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Relationships between carbon turnover and bioavailable energy fluxes in two temperate forest soils

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Abstract

Recent research has shown that the broad empirical relationships used in many ecosystem models to predict carbon turnover and stabilization in soils can fail to capture differences across vegetation types or climates. Theoretically, because energy flow is fundamental to the function of decomposer organisms and ecosystems, energetics could provide complimentary fundamental constraints on soil C dynamics. Often, however, C is considered as a surrogate for energy in studies of detrital decay and C turnover in soil. Bomb calorimetry has long been used to measure stored energy in organic matter, but in detritus not all of the energy is bioavailable. Here I outline an approach to quantify the flux of bioavailable energy dissipated by resident heterotrophic communities in soil organic horizons *in situ*. I used the principle of energy balance together with a biogeochemical process model parameterized through calorimetric analysis of field samples. I also tested relationships between C and energy across samples of forest detritus (foliar and fine root litter, well-decayed Oea material, and woody debris), across decay stages, and between a deciduous and coniferous forest at the Harvard Forest, MA, USA. As a first approximation, energy and C concentrations were closely related (within ca. 10%), as were ratios of heterotrophic energy dissipation to C mineralization across types of detritus (within 16%). Differences in energy content and energy : C ratios were measurable in forest detritus (particularly woody vs nonwoody), but did not vary reliably enough between forest types or through detrital stages to indicate that soil C models could be improved by including energetics. Model results indicated that there are strong similarities in energy flows and storage in the O horizons of the contrasting forest types studied at this location. Future research could focus on broader patterns across climates or biomes.

Keywords: carbon cycling, coarse woody debris, decomposition, energetics, litter quality, soil ecology

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Introduction

Developing a predictive understanding of the turnover and stabilization of carbon in soils is a key goal for global change research. The turnover and stabilization of soil C exert both direct and indirect controls (through effects on nutrient cycling and soil water holding capacity) on ecosystem-level C balances. Ecosystem models typically employ broad empirical relationships among climate and litter quality as controlling factors of decay (Moorhead *et al*., 1999; Cramer *et al*., 2001), together with broadly averaged parameters controlling stabilization of litter fractions as soil organic matter. Models require generalized relationships. However, recent research has shown that many typical model relationships and parameters, as currently generalized, can fail to capture differences in rates of litter decay and stabilization across regions or across novel combinations of vegetation floristics, litter types and climates (Moorhead *et al*., 1999; Berg, 2000; Gholz *et al*., 2000).

Because energy flow is fundamental to the function of organisms and ecosystems, the question arises whether the incorporation of energetics into models of detrital decay could provide complimentary fundamental constraints and thus improve our predictive understanding

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(Reiners, 1986). Soil heterotrophs oxidize C compounds in plant litter to acquire the energy needed to drive life processes. The energy stored in detritus can be measured directly through bomb calorimetry: chemical energy is converted to heat during rapid oxidation in O_2 and one measures the gross production of heat. Calorimetry has a long history of use in ecology, including previous applications to the study of detritus and nutrient turnover in soils (Golley, 1961; Reiners & Reiners, 1970; Weigert *et al*., 1970). Today, however, the commonplace approach to study energetics in soil litter and organic matter (OM) is to measure quantities or characteristics of C and to assume that these correspond to energy. For example, measures of microbial C-use efficiency, litter C quality, and CO_2 mineralization have all been described as assessing the bioavailability of energy to soil microorganisms (Smith *et al*., 1986; Yarie & Van Cleve, 1996). The conceptual substitution of C for energy is so widespread that it is typically assumed and unstated. Yet different C bonds store different amounts of energy, and energy is also stored in other forms (such as NH_4^+, which is oxidized by soil nitrifiers to provide metabolic energy). Furthermore, energy has thermophysical properties, distinct from those of C, that link to biological processes (Morowitz, 1968). For example, portions of biologically stored energy are converted to sensible and latent heat during respiration and decomposition.

Bomb calorimetry alone, unfortunately, cannot determine the proportion of stored energy that is bioavailable. This has been widely and correctly viewed as a limitation of bomb calorimetry. Energy stored in lignin, for example, is bioavailable to soil heterotrophs not to the extent that lignin can be combusted in O_2, but to the extent that the heterotrophic community can catabolize the substrate using lignolytic enzymes. Here I outline a simple approach to quantify the flux of bioavailable energy dissipated by resident heterotrophic communities in soil organic horizons *in situ*. The approach uses a biogeochemical process model to calculate energy flows by difference based on the principle of energy balance. Model calculations are parameterized with the energy contents of different components of soil organic horizons as determined through bomb calorimetry.

Bosatta & Ågren (1999) derived a general theory of litter quality that used energy content as an organizing principle and that was proposed as a key link between theoretical and experimental studies of litter decomposition and nutrient dynamics (Ågren & Bosatta, 1996). The incorporation of energy and carbon relationships in a biogeochemical decomposition model aimed at quantifying fluxes of bioavailable energy could help to explore such a link and to assess whether this approach is likely to provide insights into the ecology of decomposition.

