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## MODELING LEACHING AS A DECOMPOSITION PROCESS IN HUMID MONTANE FORESTS

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**Abstract.** Forests in the White Mountain region (New Hampshire, USA) range from northern hardwoods and pine at low elevations to spruce–fir at middle elevations, subalpine fir, and krummholz on mountain peaks. We studied landscape-scale effects of gradients in forest cover type, litter chemistry, rates of litter input (including fine woody litter), temperature, and moisture on forest-floor pools and input–output fluxes of C and N. We coupled a new model of decomposition processes to a Geographic Information System (GIS) and applied it in 10-ha cells in the White Mountain National Forest. We sought to synthesize current understanding of forest-floor leachate qualities and quantities in humid forests with measured changes in carbon fractions (“lignin,” “cellulose,” and “extractives”) in decomposing litter. We included N dynamics as transfers of N among C fractions, including the production of dissolved organic N in leachate from the forest floor. We calibrated fluxes of dissolved organic C and N (DOC and DON) to measurements from two stands at the Harvard Forest, Massachusetts, USA. We calibrated rates of humus decay to two sites at the Hubbard Brook Experimental Forest. By including leaching as a mechanism of mass loss from the forest floor, we were able to calculate CO<sub>2</sub> mineralization fluxes by difference.

Predicted masses of forest floor were higher and peaked over a broader elevational range in spruce–fir forest than in hardwoods, due primarily to a slower decay rate of humus in coniferous forests. DOC and DON fluxes were higher in coniferous forests, while CO<sub>2</sub> fluxes were higher in hardwood forests. Predicted residence times for C in the forest floor were longer, and organic N concentrations were higher, in spruce–fir forests than in hardwood forests. Along a generalized elevational ecotone from hardwood to spruce–fir forests in the region, predicted mass and N in the forest floor increased and DOC and DON fluxes increased, while CO<sub>2</sub> fluxes decreased.

**Key words:** biogeochemistry; carbon stocks; CO<sub>2</sub> fluxes; decomposition; dissolved organic carbon; dissolved organic nitrogen; Geographic Information System (GIS); humic substances; landscape; leaching; litter quality; nutrient cycling; White Mountains, New Hampshire.

### INTRODUCTION

Linked models of production and decomposition attempt to characterize the dominant controls on C and nutrient stores and interactions in ecosystems (Pastor and Post 1986, Rastetter et al. 1991). A process model coupled to a GIS (Geographic Information System) enables investigators to model landscape-scale patterns in ecosystem function (Running and Coughlan 1988, Burke et al. 1990, King 1991, Aber et al. 1993a). The success of such an approach depends upon capturing the dominant controls on the processes of interest across patches and gradients present within the region of interest (Gosz 1992, Alperin et al. 1995).

At the foundation of virtually all decomposition models is a single or multiple empirical constant,  $k$  in the expression  $e^{-kt}$ , indicating the rate of detrital mass

loss over time (Olson 1963). Leaching and CO<sub>2</sub> mineralization are two separate mechanisms of mass loss (Gosz et al. 1973, Berg and Staaf 1980b, Schlesinger and Hasey 1981, McClaugherty 1983, Cronan 1985, Yavitt and Fahey 1986). However, because of the difficulty of distinguishing between these mechanisms in the field, mass loss in litter decay studies has typically been measured as a single process (e.g., Aber et al. 1984, Fahey et al. 1988).

Fluxes of the downward leaching of organics from the forest floor (the O horizon) into mineral soil have been made in a few humid, temperate forests (McDowell and Likens 1988, Qualls et al. 1991, Vance and David 1991, Currie et al. 1996). Compounds that comprise dissolved organic carbon (DOC) in forest-floor leachate have been characterized as primarily high-molecular-mass, complex organic acids (Cole et al. 1984, David et al. 1989, Vance and David 1989, Qualls and Haines 1991, 1992, Cronan et al. 1992). These can be categorized as humic substances or prehumic substances, consisting of incomplete products of decomposition and microbial modification (Cronan and Aiken 1985, Guggenberger and Zech 1994).

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Our goal was to synthesize current understanding of qualities and quantities of leachate from forest floors in a process model of decomposition that included leaching, and to predict patterns in leaching relative to other processes in a heterogeneous landscape. We studied relationships among types of forest, rates of litter input, fluxes of CO<sub>2</sub> mineralization, mass of the forest floor, capital of organic N, and leaching of DOC and DON (dissolved organic nitrogen) as they varied with elevation in an upland-montane region. The decomposition model derives from a series of field studies and analyses of litter decomposition and N dynamics conducted in temperate forests over the past 15 yr (Aber and Melillo 1982, Melillo et al. 1982, McLaugherty et al. 1985, Melillo et al. 1989, Aber et al. 1990). Major pools in the model represent carbon fractions, operationally defined as extractives, acid-soluble material (holocellulose) and acid-insoluble material (conventionally referred to as "lignin") (Berg et al. 1984, Taylor and Parkinson 1988, White et al. 1988, Harmon et al. 1990, Ryan et al. 1990, Means et al. 1992). We included microbial turnover in order to account for the production of secondary compounds (Van Veen et al. 1984). We included N dynamics as transfers of N among the C fractions and thereby accounted for measured fluxes of dissolved organic N (DON) in leachate from the forest floor. Because it simulates leaching fluxes, we call the model DocMod (Dissolved Organic Carbon Model).

The ability to model DOC and DON fluxes resulting from incomplete decomposition processes in the forest floor distinguishes DocMod from other decomposition models. DocMod is currently being used in a standardized model intercomparison as part of the LIDET study (Long-Term Ecological Research Network Inter-site Decomposition Experiment Team), a broad field experiment designed to test the effects of substrate quality and macroclimate on decomposition processes (M. E. Harmon, *unpublished manuscript*; D. Moorhead, *unpublished manuscript*). The other models included in the comparison, CENTURY (Parton et al. 1987), GENDEC (Moorhead and Reynolds 1991), and MBL-GEM (Rastetter et al. 1991) refer to C fractions as determinants of C and N dynamics in detritus, but do not distinguish leaching as a mechanism of detrital mass loss. CENTURY, for example, was originally developed for grassland ecosystems. Leaching is typically not an important mechanism of transfer of C and nutrients in semiarid grasslands (Burke and Lauenroth, *in press*).

In humid forests, organics eluviated downward from the forest floor comprise important transfers of C and nutrients to mineral soil (Schoenau and Bettany 1987, Qualls et al. 1991). When DON is measured, it is typically found to be the dominant form of N leaching from the forest floor in undisturbed forests (Sollins and McCorison 1981, Fahey et al. 1985, Qualls et al. 1991, Currie et al. 1996). DON was found to be the dominant

form of N exported in streams from an unpolluted, old-growth, temperate forest in Chile (Hedin et al. 1995). Production of DON in the forest floor, followed by uptake of DON, has also recently been implicated as a means of competition for N between mycorrhizae (and their plant hosts) and free-living microorganisms in soil (Northup et al. 1995). The synthesis presented here should help to bridge the gap between studies of decomposition and studies of the leaching and transport of dissolved organics.

#### STUDY AREA

The White Mountain National Forest (WMNF) covers ~340 000 ha in Northern New Hampshire (Fig. 1). The northern hardwood forest predominates at mid and low elevations, comprising *Prunus pennsylvanica* or *Betula papyrifera* as pioneers, yielding to *Acer saccharum*, *Fagus grandifolia*, and *Betula alleghaniensis* in later succession (Bormann and Likens 1979, Federer et al. 1990, Botkin 1993). *Tsuga canadensis* is present at low elevations, grading to *Picea rubens* above ~450 m (Reiners and Lang 1979). *Pinus strobus* is also present at lower elevations in some locations with agricultural history (M.-L. Smith, *personal communication*). Spruce-fir forests occur from ~760 m to ~1220 m with *Abies balsamea* predominating over *P. rubens* at higher elevations (Reiners and Lang 1979). The subalpine fir zone begins above ~1220 m, comprising largely *A. balsamea* with some *B. papyrifera* var. *cordifolia*. Above tree line (~1450 m), low krummholz is present (Reiners and Lang 1979), above which the vegetation community is alpine tundra.

At Hubbard Brook Experimental Forest (HBEF) at ~500 m elevation (weather station 1) long-term mean daily temperature is -8.8°C in January and 18.7°C in July. At the same point, average annual precipitation is 1327 ± 203 mm (SD), distributed evenly throughout the year (Federer et al. 1990). In the region, precipitation increases with elevation though data are sparse for sites above 600 m (Ollinger et al. 1993). Soils at HBEF in the northern hardwoods and lower spruce-fir zone are predominantly Haplorthods with a thick mor organic horizon (Gosz et al. 1976). Soils in the subalpine fir zone in WMNF are lithic Cryorthods or Cryorhumods where there is well-drained mineral material (Reiners and Lang 1979). Current land use in WMNF is 46% designated multiple use with timber management, 34% recreation without timber management, 14% wilderness, and 6% other land use (Harper et al. 1990).

