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Soil Carbon Accumulation During Temperate Forest Succession on Abandoned Low Productivity Agricultural Lands

Robyn L. Foote and Paul Grogan*

Department of Biology, Queen's University, Kingston, Ontario K7L 3N6, Canada

Abstract

Carbon sequestration in soils that have previously been depleted of organic matter due to agriculture is an important component of global strategies to mitigate rising atmospheric CO_2 concentrations. Extensive areas of low productivity farmland have been abandoned from agriculture in eastern North America and elsewhere over the past century, and are naturally regenerating to temperate forests. We investigated the soil carbon sequestration potential of such lands by sampling adjacent mature forest and agricultural field sites, and replicated chronosequences of forest succession on Podzol, Brunisol, and Luvisol soil types that are considered 'marginal' for agriculture and have been abandoned extensively across southeastern Ontario, Canada. Total soil organic carbon and nitrogen stocks to 10 cm depth were approximately 32% and 18% lower, respectively, in agricultural fields compared to mature forests. Furthermore, carbon stocks across our 100-year chronosequences increased most within the 0–5 cm soil depth interval, tended to increase within the 5–10 cm interval, and were unaltered within the 10–20 cm interval. Soil type had little effect on the potential magnitude or rates of soil carbon sequestration (~10 g C m^{-2} y^{-1} in the top 10 cm), perhaps because all sites shared a common vegetation successional pattern. Finally, our investigations of the 'labile' free-light carbon and nitrogen fractions in the Brunisol soil type indicated no increases across the chronosequence, implying that soil carbon accumulation was primarily in more recalcitrant pools. Our results indicate that each of these low productivity soil types can be moderate carbon sinks for a century following agricultural abandonment, and strongly suggest that time since abandonment is more important than soil type in determining the potential magnitude of carbon sequestration within this climatic region.

Key words: agriculture; organic matter; soil carbon; soil nitrogen; light fraction carbon; succession; texture; temperate forest.

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Author contributions: PG conceived of the experimental design consisting of replicated forest and field sites and chronosequences on different soil types in the region. As a master's student, RLF worked in collaboration with PG to develop the specific questions and hypotheses for the paper. RLF conducted field work for hypotheses 2 and 4 and lab work for hypotheses 1 to 4. RLF performed the statistical analyses for the paper and prepared the figures and tables with guidance from PG. RLF and PG contributed to the writing and editing of the manuscript.

**Corresponding author; e-mail:* groganp@queensu.ca

Introduction

Land-use changes have resulted in a net release of about 124 Pg of organically bound carbon (C) from terrestrial ecosystems since 1850, and are responsible for approximately one-third of the total CO_2 increase in the atmosphere over that period (Houghton 1999; Malhi and others 2002). Clearance and subsequent tillage for agriculture has been an important component of that land-use change impact, releasing about 54 Pg of C that had been stored in soil organic matter (Paustian and others 1997). In recent years, however, extensive areas of agricultural land have been abandoned in many regions including eastern North America, and parts of Europe, East Asia, and South America (McLauchlan 2006a; Tasser and others 2007; Kuemmerle and others 2008). For example, 35% of farm grasslands that had been drained or otherwise improved for increased pasture production in the eastern half of Canada (Ontario–Newfoundland) was abandoned between 1951 and 1991 (Osborne 1978; Parson 1999). Abandoned agricultural land may be a significant C sink and therefore could be an important naturally occurring, low cost mechanism to mitigate anthropogenic CO_2 emissions.

Comparisons of native ecosystems (for example, mature forests) with adjacent agricultural fields across Canada and globally suggest soil C losses of 20–25% when land is cleared and tilled for agricultural use (Davidson and Ackerman 1993; Murty and others 2002; VandenBygaart and others 2003). Such comparisons provide an indication of the potential for soil C sequestration when farmland is abandoned and allowed to revert back to forest (Paustian and others 1997). Experimental research on the potential for soil C sequestration when agricultural management intensity is reduced (for example, 'conservation tillage'), abandoned (Murty and others 2002; Six and others 2002; Paul and others 2003; Poulton and others 2003; VandenBygaart and others 2003; DeGryze and others 2004), or switched to afforestation (Richter and others 1999) have mostly been on good quality productive agricultural lands that had hitherto been intensively managed (that is, tilled and fertilized annually). Paradoxically, technical, economic, social, and cultural factors over the past 50–100 years have tended to result in increasing agricultural *intensification* of such lands. By contrast, relatively unproductive or 'marginal' lands have been abandoned extensively in eastern North America and elsewhere (Hart 1968; Parson 1999). Such lands have relatively low productivity due to shallow soil depths, high stone or clay contents, drainage issues, and so on, and therefore are inherently less favored for agriculture. Accordingly, these marginal lands were usually not intensively managed for agriculture in the first place, and therefore their potential for soil C accumulation after abandonment may differ substantially from more productive soils. Several fundamental research questions arise. Is total C in marginal soils significantly depleted by agriculture? *If* there has been substantial depletion, does inherently low productivity result in slow rates of soil C recovery relative to more productive soils? Even if sequestration rates are low, do the extensive areas of abandoned marginal land suggest that these soils could be regionally significant C sinks? In summary, a better understanding of the distinctive features of soil C cycling in *marginal* agricultural lands would substantially improve estimations of global soil C sequestration potential.

The temporal pattern of soil C accumulation following agricultural abandonment for either marginal or more productive lands is not well documented, especially for the later phases of succession. Conceptually, net primary production (NPP) increases between early and mid-secondary succession until peak leaf area index is reached (50–80 years), and then begins a slow decline that may, or may not, stabilize late in succession (Odum 1969; Chapin and others 2002). Because soil organic matter decomposition rates are linked to plant C inputs (that is, NPP), they follow a corresponding pattern, although with a lag that results in a slow recovery of soil C up toward some steady-state asymptote in late succession (Chapin and others 2002). Patterns and rates of change in soil C following agricultural abandonment have been estimated using repeated sampling, chronosequences, and comparing sites of two different ages (Post and Kwon 2000; Six and others 2002; Del Galdo and others 2003; Poulton and others 2003; DeGryze and others 2004; Knops and Tilman 2000; McLauchlan and others 2006). However, most research on C cycling across successional sequences of natural vegetation regeneration has focused on the first few decades following abandonment, with only very few studies in temperate regions extending beyond 60 years (Post and Kwon 2000). Here, we characterize the longer term (that is, century scale) pattern of soil C accumulation following agricultural abandonment using multiple chronosequence sites that are scattered 0.1–60 km apart across a much larger area than most previous studies.

Parent material, one of the five 'state factors' along with climate, topography, vegetation, and time (Jenny 1941) may influence soil C dynamics because it leads to the development of soils of different textures. The onset of agricultural practices generally results in relatively large C losses from coarse-textured soils (Burke and others 1989; Jarecki and Lal 2005), but organic matter in finer-textured soils seems to be more highly protected from decomposition. For example, clay concentration is positively correlated with soil C storage across the Great Plains (Nichols 1984; Burke and others 1989; Plante and others 2006) suggesting that finer texture enhances physical protection within aggregates and chemical protection as humified organic matter (Six and others 1998, 2000). Silt and clay content may also enhance soil moisture retention, potentially prolonging plant growth and therefore C inputs to soils in seasonally dry ecosystems at least (Burke and others 1989; Chapin and others 2002). In summary, these results suggest that organic matter in finer-textured soils is more protected against C losses following conversion to agriculture, but also accumulates more quickly after abandonment. However, clay concentrations did not correlate with rates of total, labile, or non-acid hydrolyzable C accumulation over a 40-year perennial grassland chronosequence in western Minnesota (McLauchlan 2006b). Studies of abandoned sites that are naturally regenerating toward forests as well as longer-term grassland studies are required to adequately evaluate the potentially critical influence of texture as a control on regional patterns of soil C sequestration. Here, we sampled replicated sites that differed in soil type but that share a common climate, topography, and vegetation succession to investigate the influence of texture on both the potential for C sequestration as well as the temporal patterns of soil C accumulation.

Soil C is heterogeneous, consisting of a continuum ranging from relatively small labile fractions with short turnover times through to larger more recalcitrant fractions with slower turnover times (Chapin and others 2002). The relative amounts of C accumulating in these different fractions can provide insights into the mechanisms of C sequestration as well as the pools which are most sensitive to land-use change (Post and Kwon 2000; Six and others 2002; Del Galdo and others 2003; DeGryze and others 2004). Several studies have documented substantial decreases in labile C pools upon conversion of land to agricultural use (Besnard and others 1996; Carter and others 1998; Gregorich and others 2006), but little is known about changes following agricultural abandonment. Labile C pools were higher after 10 years of succession in Michigan (DeGryze and others 2004), and increased over the first 40 years of grassland development (McLauchlan and others 2006), but in both cases labile C accounted for only about 10% of the total C increase. These results suggest that C accumulates in both labile and more recalcitrant pools in the early decades following agricultural abandonment, but the longer-term patterns have not yet been determined despite the particular significance of the latter pool to prolonged and stable C storage.

We investigated soil C dynamics on three widespread distinct soil types that are considered 'marginal' (that is, low productivity) for agriculture (Gillespie and others 1966) within the mixed hardwood–conifer forest ecozone of southeastern Ontario, Canada. This region experienced extensive forest clearance and settlement by the early Europeans beginning in the late 1700s, followed by widespread abandonment of agricultural land from the late 1800s (Osborne 1978) in a pattern that was common across much of eastern North America (Hart 1968; Parson 1999). The three soil types are classified as differing in texture (Gillespie and others 1966; Gillespie and Wicklund 1968) and are from three different soil orders: a Podzol characteristic of the acidic Canadian Shield bedrock, and a Brunisol and Luvisol that are characteristic of the Limestone Plains in this region. We used our data to test the following hypotheses using replicated pairs of adjacent mature forest and agricultural field sites, and replicated chronosequences of abandoned agricultural land. The first three hypotheses refer to all three soil types, whereas the fourth was tested on one soil type only for logistical reasons.

1. Soil C and N pools on marginal (that is, low productivity) land can be depleted by agriculture.
2. Soil C in marginal lands accumulates over a century following agricultural abandonment.
3. Fine-textured soils lose less C than coarse-textured soils after conversion to agriculture, and accumulate C more rapidly following agricultural abandonment.
4. Free-light fraction C in Brunisol soils accumulates over a century following agricultural abandonment.

Methods

Study Area

This study was conducted near Kingston in southeastern Ontario, Canada (44°14′N 76°30′W) in the summers of 2004–2007. Warm summers and cold winters (mean temperatures of 16 and −4°C, respectively) are common within this region, and on average there are 222 days with a mean temperature above 0°C. Mean annual precipitation ranges from 700 to 900 mm and is fairly evenly distributed throughout the year with at least half occurring as snow between December and March (Environment Canada 2009). The study area is in the Mixedwood Plains ecozone where agriculture is a major land use, but there is also a considerable amount of mixed coniferous–deciduous forest (Wiken 1996). Mature forests are dominated by sugar maple (*Acer saccharum* Marsh.) and red oak (*Quercus rubra* L.), with some white oak (*Quercus alba* L.), red maple (*Acer rubrum* L.), basswood (*Tilia* *americana* L.), eastern hemlock (*Tsuga canadensis* L.), white pine (*Pinus strobus* L.), ironwood (*Ostrya virginiana* (P. Mill) K. Koch), and blue beech (*Carpinus caroliniana* Walt.) (Ecological Stratification Working Group 1995; Wiken 1996).

Our study focused on three common soil series that are characteristic of the northern portion of the Mixedwood Plains ecozone, and that represent three different soil orders (Podzolic, Brunisolic [equivalent to W.R.B. 'Cambisol'], and Luvisolic) within the Canadian Classification System. These soil types correspond to Spodosol, Inceptisol, and Alfisol orders, respectively, in the United States soil classification system. The Podzol (Monteagle soil series) (Gillespie and others 1966) is a well-drained sandy loam that is common across the siliceous Canadian Shield (Figure 1). This shallow and stony soil (typically 20–30 cm) is derived from glacial till that occurs amongst the numerous bedrock outcrops on the landscape, and is of very limited agricultural use (Gillespie and others 1966). The Brunisol (Farmington soil series) is a well-drained loam or sandy loam (Gillespie and others 1966) of about 20 cm depth that occurs extensively on limestone in Eastern Ontario (Figure 1). The shallowness of this soil type is the primary restriction on its agricultural productivity, although it is farmed more intensively where the soil depth permits (Gillespie and others 1966). The Luvisol (Lansdowne soil series) is an imperfectly drained clay soil formed on late glacial lacustrine sediments close to Lake Ontario (Figure 1). The Luvisol is generally deeper than the other two soil types (typically ~30–50 cm of gleyed non-calcareous material above 20–30 cm of highly calcareous sub-soil (Gillespie and others 1966)), and is considered the most productive of the region's soil types, mostly likely due to its superior water holding capacity during the summer months (Gillespie and others 1966).

History of Study Area

Colonization and establishment of agriculture in the region began around 1783 (Gillespie and others

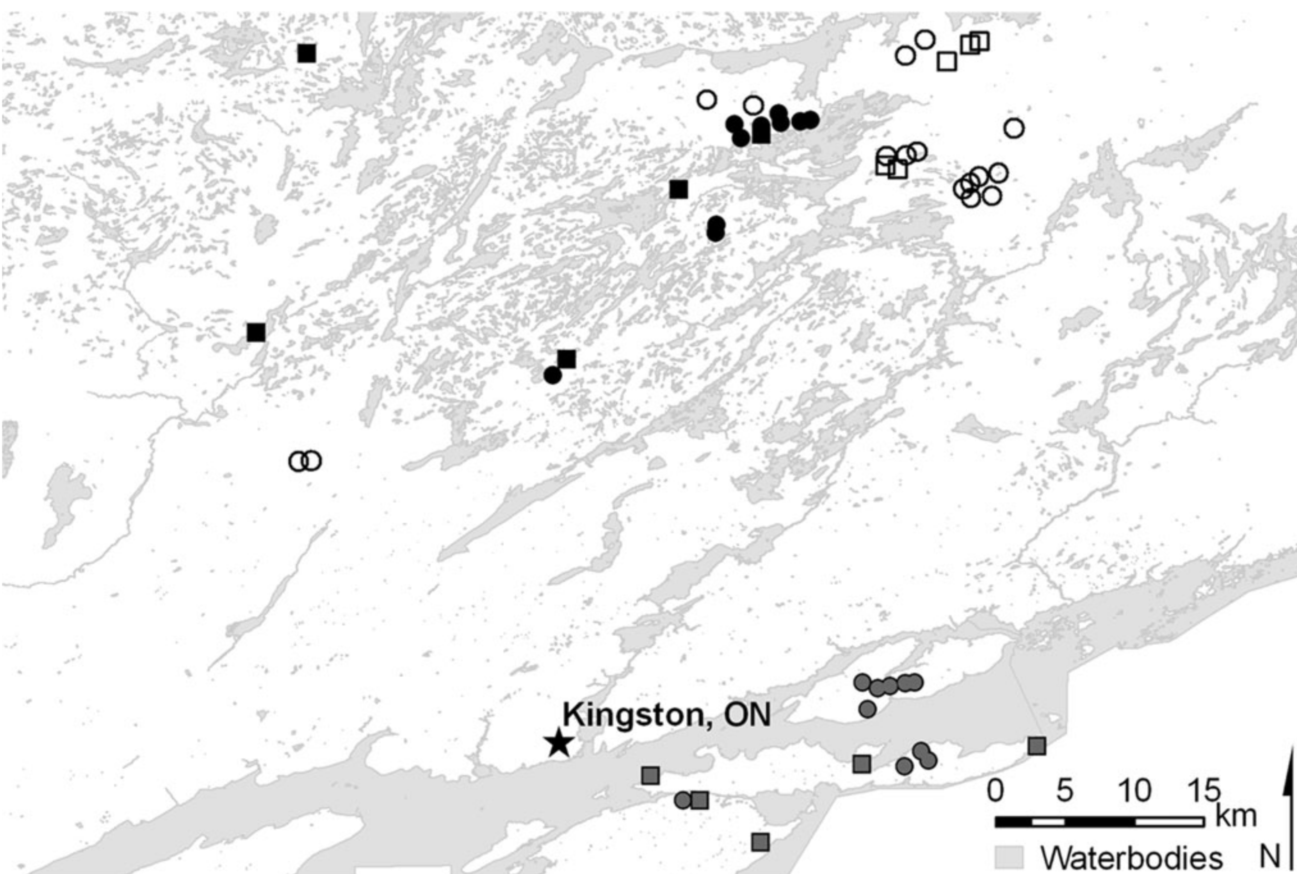

Figure 1. Sampling locations on the three major soil types in the region around Kingston, Ontario, Canada. Podzol, Brunisol and Luvisol sites are indicated by *black*, *open*, and *grey* symbols, respectively. Mature forest and adjacent agricultural field sites are indicated by *squares*; chronosequence sites are indicated by *circles*.

1966; Osborne 1978). A lack of roads as well as the presence of the agriculturally unfavorable Canadian Shield surfaces restricted initial settlement to the Limestone Plains on the edge of Lake Ontario (Osborne 1978). However, continuing population growth and demand for new farmland in the 1850s pushed settlers northward onto the Shield to clear the flatter and less rocky tracts of land for agriculture, whereas the more rocky areas were logged to provide wood for building construction, fuel, and export (Osborne 1978). Logging and clearance were so intense across Eastern Ontario that most townships had less than 30% forest cover by 1880, and wood was apparently so scarce by 1900 that many townhouses were heated primarily by coal (Keddy 1993). Oats, peas, and spring wheat were the region's most popular crops in the mid-1800s, but hay soon became strongly dominant and still is today, along with some corn, barley, and oats (Osborne 1982). Production in the region is generally highest on the Luvisol soils where these crops are grown primarily to support the livestock industry (Gillespie and others 1966). Rural populations peaked around 1881, after which an ongoing pattern of abandonment of agricultural land began (Gillespie and Wicklund 1968; Osborne 1978).

Site Identification and Description

We used aerial photos of the Kingston region from 1925 to 1930 (1:15,000), 1953 (1:15,840), 1978 (1:10,000) and 1991 (1:30,000) (Map and Air Photo Collection at Queen's University Library) to locate adjacent mature forests and agricultural fields that had been under the same land-use management practice since at least 1953 (that is, about 50 years ago). Thus, assuming that mature (second growth) forests take at least 100 years to regenerate, the minimum period since abandonment for our selected mature forest sites must be at least 150 years. Aerial photographs were also used to identify successional sites that had been cleared for agriculture at some point in the past and have since been abandoned and allowed to revert to forest. These sites and the current agricultural field sites constitute the chronosequences in our study; mature forests were not included because aging them was too speculative. We used local soils maps (Gillespie and others 1966; Gillespie and Wicklund 1968) to screen the sites for the chosen soil series. Afterwards, we visited all sites to make final selections of replicate pairs of mature forest and agricultural field sites (n = 5 for each soil type) and successional sites on the Podzol (n = 10), Brunisol (n = 16), and Luvisol (n = 10) that fit the following criteria: soil profile in the field was consistent with soil maps, similar flat topography, similar well to moderately well-drained soils, minimum size of about 1 ha, and minimal evidence of logging in the forest sites. Therefore, of the five state factors that influence soil development (Jenny 1941) and ecosystem C cycling (Chapin and others 2002), three have been specifically included as part of the study (soil parent material, vegetation-type, and time since agricultural abandonment) and two were equivalent among all sites (flat relief, and a broadly similar climate because they are all located within 45 km of each other). To determine the effects of agriculture using meaningful forest–field comparisons, we were careful to select pairs of sites in which the adjacent mature forest had no obvious features that would likely have precluded agriculture by the early European colonizers (for example, exposed bedrock, extremely shallow or rocky soils, steep topography). The time series of aerial photos for each successional site was used to estimate time since abandonment from agriculture. Specifically, the extent of new shrub cover within a field that had clearly been under agriculture in the previous photograph of the time series was used to estimate when agriculture was likely abandoned. Because the time series of photos were at approximately 25 year intervals, the likely range of error with this approach should be within ±12 years. Current landowners were an important source of information, confirming estimates of time since agricultural abandonment for some of the abandoned sites, describing management practices for the current fields, and providing histories of some of the mature forest sites. Thirteen of our agricultural field sites had been repeatedly used to grow hay, which was cut once or twice per year. The two other fields were also used for hay, but corn and barley crops were grown every few years. Landowners indicated that tillage is occasional and rarely exceeds 20 cm in depth on even the most productive soils, and that manure and/or inorganic fertilizer applications have been infrequent in the region.

Grasses, forbs, and just a few small shrubs and trees dominated early successional sites. By contrast, shrubs including dogwood (*Cornus* spp.), prickly ash (*Zanthoxylum americanum* P. Mill.), and juniper (*Juniperus virginiana* L.) were dominant 40–50 years after abandonment, though trees such as ash (*Fraxinus americana* L.) and hop hornbeam (*O. virginiana*) were also common. Some mid-successional sites were patchy with areas dominated by shrubs intermixed with grassy areas and numerous small trees such as young maples 1–3 m high. The tree canopy in later successional sites was mostly closed after 80 years of abandonment. These sites were dominated by trees (10–15 cm in diameter at breast height—DBH), with a limited understory of grasses and a few small saplings.

Field Sampling and Measurements

'Site' was the experimental unit in our study and the basis of the statistical analyses. We composited (that is, pooled together) soil samples at each site to mask out small-scale variation in favor of examining larger scale patterns across the region (that is, among the groups of sites for each soil type). Furthermore, the pairs of adjacent mature forest and agricultural field sites (n = 15) and the successional sites (n = 51 including the fields) for each soil type were well separated (0.1–60 km, see Figure 1) so that although local disturbances or differences in agricultural management might have affected one site, other replicate sites within a group were unlikely to be affected. Each site (minimum area 1 ha) was initially surveyed to avoid sampling any patches that did not fit the original selection criteria. All soils were sampled along line transects in a randomly chosen direction across the site and at least 15 m from any edge, and away from human modifications such as trails. Any litter that rested loosely on the soil surface (that is, the Oi forest floor layer consisting of the previous year's litterfall) was brushed away before the soil core was taken. No underlying OeOa (that is, -FH') layer of moderate-highly decomposed litter was found in any of the agricultural field sites, or in any of the chronosequence sites, nor in most of the mature forest sites. There was, however, a thin OeOa layer (mean depth 1 cm) in three of the mature forest sites on the Brunisol that was included in the cores.

We used a 5 cm diameter split corer (AMS Inc, American Falls, ID) to sample 10 locations approximately 20 m apart in each of the five mature forest and agricultural field sites. Cores were divided into 0–5 and 5–10 cm sections and bulked into sealable plastic bags to form one composite sample for each depth interval at each site. Minimum soil depth at each sampling location within each site was determined using a 2-cm diameter soil corer that was pushed down as deep as physically possible, hitting rock in one-third of all sites and hard compacted subsoil in the remainder. Depth to the base of the A horizon in each core was determined by the presence of a clear color boundary between surface dark organic and lower greyer more mineral soil.

The successional sites were also sampled with the split corer at five locations approximately 20 m apart, but to a depth of 20 cm. Cores were checked for compression and where there was a difference in distance between depth to the base of the sampled hole and length of the sampled soil core, we discarded the sample and took another core from a nearby location. Likewise, on the several occasions where the soils were so shallow that the corer could not be pushed to at least 10 cm, an alternative nearby location was sampled. Cores were divided into 0–5, 5–10, and 10–20 cm sections that were bulked into composite samples for each site. In addition to the total C and N analyses on all soil types, we also investigated changes in free-light fraction C and N over time in the Brunisol soil type (only) using five separate cores (to 10 cm depth) that were taken along transects through each of the successional, mature forest, and agricultural field sites of that soil type using the same sampling protocol as described above.

We characterized the vegetation on each soil type by collecting tree biomass and species composition data at all of the five mature forest sites. Species identity and DBH of all trees greater than 1.3 m in height within ten randomly located plots (10 × 10 m) along transects (>400 m) at each site (n = 5 per soil type) were determined, and these plot data were pooled to calculate composite values for each site.

Biogeochemical Analyses

All soil samples were air-dried (3 days at 21°C), weighed, sieved to 2 mm, and the remaining roots and stones were separated and weighed. Roots from the mid-summer 2004 cores were soaked and washed in de-ionized water prior to drying at 65°C for biomass determination. Dry soil bulk density for each depth at each site was calculated as mass of oven-dry (105°C) sieved soil per core volume (that is, the mass of roots and stones larger than 2 mm in diameter were not included). Soil samples from each site (10 g air-dried soil: 10 ml deionized water) were analyzed for pH (AB15 pH meter; Fisher Scientific, Pennsylvania, USA). Sub-samples were oven-dried and ground with a planetary ball mill (Retsch, Newtown, Pennsylvania, USA) and analyzed (1.25 g) for C and N by combustion and elemental determination using infrared gas analysis and thermal conductivity, respectively (CNS-2000 analyzer, LECO Corporation, Michigan, USA). Soil carbon and nitrogen pools for each depth interval were calculated by multiplying the dry soil bulk density of the less-than-2-mm fraction by the elemental concentrations. Inorganic C in all three soil types was very low or below detection as determined by bubbling and mass loss following 3 M HCl addition (Loeppert and Suarez 1996). Particle size was determined for the five oldest successional sites of each soil type (that is, 15 in total, mean age = 74 years) using the hydrometer method after dispersing the soils with 5% sodium hexametaphosphate solution (Gee and Bauder 1986).

We used density fractionation to isolate the free-light fraction, which is the light fraction outside soil aggregates, from the five cores at each Brunisol site (Six and others 1998; Compton and Boone 2000). Sub-samples (15 g) were weighed into 50 ml centrifuge tubes, 40 ml of 1.7 g cm^{-3} NaI was added, and slowly shaken by hand end over end 10 times. Samples were centrifuged for 45 min, allowed to settle for 1 min, and then the top 20 ml of NaI containing the free-light fraction was suctioned off using a pipette. The free-light fraction was filtered through 0.45 µm nylon membrane filters, and then washed with 40 ml of 0.1 M $CaCl_2$ and 40 ml of distilled water. The centrifugation and suctioning process was then repeated and the accumulated material retained by the filter at the end of the second filtering was dried at 65°C for 48 h and weighed to the nearest 0.01 mg. The samples were ground and sieved (250 µm sieve) prior to C and N analyses by dry combustion (Carlo Erba NA 2500, Milan, Italy). Macroscopic charcoal fragments were occasionally observed within the light fraction.

Statistical Analyses

We used a three factor partial hierarchal analysis of variance design (Winer and others 1991) to compare the influences of soil type, land use (that is, mature forests and agricultural fields), and depth (0–5 and 5–10 cm intervals) on soil C, soil N, soil C:N, pH, bulk density, and root biomass among sites. Soil type was tested in the statistical model's main stratum (that is, relative to the random factor 'site' nested within soil type), whereas land use, depth, and their interactions with each other and soil type were tested within the model's substratum (that is, relative to the error term 'site' nested within soil type × land use × depth).

Analysis of covariance models were constructed to test for the effect of soil type (with time since agricultural abandonment as the covariate) and their interaction on soil C, N, soil C:N, and soil bulk density for each of the three depths (0–5, 5–10, and 10–20 cm). The interaction between time and soil type tested for differences in C accumulation rates (that is, slopes) among soil types. Relationships between total soil C or soil N or free-light fraction pools and time since abandonment for each depth and soil type were calculated using simple linear regressions. We used paired *t*-tests to compare the influences of land use (that is, mature forests and agricultural fields) on free-light fraction C and N. To focus on the mineral soil light fraction only, we excluded cores with OeOa layers from this analysis, reducing our paired comparison of mature forests and agricultural fields to three sites, each based on five within-site sample cores except for one of the forest sites where two cores were excluded.

Tree aboveground biomass was estimated using allometric equations relating biomass to DBH for each species that were developed for the closest possible geographic location (Ter-Mikaelian and Korzukhin 1997; Lambert and others 2005). Simpson's index was used to calculate tree species diversity among soil types. Data from the 10 plots in each site were composited to compare tree aboveground biomass, number of stems per plot, and species diversity among soil types using one-factor analyses of variance. All statistical analyses were done using JMP 6.0 (SAS Institute 2006; Cary, North Carolina), and no data transformations were necessary to pass normality. All statistically significant effects and their interactions are reported in the text.

Results

Soil Carbon and Nitrogen in Forests and Adjacent Fields

Soil C and N stocks were significantly smaller in agricultural fields than adjacent mature forests at both 0–5 and 5–10 cm depths ($F_{1,36} = 60.4$, $P < 0.0001$ and $F_{1,36} = 22.3$, $P < 0.0001$, respectively; Figure 2), strongly suggesting that agricultural practices in this region had depleted the soils of these elements. Carbon stocks in agricultural fields were approximately 32% lower relative to mature forests when averaged over the top 10 cm of the three soil types. The decrease in soil N was smaller (averaging 18%) and more variable than for C, resulting in significantly lower soil C:N in agricultural fields relative to mature forests for all soil types and both 0–5 and 5–10 cm depth intervals ($F_{1,36} = 137.6$, $P < 0.0001$; Table 1). To our surprise, soil type did not significantly influence C or N stocks at either depth, and there were no significant interactions between land use and soil type (Figure 2).

Because bulk density differed significantly among land uses, soil types, and depths (Table 1), we also analyzed these data as concentrations of soil C and N (g/100 g dw) to assess the robustness of the above conclusions. The pattern of results was almost identical (land use: $F_{1,36} = 65.5$, $P < 0.0001$ and $F_{1,36} = 48.7$, $P < 0.0001$ for C and N, respectively), except that there were significant interactions

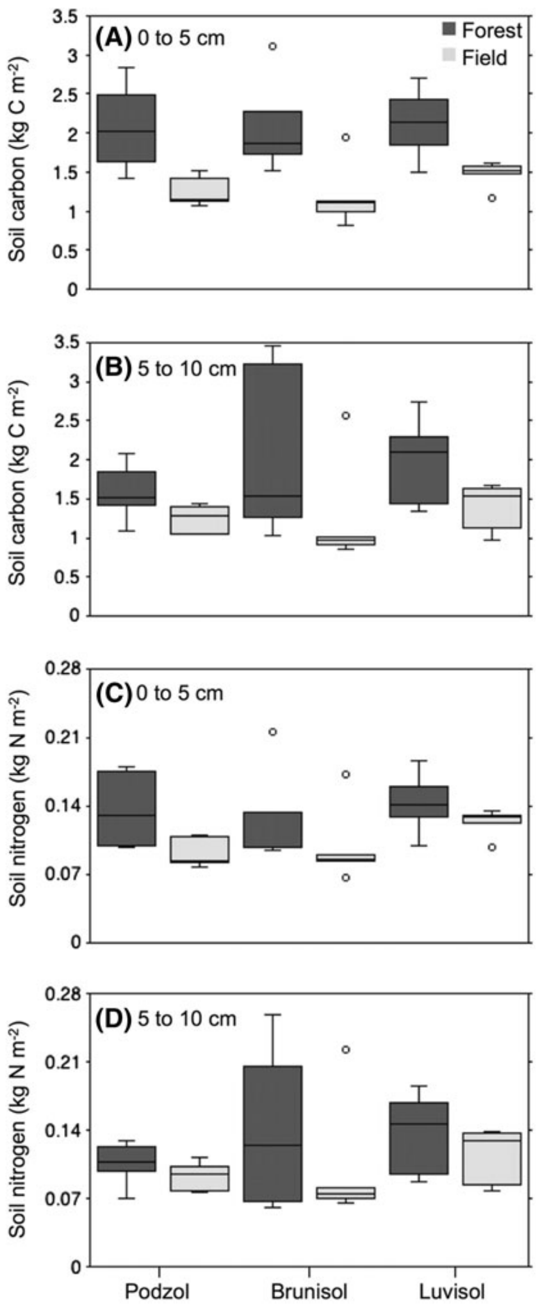

Figure 2. Soil carbon stocks from 0 to 5 cm (**A**) and 5 to 10 cm (**B**), and nitrogen stocks from 0 to 5 cm (**C**) and 5 to 10 cm (**D**) in pairs of mature forests and adjacent agricultural fields (n = 5,) for each soil type. *Box plots* show 10, 25, median, 75, and 90th percentiles as *horizontal lines* and outlying values as *circles.*

between land use and soil type for both C and N ($F_{2,36}$ = 9.4, $P < 0.0005$ and $F_{2,36}$ = 9.0, $P <$ 0.0007, respectively). Mature forest soils on the Brunisol had about 50% higher C and N concentrations compared to mature forests of the other two soil types (Table 1), resulting in relatively large differences between mature forests and agricultural fields on this soil type. Furthermore, the difference in soil C:N between forests and fields was highest in the Brunisol, resulting in a significant land use × soil type interaction ($F_{2,36}$ = 5.1, $P < 0.01$). Finally, there were significant effects of depth, indicating that C and N concentrations were larger in the 0–5 cm than the 5–10 cm depth interval ($F_{1,36}$ = 11.3, $P < 0.002$ and $F_{1,36}$ = 10.9, $P < 0.002$, respectively).

Total Soil Carbon and Nitrogen During Forest Regeneration After Agricultural Abandonment

Total soil C over time since agricultural abandonment increased significantly in the 0–5 cm depth interval ($F_{1,45}$ = 23.8, $P < 0.0001$; Figure 3), tended to increase significantly in the 5–10 cm interval ($F_{1,45}$ = 3.4, $P < 0.07$; Figure 4), but did not change in the 10–20 cm interval. Overall mean rates of soil C accumulation for the top 10 cm were 8.5, 10.3, and 11.4 g C m^{-2} y^{-1} for the Podzol, Brunisol, and Luvisol, respectively. A comparison of the slopes at 0–5 cm and 5–10 cm revealed that approximately 70% of the C accumulation occurred in the top 5 cm (Table 2).

There were no significant interactions between soil type and time for any of the depth intervals, indicating that the rates of increase were statistically similar among soil types (Table 2; Figure 3). Nevertheless, the Luvisol chronosequence soils generally had slightly more C in the top 5 cm (Figure 3), resulting in a larger intercept compared to the other two soils (Tukey's HSD, $P < 0.05$, Table 2), and a significant influence of soil type on total soil C ($F_{2,45}$ = 5.4, $P < 0.008$). Thus, although the paired forest–field comparisons above indicated no differences in total C among soil types, the larger chronosequence data sets indicated slightly more C near the surface of the Luvisol soils.

Soil N increased significantly with time since agricultural abandonment between 0 and 5 cm ($F_{1,45}$ = 9.7, $P < 0.003$), but did not change at lower depths. Although there were no significant soil type × time interactions, the relationship between N accumulation and time was strongest in the Luvisol (Table 2). Analogous to the results for C above, N stocks differed significantly among soil types at 0–5 cm ($F_{2,45}$ = 10.0, $P < 0.0003$) due to significantly higher N in the Luvisol chronosequence soils compared to the others (Tukey's HSD, $P < 0.05$). These soils also had higher N stocks in the 5–10 and 10–20 cm depth intervals ($F_{2,45}$ = 2.5, $P < 0.09$ and $F_{2,30}$ = 4.9, $P < 0.01$, respectively),

Table 1. Mean Soil C and N Concentrations, C:N, pH, Bulk Density, Root Biomass, Topsoil and A Horizon Depths for Mature Forests and Agricultural Fields on the Three Soil Types for 0–5 cm and 5–10 cm Depth Intervals ($n = 5$)

Soil property	Podzol		Brunisol		Luvisol	
	Forest	Field	Forest	Field	Forest	Field
Soil C (g/100 g dw)						
0–5 cm	6.63 (1.01)	2.95 (0.20)	10.80 (2.63)	2.65 (0.51)	5.86 (0.85)	3.83 (0.44)
5–10 cm	4.24 (0.88)	2.22 (0.12)	7.54 (2.71)	2.30 (0.63)	4.37 (0.77)	2.48 (0.34)
Soil N (g/100 g dw)						
0–5 cm	0.43 (0.06)	0.22 (0.02)	0.68 (0.18)	0.22 (0.05)	0.39 (0.06)	0.32 (0.03)
5–10 cm	0.28 (0.05)	0.17 (0.01)	0.51 (0.21)	0.19 (0.06)	0.30 (0.05)	0.20 (0.03)
Soil C:N						
0–5 cm	15.3 (0.4)	13.7 (0.1)	16.0 (1.1)	12.2 (0.3)	14.9 (0.2)	12.0 (0.2)
5–10 cm	15.1 (0.4)	13.4 (0.1)	15.5 (1.2)	12.7 (0.4)	14.8 (0.5)	12.4 (0.3)
pH						
0–5 cm	5.2 (0.4)	5.7 (0.2)	5.3 (0.4)	5.4 (0.3)	5.4 (0.2)	5.4 (0.1)
5–10 cm	5.1 (0.4)	5.8 (0.2)	5.1 (0.3)	5.4 (0.3)	5.4 (0.2)	5.5 (0.2)
Bulk density (g/cm^3)						
0–5 cm	0.65 (0.06)	0.86 (0.05)	0.45 (0.07)	0.93 (0.05)	0.75 (0.06)	0.80 (0.06)
5–10 cm	0.75 (0.05)	1.12 (0.03)	0.67 (0.10)	1.13 (0.07)	0.94 (0.05)	1.14 (0.05)
Root biomass (g/m^2)						
0–5 cm	138.2 (15.3)	219.4 (34.5)	137.3 (16.9)	95.9 (43.1)	102.0 (16)	164.6 (42.9)
5–10 cm	128.5 (18.7)	74.1 (9.5)	135.7 (22.8)	18.1 (7.7)	104.7 (26)	66.9 (16.9)
Minimum soil depth (cm)	19.7 (4.2)	25.0 (5.7)	20.8 (3.3)	22.1 (2.2)	24.2 (3.3)	24.9 (5.9)
A horizon depth (cm)	13.3 (3.6)	Not distinct	13.9 (3.1)	Not distinct	17.6 (2.5)	Not distinct

Parentheses indicate standard errors.

the latter of which is likely due to significantly higher bulk density at this depth (Tukey's HSD, $P < 0.05$; Appendix 1 in Supplementary materials).

Soil C:N increased significantly over time in both the 0–5 and 5–10 cm depth intervals ($F_{1,45} = 22.8$, $P < 0.0001$ and $F_{1,45} = 13.6$, $P < 0.0006$, respectively). Again, although the rates of increase were similar among soil types (that is, no significant interactions), there were significant soil type effects at both depths ($F_{2,45} = 7.8$, $P < 0.001$ and $F_{2,45} = 4.7$, $P < 0.01$, respectively) due to significantly lower C:N ratios (by ~1) in the Luvisol chronosequence soils compared to the others (Tukey's HSD, $P < 0.05$). Soil C:N in the 10–20 cm interval tended to increase over time ($F_{1,30} = 2.3$, $P < 0.10$), and again was lower in the Luvisol (soil type: $F_{2,30} = 3.9$, $P < 0.03$) compared to the Brunisol (Tukey's HSD, $P < 0.05$).

Free-Light Fraction Soil Carbon and Nitrogen During Forest Regeneration on the Brunisol

Our analyses of free-light fraction in the Brunisol indicated few consistent patterns of change over time since agricultural abandonment, and therefore few statistically significant results. Mature forests and agricultural fields had similar mineral soil free-light fraction C and N stocks (paired t-tests: $t_2 = 2.24$, $P = 0.15$ and $t_2 = 0.93$, $P = 0.45$, respectively) (Figure 5, Appendix 2 in Supplementary materials). The soil free-light fraction C stock did not change consistently across the chronosequence (Figure 5), but the concentration of free-light fraction C in soil tended to increase over time (linear regression $F_{1,19} = 2.9$, $P < 0.10$; $r^2 = 0.13$; data not shown). There were no significant changes in the free-light fraction N stock or concentrations over time since abandonment (Figure 5). Neither the proportion of total soil N nor total soil C as free-light fraction changed consistently across the chronosequence (Appendix 3 in Supplementary materials). Accordingly, the C:N ratio of the free-light fraction pool increased significantly over time (linear regression, $F_{1,19} = 15.1$, $P = 0.001$; $r^2 = 0.44$) (Figure 5), and was wider than the total soil C:N ratio, averaging 20:1 as compared to about 13:1 in the agricultural fields (Table 1).

Soil Properties Among Soil Types and Between Land Uses

The Luvisol soils contained more than three times the clay and approximately one-fourth of the sand

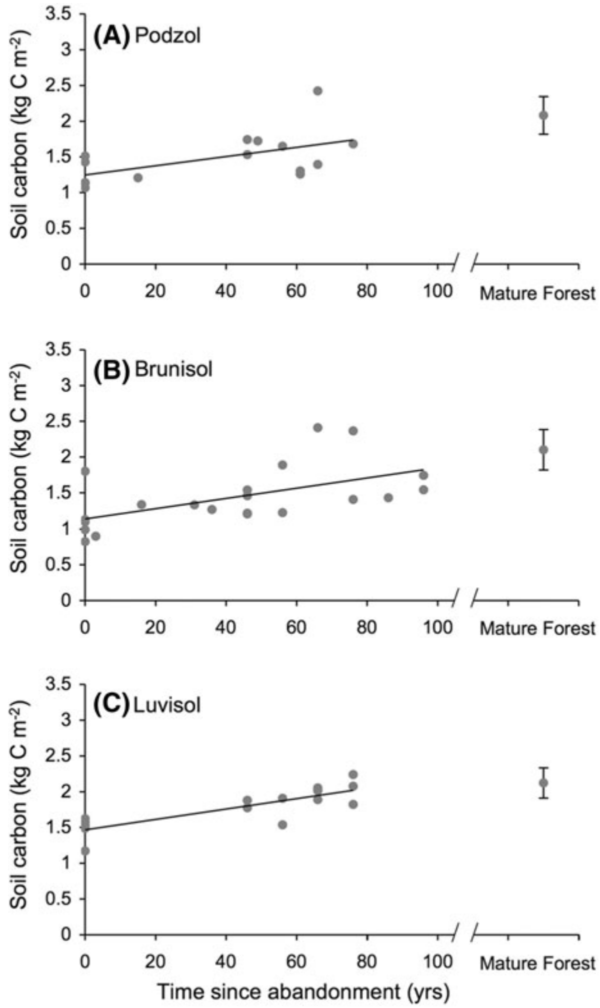

Figure 3. Soil carbon stocks (0 to 5 cm depth) in the chronosequence sites of the Podzol (**A**), Brunisol (**B**), and Luvisol (**C**) soil types (n = 15, 21, and 15 sites respectively). *Lines* are linear regressions (Table 2). Means for mature forests are also included (n = 5, bars = ± 1 SE).

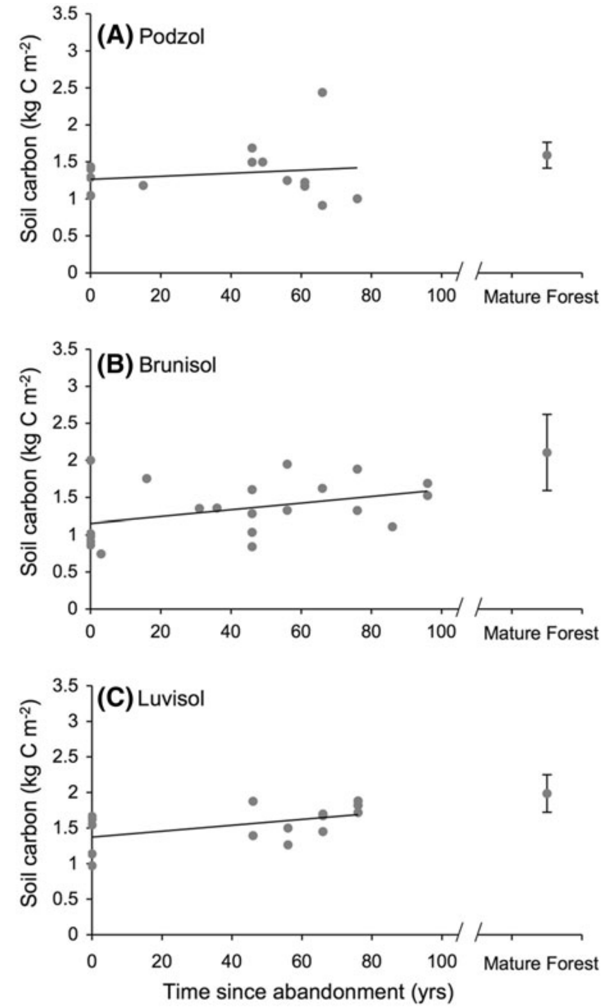

Figure 4. Soil carbon stocks (5 to 10 cm depth) in the chronosequence sites of the Podzol (**A**), Brunisol (**B**), and Luvisol (**C**) soil types (n = 15, 21, and 15 sites, respectively). *Lines* are linear regressions (Table 2). Means for mature forests are also indicated (n = 5, *bars* = ±1 SE).

contents of the Brunisol and Podzol soils (Table 3), but the latter two had similar textures due to higher than expected sand concentrations in the Brunisol (Table 3). This pattern of textural differences among soil types was observed in both surface and deeper soil intervals (Table 3). Soil pH differed significantly among land uses and there was a significant interaction with soil type ($F_{1,36} = 8.5$, $P < 0.006$ and $F_{2,36} = 3.1$, $P < 0.06$, respectively). The Podzol in particular had relatively high pH in the fields, whereas the Brunisol had a substantially lower pH than expected for soils over limestone bedrock (Table 1). In summary, the Brunisol and Podzol soil types had quite similar pH and texture despite their different parent materials whereas the Luvisol clearly had a much finer-grained texture.

As expected, soil bulk density was significantly lower in the 0–5 compared to the 5–10 cm depth intervals in both mature forest and field sites, but especially in the Brunisol and Luvisols (depth: $F_{1,36} = 107.7$, $P < 0.0001$; depth × soil type: $F_{2,36} = 5.9$, $P < 0.02$; Table 1). Bulk densities were substantially lower in mature forest sites than in adjacent fields ($F_{1,36} = 195.1$, $P < 0.0001$; Table 1), except in the Luvisols where their finer texture resulted in relatively high bulk densities and negligible effects of agriculture (land use × soil type: $F_{2,36} = 21.8$, $P < 0.0001$; Table 1). The chronosequence data indicate significant decreases in soil bulk density within the 0–5 and 5–10 cm depth intervals following agricultural abandonment ($F_{1,45} = 18.3$, $P < 0.0001$ and $F_{1,45} = 52.9$,

Table 2. Simple Linear Regressions Between Soil Carbon or Nitrogen Stocks and Time Since Agricultural Abandonment ('*x*' = years) for Each Soil Type at Each Depth Where the 'Time' Factor in the Chronosequence ANCOVA Statistical Analyses was Significant at $P < 0.1$

Soil property	Soil type	d.f.	*F* ratio	*P* value	R^2	Equation
Carbon (kg C m^{-2})						
0–5 cm	Podzol	14	5.8	0.03	0.31	$0.00645x + 1.25$
	Brunisol	20	7.7	0.01	0.29	$0.00690x + 1.15$
	Luvisol	14	27.7	0.0002	0.68	$0.00726x + 1.47$
5–10 cm	Podzol	14	0.4	0.6	0.03	$0.00205x + 1.26$
	Brunisol	20	1.3	0.3	0.07	$0.00343x + 1.22$
	Luvisol	14	4.4	0.06	0.25	$0.00417x + 1.37$
Nitrogen (kg N m^{-2})						
0–5 cm	Podzol	14	3.5	0.08	0.21	$0.000349x + 0.094$
	Brunisol	20	2.14	0.2	0.10	$0.000286x + 0.092$
	Luvisol	14	10.3	0.007	0.44	$0.000375x + 0.120$

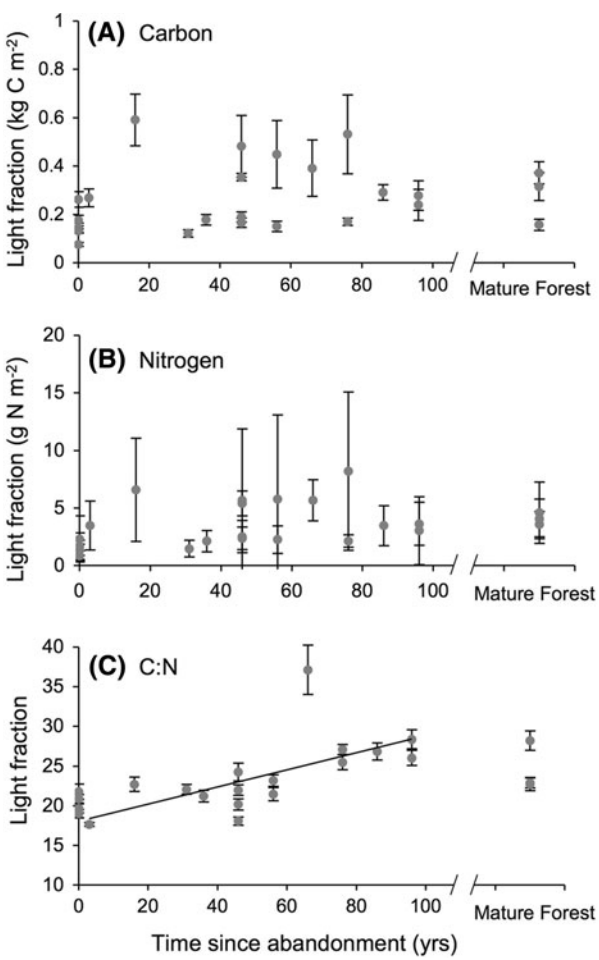

Figure 5. Soil free-light fraction carbon stocks (**A**), nitrogen stocks (**B**), and C:N ratios (**C**) within 0–10 cm depth in the chronosequence sites on the Brunisol soil type. Means for the three mature forest sites without a continuous OeOa layer are also shown. Each data point is the mean of five cores per site except for one mature forest site that had three cores without an OeOa layer (*bars* = ±1 SE).

$P < 0.0001$, respectively), and no differences in rates among soil types. By contrast, there was no significant change in bulk density across the chronosequences for any of the soil types in the 10–20 cm depth interval.

Minimum soil depth (that is, topsoil cover to bedrock or compacted subsoil) ranged from 20 to 25 cm, and did not differ significantly amongst land uses or soil types (Table 1). A distinct A horizon was present at 13–18 cm depth in the mature forest soils, but was rare in the agricultural fields (Table 1).

Vegetation Characteristics Among Soil Types and Between Land Uses

We characterized the mature forest vegetation associated with each soil type because differences in soil carbon inputs due to variation in plant species composition or productivity could explain potential differences in soil C sequestration among the soil types. Aboveground tree biomass, stem density, and tree species diversity in mature forests did not significantly differ among soil types (Table 4). Sugar maple was the clear dominant tree species on all soil types, although ash tended to be a relatively large subsidiary component in the Luvisol compared to the other soil types (Table 4).

Root biomass was larger in the 0–5 cm than the 5–10 cm depth intervals of agricultural fields but not mature forests (depth: $F_{1,36} = 18.2$, $P < 0.001$; depth × land use: $F_{1,36} = 14.5$, $P < 0.0005$; Table 1). There was also a significant interaction between soil type and land use ($F_{2,36} = 5.9$, $P < 0.006$), indicating that root biomass at both depths in agricultural fields was smaller on the Brunisol compared to the other soil types (Table 1).

Table 3. Textural Analyses of Soils at 0–5 and 10–20 cm Depth Intervals from the Oldest Chronosequence Sites (n = 5; average age = 74 years) of the Three Soil Types

Soil type	Measured			Classification	
	% Sand	% Silt	% Clay	USDA classification	Expected
Podzol					
0–5 cm	60 (3)	32 (2)	8 (1)	Sandy loam	Sandy loam
10–20 cm	61 (3)	29 (2)	10 (1)	Sandy loam	Sandy loam
Brunisol					
0–5 cm	58 (6)	32 (6)	9 (2)	Sandy loam	Loam or sandy loam
10–20 cm	59 (4)	29 (4)	12 (1)	Sandy loam	Loam or sandy loam
Luvisol					
0–5 cm	18 (7)	50 (5)	32 (4)	Silty clay loam	Clay
10–20 cm	13 (3)	46 (2)	41 (4)	Silty clay	Clay

Parentheses indicate standard errors. Measured values were classified according to the USDA classification (Gee and Bauder 1986) and compared to our expectations based on Canadian soil survey map classifications for the sampling sites (Gillespie and others 1966; Gillespie and Wicklund 1968).

Table 4. Aboveground Tree Biomass, Stem Density, and Simpson's Diversity Index for Mature Forests (n = 5) on the Three Soil Types

Variable	Podzol	Brunisol	Luvisol	F ratio	P value
Aboveground biomass (kg/m^2)					
Sugar Maple	15.4 (2.6)	17.8 (5.4)	9.0 (4.0)	1.2	0.3
Ash	0.9 (0.5)	1.4 (0.9)	5.0 (1.8)	3.5	0.06
Red Oak	2.3 (1.4)	0.20 (0.20)	8.7 (4.8)	2.1	0.2
American Beech	0.5 (0.5)	5.1 (5.1)	0.5 (0.4)	0.1	0.9
Total	21.7 (2.1)	28.4 (7.1)	27.4 (3.7)	0.6	0.6
Stem density (number per 1000 m^2)					
Sugar Maple	210 (40)	82 (23)	116 (58)	2.3	0.1
Ash	30 (12)	27 (13)	30 (7)	0.02	0.9
Red Oak	1 (1)	2 (1)	7 (6)	1.4	0.3
American Beech	16 (15)	32 (23)	9 (8)	0.4	0.7
Total	310 (39)	228 (13)	247 (46)	1.5	0.3
Simpson's diversity index (D)	1.53 (0.12)	1.62 (0.13)	1.77 (0.22)	0.6	0.6

Biomass and number of stems are shown for all tree species that make up at least 5% of the total plant aboveground biomass on at least one of the soil types. Parentheses indicate standard errors, and one-way ANOVA results are shown (d.f. = 2, 12).

Discussion

We investigated patterns, controls, and component pools of C accumulation in marginal (that is, low productivity) shallow soils of southeastern Ontario that have been farmed using low intensity practices for the past one to two centuries. Fields had substantially less soil C in the top 10 cm than adjacent mature forests (whether expressed as stocks or concentrations), demonstrating that even low intensity agriculture on marginal soils results in carbon losses (Table 1; Figure 2). Using replicated chronosequences across an extensive area, we have also shown that soil C increased for at least 100 years during natural regeneration of mixed hardwood–conifer forests in this region, implying some potential for C sequestration when such lands are abandoned. These results support our first two hypotheses. Surprisingly, the losses of soil C in the top 10 cm due to agriculture were similar among soil types of three different soil orders (Table 1), one of which had a much finer texture. Similarly, the rates of C accumulation across the chronosequences were not significantly influenced by soil type (insignificant interactions between soil type and time), refuting our third hypothesis that differences in texture among soil types would affect both the potential magnitude and rate of C sequestration. Finally, the soil free-light fraction C in the Brunisol did not significantly increase following agricultural abandonment (Figure 5), refuting our fourth hypothesis. Together these findings make a unique contribution to our knowledge of the patterns and controls on soil C sequestration because they are focused on lands of low agricultural productivity that are being abandoned extensively. Furthermore, because our replicated chronosequence sites ($n = 15$–21 per soil type) were scattered across a large area of southeastern Ontario (~200,000 ha) and range over approximately 100 years, the conclusions may be more confidently applied to larger spatial and temporal scales than most previous studies on this topic (Post and Kwon 2000).

Soil Carbon and Nitrogen Depletion by Agriculture

Total soil C and N pools were 32 and 10–25% lower, respectively, in the top 10 cm of agricultural fields as compared to adjacent mature forest sites. We sampled more deeply in the chronosequence component of the study and found that soil C concentrations were at least 25 and 50% lower in the 10–20 cm depth interval than in the overlying 5–10 and 0–5 cm intervals, respectively (Table 1, Appendix 1 in Supplementary materials). Mixing during tillage could have reduced field C and N pools in the top 10 cm but enhanced them at depth, resulting in overestimates of total C and N depletion due to agriculture because the entire soil column was not included. The base of the A horizon was observed in mature forests at 13–18 cm depth but neither it nor the base of a plow layer (the plow pan) were apparent in most samples from the adjacent fields (Table 1). Together, these results strongly suggest that the fields had been tilled to at least 15 cm at some point in the past, but that the number of tillage events was low (restricting plow pan development), and that sufficient time had since elapsed to decompose surface organic material that had been buried during plowing. In any event, although our forest–field comparison to 10 cm depth may have overestimated total C and N losses due to agriculture, the chronosequence study clearly indicates that C sequestration after abandonment was confined to the uppermost soil layers. The largest and most statistically significant C (and N) increases following agricultural abandonment occurred in the 0–5 cm interval for all soil types. There was a statistical trend toward some increase in soil C within the 5–10 cm interval, but soil C within the 10–20 cm interval did not change over the chronosequences, strongly suggesting negligible sequestration potential below 10 cm.

Studies of more productive (and therefore usually deeper) agricultural soils have generally reported either similar or substantially higher losses, especially for the uppermost layers. For example, conversion of forested lands to crop agriculture resulted in a 4–68% decrease in soil C (at 0–30 cm depth) across Ontario (Ellert and Gregorich 1996); an approximately 45% decrease in soil C (at 0–15 cm) in a global review (Murty and others 2002), and an approximately 40% decrease in the surface soil layers (A Horizon) in another global review (Davidson and Ackerman 1993). Even in those studies where the proportional C losses in productive soils are similar to those at our sites, the total magnitudes of the losses are usually much larger because they extend to a greater depth due to more frequent and deeper tillage. Therefore, because initial soil C depletion by agriculture is a critical factor determining subsequent C accumulation rates (Grogan and Matthews 2002), these factors together indicate that the overall C sequestration potential of our soils (per unit area) is undoubtedly considerably lower than those reported for more productive soils. Nevertheless, this conclusion must be balanced against the relatively large areal extent of abandonment of marginal as compared to more productive lands in any full evaluation of their potential contributions to global soil C sequestration.

The Potential for Soil Carbon and Nitrogen Accumulation in Abandoned Marginal Agricultural Lands

The patterns of soil C increases during forest succession in our chronosequences on the three soil types appear linear over the sampling time frame (that is, *within* 80–100 years of agricultural abandonment) (Figures 3, 4). Previous studies reported linear increases in soil C over the first few decades following abandonment (Knops and Tilman 2000; McLauchlan 2006b; McLauchlan and others 2006). In contrast, theory on ecosystem development predicts that there should be a decline in the rate of soil C sequestration late in succession as rates of NPP and soil decomposition converge (Odum 1969; Chapin and others 2002). Total soil C stocks of the oldest chronosequence sites were close to those of the mature forests on the Podzol and Brunisol, and were equal to the mature forests on the Luvisol, suggesting that the majority of the C sequestration potential had been achieved by approximately 80–100 years. We anticipate that C accumulation rates in our oldest chronosequence sites will slow in the future (especially in the Luvisol) as soil C reaches the levels in the mature forests, assuming that the latter are close to full development and therefore provide an indication of the maximum soil C stock.

The mean rate of soil C accumulation over 100 years of succession across soil types was approximately 10 g C m^{-2} y^{-1} in the top 10 cm (64–76% occurring in the top 5 cm). C accumulation may also be calculated to constant mass (as opposed to constant depth) to correct for differences in soil mass across the chronosequences due to decreasing bulk density following agricultural abandonment (Poulton and others 2003). Note that because the bulk density changes across the chronosequences were similar among soil types, statistical analyses of our data on a constant mass basis does not alter any of the outcomes of the hypothesis tests in this study. Nevertheless, calculation to a constant mass of 78 kg/m^2 (~10 cm depth in the agricultural fields) elevates the mean soil C accumulation rate in our study by 40% (to 14 g C m^{-2} y^{-1}). In any event, comparisons with other studies, most of which express C accumulation to a constant depth, indicate that the rates we observed are quite low—about one-third of the global average for forest re-establishment (Post and Kwon 2000).

The large variation in soil C accumulation rates among studies is broadly attributed to site variations in vegetation productivity, physical and biological conditions in the soil, and the previous history of C inputs and physical disturbance (Post and Kwon 2000). For example, C accumulation over a 60-year chronosequence of prairie–savanna–oak woodland on a sandy soil in Minnesota was 20 g C m^{-2} y^{-1} in the top 10 cm (Zak and others 1990; Knops and Tilman 2000). Rates during temperate perennial grassland development can be as high as 52 g C m^{-2} y^{-1} in the top 10 cm (McLauchlan 2006a; McLauchlan and others 2006). In contrast, low rates (3–4 g C m^{-2} y^{-1}) are reported for development of white pine forests in the top 10 cm (Hooker and Compton 2003) and for pine afforestation plantations in the top 15 cm (Richter and others 1999), presumably due to slow decomposition and soil incorporation of pine litter. In our study, a very similar mixed hardwood–conifer forest tree community occurred at all sites (Table 4), allowing us to investigate the specific influence of differences in soil type on soil C accumulation *without* confounding effects of differing vegetation. Our results together with the above cited studies, suggest that soil C accumulation rates on abandoned agricultural land vary more among vegetation types (that is, climatic ecozones) than among soil types.

Our conclusions about soil C and N accumulation rates assume that the chronosequences are accurate 'space for time' substitutions. First, this approach assumes that all successional sites within a soil type had similar soil C and N levels when abandoned. The majority of soil C losses occur within the first few years or decade of agricultural practices (Davidson and Ackerman 1993). Our oldest successional sites were abandoned around 1910 and were likely farmed for at least a couple of decades prior to abandonment (because agriculture was widespread by the mid-1800s), suggesting that all chronosequence sites had undergone similar initial C and N losses. Second, soil C can vary widely between agricultural fields on the same soil type even within a small area due to differences in management practices (Paul and others 2003) as well as natural spatial heterogeneity. Our experimental design included replicated pairs of adjacent agricultural field and mature forest sites for each soil type and replicated sites for most ages along the chronosequences to account for this variability. By contrast, replication in most of the soil C sequestration studies cited in this paper is based on multiple plots within a site, rather than multiple sites. Third, all sites should have experienced the same ecological conditions so that the rates and trajectories of vegetation succession are not affected by the point in time when abandonment began. Seed dispersal and colonization are unlikely to have been limiting at any time because mature forests are, and have been, scattered extensively throughout the region. Nevertheless, other factors such as atmospheric N deposition, invasive earthworms, and deer populations have all increased in the region within the past century and therefore could have exerted stronger influences on forest development and soil C accumulation in more recent years.

The Influence of Texture on Soil Carbon and Nitrogen Accumulation

Soil particle size analyses revealed that our three soil series were not as different texturally from each other as we expected from the classification descriptions (Gillespie and others 1966; Gillespie and Wicklund, 1968). Strong spatial heterogeneity in soil texture has been observed in the region, even at scales of 10–100 m within hayfields (Crowder and Harmsen 1998). Furthermore, many of the Brunisol sites were located in an area where the classification for that soil series combines both loam and sandy loam textural classes (Gillespie and Wicklund 1968). In any event, the Luvisol was clearly distinct from the other two, having less than one-third the amount of sand and more than four times the amount of clay. Evidence for the influence of clay on C sequestration is based on correlations between soil C and clay concentration across the various ecosystems of the Great Plains and elsewhere (Nichols 1984; Burke and others 1989; Plante and others 2006), but this relationship was not observed in studies focused on single ecosystem-types (for example, grasslands) within particular climatic regions (Percival and others 2000; McLauchlan 2006b). We found no differences in soil C loss or C accumulation rates between the clearly finer-textured Luvisol and the other soil types, supporting the latter studies. Together, these results suggest that clay content may have relatively little influence on soil C stocks within ecosystems that share a common climate and vegetation successional pattern as compared to across markedly different ecosystems. More specifically, climate, vegetation successional pattern, and topography were broadly similar across all of our sites, meaning that this study was well poised to detect the influence of soil type on C accumulation without confounding effects. We conclude that the expected influence of soil textural differences on C accumulation rates was not observed in our study because its influence was small relative to the over-riding impact of forest clearance and subsequent cultivation on initial C stocks. In other words, C accumulation rates may not have differed across soil types of varying texture because all of the soils had been substantially and similarly depleted in C (by ~32%) as a result of forest clearance and subsequent agriculture, and the rates of recovery were determined more by the extent of initial depletion than by differences in soil texture.

Soil Free-Light and Heavy Fraction Pool Dynamics Following Agricultural Abandonment

Our final objective was to investigate the long-term dynamics of the free-light fraction C pool following agricultural abandonment on the Brunisol. Free-light fraction consists of organic matter not associated with mineral particles, whereas the heavy fraction tends to have a relatively slow turnover and includes organic matter that is physically protected within soil aggregates or chemically bound to silt or clay particles (Baisden and others 2002; Yamashita and others 2006). In addition to the free-light fraction, many studies use techniques that disrupt aggregates to include light fraction material occluded within aggregates that consists of more highly decomposed compounds and has a longer turnover time than the free-light fraction (Golchin and others 1994; Baisden and others 2002). Here, we focused on the free-light fraction only, as representing a particularly active labile C pool that should be sensitive to changes in land use (Post and Kwon 2000).

Free-light fraction C was about 10% of total soil C, and did not change significantly over the century-long chronosequence of agricultural abandonment. Furthermore, the free-light fraction C and N stocks in our mature forests were not significantly different from adjacent agricultural fields (Appendix 2 in Supplementary materials). A New England study of the long-term impacts of agriculture found that soil light fraction C (equivalent to our free-light fraction) was about 60% lower in abandoned soils that had been plowed 90–120 years ago compared to abandoned soils that were relatively undisturbed because they had been under woodlot management at that time (Compton and Boone 2000). The authors conclude that disturbance of the soil by plowing substantially depleted light fraction C and that this impact persists for at least a century after abandonment. Because light fraction C stocks in our forest and field sites were similar, and about one-fifth of the New England woodlot values (to 10 cm depth), these results suggest that the land on which our mature forests had regenerated had previously been plowed. Free-light (and occluded) fractions increased over the first decade of succession in Michigan, but most C accumulated in soil pools associated with mineral particles (DeGryze and others 2004). Similarly, increases in recalcitrant C accounted for 92% of total C accumulation across a 40-year grassland chronosequence in Minnesota (McLauchlan and others 2006). Rapid microbial processing of the more labile components of incoming plant litter, and the microbial synthesis of biochemically recalcitrant byproducts, may be major components of accumulating soil organic matter during succession (McLauchlan and others 2006). Our findings that the free-light fraction—and therefore presumably the most labile fraction—was small and unchanging are consistent with this concept, and provide empirical evidence that most of the increase in total C observed in the Brunisol at least was due to the accumulation of relatively recalcitrant C compounds.

Forest Floor Litter Layer Accumulation Across the Region

The forest floor litter layer (OeOa) was present in only three of the fifteen mature forest sites, and furthermore no surface litter accumulation was observed in any of our chronosequence sites. Earthworms can affect the forest floor litter layer by moving surface material downwards and mixing it with mineral particles to form aggregates (Fox and others 2006). Earthworms were particularly frequent in the forest sites within our study, occurring in 23% of all cores in the mature forests as compared to 4% in adjacent fields (with no significant differences among soil types). Furthermore, populations of the invasive night crawler earthworm (*Lumbricus terrestris* L.) are increasing in this region and can greatly decrease forest floor litter mass (Bohlen and others 2004), potentially explaining why OeOa layer development was uncommon in our mature forest sites and absent from even the oldest chronosequence sites.

The Potential Magnitude of Carbon Sequestration on Abandoned Agricultural Lands in This Region

Our data can be used to estimate the magnitude and significance of carbon sequestration on abandoned low productivity agricultural land. For example, approximately 3 Mha (that is, 35% of the total area) of agriculturally improved pasture farmland in Ontario (a province twice the size of France) has been withdrawn from agriculture between 1951 and 1991 (Parson 1999; Anonymous 2004). Assuming that 75% of this abandoned land area (~2.24 Mha) (Anonymous 2004) has been allowed to naturally revert to mixed hardwood–conifer forest, our data suggest that 8.95 Tg C (Tg = 10^{12}g) would have been sequestered in soil in that period (that is, mean C accumulation rate of 0.22 Tg C y^{-1}). Mean aboveground biomass in our mature forest stands was 12.9 kg C m^{-2} (Table 4, assuming C concentration of 50%), in very close agreement with a previous extensive study of Canadian moderate temperate forests (Kurz and Apps 1999), that also estimated belowground tree biomass at 2.5 kg C m^{-2}. Assuming that mature forest stands take 130 years to fully develop, these data together suggest a mean total tree biomass C accumulation rate of about 118 g C m^{-2} y^{-1} (that is, ~12 times the soil C sequestration rate quantified in this study). Because Ontario's greenhouse gas emissions are about 55 Tg CO_2–C equivalents per year (Environment Canada 2005), this analysis suggests that total annual C accumulation in regenerating forests on abandoned farmland is approximately 5% of the province's current annual CO_2–C emissions, and that trees rather than soils are the main sink.

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