Objectives

By structuring and parameterizing a decomposition model to include both C and energy fluxes explicitly, I sought to examine relationships between the rate of energy dissipation and the rates of C turnover and storage. An additional objective was to complete a field study that could serve both to parameterize the model and to examine relationships between energy and C content across types of plant litter (foliar, fine root, and woody litter) in a coniferous vs a deciduous forest. Previous studies of energy content of plant material showed little regular variation among seasons or across environmental gradients, although some differences were observed among plant tissues and among species (Reiners & Reiners, 1970; Hickman & Pitelka, 1975; Pitelka, 1978; Reiners, 1988). Another goal of the field study was to examine relationships between C and energy in sequences of decay stages. My null hypothesis was that C would function as a surrogate for energy as usually assumed: energy content would be closely related to C concentrations across litter types and stages of decay. My alternative hypotheses were that energy : C ratios would vary among forest types, litter types, or stages of decay.

I focused on the forest floor (O horizon), the layer of fine litter, woody debris, and humified matter that accumulates atop the mineral soil in temperate forests. The relatively low mineral (ash) content of the O horizon makes the technical aspects and interpretation of bomb calorimetry more straightforward; in addition, litter types, and decay stages can be recognized relatively well in the O horizon. In the forests I studied here it is also the soil component where most litter inputs occur and where the bulk of litter decomposition takes place.

I worked in a coniferous and a deciduous forest at the same location, thus controlling for soil type and climate. I expected to find differences in the relationships between modeled rates of C turnover and bioavailable energy dissipation in the O horizons of the contrasting forests.

Materials and methods

Site description

This study took place in two forest stands at the Harvard Forest in central Massachusetts, USA. The first is an even-aged red pine (*Pinus resinosa* Ait.) stand planted in 1926 on land previously in agriculture (Foster, 1992). There is no woody debris predating the present stand; the decaying wood derives from the self-thinning phase of the present stand and is almost exclusively *P. resinosa* (Currie & Nadelhoffer, 2002). The second forest is a predominantly oak (*Quercus velutina* Lam., *Q rubra* L., *Betula lenta* L., *Acer rubrum* L.) stand that naturally regenerated

after selective logging that took place from 1885 to 1900 (Foster, 1992). The oak forest was heavily damaged by catastrophic windthrow during a hurricane in 1938 (Motzkin *et al*., 1999), producing some of the older pieces of coarse woody debris (CWD) present today (Currie & Nadelhoffer, 2002). Soils in both stands are coarse loamy (in the oak stand, coarse loamy over sandy skeletal), mixed, frigid Typic Dystrochrepts. Soils are well drained and contain well-defined O horizons (mor type). Elevations in these forest stands are ~400 m; monthly mean temperatures are −7 °C in January and 19 °C in July. Precipitation averages 110 cm yr^{-1}, distributed fairly evenly throughout the year (Van Cleve & Martin, 1991).

Sample collection and laboratory analysis

Samples were collected in the vicinities of six 100 m transects and from four permanent, $30 \times 30\ m^2$ experimental plots. The permanent plots are part of the Chronic N study, a continuing study of nitrogen (N) amendments under way since 1988 (Aber *et al*., 1993; Magill *et al*., 1997). In each forest type, the three transects were located randomly, orientated 120° relative to one another and within approximately a 1 ha area surrounding the set of experimental plots.

Woody debris Along each transect, fine and CWD were sampled, together with sloughed bark. Fine woody debris (FWD, < 10 cm diameter) was separated into four size classes based on diameter: 0.5 to < 1.0 cm, 1.0 to < 2.5 cm, 2.5 to < 5.0 cm, and 5.0 to < 10.0 cm. Coarse woody debris was separated into three size classes: 10.0 to < 25.0 cm diameter, 25.0 to < 50 cm, and 50 cm or greater. Woody debris was further sorted into decay classes, with an increasing number of decay classes for larger size classes (Polit & Brown, 1996). In the largest two size classes of FWD, we distinguished three categories: sound, intermediate, and rotten. CWD was sorted into the five decay classes commonly used (Sollins, 1982; McCarthy & Bailey, 1994; Krankina & Harmon, 1995), from sound wood (decay class 1) to the most advanced stage of decay (class 5). Stage of decay was determined by the presence of bark and branches, the degree of sapwood degradation, soundness of the heartwood, and the presence of moss and fungi. In addition to the collections of all size classes along transects, collections of the finer size classes of FWD (those < 5.0 cm) were collected from the experimental plots of the Chronic N Study. FWD was collected in nested $2.5 \times 2.5\ m^2$ and $1 \times 1\ m^2$ quadrats established randomly in ambient plots (no N amendments) and low-N addition plots (receiving ambient + 5 g N m^{-2} yr^{-1} as NH_4NO_3). The same size and decay classes were used in the quadrat and transect sampling. Testing the effects of N amendment was not an objective; these samples simply allowed me to include a larger number of FWD samples. I tested for confounding effects of N treatment.

Fine litter and humus In the vicinities of the three 100 m transects in each forest type, I collected fresh foliar litter and slabs of forest floor material. Near each transect, I randomly located four sampling points (12 in each forest type). I collected a sample of freshly fallen foliar litter at each point (exclusively red pine litter in the red pine forest and oak spp. litter in the oak forest). I sampled in early October 1999, when freshly fallen litter was easily distinguished from the one year old litter beneath. I then collected a slab of forest floor material ($10 \times 10\ cm^2$), including Oi, Oe and Oa horizons, at each point. I carried samples on ice in the field and shipped them on ice overnight to the Appalachian Laboratory in Frostburg, MD, USA.

Sample preparation Samples of fresh litter and woody debris were dried at 70 °C; forest floor slabs were refrigerated (4 °C) for up to 10 days during sorting, then dried at 70 °C. Detritus from forest floor slabs was sorted into four categories: foliar litter that was one year old, foliar litter that was two or more year old, fine roots, and well-decayed Oea material. The latter category refers to commingled material unidentifiable as to source; recognizable foliar, fine root, or woody detritus was carefully removed with tweezers, as were visible and easily removable soil fauna and fungal hyphae. During sorting, only red pine litter was kept for the pine forest, while only oak spp. litter was kept for samples from the oak forest. For the oak forest, categories of one year and two or more year old foliar litter were composited because of difficulty in accumulating older litter fragments that could be positively identified as oak spp. Fine roots (< 2 mm) were not identified to species, and included root litter together with roots alive at the time of collection. Fine roots were rinsed gently with deionized water (DIW) to remove mineral grains before drying at 70 °C. All samples were composited by paired, adjacent sampling points, leaving six composites in each forest for each sample category. Samples were ground in a Wiley mill, re-dried at 70 °C and refrigerated until analysis; before analysis, all samples were dried at 70 °C a third time, and cooled in an evacuated desiccator.

Laboratory analyses Concentrations of C and N were determined through dry combustion followed by gas chromatographic analysis on a Carlo-Erba NA 2100. Analytical sample sizes of 10 mg were weighed to the microgram. Calorimetry was performed on analytical samples of 0.3–0.6 g using an isoperibol bomb calorimeter (Parr Instrument Co. Moline, Illinois, USA). Benzoic acid

standards tested as unknowns were recovered within 0.1% of the standard value. For nonwoody detritus, all caloric determinations were made in duplicate or until duplicate values were obtained that measured within $< 1.5\%$ of each other. For woody detritus, 17% of samples were chosen at random for duplicate analyses. Duplicate means were used in subsequent calculations. Corrections were made for combustion of fuse wire. Ash concentrations were measured by combustion at 500 °C for 4 h in a muffle furnace (Paine, 1971). Corrections for oven-dry weight (105 °C) and ash content were determined on each sample and were applied to %C and caloric results. The caloric unit used here is the kilocalorie (kcal), equal to 10^3 gram calories. (1 kcal = 4.184 kJ). Results are expressed as ash-free caloric value (kcal g^{-1}), also referred to here as energy content. Caloric value was also divided by C concentration (both ash-free) to be expressed as the ratio of energy : C (kcal g^{-1} C).

Statistics Results were tested for normality, and log transformations were made where necessary to obtain normal distributions. Effects of forest type and detrital category were tested using analysis of variance (ANOVA), followed by pairwise *t*-tests for significant differences among individual means ($P < 0.05$) in cases where ANOVA indicated differences existed.

Model description and application

I developed a modeling approach based on the principles of mass and energy balance to calculate, by difference, the energy dissipated through heterotrophic activity in the soil O horizons. Briefly, given the biomass of litter entering a detrital pool together with its caloric value, and given the fractional mass stabilized in well-decayed material together with its caloric value, then by difference I was able to calculate the amount of energy dissipated during the process of litter decomposition *in situ*. I used the Tracer Redistributions Among Compartments in Ecosystems model (TRACE), an ecosystem model previously applied to study C and N cycling, together with ^{15}N redistributions, in the two forest stands considered here (Currie *et al*., 1999; Currie & Nadelhoffer, 1999). TRACE combines the vegetation processes of PnET-CN (Aber *et al*., 1997), with a more complex model of soil processes, including separation of pools and processes in forest floors from those in mineral soils. PnET-CN embodies a plant-internal source-sink model for C that includes photosynthesis, allocation, growth and respiration in foliage, wood, and fine root tissues, previously parameterized for the present forests.

Modeled rates of tissue production and turnover derive from previous field and modeling work at these sites (Aber & Federer, 1992; Aber *et al*., 1993; Aber *et al*., 1997; Magill *et al*., 1997; Currie *et al*., 1999). Comparison of selected model pools and fluxes of OM against field data show reasonable agreement (Table 1). Rates of production of woody litter are altered from previous uses of TRACE at this site, because field measures of pool sizes of downed woody debris at this site are newly available (Table 1). Rates of woody litter production were calibrated, given the decay rates of wood in the model, and given the well-known histories of forest growth and disturbance (Foster, 1992; Motzkin *et al*., 1999; Currie & Nadelhoffer, 2002), to produce present-day pool sizes of downed woody debris in appropriate size classes. To compare modeled fluxes of fine root production against field measurements, I used values derived from a

Table 1 Comparisons between selected simulated and field-measured pools and fluxes of organic matter

	Pine forest		Oak forest	
	TRACE model	Field data*	TRACE model	Field data*
(A) Throughfall DOM (g OM m^{-2} yr^{-1})	28	28	23	23
(B) Foliar litter inputs (g OM m^{-2} yr^{-1})	335	320	278	290
(C) DOM leaching losses† (g OM m^{-2} yr^{-1})	78	80	45	45
(D) Forest floor mass‡ (g OM m^{-2})	5190	5480	4920	5250
(E) Downed woody debris (g OM m^{-2})	3850	3960	2600	2660
(F) Fine root production (g OM m^{-2} yr^{-1})	299	254 ± 120	245	231 ± 120

DOM = dissolved organic matter; OM = organic matter mass (ash free).

*Sources and dates of measurement: (A) and (C), Currie *et al*. (1996), for 1994; DOM fluxes are approximated as two times fluxes of dissolved organic C; (B) Magill *et al*. (1997), averages 1989–1993; (D) Magill *et al*. (1997), for 1992; (E) Currie & Nadelhoffer (2002), for 1999 (after ash correction); (F) mean values with 95% confidence intervals from a regression meta-analysis against foliar litter production in forests based on a N-budget technique (Fig. 1(D) in Nadelhoffer & Raich, 1992).

†Vertical fluxes of DOM leaving the Oa horizon of the forest floor.

‡Excluding fine and coarse woody debris in both field data and model results shown on line (D).

meta-analysis regression against foliar litterfall across a range of forests (Nadelhoffer & Raich, 1992), together with foliar litterfall flux measured at the site (Table 1). Below, I provide a brief description of forest floor decomposition processes in TRACE and model augmentations made to incorporate energetics.

Decomposition processes in TRACE Decomposition of foliar and fine root litter follows two phases in the model: short-term decay of fresh litter with stabilization of decomposition intermediates (henceforth 'phase I'), followed by the much slower process ('phase II') of humus turnover (Berg, 1986; Melillo *et al*., 1989; Aber *et al*., 1990; Nadelhoffer *et al*., 1995; Coleman & Crossley, 1996; Gholz *et al*., 2000). In TRACE, mass is lost in phase I through C mineralization and leaching until 20% of the original litter mass remains. The rate of decay in this phase is determined by climate (as represented by actual evapotranspiration) and litter quality (Meentemeyer, 1978; Berg *et al*., 1993). Litter quality controls decay rates through the mixture of operationally defined classes of carbon known as proximate C fractions (henceforth 'C classes'), representing extractives, acid-soluble, and acid-insoluble material (McClaugherty *et al*., 1985; Aber *et al*., 1990; Ryan *et al*., 1990; Preston *et al*., 1997; Moorhead *et al*., 1999). The present analysis, in an improvement on previous energy budgets, explicitly includes leaching of DOC (dissolved organic carbon) as a loss of mass and energy from decaying litter in the forest floor, a loss distinct from energy dissipation associated with mineralization. This is particularly important to include when comparing across forest types (Currie & Aber, 1997).

In TRACE, fine litter and woody detritus in advanced decay are transferred to the same humus pool. Humification in the model is conceived as a convergence of material that may have had differing initial characteristics (Melillo *et al*., 1982; Zech & Kögel-Knabner, 1994; Coleman & Crossley, 1996).

Incorporation of energetics in TRACE Pools and fluxes of energy (kcal m^{-2} and kcal m^{-2} $month^{-1}$) were created in the model, linked to pools and transfers of OM in the forest floor. Caloric values of fresh foliar litter and fine roots were used to parameterize the appropriate energy inputs in litter production. Caloric values of older categories of foliar litter and of well-decayed Oea material were used to set the average energy contents of material in phase I and phase II decay, respectively. Energy fluxes included those associated with leaching losses of DOM from the forest floor, transfers of material from the phase I fine litter and woody debris pools (FWD and CWD pools) to phase II decay, and energy dissipation associated with mass loss through oxidation of organic constituents. In phase I decay, energy dissipation was calculated as the net effect of two processes, the loss of stored energy due to mass loss and the change in energy content (kcal g^{-1}) of a proportion of the material as it was humified.

Results

Carbon and energy aggregated over stages of decay

When combined across stages of decay, mean caloric values of different types of detritus fell between 4.8 and 5.8 kcal g^{-1} (Table 2). No consistent differences were observed between the pine and oak forest types. In both forests, woody debris consistently had lower energy content than all other types of detritus. Some differences were observed among other types of detritus in the pine forest, most notably between foliage and fine roots. Interestingly, well-decayed Oea material had energy content that was similar between forests, but resembled a different set of fine-litter categories in each forest. Its energy content resembled that of only foliage in the pine forest but resembled that of foliage, fine roots, and sloughed bark in the oak forest.

Carbon concentrations showed patterns similar to those in caloric values in some respects, but some differences were evident in comparing patterns of C concentration and energy content (Table 2). As with caloric values, C concentrations showed no significant differences between forests in most detrital categories. Likewise, C concentrations in woody debris of both forests were consistently lower than in other types of detritus (Table 2). Not only were woody debris categories different from other detrital categories in C concentrations and caloric values, but also in the energy : C ratios (Table 2). This occurred in both forests, where energy : C ratios were significantly lower for woody debris than for all other types of detritus. Some other patterns in energy : C ratios were evident, but exhibited differences of 8% or less.

Because some samples of FWD in finer size classes (< 5.0 cm) were taken from a concurrent study in N-amendment plots, I tested for confounding effects of N treatment. Most comparisons exhibited no such effects, although there was a significant overall difference in C concentrations between N treatments in this detritus. However, these differences were small (2% or less) and were in the opposite direction in the two forests. In the present results, these samples were combined with samples collected along transects (well outside the N-treatment study plots). This strengthened the sampling design, resulted in no confounding effects on energy content, and produced only negligible effects in C concentration at the level of aggregation used here.

Table 2 Characteristics* of detritus by forest type and detrital type, combined across stages of decay

	n	Ash (%)	C (%)	Caloric value (kcal g^{-1})	Caloric value per unit C (kcal g^{-1} C)
Pine forest					
Foliar litter	18	5.19 ± 0.70	55.6 ± 0.4 a	5.63 ± 0.03 a	10.12 ± 0.06 a
Fine roots†	6	1.83	56.3 ± 1.8 a	5.26 ± 0.04 b	9.37 ± 0.29 b
Fine woody debris	97	1.04 ± 0.16	52.2 ± 0.3 b(‡)	4.89 ± 0.03 c	9.39 ± 0.05 b
Coarse woody debris	26	1.01 ± 0.16	51.6 ± 0.3 b	4.95 ± 0.03 d	9.60 ± 0.04 c
Sloughed bark	6	2.95 ± 0.80	52.0 ± 1.0 b	5.21 ± 0.08 b	10.03 ± 0.16 a
Well-decayed Oea material	6	16.25 ± 3.58	56.3 ± 0.6 a	5.60 ± 0.07 a	9.94 ± 0.10 a
Oak forest					
Foliar litter	12	4.33 ± 0.35	55.0 ± 0.5 a	5.57 ± 0.06 a	10.14 ± 0.10 a
Fine roots	6	2.78 ± 0.50	55.2 ± 1.5 a	5.62 ± 0.08 a	10.21 ± 0.28 a
Fine woody debris	115	1.30 ± 0.08	51.1 ± 0.2 b(‡)	4.83 ± 0.02 b	9.47 ± 0.03 b
Coarse woody debris	24	1.21 ± 0.42	51.3 ± 0.6 b	4.87 ± 0.06 b	9.52 ± 0.07 b
Sloughed bark	7	4.78 ± 1.18	55.5 ± 2.3 a	5.64 ± 0.37 a	10.12 ± 0.28 a
Well-decayed Oea material	6	14.85 ± 3.34	55.3 ± 0.9 a	5.67 ± 0.09 a	10.27 ± 0.27 a

*Results for C and caloric value are given on an ash-free, dry-weight (105 °C) basis; ash concentration is given on a dry-weight (105 °C) basis. Means and standard errors are given; *n* = number of field samples analyzed. Within each forest, means followed by a common letter do not differ at the 0.05 significance level. Between forests, within each detrital category, means followed by a double dagger (‡) do differ at the 0.05 significance level. Ash concentrations were not tested for differences. Differences in caloric value per unit C were tested only within each forest, because data were not normally distributed across both forests combined.
†For ash determination in pine fine roots, *n* = 1 (a composited sample).

Carbon and energy changes over decay sequences

In the CWD of each forest, significant differences were observed in both C and energy among the five decay classes (oak forest, Fig. 1; pine forest not shown). (Note that downed woody debris in decay class 1 was rare in the pine and absent from the oak forest even though large areas were searched; Currie & Nadelhoffer, 2002). Measurements of C concentrations and caloric values on an ash-free basis were highly repeatable when grouped by forest, detrital category, and stage of decay, with standard errors typically < 1.7% of mean values for C and energy. Partly as a result of this precision, trends of both increasing C concentration and increasing energy content with decay were evident in the CWD of both forests.

