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Reconciling Change in Oi-Horizon ^{14}C With Mass Loss for an Oak Forest

ABSTRACT

First-year litter decomposition was estimated for an upland-oak forest ecosystem using enrichment or dilution of the ^{14}C-signature of the Oi-horizon. These isotopically-based mass-loss estimates were contrasted with measured mass-loss rates from past litterbag studies. Mass-loss derived from changes in the ^{14}C-signature of the Oi-horizon suggested mean mass loss over 9 months of 45% which was higher than the corresponding 9-month rate extrapolated from litterbag studies (~35%). Greater mass loss was expected from the isotopic approach because litterbags are known to limit mass loss processes driven by soil macrofauna (e.g., fragmentation and comminution). Although the ^{14}C-isotope approach offers the advantage of being a non-invasive method, it exhibited high variability that undermined its utility as an alternative to routine litterbag mass loss methods. However, the ^{14}C approach measures the residence time of C in the leaf litter, rather than the time it takes for leaves to disappear; hence radiocarbon measures are subject to C immobilization and recycling in the microbial pool, and do not necessarily reflect results from litterbag mass loss.

The commonly applied two-compartment isotopic mixing model was appropriate for estimating decomposition from isotopic enrichment of near-background soils, but it produced divergent results for isotopic dilution of a multi-layered system with litter cohorts having independent ^{14}C-signatures. This discrepancy suggests that cohort-based models are needed to adequately capture the complex processes involved in carbon transport associated with litter mass-loss. Such models will be crucial for predicting

intra- and interannual differences in organic horizon decomposition driven by scenarios of climatic change.

ABBREVIATIONS USED IN THE TEXT

(Excluding variables defined with equations.)

AMS = accelerator mass spectrometer

C = carbon

N = nitrogen

C/N = C to N ratio

DOE = U.S. Department of Energy

EBIS = Enriched Background Isotope Study

ORR = Oak Ridge Reservation

P = probability

SE = standard error

SOM = soil organic matter

TVA = Tennessee Valley Authority

‰ = per mil

Fundamental knowledge of soil organic matter (SOM) dynamics is critical to understanding carbon (C) sequestration, ecosystem C and nutrient cycling processes and ultimately forest growth. Unfortunately, we still lack critical information regarding how soil organic matter is formed and the mechanisms whereby it is distributed within the soil profile. Annual leaf-litter inputs are an obvious potential source of mineral soil C, but significant mass loss of annual leaf-litter cohorts occurs during their migration to the underlying mineral soil (Edwards et al., 1970). Litter mass-loss is a multifaceted process involving leaching of soluble chemicals, faunal facilitated comminution and fragmentation, and decomposition (catabolic degradation of litter constituents) by soil microorganisms (Edwards et al., 1970; Anderson, 1973; Singh and Gupta, 1977). Unambiguous estimates of the rate of accumulation of forest litter and/or the rate at which it transfers C to long-term storage pools are needed.

Litter decomposition bags, tethered leaves, or the isolation of litter cohorts in layered mesh are all methods that have been used to quantify the processes of litter decomposition (Anderson, 1973; Singh and Gupta, 1977; Jorgensen et al., 1980; Binkley, 2002). Disturbance to the litter microclimate, interruption of faunal access to the litter, and mass-accumulation from mineral contamination are, however, common problems confounding the interpretation of cohort mass loss measurements (Robertson and Paul, 2000; Bradford et al., 2002; Idol et al., 2002; Gartner and Cardon, 2004).

Isotopic tracer studies using ^{13}C or ^{14}C have obvious potential for tracking litter mass loss without the disturbance artifacts of the manipulative approaches, and a number papers have reported on the application of such methods to field measurements of the decomposition of crop/grassland litter (Nyhan, 1975; Wedin et al., 1995; Milchunas and

Lauenroth, 1992), forest litter (Hobbie et al., 2004), peat (Domisch et al., 2000) and fine roots (Dahlman and Kucera, 1965; Balesdent and Balabane, 1996). Unfortunately, past isotope studies had to depend on short-term pulse labeling methods as a source for isotopically enriched plant tissues. Those methods may not produce uniformly labeled plant material (Robertson and Paul, 2000; Schimel, 1993), and therefore could lead to estimates of litter turnover inconsistent with true changes in bulk tissue mass loss or decomposition. Conversely, Bromand et al. (2001) have documented experimental methods for generating small quantities of uniformly labeled ^{13}C-litter in wheat appropriate for lab and mesocosm studies (e.g., Lin et al., 1999; Hobbie et al., 2004).

Elevated levels of ^{14}C-CO_2 in the air and soil atmosphere as well as in leaf, stem, and root tissues were observed on the Oak Ridge Reservation (ORR) in east Tennessee during the summer of 1999 as a part of a latitudinal study of soil C cycling from Tennessee to Maine (Gaudinski et al., 2003). The rapid rise in the background ^{14}C-signature of soil-derived CO_2 was the result of a local release of ^{14}C in the form of $^{14}CO_2$ gas from local industrial incinerator (Trumbore et al., 2002). Subsequent measurement of $\Delta^{14}C$ in the cellulose from tree rings formed in 1999 showed that the localized growing-season release was unique in its magnitude, and additional surveys of 1999 tree wood and 2000 leaves showed that the release encompassed a significant portion of the ORR. The highest amounts of the ^{14}C-enriched 2000 leaf tissues ($\Delta^{14}C$ of 1000 to 2000 ‰) were found in vegetation from the western portion of the ORR (Trumbore et al., 2002). The ecosystem-scale enrichment of ^{14}C represented a unique opportunity to study C cycling processes within undisturbed stands of the eastern deciduous hardwood forest. Because the $^{14}CO_2$-release occurred following canopy leaf production and maturation in 1999, foliar litterfall from 1999 was not expected to be highly enriched. However, the 2000 canopy leaf growth from stored 1999-carbohydrates was indeed enriched by the 1999 ^{14}C-pulse. Therefore, the 2000 mixed-species litterfall represented a unique source of ^{14}C enriched foliar tissues for application to a number of edaphic, physiological and ecosystem-scale research questions. To take advantage of this opportunity, large quantities of leaf litter were collected from the west and east ends of the ORR during fall canopy senescence in 2000. The collections included enriched ($\Delta^{14}C$ of ~1000 ‰) and near-background ($\Delta^{14}C$ of ~220 ‰) litter for use in subsequent studies of soil C cycling as a part of the DOE funded Enriched Background Isotope Study (EBIS) described further on the project's Web page (http://ebis.ornl.gov/). As one component of the EBIS project, this paper reports on the use of the uniquely-labeled forest litter for measuring annual rates of Oi-horizon litter decomposition in replicated and undisturbed plots under natural forest-floor conditions. It evaluates the utility of the isotopic approach for stable ^{14}C-input versus transient conditions, and for ^{14}C enrichment versus dilution of the Oi-layer. The isotopic estimates of litter turnover are also contrasted with traditional litter decomposition observations from past studies on the ORR.

