

Forest and Pasture Carbon Pools and Soil Respiration in the Southern Appalachian Mountains

Paul V. Bolstad and James M. Vose

Abstract: Our ability to estimate the changes in carbon (C) pools and fluxes due to forest conversion is hampered by a lack of comparative studies. We measured above- and belowground C pools and soil respiration flux at four forested and four pasture sites in the southern Appalachian Mountains. Above- and belowground C pools were significantly larger ($P < 0.01$, t -test) at forested sites relative to pasture sites. The largest differences were in aboveground live biomass, which averaged $152 \text{ Mg ha}^{-1} \text{ C}$ at the forested sites and 1.9 Mg ha^{-1} at the pasture sites. Coarse root and stump C and surface detritus were also substantially different, averaging 41.3 and $32.6 \text{ Mg ha}^{-1} \text{ C}$, respectively, at the forested sites, and less than 1 Mg ha^{-1} at the pasture sites. Fine root C was higher and mineral soil C lower at pasture sites relative to comparable forested sites, but neither difference was statistically significant. Soil respiration at a given temperature was generally lower at pasture sites relative to forest sites. However, soil temperatures at pastures were consistently higher than at forest sites. Estimated annual soil respiration flux averaged $10.9 \text{ Mg C ha}^{-1}$ at the pasture sites and $12.6 \text{ Mg C ha}^{-1}$ at the forested sites. *FOR. SCI.* 51(4):372–383.

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HUMANS HAVE SIGNIFICANTLY ALTERED global carbon (C) pools and fluxes by altering land cover and land use. Land use change, particularly the conversion of forest lands to other land covers and uses, is a primary way in which humans are altering the global C cycle (Post et al. 1990, Conway et al. 1994, Ciais et al. 1995, Cannel 1996, Schlesinger 1997, Sellers et al. 1997). Unfortunately, we have quantified the impacts of land use change on C cycles for relatively few ecosystems and regions, and this hinders our ability to adequately estimate the impacts of past land use changes and predict the outcomes of future changes.

Forest conversion to agriculture has historically been the most common land use change, and typically results in the reduction of terrestrial carbon pools (Davidson and Ackerman 1993, Pennock and Vankessel 1997), although the amount and rate of C loss depend on agricultural practices (Buyanovsky et al. 1987, Buyanovsky and Wagner 1998). Carbon in standing vegetation and the forest floor is lost from the site through direct removal and combustion during clearing. Losses continue for some time after clearing, primarily due to erosion, detrital decomposition, and increased soil respiration. Soil respiration, soil C, and litter pools may increase or decrease after forest harvest (Covington 1981, Fernandez et al. 1989, Mattson and Swank 1989, Johnson et al. 1991, Johnson 1992, Toland and Zak 1994, Yanai et al. 1999, Laporte et al. 2003), but respiration typically decreases over time after conversion to nonforest land uses

due to a variety of mechanisms. Organic matter inputs into the soil are typically lower in nonirrigated agriculture when compared to the native forests they replace. Under many agricultural regimes the soils are plowed, disked, or otherwise disturbed on an annual basis, mechanically breaking vegetation detritus and exposing deeper soils to the surface. Reduced cover, particularly during spring, often results in warmer soils and speeds respiration (Lal et al. 1995).

To understand the impacts of land use activities on C-cycling we must know (1) how human land use activities have altered soil and aboveground C pools, and (2) how changes in land use have had impacts on annual soil/atmosphere carbon flux. Unfortunately, the amount of C stored in the soil and the impacts of land clearing and land use on the soil C pools and fluxes are difficult to quantify. Not surprisingly, there are relatively few studies that have directly measured ecosystem C pools and fluxes in forests and the agricultural ecosystems that replace them. The rates of soil C respiration flux under native vegetation and agricultural land uses on similar sites are known in relatively few instances.

We report measurements of vegetation and soil C pools and soil respiration fluxes for a set of sites in western North Carolina. Sites were chosen for two main purposes: (1) compare aboveground and soil C pools at forest and comparable cleared, pasture sites, and (2) to measure and compare instantaneous and annual soil C respiration fluxes for forested and comparable agricultural sites.

Paul V. Bolstad, Department of Forest Resources, University of Minnesota, St. Paul, MN 55108—pbolstad@umn.edu. James M. Vose, Coweeta Hydrologic Lab, USFS Southern Forest Experiment Station, Otto, NC 28763—jvose@fs.fed.us.

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Methods

Site Selection

A subset of ecosystem C pools and fluxes were measured and modeled at eight sites in the southern Appalachian Mountains between 1996 and 2001 (Table 1). All study sites are located within 10 km of 83°30'W, 35°5'N. We attempted to control soil and terrain variables by selecting a comparable set of sites across differing land uses (Garten et al. 1999). Sites were in similar slope positions, coves, or low flat areas. Sites were also limited to similar igneous parent materials and restricted to a narrow range of elevations, between 670 and 865 m. All sites were on soils in the Saunook complex, comprising deep, well-drained soils formed on colluvium deposited from adjacent gneiss uplands (USDA-Natural Resources Conservation Service (NRCS), 1996).

We used historical aerial photographs to select sites with unchanging land use over at least the 45-year time period preceding our measurements. Pasture sites were continuously occupied by grasses as viewed on 1950s, 1970s, and 1990s aerial photographs. Forested sites were on the USDA Forest Service Coweeta Hydrologic Laboratory and had not been harvested, thinned, or undergone human disturbance since 1930. Stands were free from visible signs of significant natural disturbance, although all stands were probably affected by the loss of American chestnut (*Castanea dentata*) in the 1930s. Forests were uneven-aged. However, trees cored on all sites were between 60 and 90 years old, consistent with previous measurements in the basin. Although forested sites showed no evidence of previous cultivation, humans have farmed in the region since at least 800 AD, and more than 20% of the land was in cultivation during the late 1800s. Forested sites may have been cultivated in the past, but we chose sites to avoid areas that had been in agriculture since 1900. Evidence for noncultivation includes a lack of berms or furrows, distance from current cultivation, lack of rock piles, relatively high understory diversity, the absence of weedy species, the presence of large woody debris, and the occurrence of large trees more than 80 years old. Four pasture sites were selected to match the soils, elevation, and topography of the forested sites. Plot location was randomly selected within each site.

Field Sampling

Carbon pools were estimated by direct field sampling of biomass and soils. These measurements were combined with subsequent laboratory analysis of C content. Soil and biomass samples were collected between Nov. 1996 and Apr. 2000. All samples were collected during the nongrowing season, most in Jan. and Feb. Soil samples were collected with a 5-cm-diameter tube sampler to a depth of 30 cm. At least 15 subsamples were collected per site. Subsample locations were selected at random within 30 m of the site center. Three intact subsamples were saved for subsequent bulk density measurements. The remaining subsamples were placed in a plastic bucket, well-mixed, and a 1-kg subsample removed and placed in a plastic bag for transport and storage until laboratory processing and analyses. Litter was removed and bagged for subsequent C determination. Soil C below 30 cm was calculated from the measured pedon average organic matter and bulk densities for these soil types because C below this depth varies considerably less than at upper horizons over the range of land uses observed here (J. Knoepp, USFS Southern Station, personal communication, June 2004). Soils below 30 cm were largely undisturbed by plows typical of the region.

Overstory species composition was noted for all trees greater than 30 cm diameter within 15 m of the plot center, and basal area was determined using a 10-factor angle prism. Diameter and height on all trees greater than 10 cm diameter were measured for a 0.1 ha circular plot. Diameter and height on trees less than 10 cm diameter were measured on a 0.0125 ha subplot of the 0.1 ha plot. Understory density was determined with 40 vertical point samples, noting presence/absence of understory (<1.5 m) vegetation contacts at each point. Stem diameters and heights were then used to calculate stem and branch biomass for each tree with locally developed allometric equations (Martin et al. 1998).