#### METHODS

DocMod is an empirically based process model. Many equations quantifying processes derive from regressions over field data. Another model is needed to supply predictions of litter production and AET (actual evapotranspiration). Here we linked DocMod to the PnET-II model (Aber et al. 1995). Through a single

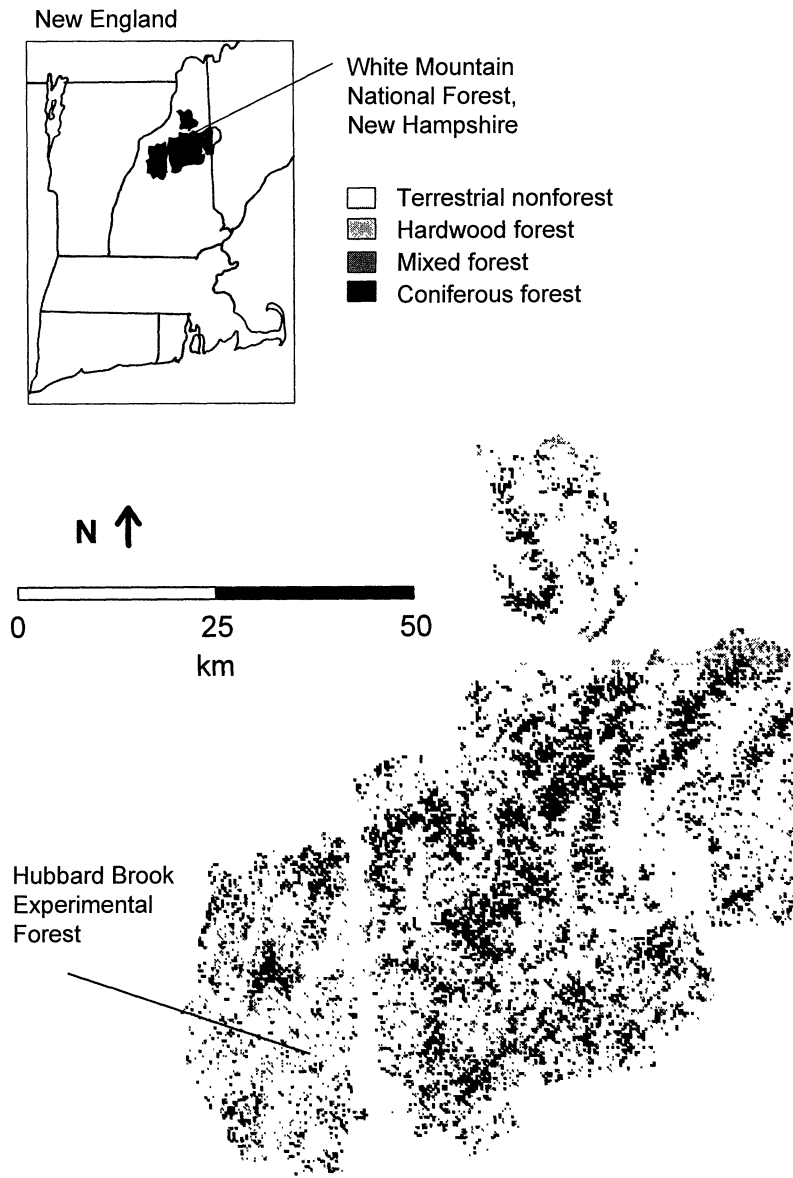


FIG. 1. Location of the study area, the White Mountain National Forest, and distribution of forest types within the categories of forest cover used in the study.

parameter, the decay constant of humus, we then calibrated predicted masses of the forest floor to two measurements at HBEF. We coupled the linked process models to a GIS and applied them in 10-ha cells across WMNF.

#### *DocMod mass dynamics*

For each tree species, chemistry of foliar and fine root litter are specified as model inputs (Table 1). Ash-free mass from this litter enters three pools (Fig. 2): lignocellulose (LC), unprotected cellulose (C), and extractives (E). (LC, C, and E are hereafter referred to as carbon classes.) All of the acid-insoluble mass, together with an equivalent amount of acid-soluble mass,

enters the pool of LC-class material; this represents the bound nature of lignin and celluloses in plant tissue (Swift et al. 1979). The remainder of the acid-soluble mass enters the C-class pool. Throughfall DOC is included as a carbon input to the forest floor in DocMod as a flux of  $13 \text{ g C} \cdot \text{m}^{-2} \cdot \text{yr}^{-1}$  (Currie et al. 1996). This enters the E-class pool because it comprises relatively labile material (Qualls and Haines 1992).

DocMod runs on a monthly time step. The decay parameter  $k$  for each carbon class is calculated from the current value of the lignocellulose index (LCI), where  $\text{LCI} = \text{lignin}/(\text{lignin} + \text{holocellulose})$  (Melillo et al. 1989). Rates of decay of material in each carbon class change through time as LCI of the detritus

TABLE 1. Litter chemistry used in DocMod simulations.

Species and tissue	Lignin† (%)	Cellulose (%)	Extractives (%)	N (%)
<i>Acer saccharum</i> : foliage (Aber et al. 1984)	12.1	43.1	44.8	0.83
<i>Fagus grandifolia</i> : foliage‡	30.6	49.2	20.2	0.78
<i>Betula papyrifera</i> : foliage (mixed-hardwoods zone) (Aber et al. 1990)	20.7	37.6	41.7	0.9
<i>Betula papyrifera</i> : foliage ( <i>Abies balsamea</i> zone) (Lang et al. 1982)				2.47
<i>Quercus velutina</i> / <i>Q. borealis</i> : foliage (Currie et al. 1996)	31.4	38.9	29.7	0.70
<i>Betula alleghaniensis</i> : foliage‡	35.8	41.5	22.7	1.53
<i>Tsuga canadensis</i> : foliage (Aber et al. 1984)	20.6	39.6	35.8	0.83
<i>Abies balsamea</i> : foliage§	25.0	37.5	37.5	2.26
<i>Picea rubens</i> : foliage (McLellan et al. 1991)	20.0	39.9	40.1	1.15
<i>Betula alleghaniensis</i> : fine roots	25.7	35.6	38.9	1.01
<i>Acer saccharum</i> : fine roots	31.1	38.9	30.5	1.01
<i>Fagus grandifolia</i> : fine roots	25.4	41	33.7	0.98
<i>Picea rubens</i> : fine roots	24.5	29.0	46.5	0.91
<i>Abies balsamea</i> : fine roots (Lang et al. 1982)				1.50
<i>Betula papyrifera</i> : fine roots (Lang et al. 1982)				1.51
Mixed hardwoods: fine roots (Harvard Forest) (McClougherty et al. 1982)			22.9	0.94
Mixed hardwoods: wood¶				0.15
<i>Picea/Abies</i> : wood¶				0.20

† Lignin (acid-insoluble), cellulose (acid-soluble), and total extractives (polar plus nonpolar) are specified on an ash-free dry mass basis (Ryan et al. 1990); N content is specified on an ash-included dry mass basis.

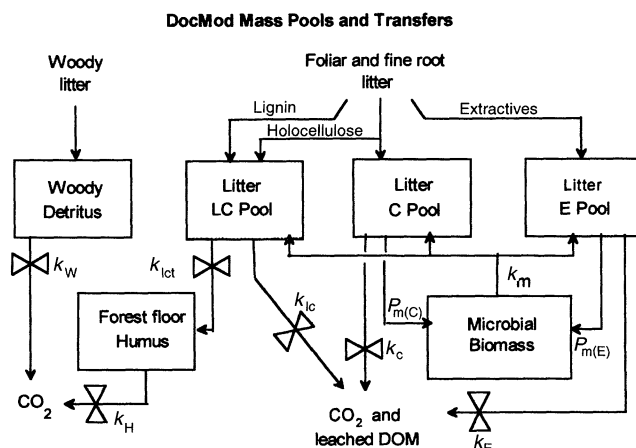
‡ LIDET (Long-term ecological research Intersite Decomposition Experiment Team); M. E. Harmon et al. (*unpublished data*).

§ N content is from Lang et al. (1982); proximate C fractions are our estimates.

|| Fahey et al. (1988). (Biomass-weighted bulk chemistry for combined size classes 0.6–1.0 mm and 1.0–2.5 mm. Corrected in order to be reported on an ash-free basis.)

¶ Wood N contents represent our estimates for FWD (fine woody debris) based on Whittaker et al. (1979), Lambert et al. (1980), Lang et al. (1982), Melillo et al. (1983), Aber et al. (1984), and Edmonds (1987).

FIG. 2. Pools and transfers of detrital mass in DocMod.  $K_{lct}$  indicates lignocellulose transfer, the movement of mass from the lignocellulose pool to the humus pool.  $P_{m(C)}$  and  $P_{m(E)}$  indicate production of microbial biomass from substrates in the C and E pools. See Table A.1 for description of other parameters. DOM = dissolved organic matter.