MATERIALS AND METHODS

Site Description

The EBIS project (Trumbore et al., 2002) was established in the autumn of 2000 on the ORR, in the U.S. Department of Energy's National Environmental Research Park near Oak Ridge, Tennessee (latitude N 35° 58'; longitude W 84°16'). The mean annual precipitation is 1358 mm and mean annual temperature is 14° C (Johnson and Van Hook, 1989). All EBIS research plots are located on up-slope, ridge-top positions in the upland oak forest type (*Quercus* spp.; *Acer* spp.) with scattered pine (*Pinus echinata* Mill. and *P. virginiana* Mill.), mesophytic hardwoods (*Liriodendron tulipifera* L., *Fagus grandifolia* J.F. Ehrh.), and some hickory (*Carya* spp.). The ages of the over-story trees cover a broad range from about 40 to 150 years, and the maximum canopy height is approximately 26 m. Maximum leaf area index is typically about 6 m^2 m^{-2}. The EBIS sites on the ORR encompass two soil types and two levels of ^{14}C exposure in 1999. At all sites, replicated permanent plots were established for the manipulation of forest litter through reciprocal transplants of enriched versus near-background litter among sites.

The EBIS Experimental Design

Prior to leaf senescence in the fall of 2000, ≈150 4.6 x 9 m plastic tarps were laid out on the forest floor along Pine Ridge for the collection of all forest leaf litter in the vicinity of the 1999 ^{14}C release. A similar number and distribution of tarps were laid out on Walker Branch Watershed at the east end of the ORR to represent near-background conditions. Litter was manually collected from the tarps weekly from September through mid-December 2000. Collected litter was transferred to ORNL greenhouses for air-drying and subsequent storage in large (1 x 1.5 m) vacuum bags. The dried litter was stored in rodent free trailers until needed for the experimental manipulations. Sufficient enriched (1005±19 ‰) and near-background (221±2 ‰) litter was collected in the fall of 2000 to conduct a plot-level litter manipulation study (3 years of litter additions). The near-background litter's ^{14}C-signature was slightly elevated with respect to the expected northern hemisphere data (Levin and Hessshaimer, 2000) because the 1999 ^{14}C-release also produced limited exposure of eastern portions of the Oak Ridge Reservation (Figure 1 and Trumbore et al., 2002).

Four research sites were established on the ORR. Two 'enriched' sites on the west end of the ORR were established on Ultisol and Inceptisol soils of Pine Ridge and on Tennessee Valley Authority land on Chestnut Ridge (TVA), respectively. Two 'near-background' sites were established approximately 10 km further east away from the influence of the 1999 ^{14}C pulse. The near-background sites included a site with Ultisol soils within Walker Branch Watershed on Chestnut-Ridge, and a site with Inceptisol soils on Haw Ridge. The Ultisols are deep, highly weathered soils derived from dolomitic parent material. The Inceptisols are shallow, less weathered soils derived from limy shale/sandstone formations. According to the classification scheme of Green et al. (1993) the organic horizon for both of these soils would be classified as a Leptomoder (a transitional state between mor and mull forest humus). A detailed description of the hydrologic, physical, geochemical, and mineralogical properties of these soils can be found in previous studies (Wilson and Luxmoore, 1988; Jardine et al., 1988; Wilson et al., 1989 and 1990).

At each of the four research sites on the ORR, eight square 7x7 m plots were delineated with metal fence posts and plastic fencing (~61 cm tall). From late September through early December of 2000, the forest floor within each plot was covered with landscape cloth, and the ambient litterfall was periodically blown off the landscape cloth. After the landscape cloth was removed in mid-December, ^{14}C enriched or near-background litter was added back to the respective treatment plots (500 g dry mass m^{-2}) in May 2001. Treatment litter was not added to the experimental plots earlier in the annual cycle pending project funding decisions. Litter treatments were randomly applied to the eight plots at each of the four research sites. The following combination of replicated research plots was created by the experimental design:

(1) plots with ^{14}C-enriched root litter, ^{14}C-enriched soil C, and applied ^{14}C-enriched leaf litter (Pine Ridge and TVA western ORR)

(2) plots with ^{14}C-enriched root litter, ^{14}C-enriched soil C, and near-background 2000 litter, (Pine Ridge and TVA, western ORR),

(3) plots with background roots and soil C, and ^{14}C-enriched 2000 litter (Walker Branch and Haw Ridge, eastern ORR), and

(4) plots with background roots and soil C and near-background 2000 litter (Walker Branch and Haw Ridge, eastern ORR).

This paper deals only with first-year manipulations of the organic horizons of these plots.

Oi-Horizon Sampling

Time-zero and 1st-year litter-layer and mineral soil core samples were collected in March of 2001 and January 2002, respectively. Time-zero O-horizon samples for a given plot within each research site represented a pooled sample of three randomly selected 0.25 m^2 rings for a total sampled area of 0.75 m^2. Each pooled sample was separated into Oi-horizon leaf-litter greater than approximately 1-year of age (i.e., the recognizable litter under the landscape cloth), and the Oe/Oa-horizon litter consisting mostly of humus with small amounts of decomposed leaf litter without distinguishable features indicative of the species of origin. One-year samples were collected similarly, but with smaller rings (0.062 m^2) having a total collection area of 0.185 m^2. Corresponding mineral soil samples were collected with a 0.1 m diameter circular coring device from the center of the sampled ring to a depth of 0.9 m, but are not discussed in this paper.

Litterbag Mass-loss Observations

Although not a part of the EBIS project, comparable data for litter mass-loss from litterbag studies were available from a number of studies on the ORR. These studies included mass loss of litter from various tree species [*Morus rubra* L., *Cercis Canadensis* L., *Quercus alba* L., *Pinus taeda* L.] from November 1960 to December 1961 (Witkamp, 1966), *A. rubrum*, *Nyssa sylvatica* L., and *Q. alba* litter from November 1970 to March 1972 (Kelly, 1973), *Liriodendron tulipifera* L. from November 1990 to November 1991 (O'Neill and Norby, 1996), and mixed-tree-species litter [*Acer rubrum* L., *Cornus florida* L., *Quercus prinus* L.] from March 1996 to October 2000 (Hanson et al., 2003b). All data were combined to generate a 'mixed-species' estimate of litter mass loss for closed-canopy, deciduous forests occupying the ORR. Temperature and rainfall data for the studies listed above were comparable, albeit not identical, to the weather during first-year of O-horizon decomposition described in this paper (Figure 2). Abundant and seasonally uniform monthly precipitation in the years studied suggested that these data were appropriate for comparison against the changing ^{14}C-signatures studied in this paper.