Five 4,600 cm² litter traps were randomly located within each plot. Litterfall was collected approximately monthly during periods of peak leaf fall in 1996 and 1997, and twice during the rest of each year, and data from each year averaged. Litter was sorted by tissue type (e.g., leaf, wood, flowers, and seeds), and by species or closely related species groups. Leaves were dried at 70°C for 48 h and weighed. Leaf biomass per unit area was estimated by

Table 1. Site Characteristics

Site ID	Type	Dominant Species	Tree Basal Area (m ² /ha)	Slope (%)
F1	Forest	<i>L. tulipifera</i> , <i>A. rubrum</i>	27.6	3
F2	Forest	<i>Q. prinus</i> , <i>L. tulipifera</i>	30.1	5
F3	Forest	<i>A. rubrum</i> , <i>Q. alba</i>	25.3	0
F4	Forest	<i>L. tulipifera</i> , <i>Q. prinus</i>	30.2	4
P1	Pasture	<i>Festuca-Panicum</i> mix	0.0	0
P2	Pasture	<i>Festuca-Panicum</i> mix	0.0	4
P3	Pasture	<i>Festuca-Panicum</i> mix	0.0	2
P4	Pasture	<i>Festuca-Panicum</i> mix	0.0	4

summing leaf biomass within each basket, dividing by basket area, and averaging across baskets. Litter basket leaf mass was expanded to per hectare mass using appropriate area conversions.

Forest floor biomass and small woody debris were estimated from the removed litter sampled at each soil coring location. Samples were dried at 70°C for 2 days, weighed, and C determined. Coarse woody debris was estimated at the forested sites from 16 1-m² subplots within each plot. Length and diameter of large coarse woody debris were measured in each subplot and carbon content was assumed to be 48% (Harmon 1982).

Aboveground biomass at pasture sites was determined with eight 0.49-m² clipped plots, randomly selected within 30 m of plot center. Samples were dried at 70°C for 48 h, weighed, and C content determined. In those pasture sites where multiple annual harvests occurred, each harvest biomass was calculated assuming a 10-cm crown height and multiplying sampled biomass by the removed proportion to total height. Removed C was multiplied by the number of harvests.

Carbon flux via soil respiration was measured approximately monthly with portable IRGA-based analyzers. Because one analyzer had limited availability, two sampling systems were used. The first sampling system was based on five independent chambers connected to the IRGA via a multiplexed valve assembly (Vose et al. 1997). Airflow to and from each chamber was controlled with balanced input and output pumps to maintain pressure balance. The system would typically collect samples over a 28-h period, one sample approximately every 2 hours from each chamber. We also measured soil respiration with a PP-Systems EGM-1. Three replicate measurements were made at each of the eight locations within each plot. Extensive cross-comparisons using both systems on the same plots indicate that respiration response models based on the two measurement systems are not significantly different, although measurements from the EGM-1 were more variable. Soil temperature at 20 cm and soil moisture at a 15 cm depth were measured simultaneously with respiration.

Laboratory Methods

Soils and litter were stored at 2°C in plastic bags until processing. The samples were pulverized with a rubber mallet and well-mixed, then dried at 70°C for 48 h and washed through a 2-mm sieve. Roots and coarse fraction were sorted and weighed. A subsample was ground with a mortar and pestle and C content determined with a Perkin-Elmer CHN analyzer. Soil C on mass and area bases were calculated using coarse fraction and bulk density measurements.

Root biomass was determined per unit area by the proportional weights of the total sampled soil mass versus the sorted subsample mass, adjusted for bulk density and coarse fraction. Our sampling protocol undersampled coarse roots in three ways, first because our sampler could not cut through roots larger than approximately four centimeters in

diameter, second because vertical samples missed the main root mass directly below tree stems, and third, because we sampled only to a 30-cm depth. Root biomass was multiplied by 1.39 to account for root mass below 30 cm (McGinty 1972, Harris et al. 1977). Forest coarse root biomass was subsequently multiplied by 2.2, a factor derived from a nearby study, to adjust for unsampled stump root mass directly below the main stem of each tree (Harris et al. 1977).

Carbon Pool and Flux Calculations and Statistical Analyses

Total and component carbon pools at each site were calculated on an area basis from site measurements. Aboveground stem and branch biomass were calculated by summing across all measured trees for the 0.1-ha plot and all saplings and shrubs measured on the 0.0125 ha subplot. Woody biomass was converted to per hectare C by appropriate wood mass and tissue C content measurements. Leaf biomass was estimated from littertraps, and forest floor and pasture litter biomass and root biomass were estimated from field samples. These mass measurements were scaled by appropriate sampling areas and multiplied by measured C content to estimate component C values. Components were then summed to estimate ecosystem C pools.

Soil respiration was calculated based on site-specific models developed from respiration, temperature, and moisture measurements. Two-parameter exponential models were fit, and converted by appropriate units to predict respiration flux (Kicklighter 1994, Fang and Moncrieff 2001). The model took the form

$$\text{Soil C Flux} = \beta_0 e^{\beta_1 T} (1 + \beta_2 W),$$

where soil flux is expressed in $\mu\text{mol m}^{-2} \text{s}^{-1}$, T is soil temperature at a 20-cm depth in °C, W is measured volumetric soil water content, and β_0 , β_1 , and β_2 are estimated coefficients.

Because soil temperature was continuously measured at only three sites, site-to-site regressions were fit to predict daily soil temperatures at the remaining plots. Daily mean 20-cm soil temperature data for continuously measured sites were combined with soil temperature measurements taken at all sites coincident with respiration measurements. Simple linear models were fit between sites, and these models applied using the continuously measured data to predict daily temperature at each unmeasured plot. Daily soil moisture was linearly interpolated for days between monthly sampling dates. Soil respiration may respond strongly and nonlinearly to precipitation, particularly when there is substantial drying (Davidson et al. 1998, Martin and Bolstad 2005). Daily respiration was predicted for each site and date, and summed over a 1-year period.

All statistical analyses were performed using SAS software. Differences among C pools were tested via Student's t -test of means across land use type. Nonlinear regression models were fit using a Gaussian method, and asymptotic

Table 2. Soil pools and flux observed at forested (F1-F4) and pasture (P1-P4) sites in the southern Appalachian Mountains.

C category (all in Mg ha ⁻¹)	F1	F2	F3	F4	Mean Forest	s.e. Forest	P1	P2	P3	P4	Mean Pasture	s.e. Pasture
Mineral soil	154.3	240.6	205.8	129.8	182.1	41.8	131.8	120.6	211.8	121.7	146.2	36.6
Fine root (top 30 cm)	4.7	2.3	7.4	3.9	4.6	2.1	6.3	3.9	7.1	2.8	5.0	2.0
Coarse root and stump C (all depths)	43.0	27.2	52.4	42.7	41.3	10.4	0.0	0.0	0.0	0.0	0.0	0.0
Surface detritus and standing dead mass	34.8	34.5	33.5	27.5	32.6	3.4	0.0	0.0	0.0	0.0	0.0	0.0
Aboveground live biomass C	161.6	181.0	147.9	117.6	152.0	26.7	1.6	2.4	1.4	2.2	1.9	0.5
Site Total C	398.4	495.5	436.9	321.6	412.6	62.9	139.7	126.8	220.4	126.8	153.2	37.8
Predicted annual soil respiration (Mg C ha ⁻¹)	12.5	12.4	12.2	13.2			10.0	11.7	10.3	11.8		

variances used in significance tests. Regression diagnostics included scatter diagrams, R^2 , Cook's-D, and K-S tests for normality.

