

The legacy of harvest and fire on ecosystem carbon storage in a north temperate forest

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Abstract

Forest harvesting and wildfire were widespread in the upper Great Lakes region of North America during the early 20th century. We examined how long this legacy of disturbance constrains forest carbon (C) storage rates by quantifying C pools and fluxes after harvest and fire in a mixed deciduous forest chronosequence in northern lower Michigan, USA. Study plots ranged in age from 6 to 68 years and were created following experimental clear-cut harvesting and fire disturbance. Annual C storage was estimated biometrically from measurements of wood, leaf, fine root, and woody debris mass, mass losses to herbivory, soil C content, and soil respiration. Maximum annual C storage in stands that were disturbed by harvest and fire twice was 26% less than a reference stand receiving the same disturbance only once. The mechanism for this reduction in annual C storage was a long-lasting decrease in site quality that endured over the 62-year timeframe examined. However, during regrowth the harvested and burned forest rapidly became a net C sink, storing $0.53 \text{ Mg C ha}^{-1} \text{ yr}^{-1}$ after 6 years. Maximum net ecosystem production ($1.35 \text{ Mg C ha}^{-1} \text{ yr}^{-1}$) and annual C increment ($0.95 \text{ Mg C ha}^{-1} \text{ yr}^{-1}$) were recorded in the 24- and 50-year-old stands, respectively. Net primary production averaged $5.19 \text{ Mg C ha}^{-1} \text{ yr}^{-1}$ in experimental stands, increasing by $<10\%$ from 6 to 50 years. Soil heterotrophic respiration was more variable across stand ages, ranging from $3.85 \text{ Mg C ha}^{-1} \text{ yr}^{-1}$ in the 6-year-old stand to $4.56 \text{ Mg C ha}^{-1} \text{ yr}^{-1}$ in the 68-year-old stand. These results suggest that harvesting and fire disturbances broadly distributed across the region decades ago caused changes in site quality and successional status that continue to limit forest C storage rates.

Keywords: aspen, carbon storage, disturbance, fire, legacy effects, logging, net ecosystem production, net primary production, northern hardwoods, succession

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Introduction

Historical legacies of disturbance and land-use shape current ecosystem function and affect long-term trajectories of ecological change (Foster *et al.*, 2003; Chen *et al.*, 2004a). The pine and hemlock forests in the upper Midwest of North America were disturbed on a large scale by logging and wildfire from the late 19th to early 20th centuries (Karamanski, 1989; Frelich, 1995; Friedman & Reich, 2005). These stand-replacing disturbances led to the establishment of broad areas of aspen-

dominated forests that differ in their capacity to store carbon (C) due to variation in disturbance frequency and intensity, successional status, soil nutrition, and climate (Birdsey & Heath, 1995). Although postdisturbance regrowth of these and other forests contributes to a North American terrestrial C sink (Potter & Klooster, 1999; Caspersen *et al.*, 2000), the extent to which historical legacies of disturbance affect current rates of forest C storage has not been quantified for most ecosystems (Chen *et al.*, 2004a). Modeling work by Euskirchen *et al.* (2002) suggests that repeated stand-replacing disturbances may prevent forests in the upper Midwest from reaching maximum C storage capacity, but empirical evidence in support of their prediction is limited

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(Dale *et al.*, 2001; Chen *et al.*, 2004a). Understanding how historical legacies of disturbance alter forest C cycling is essential to the development of effective C management strategies (Foster *et al.*, 2003).

Disturbance, successional status, and climate simultaneously constrain net ecosystem production (NEP) and may be equally important sources of variation in forest C storage over time (Fig. 1; Chen *et al.*, 2004a). The long-term effects of logging and fire disturbance on forest C cycling are variable and depend on disturbance severity and ecosystem type (Johnson & Curtis, 2001). For example, in several northern hardwood forests, logging followed by fire reduced both aboveground C pools (Bergeron & Harvey, 1997) and soil C (Reich *et al.*, 2001; Latty *et al.*, 2004; Fahey *et al.*, 2005), while Hicke *et al.* (2003) reported a relatively minor reduction in annual forest C storage for a Canadian boreal forest 23 years following severe fire. Ecosystem C storage was reduced by logging and fire in hardwood and conifer forests of Western Oregon (Law *et al.*, 2004) and by repeated fire in an oak-savanna community in Minnesota (Tilman *et al.*, 2000). These disturbances reduced site quality in southern Canadian boreal forests, thereby slowing forest growth (Bergeron & Harvey, 1997). Clearly, broadly distributed human disturbances may have lowered the successional trajectory of NEP in numerous ecosystems, reducing C storage in large forested areas that contribute to the terrestrial North American C sink (Fig. 1).

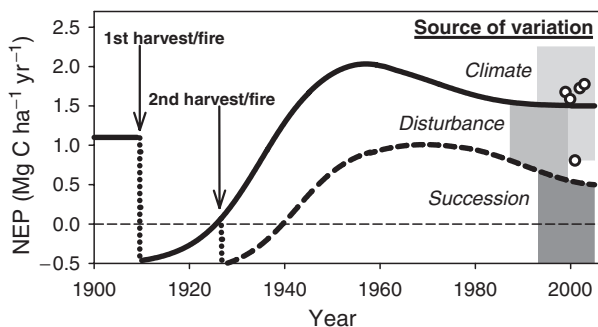


Fig. 1 Sources of variation in net ecosystem production (NEP) following stand-replacing harvest and fire. Annual carbon (C) storage in an ~85-year-old northern Michigan forest disturbed once by harvest and fire averaged $1.5 \text{ Mg C ha}^{-1} \text{ yr}^{-1}$ from 1999 to 2003, varying annually by $>100\%$ in response to climate (○, Gough *et al.*, 2007a). An additional harvest and fire disturbance is hypothesized to lower the successional trajectory of NEP, preventing the stand from reaching a maximum NEP equal to that of the forest disturbed only once. Forest successional status is an additional source of variation in NEP that may be detectable over longer, decadal timescales. Predisturbance NEP is from Desai *et al.* (2005) for an old-growth forest in Wisconsin, USA.

Postdisturbance succession also fundamentally shapes the trajectory of forest C storage (e.g. Law *et al.*, 2001, 2003; Humphreys *et al.*, 2005). Odum (1969) hypothesized that forest stands experience an initial postdisturbance reduction in C storage due to higher respiration rates, with NEP increasing to a maximum as canopy assimilation peaks and declining thereafter (Fig. 1). Such a pattern of C storage over time has been found in a few ecosystems using data from forest chronosequences established from clearcuts or wildfire, including ponderosa pine (*Pinus ponderosa*) forests of western Oregon (Law *et al.*, 2001, 2003), black spruce (*Picea mariana*) forests of Manitoba (Bond-Lamberty *et al.*, 2004a), and jack pine (*Pinus banksiana*) forests of Saskatchewan (Howard *et al.*, 2004). These ecosystems were strong sources of C to the atmosphere for up to four decades following stand-replacing disturbance and, after maximum NEP was attained, all forests exhibited a gradual decline in NEP as they approached maturity. In the upper Midwest, forest NEP studies generally have taken place in late-successional stands (Schmid *et al.*, 2003; Desai *et al.*, 2005). Despite the distribution of multiple age classes across the landscape (Schimel *et al.*, 2000; Chen *et al.*, 2004a), annual forest C storage is rarely examined in young stands or over successional time.