Environmental Monitoring

A single solar-powered, weather station with data logger was placed at each research site for the collection of hourly measurements of air temperature, relative humidity, throughfall, litter layer water content, and other environmental variables not discussed here. Air (1.5 m aboveground) and Oi-horizon temperatures were logged at all long-term reference plots starting in 2001. Air temperature and relative humidity were measured with a shielded combination sensor (Rotronic Model MP101; Huntington, New York). Oi-horizon temperatures were obtained with independent sealed thermistor probes (Stowaway Tidbit, ONSET Corporation, Bourne, MA). Continuous direct measurements of forest litter water content were based on the electrical resistance characteristics of wet versus dry litter (Hanson et al., 2003a). All environmental data was logged as hourly means or sums and stored on a data logger (CR10; Campbell Scientific, Inc., Logan, Utah).

Elemental Measurements

Subsamples of enriched and near-background litter and all O-horizon plot samples were analyzed for ^{14}C, total C, and total N. Radiocarbon values were measured on the Van de Graaff FN accelerator mass spectrometer (AMS) at the Center for Accelerator Mass Spectrometry, Lawrence Livermore National Laboratory, Livermore California. In preparation for AMS analysis, samples were combusted in evacuated, sealed tubes in the presence of CuO and Ag, then reduced onto iron powder in the presence of H_2 (Vogel et al., 1984). Splits of combusted sample were taken for ^{13}C analysis from each organic and mineral horizon, for correction of the AMS values, and all radiocarbon values are presented as $\Delta^{14}C$ (‰) according to Stuiver and Polach (1977).

Samples were analyzed for total C and N on a LECO CN-2000 (LECO Corporation, St. Joseph, Michigan) using secondary standards traceable to NIST reference materials. Soil C and N concentrations (g element g dry mass^{-1}) in combination with average measurements of forest floor dry mass (g m^{-2}) were used to calculate C and N stocks (g m^{-2}) for O-horizon layers.

Data Analysis

A two-compartment stable-isotope mixing model was used to evaluate the percent contribution of current litterfall to 9-month-old Oi-horizon litter (L%):

$$L\% = (S_1 - S_0)/(L - S_0)*100 \quad (1a)$$

$$f_1 * S_1 = f_a L + f_b S_0 \quad (1b)$$

$$f_1 = 1 = f_a + f_b \quad (1c)$$

where S_0 is the Oi-$\Delta^{14}C$ signature at time zero, S_1 is the Oi-$\Delta^{14}C$ signature after one period of decomposition (i.e., 9-months in this paper), L is the $\Delta^{14}C$ signature of added litter cohorts, and f_x is the fractional mass of the Oi-horizon or its components. For a 9-month increment of time, radioactive decay (1/8267 y) is negligible in this calculation and is ignored. The mean and 95% confidence intervals for L% were calculated according to Phillips and Gregg (2001) using their Web-accessible Excel spreadsheet program ISOERROR 1.04 (Phillips and Gregg, 2003). This model is appropriate for stable systems where two uniform materials are mixed. An eight-year record of litter inputs to the Throughfall Displacement Experiment on Walker Branch Watershed (Hanson et al., 2003c) demonstrated that inter-annual variation in above-ground litter production was low on the ORR (maximum range was 480 to 520 g m^{-2} from 1994 through 1998) suggesting that stable inter-annual litter production (and perhaps standing Oi-horizon stocks) could be assumed in the calculations.

Measurements of litterbag mass loss from the studies described above (see litterbag mass loss observations) were fitted to the following exponential relationship of litterbag mass remaining (MR_{LB}) versus time that allows for variable loss rates over time (Kelly and Beauchamp, 1987):

$$MR_{LB} = 100 \exp(-kt^{p}) + \text{error} \qquad (2)$$

where MR_{LB} is the percent mass remaining in an individual litter cohort over time, t is time in years, *k* is the mass loss coefficient, *p* is the parameter that allows the rate of mass loss to change with time, and error is the sampling error associated with measurements of mass loss. Estimates of *k* and *p* in Equation 2 were obtained from nonlinear regression of the data in Figure 3. For the ORR, values of MR_{LB} following more than 3 years of decomposition are assumed to approximate the ash content plus recalcitrant chemical matter of the original litter cohort.

Using the calculated values of L% from Equation 1a an alternate estimate of the current-year litter cohort mass remaining after the 2001 growing season can be derived from the following equation:

$$MR_{14C} = 100*(L\%*M_1)/ M_L \qquad (3)$$

where MR_{14C} is the percent mass of litter remaining estimated from isotopic data, M_1 is the mass of the Oi-horizon after one growing season and M_L is the mass of the litter-cohort originally added to the Oi-horizon at time zero. The numerator ($L\%*M_1$) is the estimated mass of the newly added litter cohort after 9-months.

One-way analysis of variance was used to test for time-zero differences in Oi-horizon mass and C/N ratio across research sites, and to test for within site differences in litter mass, $\Delta^{14}C$ signature, and C/N ratio following litter addition treatments. The litterbag mass loss function was fitted using nonlinear regression. All statistical analyses were conducted using SPSS 11.0 for Macintosh (SPSS, Inc., Chicago, Illinois).

RESULTS

Litterbag Mass-loss Studies

Historical litterbag decomposition studies on the ORR, all conducted under similar weather conditions (Figure 2), show similar rates of mass loss over time for species-mixtures and for *Acer*, *Quercus*, and *Liriodendron* species-specific studies (Figure 3). *Nyssa* foliage (a common mid-canopy tree species) exhibited higher rates of mass loss over time and was not included in the fitted relationship (Figure 3, lower graph). The Kelly and Beauchamp (1987) equation for residual litter mass with time (Equation 2) provided a significant fit to the multi-study data set ($r^2 = 0.86$) showing effective losses of 42.5, 27.5, and 23.5 % of remaining mass per year for a single litter cohort through 3 annual cycles of litter decomposition, by which time the initial litter cohort would have moved below the Oi-horizon. Notwithstanding small adjustments due to influx of fungal C and influx/leaching of nutrients, this fitted relationship suggests that ≈20% of the initial litter cohort mass is resistant to decomposition. Application of the traditional litter mass loss equation ($MR = \exp^{-kt}$; Jenny et al., 1949; Olson, 1963) would have produced an estimate of residual recalcitrant mass closer to zero after 5 years with a correspondingly reduced r^2.