Land Use History and Changes in Carbon Pools

Agriculture and forestland uses were mapped for 1904, 1950, and 1990. The 1904 land use was based on a USGS map and publication based on surveys near the turn of the last century (Ayers and Ashe, 1905). A regional field survey of land use, land condition, and standard timber volumes was conducted by the US Geological Survey. The 1950 land use was based on the manual interpretation of panchromatic 1:20,000 aerial photographs. Forest/agriculture land uses were delineated on clear Mylar sheets attached to the photographs. A minimum mapping unit of 2 hectares was specified. These sheets were digitized and terrain-corrected using a single-photoressection procedure. Elevation data were obtained from 1:24,000 US Geological Survey digital elevation models with a resolution of 30 meters. Control points used in the photoressection were obtained from differentially corrected global positioning systems (GPS) (5 meter accuracy or better), or from USGS topographic quadrangles (15 meter accuracy or better). Resected data from each photo were combined in a mosaic and land use polygons constructed for the upper Little Tennessee River (LTR) watershed.

Land use in 1990 was based on the classification of Landsat thematic mapper (TM) data. Cloud-free images were obtained for the upper LTR. Images were geo-referenced and registered to a coordinate system compatible with the 1950s aerial photographic data. Four images collected between 1990 and 1993 were used. Images were collected between May and Sept., during full leaf-on conditions. A supervised maximum-likelihood classification was performed (Bolstad and Lillesand 1991), using 86 spectral training sets and bands 3, 4, and 5 of the Landsat TM imagery. Accuracy of better than 96% was obtained for forest/agriculture classification based on standard assessment procedures (Congalton et al. 1987).

Land use data were combined with carbon pool estimates to expand plot measurements to estimates for the upper LTR watershed. The change in carbon pools and annual carbon flux due to land clearing was estimated by area-weighted expansion. Average estimates of C pools for each land use

type were combined with the transition area to estimate carbon lost due to land clearing.

Results and Discussion

Ecosystem C Pools and Land Use

Carbon pool sizes and distributions differed among land use types. At the forested sites, C was primarily in the aboveground live biomass and subsurface soil organic matter (Table 2); these composed approximately 37 and 44%, respectively, of total ecosystem C. Coarse root and forest floor and surface detritus C were the next most important components, averaging 10% and 8% of total ecosystem C, respectively. Fine roots were a relatively minor component, composing less than 1% of total ecosystem C.

Total carbon at the forest sites was substantially higher than at the comparable pasture sites (Table 2). Total carbon averaged 413 Mg ha⁻¹ at the forested sites, and 153.2 Mg ha⁻¹ at the pasture sites. Total ecosystem carbon varied considerably within the forest and pasture classes; however, the mean difference in total ecosystem C between forest and pasture sites was significant ($P < 0.05$, t -test).

Most of the difference in total ecosystem C was due to a difference in the aboveground live biomass. Aboveground live biomass was the first- or second-largest C pool at all forested sites, and averaged 152 Mg ha⁻¹. Carbon averaged 2 Mg ha⁻¹ in the aboveground live biomass at the grassland sites. The one grazed pasture site (P3) had the lowest leaf biomass (Table 2).

Aboveground carbon amounts found here are within the ranges reported for similar ecosystems elsewhere (Raich and Schlesinger 1992). As noted by others (Raich and Schlesinger 1992, Davidson and Ackerman 1993), there are relatively few studies that report either total or component ecosystem C content for human land uses in the temperate zone. Previous studies have reported aboveground C in mature southern Appalachian forests ranges from 68 to 300 Mg ha⁻¹ (assuming biomass is 50% C; Whittaker 1966, Monk et al. 1970, Harris et al. 1977, Delcourt and Harris 1980), and averaged near 170 Mg ha⁻¹ for cove forests, very near the 152 Mg ha⁻¹ reported for this study. Aboveground C in the pasture sites, derived from production data, has been reported at 2.3 Mg ha⁻¹ (Delcourt and Harris 1980), similar to our average estimate of 1.9 Mg ha⁻¹.

There were large differences among land use types in site root carbon, particularly for coarse roots. Root C averaged 45.9 Mg ha^{-1} on forested sites and 5.1 Mg ha^{-1} on pasture sites. In contrast, fine root amounts were quite similar at the pasture and forest sites. As a result, coarse and central roots composed the majority of forest root biomass and accounted for most of the difference among pasture and forest root C pools.

Average soil C was lower at the pasture sites (122.2 Mg ha^{-1}) than at the comparable forest sites (152.1 Mg ha^{-1}). However, the differences between forest and pasture were not statistically significant (*t*-test, $P > 0.05$). These differences in soil C are consistent with a reported loss of from 20% to 40% of soil C on clearing and cultivation (Houghton et al. 1983, Schlesinger 1984, Mann 1986, Davidson and Ackerman 1993).

There were substantial and significant ($P < 0.01$, *t*-test) differences in the aboveground detritus between the forest and pasture sites. Forests averaged 32.6 Mg ha^{-1} C in the forest floor litter and coarse woody debris, while pasture sites averaged less than 0.1 Mg ha^{-1} . The forest floor in the southern Appalachians typically receives from 1 to $6 \text{ Mg C ha}^{-1} \text{ year}^{-1}$ in leaf and coarse woody litterfall (Whittaker 1966, Monk et al. 1970, Harris et al. 1977, Bolstad et al. 2000). Litterfall decomposition is rapid in the warm, wet environments of southern Appalachian cove forests relative to other temperate forest locations (Abbott and Crossley 1982, Harmon 1982, Seastedt and Crossley 1988), and substantial forest floor C accrues, at least relative to the pasture sites. Surface litter quantities were quite small in the pasture sites. Higher temperatures, coupled with ample moisture and high-quality substrate, apparently result in rapid litterfall decomposition at the pasture sites.

Taken together, our results suggest an average loss of 252.8 Mg C/ha from cove forested sites when they are converted to pasture. Most of this loss on conversion to pasture appears to be due to the removal of above- and belowground woody biomass and surface detritus. The losses reported here may be an estimate of the lower bounds on ecosystem C losses from terrestrial ecosystems after conversion to pasture in the southern Appalachian Mountains. Old-growth cove forests probably had higher standing live and dead biomass and substantially more surface litter, particularly in coarse woody debris (Whittaker 1966, Lorimer 1980). Our study forests were likely to have been cut during the early 1900s (Ayers and Ashe 1905). Carbon storage in aboveground and detrital pools is likely to be lower in these second-growth forests than in old-growth forests. However, the region has a complex and long history of forest disturbance, with human occupation as early as 800 AD. There is evidence of extensive pre-European burning and agriculture that was concentrated on low-elevation, near-stream sites such as those measured in this study. Without direct measurements, our measurements may provide at best approximate estimates of the carbon loss due to conversion of primary forests to pastures.

An approximate estimate of changes in C storage with changes in land use for the upper LTR watershed may be

obtained by combining our carbon pool measurements with land use data (Table 3). We estimated the increase in carbon storage with agricultural abandonment by summing the difference in above- and belowground plant and detrital C components for forest sites relative to agricultural sites. This assumes there is no recovery of bulk soil C, as indicated by Schlesinger (1990), and that carbon stores in our measured sites are representative of abandoned agricultural sites of similar age. This latter assumption may result in an overestimation of regional carbon accrual because our forest sites were likely to have originated from a harvest, which may have resulted in higher detrital and understory C pools relative to abandoned agricultural sites. These pools form a relatively small portion of stand totals, so overestimation due to errors in this assumption is likely to be small.