Climate effects on C fluxes now have been quantified for many North American forests. We observed immediate effects of climate on canopy photosynthesis and ecosystem respiration in an aspen-dominated northern hardwood forest (Schmid *et al.*, 2003; Curtis *et al.*, 2005). In a structurally similar forest in Wisconsin, Bolstad *et al.* (2004) found that air and soil temperatures affected short-term respiratory fluxes from soils, boles, and leaves. Gough *et al.* (2007b) found that annual forest NEP varied by $>100\%$ in response to changes in growing season photosynthetic photon flux density and soil temperature (Fig. 1). Similar climate controls on short-term C fluxes have been documented for other forest types, including coniferous forests of Oregon, mixed-deciduous forests of Indiana, and southeastern pine plantations (Law *et al.*, 2001; Ehman *et al.*, 2002; Clark *et al.*, 2004).

In this study, our primary objective was to quantify the legacy of disturbance on annual C storage in a northern hardwood forest over successional time. We hypothesized that repeated harvesting and fire disturbance would reduce current rates of C storage in this forest by degrading site quality. We quantified C pools and fluxes through multiple decades of successional change following stand-replacing disturbance. This work complements previous efforts to quantify short-term, climate-driven variability in forest C fluxes and storage in the upper Great Lakes region (Curtis *et al.*,

2002; Schmid *et al.*, 2003; Bolstad *et al.*, 2004; Curtis *et al.*, 2005; Desai *et al.*, 2005; Gough *et al.*, 2007b). Our study forest is part of the Fluxnet network of long-term C cycle research facilities (Balducchi *et al.*, 2001).

Methods

Study site

Our study was conducted in 2004 and 2005 at the University of Michigan Biological Station (UMBS) in northern lower Michigan, USA (45°35.5'N 84°43'W). The research site is located in the transition zone between mixed hardwood and boreal forests. The study forest is on a level to gently sloping (<5%) high outwash plain derived from glacial drift. Soils are well-drained, sandy, mixed frigid Entic Haplothods (Rubicon series) consisting of 92% sand, 7% silt, and 1% clay. Mean (1942–2003) annual temperature is 5.5°C and mean annual precipitation is 817 mm. The growing season is ~120 days.

A chronosequence of stand age and disturbance history was created in five, ~1 ha contiguous stands which were clear-cut and burned in 1936, 1948, 1954, 1980, and 1998. This treatment was intended to reproduce the logging and slash-fueled wildfire disturbances that were common in the upper Great Lakes region in the early 20th century (Gates, 1930). A common clear-cut harvest and burn protocol was followed in all experimental stands in which residual bole, branch, and leaf mass was evenly distributed across sites following harvest to provide fuel for controlled fires. This experimental disturbance was in addition to that

experienced at each site during the time of general deforestation. The uniform disturbance history of these stands, together with their common original vegetation, soils, slope, and climate afforded us the opportunity to investigate forest C storage over time.

Experimental stands were compared with 35 replicate plots within a single disturbance reference stand located ~500 m away. The reference stand was disturbed by harvest and fire once during the time of general deforestation in the early 20th century, but did not receive the additional experimental disturbance used to create the chronosequence. Chronosequence and reference stands differed only in disturbance frequency, sharing common species, soils, and climate (Table 1). Gough *et al.* (2007b), using both biometric and meteorological methods, reported 5-year (1999–2003) NEP for the reference stand. To compare site quality in the experimental and reference stands, we calculated site index by measuring the height and age of six dominant bigtooth aspen (*Populus grandidentata*) trees per stand. Height was determined geometrically using a clinometer and age was calculated from growth rings. Site index (m, height), a metric of site productivity, for 50-year-old trembling aspen was estimated from Lundgren & Dolid (1970).

Presettlement vegetation in this area was dominated by white pine (*Pinus strobus*), red pine (*Pinus resinosa*), and eastern hemlock (*Tsuga canadensis*) (Gates, 1926). Harvesting and repeated fires in the early 20th century promoted the current aspen-dominated composition (Gough *et al.*, 2007b). In the experimental and reference stands, a majority of the standing live mass was bigtooth aspen (Table 1). Other common overstory species included northern red oak (*Quercus rubra*) and red

Table 1 Composition and structure of experimentally harvested and burned stands in a chronosequence, and the reference stand at the University of Michigan Biological Station

	Stand age (years)					Reference, 85
	6	24	50	56	68	
Tree height (m)	2.8 (0.03)	5.6 (0.05)	8.2 (0.18)	9.3 (0.21)	8.0 (0.26)	–
Dominants only	–	–	11.1 (0.41)	14.2 (0.47)	14.5 (0.27)	21 (–)
<i>D</i> (cm)	2.8 (0.10)	5.3 (0.08)	9.9 (0.28)	9.6 (0.26)	10.7 (0.37)	19.3 (0.34)
Tree density (ha ⁻¹)	7249 (1372)	6047 (938)	1747 (164)	2680 (12)	2133 (256)	714 (29)
Basal area (m ⁻² ha ⁻¹)	5.9 (1.9)	16.3 (2.4)	16.4 (1.4)	25.1 (0.90)	26.7 (1.7)	24.7 (0.9)
<i>A</i> _{lmax} (m ² m ⁻²)	1.8	3.0	3.6	3.5	3.4	3.5
Site index (m)	13.4 (0.14)	8.9 (0.08)	11.1 (0.24)	13.4 (0.30)	12.6 (0.41)	19.8 (0.51)
Overstory composition (%)	<i>Populus grandidentata</i> (93)	<i>P. grandidentata</i> (92)	<i>P. grandidentata</i> (68)	<i>P. grandidentata</i> (76)	<i>P. grandidentata</i> (84)	<i>P. grandidentata</i> (35)
	<i>Acer rubrum</i> (6)	<i>A. rubrum</i> (5)	<i>Quercus rubra</i> (28)	<i>Q. rubra</i> (12)	<i>A. rubrum</i> (4)	<i>A. rubrum</i> (19)
	<i>Q. rubra</i> (1)	<i>Q. rubra</i> (3)	<i>A. rubrum</i> (4)	<i>A. rubrum</i> (4)	<i>Q. rubra</i> (2)	<i>P. trem.</i> (16)

D, diameter at breast height, *A*_{lmax}, maximum overstory leaf area index. Mean ± (SE).

maple (*Acer rubrum*) with lesser representation of trembling aspen (*Populus tremuloides*), paper birch (*Betula papyrifera*), American beech (*Fagus grandifolia*), sugar maple (*Acer saccharum*), and white pine. The understory was dominated by bracken fern (*Pteridium aquilinum*) and red maple, red oak, American beech, and white pine seedlings and saplings. Maximum overstory leaf area index (A_{lmax}) ranged from 1.8 to 3.6 in the experimental stands (Table 1).

