 using the whole dataset, and 2.1 when only fine roots were considered. The Q_{10} values for root decomposition by life form ranged from 1.0 (fine broadleaf roots in litterbags) to 2.5 (fine graminoid roots, all methods combined). In general, broadleaf species exhibited the lowest Q_{10} values, and graminoid species the highest Q_{10} values. These data

should be treated with caution, however, because our results indicate that MAT was not a particularly strong predictor of root decay rates.

The strongest relationship between environmental variables and root decomposition was a decrease in fine root decay with increasing latitude, which likely results from a complex interaction of climate, soil, and biological factors that change in relation to the distance from the equator. The relationship was significant for broadleaf species and graminoids, but not for conifers. The fact that studies of coniferous root decomposition are limited to northern latitudes, as opposed to the widespread distribution of other plant life forms, may contribute to the lack of an observable pattern.

AET had a large and significant impact on rates of graminoid root decomposition, but little or no effect on decomposition rates of roots of other life forms, or decay rates when life forms were combined. Broadleaf roots spanned a wide range of AET, while roots of conifer species did not. In a review of root decomposition from 37 sites and plots in northern Europe, Berg et al. (1998) found that conifer root decomposition was also relatively insensitive to AET. In general, root decay appears to be less sensitive to AET than leaf litter decay; AET has been widely used to characterize climatic control of leaf litter decomposition (Meentemeyer and Berg 1986; Dyer et al. 1990), and is often the best predictor of leaf litter decay at large spatial scales (Meentemeyer 1978; Aerts 1997).

Substrate quality

Root chemistry appears to be the dominant factor controlling patterns in decomposition rates at a global scale. Root Ca had the strongest impact on decay rates. The dominant role of Ca in root decay is intriguing, and suggests several possible alternative explanations. First, Ca concentrations in roots are likely to result from a combination of root tissue concentrations and those of associated microbes. No distinctions are made between root Ca and nutrient contributions from root-associated microbes (e.g., mycorrhizal associations) in root decomposition studies. Fungal and bacterial heterotrophs may access and accumulate root Ca to form an oxalate salt (Cromack et al. 1979). Oxalates serve as a pool of reserve organic matter that can be used to maintain microbial metabolism under unfavorable soil conditions (Grabovich et al. 1995). Various forms of Ca in vesicular-arbuscular mycorrhizal tissue, such as Ca-polyphosphates on the cell surface near the cytoplasmic membrane, may also contribute significantly to the overall root Ca levels when such associations occur (Kulaev 1975; Peterson and Howarth 1991).

Second, root Ca concentrations could be an index of soil conditions that in turn exert a strong influence on decomposition rates. For example, lower root Ca concentrations were reported in root tissues from northern New Hampshire, USA, and Scandinavia (Berg 1984;

Fahey et al. 1988; Fahey and Arthur 1994; Berg et al. 1998), both regions of potential anthropogenic acid deposition (Adriano and Havas 1989), and/or soils with low Ca availability. Ca plays an essential role in regulating many plant physiological processes including water and solute movement, cell division and cell wall synthesis, signaling roles in plant defense and damage repair systems, and structural chemistry and function of support tissues (McLaughlin and Wimmer 1999). Unfavorable ratios of root Ca to Al can produce symptoms of Al toxicity in roots and decrease rates of microbial degradation (Vogt et al. 1987). This is likely to occur in soils exposed to acidic deposition (Lohmus and Lasn 1990) and tropical soils with high exchangeable Al concentrations (Bloomfield et al. 1993). Furthermore, leaching or displacement of Ca by exposure to increased soil acidity has been shown to lead to altered permeability of root membranes (Zhao et al. 1987). In summary, the positive relationships between root decomposition and initial Ca concentrations warrant further study. Analyses should include studies of the contribution of microbial Ca to bulk tissue analyses, together with an examination of the role of acidification, Al toxicity, and Ca leaching on root and microbial processes.

Root C:N ratios also played an important role in predicting patterns in root decay globally. The importance of substrate C:N ratios in governing the rate of organic matter decomposition was recognized as early as 1916 (Jensen 1929). Theoretically, the optimum C:N ratio for microbial growth is approximately 25, but fungi and bacteria can decompose substrates with much higher ratios (Heal et al. 1997). The C:N ratios of medium- and large-diameter roots, and those of conifer species regardless of size class, had high (>75) C:N ratios. Substrates with C:N ratios of <20 decompose rapidly and NH_4 is released through mineralization. Plant material with intermediate C:N ratios of 25–75 can also decompose quickly, but N mineralization activity is often reduced by increased microbial immobilization as well as protein complexation by polyphenols when the cells lyse. Substrates with high C:N ratios (>75) are often much more difficult to break down and are generally characterized by greater amounts of structural woody materials such as lignin, condensed tannins and terpenes, as well as low available N for decomposer organisms (Heal et al. 1997).

The C:N ratio by itself merely describes the proportions of C to N, without revealing how these elements are distributed among the important chemical classes of the plant cell (Cromack and Monk 1975). Regardless of this simplification, the C:N ratio has been shown to be a valuable predictive tool in numerous studies of litter decomposition at local, regional, and global scales (Flanagan and Van Cleve 1983; Fog 1988; Taylor et al. 1989; Aerts 1997; and others).