Isotopic Enrichment or Dilution of the Oi-Horizon

Mean mixed-species litter quantity (454 g m^{-2}) and the litter C-to-N ratio (92.2 gC gN^{-1}) of the added 2000 litter cohort were not significantly different among sites, but initial mass of the Oi-horizon at time-zero did vary from site to site (Table 1). The west-end enriched sites (TVA and Pine Ridge) had the lowest starting Oi-horizon masses ranging from 312 to 379 g m^{-2}, Walker Branch was intermediate from 414 to 477 g m^{-2}, and Haw Ridge had the highest initial mass at 550 to 567 g m^{-2}. No significant differences in initial Oi-horizon mass were found for the designated treatment plots (i.e., litter enrichment or near-background litter additions). Site to site differences in Oi-horizon mass were no longer apparent after the first-year litter additions (Table 1). On average, Oi-horizon temperatures and leaf-litter water content did not differ among research sites or treatments, but brief periods of variable litter water content were occasionally observed in association with isolated summer precipitation events (data not shown).

As expected by the nature of the 1999 ^{14}C-pulse, the litter $\Delta^{14}C$-signatures of extant Oi-horizons at time-zero (March 2001) differed between sites but not by plots within sites (Table 2). Haw Ridge and Walker Branch, located on the east end of the ORR, had initial $\Delta^{14}C$-signatures ranging from 190 to 260 ‰; near expected average values in the North Hemisphere for 2000 (Levin and Hesshaimer, 2000; Trumbore et al., 2002). Sites on the west-end of the ORR had higher $\Delta^{14}C$-signatures, with means ranging from 515 ‰ (Pine Ridge) to 627 ‰ (TVA). The initial differences between sites were driven by wind direction and proximity of a given site to the ^{14}C-source in 1999 (Trumbore et al., 2002).

Near-background (221 ‰) and ^{14}C-enriched (1005 ‰) litter additions were made from pooled materials collected in the fall of 2000 (see methods) and their respective $\Delta^{14}C$-signatures did not differ between research sites. One growing season (8-months) after the application of near-background versus enriched litter to the forest floor, significant changes in Oi-horizon $\Delta^{14}C$-signatures were observed at all sites (Table 2). ^{14}C-enriched treatments produced significant increases in $\Delta^{14}C$-signatures on the Walker

Branch (+415 ‰), Haw Ridge (+406 ‰), and Pine Ridge (+181 ‰) sites. The magnitude of the difference was proportional to the difference between the initial conditions and enriched litter. Substantial within-site variability at the TVA site precluded detection of a significant $\Delta^{14}C$ difference between time-zero and 9 months of decomposition even though the mean $\Delta^{14}C$-signature of the enriched TVA plots was 173 ‰ greater than the time zero values. Adding near-background litter to Walker Branch and Haw Ridge plots did not produce a significant change in Oi-horizon $\Delta^{14}C$-signatures, but the same additions resulted in a significant dilution of the $\Delta^{14}C$-signature of both the TVA (-317 ‰) and Pine Ridge (-201 ‰) Oi-horizons.

The percent of the residual Oi-horizon contributed by the 2000 litter cohort (L%) was calculated only for those systems demonstrating a significant change in $\Delta^{14}C$-signatures (Table 2). Enrichment data for the Walker Branch and Haw Ridge sites yielded L% values of 55 and 50 %, respectively. Enrichment data for Pine Ridge indicated a lower value around 38%, and the dilution of Pine Ridge and TVA plots from the addition of near-background litter suggested unexpectedly high L% values of 71 and 78%.

Residual Mass: Litterbags Versus Isotopic Change

Interpolation of the fitted equation for litterbag mass change over an 8-month period (May 2001 to January 2002) indicated that the expected mass remaining (MR_{LB}) from the previous year's cohort of litter would have been 65.4 % plus or minus a rather narrow confidence interval (Figures 3 and 4). Applying the significant L% values from Table 2 to the mass-dependent calculations of Equation 3, the isotopic enrichment approach yielded MR_{14C} values ranging from 45 to 59%, and the isotopic dilution value for the Pine Ridge site gave an MR_{14C} of 63%. The calculated MR_{14C} value for the dilution treatment at the TVA site yielded an unrealistic estimate of 105%. All estimate of MR_{14C} were found to have substantial variation driven by spatial variability in Oi-horizon mass (Table 1) and $\Delta^{14}C$ measurements (Table 2).

DISCUSSION

Mean mass-loss estimates derived from past ORR litterbag studies provided a solid baseline from which to compare isotopically derived measurements of litter decomposition. The *k* value of 0.55 for the combined data set projects a first-year mass loss of 42.5% which is within the range of similar values for deciduous hardwood forests (Hanson et al., 2003a). Gartner and Cardon (2004) reported that decomposition rates of mixed-species litter is often not scaleable from single-species experiments and reported that litter mixtures can produce ~20% greater rates of mass loss than observed in single species studies. The ORR data for *Acer* and *Liriodendron* litter in Figure 3, however, coincide nicely with the *Quercus* and mixed-litter data sets for mass-loss on the ORR.

One-year mass loss from the combined time-zero Oi-layer plus new litter additions ranged from 45 to 48 percent for the Walker Branch and Haw Ridge (Table 1) consistent with anticipated first-year mass loss from litterbags previously discussed. No statistically significant changes in mid-winter (i.e., January) dry mass of the Oi-horizon were observed for Walker Branch and Haw Ridge (Table 1) suggesting that the litter turnover rates were balanced by the 500 g m^{-2} experimental litter additions. Conversely, the Oi-horizon mass of the TVA and Pine Ridge sites showed significant accumulation between time zero and the January 2002 sampling (*P*-values of 0.01 and 0.07, respectively), and a correspondingly lower mean mass losses between 29 and 42% during 2001. Litter C-to-N ratios, an important variable associated with the rate of decomposition (Flanagan and Van Cleve, 1983; McClaugherty et al., 1985) were unchanged over time for Walker Branch and Haw Ridge sites, but were significantly greater for TVA and Pine Ridge sites (*P*-values of <0.001 and 0.035, respectively) confirming the accumulation of litter mass at the latter sites.