Aboveground wood and understory mass

We measured aboveground wood mass (M_a) in 3, 0.1 ha plots within each of the five experimental stands using allometric equations relating bole diameter at 1.33 m height (D) to M_a by

$$M_a = aD^b, \quad (1)$$

where a and b are species-specific coefficients developed from data collected at UMBS (Koerper, 1977; Cooper, 1981; A. W. Cooper, personal communication) or obtained from published reports from the Great Lakes states and eastern North America (Wiant *et al.*, 1977; Ker, 1980; Young *et al.*, 1980; Schmitt & Grigal, 1981; Crow & Erdmann, 1983; Hocker & Early, 1983; Perala & Alban, 1994; Ter-Michaelian & Korzukhin, 1997). All woody plants with $D > 1$ cm were measured.

Bracken fern was the primary understory component, which we measured in nine, 1 m² plots located in each of the five experimental stands. In an adjacent stand, 35 mature ferns were harvested, dried, and weighed. Understory mass was estimated as the product of mean individual fern mass and fern density. All dry live and dead mass components were converted to C mass using a fraction of 0.49, except for fine roots in which 0.47 was used.

Leaf litter and woody debris mass

We estimated overstory leaf litter mass (M_{ll}), fine debris mass (M_{fd}), and maximum overstory leaf area index (A_{lmax}) in 2004 with three litter traps (0.264 m²) randomly located in each of the five experimental stands. Litter traps were emptied weekly during leaf abscission in the autumn and monthly otherwise.

We measured coarse woody debris (CWD) mass (M_{cd}) in three, 0.02 ha plots located within each of the five experimental stands. We recorded the lengths and diameters of the distal ends and midpoints of all samples with a midpoint diameter ≥ 50 mm. We calculated CWD volume using the equation for the frustum of a cone. Each sample was assigned to one of five decay classes, depending on the level of decay (Marra & Edmonds, 1994). To estimate CWD density, six samples

from each decay class were dried and weighed, and volume was determined using water displacement.

Herbivory

We previously estimated annual foliar C losses to herbivory (H) in a neighboring stand by measuring damage to green leaves, collection of insect frass below the canopy, and through caterpillar feeding trials relating leaf mass loss to frass production (Gough *et al.*, 2007b). The proportion of leaf area lost to herbivory was determined using a LAI-3100 leaf area meter (LI-COR Inc. Lincoln, NE, USA). Insect frass collected in traps on the forest floor and from caterpillar feeding trials was dried and weighed to estimate the fraction of fresh leaf mass consumed. Annual H in 2004 was assumed to be the same as reported previously (4% of M_{ll}).

Root mass and fine root turnover

We estimated belowground wood or coarse root mass (M_b) using an allometric equation relating M_b – M_a (Cairns *et al.*, 1997). We examined the ability of this model to accurately predict belowground wood mass by extracting 90, 0.6 m soil cores (0.0014 m³ core⁻¹) from the reference forest. Roots (diameter > 2 mm) were separated from soil, dried, weighed, and burned in a muffle furnace to determine ash-free weight. The two approaches yielded estimates that differed by only $\sim 1\%$.

We intensively sampled standing fine root mass (M_{sfr}) in experimental stands that were disturbed in 1998, 1954, and 1936. Soil cores were collected at 20 cm increments (425 cm³ sample⁻¹) to a depth of 80 cm in 18 locations within each stand. Fine roots (diameter ≤ 2 mm) were separated from soil using a 2 mm mesh sieve. Soil was sieved multiple times to maximize root recovery and remaining roots were manually removed from the soil. Roots were washed, dried, weighed, and burned in a muffle furnace to determine ash-free mass. We estimated M_{fr} from 0.8 to 1 m from a regression model relating root depth to root mass that was developed for the reference stand ($M_{fr} = 8.45e^{(-0.0363 \times \text{depth[cm]})} \times 0.47$, $r^2 = 0.89$, $P < 0.0001$). A site-specific C fraction of M_{fr} (0.47) was used to convert dry mass to C mass. We estimated annual fine root turnover (T_{fr} year⁻¹) from an empirical relationship relating available soil N to T_{fr} (Aber *et al.*, 1985)

$$T_{fr}(\text{year}^{-1}) = 0.789 - 0.0191N_{\text{avail}} + 0.000211N_{\text{avail}}^2, \quad (2)$$

where N_{avail} is the sum of mineralized and nitrified soil N, and atmospheric N deposition. We calculated N mineralization and nitrification using site-specific equations that relate stand age to net N mineralization and nitrification (White *et al.*, 2004). Atmospheric N deposition (wet + dry)

was estimated from Baumgardner *et al.* (2002). Annual production of fine root litter (M_{fr}) was estimated as the product of M_{sfr} and T_{fr} .

Organic and mineral soil C mass

We sampled O-horizon and mineral soil C in each of the five experimental stands. Additionally, mineral soil C was measured in an adjacent reference stand that was not experimentally harvested and burned. We collected six, 21.2 cm² O-horizon samples in each stand. To estimate O-horizon C mass (M_o), samples were dried, weighed, and loss on ignition (LOI) was used to calculate C content. A subset of O-horizon samples was analyzed for C content using an elemental analyzer (PerkinElmer 2400; PerkinElmer Inc., Wellesley, MA, USA) to verify the accuracy of the LOI approach. In each experimental stand and in the reference stand, we excavated 20 cm increments of mineral soil to a depth of 80 cm from 60 locations using a soil corer (diameter = 5.2 cm). Ten soil cores from the same stand and depth were pooled for analysis. Mineral soil was sieved through a 2 mm mesh screen. Remaining roots were manually removed, and soil was dried and ground with a mortar and pestle. Soil C concentration was assessed using an elemental analyzer (PerkinElmer 2400) following acid fumigation to remove carbonates (Sollins *et al.*, 1999). To estimate mineral soil C mass (M_{ms}), we first measured bulk density from six soil cores taken at each 20 cm depth increment in all five experimental stands and the reference stand. Soil of a known volume was dried and weighed to calculate bulk density, and this value was multiplied by C% to determine soil C content.

Heterotrophic soil respiration

We measured soil respiration (R_s) in 15 locations within each experimental stand using a LI-COR LI-6400 and a LI-6400-09 soil CO₂ flux chamber (LI-COR Inc.). Soil collars constructed from polyvinyl chloride (PVC) pipe were installed at each location and R_s , soil temperature (T_s), and soil moisture (θ_s) were measured on eight dates (May to November) in 2004 using standard methods described by Curtis *et al.* (2005). For each stand, we modeled R_s as a function of T_s (from ~5 to 20 °C) using a two-parameter exponential function (SAS PROC NLIN procedure; SAS v. 8.2, SAS Inst., Cary, NC, USA). Soil moisture did not explain a significant amount of the variance in R_s and, therefore, was not included in the model. Hourly R_s was estimated for 2004 using continuous T_s data (0.075 m depth) collected in five locations at a nearby site and was summed over the year to determine annual soil respiratory flux (F_s). There were

no significant differences between point measurements of T_s in the experimental stands and overlapping continuous measurements of T_s taken at the reference stand ($P > 0.1$). Point measurements of T_s did not differ among experimental stands ($P > 0.1$); therefore, the same temperature data were used to estimate annual R_s for each stand. The standard errors of hourly R_s were summed to calculate the standard error of F_s .