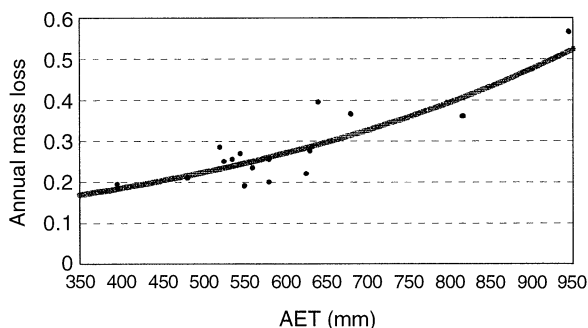


FIG. 3. AET effect on mass loss for all mass compartments in DocMod. Annual fractional mass loss is plotted against actual evapotranspiration (AET, in mm). Data shown are from Berg et al. (1993); regression fit is our own ( $r^2 = 0.72$ ).

changes. Equations for  $k$  values derive from dynamics in carbon classes in decomposing litter from three locations: Blackhawk Island, Wisconsin; the Harvard Forest, Massachusetts; and Hubbard Brook, New Hampshire (Appendix; Aber et al. 1990). Loss of C and E material dominates mass losses in the early stages, while the rate of LC decay controls the later stages (Berg and Staaf 1980a, McLaugherty 1983, McLaugherty and Berg 1987). Examples exist in the literature in which litter N content either correlates or does not correlate with decay rates (e.g., Prescott 1995); we have adopted the null hypothesis that N content does not affect rates of decay.

Climatic controls on decay rates are included as a function of AET (actual evapotranspiration), a convenient climatic surrogate because it combines temperature and moisture information. We derived an AET effect (Fig. 3; Appendix) from data published by Berg et al. (1993) for pine needle litter studied in 17 sites in Central Europe and North America. We normalized the AET effect to Blackhawk Island, Wisconsin, the site from which our litter decay constants derive (Aber et al. 1984, 1990).

Each month, a quantity of material equal to one-third the mass lost from the LC class is transferred to humus (Fig. 2). This flux corresponds to an ultimate transfer of ~20% of initial litter mass to humus (Aber et al. 1990). Using the LC pool as the source means that the mass ratio of lignin:cellulose in well-decayed litter is ~1:1 (Berg 1986).

**Microbial production and turnover.**—In the model, microbes grow with different efficiencies on material in each carbon class. The primary limitation on microbial production is thus availability of readily decomposable carbon (Lynch 1982, Zak et al. 1990). We set the microbial efficiency on holocellulose at 0.35. The lowest microbial efficiency observed by Ladd et al. (1992) for soil microbes metabolizing glucose was 0.4; holocellulose should be more difficult to metabolize because it requires at least two additional types of enzymes, endoglucanases and exoglucanases (Ljung-

dahl and Eriksson 1985). We assigned a microbial efficiency of zero to lignin decomposition based on  $^{14}\text{C}$  tracer observations that carbon in lignin may not be incorporated into microbial biomass (Tate 1987, Paul and Clark 1989). The microbial efficiency on LC material was estimated as 0.175, the average of the efficiencies for lignin (zero) and holocellulose. We calculated a microbial efficiency for extractives that was consistent with the above plus the constraint that efficiency on whole litter ( $e_{\text{overall}}$ ) should be ~0.4 (Hadas et al. 1992). We solved Eq. 1 for  $e_{\text{E}}$ , where  $e_x$  parameters represent microbial efficiency on each carbon-class substrate and  $F_x$  parameters represent the fractions of each carbon class in whole litter (we used representative values for  $F_x$  from Table 1):

$$e_{\text{L}}F_{\text{L}} + e_{\text{C}}F_{\text{C}} + e_{\text{E}}F_{\text{E}} = e_{\text{overall}} \quad (1)$$

This yielded a value of 0.7 for  $e_{\text{E}}$ , which we found reasonable since our formulation included lignin as a cometabolite at an efficiency of zero, and since Ladd et al. (1992) reported efficiencies ranging from 0.5 to 0.9 on a highly labile substrate (glucose).

We assumed microbial turnover to be equal to  $1/e$  or 63% of microbial production in each month. This is roughly equivalent to a 2% per day turnover observed for the unprotected fraction of microbial biomass in soil by Gregorich et al. (1991). Upon turnover in the model, microbial biomass enters the LC, C, and E pools in detritus. We hypothesized that microbial biomass contains 50% LC, 10% C, and 40% E material. The high amount of acid-insoluble material includes chitin, a constituent of fungal cell walls; other material we placed primarily in the E pool because we consider cytoplasm and proteins to be highly labile to decomposition. However, it was necessary to have some quantity of C-class material in microbial litter in order to effect an increase in nitrogen in the acid-soluble fraction of decomposing litter shown in the field data of Aber et al. (1984).

**C leaching and mineralization fluxes.**—Within each carbon class, the model partitions mass loss into fluxes of DOC and  $\text{CO}_2$ . We calibrated the partitioning parameters (Appendix) based on fluxes of litterfall, chemistry of litter, and fluxes of DOC in Oa leachate from the Harvard Forest, Massachusetts (Aber et al. 1993b, Currie et al. 1996). We performed separate calibrations for a mixed-hardwood stand and a red pine stand (Table 2) because the hardwoods and conifers showed markedly different DOC leaching fluxes (Cronan and Aiken 1985, Currie et al. 1996). First it was necessary to express Oa-leachate DOC in terms of the carbon classes in DocMod. McDowell and Likens (1988) calculated that C in monomeric and polymeric carbohydrates composed 6% of the DOC flux in Oa leachate at Hubbard Brook, New Hampshire; we consider this to be “unprotected C” material. Consistent with this, Qualls and Haines (1992) found that 70–80% of DOC in Oa leachate was not biodegradable in 120-d laboratory incu-

TABLE 2. Annual fluxes of dissolved organic C (DOC) leaching from the forest floor (Oa horizon) as calculated by DocMod and as measured in the field. Units are  $\text{g C}\cdot\text{m}^{-2}\cdot\text{yr}^{-1}$ .

Location (forest type)	DOC flux		Reference for measurement
	DocMod	Measured	
Harvard Forest (mixed-hardwood stand)	22.5†	22.5	Currie et al. 1996
Harvard forest (red pine stand)	39.8†	39.8	Currie et al. 1996
Hubbard Brook Experimental Forest (northern hardwoods)	25.2	26.3	McDowell and Likens 1988
Bear Brooks Watershed, Maine (northern hardwoods)	24.5	11–26	Vance and David 1991
Coweeta, North Carolina (mixed hardwoods)	31.7	40.5	Qualls et al. 1991

† DocMod fluxes were calibrated to Harvard Forest values.

bations. We considered this to indicate primarily LC-class material, the most recalcitrant pool of litter material in DocMod. By reviewing literature on fractionation of, biodegradability of, and chemical characterization of DOC we thus hypothesized that organics in Oa-leachate were composed 75% of LC-class material, 10% of C-class material, and 15% of E-class material (Leenheer 1981, McClaugherty 1983, Cronan and Aiken 1985, McDowell and Likens 1988, David et al. 1989, Vance and David 1989, Qualls et al. 1991, Qualls and Haines 1991, Cronan et al. 1992, Guggenberger and Zech 1994). Humus does not contribute to the leaching flux. Qualls et al. (1991) reported that DOC and DON fluxes were at least as great from the Oi as from the Oa horizon in a forest at Coweeta, North Carolina. Guggenberger and Zech (1994) stressed the importance of humus precursors in forest-floor leachate; also the DOC:DON ratio in Oa leachate (discussed below) is much higher than the C:N ratios of humus.

#### Woody litter dynamics

DocMod includes woody litter (branches, twigs, boles, and woody roots) initially 5 cm in diameter or smaller, which by convention (Mattson et al. 1987) we refer to as fine woody debris (FWD). This size material would be distributed more homogeneously than larger woody litter, would be included in measurements of forest-floor mass that avoided stumps or large boles, and on the time scale of decades would be more likely to be incorporated into the forest floor beyond the point of separation with laboratory sieves. Woody detritus is kept separate from the carbon-class pools because we found published data insufficient to establish whether a litter-quality index could predict rates of wood decomposition.

For similar reasons, and because the interaction between temperature and moisture in controlling wood decay is probably complex, the decomposition of FWD in DocMod is independent of AET. Decomposition of wood can be inhibited when moisture is either too low or too high (Boddy 1986). Amounts of precipitation are sometimes observed to correlate inversely with

rates of wood decay (Harmon et al. 1987, Harmon and Hua 1991). We set woody  $k$  at the average mass loss rate (corrected for fragmentation) observed over all sizes of FWD by Mattson et al. (1987) over a 6-yr period (Appendix).

Well-decayed wood is not passed to humus in DocMod. An exponential decay rate with a single  $k$  value described bolewood decomposition in the White Mountains throughout a chronosequence spanning 64 yr (Foster and Lang 1982). All C is assumed mineralized to  $\text{CO}_2$ . Leaching of DOC from wood has been suggested by declining concentrations of DOC in interstitial water during snowmelt-induced flushing of woody detritus in Wyoming (Yavitt and Fahey 1985). However, *Fagus sylvatica* wood in a temperate deciduous forest retained water to 300% of its oven-dry mass (Boddy 1986), suggesting that gravitational leaching could be minimal in the absence of strong flushing. Because the contribution of wood to leaching fluxes of dissolved organics in this region is an open question, we adopted the null hypothesis that these fluxes are zero.