Because isotopic methods allow litter mass-loss to proceed normally without experimental artifacts, we might have expected the MR_{14C} values to be lower than the values for litterbags. Litterbags are known to limit faunal facilitated comminution and fragmentation of organic debris, and may modify environmental conditions driving microbial decomposition (Anderson, 1973; De Santo et al., 1993; Gartner and Cardon, 2004). Observed MR_{14C} values were lower for four of five estimates (Figure 4), but the substantial variability around all estimates of MR_{14C} suggests the need to consider potential sources of error involved in the measurement and calculation of MR_{14C}.

Sources of Error

Observed variation in Oi-horizon mass is not consistent with the assumptions of the stable isotopic mixing model (Equation 1a). Changing mass of the Oi-horizon from time-zero to January 2002 at both Pine Ridge and TVA is partly responsible for the disproportionate decrease and increases in L% for the enriched and near-background litter addition treatments, respectively, at those sites. Random variation in thickness of the Oi-horizon within sampling plots also contributes to variability in the interpretation of the isotopic data. Furthermore, because the manual separation of the Oi- from the Oe/Oahorizons is rather subjective (Federer, 1982), errors associated with the collection of the Oi-layer are compounded. These particular sources of error seem to have been minimal in the near-ambient Walker Branch and Haw Ridge plots (Table 1; SE ranging from 33 to 51 g m^{-2}), but greater in the west-end TVA and Pine Ridge plots (Table 1; SE ranging from 34 to 114 g m^{-2}). Interannual variation in weather conditions may have also contributed to inconsistent Oi-horizon mass, but the uniformity of temperature and moisture at all four research sites suggests that this was not the cause of differences between eastern and western sites on the ORR.

Dilution of isotopic signals from unmeasured C inputs having variable $\Delta^{14}C$-signatures is another potential confounding influence. Leake et al. (2001) reported significant changes in isotopic signatures for *Pinus sylvestris* litter from its exploitation by ectomycorrhizal fungal mycelium. Inputs of reproductive tissues (e.g., bracts, flowers, seeds), especially from *Acer* and *Liriodendron* species, were not quantified and would also result in the addition of near-background ^{14}C-signatures onto the 1999-enriched TVA and Pine Ridge plots.

Finally, unequal losses of ^{14}C-signatures from leaching, litter comminution, and decomposition processes represents yet another possible way for the assumptions of the two-compartment mixing model to be compromised. Anderson (1973) suggested that as much as 30% of the organic mass of a fresh litter cohort was soluble material with the potential to leach from litter and percolate out of the Oi-horizon. Experiments on additional samples of archived 2000 litter are underway to evaluate the importance of this source of error.

Evaluating Complex Mixtures

While it is not possible to derive explicit solutions for equations with multiple unknowns, data from multiple sources can be used to bracket the range of possible isotopic signatures and cohort masses in an attempt to explain the very high L% and MR_{14C} for the TVA site. Because the Oi-horizon sampled after an annual cycle is likely to contain layered-litter from at least 2 annual cohorts, a three-compartment model can also be considered:

$$f_1 S_1 = f_a L + f_b S_0 + f_c S_{-1} \quad (4a)$$

$$f_1 = 1 = f_a + f_b + f_c \quad (4b)$$

where S_{-1} is the $\Delta^{14}C$-signature of residual C from a litter cohort laid down approximately one year before time-zero. The 3-compartment mass balance equation can then be obtained by substituting litter cohort mass values for the mass fractions (f_x) of Equation 4a and the conversion of $\Delta^{14}C$-signature data to appropriate 'relative concentrations' ($[^{14}C] = \Delta^{14}C/1000+1$):

$$MR_1*[^{14}C_1] = M_L*[^{14}C_L] + M_0*[^{14}C_0] + M_{-1}*[^{14}C_{-1}] - D_L*[^{14}C_L] + D_0*[^{14}C_0] + D_{-1}*[^{14}C_{-1}] \quad (5)$$

where MR_1 and $[^{14}C_1]$ are, respectively the Oi-horizon mass and $[^{14}C]$ remaining after 9 months, and M_x and $[^{14}C_x]$ are the initial mass and $[^{14}C]$ contributions of the 2000 litter (x = L) and previous litter cohorts (x = 0 or –1). D_x is the annual decomposition from the respective cohorts (x = L, 0, -1). Carbon lost from the Oi-horizon is based on mass loss estimates, and does not necessarily represent the differential losses associated with comminution and leaching processes.

Equation 5 can be rearranged with assumptions about time-dependent cohort masses derived from litterbag mass-loss information in Figure 3 to yield unique solutions that can be contrasted with the ^{14}C-signatures of measured litter and Oi-horizon mass and $\Delta^{14}C$. Figure 5 is a diagrammatic representation of this approach showing approximations of mass loss estimates and multiple cohort contributions for examples of Oi-horizon ^{14}C enrichment and dilution cases: Walker Branch and TVA. We assume that litter cohorts prior to 1999 had nearly uniform ^{14}C-signatures consistent with small changes observed for the northern hemisphere (Levin and Hessshaimer, 2000).

In a stable natural system (approximated by Walker Branch and Haw Ridge) pre-treatment litter cohorts making up the layers of the Oi-horizon were assumed to have similar $\Delta^{14}C$-signatures (≈245 ‰). Given this assumption, we see that the application of litterbag decomposition assumptions for one season to the data allows Oi-horizon $\Delta^{14}C$ estimates to range from 617 to 696 ‰ overlapping the measured value of 660 ‰ (Figure 5a). For the divergent case of the TVA Oi-horizon diluted by near-background litter (Figure 5b), we need to consider that the original 1999-^{14}C pulse may have incorporated a disproportionately enriched 1999 litter cohort (≈674 ‰) into the Oi-horizon. Including this assumption in the 3-compartment model allows us to evaluate the Oi-horizon remaining after one season of decomposition to be a variable combination of ^{14}C-signatures associated with independent litter cohorts. Unfortunately, the results (397 to 406 ‰) still show limited agreement with the measured Oi-horizon data (308 ‰) after one season of decomposition, suggesting the need to include explicit measurements and parameterization of $\Delta^{14}C$-signatures and C losses associated with faunal comminution and leaching processes in our mass balance calculations. Such work is underway.