The upper LTR watershed encompasses $1,465 \text{ km}^2$, of which $1,322 \text{ km}^2$ (90.3%) were in forest in 1990. Forest composed $1,197 \text{ km}^2$ (81.7%) in 1950, indicating a substantial reduction in agricultural land use during the 40-year period. Approximately 125 km^2 were converted from agricultural to forested land use between 1950 and 1990. Using our observed differences in carbon pools among land use, we calculate this corresponds to a 19.3 Mg ha^{-1} increase in C storage due to land use change over the upper LTR when averaged over the entire watershed, in addition to any accrual due to increased storage in continuously forested areas.

Our carbon pool change estimates are a first approximation, based on the recognition that eight sites is a small sample size from which to extrapolate for a watershed of this size. There is substantial variation in the factors that affect ecosystem carbon pools within the upper LTR watershed. Forest age in particular will substantially alter carbon pools, because old-growth forests contain large carbon stores that an old-field origin forest does not. Nonetheless, our plots represent the best and perhaps only measurements of C pools on comparable sites representative of the regional conditions. These data are crucial in reducing uncertainty in the global carbon cycle and the North American carbon sink (Houghton et al. 2003). Although we measured carbon pools in recovering forest stands in a relatively narrow range of ages, the range corresponds to that found on a majority of logged or abandoned agricultural sites in the region. Logging peaked in the early 1900s in the southern Appalachian Mountains, with near-complete harvest of the easily accessible low cove sites such as those measured in this study. Agricultural abandonment predominantly occurred between 1930 and 1970 with the integration of the regional and national economies. Most forests on abandoned agricultural land are between 30 and 90 years old, and logged forests between 70 and 100 years old. Carbon losses and pools will vary with the management regimes, terrain position, soils, previous vegetation, land use history, and other factors we did not measure. However, more than 80% of the agricultural area of the upper LTR watershed occurred on terrain similar to our sites. Moreover, pasture was the most common agricultural land use.

Soil C Respiration Flux and Land Use

Measured instantaneous soil respiration rates ranged from 0 to 12.2 $\mu\text{mol m}^{-2} \text{s}^{-1}$, and were typically between 2 and 9 $\mu\text{mol m}^{-2} \text{s}^{-1}$ (Figures 1–3). Respiration rates were strongly and exponentially dependent on soil temperature, as has been frequently reported in previous studies. The soil respiration rates observed in this study compare well to respiration rates of 0 to 10.2 $\mu\text{mol m}^{-2} \text{s}^{-1}$ reported in northern temperate deciduous forests using a variety of techniques (Froment 1972, Garrett and Cox 1972, Anderson 1973, Edwards 1975, Baldocchi et al. 1986, Baldocchi and Meyers 1991, Hanson et al. 1993, Kicklighter 1994, Davidson et al. 1998, Savage and Davidson 2001, Bolstad et al. 2004).

Soil temperatures at a 20-cm depth averaged 11.8°C at the monitored forest site and 13.0°C at the pasture site (Figure 4). Higher annual mean soil temperatures at the pasture sites are due to consistently higher spring and summer temperatures. The forest sites had denser, multistoried canopies and thick litter layers, reducing direct radiation to the soil. Soil temperatures at the pasture site tended to be the same or lower than those at the forested site during winter months; however, the differences were slight and inconsistent.

Exponential functions (Equation 1) were significant at every site ($P < 0.001$, adjusted R^2 from 0.68 to 0.89, Figures 2 and 3). Scatterplots and diagnostic tests indicate residuals were homoskedastic and not significantly different from a normal distribution. β_0 values on forested sites ranged from 0.26 to 1.55 (Figure 3). These parameters correspond to the respiration rate at 0°C, and the implied rates at 0°C are somewhat higher than those reported by a number of previous studies in eastern deciduous forest sites (Garrett and Cox 1973, Edwards 1975, Hanson et al. 1993, Kicklighter 1994). β_1 values ranged from 0.059 to 0.21, similar to reported values, once adjusted for differences in model form (Schlentner and Van Cleve 1985, Hanson et al. 1993, Kicklighter 1994, Peterjohn et al. 1994, Davidson et al. 1998, Savage and Davidson 2001).

We found no relationship between soil moisture and soil respiration at any of our sites. Previous studies have reported a relationship between respiration and soil moisture (Schlentner and Van Cleve 1985, Hanson et al. 1993), or respiration and precipitation (Raich and Schlesinger 1992). We included soil moisture as a variable in a number of linear and nonlinear models, including two-variable linear models, bivariate Gaussian models, and a modified version of the model used by Hanson et al. (1993). Moisture was not a significant parameter ($P < 0.05$) in any of these models.

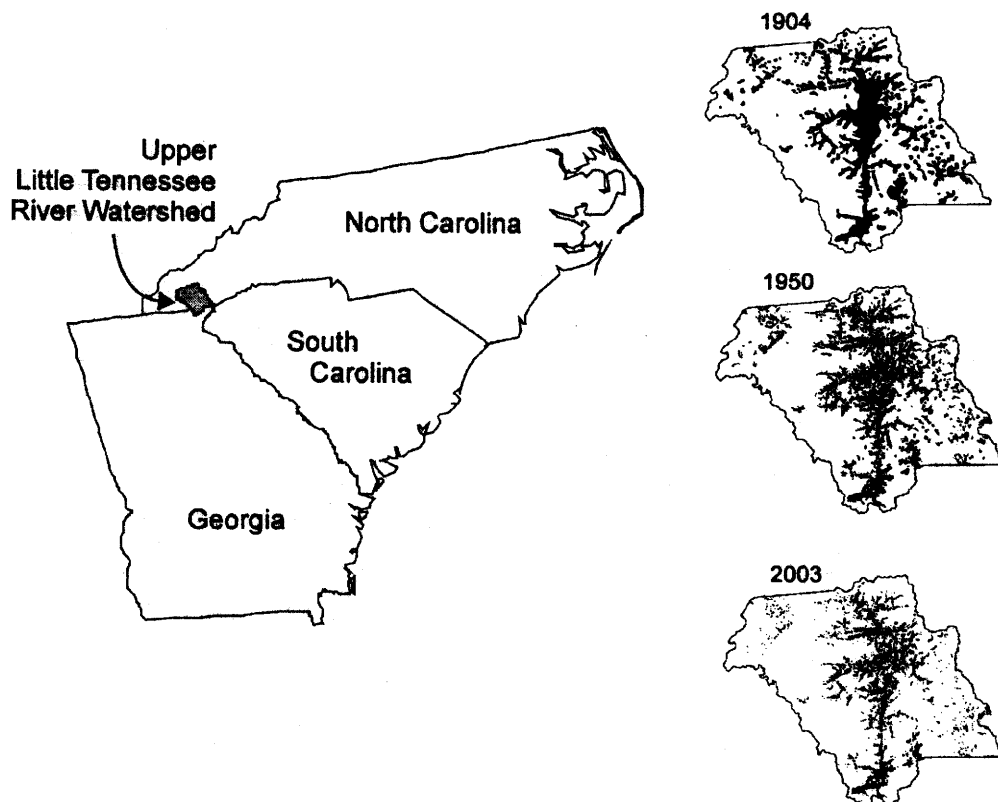


Figure 1. Location of the study area (left), and land use (right) in the upper Little Tennessee River Watershed (nonforest shown in black).

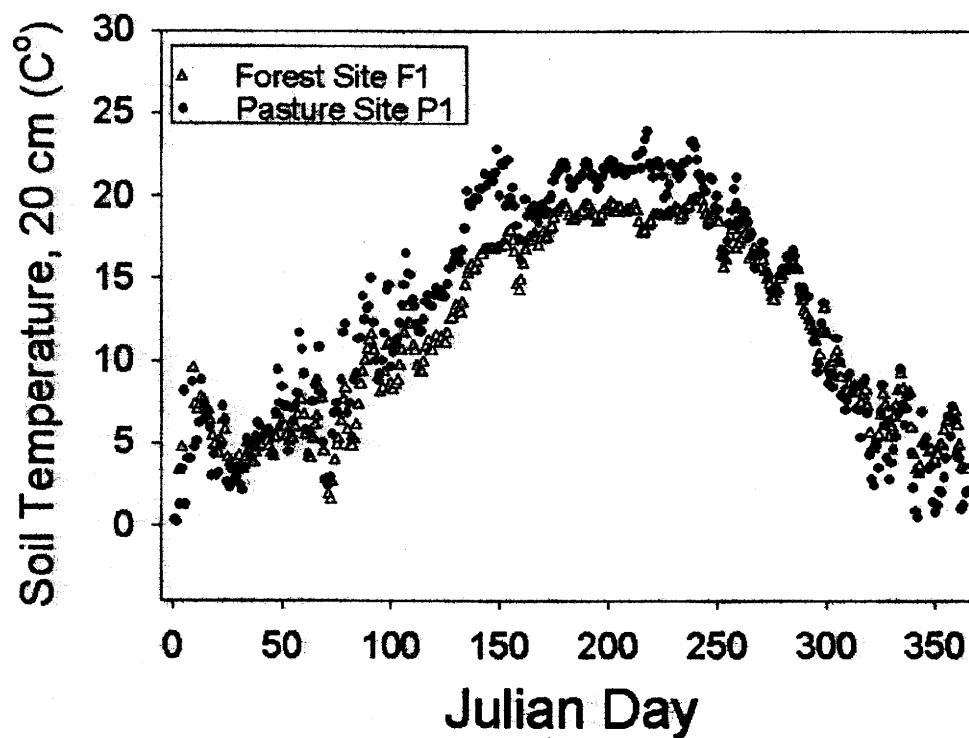


Figure 2. Soil temperature at 20 cm for continuously measured pasture (P1) and forest (F1) sites for 1997. Temperature was measured hourly, and daily averages computed.

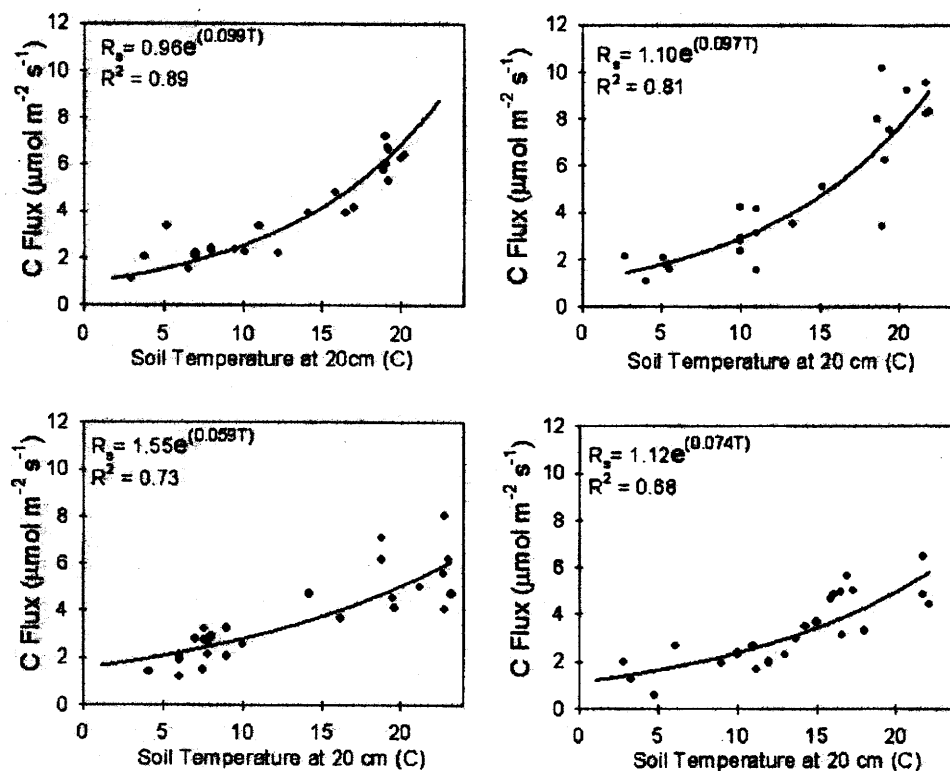


Figure 3. Soil respiration measurements and fit response functions for four pasture sites.

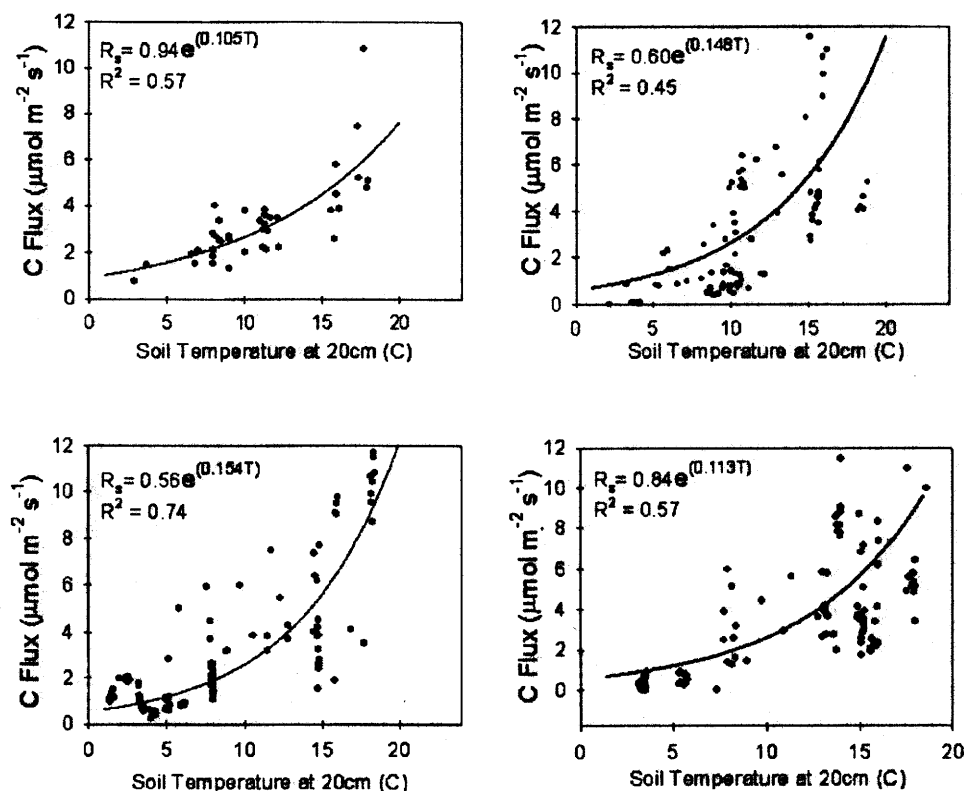


Figure 4. Soil respiration measurements and fit response functions for four forested sites.