#### DocMod N dynamics

Ash-free mass entering the LC pool has N content equal to that of fresh, whole litter; the remainder of the nitrogen in fresh litter enters the E pool, while no N in fresh litter enters the C pool (Aber et al. 1984). Microbial growth incorporates N based on the N content of microbial biomass, which is 3% (Swift et al. 1979, Tietema and Wessel 1992). Exogenous, available N (e.g., from deposition), together with any N mineralized during short-term decay, enters a pool of available inorganic N (Fig. 4). However, in the present application of DocMod, plant uptake of N is not included so the pool size of inorganic N is unrealistic. Here we consider only organic pools of N in the forest floor and we model N immobilization as being limited not by N availability, but by the availability of carbon substrates (above). We do include throughfall inputs of DON to organic N pools as a flux of  $0.31 \text{ g N}\cdot\text{m}^{-2}\cdot\text{yr}^{-1}$  (Currie

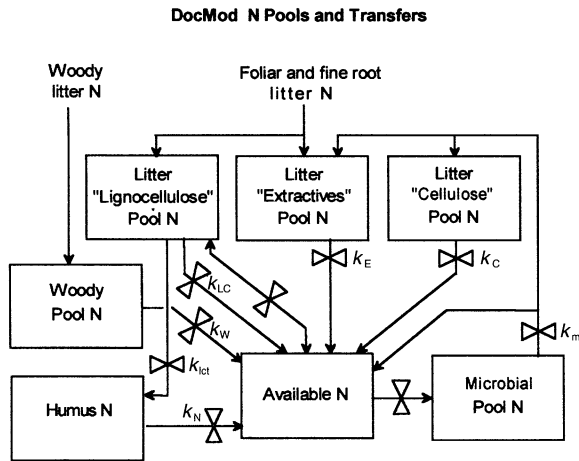


FIG. 4. Pools and transfers of nitrogen in DocMod. See Fig. 1 and Table A.1 for description of parameters.

et al. 1996). This enters the E pool in the forest floor as does the DOC in throughfall (above).

*Incorporation of N in recalcitrant pools.*—All N transfers but two are calculated as a mass transfer multiplied by the N concentration of the source pool. The two exceptions are immobilization of N by the LC pool and concentration of N in humus. From field data (Aber et al. 1984, McLaugherty et al. 1985) we derived an empirical relationship for N in the LC pool that is similar to a sorption isotherm; low N concentration in the LC pool results in immobilization, while high N concentration results in release (Fig. 5). This function is presumed to model biotic and/or abiotic mechanisms of N retention in lignocellulose (Stevenson 1982, Johnson 1992). Because both humus and dissolved organic matter in forest-floor leachate derive largely from the LC pool, this pool in part represents the formation of soluble and insoluble “prehumic” substances as lignin-rich derivatives (Melillo et al. 1982, Guggenberger and Zech 1994).

The N in woody detritus concentrates without release (Alban and Pastor 1993) until the C:N ratio of the entire pool reaches 20:1, at which level the C:N ratio is maintained through N mineralization. From humus, N is mineralized at a rate slower than mass loss (60% of

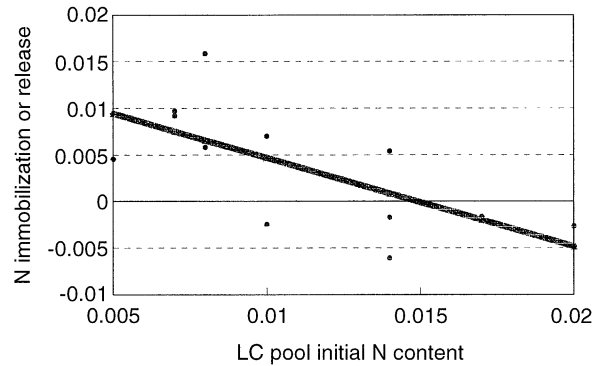


FIG. 5. Immobilization or release rate of nitrogen for the lignocellulose (LC) pool in DocMod (see Appendix: Eq. A.13). Positive y-axis values represent N immobilization; negative values, release. For regression shown,  $r^2 = 0.45$ .

the rate of mass loss), allowing humus to reach a C:N ratio lower than that of the LC pool. We chose the rate of N concentration in humus in concert with the N dynamics of woody litter to produce well-decomposed material in both pools at a C:N ratio of ~21:1. Field measurements do not distinguish humified material in the Oa horizon by original source, foliar vs. fine root vs. wood.

*DON leaching fluxes.*—In the model, dissolved organic matter leaching from the LC pool is presumed to retain all of its N because this pool contains recalcitrant and highly processed compounds. Matter leaching from the unprotected C pool is presumed to be stripped of all N content, while matter leaching from the E pool retains 30% of its N content. We consider leachate from the E pool to contain some tannins and polyphenolics, which would be relatively recalcitrant to microbial decay. The 30% parameter was calibrated, given the above constraints on LC- and C-class material, to produce the correct fluxes of total DON and overall DOC:DON ratios in Oa-leachate in both forest types studied at the Harvard Forest, Massachusetts (Table 3).

*Model linkage, parameterization, and validation*

We used the closed-canopy forest ecosystem model PnET-II (Aber et al. 1995) to supply litter inputs to the

TABLE 3. Annual fluxes of dissolved organic N (DON) fluxes leaching from the forest floor (Oa horizon) as calculated by DocMod and as measured in the field. Units for DON are  $g N \cdot m^{-2} \cdot yr^{-1}$ .

Location (forest type)	DON flux		DOC:DON ratio		Reference for measurement
	DocMod	Measured	DocMod	Measured	
Harvard Forest (mixed-hardwood stand)	0.59†	0.61	38	37	Currie et al. 1996
Harvard Forest (red pine stand)	1.0†	0.95	39	42	Currie et al. 1996
Coweeta, North Carolina (mixed hardwoods)	0.75	1.0	42	40	Qualls et al. 1991

† DocMod fluxes were calibrated to Harvard Forest values.



TABLE 4. Forest-floor mass and N capital for three elevations in WMNF in New Hampshire, USA.

Parameters	Hubbard Brook	Hubbard Brook	Mt. Moosilauke
Forest type	Northern hardwoods	Spruce–fir	Subalpine fir
Elevation	645 m	795 m	1235 m
Historical disturbance	Clearcut	Clearcut	Unlogged; fir waves
Humus decay rate, $k_H$	0.014 yr <sup>-1</sup>	0.0071 yr <sup>-1</sup>	0.0071 yr <sup>-1</sup>
PnET-II results†			
Foliar production	330 g·m <sup>-2</sup> ·yr <sup>-1</sup>	270 g·m <sup>-2</sup> ·yr <sup>-1</sup>	270 g·m <sup>-2</sup> ·yr <sup>-1</sup>
Fine root production	300 g·m <sup>-2</sup> ·yr <sup>-1</sup>	240 g·m <sup>-2</sup> ·yr <sup>-1</sup>	240 g·m <sup>-2</sup> ·yr <sup>-1</sup>
Wood production	790 g·m <sup>-2</sup> ·yr <sup>-1</sup>	410 g·m <sup>-2</sup> ·yr <sup>-1</sup>	340 g·m <sup>-2</sup> ·yr <sup>-1</sup>
AET	558 mm	521 mm	495 mm
DocMod results			
Forest-floor mass‡	7300 g/m <sup>2</sup> (age 57)	8000 g/m <sup>2</sup> (age 52)	10 000 g/m <sup>2</sup> (steady state)
Forest-floor N capital	140 g/m <sup>2</sup> (age 60)	170 g/m <sup>2</sup> (age 52)	240 g/m <sup>2</sup> (steady state)
Forest-floor N concentration§	1.9%	2.1%	2.4%
Data for comparison			
Forest-floor mass	7000 ± 1000 g/m <sup>2</sup> (age 57)	8000 g/m <sup>2</sup> (age 52)#	9500 ± 1300 g/m <sup>2</sup> (at maturity)††
Forest-floor N capital	130 g/m <sup>2</sup> (age 60)¶	...	230 g/m <sup>2</sup> (at maturity)††

† Closed-canopy production and AET (actual evapotranspiration) were calculated by the PnET-II model (Aber et al. 1995), linked to DocMod for the present study. Total production of foliage, fine roots, and wood is listed.

‡ Forest-floor mass quantified as organic-matter mass, including fine woody debris, and excluding live roots.

§ N content expressed as g N/g organic-matter mass.

|| Covington 1981, HBEF Watershed 6.

¶ Bormann and Likens 1979.

# Gosz et al. 1976.

†† Lang et al. 1981. Range in forest-floor mass was 8100–10 600 g N/m<sup>2</sup>.

forest floor. PnET also includes a model of monthly mean temperatures and monthly mean precipitation throughout the region based on latitude, longitude, and elevation (Ollinger et al. 1993). PnET-II calculated AET based on the climate model and on the type of forest cover present in each grid cell in the GIS (below).