Conclusions

This study successfully used mixed-species oak-forest litter enriched with ^{14}C to evaluate turnover rates of litter within the Oi-horizon, an approach that avoids potential artifacts associated with litter containment systems (e.g., litterbags). Normal quantities of leaf litter were applied to large replicated field plots. On average, measured annual changes in the ^{14}C-signature of the Oi-horizon of an upland-oak forest produced calculated estimates of litter mass remaining after one season that were lower than expected based on traditional litter bag studies. The difference between the two approaches was consistent with the exclusion of soil macro-fauna by litterbags.

Even though isotopic enrichment or dilution techniques offer the advantage of being a non-invasive method, a high degree of variability for some sites undermined its utility as a substitute for litterbag mass loss methods. However, the ^{14}C approach measures the residence time of C in the leaf litter, rather than the time it takes for leaves to disappear; hence radiocarbon measures are subject to C immobilization and recycling in the microbial pool, and do not necessarily reflect results from litterbag mass loss. The use of cohort-based ^{14}C-signatures for tracking C movement and cycling beyond the litter layer is also an important additional consideration justifying the application of isotopic approaches.

While the two-compartment isotopic mixing model does appear appropriate for systems with stable ^{14}C inputs, it was insufficiently robust for uniform application within the experiment. A more detailed model, as exemplified by the analysis of Figure 5, is needed to adequately capture the complex processes involved in litter mass-loss and to handle interannual differences in the isotopic signature of litter cohort additions. Future analyses of additional data from the EBIS project will attempt to reconcile the patterns of ^{14}C movement throughout the experimentally manipulated Ultisol and Inceptisol soils using sophisticated, cohort-based models of the organic horizons (e.g., Berg and Matzner, 1997; Berg, 2000).

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Table 1. Mean dry mass (±SE) and the corresponding C-to-N ratio (C/N ±SE) of the Oi-horizon at time zero, 2000 litter cohort addition, and the Oi-horizon one season after litter additions by research site and litter addition type.

Research sites	Litter-addition Type	Dry Mass			C/N Ratio		
		Oi-Layer Time-zero	Litter additions	Oi-Layer +9 Months	Oi-Layer Time-zero	Added-Litter	Oi-Layer +9 Months
		--------------g m^{-2}------------					
Near-background Sites							
Walker Branch	^{14}C-Enriched	414±52ab†	449±3	445±33a	36.0±1.1a	88.0±2.9	38.7±0.6a
Walker Branch	Background	477±68ab	431±16	494±51a	36.1±1.7a	88.0±2.9	37.1±1.3a
Haw Ridge	^{14}C-Enriched	567±87b	486±5	579±48a	39.7±0.5b	93.9±2.0	43.4±1.5b
Haw Ridge	Background	550±94b	476±4	536±36a	41.4±1.5b	93.9±2.0	40.3±1.7b
Enriched Sites							
TVA	^{14}C-Enriched	340±40a	431±7	489±89a	37.6±1.0a	90.8±1.3	41.1±0.7ab

TVA	Background	312±26a	442±3	593±114a	36.9±0.5a	90.8±1.3	40.1±0.6ab
Pine Ridge	^{14}C-Enriched	336±39a	458±1	542±91a	36.4±1.2a	98.8±5.5	39.5±1.4a
Pine Ridge	Background	379±40a	457±1	403±39a	34.0±1.7a	98.8±5.5	38.2±2.0a

†Different letters within a column represent significant (*P*<0.05) differences among research sites evaluated with post-hoc Duncan's test when the main effects for research site and/or treatment were significant. Litter-addition treatment had no significant effect on dry mass or C/N ratios for any research site.

Table 2. Litter $\Delta^{14}C$-signature (±SE) of the Oi-litter at time-zero, the 2001 enriched or background litter cohorts, and the Oi-litter 9 months after the addition of either enriched or near-background litter treatments. Also shown are the probabilities (*P*) for a test of significant changes in $\Delta^{14}C$-signature between sampling periods by treatment, and (if significant) the calculated percent contribution of litter additions onto background (Walker Branch and Haw Ridge) or recently enriched (Pine Ridge and TVA) research sites, respectively. NC = no calculation executed (see text).

Research site	Litter Treatment	$\Delta^{14}C$-signature			Treatment Main-effect		Fraction of $\Delta^{14}C$ from 2000 Litter
		Oi-horizon Time-zero	Litter Additions	Oi-horizon +9 Months	F	*P*	
		----------------(‰)---------------					---------%-------
Near-background sites							
Walker Branch	Enriched	245±15b†	1005±19‡	660±19a§	268.0	<0.001	54.6±7.8
Walker Branch	Background	260±23b	221±2	219±11b	3.1	0.137	NC
Haw Ridge	Enriched	195±7a	1005±19	601±62a	306.7	0.003	50.1±24.6

Haw Ridge	Background	190±4a	221±2	194±8b	0.2	0.717	NC
Enriched sites							
TVA	Enriched	629±25d	1005±19	802±79a	2.1	0.221	NC
TVA	Background	625±18d	221±2	308±20b	140.3	<0.001	78.4±16
Pine Ridge	Enriched	528±7c	1005±19	709±19a	27.8	0.003	37.9±13.5
Pine Ridge	Background	503±38c	221±2	302±17b	22.9	0.003	71.3±18

†Means in the same column sharing the same alphabetic postscript are not significantly different (post hoc Duncan's test; $p < 0.05$).

‡Litter addition treatments were significantly different ($P<0.001$).

§Litter additions produced statistically significant changes in treatment plots within sites ($P<0.01$).

Reconciling Change in Oi-Horizon ^{14}C With Mass-Loss for an Oak Forest

List of Figure

Figure 5. Diagram of the hypothetical path of ^{14}C-isotopes through a well-mixed Oi-horizon with stable ^{14}C-signatures (Walker Branch site), and through a manipulated Oi-horizon having distinct $\Delta^{14}C$ signatures in all measurable litter cohorts (TVA site). Values contained within bold boxes are measured data from Tables 1 and 2. All other data are estimates of cohort-specific components of the time-zero and 9-month litter Oi-horizons. Mass estimates (g dry matter m^{-2}) and decomposition losses (g dry matter m^{-2} y^{-1}) were derived from the fitted litterbag relationship in Figure 3.