We first partitioned R_s into heterotrophic and autotrophic sources using the component integration method (Hanson *et al.*, 2000). The O-horizon and top 0.2 m of mineral soil were excavated from six locations in each stand and the mineral soil was sieved through a 2 mm mesh screen to remove roots. Soil samples (200 g) were adjusted to 15% volumetric soil moisture, placed in 500 mL jars and incubated at room temperature (~20 °C) for 1–2 weeks. We measured O-horizon (R_o) and mineral soil (R_{ms}) respiration between 2 and 30 °C (Winkler *et al.*, 1996). A subsample of mineral soil was analyzed for C content and these data were used to calculate CO₂ efflux per gram of soil C. Mineral soil respiration was scaled to the surface area using estimates of C mass for a 1 m² surface × 0.8 m soil depth. O-layer respiration was scaled to the surface area from estimates of forest floor litter mass. The fraction of R_s attributed to heterotrophs at 20 °C (f_h) was calculated as

$$f_h = (R_{ms} + R_o)/R_s. \quad (3)$$

Annual soil heterotrophic respiration estimated using component integration (F_{h1}) was

$$F_{h1} = f_h \times F_s. \quad (4)$$

Total ecosystem heterotrophic respiration (F'_{h1}), including that from coarse woody decomposition, was

$$F'_{h1} = F_{h1} + |-\Delta M_{cd}|, \quad (5)$$

where only annual CWD losses ($-\Delta M_{cd}$) were added to calculations of total heterotrophic respiration. The annual loss of CWD was estimated by calculating the incremental change in mass over 1 year from an equation relating chronosequence stand age to M_{cd} . Losses of M_{cd} were included in F'_{h1} because this negative flux is a component of ecosystem respiration (Gough *et al.*, 2007a), while gains in M_{cd} were incorporated into production estimates since a positive flux indicates net growth of this pool ('Net primary production (NPP), NEP, and annual C increment').

Because belowground C flux estimates generally contain high levels of uncertainty (e.g. Law *et al.*, 2001), we also estimated annual heterotrophic soil respiration

using a mass balance approach (F_{h2})

$$F_{h2} = (M_u + M_{ll} + M_{fd} + M_{fr} + H) - (\Delta M_o + \Delta M_{ms}). \quad (6)$$

That is, F_{h2} is the sum of annual detritus production and H less the soil C increment, and assumes rapid turnover of detritus.

Total ecosystem heterotrophic respiration estimated from mass balance (F'_{h2}), including that from decomposing CWD, was

$$F'_{h2} = F_{h2} + |-\Delta M_{cd}|. \quad (7)$$

Net primary production (NPP), NEP, and annual C increment

To estimate NPP, NEP, and net annual C increment (ΔC) we first calculated the annual production or loss of each C pool. We inferred annual production or loss in slow turnover pools, ΔM_a , ΔM_b , ΔM_{cd} , ΔM_o , and ΔM_{ms} , by calculating the incremental change in pool size over 1 year from regression equations relating chronosequence stand age to mass. The production of annually cycling pools (i.e. fine detritus), M_u , M_{ll} , M_{fd} , and M_{fr} was measured as previously described.

We estimated NPP as

$$NPP = L + D + H, \quad (8)$$

where L is the annual live mass production ($= \Delta M_a + \Delta M_b$), and D is the annual dead mass production ($= M_u + M_{ll} + M_{fd} + M_{fr} + \Delta M_{cd}$; Waring & Schlesinger, 1985). CWD production (ΔM_{cd}) was included in NPP estimates only when ΔM_{cd} was positive.

NEP was

$$NEP = L + D + H - F'_{h1} = NPP - F'_{h1}, \quad (9)$$

(e.g. Curtis *et al.*, 2002, Ehman *et al.*, 2002).

The annual C increment (ΔC) was

$$\Delta C = L + S = NPP - F'_{h2} \quad (10)$$

where S is the change in soil and forest floor C stocks ($\Delta M_o + \Delta M_{ms} + \Delta M_{cd}$) (Curtis *et al.*, 2002). Note that $NEP = \Delta C$ if $F'_{h1} = F'_{h2}$.

Statistical analyses

Standard errors were calculated from the intersample variance of each C pool. The standard errors of NPP, NEP, and ΔC ($\hat{\sigma}_y$) were estimated as the quadratic sum of component errors, ($\hat{\sigma}_y = \sqrt{\sigma_i^2 + \sigma_j^2 + \dots + \sigma_x^2}$). Pairwise comparisons of C pool mass were conducted between stands using Tukey's HSD ($\alpha = 0.05$). T -tests were used to examine differences in annual C storage and site index between experimental and reference stands (SAS V8.1, SAS Institute, Cary, NC, USA). Degrees

of freedom for these tests were based on within-stand replicate plots. As with numerous other C cycling studies using experimental chronosequences (e.g. Chen *et al.*, 2002; Howard *et al.*, 2004; Desai *et al.*, 2005) the main treatment of stand age was unreplicated. However, stand location was unlikely to be confounded with treatment due to the close physical proximity of stands and the uniformity of vegetation, soils, and climate over this area.

Results

C pool mass and production

C accrued rapidly in wood and leaf litter over the first ~40 years following harvest and burning, while understory and woody debris C declined sharply between 6 and 24 years (Fig. 2a and b). C stored in aboveground wood increased >7-fold over 62 years. In stands >50 years, this pool was the largest component of ecosystem C storage. Leaf and fine detritus more than doubled over the first 50 years, peaking at 1.6 Mg C ha^{-1} and then decreasing gradually. Understory C mass decreased by ~70% between 6 and 24 years and reached an asymptotic low of $0.16 \text{ Mg C ha}^{-1}$. Woody debris C exhibited an inverse j-shaped trajectory beginning at age 6 years that was dominated by two phases, one of rapid decay in the youngest stand and another by slow accumulation in maturing stands. Woody debris mass varied by an order of magnitude from 6 to 68 years, with a high of 8.8 Mg C ha^{-1} in the youngest stand and a low of 0.8 Mg C ha^{-1} in the 50 year-old stand.

C stored over time in belowground components generally varied less than that in aboveground pools (Fig. 2c and d). The exception was belowground woody C, which paralleled aboveground wood, increasing four-fold over 62 years. Fine root mass averaged 5.7 Mg C ha^{-1} and did not vary significantly with stand age ($P > 0.05$). Soil organic-horizon C doubled over the first 40 years, but declined as leaf litter production decreased. Total mineral soil C mass (to 80 cm depth) exhibited no significant change with stand age. However, mineral soil C in the top 20 cm followed a significant u-shaped trend over time (Fig. 3a, $P < 0.05$), suggesting that harvest and burning impacted the soil surface, but not the deeper mineral soil (Fig. 3b and c). Soil C in the top 20 cm of the youngest and oldest experimental stands exceeded that of the reference stand ($P < 0.05$), while no significant variation was observed from 20 to 80 cm soil depth.

Respiration, NPP, and NEP

Total soil respiration, mineral soil, and O-horizon respiration were all strongly positively correlated with

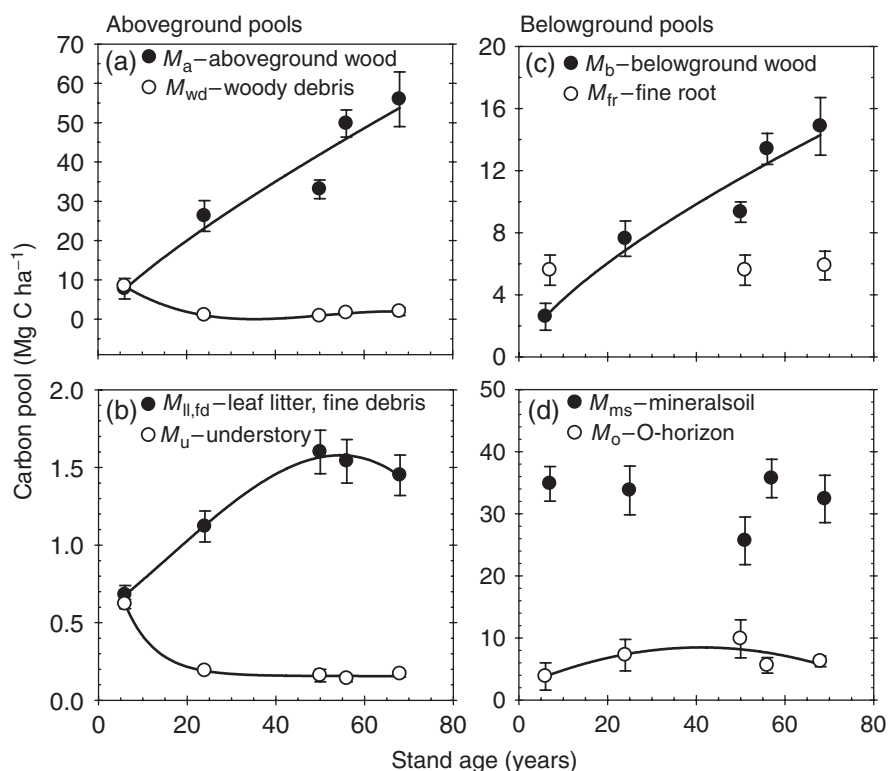


Fig. 2 Carbon pool mass of aboveground wood and woody debris (a), leaf litter, fine debris, and understory (b), belowground wood and fine roots (c), and mineral soil and O-horizon in experimental stands (d). Vertical bars indicate ± 1 SE.

soil temperature (Table 2). Temperature normalized R_s , R_{ms} , and R_o (20°C) generally increased with stand age, reaching a maximum at 50 (R_o) or 56 (R_s , R_{ms}) years. The temperature sensitivity (Q_{10}) of R_s , R_{ms} , and R_o averaged 3.21, 1.94, and 1.61, respectively, and exhibited no clear relationship with stand age. Annual soil respiratory flux, F_s , increased 60% over 50 years of stand development, reaching a maximum of $10.9\text{ Mg C ha}^{-1}\text{ yr}^{-1}$ in the 56-year-old stand. Although the soil heterotrophic respiration fraction (f_h) decreased 28% during this period, F_{h1} increased 27% from a low of $3.6\text{ Mg C ha}^{-1}\text{ yr}^{-1}$ at 24 years to a high of 4.56 at 68 years.

NPP recovered rapidly following harvest and burning, exceeding $5\text{ Mg C ha}^{-1}\text{ yr}^{-1}$ in the youngest stand (Table 3). NPP varied relatively little with stand age, increasing $<10\%$ over 50 years before decreasing somewhat at 60 years. Stability in NPP across the chronosequence was due to offsetting changes in aboveground C pools during the first 50 years of growth, with leaf and fine detritus production increasing and understory production decreasing with stand age. Fine root production typically accounted for $>50\%$ of NPP, and varied by $<10\%$ across the chronosequence. Belowground NPP (BNPP) averaged 54% of total NPP and was always greater than aboveground NPP (ANPP).

NEP and ΔC in experimental stands exhibited similar qualitative trends across stand ages, increasing to a maximum and then declining in older stands, but differed quantitatively across stand ages (Table 3). Both C storage estimates indicate that the forest was a weak C sink 6 years following disturbance (NEP = 0.55 , $\Delta\text{C} = 0.50\text{ Mg C ha}^{-1}\text{ yr}^{-1}$). NEP reached a maximum of $1.35\text{ Mg C ha}^{-1}\text{ yr}^{-1}$ at 24 years, declining three-fold in the 68-year-old stand. The annual C increment was less variable across time, reaching a maximum of $0.95\text{ Mg C ha}^{-1}\text{ yr}^{-1}$ at 50 years and varying by <2 -fold across stand ages. Woody debris losses were an important component of NEP and ΔC in the 6-year-old stand, and were similar in magnitude to leaf and fine debris detritus, and understory production. Decreasing C storage in stands >50 years was due to small reductions in the production of leaf litter and fine debris, fine roots, and wood, and to increasing F'_{h1} in the case of NEP.

Differences between NEP and ΔC estimates of 10–84% (Table 3) were due to discrepancies between estimates of annual heterotrophic respiration calculated using component integration (F'_{h1}) and mass balance (F'_{h2}) approaches, respectively. This degree of difference was less than the respective standard errors, which averaged 108% for NEP and 95% for ΔC . Estimates of F'_{h1} and F'_{h2} differed by as much as 16% in any given stand.

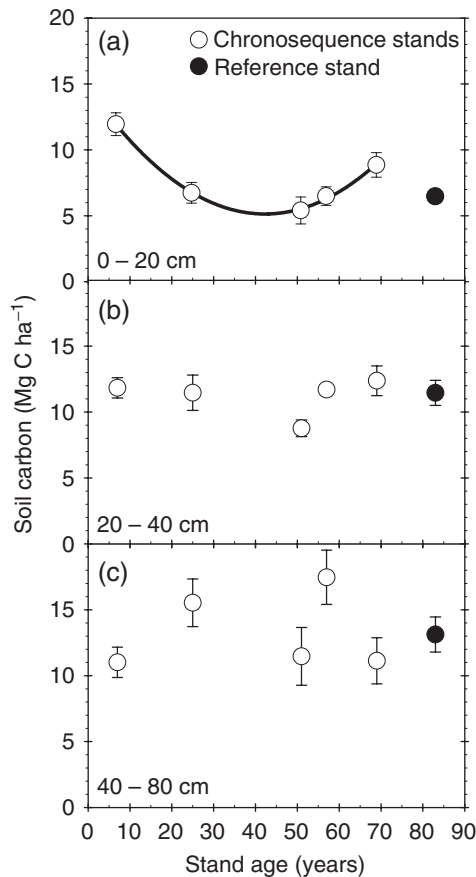


Fig. 3 Mineral soil carbon mass at 0–20 (a), 20–40 (b), and 40–80 (c) cm depths for the experimental and reference stands. Vertical bars indicate ± 1 SE.

Disturbance frequency and annual C storage

Maximum annual C storage in the chronosequence, calculated as the average of maximum NEP and ΔC , was 26% < 5-year mean NEP in the reference stand, an indication that repeated disturbance lowered the successional trajectory of C storage (Table 3, Fig. 4a). This difference was primarily due to lower wood production in experimental stands. Averaged across all experimental stands, NEP and ΔC were 45% lower than 5-year mean NEP in the reference forest ($P < 0.01$). The average of NEP and ΔC was correlated with site index ($P < 0.01$, $r^2 = 0.50$; Fig. 4b), with repeated disturbance resulting in concurrent reductions in site quality and annual C storage.

Discussion

Disturbance effects on forest C storage

A primary objective of this work was to quantify the effect of disturbance on forest C storage for several decades following stand regrowth. Repeated harvest

and fire disturbance had long-term detrimental effects on C storage in this forest, lowering the successional trajectory of NEP and ΔC for several decades. Annual C storage in experimental stands did not recover to levels observed in the less frequently disturbed reference stand over the 62-year timeframe examined, indicating that the legacy effects of harvest and fire on C storage are severe and long-lasting at our study site. Because the approach we used does not capture interannual variation in C storage due to climate variability, NEP and ΔC in experimental stands are smoothed estimates of annual C storage. However, maximum NEP and ΔC in experimental stands averaged $\sim 26\%$ < 5-year mean NEP in the 85-year-old reference stand (Gough *et al.*, 2007b).

Variation in annual C storage among hardwood forests in the upper Great Lakes region is due to multiple parameters including climate, species, and soils (Desai *et al.*, 2007). In addition, disturbance history may be an important determinant of C storage (Chen *et al.*, 2004a). We suggest that NEP and ΔC are particularly low in our experimental stands because of the effects of repeated disturbance. Maximum NEP and ΔC in experimental stands were lower than mean annual C storage in other northern hardwood forests, including mixed hardwood forests of central Massachusetts ($2.0 \text{ Mg C ha}^{-1} \text{ yr}^{-1}$; Barford *et al.*, 2001), aspen and maple-dominated forests of southern Ontario ($1.7 \text{ Mg C ha}^{-1} \text{ yr}^{-1}$; Lee *et al.*, 1999), and an aspen-dominated stand in Saskatchewan ($3.0 \text{ Mg C ha}^{-1} \text{ yr}^{-1}$; Griffis *et al.*, 2004).

Low annual C storage in experimental stands resulted from a long-term reduction in site quality caused by repeated harvest and fire. Site index, an integrated metric of site quality, was 32% lower in experimental stands than in the reference stand. Increases in fire and logging frequency and severity have been linked to reductions in forest soil fertility (e.g. Binkley *et al.*, 1992; Latty *et al.*, 2004), and concurrent decreases in forest C storage (Bergeron & Harvey, 1997). Our findings indicate that legacy effects of disturbance can persist for decades, possibly through the loss of essential nutrients such as nitrogen (Dale *et al.*, 2001). In a meta-analysis, Johnson & Curtis (2001) reported mixed effects of harvest and fire on soil nitrogen, with sawlog harvesting generally increasing soil nitrogen, and fire resulting in no net change in soil nitrogen. In contrast, fire was more detrimental than harvesting to soil nitrogen pools in ponderosa pine (*P. ponderosa*) forests (Deluca & Zouhar, 2000). In an oak-hickory forest, 5 years of atmospheric nitrogen inputs were required to replenish the soil nitrogen pool following a low intensity, controlled fire (Trammell *et al.*, 2004). High-intensity, slash-fueled wildfires once common in the

Table 2 Soil respiration across a disturbance chronosequence

	Stand age (years)				
	6	24	50	56	68
R_s 20 °C ($\mu\text{mol m}^{-2} \text{s}^{-1}$)	6.31 (0.26)	8.85 (0.24)	7.46 (0.36)	11.17 (0.29)	8.82 (0.31)
Q_{10}	2.87 (0.44)	3.88 (0.54)	2.92 (0.48)	3.38 (0.42)	2.98 (0.41)
a, b	0.763, 0.106	0.588, 0.136	0.877, 0.107	0.978, 0.122	0.995, 0.109
r^2, P	0.97*	0.97*	0.96*	0.98*	0.97*
R_{ms} 20 °C ($\mu\text{mol m}^{-2} \text{s}^{-1}$)	3.14 (0.36)	3.57 (0.35)	3.40 (0.26)	4.16 (0.27)	3.88 (0.26)
Q_{10}	1.98 (0.38)	1.72 (0.30)	1.90 (0.27)	1.95 (0.23)	2.16 (0.27)
a, b	0.797, 0.069	1.206, 0.054	0.943, 0.064	1.093, 0.067	0.834, 0.077
r^2, P	0.91*	0.95*	0.95*	0.96*	0.96*
R_o 20 °C ($\mu\text{mol m}^{-2} \text{s}^{-1}$)	0.44 (0.31)	0.53 (0.12)	0.59 (0.17)	0.46 (0.10)	0.41 (0.08)
Q_{10}	1.48 (1.28)	1.61 (0.58)	1.61 (0.68)	1.74 (0.60)	1.60 (0.50)
a, b	0.200, 0.039	0.203, 0.048	0.228, 0.048	0.153, 0.056	0.161, 0.047
r^2, P	0.52**	0.81*	0.76*	0.81*	0.86*
F_s ($\text{Mg C ha}^{-1} \text{yr}^{-1}$)	6.75 (0.54)	7.82 (0.51)	7.82 (0.72)	10.90 (0.65)	9.30 (0.66)
f_h [$= (R_{ms} + R_o)/R_s$]	0.57 (0.02)	0.46 (0.04)	0.53 (0.02)	0.41 (0.02)	0.49 (0.02)
F_{h1} ($\text{Mg C ha}^{-1} \text{yr}^{-1}$) [$= F_s \times f_h$]	3.85 (0.64)	3.60 (0.59)	4.14 (0.76)	4.47 (0.69)	4.56 (0.70)

Instantaneous respiration at 20°C, Q_{10} , model parameters (where $R = ae^{bT}$), and model goodness of fit are shown for total soil respiration measured *in situ* (R_s), mineral soil respiration (R_{ms}), and O-layer respiration (R_o). The product of the annual soil respiration flux (F_s) and the fraction of soil respiration due to heterotrophs (f_h) is annual soil heterotrophic respiration (F_{h1}). Estimate \pm (SE).

* = $P < 0.0001$, ** = $P < 0.01$.

Table 3 Annual gain or loss of carbon from ecosystem components and total annual carbon storage across a disturbance chronosequence and for the reference stand

Production/loss ($\text{Mg C ha}^{-1} \text{yr}^{-1}$)	Stand age (years)					Reference, 85
	6	24	50	56	68	
¹ Aboveground wood	1.00 (0.07)	0.78 (0.03)	0.68 (0.01)	0.66 (0.01)	0.64 (0.01)	1.73 (0.10)
² Herb layer	0.62 (0.03)	0.19 (0.01)	0.16 (0.04)	0.14 (0.02)	0.17 (0.02)	0.14 (0.01)
³ Herbivory losses	0.03 (0.01)	0.06 (0.01)	0.08 (0.01)	0.08 (0.01)	0.07 (0.01)	0.07 (0.01)
⁴ Leaf litter and fine debris	0.68 (0.06)	1.12 (0.10)	1.60 (0.14)	1.54 (0.14)	1.45 (0.13)	1.51 (0.12)
⁵ Coarse woody debris	-0.67 (0.03)	-0.18 (0.01)	0.09 (0.01)	0.08 (0.01)	-0.03 (0.02)	0.00 (0.58)
⁶ Fine roots (<2 mm)	2.44 (0.41)	2.78 (0.47)	2.67 (0.45)	2.61 (0.44)	2.56 (0.43)	2.69 (0.46)
⁷ Belowground wood (>2 mm)	0.30 (0.02)	0.20 (0.01)	0.16 (0.01)	0.16 (0.01)	0.15 (0.01)	0.40 (0.02)
⁸ Mineral soil	-0.39 (0.02)	-0.19 (0.03)	0.09 (0.04)	0.15 (0.04)	0.28 (0.05)	-
⁹ O-layer	0.26 (0.21)	0.13 (0.29)	-0.07 (0.42)	-0.12 (0.45)	-0.21 (0.50)	-
¹⁰ ANPP ^(1+2+3+4+5*)	2.33 (0.10)	2.15 (0.11)	2.61 (0.15)	2.50 (0.14)	2.33 (0.13)	3.45 (0.60)
¹¹ BNPP ⁽⁶⁺⁷⁾	2.74 (0.41)	2.98 (0.47)	2.83 (0.45)	2.77 (0.44)	2.71 (0.43)	3.09 (0.46)
¹² NPP total ⁽¹⁰⁺¹¹⁾	5.07 (0.42)	5.13 (0.48)	5.44 (0.47)	5.27 (0.46)	5.04 (0.45)	6.54 (0.76)
¹³ F'_{h1} ^(Table 2 + 15*)	4.52 (0.70)	3.78 (0.55)	4.14 (0.77)	4.47 (0.56)	4.59 (0.65)	5.01 (0.86)
¹⁴ F'_{h2} ^{(2+3+4+15*+6)-(8+9)}	4.57 (0.47)	4.39 (0.56)	4.49 (0.63)	4.34 (0.65)	4.21 (0.67)	-
NEP ⁽¹²⁻¹³⁾	0.55 (0.82)	1.35 (0.73)	1.30 (0.90)	0.80 (0.73)	0.45 (0.79)	1.53 (1.15)
ΔC ^{(1+5+7+8+9) or (12-14)}	0.50 (0.63)	0.74 (0.74)	0.95 (0.79)	0.93 (0.79)	0.83 (0.81)	-

ANP, aboveground net primary production; BNPP, belowground net primary production; NPP, net primary production, F'_{h1} , F'_{h2} , heterotrophic soil respiration; NEP, net ecosystem production; ΔC , ecosystem carbon increment. Estimate \pm (SE).

*Coarse woody debris included in ANPP calculation when positive and F'_{h1} , F'_{h2} calculations when negative.

upper Midwest and now widespread in the tropics may be even more deleterious to soil nutrient pools than low-intensity controlled burns (Pietikainen & Fritze,

1993), underscoring the need to consider long-term consequences of this disturbance in other managed ecosystems.

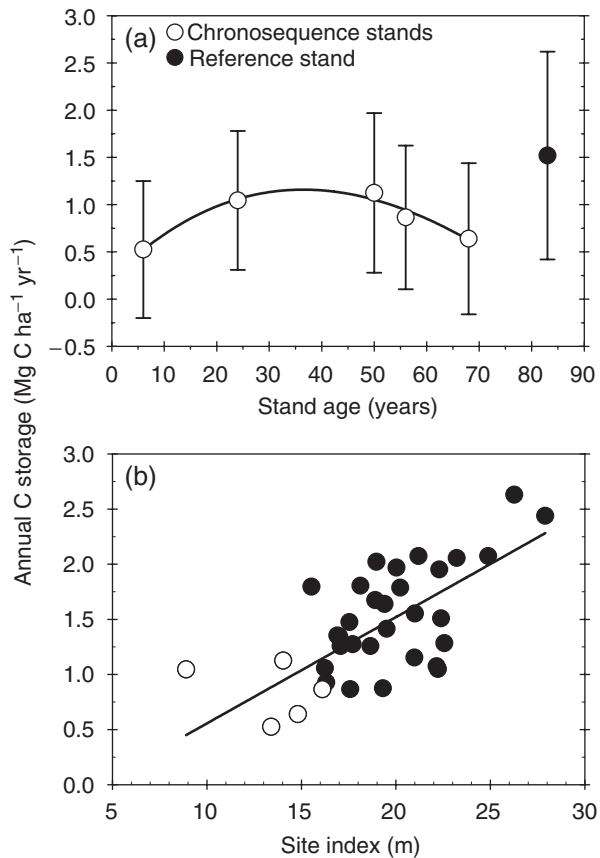


Fig. 4 The relationship between annual carbon (C) storage and stand age (a), and site index (b) for experimental stands and replicate plots within the reference stand. Annual C storage is the average of net ecosystem production and ΔC . Vertical bars indicate $\pm 1SE$.

Succession and forest C storage

Annual C storage in our forest chronosequence followed the successional trajectory predicted by Odum (1969), increasing to a maximum and then gradually declining as the forest matured. This trend has been reported for other forests following stand-replacing disturbance (Law *et al.*, 2003; Bond-Lamberty *et al.*, 2004a; Howard *et al.*, 2004). Our study forest became a sink of C to the atmosphere within 6 years following harvesting and burning. This transition time from C source to sink is less than the 10–20 observed years for Canadian boreal forests (Hicke *et al.*, 2003; Howard *et al.*, 2004) and the 39 years reported for ponderosa pine forests of central Oregon (Law *et al.*, 2003). The time required for a forest to transition from a C source to sink likely depends on the recovery of leaf area following a stand-replacing disturbance. Although $A_{I_{max}}$ in the 6-year-old stand was half that of the 50-year-old stand, understory fern mass was nearly four times greater. The inverse relationship between

overstory leaf and understory production suggests that high understory leaf area in young stands compensated for losses in overstory leaf area following disturbance, facilitating a rapid transition from C source to sink. NEP over successional time is correlated with maximum overstory leaf area ($A_{I_{max}}$) in other forest ecosystems (Arain & Restrepo-Coupe, 2005; Humphreys *et al.*, 2005).

Mineral soil C and CWD pools varied similarly over successional time, exhibiting an initial postdisturbance decline and then gradual accumulation. Mineral soil C in the top 20 cm followed a u-shaped trend with forest age, but exhibited no discernable trend over time at depths of 20–80 cm. Sun *et al.* (2004) found that mineral soil C in the top 100 cm followed a u-shaped curve over time in western US coniferous forests due to decomposition of legacy C inputs and subsequent C accrual as detritus inputs increased with forest maturation. Harvest and fire in our study did not reduce C storage in surface mineral soil. Instead, C storage in the top 20 cm of mineral soil in the youngest, 6-year-old stand was greater than that of the mature reference stand that was not subjected to experimental harvest and burning. Mature forests generally store more C in surface mineral soil than do young forests following disturbance (Gaudinski *et al.*, 2000; Law *et al.*, 2001). High levels of soil C in the 68-year-old stand suggest that harvest and fire disturbance resulted in the long-term augmentation of C in the top 20 cm of mineral soil, possibly through the production of recalcitrant charcoal. Studies conducted in fire-prone loblolly pine (*Pinus taeda*) and oak-savanna ecosystems have shown that fire results in only minor reductions in mineral soil C over the long term (Binkley *et al.*, 1992; Tilman *et al.*, 2000). In contrast, clear-cut harvest and fire reduced long-term mineral soil C storage in northern hardwood forests of New York (Latty *et al.*, 2004). CWD variation across the forest chronosequence was similar to that of the surface mineral soil, initially decreasing as legacy CWD decomposed and then accumulating slightly with forest maturation. This pattern of CWD storage over time is similar to that reported for boreal and western US coniferous forests (Sturtevant *et al.*, 1997; Janisch & Harmon, 2002).

