Available online at www.sciencedirect.com

Applied Soil Ecology 23 (2003) 165–179

Applied Soil Ecology

www.elsevier.com/locate/apsoil

Effects of disturbance and ecosystem on decomposition

D.A. Neher [a,*], M.E. Barbercheck [b,1], S.M. El-Allaf [a,2], O. Anas [a]

[a] Department of Plant Pathology, North Carolina State University, Raleigh, NC 27695-7616, USA
[b] Department of Entomology, North Carolina State University, Raleigh, NC 27695-7634, USA

Received 31 December 2001; accepted 20 March 2002

Abstract

Decomposition of organic matter integrates collective activities of organisms within the soil food web. We compared decomposition of museum board (predominantly cellulose) and balsa wood substrates in 18 sites chosen to represent a completely nested design with two disturbance levels nested within three ecosystems (agriculture, wetland, and forest) and ecosystems nested within three land resource regions (LRR) in North Carolina. Percentage mass remaining and daily rate of mass loss of museum board and balsa wood substrates were analyzed using repeated measures analysis of covariance with soil physical and chemical properties as covariates. At the end of the two-year monitoring period, the percentage of museum board and balsa wood substrates remaining was least in agricultural and wetland and greatest in forest ecosystems. Soil pH influenced the percentage of substrate remaining based on days of incubation, and its effects were greater than electrical conductivity, percentage soil organic matter, and total available soil nitrogen (N). Percentage of substrate remaining (museum board or balsa wood) was correlated negatively with pH for all sites, suggesting that pH should be included as a covariate if measures of decomposition are used as environmental indicators. Overall, rate of decomposition of museum board substrates distinguished between relative levels of disturbance in agricultural and wetland but not forest ecosystems. The rate of balsa wood decomposition distinguished between relative levels of disturbance in wetland but not forest or agricultural sites. Forest soils had consistently lower total N and electrical conductivity, and sometimes lower pH, associated with slower decomposition than disturbed wetlands or agricultural lands. We conclude that for short-term monitoring, measures of decomposition of predominantly cellulose substrates can be used to distinguish between relative levels of disturbance in agricultural and wetland but not forest systems. Differences in decomposition may signal either a change in decomposer community or condition of biotic and abiotic resources at a site.

Keywords: Agricultural ecosystems; Balsa wood; Cellulose; Decomposition; Environmental monitoring; Forests; Indicators; Lignin; Wetlands

1. Introduction

The decay of organic matter is critical to mineralization and nutrient cycling in ecosystems. Energy and nutrients obtained by plants eventually become incorporated in detritus that provides the resource base of complex food webs in soil. Because decomposition of organic materials is measured easily and serves as an integrator of the collective activities of organisms

* Corresponding author. Present address: Department of Earth, Ecological and Environmental Sciences, University of Toledo, 2801 W. Bancroft, Toledo, OH 43606, USA. Tel.: +1-419-530-2585; fax: +1-419-530-4421.
E-mail address: deborah.neher@utoledo.edu (D.A. Neher).
[1] Present address: Department of Entomology, The Pennsylvania State University, University Park, PA 16802, USA.
[2] Present address: 113 Selby, Ohio Agricultural Research and Development Center, Wooster, OH 44691, USA.

0929-1393/03/$ – see front matter © 2003 Elsevier Science B.V. All rights reserved.
doi:10.1016/S0929-1393(03)00043-X

within a soil food web, decomposition has the potential to serve as an indicator of soil condition (Moore and DeRuiter, 1993). The rate of decomposition is a function of many characteristics and processes including chemical composition or quality of the organic material, temperature, moisture and composition of the decomposer community. Therefore, a significant difference in the rate of decomposition between similar sites may signal either a change in decomposer community or condition of biotic and abiotic resources at a site.

Plant litter is a mixture of labile (e.g. cellulose and hemicellulose) and recalcitrant (e.g. lignin) substrates that decompose at progressively slower rates (Coleman and Crossley, 1996). Cellulose and the lignin polymer are among the most abundant organic compounds on earth. Cellulose is the main carbohydrate constituent of plant cell walls and is decomposed by a wide variety of microorganisms (Paul and Clark, 1996). Lignin, an aromatic compound, coats cell walls and combines chemically with cellulose to form lignocellulose. In contrast with cellulose, lignin is one of the most resistant components in plant litter and only specialized organisms decompose it (Dix and Webster, 1995). An inverse relationship between lignin concentration and the rate of decomposition has been observed previously (Fogel and Cromack, 1977; Meentemeyer, 1978; Berg and Staaf, 1980; Melillo et al., 1982). Consequently, lignin/N (Melillo et al., 1982) and cellulose/lignin/N (Entry and Backman, 1995) ratios have been suggested as predictors of soil organic matter decomposition.

We conducted an experiment to compare decomposition across ecosystems in three land resource regions (LRR). Our goal was to determine whether decomposition patterns are affected more by ecosystem type or LRR. Secondly, we wanted to determine if selected measures of decomposition or soil factors associated with decomposition distinguish between levels of disturbance, as a proxy for ecosystem condition, for use in a national environmental monitoring program. Two criteria necessary for adoption of decomposition as a reliable and interpretable indicator were defined as consistency of decomposition patterns within an ecosystem type, and ability to consistently distinguish levels of disturbance.

2. Materials and methods

2.1. Site selection

North Carolina was chosen as the initial study site for testing a range of indicators of ecosystem condition that could be applied across terrestrial ecosystems. North Carolina has a wide range of soil types and a diversity of terrestrial ecosystems including forests, wetlands, and agriculture. These terrestrial ecosystems are arranged spatially in a mosaic in three land resource regions within the state, i.e. coastal plain, piedmont, and mountains. LRR represent geographic areas with unique soil type, topography, climate and water resources (USDA-SCS, 1981).

Several criteria were established for selection of the monitoring sites. First, a forest, wetland, and agricultural site were located within a hydrogeologic unit in each of the mountain, piedmont, and coastal plain LRRs of North Carolina. The mountain, piedmont, and coastal plain sites were located in Buncombe, Lincoln, and Jones counties, North Carolina, respectively (Table 1). Overlaying maps of soil and hydrogeologic unit identified pairs of sites with similar soil type. Hydrogeologic units were chosen as the degree of resolution because they describe areas of similar geology within a watershed (Daniel and Payne, 1990). For each of the three ecosystems in each of the three LRR, one relatively undisturbed and one relatively disturbed sampling site were chosen. Undisturbed sites were defined as a forest stand >20 years old, a wetland that is functioning as a wetland, and a permanent pasture >10 years old. Disturbed sites were defined as a forest plantation that was planted <3 years before the first sample date, a wetland that had been converted to a use other than wetland within 20 years before the first sample date, and agricultural fields under annual cultivation and crop production. The final selection of the 18 sites was completed in coordination with personnel from the Natural Resources Conservation Service and US Geological Survey in Raleigh, North Carolina. USGS has delineated unpolluted or baseline conditions of forested and agricultural basins in North Carolina (Simmons and Heath, 1982; Caldwell, 1992; Gunter et al., 1993).