Because forest patches in WMNF exist in various stages of recovery from disturbance, particularly clear-cutting and fir waves (Bormann and Likens 1979, Reiners and Lang 1979), and because forest-floor mass decreases and then recovers following clear-cutting (Covington 1981), we chose 60 yr following major disturbance to use as an index. From a curve fit to chronosequence data, Federer (1984) noted that mass of the forest floor had recovered to 95% of its asymptotic value by year 64. Repeated sampling in watershed 6 at HBEF showed no significant changes in mass of the forest floor over stand ages of ~55–66 yr (T. G. Siccamo, unpublished data, cited in Yanai 1990). We ran DocMod for 400 yr to produce steady states in C and N pools, then simulated clear-cutting followed by 60 yr of forest regrowth. At the time of clear-cutting, 20% of humus mass was considered to be lost from the O horizon through mixing into the mineral soil by the heavy equipment used during harvesting operations (Ryan et al. 1992).

To produce temporal patterns in litterfall, we converted PnET-II results for closed-canopy litter fluxes into annual fluxes following disturbance. Recovery of foliar litter production was based on the data of Bormann and Likens (1979), which showed a complete recovery within 30 yr. We used the same function for

fine root litter. We modeled FWD inputs with a logistic-like function reaching its maximum at 45 yr (Appendix).

Only 48% of fine-root litter entered the forest floor; the rest was considered to enter mineral soil (McClougherty et al. 1982, Fahey et al. 1988). For woody litter, we estimated that at low elevations in WMNF, 20% of total wood production enters the forest floor as FWD, while 36% does so in the highest-elevation spruce–fir forests (Harris et al. 1973, Rolfe et al. 1978, Whittaker et al. 1979, Lambert et al. 1980, Mattson et al. 1987, Fahey et al. 1988). We hypothesized that the fraction (20–36%) increases with elevation (Appendix) because of a greater fraction of woody production occurring in small size classes at higher elevations.

The rate of decay of humus,  $k_H$ , was calibrated to different values for hardwood and coniferous forests. For mid-elevation (420–700 m) hardwood forests, we constrained total forest-floor mass at HBEF at age 57 to match the value measured by Covington (1981), which was representative of forest-floor mass measurements in a 200-yr chronosequence (Covington 1981, Federer 1984). This produced a  $k_H$  value of 0.014 yr<sup>-1</sup> (Table 4). For spruce–fir forest, we constrained humus mass at 795 m elevation at HBEF at age 52 to total ~5600 g/m<sup>2</sup> (Gosz et al. 1976). This produced a  $k_H$  value of 0.0071 yr<sup>-1</sup> (Table 4). This value for  $k_H$  also produced total mass of the forest floor in agreement with the field measurement (Gosz et al. 1976). A third value for higher elevation fir forests was not required, because the  $k_H$  calibrated for spruce–fir produced ac-

ceptable estimates of mass and N capital in the forest floor in the subalpine fir zone (Table 4).

We tested the DOC and DON flux calculations by applying the linked models at other locations in the humid, temperate forest biome for which DOC and DON flux data were available (Tables 2 and 3).

#### Landscape-scale application

Actual land use–land cover (LULC) data, interpreted from Landsat Thematic Mapper (TM) imagery, was obtained from the GRANIT project (Complex Systems Research Center, University of New Hampshire) for the portion of WMNF in the state of New Hampshire (we do not consider the small part of WMNF that extends into Maine). The LULC data were in NH State Plane format, extending from 71.0° to 72.0° W and from 43.75° to 44.65° N. Resolution was 30 × 30 m, with pixels classified as hardwood, coniferous, or mixed forest, and several nonforest categories. Nonforested pixels, ~5% of the area, contained these land-cover categories: wetland, agricultural, exposed bedrock, open, water, urban, and alpine tundra. Interpretations among forest types had been checked against reference data to ~80% accuracy. The LULC image was converted into IDRISI format (program developed by Clark University Geography Department), in which all subsequent GIS analysis (including statistical analyses of results) was performed. State Plane coordinates were converted to planar latitude and longitude using the CORPSCON program (U.S. National Geodetic Survey). Resampling to the planar latitude and longitude system was accomplished with a simultaneous coarsening of scale from 30 × 30 m pixels to 316 × 316 m (10 ha) pixels. A digital elevation model (DEM) for the region was obtained in USGS DEM format at the scale of 1:250 000 (~800 × 800 m), converted to IDRISI format, aligned with the LULC image and resampled using bilinear interpolation to 316 × 316 m scale.

Three PnET-II parameter sets were used: mixed northern hardwood forest; pine (*Pinus strobus* and *P. resinosa*); and spruce–fir. Grid cells with the LULC cover type “hardwoods” at all elevations (67.5% of the forested land) were modeled in PnET as mixed hardwoods. Litter in these grid cells was estimated as comprising 33% *Fagus grandifolia* litter, 39% *Acer saccharum*, 23% *Betula alleghaniensis*, and 5% *Picea rubens* (Bormann and Likens 1979). The cover type “coniferous forest” at 450 m elevation and higher (17.8% of the forested land) was modeled as spruce–fir in PnET-II and as 85% *Abies balsamea* and 15% *Picea rubens* litter in DocMod (Reiners and Lang 1979). We modeled coniferous forest below 450 m elevation (2.7% of the forested land) as pine in PnET-II and *Pinus strobus* for litter quality. “Mixed forest” pixels at elevations below 450 m (2.5% of total forest) were considered mixed hardwoods, hemlock phase. These were modeled in PnET-II as mixed hardwoods, and in DocMod litter was estimated as comprising 35%

*Acer rubrum*, 25% *Picea rubens*, 20% *Tsuga canadensis*, 10% *Betula alleghaniensis*, 5% *Fagus grandifolia*, and 5% *Abies balsamea* (Hornbeck and Leak 1990). Finally, mixed forest at elevations 450 m and higher (9.5% of forested land) was considered 50% mixed-hardwood forest and 50% spruce–fir.

## RESULTS

### Predicted values of mass pools and C fluxes

In both hardwood and coniferous forests, the highest predicted masses of forest floor occurred in the zone of 800–1000 m elevation (Fig. 6B). The lowest predicted masses of forest floor occurred at the highest elevations with forest trees in WMNF. We estimated the regionally averaged mass of forest floor for hardwood cover to be 7250 g organic-matter (OM) mass/m<sup>2</sup>, while we estimated the regional average for coniferous cover to be 8920 g OM mass/m<sup>2</sup> (Table 5). (OM mass excludes ash mass.)

The mean value for mass of the forest floor under hardwoods was predicted to be maximal (8000 g/m<sup>2</sup>) in the elevational zone of 800–1000 m primarily because the PnET-II model predicted production of hardwood litter to be greatest at an elevation of ~850 m. Predicted fluxes of DOC leaching and CO<sub>2</sub> mineralization from the forest floor were also high in this zone, although the relatively high values for these fluxes also extended down into the 650–800 m zone (Fig. 6D, E). Within a forest cover type in DocMod, either higher relative rates of decay or higher litterfall fluxes (and thus greater absolute decay) produced higher fluxes of DOC and CO<sub>2</sub>. Below 800 m in hardwood forest, greater decay rates due to higher temperatures offset the slightly lower fluxes of litter production.

Predicted masses of forest floors were greater under coniferous cover than under northern hardwood cover within each elevational zone in the region. In addition, coniferous forests exhibited the highest mean value of predicted mass of the forest floor, 9500 g OM mass/m<sup>2</sup>, in the elevational zone of their peak occurrence (Fig. 6A, B).

DocMod predicted fluxes of DOC and DON to be higher in coniferous forest than hardwood forest at all elevations, as expected. Mean fluxes of DOC were predicted to range from nearly zero to 26 g C·m<sup>-2</sup>·yr<sup>-1</sup> in hardwood forests and 45 g C·m<sup>-2</sup>·yr<sup>-1</sup> in coniferous forests. We estimated average fluxes across WMNF to be 24.6 g C·m<sup>-2</sup>·yr<sup>-1</sup> in hardwood forests and 33.6 g C·m<sup>-2</sup>·yr<sup>-1</sup> in coniferous forests (Table 5). The lowest fluxes were predicted in the upper *krummholz* zone (1450–1730 m). The highest fluxes were predicted in pine forest at the lowest elevations in WMNF, corresponding to both greater litter production and higher decay rates relative to coniferous forests at middle and high elevations.