Lignin (Cromack 1973; Fogel and Cromack 1977; Meentemeyer 1978; Taylor et al. 1991; and others), lignin:N (Lehmann et al. 1995; Arunachalam et al. 1996; Ostertag and Hobbie 1999), and N concentrations (Pandey and Singh 1982; Hunt et al. 1988; Aber et al.

1990) have been shown to be good predictors of litter decay, particularly of foliar tissues. We found that these indices of litter quality were not strongly correlated with root decomposition rates at a global scale. Lignin is a relatively recalcitrant organic constituent of fibrous material in plant tissue that helps to hold plant cells together and provides tissue strength. Lignin controls decomposition rates by its own resistance to enzymatic attack, as well as through physical interference with the decay of other cell wall fractions (Alexander 1977). Negative correlations between initial root lignin content and decomposition rates have been documented for tropical forests ($r^2=0.38$; $P=0.05$; Arunachalam et al. 1996), bamboo roots ($r^2=0.86$; $P<0.01$; Tripathi and Singh 1992), Scots pine roots (Berg 1984), and roots from desert plant species (Mun and Whitford 1998). In our analysis, graminoid roots had the lowest lignin concentrations of the life forms examined. Grasses often contain larger amounts of more labile forms of C (carbohydrates, sugars, amino acids) and smaller percentages of structural materials (lignin, cellulose, hemicellulose) (Seastedt et al. 1992). Interestingly, while fine broadleaf and conifer roots had comparable lignin concentrations, conifer roots still decompose at a significantly slower rate. Lignin control of decomposition is likely to appear only after the more labile nutrient forms are consumed or leached. Even then, lignin concentrations still may not be high enough to significantly inhibit decomposition (Taylor et al. 1991).

At a global scale, we found only weak correlations with root lignin:N ratios. While lignin concentrations showed little variability among the size class and life form categories examined, root N ranged from 0.09 to 2.15%, which is comparable to ranges reported for leaf litter (Taylor et al. 1991; Aerts 1997). Leaf litter decomposition is often positively correlated with tissue N concentrations, especially during the initial decomposition phase (Pandey and Singh 1982; Hunt et al. 1988; Aber et al. 1990). This pattern was not apparent for root decomposition.

Rates of root decomposition differed significantly by root diameter, most notably slower decay of roots >5 mm diameter. Some investigators have suggested that decreased mass loss from larger diameter roots may be due to slower leaching rates of water-soluble compounds (Fahey et al. 1988), a longer time required for fungal hyphae penetration (Foster and Lang 1982; Berg 1984), or increasing proportions of resistant organic substances and structural mass (Fitter 1985). Large-diameter roots are less susceptible to herbivory, mechanical damage, and desiccation compared to fine roots, which is consistent with the general observation that root longevity increases with root diameter (Boot 1990). Most studies report faster decomposition rates of fine roots, and attribute this pattern to higher inorganic nutrient concentrations and lower lignin:N ratios (Berg 1984; Camiré et al. 1991). We observed that intermediate-diameter roots (2–5 mm) had higher Ca and P, and lower lignin and lignin:P ratios than other size classes, while fine roots had the highest root N concentrations.

Climate and litter quality combined

Similar to leaf litter decay, the combination of substrate quality, climate, and environmental factors produced the strongest relationship with root decay rates globally. The combination of root Ca level and C:N ratio provided the best substrate quality model for predicting decomposition rates globally, and the inclusion of MAT or AET improved the model's predictive power. Swift et al. (1979) suggested that environmental factors (MAT, AET) set the upper and lower limits to the potential decay rate, and the "fine control" at the local level is determined by resource quality (C:nutrient ratios) and factors of the edaphic complex (soil moisture, texture, aeration, pH). At a global scale of analysis, Meentemeyer (1978) was able to account for 72% of the variation in leaf decay rates using AET and AET:lignin ratio. Aerts (1997) was able to explain 57% of the variability in leaf litter decomposition rates with the combined effects of AET and substrate C:N ratio. Unlike studies of leaf litter decay, however, substrate quality parameters described the greatest proportion of the variability in root decomposition rates. We expect that this is because roots occur in the soil where they and the community of decomposers are well buffered from extremes in temperature and precipitation relative to surface litter.

Conclusions

Our analyses show that root decomposition can be fairly well predicted by a combination of litter quality and environmental parameters. Root decomposition often plays a key role in soil C sequestration and nutrient cycling, and the C and nutrient dynamics associated with root decay represent significant components of the global C cycle. A more thorough understanding of the factors that control root decomposition will improve our ability to model global C dynamics, and predict the effects of future climate and other global changes on biogeochemical cycles. Future studies should focus on the mechanistic role of root litter chemistry, and particularly root Ca in root decomposition. These studies should incorporate analyses of soil microbial communities and fungal colonization to improve our understanding of how organisms influence rates of root decay at local, regional, and global scales.

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