Table 1
Descriptions of relatively disturbed and undisturbed study sites in North Carolina

Region	Ecosystem relative condition	
	Disturbed	Undisturbed
Forest		
Mountains	Clifton Typic Hapludults; clayey, mixed, mesic; 15–45% slope; harvested in 1990, hilltop planted to white pine, *Pinus strobus*, in 1993	Clifton Typic Hapludults; clayey, mixed, mesic; 15–45% slope; >90 year old white pine (dominant) with holly, *Ilex vomitoria*
Piedmont	Gaston sandy clay loam. Loblolly pine, *Pinus taeda*, planted in 1992	Gaston sandy clay loam. Loblolly pine planted 1939
Coastal plain	Rains fine sandy loam; fine–loamy, siliceous, thermic Typic Paleaquults; slope <2%. Loblolly pine planted in 1992	Alpin fine sand; thermic coated Typic Quartzipsamments; 0–6% slope; >80 year old longleaf pine, *Pinus palustris*, (dominant) with loblolly bay, *Gordonia lasianthus*
Wetland		
Mountain	Toxaway loam black; cumulic Humaquepts, fine–loamy, mixed, non-acid, mesic; slope 0–2%; >50 cm overwash; cultivated >45 years. Corn, *Zea mays*, planted in 1993	Toxaway loam brown; cumulic Humaquepts, fine–loamy, mixed, non-acid, mesic; slope 0–2%; 20 cm overwash. Undisturbed since 1968
Piedmont	Worsham fine sandy loam, hydric. Cultivated >55 years. Soybeans, *Glycine max*, planted in 1993	Worsham fine sandy loam, hydric; no overburden. Planted to pines in 1960.
Coastal plain	Torhunta fine sandy loam; coarse–loamy, siliceous, acid, thermic Typic Humaquepts; slope <2%; cultivation history unknown. Corn planted in 1993	Torhunta fine sandy loam; coarse–loamy, siliceous, acid, thermic Typic Humaquepts; slope <2%. Closed canopy natural pond pine, *Pinus serotina*, woodland
Agriculture		
Mountain	Iotla Aquic Udifluvents, coarse–loamy, mixed, mesic; 0–3% slope; cultivated >16 years. Field corn planted in 1993	Iotla Aquic Udifluvents, coarse–loamy, mixed, mesic; 0–3% slope. Planted in fescue, *Festuca ovina*, and ladino clover, *Trifolium repens*, >20 years
Piedmont	Cecil sandy clay loam, not very eroded. Cultivated >55 years. Wheat, *Triticum aestivum*, and soybean planted in 1993	Cecil sandy clay loam. Fescue pasture planted in 1959
Coastal plain	Alpin fine sand; thermic coated Typic Quartzipsamments; 0–6% slope. Cultivated >50 years	Alpin fine sand; thermic coated Typic Quartzipsamments. Pasture since 1956

2.2. Soil samples

Soil samples were collected at each of the 18 sites eight times per year for two years, starting in March 1994 and ending in November 1995. Because many soil characteristics are aggregated spatially, soil samples were collected using a systematic pattern. Two sets of soil samples were taken along two independent diagonal transects within a 2 ha area, with a random starting point (Neher et al., 1995). Soil samples were collected using an Oakfield Tube soil probe (2 cm diameter, 20 cm depth). Twenty soil cores were collected from each of two independent transects. Soil from each transect was pooled, forming two composite samples which were homogenized by hand in a bucket. All soil samples were stored at 14 °C until processed (Barker et al., 1969).

Characteristics determined for the soil at each study site included percentage soil organic matter, pH, electrical conductivity, total available nitrogen (N) and texture (Table 2) (Doran and Parkin, 1996). Soil organic matter was determined by loss-on-ignition (Schulte et al., 1991). A 1:1 water pH of the soil solution and electrical conductivity was determined according to Smith and Doran (1996). Available pools of N (nitrate and ammonium) were measured by colorimetric reaction (Cataldo et al., 1975; Keeney and Nelson, 1982). The indophenol blue method was used to determine ammonium concentration (Keeney and Nelson, 1982). EDTA was added to the soil filtrate to prevent interference by calcium and magnesium ions. Soil texture was determined by the hydrometer method (Gee and Bauder, 1986). Daily means for soil temperature and moisture in all forest sites were recorded with Campbell 21X dataloggers using thermistors and

Table 2
Soil analysis for relatively disturbed and undisturbed study sites North Carolina[a]

Location condition	Sand (%)	Silt (%)	Clay (%)	Total N ($\mu g\,g^{-1}$)	EC ($dS\,m^{-1}$)	SOM (%)	pH
Agriculture							
Mountains							
Disturbed	21.9	52.5	25.7	25.3 (6.37)	0.28 (0.040)	9.7 (0.20)	5.5 (0.11)
Undisturbed	18.2	60.3	21.6	6.7 (2.18)	0.19 (0.020)	9.6 (0.19)	6.6 (0.09)
Piedmont							
Disturbed	60.5	18.9	20.7	6.4 (1.16)	0.16 (0.010)	3.7 (0.15)	6.2 (0.07)
Undisturbed	57.4	18.1	24.5	3.7 (0.36)	0.17 (0.010)	4.8 (0.17)	5.7 (0.08)
Coastal plain							
Disturbed	92.9	4.0	3.2	2.7 (0.76)	0.07 (0.010)	1.6 (0.28)	5.9 (0.07)
Undisturbed	82.2	14.2	3.7	4.3 (0.98)	0.09 (0.009)	2.8 (0.11)	5.0 (0.08)
Forest							
Mountain							
Disturbed	40.9	23.3	35.9	2.3 (0.33)	0.05 (0.006)	5.8 (0.25)	4.8 (0.09)
Undisturbed	51.7	24.7	23.7	2.4 (0.27)	0.09 (0.007)	4.9 (0.15)	4.6 (0.04)
Piedmont							
Disturbed	31.2	24.3	44.5	1.7 (0.11)	0.05 (0.004)	6.7 (0.13)	4.8 (0.05)
Undisturbed	51.2	14.2	34.7	2.3 (0.16)	0.08 (0.008)	5.1 (0.07)	4.9 (0.22)
Coastal plain							
Disturbed	72.4	15.3	12.4	1.9 (0.29)	0.06 (0.006)	2.2 (0.05)	4.7 (0.07)
Undisturbed	58.0	33.5	8.6	1.7 (0.12)	0.07 (0.002)	4.9 (0.22)	4.2 (0.06)
Wetland							
Mountains							
Disturbed	45.4	35.0	19.7	7.7 (1.96)	0.18 (0.030)	5.0 (0.12)	5.4 (0.07)
Undisturbed	38.4	44.0	17.7	3.6 (0.38)	0.12 (0.020)	8.4 (0.15)	4.7 (0.06)
Piedmont							
Disturbed	66.2	16.3	17.6	5.4 (0.47)	0.16 (0.010)	6.6 (0.19)	5.6 (0.08)
Undisturbed	70.4	16.3	13.4	4.5 (0.19)	0.16 (0.010)	9.0 (0.13)	4.9 (0.05)
Coastal plain							
Disturbed	75.4	21.0	3.7	16.8 (2.62)	0.26 (0.020)	18.3 (0.93)	4.6 (0.07)
Undisturbed	90.0	7.6	2.5	3.6 (0.28)	0.14 (0.006)	41.6 (2.9)	3.3 (0.06)

[a] Values represent means and standard errors (±standard error) ($n = 30$). EC: electrical conductivity, SOM: soil organic matter.

gypsum blocks, respectively, with sensors placed at 20 cm depth. The suite of soil properties were chosen based on their demonstrated potential to influence composition and activity of microbial and faunal communities involved in decomposition.