We estimated landscape-scale means in fluxes of CO<sub>2</sub> mineralization (i.e., excluding root respiration and ex-

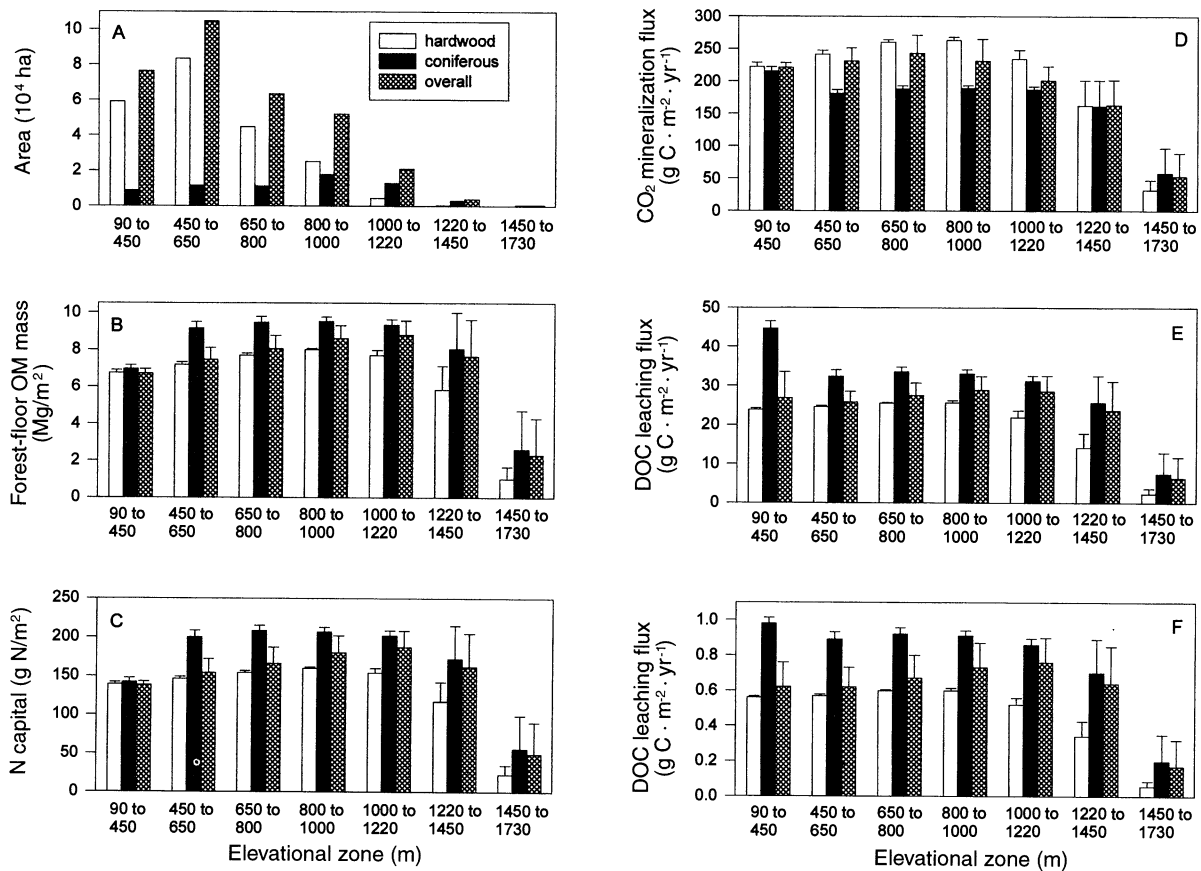


FIG. 6. Forest-floor pools and fluxes 60 yr after clear-cutting, grouped by category of forest cover and by elevational zone. (A) Area covered by each category of forest cover in the New Hampshire portion of the White Mountain National Forest (WMNF). (B) Mass of organic matter in the forest floor. (C) Capital of organic N in the forest floor. (D) Flux of CO<sub>2</sub> mineralization from the forest floor. (E) Flux of DOC leaching from the forest floor. (F) Flux of DON leaching from the forest floor. All results except (A) are independent of area covered by each category of forest cover. The "overall" category includes the "mixed" forest cover category (not shown separately) in addition to hardwood and coniferous categories. Error bars represent sample standard deviation calculated in IDRISI (software package developed by Clark University Geography Department).

cluding processes occurring in deeper soil horizons) to be 242 and 188  $g C \cdot m^{-2} \cdot yr^{-1}$  in hardwood and coniferous forests, respectively, with 228  $g C \cdot m^{-2} \cdot yr^{-1}$  as the overall mean for forests in WMNF (Table 5). Fluxes ranged from nearly zero (at the highest elevations) to 263  $g C \cdot m^{-2} \cdot yr^{-1}$  in hardwoods and 215  $g C \cdot m^{-2} \cdot yr^{-1}$  in coniferous forests (Fig. 6D). In each case, the peak

flux occurred where litter production was greatest within the forest type.

#### Relationships between mass pools and C fluxes

Within each forest type, DOC leaching and CO<sub>2</sub> mineralization correlated positively with mass of the forest floor (Figs. 7 and 8). Along transitions from hardwood

TABLE 5. Mean simulated values of forest-floor pools and fluxes 60 yr after clear-cutting. Fluxes represent outputs from the forest floor (CO<sub>2</sub> flux refers to mineralization only). Means were calculated within each category of forest cover, over all elevations in WMNF.

Cover	Area (ha)	DOC flux ( $g \cdot m^{-2} \cdot yr^{-1}$ )	CO <sub>2</sub> flux ( $g \cdot m^{-2} \cdot yr^{-1}$ )	Forest-floor OM mass ( $g \text{ mass}/m^2$ )	Forest-floor C turnover rate (%/yr)	DON flux ( $g \cdot m^{-2} \cdot yr^{-1}$ )	Forest-floor N capital ( $g/m^2$ )
Hardwood	217 550	24.6	242	7250	7.4	0.58	147
Coniferous	66 050	33.6	188	8920	5.0	0.89	193
Mixed	38 800	29.3	218	7700	6.4	0.73	164
Overall	322 400	27.0	228	7650	6.7	0.66	159

Note: DOC = dissolved organic carbon; DON = dissolved organic nitrogen; OM = organic matter.

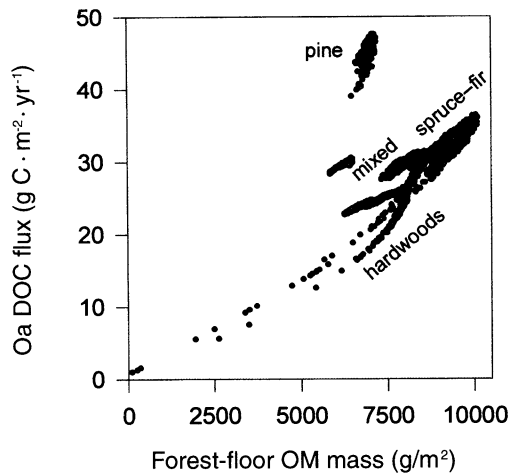


FIG. 7. Fluxes of DOC leaching from the forest floor, related to mass of organic matter in the forest floor. Shown are DocMod simulations for 10-ha cells in WMNF at 60 yr following clear-cutting. A random selection of 20% of the points in WMNF is plotted (6500 points).

to spruce–fir forest, however,  $\text{CO}_2$  mineralization fluxes decreased while DOC leaching fluxes increased (summarized in Fig. 9). DOC fluxes were higher in spruce–fir forests despite the slower rates of litter decomposition, because of the greater fraction of mass loss attributed to leaching in coniferous forests relative to hardwoods. The mean ratios of  $\text{CO}_2\text{-C}$  to DOC fluxes, as outputs from the forest floor, decreased from  $\sim 10:1$  to  $\sim 6:1$  in a generalized elevational transition from hardwood to spruce–fir forests in the region (Table 5).

On the average, we predicted forest floors under spruce–fir cover to have lower total input and output fluxes of C than under hardwood cover. In our simulations, the greater fluxes of DOC leached from the forest floor in spruce–fir forests (Fig. 7) were not high enough to overcome the lower  $\text{CO}_2$  fluxes (Fig. 8). The combination of lower input fluxes of C, lower total output fluxes of C, and higher mass in the forest floor indicates a greater residence time predicted for C in the forest floor in spruce–fir forests than in hardwood forests. This can also be expressed as a lower turnover rate in coniferous forest floors, as shown in Table 5.

#### *N capital and dissolved organic nitrogen*

Capital of organic N in the forest floor showed similar patterns to mass of the forest floor at the landscape scale (Fig. 6C). N capital was higher in coniferous forest, peaked in the 800–1000 m range in hardwood and the 650–1000 m range in coniferous forests, and declined more slowly with increasing elevation above 1220 m in coniferous forests. DocMod simulations produced higher N content (as a percentage of mass of the forest floor) at higher elevations, in agreement with observations (Table 4).

Predicted fluxes of DON in Oa leachate ranged from nearly zero in the upper krummholz zone to 0.60 g

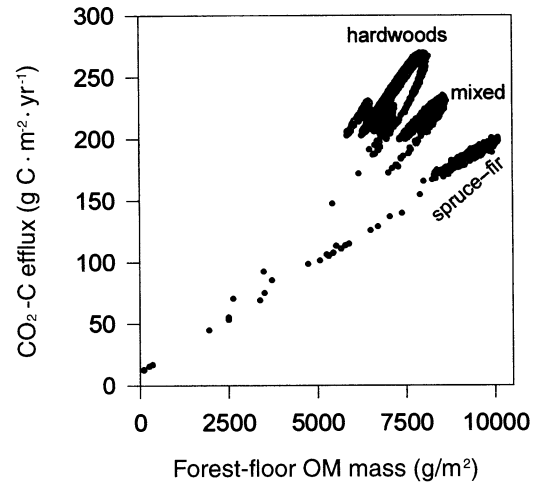


FIG. 8. Flux of  $\text{CO}_2\text{-C}$  mineralized from the forest floor, related to mass of organic matter in the forest floor. Simulated points are as in Fig. 7.

$\text{N}\cdot\text{m}^{-2}\cdot\text{yr}^{-1}$  in hardwood forests and  $0.98 \text{ g N}\cdot\text{m}^{-2}\cdot\text{yr}^{-1}$  in coniferous forests. We estimated that a scaled-up average in DON flux across the landscape is  $0.66 \text{ g N}\cdot\text{m}^{-2}\cdot\text{yr}^{-1}$  (Table 5).

#### DISCUSSION

Net flux of DOC through the forest floor has been calculated previously by subtracting DOC fluxes in throughfall from those in forest-floor (Oa) leachate (Qualls et al. 1991, Liechty et al. 1995). Our analysis allowed a more functional approach to the forest-floor DOC budget. The DOC in throughfall entered a labile pool in the forest floor, while most of the DOC in Oa leachate derived from a more recalcitrant pool containing prehumic material. This approach also allowed us to hypothesize sources of DON in Oa leachate in a manner consistent with inputs of N in litter, capital of organic N in the forest floor, and concentration of N in detrital carbon classes.

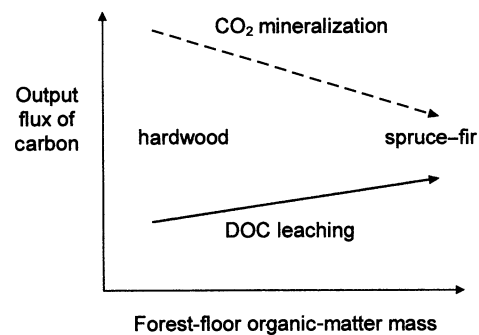


FIG. 9. Generalized relationships between hardwood and coniferous forest cover, fluxes of DOC leaching from the forest floor, and fluxes of  $\text{CO}_2\text{-C}$  mineralization from the forest floor (Figs. 7 and 8). Note that DOC and  $\text{CO}_2\text{-C}$  fluxes are not to scale.

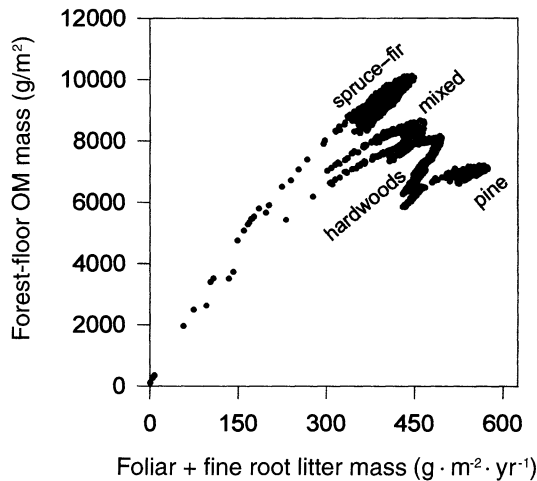


FIG. 10. Mass of organic matter in the forest floor related to fluxes of foliar plus fine root litter. Simulated points are as in Fig. 7. OM = organic matter.

Residence time for C in the forest floors increased with elevation in our simulations. Within the hardwood cover category, curves relating forest-floor mass to input or output fluxes of C exhibited hysteresis (Figs. 8 and 10; generalized in Fig. 11). On each curve, the two limbs represent different elevational zones. The transition between the two zones occurred approximately where predicted mass of the forest floor was maximal within each forest type. In the steady-state approximation, the existence of two curves relating size of the C pool to a single input or output flux of C corresponds to two different residence times for C (Nicolis and Prigogine 1989). A residence time for C (in the steady-state approximation) was 14 yr at mid and lower elevations (850 m and below), and 15 yr or greater at higher elevations. Longer residence time at higher elevation resulted from slower decay caused by cooler temperatures.

A landscape-scale ecotone between hardwood and coniferous forest (*sensu* Risser 1995) was centered at middle elevations (800–1000 m). If climatic warming caused the ecotone to shift to higher elevations, our results suggest that  $\text{CO}_2$  mineralization fluxes from the forest floor would increase in the transition zone. Storage of C and N in the forest floor, together with the downward transport of DOC and DON into mineral soil, would be reduced. Of course, climatic warming would affect production as well; to calculate net ecosystem responses, additional pools and fluxes of C and N would need to be included.

Our simulations showed a strong correlation between C capital and organic N capital in the forest floor, illustrating the importance of litter and humus in storing nutrients. There was also a positive relationship between C residence time and N capital in the forest floor, both quantities increasing with elevation at least up to 1220 m where the subalpine fir zone began. This re-

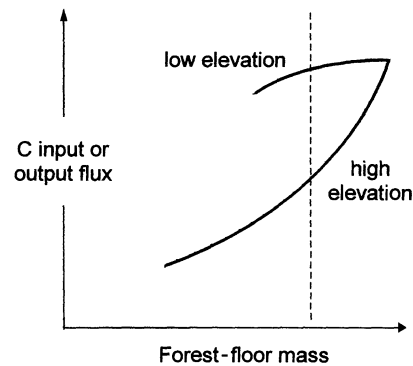


FIG. 11. A generalized curve showing hysteresis in the relationships among mass of the forest floor and input or output fluxes of C within a single cover category (hardwoods). This relationship is evident in fluxes of DOC leaching (Fig. 7), fluxes of  $\text{CO}_2$ -C mineralization (Fig. 8), and fluxes of litter input (Fig. 10). The dashed vertical line emphasizes that, for a given value of forest-floor mass, there may be two values for a given flux, arising from different residence times for C at different elevations.

lationship was strengthened by increased concentrations of organic N in the forest floor at higher elevations, arising partly from the higher N concentrations in foliar, fine root, and woody litter in *Abies* and *Picea* relative to hardwoods (Table 1), and partly from higher masses of humus. The high N contents of the forest floors at elevations above 1000 m also arose partly as a result of lower fluxes of DON leaching that resulted from reduced rates of detrital decay.

#### Methodology, data limitations, and scale

Where insufficient data were available for functional relationships, we sometimes adopted the "null model" approach of including no effect. The production and decomposition of woody litter constitute an area where our model was sensitive and where data were sparse (Alban and Pastor 1993). Woody litter makes an important contribution to forest-floor mass during aggradation after clear-cutting (Roskoski 1980, Covington 1981). Because the C:N ratio in woody litter is so high, the humification of fine woody debris may also be an important component of N retention by organic matter. We were not able to partition woody litter into C classes or otherwise synthesize the decomposition of woody litter conceptually with the decomposition of foliage and fine roots. In reality some woody material may leach from the forest floor, and some probably does become humified, although what fractions do are open questions. We also omitted potential effects of temperature and moisture on wood decomposition. In this case the use of the null model seemed particularly justified because Mattson et al. (1987) and Alban and Pastor (1993) found nearly equivalent decay rates for coarse woody debris in North Carolina and Minnesota.

In these and other cases, though null models may turn out to be inaccurate, we believe their use is a valid

and sometimes desirable approach. The more "null" relationships that are used in a complex model, the more straightforward it is to interpret predictions in terms of processes that *are* better quantified. This modeling methodology is conceptually akin to a stepwise multiple regression in statistics, where additional terms are included in the model only if they are significant. As more data become available for additional sites or for poorly characterized processes, additional functional relationships can be included if they contribute significantly to landscape patterns.

Where our model structure demanded parameters that were difficult to obtain in the literature, in some cases we back-calculated them by calibrating the model to measurements made at individual sites. An example was the humus decay rate ( $k_H$ ), a highly sensitive parameter in the model. Based on this sensitivity, together with the paucity of field measurements on the rates of humus formation and decay, we suggest that research is needed in this area. A 10% increase or decrease in  $k_H$  for northern hardwoods yielded forest-floor mass 60 yr after clear-cutting that was lower or higher by ~5%. The sharper peak we predicted in mass of hardwood forest floors with elevation, compared with the broader peak in spruce-fir forest (Fig. 6B), resulted from using different values of  $k_H$ . The higher  $k_H$  that we calculated for hardwood forests made humus a smaller fraction of total forest-floor mass and made the total mass more responsive to elevational gradients in litter production. For calibrated parameters like  $k_H$ , the value we found should be interpreted carefully in terms of our assumptions and model structure. For example, we assumed no downward mixing of organic matter into mineral soil due to invertebrate activity; if we had included such an effect, our values for  $k_H$  would have been lower.