Reconciling Change in Oi-Horizon ^{14}C With Mass-Loss for an Oak Forest

Figure 1:

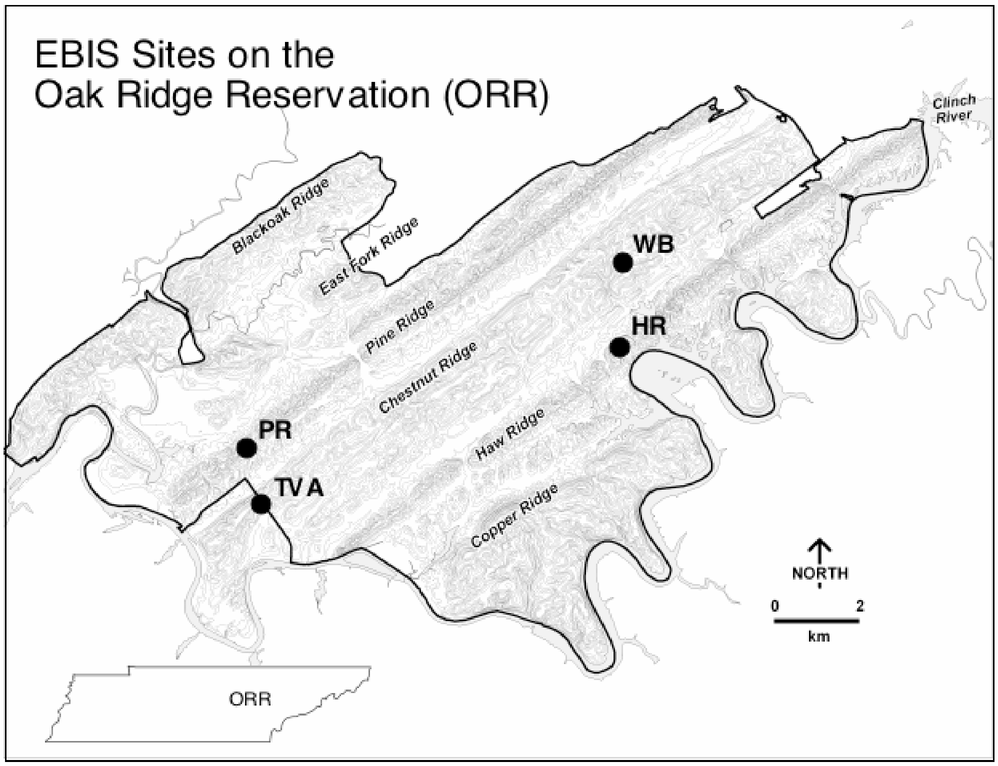
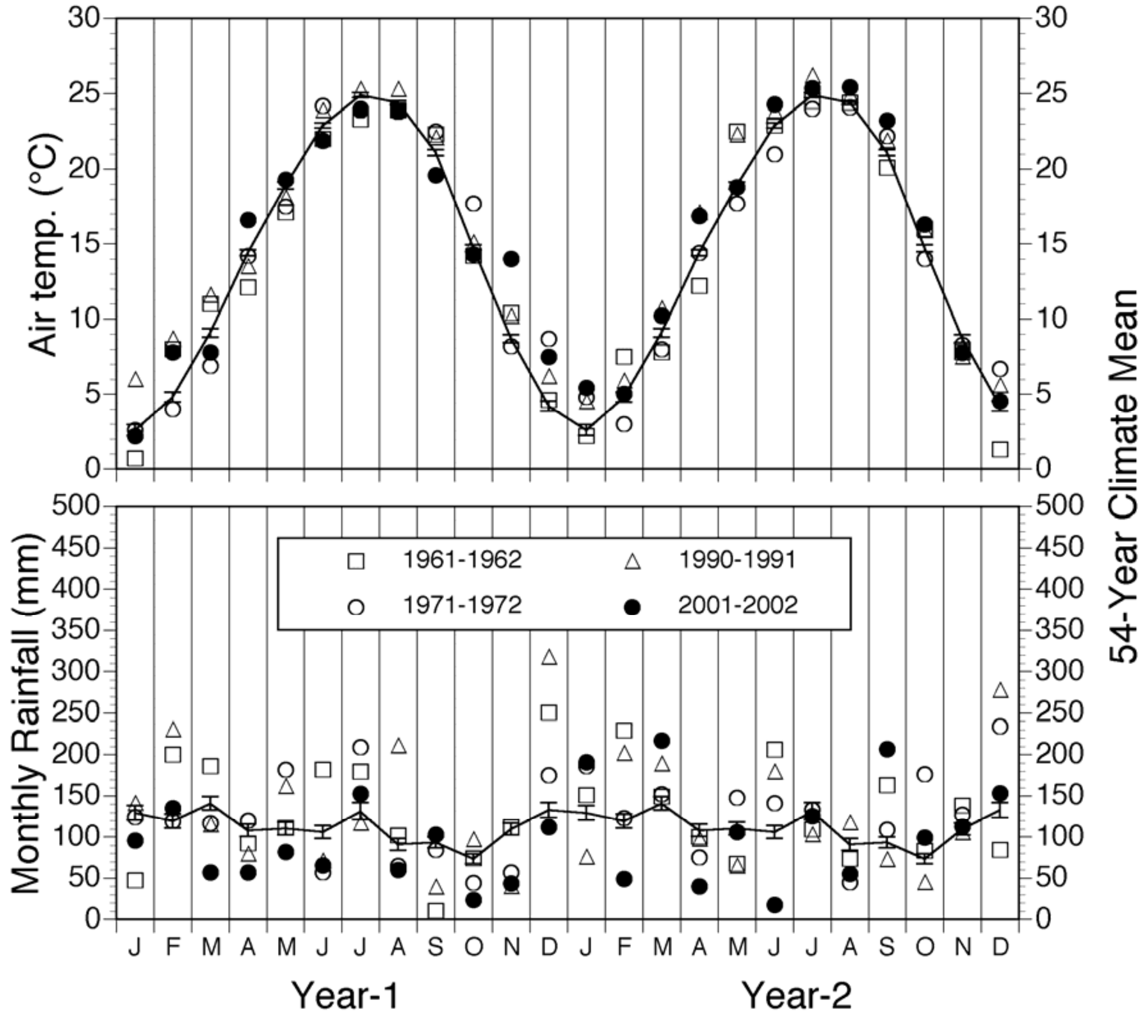


Figure 2:


Air temp. (°C)
Monthly Rainfall (mm)
54-Year Climate Mean
1961-1962
1990-1991
1971-1972
2001-2002
J F M A M J J A S O N D J F M A M J J A S O N D
Year-1
Year-2

Reconciling Change in Oi-Horizon ^{14}C With Mass-Loss for an Oak Forest

Figure 3:

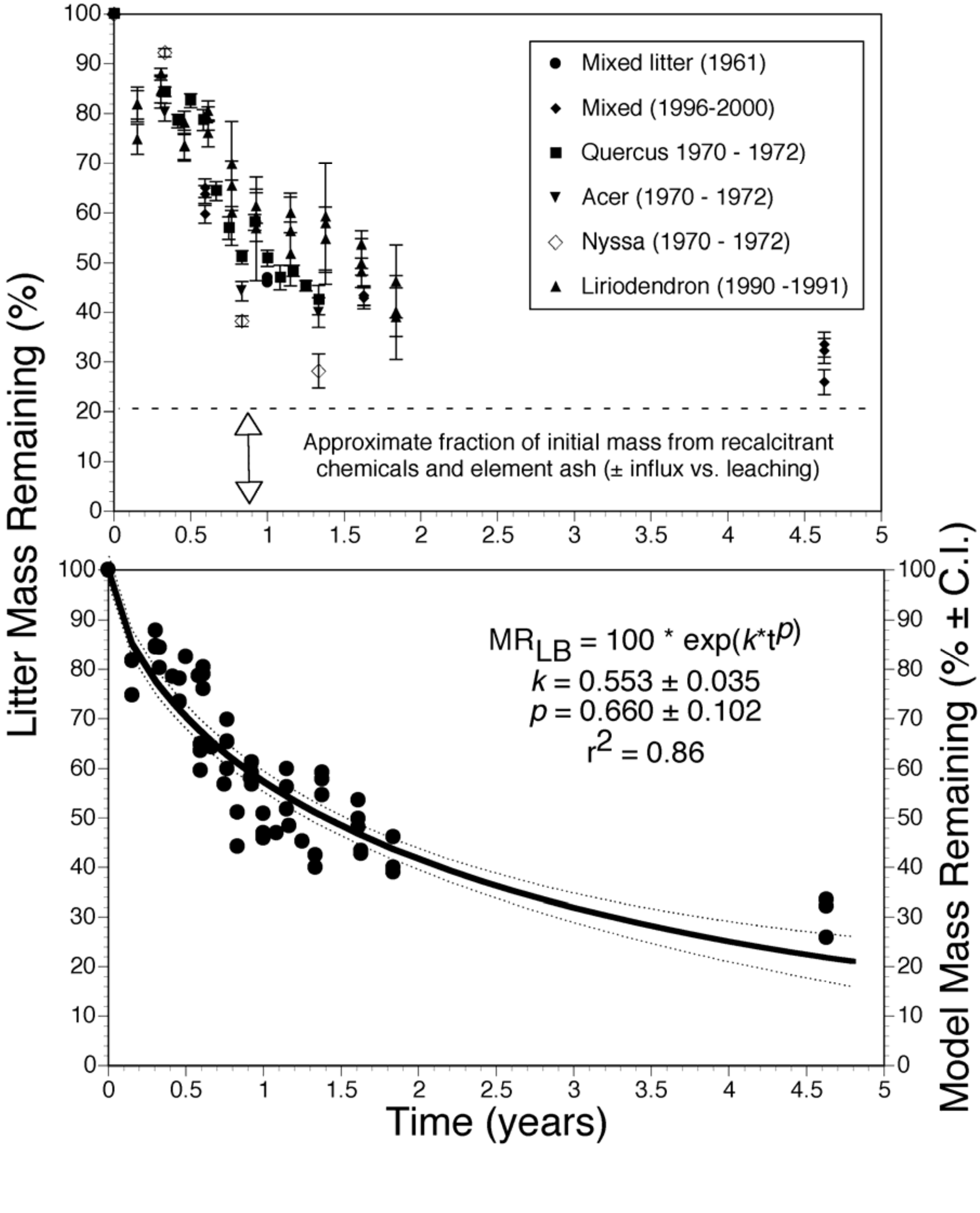
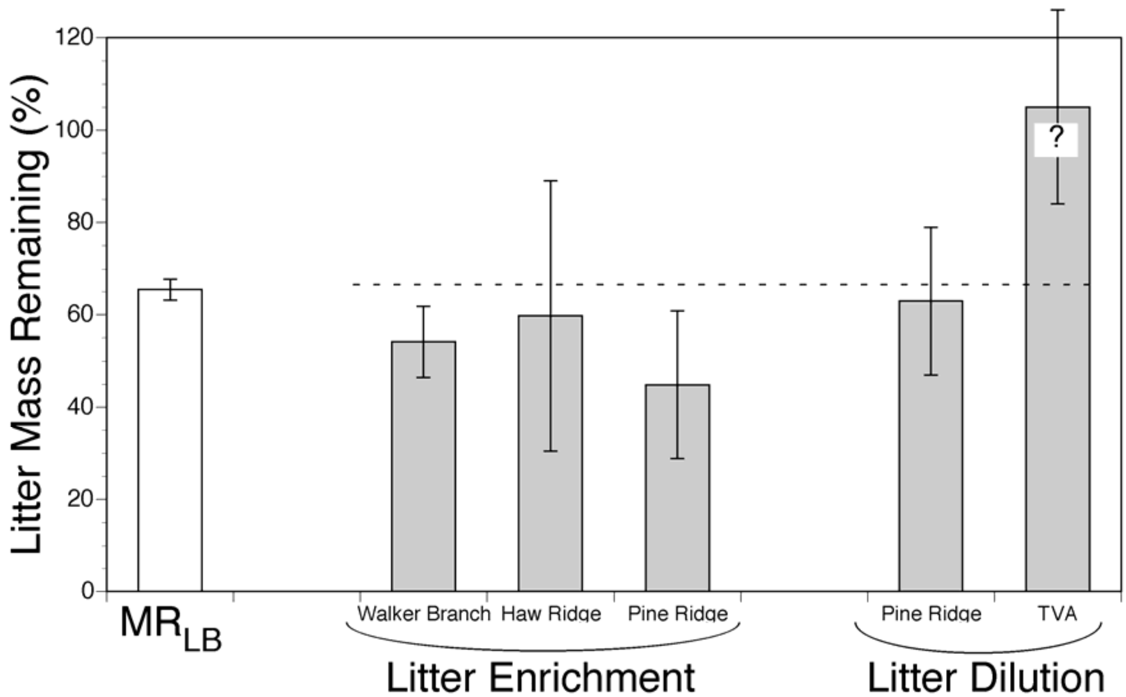


Figure 4:


Litter Mass Remaining (%)
0
20
40
60
80
100
120
?
MR$_{LB}$
Walker Branch
Haw Ridge
Pine Ridge
Pine Ridge
TVA
Litter Enrichment
Litter Dilution

Reconciling Change in Oi-Horizon ^{14}C With Mass-Loss for an Oak Forest

Figure 5: