

LONG-TERM IMPACTS OF AGRICULTURE ON SOIL CARBON AND NITROGEN IN NEW ENGLAND FORESTS

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Abstract. Abandonment and reforestation of agricultural lands has been a major influence on the landscape of eastern North America. Cultivation and soil amendments can dramatically alter soil nutrient pools and cycling, yet few studies have examined the long-term (>50 yr) influence of pasturing and cultivation on soil processes in the forests that develop after abandonment. Twelve forested sites at Harvard Forest in central New England were compared 90–120 yr after abandonment from agricultural use. We measured soil carbon (C), nitrogen (N), and phosphorus (P); light fraction C, N, and $\delta^{15}\text{N}$; microbial chloroform-N; net N mineralization and nitrification; nitrification potential; and culturable nitrifiers on sites with differing land-use history and vegetation. The sites had similar soil series and topography but were arrayed along a soil disturbance gradient from permanent woodlots (selective logging but no mineral soil disturbance) to formerly pastured sites (clearcut and grazed but no deep [>10 cm] soil disturbance) to formerly cultivated sites (cleared-with-plow horizon 15–20 cm thick). Mineral soil C (0–15 cm soil depth) was very similar among all sites, but the forest floor C was lower in the cultivated sites than in the woodlots of both stand types. Mineral soil in cultivated sites contained 800 kg N/ha and 300 kg P/ha more than woodlots, a relative increase of 39% for N and 52% for P. The cultivated soils had lower C:N and C:P ratios, largely driven by higher soil N and P. The light fraction appeared to be more sensitive to prior land use than the bulk soil organic matter. The C content and C:N ratio of light fraction were lower in cultivated soils, which suggests that input and/or turnover of organic matter pools of relatively recent origin remain altered for a century after abandonment. Similar $\delta^{15}\text{N}$ for the light and heavy fraction organic matter pools in cultivated soils suggests that cultivation accelerates the mineralization of humus N, increasing the proportion of N available for plant uptake, resulting in a convergence of the light and heavy fractions. The N pool in the woodlot soils may have been subject to preferential losses of small amounts of ^{14}N over a longer time period, resulting in a more pronounced divergence between the light fraction (reflecting recent plant inputs) and the mineral-associated heavy fraction (more recalcitrant).

Nitrification was strongly influenced by land-use history, with highest rates in formerly cultivated sites. In contrast, soil net N mineralization and chloroform-N were more strongly influenced by present vegetation. Nitrifying bacteria were relatively abundant in all pastured and cultivated sites; however, only the cultivated hardwood sites, with lowest C:N ratios (16–18), had substantial net nitrification. Historical manure inputs may explain the more rapid soil net nitrification rates, by decreasing soil C:N ratios and thus reducing nitrate immobilization in the mineral soil of cultivated sites. Regionally, 65% of the land area was pastured, and a proportion of the nutrients obtained from grazing was transferred to the cultivated croplands, which comprise $\leq 15\%$ of the land area. Pastures generally had intermediate nutrient ratios and N transformations but were often more similar to woodlots, which suggests that plowing and amendments, rather than forest clearance, have the greatest impact on soil organic matter and nutrients. The influence of land-use history on soil N and P and nitrification rates was more dramatic in hardwood sites, which indicates that characteristics of the recovering vegetation and/or changes in plant community composition associated with prior land use are important factors in the rate of recovery. Our findings lead to the surprising conclusion that 19th century agricultural practices decreased forest floor nutrient content and ratios, and increased nitrifier populations and net nitrate production for approximately a century after abandonment. Consideration of site history clearly deserves more attention in the design of field experiments, and in our understanding of patterns of element distributions and transformations in dynamic forested landscapes.

Key words: carbon; cultivation; $\delta^{15}\text{N}$ natural abundance; land-use history; light fraction organic matter; nitrification; nitrogen mineralization; pastures; phosphorus; reforestation; vegetation effects; woodlots.

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INTRODUCTION

During the last 150 yr, most of the landscape of eastern North America has been transformed from predominantly agricultural lands to forest (Williams 1990). While 45–65% of New England's landscape was cleared for pasture or cropland by the mid-1800s, much of this area was abandoned after 1850, and today 70–90% of these lands support mature forests (Hendricksen 1933, Foster et al. 1998). Abandonment of agricultural lands during the last century has also occurred in the southeastern United States (Delcourt and Harris 1980, Kalisz 1986), and Puerto Rico (García-Montiel and Scatena 1994), and is predicted to occur in portions of New Zealand and Europe over the next few decades (Houghton 1996, Maclaren 1996).

Changes in soil organic matter and nutrient pools following the conversion of native systems to agriculture are well documented. Cultivation of temperate forest soils reduces soil C by an average of 30% (see reviews by Johnson 1992, Davidson and Ackerman 1993), through accelerated decomposition in cultivated horizons, reduced plant inputs, and erosion of surface horizons. Active soil C and N fractions are even more sensitive to the effects of conversion and continuous cultivation than total soil C and N pools. Upon tillage, relative losses of 50–75% for soil microbial biomass and light fraction (or relatively undecomposed particulate) organic matter are common (Cambardella and Elliot 1994, Tiessen and Stewart 1983, Collins et al. 1992). Potentially mineralizable N is often reduced by tillage (Campbell and Souster 1982), while net nitrification is typically elevated in agricultural soils (Schimel 1986).

In the northeastern United States, trees quickly invade abandoned farmland, yet recovery of soil organic matter and nutrient dynamics may not proceed rapidly. There often is a time lag between plant production and soil C storage; for example, nearly all the increase in ecosystem C went into standing biomass, not soil organic matter, during 30 yr of old-field succession in North Carolina (Richter et al. 1995). Total soil organic matter and N content increased in an old-field chronosequence spanning 75 yr in New Hampshire, but a minimum of 200 yr was predicted to be necessary to obtain soil organic matter found in nearby primary forests (Hamburg 1984). Although the estimate of Houghton et al. (1983) that temperate soil C recovers to 90% of predisturbance levels within 50 yr was supported in the southeastern United States (Schiffman and Johnson 1989), soil organic matter had not recovered to native levels 50 yr after abandonment in Colorado semi-arid grasslands (Burke et al. 1995). This 50-yr time frame may also be too short for northern temperate forests.

Many studies examining the recovery of nitrogen dynamics after abandonment have focused on the short-term recovery from 0–60 yr after abandonment (Haines 1977, Christensen and MacAller 1985, Kalisz 1986,

Zak et al. 1990, Richter et al. 1994, Ihori et al. 1995) or have compared old fields with late successional forests which have very different plant communities and site history (Lamb 1980, Robertson and Vitousek 1981, Pastor et al. 1987). Examining changes on sites >60 yr after their abandonment is difficult in part because few aerial photos are widely available prior to the 1930s. Several recent studies, however, have used older maps or archaeological information to move back farther in time and have revealed older land-use legacies. Koerner et al. (1997), for example, compared 100-yr-old forests classified as either forest, pasture, cropland, or garden during the early 1800s, and found that soils in all former agricultural lands contained more P and lower C:N ratios than continuously forested areas. Other evidence of prior agriculture, based on soil chemistry, has been reported for Scottish highland sites last farmed in the 1700s (Entwistle et al. 1998) and for Andean grassland sites farmed 1500 yr ago (Sandor and Eash 1995).

Collectively, these findings suggest that land-use history could have an important long-term (>100 yr) legacy on nutrient pools throughout the reforested landscape of many temperate regions. Recent papers have suggested that land-use history is an important factor influencing the capacity of forested watersheds to retain increased atmospheric N inputs (Magill et al. 1997, Aber et al. 1998, Fenn et al. 1998). While there is some evidence for this (Silsbee and Larson 1982, Feger 1992, Magill et al. 1997), few replicated studies have examined the long-term (>100 yr) impacts of common land-use practices (e.g., logging, cultivation, and pasturing) on present-day nutrient transformations. Ignoring the potential importance of site history may be a significant oversight in studies of forest biogeochemistry.

Our study examines the residual impact of farming on soil C, N, and P pools; light fraction organic matter; microbial populations; and N transformations in an area of New England used for agriculture in the mid-1800s but which has been forested for >90 yr. Previous related work in a low-fertility sand plain in central Massachusetts suggested that soil C content and N transformations were influenced by prior cultivation (Motzkin et al. 1996, Compton et al. 1998). Those findings led us to design a broader study in a more fertile glacial till-derived soil, representative of a large proportion of southern New England. This study is unique in comparing three different land uses (woodlot, pasturing, and cultivation), and the recovery of two different vegetation types (hardwood vs. conifer). We also measured nitrifier populations and activity; the C, N, and $\delta^{15}\text{N}$ of the light fraction and heavy fraction organic matter pools; microbial N (chloroform fumigation-extraction); and field net N transformations during the 1994–1995 growing season. Our major questions were: (1) Are soil C, N, and P lower in areas previously used for agriculture? (2) Are N transformations and nitrifiers influ-

enced by land-use history? (3) Do nutrient ratios in recently deposited organic matter (forest floor and light fraction) vary by prior land use? (4) Does the type of agricultural use or the composition of the new forest influence these pools and transformations?

METHODS

Study site

Our study was conducted in the Prospect Hill tract of Harvard Forest (42°30' N, 72°10' W), in the central Massachusetts town of Petersham. Elevation ranges from 270 to 420 m above sea level. Soils are of the Canton and Scituate series (Typic Dystrochrepts), which are deep, well-drained loam soils derived from glacial till, and bedrock of mica-rich schist, granodiorite, and gneiss. Mean weekly air temperature varied from 20°C in July to -6°C in January, and precipitation averaged 126 cm (1990–1994 data).³ A pronounced drought occurred throughout New England in early to mid-1995: January–August 1995 rainfall was ~40% less than the previous 5-yr average rainfall during the same months (Goulden et al. 1996). The vegetation is representative of the transition between the northern hardwoods region and the southern oak–hickory forests. In recently disturbed sites, red oak (*Quercus rubra*), white pine (*Pinus strobus*), and red maple (*Acer rubrum*) dominate, and older forests are dominated by eastern hemlock (*Tsuga canadensis*), white pine, beech (*Fagus grandifolia*), and yellow birch (*Betula alleghaniensis*).

History of the Prospect Hill tract

Historical information was assembled and summarized by Raup and Carlson (1941), Raup (1966), and Foster (1992). Petersham was settled by Europeans in 1733, and little information is available regarding pre-European land use. Forest clearance in Petersham proceeded at ~1–4% per year until the late 1700s, then accelerated to meet increased demands for cattle and sheep pasture. A one-hundred-acre farm might have contained 4–6 acres of crops, 8–10 acres of upland mowing, a similar amount in meadow, and the rest in pasture and woodland. In the early to mid-1700s, crops included vegetables and rotations of cereals and grasses with 7–15 yr of fallow after a decade of use. After the introduction of organic fertilizers, the fallow period was reduced to 1–2 yr. Cleared land increased from 50% of the area in 1800 to nearly 85% during the peak of agriculture in 1840. At that time, ~15% of the landscape was cultivated, while 65% of the landscape was occupied by grasses for pasture and mowing. The remaining forests occupied rocky slopes or swamps where timber was removed and grazing animals roamed during much of the summer. Beginning in 1850, residents left for jobs in developing urban centers or for agricultural opportunities in the Midwestern United

States, and large areas of farmland were abandoned and allowed to revert to forest. In 1907 Harvard University purchased the Prospect Hill tract for use as a research forest.

Site selection and experimental design

We selected 12 plots from a subset of the study plots used for a broader vegetation survey (Motzkin et al. 1999). Three major historical land uses were identified: cultivation (frequent removal of plant biomass, removal of stumps and rocks, mixing surface organic matter and mineral soil to ≤20 cm, possible addition of animal manure), pasturing (removal of vegetation and forest floor, seeding of pasture grasses, removal of stumps and rocks, no mineral soil disturbance >5 cm), and woodlots (frequent removal of trees, no mineral soil disturbance, little forest floor disturbance). Ideally, a forest undisturbed by logging would be used for comparison of nutrient levels and transformations; however, at present estimate, all but one of the <25 old-growth stands in Massachusetts are found on steep slopes in western Massachusetts (Dunwiddie and Leverett 1996). Therefore it was not possible to find old-growth forest sites on similar soils for comparison in this study, and we use the woodlot sites as our “least disturbed” metric.

Former land use was identified based on field and historical evidence (Raup and Carlson 1941, Spurr 1950, Foster 1992; Motzkin et al. 1999), and more recent field examination. Field indicators of cultivation include the presence of an Ap horizon >10 cm deep, absence of surface stones, smooth microtopography, and bordering stone walls composed of small cobbles. Formerly cultivated sites had a 16–20 cm thick Ap horizon (plow layer) with moist soil color generally one Munsell hue darker than the B horizon below it and an abrupt lower boundary. Pastured soils refer to “unimproved pasture” of Motzkin et al. (1999), with no evidence of soil mixing to >5 cm. Woodlots were differentiated from pastures based on historical records, microtopography, and presence of old stumps or tip-up mounds, since stumps were often removed in the conversion to pasture.

Farmers tended to avoid the poorly drained areas of Prospect Hill (Raup and Carlson 1941, Foster 1992), thus land-use history and inherent site factors may be confounded. In order to minimize inherent site differences among land uses, we examined areas with slopes <10% and well-drained soils of the Canton and Scituate series. After field examination, we established four 20 m diameter plots each within former woodlots, pastures and cultivated areas (Table 1). Cultivation and logging ended on all plots ~90–120 yr prior to 1995. Since plant communities could influence soil processes, the plots were stratified into two broad vegetation classes: conifer and hardwood.

We acknowledge that increased replication is desirable in this type of study dealing with complex site

³ URL: <www.lternet.edu/hfr>.

TABLE 1. Soils, land-use history, and vegetation information for all plots.

Plot vegetation class	Prior land use	Plot no.	Soil series	Year last used	Basal area (m ² /ha)	Species (count > 1)
Conifer	Woodlot	76	Canton	1890	44	<i>Tsuga canadensis</i> , <i>Pinus strobus</i>
	Woodlot	132	Canton	1890	44	<i>T. canadensis</i>
	Pastured	218	Canton	1880	57	<i>Pinus resinosa</i> , <i>P. strobus</i>
	Pastured	227	Scituate	1880	60	<i>P. resinosa</i>
	Cultivated	155	Scituate	1908	44	<i>P. strobus</i> , <i>Acer rubrum</i>
	Cultivated	215	Canton	1908	46	<i>T. canadensis</i> , <i>Picea rubens</i> , <i>P. strobus</i> , <i>P. resinosa</i>
Hardwood	Woodlot	135	Scituate	1890	37	<i>A. rubrum</i> , <i>Quercus rubra</i> , <i>T. canadensis</i>
	Woodlot	46	Canton	1890	37	<i>Q. rubra</i> , <i>A. rubrum</i> , <i>Fagus grandifolia</i>
	Pastured	43	Canton	1908	32	<i>A. rubrum</i> , <i>Betula alleghaniensis</i>
	Pastured	91	Canton	1908	30	<i>A. rubrum</i> , <i>Q. rubra</i>
	Cultivated	235	Canton	1908	28	<i>Q. rubra</i> , <i>Acer saccharum</i> , <i>P. strobus</i>
	Cultivated	134	Canton	1908	46	<i>Fraxinus americana</i> , <i>Prunus serotina</i> , <i>A. rubrum</i> , <i>Acer pensylvanicum</i>

Note: "Last used" refers to when the area was abandoned from agriculture or last extensively logged.

histories or "treatments." Sites were selected from a larger set of ~200 plots (Motzkin et al. 1999), and no bias was used in site selection other than holding soils and topography constant. Strong consideration was given to the possibility that inherent site differences were responsible for the patterns observed.

Mineral soil nitrogen transformations

Field net nitrogen mineralization was measured in late summer 1994 and from May–October 1995 using the in situ buried bag method (Eno 1960) as modified by Boone (1992) to use intact soil cores. We only measured mineralization in the mineral soil, because the strongest impact of agriculture was expected to be observed in the former plow layer. The forest floor was removed, and a pair of soil cores collected from the mineral soil 0–15 cm depth using a cylindrical metal corer. Five pairs of soil cores were collected from random locations within each plot in August 1994, and three pairs of cores were collected during the 1995 sampling periods. Time-zero cores were stored on ice and returned to the lab for processing. The second core was kept intact within a perforated plastic tube, which was then capped and placed in a gas-permeable polyethylene bag (0.025 mm thickness) within a nylon mesh bag to prevent disturbance of the core by soil fauna. The core was placed back in the original hole, covered with forest floor and incubated in the field for six weeks per measurement period.

Soil cores were kept cool (<5°C) until returned to the lab, sieved to <2 mm, and extracted within 24 hrs of collection. Sieved fresh soil (10 g) was shaken for 1 min with 100 mL 2 mol/L KCl, allowed to stand for 24 hrs, then suction filtered through Whatman GF A/E filters (Whatman, Clifton, New Jersey, USA). Soil KCl extracts were frozen until colorimetric analysis for ammonium and nitrite plus nitrate by flow injection ion analyzer (LACHAT Instruments, Milwaukee, Wisconsin, USA). Net nitrification was calculated as the net change in nitrate between the time-zero and six-wk

cores. Net N mineralization was calculated as the change in ammonium plus nitrate. Moisture content (105°C for 24 hr) and loss-on-ignition (550°C for 4 hr) were determined, and oven-dried mass of the sieved soil in each core was used to determine bulk density of the <2 mm soil.

Forest floor and mineral soil carbon, nitrogen, and phosphorus

Forest floor (Oi, Oe, and Oa) was collected from a 15 × 15 cm area in early June 1995 from five random locations within each site, and the mass (<5.6 mm) corrected for moisture and ash content. Mineral soil was collected from the 0–15 cm soil depth at five random locations within each site in August 1995. Soil and forest floor materials were finely ground using a roller mill followed by mortar and pestle. Total C and N in the forest floor (June 1995) and 0–15 cm soil (August 1994) were determined by carbon–nitrogen analyzer (Fisons Instruments, Beverly, Massachusetts, USA) using 30 mg soil and 7 mg forest floor. Acidification of a subset of samples with 4 mol/L HCl indicated that no carbonates were present. Total P was determined by the modified Kjeldahl digest of Parkinson and Allen (1975) using 0.3 g of mineral soil and 0.2 g of forest floor. Phosphate in the digests was determined by ion analyzer using the molybdophosphate ascorbic acid technique (LACHAT Instruments, Milwaukee, Wisconsin, USA).

Light fraction carbon and nitrogen

Light fraction mass was determined on <2-mm sieved, air-dried mineral soil collected at time zero for the May 1995 sampling using a modification of Strickland and Sollins (1987). Ten grams of air-dried soil was placed in a centrifuge tube with 20 mL sodium metatungstate solution (density 1.75 g/cm³). The tubes were shaken by hand for 30 s, then centrifuged at 1000 rpm for 15 min. The floating light fraction was siphoned off with a syringe fitted with 2 cm of Tygon

tubing. The centrifugation and siphon process was repeated \geq four times until no floating material remained. The light and heavy fraction were washed over Whatman GF A/E filter paper with \geq 100 mL deionized water and dried for two hr at 65°C. Both fractions were finely ground and analyzed for C and N. Percent light fraction of the total soil was multiplied by the <2 mm soil mass per hectare to obtain light fraction C and N contents. Light fraction and heavy fraction $\delta^{15}\text{N}$ was determined for one equal-weight composite sample per site using a Europa Hydra 20/20 continuous flow isotope ratio mass spectrometer (PDZ Europa, Cheshire, UK) dedicated for natural abundance samples at the University of California–Davis.

Microbial assays

Chloroform-extractable N was determined on time-zero soils collected for in situ N mineralization in June, July, and September 1995 by the fumigation-extraction method (Brookes et al. 1985) within two days of collection. Total N in the fumigated and non-fumigated 0.5 mol/L K_2SO_4 extracts was measured as nitrate following alkaline persulfate digestion (Cabrera and Beare 1993). No correction factor (K_{EN}) was used; therefore the data are presented as chloroform-extractable N to provide an index of microbial N.

Potential nitrification was determined for the July 1995 mineral soil samples using an aerobic shaken slurry method (Schmidt and Belser 1994). This short-term assay provides an indication of the activity and size of autotrophic nitrifier populations. Soil (20 g moist) was shaken for 24 hr with 90 mL phosphate buffer plus 0.2 mL 0.25 mol/L ammonium sulfate; aliquots of the solution collected at 2, 4, 18, and 24 hours were filtered through Whatman GF/A filters and frozen until analysis of nitrite plus nitrate (<48 hr). Chlorate was not added since it did not appear to stop conversion of nitrite to nitrate. Potential nitrification was calculated by determining the linear rate of nitrate increase for the 2–24 hr time period.

Counts of culturable nitrifying bacteria were conducted using a most probable numbers technique (Schmidt and Belser 1994) for one of the two replicate plots per land use by vegetation combination, chosen at random. Nitrite oxidizers (*Nitrobacter*) were enumerated in fresh soils collected 31 August 1995 (during drought) and 12 September 1995 (after rainfall), using five replicate ten-fold dilution series initiated for each sample within 24 hr of collection. We used both the recommended media nitrite concentrations and one-tenth nitrite concentrations, since forest soil nitrifiers are inhibited by high substrate N concentrations (Donaldson and Henderson 1989). Culture tubes were checked for the presence of nitrite or nitrate every week for several months until no further changes were observed.

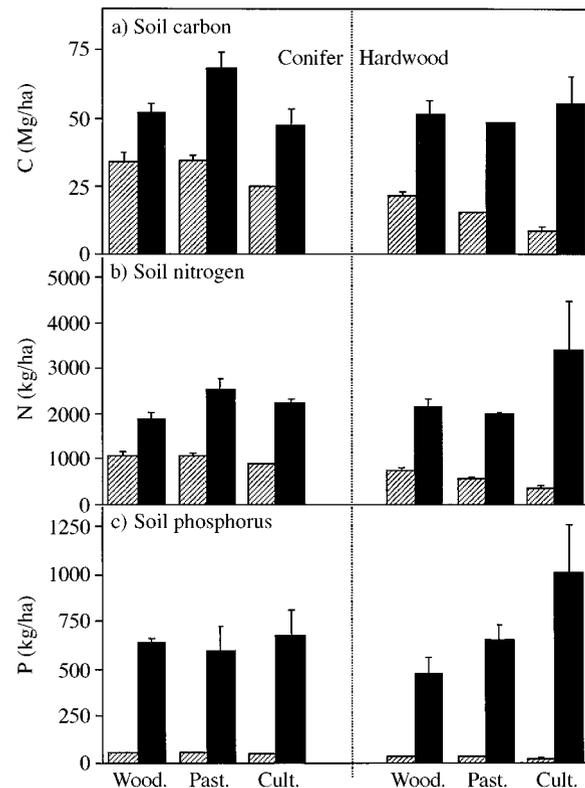


FIG. 1. Total C, N, and P in forest floor and mineral soil by prior land use (Wood. = woodlot; Past. = pastured; Cult. = cultivated) and present vegetation. Hatched bars depict data for the forest floor, and solid bars depict data for mineral soil; error bars indicate +1 SE ($n = 2$ sites).

Statistical analyses

The data were analyzed by two-way factorial analysis of variance using present vegetation (conifer or hardwood) and land-use history (woodlot, pastured, or cultivated) as main effects and site as a covariate. All ANOVAs were conducted using the general linear model in SYSTAT (Wilkinson 1992). Analyses for N mineralization and nitrification were conducted within each time period since it was expected that the rates would vary across time. Nitrification data were log-transformed because of non-normal distribution. Potential nitrification was ranked to avoid both non-normal distribution and nonhomogeneous variances, and the ANOVA performed using ranked data in SYSTAT (non-parametric ANOVA). Post hoc pairwise multiple comparisons were conducted using Tukey's honestly significant difference procedure.

RESULTS

Forest floor and mineral soil carbon, nitrogen, and phosphorus

Forest floor carbon was lower in previously cultivated sites than woodlots (Fig. 1, Tables 2 and 3), while mineral soil C did not vary significantly by prior land

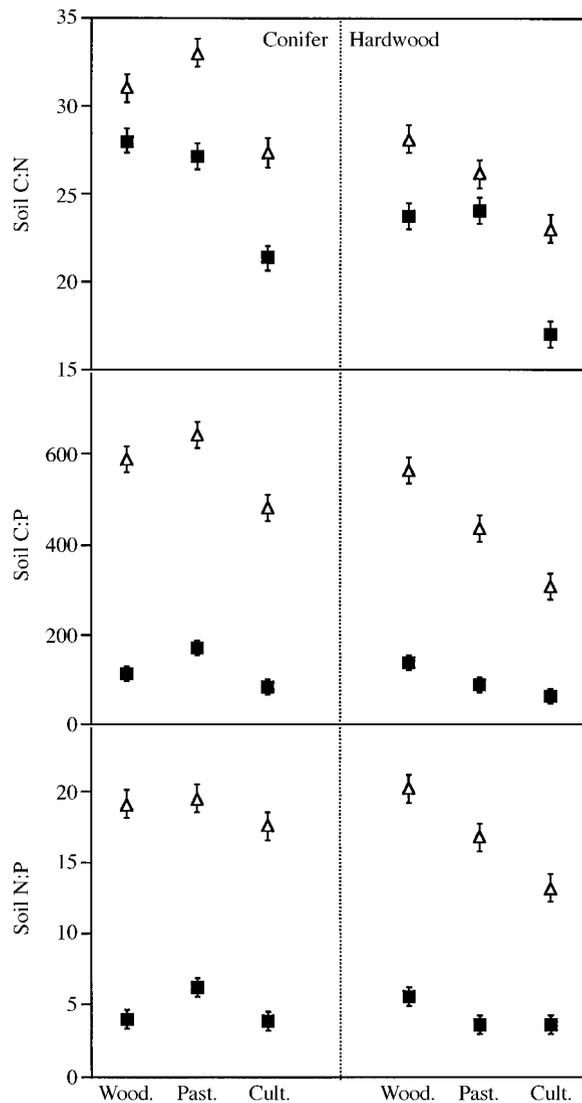


FIG. 2. Ratios of total C, N, and P in forest floor (open triangles) and 0–15 cm soil (solid squares) by prior land use (abbreviations as in Fig. 1) and present vegetation. Error bars indicate ± 1 SE ($n = 2$).

use ($P = 0.072$). Forest floor plus mineral soil C to 15 cm depth was influenced by land-use history, and was 13–16% greater in the woodlots than cultivated sites. Forest floor mass in cultivated sites averaged 20 Mg/ha under hardwoods and 59 Mg C/ha under conifers, while woodlots had 29 and 10 Mg C/ha greater forest floor mass under hardwood and conifer, respectively. Hardwood sites had less soil C to 15 cm than conifer sites, because they contained less forest floor mass. Loss-on-ignition was significantly lower in the hardwood forest floor (Table 2).

Mineral soil N and P contents were influenced by land-use history (Table 3), and were slightly greater in formerly pastured and cultivated sites relative to woodlots (Fig. 1). The cultivated hardwood sites had the

highest soil N and P concentrations, and highest P concentrations in the forest floor. Forest floor N or P concentrations did not vary consistently between conifer and hardwoods (Table 2), but the conifer sites had greater forest floor mass, leading to higher forest floor N and P contents. Because cultivated sites had slightly less forest floor mass, forest floor N was lower than in pastures or woodlots. Forest floor P content did not vary by land use, and a much smaller proportion of soil P was contained in this pool as compared to the forest floor C or N. The pastured conifer stands, dominated by red pine (90% of basal area), had the highest overall forest floor mass and mineral soil C and N content. There was a strong interaction between land-use history and present vegetation for soil N and P contents (Table 3): the hardwood sites varied more strongly by land use than did the conifer sites.

Present vegetation and prior land use influenced C:N, C:P, and N:P ratios, especially in the forest floor (Fig. 2, Table 3). Mineral soil and forest floor C:N ratios were consistently 5 units lower in cultivated sites than pastured or woodlot sites, regardless of vegetation. Forest floor C:P and N:P ratios were lower in cultivated soils, especially under hardwoods. Mineral soil C:P and N:P ratios varied strongly by land-use history only under hardwoods, since cultivated hardwood sites had higher soil P. Pastured site C:N ratios were more similar to woodlots than cultivated sites. Conifer pastures (dominated by red pine) had the highest forest floor and soil C:P ratios and higher soil N:P ratios. In contrast, hardwood pasture forest floor and soil C:P and N:P ratios were intermediate or more similar to cultivated sites.

Soil organic matter density fractions: carbon, nitrogen, and natural abundance $\delta^{15}\text{N}$

Although mineral soil carbon did not differ by prior land use, light fraction carbon was 5–11 Mg C/ha lower (36–61% less) in cultivated soils than woodlot soils (Fig. 3). Prior land use influenced light fraction mass and C content ($P = 0.019$ and $P = 0.001$, respectively), but did not influence light fraction N content. Light fraction organic matter comprised 4–10% of soil mass, 21–39% of soil C, and 16–36% of soil N. Heavy fraction C was not influenced by prior land use, while heavy fraction N was slightly greater in the cultivated sites ($P = 0.084$). Carbon to nitrogen ratios were generally lower in the heavy fraction than the light fraction. Cultivated sites had lower C:N ratios in both the light fraction and heavy fraction (Fig. 3). The heavy fraction C:N ratio was lower for hardwoods than for conifers.

Strong trends were observed for natural abundance $\delta^{15}\text{N}$ in the light and heavy fraction organic matter pools (Fig. 4). The heavy fraction was enriched by 1–3% compared to the light fraction, with little overlap of values. No statistical comparisons were made due to low sample sizes (one composite sample per site).

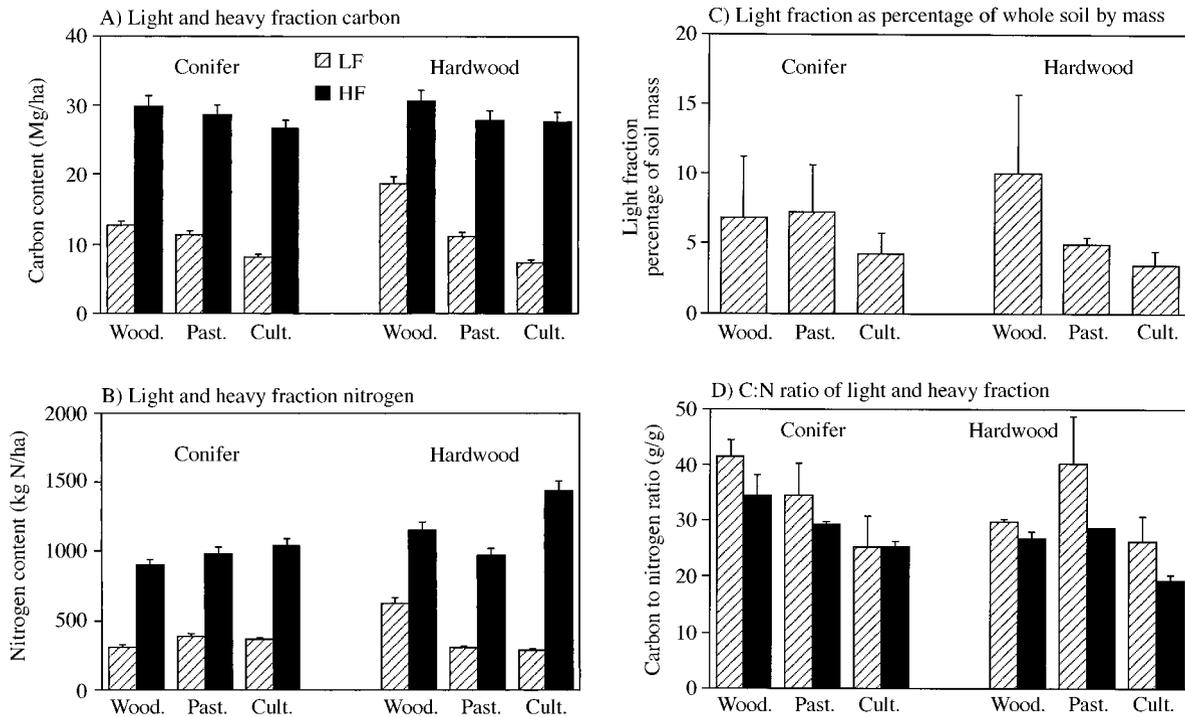


FIG. 3. Light-fraction (LF) and heavy-fraction (HF) mass, C:N ratio, and C and N content in mineral soil collected in May 1995 (0–15 cm depth). Error bars indicate + 1 SD. Prior land use abbreviations are as in Fig. 1.

The variability between replicate plots was generally low ($CV = 10\%$), but the conifer sites showed greater variability than hardwoods. Pastured and cultivated heavy fraction pools were depleted in ^{15}N compared to the woodlot soils. In contrast, the light fraction $\delta^{15}N$ was higher in the pastured and cultivated sites. For both vegetation types, the light fraction and heavy fraction

of the cultivated sites were most similar, while the greatest divergence between light fraction and heavy fraction $\delta^{15}N$ values occurred in the woodlots.

Nitrogen mineralization and nitrification

Net N mineralization was quite variable within plots and over time, and was greater under hardwoods than

TABLE 2. Soil properties for the forest floor (<5.6 mm) and mineral soil (0–15 cm depth).

Site	Mass (Mg/ha)	BD (g/cm ³)	LOI (g/g)	pH [2:1, water]	C (g/kg)	N (g/kg)	P (mg/kg)
Forest floor							
Conifer							
Woodlot	69 ^a	0.13 ^a	0.92	3.36 ^c	487 ^a	15.9	842 ^{bc}
Pastured	74 ^a	0.12 ^{ab}	0.86	3.48 ^{bc}	460 ^{ab}	14.0	720 ^c
Cultivated	59 ^{ab}	0.10 ^{abc}	0.83	3.71 ^b	418 ^{ab}	15.3	880 ^{bc}
Hardwood							
Woodlot	49 ^b	0.13 ^a	0.79	3.61 ^{abc}	428 ^{ab}	15.3	768 ^c
Pastured	36 ^{bc}	0.09 ^{bc}	0.78	3.70 ^{abc}	419 ^{ab}	16.1	958 ^b
Cultivated	20 ^c	0.08 ^c	0.77	4.27 ^a	393 ^b	17.0	1321 ^a
Mineral soil							
Conifer							
Woodlot		0.86	0.11	4.29 ^{ab}	58.2 ^b	2.10 ^b	636 ^{ab}
Pastured		0.80	0.09	4.08 ^b	83.6 ^a	3.09 ^{ab}	598 ^b
Cultivated		0.84	0.11	4.41 ^{ab}	54.6 ^b	2.53 ^b	677 ^{ab}
Hardwood							
Woodlot		0.86	0.10	4.29 ^{ab}	58.6 ^b	2.46 ^b	476 ^b
Pastured		0.86	0.14	4.46 ^a	51.8 ^b	2.17 ^b	652 ^{ab}
Cultivated		0.86	0.09	4.44 ^a	58.8 ^b	3.66 ^a	1009 ^a

Notes: Within each column and material type, values with the same superscript letter are not significantly different ($P > 0.05$). Abbreviations: BD = bulk density; LOI = loss-on-ignition.

TABLE 3. Effects of present vegetation and land-use history on soil properties and processes as indicated by *P* values for a two-way ANOVA, using site as a covariate.

Property or process	Variable	Source of variation		
		Vegetation	Land use	Interaction
Forest floor + mineral soil (kg/ha)	C	0.000	0.001	0.001
	N	NS	0.010	0.000
	P	NS	0.002	0.010
Mineral soil (0–15 cm; kg/ha)	C	NS	NS	0.000
	N	0.013	0.000	0.000
	P	NS	0.001	0.008
Forest floor (kg/ha)	C	0.000	0.002	NS
	N	0.000	0.007	NS
	P	0.000	NS	NS
Mineral soil (g/g)	C:N	0.000	0.000	NS
	C:P	NS	0.002	0.010
	N:P	NS	NS	0.007
Forest floor (g/g)	C:N	0.000	0.000	NS
	C:P	0.000	0.000	0.007
	N:P	0.017	0.000	0.013
Light fraction (kg/ha)	C	NS	0.001	NS
	N	NS	NS	0.024
	C:N	NS	0.007	0.029
Heavy fraction (kg/ha)	C	NS	NS	NS
	N	0.041	NS	NS
	C:N	0.000	0.000	0.022
N mineralization (kg·ha ⁻¹ ·28 d ⁻¹)				
Aug 1994		NS	0.017	0.000
May 1995		0.007	NS	NS
June 1995		0.003	NS	NS
July 1995		NS	NS	NS
Sept. 1995		0.031	NS	NS
Nitrification (kg·ha ⁻¹ ·28 d ⁻¹)				
Aug 1994		NS	0.009	0.011
May 1995		NS	0.010	0.001
June 1995		0.001	0.002	0.016
July 1995		0.018	0.001	0.042
Sept. 1995		0.017	0.000	0.009
CHCl ₃ -extractable N (mg/kg)				
June 1995		0.019	NS	NS
July 1995		0.039	NS	NS
Sept. 1995		NS	NS	0.005
Potential nitrification (mg/kg)				
Per unit soil		0.006	0.020	NS
Per unit organic matter		0.010	0.015	NS
1995 net mineralization (kg N/ha)		0.002	NS	NS
1995 net nitrification (kg N/ha)		0.010	0.010	NS

Note: NS, not significant ($P > 0.05$).

conifers (Fig. 5, Table 3). During two time periods (May and June 1995) the hardwood cultivated sites had much higher net N mineralization rates than all other sites. In August 1994, net N mineralization was much higher in conifer pastured and woodlot sites than other sites. Present vegetation was a more important factor influencing net N mineralization than land-use history (Table 3). Vegetation was a significant factor in May, June, and September 1995, while land-use history was significant only in August 1994, when there was also a significant interaction between land-use history and present vegetation. Comparing growing season N mineralization rates (Table 4), present vegetation appears

to have a greater influence, with rates being more than two times higher in hardwoods than conifers.

Nitrification varied by land-use history and vegetation (Fig. 6; Table 3). Land-use history was a significant factor during all five time periods, while vegetation was a significant influence during three time periods. Net nitrification was 2–24% of total N mineralization (Table 4), and was less variable over time than N mineralization. Although nitrification was detected for at least one time period in all sites, substantial nitrification occurred only in the hardwood cultivated sites. There was a significant interaction between land-use history and vegetation during all time periods, largely because

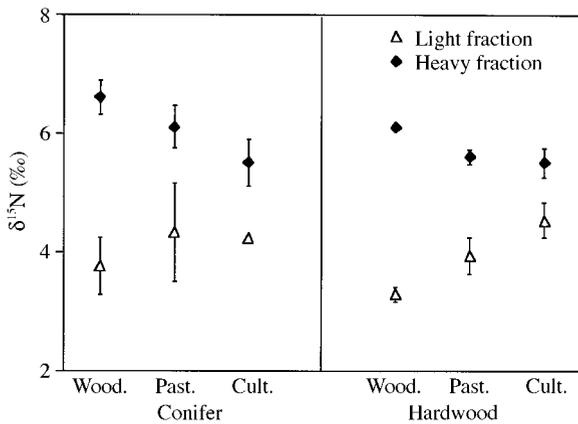


FIG. 4. Natural abundance of $\delta^{15}\text{N}$ in light and heavy fraction soil. Error bars represent ± 1 SD ($n = 2$ sites). Prior land-use abbreviations are as in Fig. 1.

cultivation had a more pronounced effect on net nitrification under hardwoods than conifers.

Net N mineralization was lowest in July 1995, the driest sampling period; gravimetric soil moistures (0–15 cm depth) dropped from 25% at the previous sampling date to 15%. Net nitrification did not decrease as markedly as N mineralization during the drought, implying that nitrification is not as sensitive to moisture changes or could occur within moist microsites in drying soils. Net nitrification was highest in June.

Chloroform-nitrogen and nitrifying bacteria

Although cultivated hardwood sites consistently had the highest chloroform fumigation-extraction N, land-use history was not a significant factor during any time period (Fig. 7, Table 3). As observed for N mineralization, present vegetation appeared to have more influence on chloroform-N than did land-use history. Chloroform-N was similar across plots and less temporally variable than N mineralization. The interaction between vegetation and land-use history was a significant term in June and September, since formerly cultivated hardwood sites had much greater chloroform-N.

Vegetation and prior land use influenced potential nitrification. While only the cultivated hardwood sites had appreciable net nitrification (Fig. 6: July 1995), both former pastures and cultivated sites had high potential nitrification relative to the woodlots (Fig. 8a). Hardwood sites had higher potential nitrification than conifer sites. Potential nitrification and in situ net nitrification in July 1995 were not well correlated ($R^2 = 0.025$).

Culturable autotrophic nitrifying bacteria were more abundant in pastured and cultivated sites than in woodlot sites (Fig. 8b). These data were quite variable, but autotrophic nitrifiers were observed in all stands. The more dilute media (10% the concentrations of Schmidt and Belser 1994) generally yielded higher nitrifier counts, as observed by Donaldson and Henderson

(1989). Counts were much higher in early September, when the drought ended, than in late August.

DISCUSSION

Persistent effects of land-use history on total soil carbon, nitrogen, and phosphorus

The cultivation of forest soils reduces soil carbon by an average of 30% (Johnson 1992, Davidson and Ackerman 1993). Soil carbon (forest floor + mineral soil 0–15 cm depth) for both vegetation types was 13–16% lower in sites last cultivated 90–120 yr prior to sampling than in permanent woodlots, mainly because of lower forest floor C content in the cultivated sites. Although we expected the Ap horizon to more strongly reflect prior land use, mineral soil C content (0–15 cm depth) did not vary by prior land use. There are several possible explanations for this result: (1) soil C was not reduced by 19th century agricultural practices, (2) soil C has recovered within a century, (3) logging also reduces soil C, and (4) the 0–15 cm depth mineral soil samples do not accurately reflect the full mineral soil profile. The first two possibilities may not be the case in glacial till soils of New England: Hamburg (1984) indicates that soil organic matter was lower in sites abandoned <70 yr prior to sampling than in an uncultivated stand, and forest floor mass was still accu-

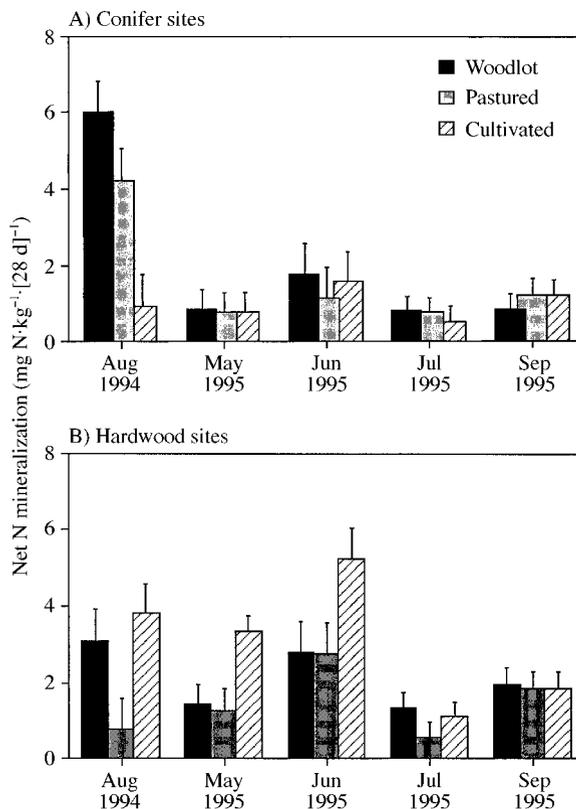


FIG. 5. In situ net nitrogen mineralization rates per gram soil in the 0–15 cm mineral soil. Error bars indicate +1 SE ($n = 2$ plots).

TABLE 4. Growing season net nitrogen mineralization (net ammonium plus nitrate accumulation in buried bags), nitrification, and nitrification as a percentage of N mineralization.

Plot type	N mineralization (kg·ha ⁻¹ ·yr ⁻¹)	Nitrification (kg N·ha ⁻¹ ·yr ⁻¹)	Nitrification as a percentage of N mineral- ization
Conifer			
Cultivated	7.9 ^b (3.5)	0.8 ^{ab} (0.5)	9.3 (2.4)
Pastured	8.2 ^b (0.6)	0.5 ^b (0.2)	6.0 (2.1)
Woodlot	7.7 ^b (0.1)	0.1 ^b (0.0)	1.6 (0.1)
Hardwood			
Cultivated	18.1 ^a (0.7)	4.3 ^a (0.3)	23.7 (2.5)
Pastured	11.8 ^{ab} (1.6)	0.6 ^{ab} (0.2)	4.6 (1.3)
Woodlot	14.7 ^{ab} (0.0)	0.6 ^{ab} (0.1)	4.2 (0.5)

Notes: The time period is 11 May through 31 October 1995. One standard error of the mean of two plots is shown in parentheses. Within the same column, values with the same superscript letter are not significantly different ($P > 0.05$).

mulating at a linear rate. Logging can reduce soil C to some extent, although the reduction is less dramatic than for agriculture (Johnson 1992). Downward translocation of organic matter (Motzkin et al. 1996) and absence of woody root inputs (Richter et al. 1990) during the agricultural period are important factors that may influence C content of soil below the Ap horizon. While carbon in the 0–15 cm mineral soil depth did not vary by land-use history, deeper mineral soil must be considered in any assessment of land-use effects on soil C.

The forest floor was influenced by land-use history and accumulated more rapidly under conifers than hardwoods: accumulation in the cultivated sites after abandonment was ~ 0.23 Mg·ha⁻¹·yr⁻¹ under hardwoods and 0.68 Mg·ha⁻¹·yr⁻¹ under conifers. Forest floor mass was not strongly related to basal area ($R^2 = 0.34$). Accumulation of the forest floor is regulated by the balance between litter inputs and outputs, including decomposition and organic matter transfer to the mineral soil through mixing and to a lesser extent leaching. The lower forest floor masses in the cultivated soils, as compared to woodlot soils, may result from increased turnover or less litter production in the cultivated sites.

Our findings suggest that cultivation increased soil N and P levels, persisting long after the agricultural period ended. In contrast, modern-day temperate-zone agriculture, despite addition of inorganic N and P fertilizers, generally reduces soil N and P (Tiessen et al. 1982, Post and Mann 1990). Organic amendments may yield a different result. In the Hoosfield continuous barley experiment at Rothamsted, an agricultural plot

manured from only 1852–1871 had 26% more N and 56% more C to 23 cm soil depth in 1975 than an adjacent unamended plot (Jenkinson and Johnston 1976). In contrast, soil C and N were lower where inorganic NPK fertilizers were added for over a century. In our study, mineral soil in cultivated sites contained 2800 kg N/ha and 843 kg P/ha, compared with 2010 kg N/ha and 556 kg P/ha in woodlots, a relative increase of 39% for N and 52% for P.

There is evidence that animal manures were added to cultivated soils at Prospect Hill. In the mid-1800s $\sim 65\%$ of the landscape was used for pasturing of cattle and sheep in Petersham (Raup and Carlson 1941), and spring plowing of manure into the soil was practiced at Prospect Hill during the 1800s (Raup and Carlson 1941; F. M. Wheeler, *unpublished manuscript*) (see *Discussion: Long-term effects on organic matter density fractions* [last paragraph]). Animal densities in 1831 were 0.66 animal units/ha of pasture and meadow (includes horses, oxen, steers, cows, heifers, sheep, and swine; Petersham tax records in Harvard Forest Archives). Hamburg (1984) did not observe higher N in cultivated soils in central New Hampshire, where domestic animal densities were lower (peak of 0.3 animal units/ha in 1845; 0.15 units/ha from 1825–1925). The addition of ~ 800 kg N/ha and 300 kg P/ha to the Ap horizon during the >100 -yr agricultural period is quite possible, considering that $\sim 65\%$ of the landscape was used for pasture. Animal manure derived from some fraction of the pastures would have been added to cultivated lands, which comprised ≤ 10 –15% of the area. Manures also have low N:P ratios, and the cultivated forest floor and the hardwood cultivated soil reflected this. Rough calculations for the Sanderson farm indicate that of the ~ 100 kg N in manures produced from two oxen and one cow in 1771, ~ 10 kg N/ha might have made its way to the 0.25 ha cultivated area (Raup and Carlson 1941; Harvard Forest Research File 1974–04); continuation of this practice for 80 yr could roughly explain the accumulation of N in the cultivated sites.

Soil nutrient levels appear to have been enhanced by 19th century farming practices, reflected as increased N and P levels and lower C:N and C:P ratios. Altered nutrient ratios may be the result of manure additions, or may reflect the influence of an altered decomposition environment. The ratios were largely influenced by higher N and P levels, rather than lower C; hence, addition of animal manure as a farming practice may be an important factor in the postagricultural recovery of soil nutrient dynamics. While inorganic fertilizers may result in net N losses, organic amendments may accumulate in the soil (Drinkwater et al. 1998). In the Andes, agricultural practices 1500 yr ago included adding large amounts of guano to terraced Mollisols, and these sites still have higher C, N, and P than native soils (Sandor and Eash 1995). Our findings also suggest that the effects of animal manure amendments can per-

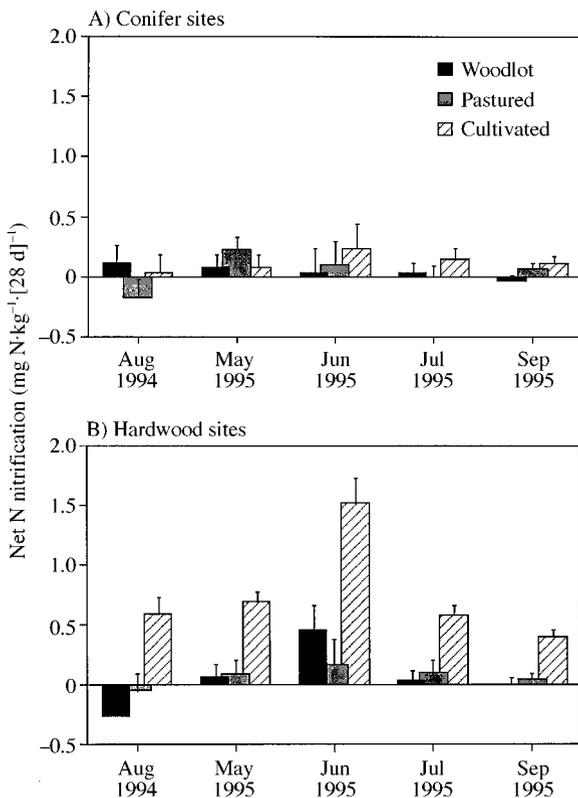


FIG. 6. In situ net nitrification rates per gram soil in the 0–15 cm mineral soil. Error bars indicate +1 SE ($n = 2$ plots).

sist for at least a century in the form of elevated N and P and lower C:N and C:P ratios.

Long-term effects on organic matter density fractions

While bulk mineral soil C did not vary by prior land use, cultivated mineral soil had substantially less light fraction C (36–61% less) than did woodlot soils. The light fraction is largely derived from below- and above-ground litter, and is likely to be of more recent origin, as indicated by lower $\delta^{15}\text{N}$ and higher C:N ratios than the mineral-associated heavy fraction. The higher C:N ratios of the light fraction suggest that in the short term it could be a site for N immobilization; however, over the long term, there is a net transfer of organic matter and N from the light fraction to the heavy fraction. Light fraction dynamics might then parallel inputs and decomposition of litterfall, and would exhibit a pattern similar to forest floor mass, which is also lower in the cultivated sites.

The decline in total soil organic matter in agricultural soils has been attributed to losses of the light fraction (Cambardella and Elliott 1994). Agricultural soils tend to have lower light fraction masses, usually <2% of the soil (Janzen 1987, Janzen et al. 1992, Boone 1994). Our light fraction masses of 4–10% of the soil are within the range of those observed in forest soils (Spycher et al. 1983, Sollins et al. 1984, Strickland and

Sollins 1987, Boone 1994), although the cultivated soils had much less light fraction mass and C than did the woodlot soils. While the light fraction N in cultivated soils was similar to or lower than that in pastured or woodlot soils, heavy fraction N was greater in cultivated soils, indicating an accumulation of N in this pool.

The natural variation in the ratio of $^{15}\text{N}/^{14}\text{N}$ in soils can reflect both differences in sources of N and fractionation of N during decomposition (Delwiche and Steyn 1980, Shearer et al. 1978, Nadelhoffer and Fry 1988, 1994). The lighter isotope is preferentially released during decomposition, and losses of inorganic N through leaching, denitrification, and ammonia volatilization result in preferential losses of ^{14}N from soils, resulting in an increase in soil $\delta^{15}\text{N}$ over time (Nadelhoffer and Fry 1988, 1994, Handley and Raven 1992). Plants are depleted in ^{15}N relative to soil nitrogen (Nadelhoffer and Fry 1994). The light fraction is mostly sand-sized leaf and root fragments of recent plant origin, and therefore has a lower $\delta^{15}\text{N}$ than bulk soil or heavy fraction N.

By more rapidly incorporating isotopically light plant inputs into the mineral soil, cultivation and pasturing can decrease soil $\delta^{15}\text{N}$. Soil $\delta^{15}\text{N}$ has been found to be lower in cultivated soils than in native grassland (Tiessen et al. 1984) or zero-till agriculture (Selles et al. 1984). Pasturing also decreased the surface soil $\delta^{15}\text{N}$ in several tropical grasslands (Piccolo et al. 1994). The heavy fraction (mineral-associated) $\delta^{15}\text{N}$ was lower in the cultivated and pastured soils than in woodlot soils. These observed patterns could be driven by similar mechanisms.

Cultivation may increase the mixing of light fraction and heavy fraction, resulting in a convergence of $\delta^{15}\text{N}$ values between the two fractions. Tiessen et al. (1984) reported that long-term cultivation of a grassland soil resulted in lower $\delta^{15}\text{N}$ in the bulk soil and coarse clay and silt fractions, but higher $\delta^{15}\text{N}$ in the sand fraction. These observations were interpreted as a greater accumulation of more labile N compounds depleted in ^{15}N (from byproducts of microbial decomposition) in the mineral-associated fractions under cultivation. Although we measured soil density fractions rather than size fractions, our findings are similar. The $\delta^{15}\text{N}$ values for the light fraction and heavy fraction were most similar in cultivated sites, which suggests that turnover of light fraction and incorporation of N into the heavy fraction is more rapid in these soils. Compared to woodlot soils, the heavy fraction N (mineral-associated) of the cultivated soils was depleted in ^{15}N , while the light fraction was enriched in ^{15}N . The closer $\delta^{15}\text{N}$ values in the previously cultivated soils suggest a tighter coupling between the two fractions in the cultivated soils than in woodlots.

The $\delta^{15}\text{N}$ of soil amendments in cultivated sites is not known, therefore we cannot directly implicate animal wastes as a source of N in the cultivated soils

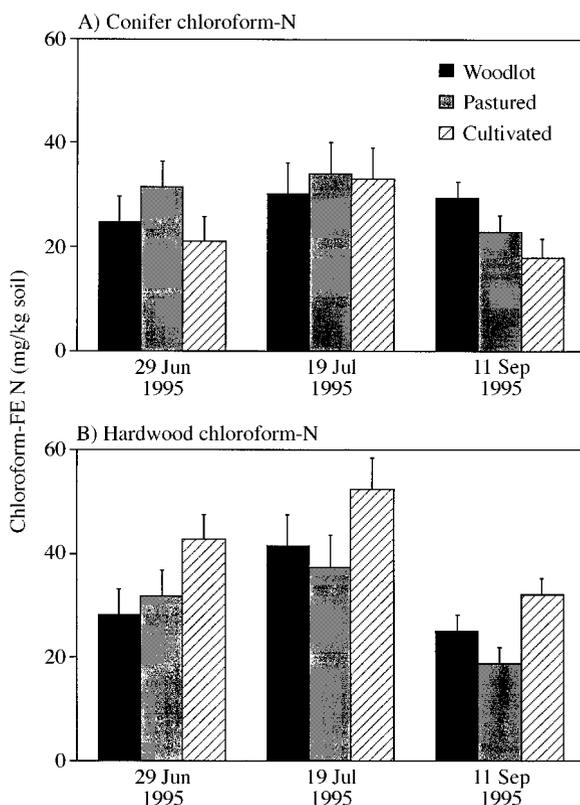


FIG. 7. Chloroform fumigation-extraction (FE) nitrogen as a relative estimate of microbial N by vegetation type and land use. Error bars represent +1 SD ($n = 2$ plots).

using these values. The $\delta^{15}\text{N}$ of animal wastes varies widely depending upon the diet, type of waste, and time of day (Steele and Daniel 1978, Kerley and Jarvis 1996, Kielland and Bryant 1998). Consumption of N_2 -fixing plants such as red and white clover (*Trifolium repens* and *Trifolium pratense*), as well as application of urine (Lincoln 1851) which has a lower signature (Steele and Daniel 1978), might have caused the $\delta^{15}\text{N}$ values of amendments to be relatively low. The $\delta^{15}\text{N}$ values of fresh animal wastes may not be outside the range of soil values (Macko and Ostrom 1994), therefore we cannot use the actual $\delta^{15}\text{N}$ values to directly implicate manure N as a source.

Early land-use practices would have increased losses of nitrogen from the soil via harvest, leaching, and erosion, and therefore depleted native soil nitrogen pools. There is widespread discussion of exhaustion of the native soil nutrient capacity after a few years of growing crops on a recently cleared site (see references in Whitney 1994). However, manures were used widely as a soil amendment in the 1800s (Bidwell and Falconer 1941, Russell 1982), including in Petersham (Raup and Carlson 1941; F. M. Wheeler, Diary from 1881–1882, File No. HF 1882–1 in Harvard Forest Archives); thus the re-accumulating active N pool at this time would be largely composed of manure N. The cumulative ef-

fect of these practices would be to deplete the native N pool and cause manure N inputs to dominate the actively cycling N pools. In the woodlot soils, little N would have been lost, and the slow process of losing small amounts of ^{14}N over the long term would result in a divergence between the light fraction (recent plant inputs) and the more recalcitrant and older heavy fraction. In the cultivated areas, frequent incorporation of amendments into the soil may have also strongly influenced the $\delta^{15}\text{N}$ signal. By increasing the mineralization of humus N and the addition of easily soluble animal wastes, annual cultivation would have made much of the soil N available to plants, resulting in a convergence of the light and heavy fractions. In the woodlot soils, plant uptake and ecosystem losses of N may have preferentially removed ^{14}N from the soil humus for a longer time period, allowing the heavy fraction to become more enriched in ^{15}N over time. We suggest that more than a century after abandonment is required to establish this divergence of $\delta^{15}\text{N}$ values for the light and heavy fraction.

Recovery of processes after agricultural abandonment

Nitrification rates and nitrifiers remain elevated 90–120 yr after abandonment of cultivated sites. Nitrification as a percentage of N mineralization was higher in previously cultivated sites (9% and 24% in conifer and hardwoods) than in pastured and woodlot sites (1–6%, Table 4). The 1995 growing season N mineralization rates ranged from 7 to 18 $\text{kg}\cdot\text{ha}^{-1}\cdot\text{yr}^{-1}$ (Table 4). These values are low for this forest type (Magill et al. 1997), presumably because of the summer 1995 drought.

Several mechanisms explain the higher net nitrification found in cultivated sites relative to uncultivated sites 90–120 yr after their abandonment. Cultivation generally increases net nitrification through liming, aeration, enhanced ammonium levels, and lower immobilization (Schimel 1986). Soil pH was slightly higher in formerly cultivated sites (Table 2). Lime was not locally available at Prospect Hill during the 1800s, but burning was the predominant method of land clearing in New England in the 17th and 18th centuries (Bidwell and Falconer 1941), which can increase soil pH and extractable cations (Woodmansee and Wallach 1981). Autotrophic nitrifiers were present at low levels in all stands, and relatively abundant and active in all cultivated and pastured sites. However, net nitrification was substantial only in the cultivated hardwood sites. Potential nitrification and net nitrification rates were not well correlated ($R^2 = 0.025$), which suggests that factors other than the presence and activity of nitrifiers determines whether a soil will exhibit net nitrification. Immobilization of nitrate is expected to be lower in the cultivated sites, as seen by Schimel (1986) for cultivated grassland soils as compared to native grassland soils. Soil C:N ratios strongly reflect the agricultural

legacies, and relatively low ratios (16–18) in the hardwood cultivated sites may shift the nitrate immobilization–mineralization balance, resulting in net nitrate release during decomposition.

Land-use history may influence forest response to increasing N supply. Specific farming practices, in this case the addition of organic amendments during the 1800s, appear to be important in the rate and direction of the long-term postabandonment N transformations, as was suggested by Vitousek et al. (1989). If formerly cultivated soils have higher net nitrate release, then nitrate leaching and ecosystem N retention might be lower in formerly cultivated areas. In a study designed to mimic dramatic increases in atmospheric N inputs, Magill et al. (1997) cite land-use history as a possible explanation for more rapid initiation of N saturation of a formerly cultivated red pine stand than a formerly pastured hardwood stand at Harvard Forest. Consideration of site history may be critical in understanding N retention and response to changing atmospheric loading across the diverse landscape mosaic of the eastern United States.

Vegetation effects—also a land-use legacy?

The interaction between land-use history and vegetation was almost always a significant factor influencing soil properties and transformations (Table 3). Soil nutrients and nitrification appeared to vary more by land use in hardwood stands than in conifer stands. Several explanations are possible: (1) sites presently occupied by hardwoods had a more intensive cultivation history (longer cultivation, higher rates of fertilization), (2) the variation in stand composition within the categories “conifer” and “hardwood” has an important effect on soil nutrient processes, and (3) nutrient use and allocation vary between hardwoods and conifers. To address the first point, the hardwood cultivated plot 134 (see Table 1) was classified as farmland from 1805 until 1908, and did have the highest mineral soil N and P content of all sites (1266 kg N/ha and 752 kg P/ha), while rates of net mineralization and nitrification were very similar to the other hardwood cultivated plot. The other cultivated sites were also farmed for ≥ 100 yr by the Sandersons and subsequent land-owners (Raup and Carlson 1941, Raup 1966).

Although land-use history was a statistically significant factor in many of our measures, we acknowledge that greater replication would have increased the strength of our findings, since the history or “treatment” effects are possibly confounded with inherent site properties. We cannot reconstruct specific site histories because this level of detail is not available (e.g., crops grown, duration of different uses, or amount of manures added). However, we were still able to detect strong differences among our general land-use categories. Error values were generally low between replicates (with exceptions), indicating that the sites within a “treatment” were relatively similar.

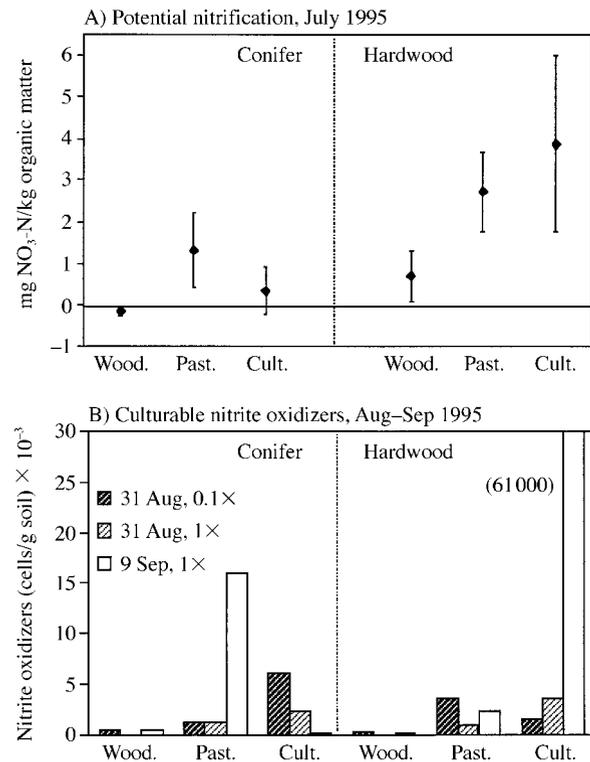


FIG. 8. Potential nitrification and most-probable-numbers (MPN) estimates of nitrite oxidizers. Error bars represent ± 1 SE for potential nitrification. For MPN estimates, media nitrite concentrations were full strength (1 \times) or diluted to one-tenth of those recommended (0.1 \times) in Schmidt and Belser (1994). The August MPN data were during the height of the drought, while the September sampling occurred after a rain.

Land-use history has influenced the distribution of several plant species across Prospect Hill (Motzkin et al. 1999), although not as dramatically as on a nearby low-fertility sand plain (Motzkin et al. 1996). It is possible that the presence of certain species is facilitated by agricultural practices at Prospect Hill. Out of a wide range of edaphic and disturbance factors at this site, the presence of *Prunus* spp. and *Acer saccharum* was best predicted by soil N and the C:N ratio (Motzkin et al. 1999). The variation in species composition within and between the “hardwood” and “conifer” categories could subsequently influence soil processes. Organic matter produced by the fertile-site species listed above can support higher N mineralization and nitrification rates than oaks and conifers (Zak et al. 1986, Boerner and Koslowsky 1989). While conifer woodlots were dominated by hemlocks and/or white pine, the conifer pastured plots were red pine (*Pinus resinosa*) plantations. Red pine litter has high lignin:N ratios and slow decomposition rates (Bockheim and Leide 1986), and the low soil pH, high forest floor and soil C, and high C:N ratios found here support this. Both conifer woodlots were dominated by hemlock (Table 1); the presence

of hemlock has been shown to be associated with low nitrification rates (Mladenoff 1987).

Present vegetation (hardwood or conifer) was an important factor controlling many soil properties. Net N mineralization and chloroform-extractable N were greater in hardwood stands, and not consistently influenced by land-use history (Table 3). Soil microbial biomass may reflect present-day organic matter supply and quality, rather than total soil nutrient content.

Forest floor mass recovered more quickly after abandonment under conifers than under hardwoods. Litterfall may be slightly higher in conifer and hardwood stands (3.2 Mg·ha⁻¹·yr⁻¹ in red pine vs. 2.9 in oak-maple [Magill et al. 1997]); this combined with slower decomposition under conifers than hardwoods (Nadelhoffer et al. 1982, Berg and McLaugherty 1987) would promote more rapid accumulation of the forest floor under conifers. There also appeared to be slightly more mixing of the forest floor with underlying mineral soil in hardwoods, as evidenced by the higher ash content of the hardwood forest floor (Table 2). Recovery of soil C pools may be more rapid under conifers.

Importance of specific management practices

By altering site nutrients and increasing nitrification rates, we speculate that each of the three land uses we examined could have important long-term effects on carbon storage, nitrogen retention, and nutrient cycling. Values for forest floor C, N, and P in the pastured sites were generally intermediate between the cultivated and woodlot sites; while pasture soil C:N ratios and N transformations rates were more similar to woodlots. Nitrifier levels and activity were similar in cultivated and pastured sites (Fig. 8), but net nitrification was consistently higher in the cultivated sites, perhaps because of lower C:N ratios, as discussed above. Our results indicate that cultivation has the most persistent influence on soil nutrients and nitrification, perhaps driven by the addition of amendments combined with the depletion and subsequent slow accumulation of the forest floor and mineral soil light fraction organic matter.

Our findings are somewhat in contrast to the view that early New England agriculture decreased soil fertility (Cronon 1983, Merchant 1989). Agricultural practices in the early 1800s included manure amendments (Bidwell and Falconer 1941), which appear to have enriched soil N and P levels, and decreased C:N and C:P ratios. These amendments and lower C:N ratios persist over a century after abandonment, and may stimulate soil nitrification. However, agriculture also depleted forest floor and light fraction organic matter, and complete recovery of these levels has not occurred. We also have no information on soil erosion rates, which could have influenced soil fertility and affected aquatic ecosystems.

Implications for ecosystem recovery from disturbance

Few long-term studies of human disturbances on ecosystem processes exist, except in unusual cases,

such as the long-term agricultural record at Rothamsted, UK (Leigh and Johnston 1994). Therefore we must rely on historical reconstruction, archaeology, dendrochronology, and paleoecology to see the long-term effects of disturbance (Foster et al. 1996, 1998, Entwistle et al. 1998, Fuller et al. 1998). Response to disturbance has been a major focus in ecology, but it is important to develop an understanding of not only immediate but long-term effects and recovery. A literature survey in 1984 found that site history was rarely mentioned in ecological studies (Hamburg and Sanford 1986); more recent studies document the persistent importance of agricultural impacts on vegetation dynamics, soil nutrient pools, and microbial activity (García-Montiel and Scatena 1994, Burke et al. 1995, Fernandes and Sanford 1995, Motzkin et al. 1996, Garcia et al. 1997, Koerner et al. 1997).

Consideration of site history is important in ecosystem process studies. Our study concludes that nutrient levels, microbial processes, and actively cycling organic matter fractions of cultivated sites may be distinctly different from less-disturbed sites even after a century of recovery via reforestation. The nature and specific impacts of a disturbance (i.e., cultivation vs. pasturing) are important in determining subsequent soil processes, as is the litter quality and productivity of the recovering plant community. Alteration of nutrient content, ratios, and form may continue to have long-term feedbacks (>100 yr) on soil organic matter dynamics and microbial populations. The underlying importance of site history deserves more thought and attention in the design of field studies and in our understanding of biogeochemical processes in dynamic forested landscapes.

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LITERATURE CITED

- Aber, J., W. McDowell, K. Nadelhoffer, A. Magill, G. Berntsen, M. Kamakea, S. McNulty, W. Currie, L. Rustad, and I. Fernandez. 1998. Nitrogen saturation in temperate forest ecosystems: hypotheses revisited. *BioScience* 48:921–34.
- Berg, B., and C. McLaugherty. 1987. Nitrogen release in relation to the disappearance of lignin. *Biogeochemistry* 4: 219–224.
- Bidwell, P. W., and J. I. Falconer. 1941. History of agriculture in the northern United States 1620–1860. Peter Smith, New York, New York, USA.

- Bockheim, J. G., and J. E. Leide. 1986. Litter and forest-floor dynamics in a *Pinus resinosa* plantation in Wisconsin. *Plant and Soil* **96**:393–406.
- Boerner, R. E. J., and S. D. Koslowsky. 1989. Microsite variations in soil chemistry and nitrogen mineralization in a beech–maple forest. *Soil Biology and Biochemistry* **21**:795–801.
- Boone, R. D. 1992. Influence of sampling date and substrate on nitrogen mineralization: comparison of laboratory-incubation and buried-bag methods for two Massachusetts forest soils. *Canadian Journal of Forest Research* **22**:1895–1900.
- Boone, R. D. 1994. Light-fraction soil organic matter: origin and contribution to net nitrogen mineralization. *Soil Biology and Biochemistry* **26**:1459–1468.
- Brookes, P. C., A. Landman, G. Pruden, and D. S. Jenkinson. 1985. Chloroform fumigation and the release of soil nitrogen: a rapid direct extraction method to measure microbial biomass nitrogen in soil. *Soil Biology and Biochemistry* **17**:837–842.
- Burke, I. C., W. K. Lauenroth, and D. P. Coffin. 1995. Soil organic matter recovery in semiarid grasslands: implications for the conservation reserve program. *Ecological Applications* **5**:93–801.
- Cabrera, M. L., and M. H. Beare. 1993. Alkaline persulfate oxidation for determining total nitrogen in microbial biomass extracts. *Soil Science Society of America Journal* **57**:1007–1012.
- Cambardella, C., and E. Elliott. 1994. Carbon and nitrogen dynamics of soil organic matter fractions from cultivated grassland soils. *Soil Science Society of America Journal* **58**:122–130.
- Campbell, C. A., and W. Souster. 1982. Loss of organic matter and potentially mineralizable nitrogen from Saskatchewan soils due to cropping. *Canadian Journal of Soil Science* **62**:651–656.
- Christensen, N., and T. MacAller. 1985. Soil mineral nitrogen transformations during succession in the piedmont of North Carolina. *Soil Biology and Biochemistry* **17**:675–681.
- Collins, H. P., P. E. Rasmussen, and C. L. J. Douglas. 1992. Crop rotation and residue management effects on soil carbon and microbial dynamics. *Soil Science Society of America Journal* **56**:783–788.
- Compton, J. E., R. D. Boone, G. Motzkin, and D. R. Foster. 1998. Soil carbon and nitrogen in a pine–oak sand plain in central Massachusetts: role of vegetation and land-use history. *Oecologia* **116**:536–542.
- Cronon, W. S. 1983. *Changes in the land*. Hill and Wang, New York, New York, USA.
- Davidson, E., and I. Ackerman. 1993. Changes in soil carbon inventories following cultivation of previously untilled soils. *Biogeochemistry* **20**:161–193.
- Delcourt, H., and W. Harris. 1980. Carbon budget of the southeastern U. S. biota: analysis of historical change in trend from source to sink. *Science* **210**:321–323.
- Delwiche, C. C., and P. L. Steyn. 1980. Nitrogen isotope fractionation in soils and microbial reactions. *Environmental Science and Technology* **4**:929–935.
- Donaldson, J. M., and G. S. Henderson. 1989. A dilute medium to determine populations size of ammonium oxidizers in forest soils. *Soil Science Society of America Journal* **53**:1608–1611.
- Drinkwater, L. E., T. Wagoner, and M. Sarrantonio. 1998. Legume-based cropping systems have reduced carbon and nitrogen losses. *Nature* **396**:262–265.
- Dunwiddie, P. W., and R. T. Leverett. 1996. Survey of old-growth forest in Massachusetts. *Rhodora* **98**:419–444.
- Eno, C. F. 1960. Nitrate production in the field by incubating the soil in polyethylene bags. *Soil Science Society of America Proceedings* **24**:277–279.
- Entwistle, J. A., P. W. Abrahams, and R. A. Dodgshon. 1998. Multi-element analysis of soils from Scottish historical sites: interpreting land-use history through the physical and geochemical analysis of soil. *Journal of Archaeological Science* **25**:53–68.
- Feger, K. H. 1992. Nitrogen cycling in two Norway spruce (*Picea abies*) ecosystems and effects of a $(\text{NH}_4)_2\text{SO}_4$ addition. *Water, Air and Soil Pollution* **61**:295–307.
- Fenn, M. E., M. A. Poth, J. D. Aber, J. S. Baron, B. T. Borrmann, D. W. Johnson, A. D. Lemly, S. G. McNulty, D. F. Ryan, and R. Stottlemyer. 1998. Nitrogen excess in North American ecosystems: predisposing factors, ecosystem responses and management strategies. *Ecological Applications* **8**:706–733.
- Fernandes, D., and R. L. Sanford. 1995. Effects of recent land-use practices on soil nutrients and succession under tropical wet forest in Costa Rica. *Conservation Biology* **9**:915–922.
- Foster, D. R. 1992. Land-use history (1730–1990) and vegetation dynamics in central New England, USA. *Journal of Ecology* **80**:753–771.
- Foster, D., G. Motzkin, and B. Slater. 1998. Land-use history as long-term broad-scale disturbance: regional forest dynamics in central New England. *Ecosystems* **1**:96–119.
- Foster, D. R., D. A. Orwig, and J. McLachlan. 1996. Ecological and conservation insights from retrospective studies of old-growth forests. *Trends in Ecology and Evolution* **11**:419–424.
- Fuller, J. L., D. R. Foster, J. S. McLachlan, and N. Drake. 1998. Impact of human activity on regional forest composition and dynamics in central New England. *Ecosystems* **1**:76–95.
- García, C., A. Roldan, and T. Hernandez. 1997. Changes in microbial activity after abandonment of cultivation in a semiarid mediterranean environment. *Journal of Environmental Quality* **26**:285–291.
- García-Montiel, D. C., and F. N. Scatena. 1994. The effect of human activities on forest structure and composition in Puerto Rico. *Forest Ecology and Management* **63**:57–78.
- Goulden, M. L., J. W. Munger, S.-M. Fan, S. C. Wofsy, and B. C. Daube. 1996. Exchange of carbon dioxide by a deciduous forest: response to interannual climate variability. *Science* **271**:1576–1578.
- Haines, B. 1977. Nitrogen uptake: apparent pattern during old-field succession in southeastern U.S. *Oecologia* **26**:295–303.
- Hamburg, S. P. 1984. Effects of forest growth on soil nitrogen and organic matter pools following release from subsistence agriculture. Pages 145–158 in E. L. Stone, editor. *Forest soils and treatment impacts*. Proceedings of the Sixth North American Forest Soils Conference (June 1983). University of Tennessee, Knoxville, Tennessee, USA.
- Hamburg, S. P., and Sanford, R. L. 1986. Disturbance, *Homo sapiens* and ecology. *Bulletin of the Ecological Society of America* **67**:169–171.
- Handley, L. L., and J. A. Raven. 1992. The use of natural abundance of nitrogen isotopes in plant physiology and ecology. *Plant, Cell and Environment* **15**:965–985.
- Hendricksen, C. I. 1933. The agricultural land available for forestry. Pages 151–169 in *A national plan for American forestry* (Copeland Report). Document No. 12. Vol. 1. U.S. Senate. U.S. Government Printing Office, Washington, D.C., USA.
- Houghton, R. A. 1996. Land-use change and terrestrial carbon: the temporal record. Pages 117–134. in M. J. Apps and D. T. Price, editors. *Forest ecosystems, forest management and the global carbon cycle*. North Atlantic Treaty Organization Advanced Science Institute Series. Springer-Verlag, Berlin.
- Houghton, R. A., J. E. Hobbie, J. M. Melillo, B. Moore, B.

- J. Peterson, G. R. Shaver, and G. M. Woodwell. 1983. Changes in the carbon content of terrestrial biota and soils between 1860 and 1980: a net release of CO₂ to the atmosphere. *Ecological Monographs* **53**:235–262.
- Ihori, T., I. C. Burke, and P. B. Hook. 1995. Nitrogen mineralization in native cultivated and abandoned fields in shortgrass steppe. *Plant and Soil* **171**:203–208.
- Janzen, H. H. 1987. Soil organic matter characteristics after long-term cropping to various spring wheat rotations. *Canadian Journal of Soil Science* **67**:845–856.
- Janzen, H. H., C. A. Campbell, S. A. Brandt, G. P. Lafond, and L. Townley-Smith. 1992. Light-fraction organic matter in soils from long-term crop rotations. *Soil Science Society of America Journal* **56**:1799–1806.
- Jenkinson, D. S., and A. E. Johnston. 1976. Soil organic matter in the Hoosfield continuous barley experiment. Pages 87–101 *in* Annual report for 1976, Part II. Rothamsted Experiment Station, Harpenden, UK.
- Johnson, D. W. 1992. Effects of forest management on soil carbon storage. *Water, Air and Soil Pollution* **64**:83–120.
- Kalisz, P. 1986. Soil properties of steep Appalachian old fields. *Ecology* **67**:1011–1023.
- Kerley, S. J., and S. C. Jarvis. 1996. Preliminary studies of the impact of excreted N on cycling and uptake of N in pasture systems using natural abundance stable isotopic discrimination. *Plant and Soil* **178**:287–294.
- Kielland, K., and J. P. Bryant. 1998. Moose herbivory in taiga: effects on biogeochemistry and vegetation dynamics in primary succession. *Oikos* **82**:377–383.
- Koerner, W., J. L. Dupouey, E. Dambrine, and M. Benoit. 1997. Influence of past land use on the vegetation and soils of present day forest in the Vosges mountains, France. *Journal of Ecology* **85**:351–358.
- Lamb, D. 1980. Soil nitrogen mineralization in a secondary rainforest succession. *Oecologia* **47**:257–263.
- Leigh, R. A., and A. E. Johnston. 1994. Long-term experiments in agricultural and ecological sciences. CAB International, Wallingford, UK.
- Lincoln, J. W. 1851. Farming in Worcester, Massachusetts. Pages 268–277 *in* Report of the commissioner of patents for the year 1850. Part II. Agriculture. Printer to the House of Representatives, Washington, D. C., USA.
- Macko, S. A., and N. E. Ostrom. 1994. Pollution studies using stable isotopes. Pages 45–62 *in* K. Lajtha and R. H. Michener, editors. *Stable isotopes in ecology and environmental science*. Blackwell Scientific, Oxford, UK.
- Maclaren, J. P. 1996. Plantation forestry: its role as a carbon sink. Pages 117–134 *in* M. J. Apps and D. T. Price, editors. *Forest ecosystems, forest management and the global carbon cycle*. North Atlantic Treaty Organization Advanced Science Institute Series. Springer-Verlag, Berlin.
- Magill, A. H., J. D. Aber, J. J. Hendricks, R. D. Bowden, J. M. Melillo, and P. A. Steudler. 1997. Biogeochemical response of forest ecosystems to simulated chronic nitrogen deposition. *Ecological Applications* **7**:402–415.
- Merchant, C. 1989. *Ecological revolutions: nature, gender, and science in New England*. University of North Carolina Press, Chapel Hill, North Carolina, USA.
- Mladenoff, D. J. 1987. Dynamics of nitrogen mineralization and nitrification in hemlock and hardwood treefall gaps. *Ecology* **68**:1171–1180.
- Motzkin, G., D. Foster, A. Allen, J. Harrod, and R. Boone. 1996. Controlling site to evaluate history: vegetation patterns of a New England sand plain. *Ecological Monographs* **66**:345–365.
- Motzkin, G., P. Wilson, D. R. Foster, and A. Allen. 1999. Vegetation patterns in heterogeneous landscapes: the important of history and environment. *Journal of Vegetation Science* **10**:903–920.
- Nadelhoffer, K. J., J. D. Aber, and J. M. Melillo. 1982. Leaf-litter production and soil organic matter dynamics along a nitrogen-availability gradient in Southern Wisconsin (USA). *Canadian Journal of Forest Research* **13**:12–21.
- Nadelhoffer, K. J., and B. Fry. 1988. Controls on natural nitrogen-15 and carbon-13 abundance in forest soil organic matter. *Soil Science Society of America Journal* **52**:1633–1640.
- Nadelhoffer, K. J., and B. Fry. 1994. Nitrogen isotope studies in forest ecosystems. Pages 22–44 *in* K. Lajtha and R. Michener, editors. *Stable isotopes in ecology and environmental science*. Blackwell, Oxford, UK.
- Parkinson, J. A., and S. E. Allen. 1975. A wet oxidation procedure suitable for the determination of nitrogen and mineral nutrients in biological material. *Communications in Soil Science and Plant Analysis* **6**:1–11.
- Pastor, J., M. A. Stillwell, and D. Tilman. 1987. Nitrogen mineralization and nitrification in four Minnesota old fields. *Oecologia* **71**:481–485.
- Piccolo, M. C., C. Neill, and C. C. Cerri. 1994. Natural abundance of ¹⁵N in soils along forest-to-pasture chronosequences in the western Brazilian Amazon Basin. *Oecologia* **99**:112–117.
- Post, W. M., and L. K. Mann. 1990. Changes in soil organic carbon and nitrogen as a result of cultivation. Pages 401–407 *in* A. F. Bowman, editor. *Soil and the greenhouse effect*. Wiley, New York, New York, USA.
- Raup, H. 1966. The view from John Sanderson's farm. *Forest History* **10**:2–11.
- Raup, H. M., and R. E. Carlson. 1941. The history of land use at the Harvard Forest. Bulletin No. 20. Harvard Forest, Petersham, Massachusetts, USA.
- Richter, D. D., L. I. Barbar, M. A. Huston, and M. Jaeger. 1990. Effects of annual tillage on organic carbon in a fine-textured Udalf: the importance of root dynamics to soil carbon storage. *Soil Science* **149**:78–83.
- Richter, D. D., D. Markewitz, J. K. Dunscomb, P. R. Heine, C. G. Wells, A. Stuanes, H. L. Allen, B. Urrego, K. Harrison, and G. Bonani. 1995. Carbon cycling in a loblolly pine forest: implications for the missing carbon sink and the concept of soil. Pages 233–251 *in* W. W. McFee and J. M. Kelly, editors. *Carbon forms and functions in forest soils*. Soil Science Society of America, Madison, Wisconsin, USA.
- Richter, D. D., D. Markewitz, C. G. Wells, H. L. Allen, R. April, P. R. Heine, and B. Urrego. 1994. Soil chemical change during three decades in an old-field loblolly pine (*Pinus taeda* L.) ecosystem. *Ecology* **75**:1463–1473.
- Robertson, G. P., and P. M. Vitousek. 1981. Nitrification potentials in primary and secondary succession. *Ecology* **62**:376–386.
- Russell, H. S. 1982. *A long deep furrow: 400 years of farming in New England*. University Press of New England, Hanover, New Hampshire, USA.
- Sandor, J. A., and N. S. Eash. 1995. Ancient agricultural soils in the Andes of southern Peru. *Soil Science Society of America Journal* **59**:170–179.
- Schiffman, P., and W. C. Johnson. 1989. Phytomass and detrital carbon storage during forest regrowth in the southeastern United States Piedmont. *Canadian Journal of Forest Research* **19**:69–78.
- Schimel, D. S. 1986. Carbon and nitrogen turnover in adjacent grassland and cropland ecosystems. *Biogeochemistry* **2**:345–357.
- Schmidt, E. L., and L. W. Belser. 1994. Autotrophic nitrifying bacteria. Pages 159–177 *in* R. W. Weaver, S. Angle, P. Bottomley, D. Bezdick, S. Smith, A. Tabatabai, and A. Wollum, editors. *Microbiological and biochemical properties*. Part two. *Methods of soil analysis*. Volume five. Soil Science Society of America, Madison, Wisconsin, USA.
- Selles, F., R. E. Karamanos, and K. E. Bowren. 1984. Chang-

- es in natural ^{15}N abundance of soils associated with tillage practices. *Canadian Journal of Soil Science* **64**:345–354.
- Shearer, G., D. H. Kohl, and S.-H. Chien. 1978. The nitrogen-15 abundance in a wide variety of soils. *Soil Science Society of America Journal* **42**:89–902.
- Silsbee, D. G., and G. L. Larson. 1982. Water quality of streams in the Great Smoky Mountains National Park. *Hydrobiologia* **89**:97–115.
- Sollins, P., G. Spycher, and C. A. Glassman. 1984. Net nitrogen mineralization from light- and heavy-fraction forest soil organic matter. *Soil Biology and Biochemistry* **16**:31–37.
- Spurr, S. H. 1950. Stand composition in the Harvard Forest as influenced by site and forest management. Dissertation. Yale University, New Haven, Connecticut, USA.
- Spycher, G., P. Sollins, and S. Rose. 1983. Carbon and nitrogen in the light fraction of a forest soil: vertical distribution and seasonal patterns. *Soil Science* **135**:79–87.
- Steele, K. W., and R. M. Daniel. 1978. Fractionation of nitrogen isotopes by animals: a further complication to the use of variations in the natural abundance of ^{15}N for tracer studies. *Journal of Agricultural Science Cambridge* **90**:7–9.
- Strickland, T. C., and P. Sollins. 1987. Improved method for separating light- and heavy-fraction material from soil. *Soil Science Society of America Journal* **51**:1390–1393.
- Tiessen, H., R. E. Karamanos, and J. W. B. Stewart. 1984. Natural nitrogen-15 abundance as an indicator of soil organic matter transformations in native and cultivated soils. *Soil Science Society of America Journal* **48**:312–315.
- Tiessen, H., and J. W. B. Stewart. 1983. Cultivation effects on organic matter composition and size fractions. *Soil Science Society of America Journal* **47**:509–514.
- Tiessen, H., J. W. B. Stewart, and J. R. Bettany. 1982. Cultivation effects on the amounts and concentrations of carbon, nitrogen, and phosphorus in grassland soils. *Agronomy Journal* **74**:831–835.
- Vitousek, P. M., P. A. Matson, and K. Van Cleve. 1989. Nitrogen availability and nitrification during succession: primary, secondary and old-field seres. *Plant and Soil* **115**:229–239.
- Whitney, G. 1994. From coastal wilderness to fruited plain: a history of environmental changes in temperate North America, 1500 to the present. Cambridge University Press, Cambridge, UK.
- Wilkinson, L. 1992. SYSTAT: the system for statistics. SYSTAT, Evanston, Illinois, USA.
- Williams, M. 1990. Deforestation. Pages 179–201 in B. Turner, W. Clark, R. Kates, J. Richards, J. Mathews, and W. Meyer, editors. *The earth as transformed by human action*. Cambridge University Press, Cambridge, UK.
- Woodmansee, R. G., and L. S. Wallach. 1981. Effects of fire regimes on biogeochemical cycles. Pages 649–669 in F. E. Clark and T. Rosswall, editors. *Terrestrial nitrogen cycles*. Volume 33. Swedish Natural Resource Science Council, Stockholm, Sweden.
- Zak, D. R., D. F. Grigal, S. Gleeson, and D. Tilman. 1990. Carbon and nitrogen cycling during old-field succession: constraints on plant and microbial biomass. *Biogeochemistry* **11**:111–129.
- Zak, D. R., K. S. Pregitzer, and G. E. Host. 1986. Landscape variation in nitrogen mineralization and nitrification. *Canadian Journal of Forest Research* **16**:1258–1263.