Fine root mass did not vary with stand age, indicating that either regrowth occurred within 6 years following disturbance or fine root mortality was minimal following harvest and fire. Root production in forests is globally correlated with litterfall (Raich & Nadelhoffer, 1989) and at our site fine root mass may have paralleled recovery of understory and overstory leaf area. Aspen roots also may be resilient following aboveground disturbance. Clear-cut harvesting stimulated aspen regeneration from root sprouts after 3 years in British

Columbia (Simard *et al.*, 2005), suggesting that root survival following disturbance was substantial. Consistent with our findings, fine root mass did not change with forest age in a mature tropical forest (Cavelier *et al.*, 1996). This is in contrast to several studies that have shown fine root mass increases leading up to forest maturation and then decreases as mature trees senesce (Cairns *et al.*, 1997; Chen *et al.*, 2004b; Claus & George, 2005). Although fine root mass was remarkably stable across our forest chronosequence, this pool may begin to decline as aspen mortality increases over the next several decades.

Estimates of annual heterotrophic respiration varied across the chronosequence in response to shifts in the heterotrophic contribution to total soil respiration, changes in the annual soil respiratory flux, and decomposition of CWD. Heterotrophic contributions were 41–57% of total soil respiration, with the highest percentage in the 6-year-old stand. Our estimates of F_h are similar to those predicted from a global relationship relating F_h to F_s , averaging only $\sim 10\%$ less (Bond-Lamberty *et al.*, 2004b). The balance between heterotrophic and autotrophic soil respiration varies across ecosystem developmental gradients in response to changes in soil microclimate, C substrate available to heterotrophs, and root mass (Fu & Cheng, 2002). Annual heterotrophic respiration in our study generally paralleled changes in annual soil respiration, which peaked in the 56-year-old stand. Soil respiration has been shown to increase with stand age in other forest ecosystems (Litton *et al.*, 2003; O'Neill *et al.*, 2003; Gough *et al.*, 2005).

Measurement uncertainty

We used two metrics to quantify annual C storage, NEP, and ΔC , which entailed different approaches to estimating annual soil heterotrophic respiration (F_h). These methods generally yielded comparable estimates of annual C storage, with ΔC averaging 11% lower than NEP across the experimental stands. Differences between the metrics resulted exclusively from minor incongruence between independent calculations of F_h . Our mass balance and soil respiration partitioning methods produced comparable estimates of F_h , despite uncertainty in the turnover time of soil C inputs and even though we did not take into account seasonal variability in heterotrophic soil respiration due to changes in environmental conditions or phenological events (Lee *et al.*, 2003; DeForest *et al.*, 2006). Annual soil respiration at our site was calculated using a simple equation that relates soil respiration to temperature. Although we did not include soil moisture in the model, Curtis *et al.* (2005) showed that soil moisture was not a consistent source of variation in soil respiration in the

reference stand. Our maximum estimate of F_s ($11.17 \text{ MgC ha}^{-1} \text{ yr}^{-1}$) is only 9% higher than the 5-year average for the reference stand, but accuracy of these estimates is difficult to assess. Chamber-based methods may overestimate soil respiration (Curtis *et al.*, 2005). Additional uncertainty in belowground C fluxes is frequently associated with estimates of fine root production (Clark *et al.*, 2001), which constitute the largest component of NPP at our site. Numerous studies have shown that uncertainty in annual C storage estimates is derived primarily from the limited precision of belowground C flux estimates (Curtis *et al.*, 2002; Ehman *et al.*, 2002; Law *et al.*, 2003; Howard *et al.*, 2004; Gough *et al.*, 2007b).

Our estimates of NEP and ΔC were derived from a combination of direct flux measurements and simple regression-based calculations of fluxes. Annual fluxes from slow C pools were estimated using equations relating forest age to mass, while fluxes from detrital pools were measured directly during a single year. The latter approach is sensitive to annual variation in climate and may not represent the mean response over longer, decadal scales (Gough *et al.*, 2007b). Despite uncertainties associated with estimates of NEP and ΔC , biometric estimates of NEP converged to within 1% of independent meteorological estimates of NEP over 5 years at our site (Gough *et al.*, 2007a), demonstrating that our methods yield accurate estimates of annual C storage.

We did not independently measure annual CWD production and losses in experimental stands, but instead evaluated the net change in this pool over time (Table 3). Studies conducted in the reference stand show that this pool is a minor component of total NPP ($< 1\%$). CWD production may be even less in the younger experimental stands because tree mortality is lower than that of the reference stand. CWD is a minor component of NPP in other young temperate forests (Sturtevant *et al.*, 1997; Janisch & Harmon, 2002). CWD losses from respiration are typically high in young, recently disturbed stands (Clark *et al.*, 2001). However, the respiratory flux of C from CWD in the mature reference stand is only 1% of ecosystem respiration (Gough *et al.*, 2007a). CWD is a substantial component of NPP and respiration in forests with high tree mortality, including old-growth forests and ecosystems that experience frequent disturbance (Clark *et al.*, 2001).

Conclusions

We have shown that a northern hardwood forest was a net C sink only 6 years following harvest and fire disturbance. However, this disturbance had long-term negative effects on the capacity of this forest to store C,

lowering the successional trajectory of annual C storage (NEP and ΔC) for several decades. Stands that were disturbed by harvest and fire twice stored on average 45% less C annually than those receiving the same disturbance only once. The mechanism for this reduction in annual C storage is a lasting reduction in site quality. These results confirm that disturbance history, together with succession and climate, is an important source of variation in annual forest C storage. Our results also serve as an important example of how once common forestry practices can have long-lasting, detrimental effects on ecological processes of importance to climate change policy.

Disturbance regimes that forests of the upper Midwest currently experience are considerably different from those of a century ago (Frelich, 1995). Harvest intensity has declined and contemporary management practices emphasize sustainability of wood production and site quality (Frelich & Reich, 1995; Houghton *et al.*, 1999). However, fire frequency in the upper Midwest is predicted to increase by 20–40% over the next half century due to climate change (Dale *et al.*, 2001), suggesting that anthropogenic disturbance may once again play a primary role in shaping regional forest C storage. Severe disturbances analogous to those that occurred in the upper Midwest a century ago are increasingly common in tropical regions such as the central Amazon and equatorial Asia (Fearnside, 2005; Toma *et al.*, 2005). The legacy of historically poor forest management practices on modern C storage in the United States may thus serve as an important example for land and forest managers in developing countries where logging and wildfire are common due to rapid land development and high wood demand.

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