2.3. Decomposition substrates

We used standardized substrates that contained either predominantly cellulose or lignin to track decomposition through two years. Although the decomposition of museum board (Strathmore, 100% cotton fiber, acid free and buffered with 2% calcium carbonate) and balsa wood (Midwest Co., 0.793 mm thick) substrates does not necessarily mimic the complexity of decomposition processes in native materials (Nieminen and Setälä, 1998; Butterfield, 1999), they provide a standard means of comparison across systems. We chose these two types of substrate because organic litter in most terrestrial ecosystems is a mixture of relatively labile and recalcitrant substrates, each with different rates of degradation.

To estimate rates of decomposition at the 18 sites, baskets (10 cm × 10 cm × 10 cm) constructed of galvanized hardware cloth (0.5 cm mesh) were buried at each site (Blair et al., 1991). Three baskets were placed along each of two transects at equal intervals. To install the baskets, a 10 cm × 10 cm × 10 cm cube of soil was removed carefully so that the structure and litter layer of the soil were disturbed minimally. The cube of excavated soil was placed inside the basket and the baskets placed in the excavation hole so that the top of the basket was flush with the soil surface. After the baskets were placed in the soil, 20 round disks (2-cm diameter) each of museum board (mean initial weight (±standard error) 184.7 mg (±0.39)) and balsa wood (mean initial weight 61.0 mg (±0.41)), dried at 70 °C and weighed, were placed between two 10 cm × 10 cm sheets of plastic window screen to exclude predation by macrofauna. This decomposition substrate-screen "sandwich" was placed on the soil surface inside the basket and the lid of the basket closed to maintain structural stability while exposed to any routine land management practices. At every sample date, one disk each of museum board and balsa wood were removed from the basket and returned to the laboratory for analysis. Museum board discs were retrieved and weight loss estimated by differential moisture contents of substrates incubated at constant water potential (Herrick, 1995). Balsa wood disks were cleaned gently under running tap water with a soft toothbrush to remove adhering soil particles. Mass of substrate remaining was calculated as the difference between initial and final weight, expressed as a percentage of initial weight at each collection time. Soil characteristics and decomposition were both measured along the same transects at concurrent times.

2.4. Cellulose and lignin in balsa wood substrates

We analyzed cellulose, soluble lignin, and insoluble lignin content in balsa wood substrates placed in undisturbed forests and wetlands in 1995 (Chen, 1988). Six disks (three baskets × two transects) from each sample date were combined per site and ground in a Wiley mill. Terpenes and similar compounds were removed from the 1 g samples with acetone (10:1) in a Soxtec System HT tecator. The dried ground balsa sample was transferred into 500 ml Erlenmeyer flasks with 10 ml of 75% sulfuric acid and 390 ml nanopure water and placed on a hot plate to boil and acid reflux gently for 4 h. The warm contents of the flasks were vacuum filtered through glass filters of known weight. Glass filters were dried and weighed to determine the amount of insoluble lignin. Concentration of soluble lignin in the solution was determined by ultraviolet spectrophotometry at 205 nm. Total cellulose was determined by subtracting the mass of insoluble and soluble lignin from total wood mass.

2.5. Data analysis

To meet assumptions of normality, proportions of remaining balsa wood and museum board decomposition substrates were transformed by arcsin of the square root, and rate (mg per day) of decomposition was transformed as $\ln(x + 1)$. Data were analyzed as a nested design (Type II sums of squares) with fixed, independent variables defined as ecosystem type and disturbance nested within ecosystem; LRR was a random block variable. Repeated measures analysis of covariance was performed using the MIXED procedure in SAS Version 8 (Cary, NC). Separate analyses were performed for two types of substrate (museum board, balsa wood) at the time scale of days of incubation in the field and two measures of decomposition (proportion of substrate remaining and rate of decomposition (mg per day) as dependent variables). Covariates included soil organic matter, pH, electrical conductivity and total available N. To meet assumptions of normality, proportion of organic matter and electrical conductivity were transformed as $\ln(x + 0.01)$ and total nitrogen availability as $\ln(x+0.1)$. Repeated measures analysis of covariance was performed for the forest sites with the additional factors of cumulative temperature (°C) and moisture (MPa) for the 7 days prior to estimating decomposition. Hereafter, temperature and moisture will be referred to as cumulative temperature or moisture. Repeated measures analysis of covariance was performed for the 1995 undisturbed forest and undisturbed wetland sites with percentage of cellulose, soluble lignin and insoluble lignin in balsa wood decomposition substrates with the soil physical and chemical covariates listed above.

A dummy variable regression was performed to test for commonality of slopes and/or intercepts of disturbed and undisturbed sites in each of the six combinations of ecosystem and decomposition substrate. Slope was estimated by linear regression for percentage of total mass remaining and log-linear transformation for mass (mg) substrate lost per day. In addition, slopes and intercepts were compared for percentage of cellulose, insoluble lignin and soluble lignin remaining in balsa wood disks in undisturbed forest and wetland sites in 1995.

3. Results

3.1. Decomposition based on proportion of substrate remaining

3.1.1. Ecosystem

Generally, percentage of mass of decomposition substrate remaining in each ecosystem type decreased linearly through time of incubation in the field (Fig. 1). Based on calculations of percentage mass remaining through time, decomposition of museum board was more rapid than balsa wood. At the end of the monitoring period, percentage of museum board (d.f. = 2, 419; $F = 31.19$, $P \leq 0.0001$) and balsa wood (d.f. = 2, 421; $F = 15.29$; $P \leq 0.0001$) substrates remaining was least in

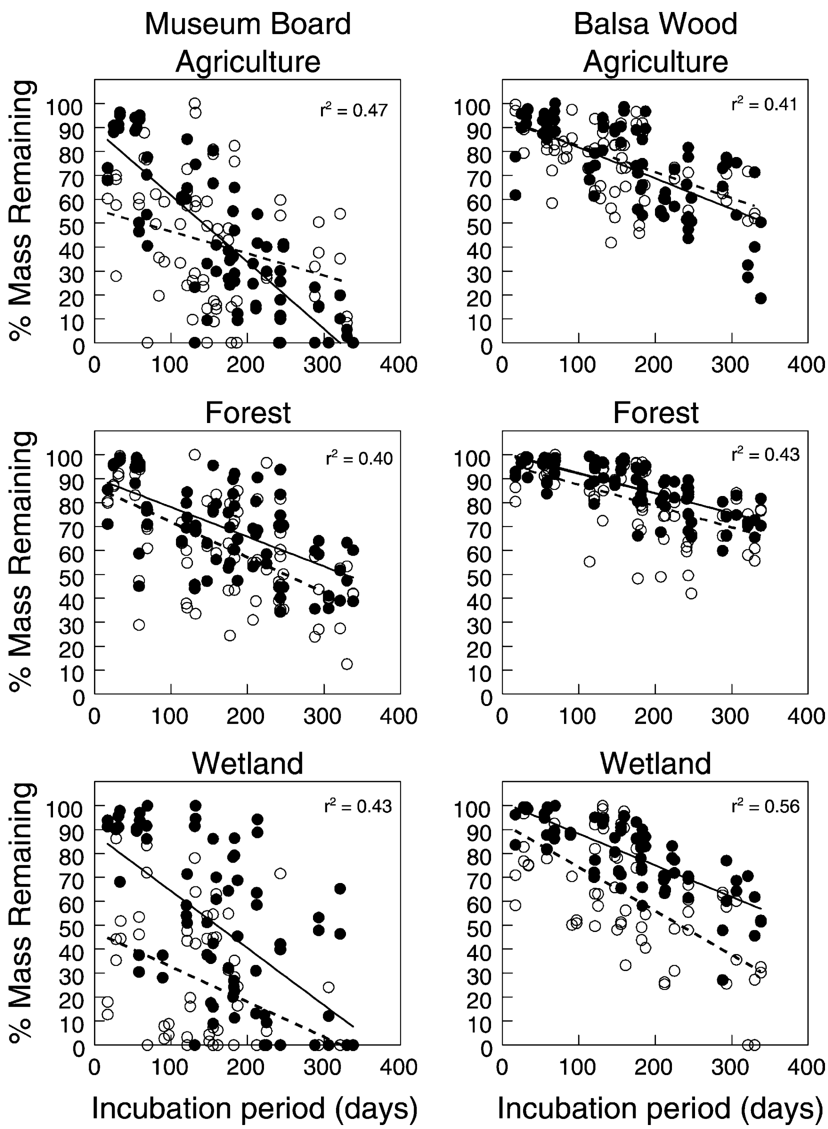

Fig. 1. Percentage of mass remaining of substrate (left, museum board; right, balsa wood) through time in field of relatively disturbed (dashed line, open symbols) and undisturbed (solid line, closed symbols) agricultural (top row), forest (middle row), and wetland (bottom row) ecosystems. The full model r^2 is reported for each linear regression.

agricultural and wetland sites, and greatest in the forest sites.

3.1.2. Disturbance

Disturbance nested within ecosystem affected decomposition rate of balsa wood (d.f. = 3, 421; F = 3.67; P = 0.0124) but not museum board (P = 0.1653). In agricultural sites, decomposition of museum board was more rapid initially in relatively disturbed than undisturbed sites, but slowed progressively through time so that percentage substrate remaining was greater in relatively disturbed sites at the end of the monitoring period canceling each other to give a net of no difference by levels of disturbance (Figs. 1 and 2). Linear regression models of percentage of museum board substrates remaining in relatively disturbed and undisturbed agricultural sites had heterogeneous slopes and heterogeneous intercepts. Disturbance had no effect on decomposition of museum board in forests (Table 3). Similar to agricultural sites, decomposition of museum board in wetland soils was greater initially in relatively

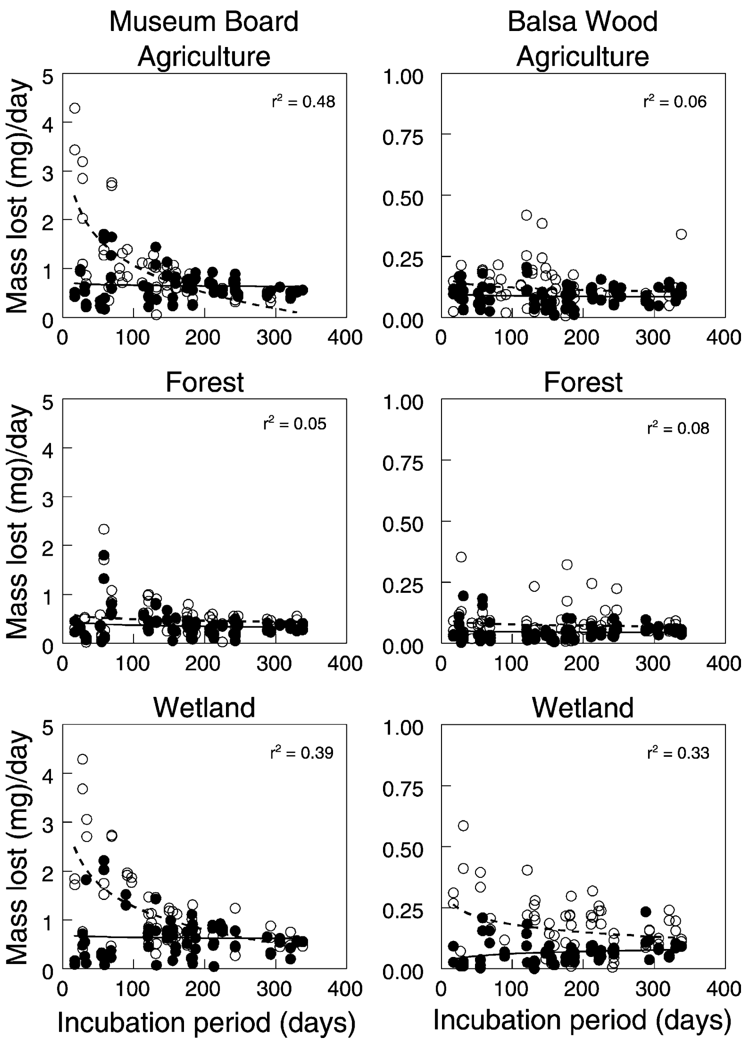

Fig. 2. Rate (mg per day) of decomposition of substrate (left, museum board; right, balsa wood) through time in field in relatively disturbed (dashed line, open symbols) and undisturbed (solid line, closed symbols) agricultural (top row), forest (middle row), and wetland (bottom row) ecosystems. Data are log-linear transformed and the full model r^2 is reported for each linear regression.

Table 3
Intercepts and slopes of linear regression equations for the relationship between percentage mass remaining of museum board and balsa wood substrates vs. days of incubation in the field in relatively disturbed and undisturbed sites in North Carolina

Decomposition substrate	Ecosystem	Relative condition	Intercept	Slope
Museum board	Agriculture	Disturbed	55.84*	−0.092*
		Undisturbed	89.47	−0.278
	Forest	Disturbed	86.77	−0.147
		Undisturbed	90.43	−0.124
	Wetland	Disturbed	47.55*	−0.147
		Undisturbed	88.15	−0.238
Balsa wood	Agriculture	Disturbed	93.26	−0.109
		Undisturbed	94.42	−0.128
	Forest	Disturbed	96.54	−0.089
		Undisturbed	100.24	−0.082
	Wetland	Disturbed	92.87	−0.183
		Undisturbed	101.43	−0.132

* Significant at $P \leq 0.05$ between disturbed and undisturbed.

disturbed than undisturbed sites, illustrated by contrasting values of y-intercept. In wetlands, however, after the initial incubation period, regression lines for percentage of museum board substrates were parallel suggesting similar magnitudes of decay (Table 3). In contrast, linear regression models of percentage of balsa wood decomposition substrates remaining through time were homogenous in both slope and intercept in relatively disturbed and undisturbed sites in all three ecosystem types (Fig. 1, Table 3).

3.1.3. Soil characteristics (covariates)

Soil characteristics, including soil pH, electrical conductivity and total N were associated with percentage of substrate remaining through time and daily rate of decomposition (Table 4). Soil pH influenced percentage of museum board ($F = 110.50$; $P \leq 0.0001$) and balsa wood ($F = 19.2$, $P \leq 0.0001$) remaining through time, and its effects were greater than electrical conductivity, percentage soil organic matter, or total available N. pH was correlated negatively with percentage of museum board substrate remaining in agricultural, forest and wetland ecosystems, and with percentage of balsa wood substrate remaining in forest and wetland sites (Table 5). Low pH soils in undisturbed wetlands and forests corresponded with relatively slow decomposition rates.

Electrical conductivity and total available N correlated negatively with percentage of museum board and balsa wood substrates remaining (Table 4). Although not significant, there was a trend for the percentage of soil organic matter content to correlate negatively with percentage of remaining museum board ($F = 3.25$; $P = 0.0723$) but not balsa wood substrates.

3.2. Decomposition rate

3.2.1. Ecosystem

Generally, daily rate (mg of mass loss per day) of decomposition was described best by a log-linear relationship (Fig. 2). Rates of decomposition of museum board (d.f. = 2, 421; $F = 23.11$; $P \leq 0.0001$) and balsa wood (d.f. = 2, 420; $F = 11.50$; $P \leq$

Table 4
Correlation of covariates with measures of decomposition across ecosystems and relative disturbance levels at study sites in North Carolina[a]

Decomposition substrate	Measure	pH	EC ($dS\,m^{-1}$)	SOM (%)	Total N ($\mu g\,g^{-1}$)
Museum board	Percentage of mass remaining	$r = -0.44$*** d.f. = 432	$r = -0.33$*** d.f. = 432	$r = -0.12$** d.f. = 432	$r = -0.26$*** d.f. = 434
	Mass (mg) loss per day	$r = 0.48$*** d.f. = 434	$r = 0.30$*** d.f. = 434	$r = -0.01$ d.f. = 434	$r = 0.25$*** d.f. = 436
Balsa wood	Percentage of mass remaining	$r = -0.28$*** d.f. = 434	$r = -0.19$*** d.f. = 434	$r = -0.04$ d.f. = 433	$r = -0.20$*** d.f. = 434
	Mass (mg) loss per day	$r = 0.33$*** d.f. = 433	$r = 0.22$ d.f. = 433	$r = -0.02$ d.f. = 433	$r = 0.28$*** d.f. = 433

[a] EC: electrical conductivity, SOM: soil organic matter.
** Significant at $P \leq 0.01$.
***Significant at $P \leq 0.0001$.

Table 5
Correlation between pH and measures of decomposition in agricultural, forest and wetland ecosystems, combined across relative disturbance levels and land resource regions (LRR)

Substrate	Measure	Agriculture	Forest	Wetland
Museum board	Percentage of mass remaining	$r = -0.35$*** d.f. = 140	$r = -0.60$*** d.f. = 155	$r = -0.56$*** d.f. = 137
	Mass (mg) loss per day	$r = 0.35$*** d.f. = 142	$r = 0.53$*** d.f. = 155	$r = 0.59$*** d.f. = 137
Balsa wood	Percentage of mass remaining	$r = -0.09$ d.f. = 140	$r = -0.33$*** d.f. = 156	$r = -0.39$*** d.f. = 138
	Mass (mg) loss per day	$r = 0.03$ d.f. = 140	$r = 0.24$** d.f. = 155	$r = 0.47$*** d.f. = 138

** Significant at $P \leq 0.01$.
*** Significant at $P \leq 0.0001$.

0.0001) substrates differed among ecosystems. Typically, rates were greater in agricultural or wetland than forest ecosystems (Fig. 2).

3.2.2. Disturbance

Relative level of disturbance affected decomposition rates of balsa wood (d.f. = 9, 420; $F = 9.07$; $P \leq 0.0001$) but not museum board (d.f. = 3, 421; $F = 2.26$; $P = 0.0805$) substrates. Based on r^2 values, ecosystems with cultivation (i.e. disturbed agriculture and disturbed wetland sites) were explained better by a log-linear relationship than ecosystems without cultivation (i.e. undisturbed agriculture, undisturbed wetland, disturbed and undisturbed forests) (Fig. 2). Without cultivation, log-linear regression models of decomposition through time of museum board substrates were similar to those of percentages of substrate remaining in relatively disturbed and undisturbed sites. Specifically, there was no effect of disturbance on intercept or slope of regression lines in forest sites (Table 6, Fig. 1). However, in agricultural and wetland sites, decomposition rates of museum board were greater initially (y-intercepts) in relatively disturbed sites and declined progressively through the incubation period to eventually match rates of relatively undisturbed sites (Table 6, Fig. 2). Disturbance had less effect on decomposition rates of balsa wood than museum board. For example, decomposition rate of balsa wood was similar among levels of disturbance in agricultural and forest ecosystems. In contrast, both initial mass (y-intercept) and change in mass (mg) loss per day (slope) of balsa wood substrates were greater in relatively disturbed than undisturbed wetland sites (Table 6, Fig. 2).

3.2.3. Soil characteristics (covariates)

Soil pH, electrical conductivity, and total available N were correlated positively with decomposition rate of both museum board and balsa wood substrates (Table 4). Soil pH influenced rates of mass loss (mg per day) of museum board ($F = 57.20$; $P \leq 0.0001$) and balsa wood ($F = 7.60$; $P = 0.0061$) substrates.

Table 6
Intercepts and slopes for linear regression equations for the relationship between mass (mg) loss per day of museum board and balsa wood substrates vs. days of incubation in relatively disturbed and undisturbed sites in North Carolina

Decomposition substrate	Ecosystem	Relative condition	Intercept	Slope
Museum board	Agriculture	Disturbed	4.78*	−0.806*
		Undisturbed	0.75	−0.019
	Forest	Disturbed	0.72	−0.048
		Undisturbed	0.55	−0.039
	Wetland	Disturbed	4.44*	−0.686*
		Undisturbed	0.73	−0.018
Balsa wood	Agriculture	Disturbed	0.19	−0.015
		Undisturbed	0.11	−0.004
	Forest	Disturbed	0.11	−0.007
		Undisturbed	0.06	−0.003
	Wetland	Disturbed	0.39*	−0.046*
		Undisturbed	−0.0002	+0.014

* Difference between disturbed and undisturbed sites significant at $P \leq 0.05$.

Soil pH was correlated positively with decomposition rate of museum board substrate in agricultural, forest and wetland sites, and with balsa wood in the forest and wetland sites (Table 5).

There was a trend for total available N concentration to positively influence the rate of balsa wood ($F = 3.37$, $P = 0.0669$) and museum board ($F = 2.95$, $P = 0.0864$) decomposition. Soil organic matter and electrical conductivity were not associated significantly with rate of decomposition of either substrate.

3.3. Forest system

In forests sites, soil pH, cumulative temperature and cumulative moisture influenced percentage of museum board and balsa wood substrate remaining. Soil pH affected percentage of substrate remaining and decomposition rate of both substrates (Table 7). As pH decreased, rates of decomposition slowed and amount of substrate remaining was greater. As soil temperature increased, rate of museum board decomposition decreased and percentage remaining of museum board and balsa wood was smaller. Soil moisture affected percentage of substrate remaining but not rate of decomposition of both substrate types. As moisture decreased, a greater proportion of museum board and smaller proportion of balsa wood remained (Table 7). Of the remaining covariates, greater organic matter content in soil was associated negatively with percentage of museum board remaining ($F = 4.60$; $P = 0.0337$) but not decomposition rate of museum board ($F = 1.18$, $P = 0.2801$). In contrast, greater electrical conductivity was associated positively with percentage of balsa wood remaining ($F = 3.06$; $P = 0.0826$) and negatively with decomposition rate of balsa wood ($F = 3.81$; $P = 0.0529$).

Decomposition rate of museum board (d.f. = 1, 141; $F = 4.54$; $P = 0.0348$) and balsa wood (d.f. = 1, 141; $F = 4.36$; $P = 0.0386$) substrates was greater in relatively disturbed than undisturbed forest sites. Association among covariates and measures of decomposition differed by level of disturbance (Table 8). For example, pH correlated negatively with percentage remaining and positively with decomposition rate of both substrate types in disturbed forests. The same relationship occurred in undisturbed forests except there was no association between pH and decomposition rate of balsa wood. There were no clear relationships between disturbance level and the remaining covariates.

3.4. Decomposition of cellulose and lignin in balsa wood

Length of incubation, LRR, ecosystem, pH, percentage soil organic matter, total available N, electrical conductivity, cumulative soil temperature (°C) and moisture (MPa) had no effect on the percentage of insoluble lignin, soluble lignin, or cellulose in balsa wood substrates placed in undisturbed forests and wetlands in 1995. The mean (±standard error) percentages of insoluble lignin, soluble lignin, and cellulose in the balsa wood decomposition substrates were 19.93 (±1.44), 0.42 (±0.03), and 77.08 (±1.41), respectively.

Table 7
F-statistics from repeated measures analysis of covariance among measures of decomposition and climate covariates in relatively disturbed and undisturbed forest sites

Condition substrate	Measure	pH	Temperature (°C)[a]	Moisture (MPa)[a]
Museum board	Percentage of mass remaining	84.89***	6.71*	11.80**
	Mass (mg) loss per day	35.55***	9.66**	0.12
Balsa wood	Percentage of mass remaining	33.38***	38.79***	11.37**
	Mass (mg) loss per day	6.50*	1.10	1.62

Associations between percentage organic matter, electrical conductivity, total available N and measures of decomposition were not significant and are not shown.

[a] Accumulated for 7 days before measurement made.

* Significant at $P \leq 0.05$.

** Significant at $P \leq 0.01$.

*** Significant at $P \leq 0.0001$.

Table 8
Linear correlations among covariates and measures of decomposition in relatively disturbed and undisturbed forest sites

Condition substrate	Measure	pH	Electrical conductivity	Temperature (°C)[a]	Moisture (MPa)[a]
Disturbed					
Museum board	Percentage of mass remaining	$r = -0.59$*** d.f. = 77	$r = -0.13$ d.f. = 77	$r = 0.06$ d.f. = 77	$r = 0.18$ d.f. = 73
	Mass (mg) loss per day	$r = 0.40$*** d.f. = 77	$r = 0.03$ d.f. = 77	$r = -0.36$** d.f. = 77	$r = -0.21$ d.f. = 73
Balsa wood	Percentage of mass remaining	$r = -0.36$** d.f. = 78	$r = -0.02$ d.f. = 78	$r = -0.15$ d.f. = 78	$r = 0.01$ d.f. = 74
	Mass (mg) loss per day	$r = 0.29$** d.f. = 77	$r = -0.13$ d.f. = 77	$r = -0.11$ d.f. = 77	$r = -0.06$ d.f. = 73
Undisturbed					
Museum board	Percentage of mass remaining	$r = -0.60$*** d.f. = 78	$r = -0.24$* d.f. = 78	$r = -0.17$ d.f. = 78	$r = -0.19$ d.f. = 78
	Mass (mg) loss per day	$r = 0.57$*** d.f. = 78	$r = 0.07$ d.f. = 78	$r = -0.14$ d.f. = 78	$r = 0.29$** d.f. = 78
Balsa wood	Percentage of mass remaining	$r = -0.24$* d.f. = 78	$r = -0.09$ d.f. = 78	$r = -0.53$*** d.f. = 78	$r = -0.05$ d.f. = 78
	Mass (mg) loss per day	$r = 0.04$ d.f. = 78	$r = -0.07$ d.f. = 78	$r = 0.23$* d.f. = 78	$r = -0.16$ d.f. = 78

Correlations between percentage organic matter, total available N and measures of decomposition were not significant and are not shown.
[a] Accumulated for 7 days before measurement.
* Significant at $P \leq 0.05$.
** Significant at $P \leq 0.01$.
*** Significant at $P \leq 0.0001$.

4. Discussion

Decomposition of organic matter is a useful indicator of soil condition because it is measured easily and serves as integrator of the collective activities of organisms within the soil food web. We suggest that a significant difference in the measures of decomposition between similar sites signals either a change in the decomposer community or condition of the biotic and abiotic resources at a site. Consequently, if observed differences in decomposition can distinguish between relative levels of disturbance, decomposition can serve as an indicator of ecosystem condition.

Instantaneous rate of decay of organic matter decreases through time (asymptotic model) with two phases, the first being a simple exponential decay and the second an asymptotic slowing. Typically, cellulose and hemicellulose are decomposed rapidly followed by a slowing rate of decay of lignin (Johansson, 1994; Johansson et al., 1995). As litter decomposition proceeds, concentration of lignin and lignin-like substrates increase because they are resistant to decay and enzymes can catalyze the polymerization of lignin-like substances and other forms of stabilized organic matter (Kondo et al., 1990; Rutigiano et al., 1996). We observed a log-linear rate of decay of decomposition substrates in disturbed sites, but this was not related to a change in lignin content of the balsa wood substrates. Taylor et al. (1989) recommended C/N ratios as a better predictor of decomposition rate than lignin content or lignin/N ratio for substrates low in lignin, or where a broad range of lignin contents is considered.

During the two-year monitoring period, we measured effects of disturbance and other soil factors on the decomposition of museum board and balsa wood substrates. Rate of decomposition of museum board substrate distinguished between relative levels of disturbance in agriculture and wetland but not forest ecosystems. Rate of balsa wood decomposition distinguished between relative levels of disturbance in wetland sites but not forest or agriculture sites. Visser et al. (1983) also observed more rapid decomposition of filter paper (i.e. cellulose) substrates in disturbed than undisturbed sites. Our results support those of Coleman and Crossley (1996) who suggest woody litter may have breakdown rates measured in decades or more. In contrast, Johansson et al. (1986) reports that soluble and insoluble lignin can decompose 37–60 and 5–52% of its original mass, respectively, within two years in coniferous forests.

In agricultural sites in our study, decomposition of museum board substrates was greater initially in relatively disturbed than undisturbed sites. We attribute this observation to differences in soil environment related to tillage and other early season production practices (e.g. fertilization, planting) that stimulate biological activity. Later in the monitoring period, rate of museum board decomposition in relatively disturbed agricultural sites diminished so that decomposition rate was less, and percentage of museum board substrate remaining was more, than relatively undisturbed agricultural sites, which had a more constant rate of decomposition.

Variation in environmental factors may cause a change in decomposition of organic matter in soils. Of these factors, oxygen, moisture content, temperature, pH and available minerals have been reported to be most important (Kowalenko et al., 1978). Nitrogen fertilizer was applied annually to disturbed agricultural and wetland sites in this study; nitrogen was correlated positively with decomposition rate of both museum board and balsa wood substrates. Addition of mineral nutrients may accelerate decomposition of nutrient-limited substrates (Newell et al., 1996), and high concentrations of N can favor high initial rates of decomposition (Berg, 1986). However, many examples exist in which addition of N to a N-deficient system slows down decomposition, especially where organic matter with high lignin content is present (Verhoef and Brussaard, 1990; Carreiro et al., 2000). Nitrogen and other fertilizers may negatively influence specific groups of organisms, particularly microbes. Any shift in microbial composition can have a negative effect on other soil fauna. As a result, decomposition and mineralization may decrease. Additionally, plants can compete successfully with decomposers for nutrients, and litter decay may be reduced under conditions of nutrient immobilization by uptake of nutrients by plants (Kaye and Hart, 1997; Moorhead et al., 1998).

At our sites, soil pH had the greatest influence on percentage of substrate remaining through time, and its effects were greater than electrical conductivity, percentage soil organic matter content, or total available N. Low pH soils in undisturbed wetlands and forests corresponded with slowest decomposition rates in our study. pH was correlated negatively with percentage of cellulose substrate remaining in agricultural, forest and wetland sites, and with the percentage of balsa wood substrate remaining in forest and wetland sites. In a review of 58 studies, Wardle (1998) found that temporal variability in soil carbon (C) was related most closely to soil N content in forests and soil pH in arable and grassland ecosystems. Relationships involving soil N, pH and soil C were negative. High soil acidity is often associated with loss of base cations, reduction in cation exchange capacity, increased solubility of potentially toxic metals such as aluminum and manganese, reduction in the solubility of phosphorus and molybdenum, reduction in plant growth and functioning of decomposer community (Kuperman and Edwards, 1997). In an experimental manipulation of soil pH, soil acidification in a spruce forest was associated with a pronounced decrease in soil ATP content (Wanner et al., 1994). pH values at some of our sites were below those known to reduce numbers and activity of bacteria.

Forest sites were lower consistently in total N, electrical conductivity, and sometimes had a lower pH than disturbed wetlands or agricultural lands, and this was associated with slower decomposition. In contrast to other studies, maturity of forests did not affect percentage of substrate remaining or decomposition rate of either substrate. For example, in young plantations of sitka spruce, *Picea sitchensis* Bong., decomposition rate of cotton cloth decreased with increased plantation age (Butterfield, 1999). Butterfield hypothesized that shading increases and the amplitude of diurnal temperature cycles decreases with plantation age. Artificial shading reduces decomposition rates in an open prairie to levels found in an adjacent aspen forest (Kochy and Wilson, 1997). Although disturbance level affected soil moisture and temperature similarly to those observed by others, we found no consistent pattern of soil climate on decomposition of either museum board or balsa wood.

We did not observe a direct relationship between soil climate and decomposition which demonstrates the complexity of the interaction between soil abiotic and biotic factors. Temperature and soil moisture levels were correlated negatively in both types of forests, i.e. as temperature increased, moisture decreased. High and fairly constant soil moisture occurred during relatively cold winters, whereas moisture fluctuated greatly during relatively hot summers. Both climatic and chemical factors regulate decomposition mainly by affecting abundance and community composition of soil microorganisms (Berg, 1986). In soils that retain adequate moisture, higher temperatures increase rates of litter decomposition (Hobbie, 1996; Verhoef and Brussaard, 1990). However, microbial activity is depressed in conditions of extreme temperature and moisture. Perhaps, lack of moisture during warm periods limited microbial activity under temperature conditions that would otherwise favor decomposition in our forest sites.

We did not observe changes in percentages of insoluble lignin, soluble lignin, and cellulose in the balsa wood substrates in undisturbed forests or wetlands. Decomposition varies by geographic region which corresponds with contrasting environmental conditions, such as soil temperature, moisture, aeration and pH, that regulate microbial activity and accessibility of lignin to enzyme degradation (Aber et al., 1990; Dilly and Irmler, 1998; Hobbie, 1996; Kochy and Wilson, 1997). None of our measured environmental factors were associated directly with percentage of insoluble lignin, soluble lignin, or cellulose in balsa wood decomposition substrates placed in undisturbed forests and wetlands. In a seven-year experiment, mass loss of beech and fir litter was influenced by lignin concentrations only in the later stages of decomposition (Berg and Staaf, 1980; Berg et al., 1996). We may have observed changes in composition of balsa wood substrates over a longer period of time. However, we conclude that lignin composition or ratios are not a useful measure in undisturbed forests and wetlands for relatively short-term monitoring. Finally, in comparison with measuring mass changes, determinations of lignin and cellulose are time-consuming and labor-intensive procedures, and may not be appropriate for frequent measurement in a monitoring program.

5. Conclusions

From these data, we conclude that short-term measures of decomposition of predominantly cellulose substrates, such as museum board, can be used to distinguish between relative levels of disturbance in agricultural and wetland but not forest ecosystems. Measures of balsa wood decomposition distinguished between relative levels of disturbance only in wetland sites. Measures of decomposition were lower and associated with lower total N, electrical conductivity, and sometimes lower pH in forest compared to disturbed wetlands or agricultural ecosystems. If measures of decomposition are used as indicators, soil pH should be included as a covariate. Currently, we are analyzing soil invertebrate communities from these sites to identify relationships among LRR, ecosystem, soil abiotic characteristics and decomposition to assist in development of indicators of soil condition.

Acknowledgements

The authors thank W.C. Warrick, Jr., M. Moussa for technical assistance, and C.-L. Chen and A. Spongberg for advice on chemical analyses. J. Blakely, K. Given, and M. Jackson assisted with the statistical analysis. We thank T.R. Weicht for critical comments on an earlier version of the manuscript. This research was supported in part by grant no. R82-1613 from the US Environmental Protection Agency-Office of Research and Development to D.A.N. and M.E.B. and a University of Toledo Undergraduate Research Fellowship to D.A.N. and M. Moussa.

References

Aber, J.D., Melillo, J.M., McClaugherty, C.A., 1990. Predicting long-term patterns of mass-loss, nitrogen dynamics, and soil organic-matter formation from initial fine litter chemistry in temperate forest ecosystems. Can. J. Bot. 68, 2201–2208.

Barker, K.R., Nusbaum, C.J., Nelson, L.A., 1969. Effects of storage temperature and extraction procedure on recovery of plant-parasitic nematodes form field soils. J. Nematol. 1, 240–247.

Berg, B., 1986. Nutrient release from litter and humus in coniferous forest soils: a mini review. Scand. J. Forest Res. 1, 359–369.

Berg, B., Staaf, H., 1980. Decomposition rate and chemical changes of Scots pine needle litter. II. Influence of chemical composition. In: Persson, T. (Ed.), Structure and Function of Northern Coniferous Forests: An Ecosystem Study, vol. 32. Ecological Bulletins, Stockholm, pp. 373–390.

Berg, B., Ekbohm, G., Johansson, M.B., McClaugherty, C., Rutigliano, F., Desanto, A.V., 1996. Maximum decomposition limits of forest litter types: a synthesis. Can. J. Bot. 74, 659–672.

Blair, J.M., Crossley Jr., D.A., Callaham, L.C., 1991. A litterbasket technique for measurement of nutrient dynamics in forest floors. Agric. Ecosyst. Environ. 34, 465–471.

Butterfield, J., 1999. Changes in decomposition rates and Collembola densities during the forestry cycle in conifer plantations. J. Appl. Ecol. 36, 92–100.

Carreiro, M.M., Sinsabaugh, R.L., Repert, D.A., Parkhurst, D.F., 2000. Microbial enzyme shifts explain litter decay responses to simulated nitrogen deposition. Ecology 81, 2359–2365.

Cataldo, D.A., Haroon, M., Schrader, L.E., Youngs, V.L., 1975. Rapid colorimetric determination of nitrate in plant tissue by nitration of salicylic acid. Comm. Soil Sci. Plant Anal. 6, 71–80.

Caldwell, W.S., 1992. Selected Water-Quality and Biological Characteristics of Streams in Some Forested Basins of North Carolina. US Geological Survey Water-Resources Investigations Report 92-4129. Raleigh, NC, 1985–1988.

Chen, C.-L., 1988. Characterization of lignin by oxidative degradation: use of gas chromatography-mass spectrometry technique. Methods Enzymol. 161, 110–136.

Coleman, D.C., Crossley Jr., D.A., 1996. Fundamentals of Soil Ecology. Academic Press, San Diego, 205 pp.

Daniel III, C.C., Payne, R.A., 1990. Hydrogeologic Unit Map of the Piedmont and Blue Ridge Provinces of North Carolina. US Geological Survey Water-Resources Investigations Report 90-4035. Raleigh, NC.

Dilly, O., Irmler, U., 1998. Succession in the food web during decomposition of leaf litter in black alder (*Alnus glutinosa* (Gaertn.) L.) forest. Pedobiologia 42, 109–123.

Dix, N.J., Webster, J., 1995. Fungal Ecology. Chapman & Hall, New York, 549 pp.

Doran, J.W., Parkin, T.B. 1996. Quantitative indicators of soil quality: a minimum data set. In: Doran, J.W., Jones, A.J. (Eds.), Methods for Assessing Soil Quality. SSSA Special Publication 49, Madison, WI, pp. 25–38.

Entry, J.A., Backman, C.B., 1995. Influence of carbon and nitrogen on cellulose and lignin degradation in forest soils. Can. J. For. Res. 25, 1231–1236.

Fogel, R., Cromack Jr., K., 1977. Effect of habitat and substrate quality on Douglas-fir litter decomposition in Western Oregon. Can. J. Bot. 55, 1632–1640.

Gee, G.W., Bauder, J.W., 1986. Particle-size analysis. In: Klute, A. (Ed.), Methods of Soil Analysis. Part 1. Physical and Mineralogical Methods. A Agronomy Monograph 9. American Society of Agronomy, Madison, WI, pp. 383–412.

Gunter, H.C., Rinehardt, J.F., Eddins, W.H., Barker, R.G., 1993. Water Resources Data, North Carolina, Water Year 1992. United States Geological Survey Water-Data Report NC-92-1.

Herrick, J.E., 1995. Simple method for determination of mass loss rates for soil-contaminated samples in decomposition studies. Pedobiologia 39, 74–77.

Hobbie, S.E., 1996. Temperature and plant species control over litter decomposition in Alaskan tundra. Ecol. Monogr. 66, 503–522.

Johansson, M.-B., 1994. Decomposition rates of Scots pine needle litter related to site properties, litter quality, and climate. Can. J. For. Res. 24, 1771–1781.

Johansson, M.-B., Berg, B., Meentemeyer, V., 1995. Litter mass-loss rates in late stages of decomposition in a climatic transect of pine forests: long-term decomposition in a Scots pine forest. Can. J. Bot. 73, 1509–1521.

Johansson, M.-B., Kogel, I., Zech, W., 1986. Changes in the lignin fraction of spruce and pine needle litter during decomposition as studied by some chemical methods. Soil Biol. Biochem. 18, 611–619.

Kaye, J.P., Hart, S.C., 1997. Competition for nitrogen between plants and soil microorganisms. TREE 12, 139–143.

Keeney, D.R., Nelson, D.W., 1982. Nitrogen: inorganic forms. In: Page, A.L., Miller, R.H., Keeney, D.R. (Eds.), Methods of Soil Analysis. Part 2. Chemical and Microbiological Properties, second ed. Agronomy Monograph 9. Agronomy Society of America, Madison, WI, pp. 643–698.

Kochy, M., Wilson, S.D., 1997. Litter decomposition and nitrogen dynamics in aspen forest and mixed-grass prairie. Ecology 78, 732–739.

Kondo, R., Iimori, T., Imamura, H., Nishida, T., 1990. Polymerization of DHP and depolymerization of DHP-glucoside by lignin oxidizing enzymes. J. Biotechnol. 13, 181–188.

Kowalenko, C.G., Ivarson, K.C., Cameron, D.R., 1978. Effect of moisture content, temperature and nitrogen fertilization on carbon dioxide evolution from field soils. Soil Biol. Biochem. 10, 417–423.

Kuperman, R.G., Edwards, C.A., 1997. Effects of acidic deposition on soil invertebrates and microorganisms. Rev. Environ. Contam. Toxicol. 148, 35–137.

Meentemeyer, V., 1978. Macroclimate and lignin control of decomposition rate. Ecology 59, 465–472.

Melillo, J.M., Aber, J.D., Muratore, J.F., 1982. Nitrogen and lignin control of hardwood leaf litter decomposition dynamics. Ecology 63, 621–626.

Moorhead, D.L., Westerfield, M.W., Zak, J.C., 1998. Plants retard litter decay in a nutrient limited soil: a case of exploitative competition? Oecologia 113, 530–536.

Moore, J.C., DeRuiter, P.C., 1993. Assessment of disturbance on soil ecosystems. Vet. Parasitol. 48, 75–85.

Neher, D.A., Peck, S.L., Rawlings, J.O., Campbell, C.L., 1995. Measures of nematode community structure and sources of variability among and within fields. Plant Soil 170, 167–181.

Newell, S.Y., Arsuffi, T.L., Palm, L.A., 1996. Misting and nitrogen fertilization of shoots of a saltmarsh grass: effects upon fungal decay of leaf blades. Oecologia 108, 495–502.

Nieminen, J.K., Setälä, H., 1998. Enclosing decomposer food webs: implications for community structure and function. Biol. Fertil. Soils 26, 50–57.

Paul, E.A., Clark, F.E., 1996. Soil Microbiology and Biochemistry, second ed. Academic Press, New York, 340 pp.

Rutigiano, F.A., de Santo, A.V., Berg, B., Alfani, A., Fioretto, A., 1996. Lignin decomposition in decaying leaves of *Fagus sylvatica* L. and needles of *Abies alba* Mill. Soil Biol. Biochem. 28, 101–106.

Schulte, E.E., Kaufman, C., Peter, J.B., 1991. The influence of sample size and heating time on soil weight loss-on-ignition. Commun. Soil Sci. Plant Anal. 22, 159–166.

Simmons, C.E., Heath, R.C., 1982. Water-quality characteristics of streams in forested and rural areas of North Carolina. In: Water Quality of North Carolina Streams. United States Geological Survey Water-Supply Paper 2185 A-D. US Government Printing Office, Washington, DC, pp. B1–B33.

Smith, J.L., Doran, J.W., 1996. Measurement and use of pH and electrical conductivity for soil quality analysis. In: Doran, J.W., Jones, A.J. (Eds.), Methods for Assessing Soil Quality. SSSA Special Publ. 49. Madison, WI, pp. 169–185.

Taylor, B.R., Parkinson, D., Parsons, W.F.J., 1989. Nitrogen and lignin content as predictors of litter decay-rates: a microcosm test. Ecology 70, 97–104.

Verhoef, H.A., Brussaard, L., 1990. Decomposition and nitrogen mineralization in natural and agroecosystems: the contribution of soil animals. Biogeochemistry 11, 175–211.

Visser, S., Griffiths, C.L., Parkinson, D., 1983. Effects of surface mining on the microbiology of a prairie site in Alberta. Can. J. Soil Sci. 63, 177–189.

Wanner, M., Funke, I., Funke, W., 1994. Effects of liming, fertilization and acidification on pH, soil moisture, and ATP content of soil from a spruce forest in southern Germany. Biol. Fertil. Soils 17, 297–300.

Wardle, D.A., 1998. Control of temporal variability of the soil microbial biomass: a global-scale synthesis. Soil Biol. Biochem. 13, 1627–1637.