Residuals from exponential temperature models were not related to soil moisture content or water potential. Soil moisture may not have significantly affected soil respiration because soil was moist for the duration of our study. All sites were in cove or alluvial bottomland sites, and thus received downslope subsurface flow. Soil moisture was within 32% of the field capacity for all sites and all measurements, and was typically higher than 50% of field capacity. Because we selected cove sites for comparisons, all our sites are likely to be wetter than those in other land forms or the regional average soil moisture. Moisture effects may occur on other sites or on our sites in drier years, but we did not observe any moisture effects on soil respiration.

Predicted daily and annual respiration were higher at forested sites than at pasture sites (Figure 5, Table 2). Cumulative soil respiration at forest sites averaged 13.8 Mg ha⁻¹ year⁻¹ and respiration at the pasture sites aver-

aged 11.8 Mg ha⁻¹ year⁻¹, although the differences were not statistically significant ($P < 0.05$). It is perhaps surprising the differences in soil respiration for pasture and forest sites was not greater, given the differences observed in root biomass, litter, and soil C between pasture and forest sites. Belowground C averaged 230 Mg ha⁻¹ at the forested sites and only 127 Mg ha⁻¹ at the pasture sites. A larger proportion of the forest belowground C may have been less active, given the rather narrow difference in cumulative respiration. Root respiration rates, allocation, and turnover may have been higher in the pasture sites. Various studies have reported fine-root turnover times of 1 to 2 years in eastern deciduous forests (Hendrick and Pregitzer 1993, Fahey and Hughes 1994), and coarse root turnover times may be from decades to centuries. Surface soil C in pastures was approximately 20% lower than in forests, and the difference is most likely due to the loss of a portion of the active soil C

Table 3. Land use by time period in the upper watershed of the Little Tennessee River. Landuse classification accuracies are higher than 95% for both the 1950 and 2003 data sets. C loss is based on the area in non-forest landuse and the observed differences in C pools between forest and no-forest sites. C increase since 1904 is based on increased forest area and measured forest biomass. Aboveground biomass accumulation in 1950 on abandoned forest land was assumed to be one-half the value measured in the late 1990s. C increase due to landcover change is averaged over the entire study area, and does not include changes in carbon pools on permanently forested areas.

Year	Source	Forest area (ha)	Cleared area (ha)	C loss (Mg ha ⁻¹)	C increase from 1904 (Mg ha ⁻¹)
1904	Ashe and Ayers, USGS	114,471	32,503	57.4	—
1950	Aerial Photographs	120,884	26,090	46.0	8.0
2003	SPOT multispectral data	132,198	14,776	26.1	15.5

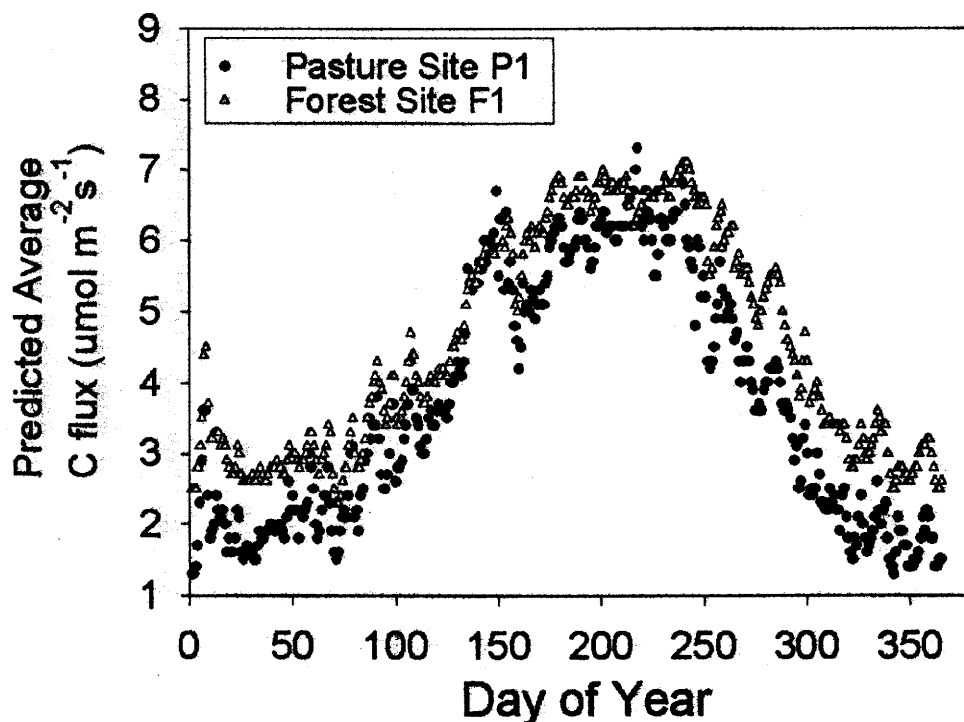


Figure 5. Daily average soil respiration for one pasture (P1) and one forested (F1) site. Respiration estimates were based on site soil temperatures and site-specific temperature-respiration response functions.

fraction. However, the 20% loss may represent a minority portion of the active soil pool. The relative size and decay rates of the various soil organic matter pools have not been well-studied in our region and with the vegetation types sampled in this study.

Observed cumulative annual soil respiration was near the upper range of data reported by previous studies in temperate forest sites. Previous studies report annual cumulative soil respiration ranging from 1.6 to 14.1 Mg ha⁻¹ year⁻¹ for mature northern temperate deciduous forests, with an average of 8.9 Mg ha⁻¹ year⁻¹ (Raich and Schlesinger 1992, Hanson et al. 1993), lower than the 12.6 Mg ha⁻¹ year⁻¹ we observed. We note that the highest previously reported are from mature mixed deciduous forests in Japan (Kirata 1971, Yoneda and Kirita 1978, Nakane 1980), and the state of Tennessee (Edwards and Harris 1977). These sites were characterized by warm, moist climates, similar to those in the present study.

The peak respiration rates we observed were at the high end of those previously reported in southern Appalachian forested sites (Edwards 1975, Edwards and Harris 1977, Hanson et al. 1993). This series of studies was at approximately the same latitude and approximately 150 km west of the current study sites. Differences in previous and our observed soil respiration rates may be the result of differences in measurement systems (Fang and Moncrieff 1996, Healy et al. 1996, Rayment and Jarvis 1997, Janssens et al. 2000), or differences in vegetation composition and age, soils, or climate.

We found no previous published reports of pasture/managed grassland soil respiration for the southeastern United States, and so we have no direct comparisons for our measurements. Respiration on tallgrass prairie sites in the southcentral United States have been reported from 4.6 to 6.6 Mg ha⁻¹ year⁻¹ (Kucera and Kirkham 1971, Buyanovsky et al. 1987, Risser et al. 1981). Data are also available for grass-covered soil (6.9 Mg ha⁻¹ year⁻¹, Dörr and Münneich 1987) under somewhat different climate regimes and soils.

Conclusions

We found large differences in total and component carbon pools in forest and sites in the southern Appalachian Mountains. Largest differences were in aboveground live biomass. Differences in soil C were substantial but smaller than aboveground biomass, as were differences in surface detritus and coarse-root biomass. There was little difference in average quantities of C stored in fine-root biomass at forest and pasture sites. These differences in ecosystem C were accompanied by lower soil respiration on the pasture and agricultural sites relative to forested sites.