It may always be necessary to calibrate  $k_H$  in ecosystem models. At the Harvard Forest, mice excavate tunnels in the humus, apparently stimulating humus decomposition because the walls of the tunnels become lined with fungal mycelia. Quantifying all faunal effects on humus decay rates mechanistically could prove very difficult. The best way to estimate rates of humus decay may be as we have done here: calibration at sites where litter inputs and forest floor mass are known. This underscores the need and the importance of long-term studies in ecosystems where climatic records are kept and rates of input of the various types of litter can be measured.

Our spatially explicit analysis was based on a mix of real and abstracted patterns. Actual LULC data were used with actual species mixes and litter quality. However, broadscale statistical generalizations were made about forest cover categories, litter production, temperature, and precipitation patterns in the region. General trends in litterfall may only be valid at large scales in WMNF (Reiners and Lang 1987). The fact that we modeled each cell at 60 yr following clear-cutting added another hypothetical element. Capturing true spatial

heterogeneity would demand data layers describing disturbance history in patches across WMNF. One could easily make isolated measurements that did not fit the patterns we found; Rustad and Cronan (1988), for example, measured forest-floor mass of 140 Mg/ha in a *Picea rubens* stand in eastern Maine at low elevation. In high-elevation forest, comparisons with field measurements are even more problematic because of patchiness, boulder fields, and potentially great variability in winds and precipitation from peak to peak. To overcome these difficulties we simulated a large number of cells (~32 000) across the region, capturing what we hypothesized to be dominant processes, and extracted landscape-scale patterns through statistical generalizations across numerous, similar gradients within the region.

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## APPENDIX

Mass is lost from each carbon class exponentially as follows:

$$\Delta M_{LC}(t) = M_{LC}(t-1)\gamma(\text{AET})(1 - e^{-k_{LC}t}) \quad (\text{A.1})$$

$$\Delta M_C(t) = M_C(t-1)\gamma(\text{AET})(1 - e^{-k_C t}) \quad (\text{A.2})$$

$$\Delta M_E(t) = M_E(t-1)\gamma(\text{AET})(1 - e^{-k_E t}) \quad (\text{A.3})$$

where  $t$  is one model timestep (one month) and  $M_{LC}$ ,  $M_C$ , and  $M_E$  represent mass in the lignocellulose (LC), unprotected cellulose (C), and extractives (E) pools. The climatic effect,  $\gamma(\text{AET})$ , derives from the data of Berg et al. (1993):

$$\gamma(\text{AET}) = e^{(0.00189\text{AET} - 2.44)} / e^{(0.00189\text{AET}' - 2.44)} \quad (\text{A.4})$$

where AET is the annual total evapotranspiration in milli-

meters, and AET' is the value used to parameterize the model, the average annual AET on Blackhawk Island, Wisconsin during the litter-decay study from which the exponential decay constants  $k_{LC}$ ,  $k_C$ , and  $k_E$  derive (Table A.1; Aber et al. 1984, 1990). The decay parameters  $k_{LC}$ ,  $k_C$ , and  $k_E$  vary in each timestep as functions of the lignocellulose index (LCI) of material summed in the LC, C, and E fraction pools where:

$$\text{LCI}(t) = \frac{\text{lignin}}{(\text{lignin} + \text{holocellulose})} \quad (\text{A.5})$$

Material is transferred to the humus pool from the LC pool at a rate equal to one-third the value of  $\Delta M_{LC}(t)$ . Mass is lost exponentially from the humus pool:

$$\Delta M_H(t) = M_H(t-1)\gamma(\text{AET})(1 - e^{-k_H t}) \quad (\text{A.6})$$

TABLE A1. Model parameters for decomposition and microbial growth. Equations for carbon-class decay constants are from Aber et al. (1990). LCI = lignocellulose index.

Model parameter	Parameter value
Decay of carbon classes	$k_{LC}(t) = 0.0011 + 0.053\text{LCI}(t)$ $k_C(t) = 0.0476[1 - \text{LCI}(t)]$ $k_E(t) = 0.115[1 - 1.5\text{LCI}(t)]$
Decay constants for humus	$k_H = 0.00116/\text{mo}$ (hardwoods, pines) $k_H = 0.0059/\text{mo}$ (spruce-fir) $k_H = 0.000875/\text{mo}$ (mixed, above 450 m)
Decay constant for woody litter	$k_W = 0.067/\text{mo}$
Time to reach closed-canopy woody litter $W_{cc}$	$T_{cc} = 45$ yr
Annual AET for Wisconsin	AET' = 595 mm
Critical C:N ratio for well-decayed wood	CNwdw = 20:1
N content of microbial biomass	$n_m = 3\%$
$e_i$ = microbial efficiency on substrate $i$	$e_{LC} = 0.175$ ; $e_C = 0.35$ ; $e_E = 0.7$
Microbial biomass proximate C fractions	$m_{LC} = 50\%$ ; $m_C = 10\%$ ; $m_E = 40\%$
Turnover of microbial biomass	$k_m = e^{-1}$ (per month)

TABLE A2. Partitioning of carbon loss into leached DOC and mineralized CO<sub>2</sub>. Values in the table indicate fraction of mass loss partitioned into DOC leaching; all remaining C loss occurs as mineralization to CO<sub>2</sub>.

C pool	Hardwood	Coniferous
Lignocellulose (LC)	0.199	0.337
Unprotected cellulose (C)	0.138	0.212
Extractives (E)	0.048	0.069
Humus (H)	0	0
Woody detritus (W)	0	0

where  $k_H$  is constant within each forest cover category (Table A.1).

For woody litter, DocMod includes only fine woody debris (FWD), defined as material initially  $\leq 5$  cm in diameter. The calculation of fine woody debris from total woody production in closed-canopy forest (as calculated by PnET) is as follows. A logistic-like relation describes the increase in woody litterfall during forest aggradation:

$$\begin{aligned} \text{fw}_{cc}(T) &= 0.5\text{FWD}_{cc}[1 - \cos(T\pi/T_{cc})] \\ &\text{for } 0 \leq T < T_{cc}, \\ \text{fw}_{cc}(T) &= \text{FWD}_{cc} \\ &\text{for } T \geq T_{cc} \end{aligned} \quad (\text{A.7})$$

where  $\text{FWD}_{cc}$  is the annual mass of FWD in litterfall in closed-canopy forest,  $T$  is time in years,  $\text{fw}_{cc}(T)$  is the annual mass of FWD in litterfall in year  $T$ , and  $T_{cc}$  is the time period (years) over which  $\text{fw}_{cc}(T)$  reaches  $\text{FWD}_{cc}$  (Table A.1).  $\text{FWD}_{cc}$  itself is calculated as a variable fraction of total woody production in closed-canopy forest,  $W_{cc}$ :

$$\text{FWD}_{cc} = W_{cc}e^{(0.008E - 2)}. \quad (\text{A.8})$$

where  $E$  is elevation in meters.

The pool of woody detritus loses mass independently of climate or litter quality, where  $t$  is the model timestep in months and  $k_w$  is the decay constant for woody detritus (Table A.1):

$$\Delta W(t) = W(t-1)(1 - e^{-k_w}) \quad (\text{A.9})$$

Carbon loss (calculated as 0.5 times mass loss) from each forest-floor pool is partitioned into leached DOC and mineralized CO<sub>2</sub> (Table A.2).

Production of microbial biomass  $P_m(t)$  in each month  $t$  is based on mass loss in each carbon class, together with the microbial production-to-respiration ratio  $\beta$  for each carbon class:

$$P_m(t) = \Delta M_{LC}(t)\beta_{LC} + \Delta M_C(t)\beta_C + \Delta M_E(t)\beta_E \quad (\text{A.10})$$

where  $e$  represents microbial efficiency on each substrate (Table A.1) and

$$\beta_i = \frac{e_i}{1 - e_i}. \quad (\text{A.11})$$

Microbial uptake of N is calculated as microbial production times the N content of microbial biomass  $n_m$ :

$$\Delta N_m(t) = P_m(t) \times n_m. \quad (\text{A.12})$$

Microbial turnover at the rate  $k_m$  results in a redistribution of mass to the LC, C, and E pools based on the fractions of microbial biomass composed by each carbon class (Table A.1). N is redistributed from microbial biomass to the C and E pools at the same rates. N is not redistributed to the LC pool based on microbial turnover, however, but based on a separate function describing the annual N dynamics of the LC pool:

$$\begin{aligned} \Delta N_{LC}(T) & \\ &= M_{LC}(T-1) \left( -0.951 \frac{N_{LC}(T-1)}{M_{LC}(T-1)} + 0.0142 \right) \end{aligned} \quad (\text{A.13})$$

where  $T$  is in years,  $N_{LC}$  represents the total N in the lignocellulose pool, and  $M_{LC}$  represents the mass in the lignocellulose pool. This function is calculated once at the start of each annual period in DocMod; the changes in N content of the LC pool in each of the subsequent 12 mo is calculated as 1/12 of this value:

$$\Delta N_{LC}(t) = \Delta N_{LC}(T)/12 \quad (\text{A.14})$$

where  $t$  is time in months.