In fine woody debris, patterns similar to those in CWD were observed in the oak forest but not the pine. In the oak forest, combined results for the two FWD size classes that used three decay categories (2.5 to < 5.0 cm and 5.0 to < 10.0 cm) showed significant trends of increasing C and energy content with increased stage of decay.

Among stages of decay of foliar litter, significant differences were observed in red pine needles. Decay stages exhibited significant differences in both C and energy content, although no trends were present with decay across stages (Fig. 2). Decay stages of foliage exhibited no significant differences in the oak forest.

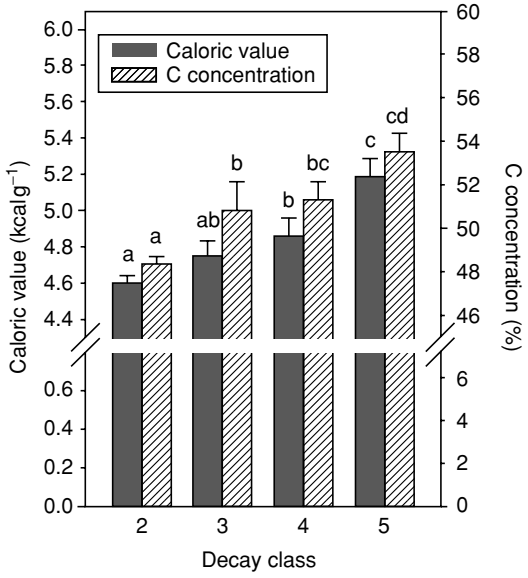

Fig. 1 Caloric value and C concentration in coarse woody debris (CWD) in the oak forest. Decay class refers to a system of five categories in which 1 = sound wood and 5 = the most highly decayed (Sollins, 1982). In this forest stand, no detritus was present in decay class 1; for decay classes shown, *n* = 5–8. Means and standard errors (SE) are shown. The same letter above two or more bars indicates no significant difference among means in either C concentration or caloric value. Note the breaks in vertical scales.

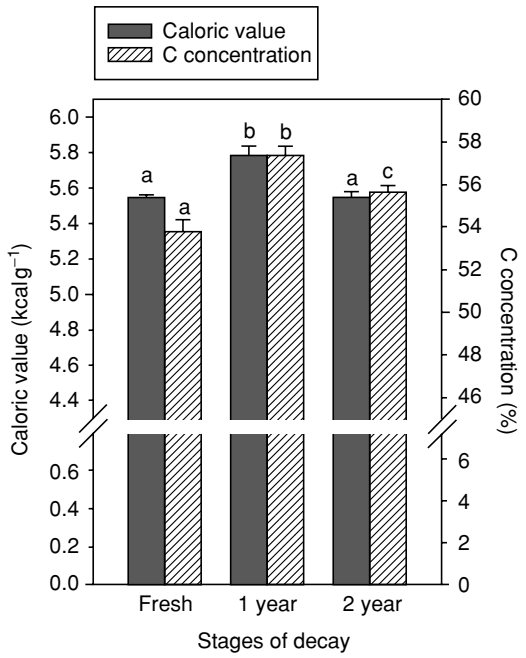

Fig. 2 Caloric value and C concentration in foliar litter in stages of decay in the pine forest. Stages of decay include freshly fallen litter, litter ≤ 1 year old, and ≤ 2 year old. Means and standard errors (SE) are shown. The same letter above two or more bars indicates no significant difference among means in either C concentration or caloric value. Vertical scales are as in Fig. 1.

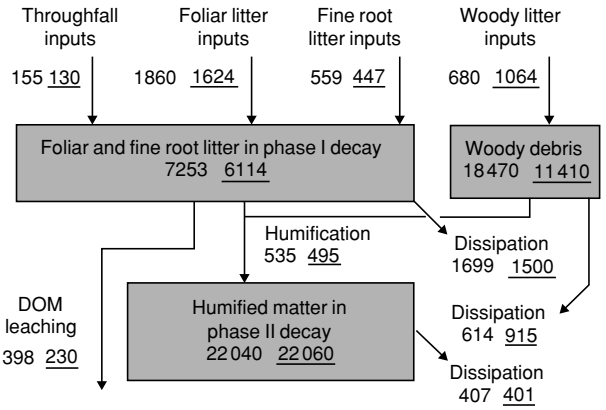

Fig. 3 Fluxes and pools of energy in two forest floors. Shown are TRACE model results for annual averages over the 10-year period 1990–1999. Energy fluxes, adjacent to arrows, are given in kcal m^{-2} yr^{-1}; pools, shown in boxes, are given in kcal m^{-2}. Each pair of values indicates results for the pine forest followed by those for the oak forest (underlined). DOM = dissolved organic matter. Note that the inputs of fine root litter here represent only the proportions entering the forest floors, not the whole solums.

In energy : C ratios assessed through the stages of decay, no trends were evident in woody detritus. Foliar litter in both forests exhibited minor trends in decreasing energy : C ratios as decay advanced (data not shown).

Modeled pools and fluxes of energy

The greatest fluxes of energy in the forest O horizon, as calculated by TRACE, were in inputs of foliar litter and in dissipation from detritus in phase I of decay (Fig. 3). Inputs of energy to the forest floor in fine roots were lower than those in foliar litter by more than a factor of 3, primarily because only a fraction of the fine root litter is deposited in the forest floor (the remainder is deposited in mineral soil horizons). After foliar litter inputs and dissipation fluxes from phase I, the next largest flux of energy was associated with inputs of woody litter (Fig. 3). Energy fluxes associated with humification amounted to 15–16% of the combined values of energy fluxes input in throughfall, foliar litter, fine root litter and woody litter in the forest floor. Fluxes of energy exported from forest floors through leaching losses of DOM (dissolved organic matter) amounted to 12 (pine) and 14% (oak) of the combined fluxes of energy input in throughfall and litter.

Simulated energy fluxes showed only slight differences between these two forests in most cases. The exceptions were input, storage and dissipation fluxes of energy in woody debris, together with DOM leaching. Because there were no significant differences between forests in the caloric values of types of detritus (Table 2), the differences in energy fluxes between forests were mainly attributable to differences in fluxes of OM. Differences in energy fluxes between forests also strongly reflected differences in C fluxes.

Differences in the modeled rates of biological energy dissipation per unit C mineralization (Table 3), calculated by the model using principles of energy balance, followed the differences in energy content among categories of detritus (Table 2). In particular, the model calculated that rates of energy dissipation per unit CO_2–C mineralization were 11–16% lower in wood than in fine litter and humus.

Discussion

Energy content and budgets

The caloric values obtained here are slightly higher than those typically reported for forest detritus. In a review of 57 plant species, Golley (1961) reported average values of 4.30 kcal g^{-1} for litter and 4.72 kcal g^{-1} for roots. Reiners & Reiners (1970), studying upland, fen and swamp communities in Minnesota reported caloric values for foliage of 13 species of trees ranging from 4.71 to 5.31 kcal g^{-1}.

Table 3 TRACE model simulations of relationships among fluxes of energy dissipation and CO_2–C mineralization

	CO_2–C mineralization	Energy dissipation/CO_2–C mineralization	
	$g\,C\,m^{-2}\,yr^{-1}$	$kcal\,g^{-1}\,C$	$kcal\,mol^{-1}\,C$
Pine forest floor			
Fine litter, phase I decay	169	10.1	121
Woody debris	68.4	9.0	108
Humus, phase II decay	39.3	10.4	124
Overall	277	9.8	118
Oak forest floor			
Fine litter, phase I decay	143	10.4	126
Woody debris	103	8.9	107
Humus, phase II decay	38.2	10.5	126
Overall	284	9.9	119

Shown are model results (forest floor only) for annual averages over the 10-year period 1990–1999.

Some disparity with previously reported values arose through my use of ash concentrations determined with a muffle furnace as opposed to the calorimeter bomb, and through my use of 105 °C (Boone *et al*., 1999) as opposed to lower temperatures for dry weight determination.

Energy budgets in forest litter and detritus have been infrequently studied. At the Hubbard Brook Experimental Forest, NH, energy dissipation through detritus was estimated to amount to ca. 3000 $kcal\,m^{-2}\,yr^{-1}$ (Gosz *et al*., 1978). This value included both the forest floor and mineral soil, but did not include DOM leaching and evidently excluded woody debris. Energy storage in the forest floor at Hubbard Brook (34 322 $kcal\,m^{-2}$; Gosz *et al*., 1978) was similar to the present results for Harvard Forest if woody debris pools are excluded: 29 293 (pine) and 28 174 $kcal\,m^{-2}$ (oak) (Fig. 3). Likewise, values of energy storage in the forest floors in an upland oak forest in Minnesota were similar, and similarly distributed between early and late stages of decay (L + F layers = 4703; H layer = 22 647 $kcal\,m^{-2}$; Reiners & Reiners, 1970), as the present results for the Harvard Forest (excluding woody debris).

Energy transport associated with DOC leaching at the Harvard Forest was on the same order of magnitude as energy fluxes associated with the process of stabilization of litter in humus (Fig. 3). The source of this DOC is believed to be litter leachates, secondary (microbial) compounds, and decomposition intermediates produced in the forest floor (Cronan, 1990; Qualls *et al*., 1991; Guggenberger & Zech, 1994; Currie *et al*., 1996). Most of this DOC typically sorbs to mineral grains in lower soil horizons, contributing to long-term storage reservoirs of C (McDowell & Wood, 1984; Schoenau & Bettany, 1987; Neff *et al*., 2000). This transport and sorption process may likewise contribute to long-term energy storage in mineral soils because the bulk of DOC leached from temperate forest floors is relatively recalcitrant to microbial decomposition (Qualls & Haines, 1992).