These results indicate that a relatively large proportion of the C loss due to land use change in the southern Appalachian Mountains has been through the removal of living and dead plant tissue from forests. This C may be recaptured relatively quickly in the southern Appalachian Mountains, where forest growth is rapid. Carbon accrual has been

taking place over the past four decades as agricultural land has been abandoned to natural forest succession. Carbon accrual is likely to continue on forested sites, as living biomass, detrital, and soil pools increase through time. The generalization of these research findings to a broader range of soils, terrain positions, land uses, and time periods, and detailed investigations on the mechanisms of carbon accrual and storage, are topics for further research.

Literature Cited

- ABBOTT, D.T., AND D.A. CROSSLEY. 1982. Woody litter decomposition following clear-cutting. *Ecology* 63:35–42.
- ANDERSON, J.M. 1973. Carbon dioxide evolution from two temperate, deciduous woodland soils. *J. Appl. Ecol.* 10:361–378.
- AYERS, H.B., AND W.W. ASHE. 1905. The Southern Appalachian forests., USGS, Washington, DC.
- BALDOCCHI, D.D., AND T.P. MEYERS. 1991. Trace gas exchange above the floor of a deciduous forest I. Evaporation and CO₂ efflux. *J. Geophys. Res.* 96:7271–7285.
- BALDOCCHI, D.D., S.B. VERMA, D.R. MATT, AND D.E. ANDERSON. 1986. Eddy-correlation measurements of carbon dioxide efflux from the forest floor of a deciduous forest. *J. Appl. Ecol.* 23:967–975.
- BOLSTAD, P.V., K.J. DAVIS, J. MARTIN, B.D. COOK, AND W. WANG. 2004. Component and whole-system respiration fluxes in northern deciduous forests. *Tree Phys.* 24:493–504.
- BOLSTAD, P., AND T. LILLESAND. 1991. Rapid maximum likelihood classification. *Photogram. Eng. Rem. Sens.* 57:67–74.
- BOLSTAD, P.V., J. VOSE, AND S. McNULTY. 2000. Forest productivity, leaf area, and terrain in southern Appalachian forests. *For. Sci.* 47:419–127.
- BUYANOVSKY, G.A., C.L., KUCERA, AND G.H. WAGNER. 1987. Comparative analyses of carbon dynamics in native and cultivated ecosystems. *Ecology* 68:2023–2031.
- BUYANOVSKY, G.A., AND G.H. WAGNER. 1998. Carbon cycling in cultivated land and its global significance. *Glob. Change Biol.* 4:131–141.
- CANNEL, M.G.R. 1996. Forests as carbon sinks mitigating the greenhouse effect. *Com. For. Rev.* 75:92–99.
- CHAPMAN, P., P.P. TANS, M. TROLIER, J.W.C. WHITE, AND R.J. FRANCEY. 1995. A large northern hemisphere terrestrial CO₂ sink indicated by ¹³C/¹²C of atmospheric CO₂. *Science* 269:1098–1102.
- CONGALTON, R., R. ODERWALD, AND R. MEAD. 1987. Assessing Landsat classification accuracy using discrete multivariate analysis statistical techniques. *Photogram. Eng. Rem. Sens.* 49:1671–1678.
- CONWAY, T.J., P.P. TANS, L.S. WATERMAN, K.W. THONING, D.R. KITZIS, K.A. MASARIE, AND N. ZHANG. 1994. Evidence for interannual variability of the carbon cycle from the National Oceanic and Atmospheric Administration/Climate Monitoring and Diagnostics Laboratory global air sampling network. *J. Geophys. Res.* 99:22831–22856.
- COVINGTON, W.W. 1981. Changes in forest floor organic matter and nutrient content following clear cutting in northern hardwoods. *Ecology* 62:41–48.
- DAVIDSON, E.A., AND I.L. ACKERMAN. 1993. Changes in soil carbon inventories following cultivation of previously untilled soils. *Biogeochemistry* 20:161–193.
- DAVIDSON, E.A., E. BELK, AND R.D. BOONE. 1998. Soil water content and temperature as independent or confounded factors controlling soil respiration in a temperate mixed hardwood forest. *Global Change Bio.* 4:217–227.
- DELCOURT, H.R., AND W.F. HARRIS. 1980. Carbon budget of the southeastern U.S. biota: Analysis of historical change in trend from source to sink. *Science* 210:321–323.
- DÖRR, H., AND K.O. MÜNNEICH. 1987. Annual variation in soil respiration in selected areas of the temperate zone. *Tellus* 39B:114–121.
- EDWARDS, N.T. 1975. Effects of temperature and moisture on carbon dioxide evolution in a mixed deciduous forest floor. *Soil Sci. Soc. Am. Proc.* 39:361–365.
- EDWARDS, N.T., AND W.F. HARRIS. 1977. Carbon cycling in a mixed deciduous forest floor. *Ecology* 58:431–437.
- FAHEY, T.J., AND J.W. HUGHES. 1994. Fine root dynamics in a northern hardwood forest ecosystem, Hubbard Brook Experimental Forest, NH. *J. Ecol.* 82:533–548.
- FANG, C., AND J.B. MONCRIEFF. 1996. An improved dynamic chamber technique for measuring CO₂ efflux from the surface of soil. *Funct. Ecol.* 10:297–305.
- FANG, C., AND J.B. MONCRIEFF. 2001. The dependence of soil CO₂ efflux on temperature. *Soil Biology and Biochemistry* 33:155–165.
- FERNANDEZ, I.J., Y. SON, C.R. KRASKE, L.E. RUSTAD, AND M.B. DAVID. 1989. Soil carbon dioxide characteristics under different forest types and after harvest. *Soil Sci. Soc. Am. J.* 57:1115–1121.
- FROMENT, A. 1972. Soil respiration in a mixed oak forest. *Oikos* 23:273–277.
- GARRETT, H.E., AND G.S. COX. 1973. Carbon dioxide evolution from the floor of an oak-hickory forest. *Soil Sci. Soc. Am. Proc.* 37:641–644.
- GARTEN, C.T. JR., W.M. POST III, P.J. HANSON, AND L.W. COOPER. 1999. Forest soil carbon inventories and dynamics along an elevation gradient in the southern Appalachian Mountains. *Biogeochemistry* 45:1115–1145.
- HANSON, P.J., S.D. WULLSCHLEGER, S.A. BOHLMAN, AND D.E. TODD. 1993. Seasonal and topographic patterns of forest floor CO₂ efflux from and upland oak forest. *Tree Phys.* 13:1–45.
- HARMON, M.E. 1982. Decomposition of standing dead trees in the southern Appalachian Mountains. *Oecologia* 52:214–215.
- HARRIS, W.F., R.S. KINERSON JR., AND N.T. EDWARDS. 1977. Comparison of belowground biomass of natural deciduous forest and loblolly pine plantations. *Pedobiologia* 17:369–381.
- HEALY, R.W., R.G. STRIEGL, T.F. RUSSEL, G.L. HUTCHISON, AND G.P. LIVINGSTON. 1996. Numerical evaluation of static-chamber measurements of soil-atmosphere gas exchange: Identification of physical processes. *Soil Sci. Soc. Am. J.* 60:740–747.

- HENDRICK, R.L., AND K.S. PREGITZER. 1993. The dynamics of fine root length, biomass, and nitrogen content in two northern hardwood ecosystems. *Can. J. For. Res.* 23:2507–2520.
- HOUGHTON, R.A. 2003. Why are estimates of the terrestrial carbon balance so different? *Global Change Biol.* 9:500–509.
- HOUGHTON, R.A., J.E. HOBBIE, AND J.M. MELILLO. 1983. Changes in the carbon of terrestrial biota and soils between 1860 and 1980. A net release of CO₂ to the atmosphere. *Ecolog. Mon.* 53:235–262.
- JANSSENS, I.A., A.S. KOWALSKI, B. LONGDOZ, AND R. CEULMANS. 2000. Assessing forest soil CO₂ efflux: An in situ comparison of four techniques. *Tree Phys.* 20:23–32.
- JOHNSON, D.W. 1992. Effects of forest management on soil carbon storage. *Water, Air, and Soil Poll.* 64:83–120.
- JOHNSON, D.W., A.H. JOHNSON, T.G. HUNTINGTON, AND T.G. SICCAMA. 1991. Whole-tree clear-cutting effects on soil horizons and organic matter pools. *Soil Sci. Soc. Am. J.* 55:497–502.
- KICKLIGHTER, D.W. 1994. Aspects of spatial and temporal aggregation in estimating regional carbon dioxide fluxes from temperate forest soils. *J. Geophys. Res.* 99:1303–1315.
- KIRATA, H. 1971. Studies of soil respiration in warm-temperate evergreen broadleaf forests of southwestern Japan. *Jpn. J. Ecol.* 21:230–244.
- KUCERA, C., AND D. KIRKHAM. 1971. Soil respiration in a tallgrass prairie in Missouri. *Ecology* 52:912–915.
- LAL, R., J.M. KIMBLE, E. LEVINE, AND B.A. STERWART. 1995. *Soils and global change*. Lewis Publishers, Boca Raton, FL.
- LAPORTE, M.F., L.C. DUCHESNE, AND I.K. MORRISON. 2003. Effect of clearcutting, selection cutting, shelterwood cutting and microsites on soil surface CO₂ efflux in a tolerant hardwood ecosystem of northern Ontario. *For. Ecol. Manage.* 174:565–575.
- LORIMER, C.G. 1980. Age structure and disturbance history of a southern Appalachian virgin forest. *Ecology* 61:1169–1185.
- MANN, L.K. 1986. Changes in soil carbon storage after cultivation. *Soil Sci.* 142:279–288.
- MARTIN, J.G., AND P.V. BOLSTAD. 2005. Soil respiration in temperate forests: Influence of soil moisture and site biological, chemical and physical characteristics. *Biogeochemistry*, in press.
- MARTIN, J.G., B.D. KLOEPPPEL, T.L. SCHAEFER, D.L. KIMBLER, AND S.G. McNULTY. 1998. Aboveground biomass and nitrogen allocation of ten deciduous Southern Appalachian tree species. *Can. J. For. Res.* 28:1648–1659.
- MATTSON, K., AND W.T. SWANK. 1989. Soil and detrital carbon dynamics following forest cutting in the Southern Appalachians. *Biol. and Fert. of Soils* 7:247–253.
- MCGINTY, S. 1972. The ecological role of *Kalmia latifolia* L. and *Rhododendron maximum* L. in the hardwood forests of Coweeta. MS thesis, University of Georgia, Athens.
- MONK, C.D., G. CHILD, AND S. NICHOLSON. 1970. Biomass, litter and leaf surface area estimates of an oak-hickory forest. *Oikos* 21:138–141.
- NAKANE, K. 1980. Comparative studies of cycling of soil organic carbon in three primeval moist forests. *Jpn. J. Ecol.* 30:155–162.
- PENNOCK, D.J., AND C. VANKESSEL. 1997. Effect of agriculture and of clear-cut forest harvest on landscape-scale soil organic carbon storage in Saskatchewan. *Can. J. Soil Sci.* 77:211–218.
- PETERJOHN, W.T., J.M. MELILLO, P.A. STEUDLER, K.M. NEWKIRK, F.P. BOWLES, AND J.D. ABER. 1994. Responses of trace gas fluxes and N availability to experimentally elevated soil temperatures. *Ecol. Appl.* 4:617–625.
- POST, W.M., T.H. PENG, W.R. EMANUEL, A.W. KING, V.H. DALE, AND D.L. DEANGELIS. 1990. The global carbon cycle. *Am. Scientist* 78:310–326.
- RAICH, J.W., AND W.H. SCHLESINGER. 1992. The global carbon dioxide flux in soil respiration and its relationship to vegetation and climate. *Tellus* 44B:81–99.
- RAYMENT, M.B., AND P.G. JARVIS. 1997. An improved open chamber system for measuring soil CO₂ effluxes of a boreal black spruce forest. *J. Geophys. Res.* 102:28779–28784.
- RISSE, P.G., E.C. BIRNEY, H.D. BLOCKER, S.W. MAY, W.J. PARTON, AND J.A. WIENS. 1981. *The true prairie ecosystems*. Hutchinson-Ross, Stroudsburg, Pennsylvania.
- SAVAGE, K.E., AND E.A. DAVIDSON. 2001. Interannual variation of soil respiration in two New England forests. *Glob. Biogeochem. Cyc.* 15:337–350.
- SCHLENTNER, R.E., AND K. VAN CLEVE. 1985. Relationship between CO₂ evolution from soil, substrate temperature, and substrate moisture in four mature forest types in interior Alaska. *Can. J. For. Res.* 15:97:106.
- SCHLESINGER, W.H. 1984. Soil organic matter: A source of atmosphere CO₂. P. 111–127 in *The role of terrestrial vegetation in the global carbon cycle: Measurement by remote sensing*. Woodwell, G.M. (ed.). John Wiley and Sons, New York.
- SCHLESINGER, W.H. 1990. Evidence from chronosequence studies for a low carbon-storage potential in soils. *Nature* 348:232–234.
- SCHLESINGER, W.H. 1997. *Biogeochemistry*. Academic Press, San Diego. 588 p.
- SEASTEDT, T.R., AND D.A. CROSSLEY JR. 1988. Soil arthropods and their role in decomposition and mineralization processes. P. 233–243 in *Forest ecology and hydrology at Coweeta*, Swank, W.T., and D.A. Crossley Jr. (eds.). Springer-Verlag, New York.
- SELLERS, P.J., R.E. DICKINSON, D.A. RANDALL, A.D. BETTS, F.G. HALL, J.A. BERRY, G.J. COLLATZ, A.S. DENNING, H.A. MOONEY, C.A. NOBRE, N. SATO, C.B. FIELD, AND C.B. HENDERSON-SELLERS. 1997. Modeling the exchanges of energy, water, and carbon between continents and the atmosphere. *Science* 275:502–515.
- TOLAND, D.E., AND D.R. ZAK. 1994. Seasonal patterns of soil respiration in intact and clear-cut northern hardwood forests. *Can. J. For. Res.* 24:1711–1716.
- USDA-NRCS. 1996. *Soil survey of Macon County*. USDA Natural Resource Conservation Service, Raleigh, North Carolina.
- VOSE, J.M., K.J. ELLIOTT, D.W. JOHNSON, D.T. TINGEY, AND M.G.

- JOHNSON. 1997. Soil respiration response to three years of elevated CO₂ and N fertilization in ponderosa pine (*Pinus ponderosa* Doug. ex Laws.). *Plant Soil* 190:19–28.
- WHITTAKER, R.H. 1966. Forest dimensions and production in the Great Smoky Mountains. *Ecology* 47:103–121.
- YANAI, R.D., T.G. SICCAMA, M.A. ARTHUR, C.A. FEDERER, AND A.J. FRIEDLAND. 1999. Accumulation and depletion of base cations in forest floors in the northeastern United States. *Ecology* 80:274–288.
- YONEDA, T., AND H. KIRITA. 1978. Soil respiration. *In* Biological production in a warm-temperate evergreen oak forest of Japan, Kira, T., Y. Ono, and T. Hosokawa (eds.). University of Tokyo Press, Tokyo, Japan.