Differences between forest stands and types of detritus

Unexpectedly, the calculated rates of energy dissipation and storage in forest floors were quite similar between the coniferous and deciduous forests studied here. This indicates that similarities in C and energy fluxes may be likely in adjacent forests or where one forest type replaces another at the same location, but it does not necessarily indicate a similarity among typical coniferous and deciduous forests in the region. Here, the two forests had substantial similarities: they grew on similar soils at nearly equivalent elevations and with equivalent temperature regimes. Forest floor masses, input rates of fine litter, litter quality, and soil C : N ratios were similar between these two forest stands (Magill *et al*., 1997). Across temperate regions, differences in C and energy fluxes between average coniferous and deciduous forest stands are likely to be greater. For example, forest floor masses are typically lower in deciduous vs. coniferous forest (Gosz *et al*., 1976; McClaugherty *et al*., 1985; Campbell & Gower, 2000).

Discussions of energy flows in the literature of soil ecology typically assume that pools and fluxes of energy are closely related to pools and fluxes of OM or C. The present results justify that assumption, at least within forests on similar soils and climate, to within a first approximation (within ca. 10%). This study also indicated that the greatest deviations from average energy content or energy : C ratios in forest floors overall may arise from differences in the relative production of foliar, fine root, and woody litter. Although only two forests were studied

here, the results suggest that in forests similar to these, the most significant differences in overall relationships between OM, C, and energy may arise from differences in amounts of woody debris.

Carbon and energy during decay

The lack of a rising or falling trend in caloric value through stages of foliar litter decay, and in comparisons of fine litter with well-decayed Oea material, are in agreement with the results of Reiners & Reiners (1970), the only previous study that addressed this question. In three forest floors along a moisture gradient in Minnesota, caloric values did not vary significantly between L and F layers. This agreement suggests that the energy content of humus, which is more difficult to measure because of its high ash content or association with mineral grains, can be reasonably extrapolated from the energy content of well-decayed Oea material. My finding of a similar energy content for this material in the pine and oak forests is also consistent with the view of decomposition as a process in which detrital materials from different tissues and species converge during stabilization (Melillo *et al*., 1989; Paustian *et al*., 1997).

There are both theoretical and practical problems in relating caloric values in soil detritus to the bioenergetics of soil organisms on a detailed molecular basis. The greatest impediment is the presence of the large variety of different, polyfunctional macromolecules in soil detritus (Zech & Kögel-Knabner, 1994; Paul & Clark, 1996). However, energy contents of important subunits of these macromolecules can serve as a rudimentary check on TRACE results. Model results for the ratios of energy dissipation to C mineralization, 121–126 kcal mol^{-1} C for fine litter and humus (Table 3), translate to an enthalpy of combustion of 123–128 kcal mol^{-1} C (enthalpies of combustion may be approximately 1.4% higher than caloric values for ecological materials; Scott, 1965). This is slightly higher than the compound phenol (a subunit of lignin), with an enthalpy of 122 kcal mol^{-1} C (Weast, 1971). For woody debris, the energy dissipation here was found to be closer to the enthalpy of combustion for glucose [Glucose is the subunit of cellulose; (112 kcal mol^{-1} C; Weast, 1971)]. Overall, these modeled energy dissipation rates may appear low, given the energetic effort presumably needed to decompose the complex, polyfunctional lignins and humic substances that comprise the bulk (excluding woody debris) of the OM in the O horizon (Stevenson, 1982; Paul & Clark, 1996). However, the present analysis indicates that the bulk of the CO_2 mineralization and energy dissipation results from the decay of fine litter before it reaches the stage of humification (Fig. 3).

Conclusion

The present analysis expands on the work of earlier energy budgets for forest soils (Reiners & Reiners, 1970; Gosz *et al*., 1976) by including DOM leaching and by including woody debris. Results showed that, in these two side-by-side but contrasting temperate forests, energy storage and flows in the soil O horizons tracked C storage and flows to a first approximation (within 16% or less; Table 3).

Reiners (1986) proposed that complementary models of C, nutrients, and energy could provide a more biologically meaningful set of fundamental constraints on ecosystem biogeochemistry. I found that differences in energy content and energy : C ratios were measurable in forest detritus, but did not vary reliably enough between forest types or through detrital stages to indicate that decomposition models could necessarily be improved by including energetics. Future studies could assess whether energetic analyses might help to address current questions concerning C controls on nutrient cycling (Hart *et al*., 1994; Aber *et al*., 1998). Future studies could also focus on potential differences in fluxes of bioavailable energy among soils, climates, or biomes. One of the goals of the present analysis was to compare energy storage and flows in forests with similar soils in the same climate but contrasting vegetation. The model results indicated that there are strong similarities in energy flows and storage in the O horizons of the contrasting forest types studied at this location. For the present, and to a first approximation, the storage and fluxes of energy should be considered closely related to the storage and fluxes of carbon in the detritus of temperate forests.

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