Forest carbon sequestration changes in response to timber harvest

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A B S T R A C T

Forest succession contributes to the global terrestrial carbon (C) sink, but changes in C sequestration in response to varied harvest intensities have been debated. The forests of the Central Appalachian region have been aggrading over the past 100 years following widespread clear-cutting that occurred in the early 1900s and these forests are now valuable timberlands. This study compared the history of ecosystem C storage in four watersheds that have been harvested at different frequencies and intensities since 1958. We compared NPP, NEP, and component ecosystem C fluxes (g C m^{-2} year^{-1}) in response to the four different harvest histories (no harvest, clear-cutting, single tree selection cutting, and 43 cm diameter-limit cutting). Clear-cutting had short-term negative effects on NEP but harvest did not significantly impact long-term average annual C sequestration rates. Average plant C (g C m^{-2}) since 1950 was about 33% lower in response to a clear-cut event than plant C in an un-harvested forest, suggesting that the C sequestration associated with clear-cutting practices would decline over time and result in lower C storage than diameter-limit cut, selective cut, or un-harvested forests. Total C stored over a 55-year period was stimulated ~37% with diameter-limit cutting and selective cutting relative to un-harvested forests.

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1. Introduction

Forest C sinks that offset greenhouse gases are threatened by socio-economic incentives (Turner et al., 1995) to harvest timber. Global terrestrial C storage currently accounts for approximately 2300 Gt C (Denman et al., 2007) that is depleted by deforestation and harvest at an estimated rate of 2.55 Gt C year^{-1} (Houghton, 2003a). Timber removal from forests is managed in many different ways and is not always considered a direct land use change even though it may affect ecosystem C budgets over time. Much of the Central Appalachian region consists of forested land that has regenerated following a major clear-cut event between 1880 and 1920 (Griffith and Widmann, 2003). There are over 9 million acres of valuable saw-timber in the state of West Virginia alone, most of which is privately owned and thus governed by diverse economic incentives (Hicks, 1998; Griffith and Widmann, 2003). The change in forest C sequestration that will result from varied management will be both temporally and spatially heterogeneous (Parker et al., 2008) and estimates of those changes require thorough evaluation of ecosystem responses to different harvest intensities. In this study, we measured the historical changes in C storage that result from different harvest histories and project the relative impact of different management decisions on forest C sinks.

Many studies have quantified the effect of land use change on terrestrial C sinks (Houghton et al., 1999; Caspersen et al., 2000; Post and Kwon, 2000; Pacala et al., 2001; Goodale et al., 2002; House et al., 2002), but the relative effect of specific harvest strategies on ecosystem C sequestration is still uncertain. Past studies suggest that terrestrial sequestration of C is increasing (Wofsy et al., 1993; Schimel et al., 2000), especially in temperate regions (Xiao, 1997; Houghton et al., 2003a), but others caution that the contribution of forest growth to terrestrial C sinks may be overestimated (Goodale et al., 2002; House et al., 2002; Beedlow et al., 2004). Net primary production (NPP) of a forest can be estimated as a biomass or C assimilation rate, *i.e.* photosynthesis minus autotrophic respiration (R_a), and is constrained by physiological characteristics of the plant community. NPP depends largely on the physiological responses of dominant timber species to climate, nutrient availability, and management practices that have not yet been validated against historical observations (Houghton, 2003b).

The long-term C balance of a whole forest ecosystem can be estimated by calculating net ecosystem production (NEP), which is

the rate of C sequestration that depends on NPP as well as C losses to decomposition and heterotrophic respiration (R_h). Plant C is an especially important component of NPP in a forest because it is proportional to live autotrophic biomass, and changes in plant C are indicative of changes in a large standing C pool as well as potential future growth. Much of the R_h flux is controlled by soil processes that are affected by biomass removal during a harvest event. NEP can be estimated using an ecosystem process model, *e.g.* PnET-CN (Aber et al., 1997), that synthesizes biotic and abiotic factors that affect R_h and soil conditions. Biotic factors that influence soil C storage include the amount and quality of plant residue additions as well as microbial biomass and activity (Matamala et al., 2003; Liebig et al., 2005; Nicolardot et al., 2007). Abiotic factors affecting R_h include soil moisture, temperature, and the proportion of mineralized N relative to soil organic matter (Lal, 2005).

Temporal changes in C sequestration rates can be used to determine the relative stability of ecosystem C storage under different management conditions. We used both field measurements and model projections to contrast short- and long-term forest C sequestration in four watersheds in the Fernow Experimental Forest (Parsons, WV) that have been harvested at different frequencies and intensities since 1958. Our objective was to compare both the rate of C sequestration and changes in C storage in response to four different harvest histories (no harvest, clear-cutting, single tree selection cutting, and 43 cm diameter-limit cutting). We hypothesized that, (1) if NEP progressively declines in response to repeated harvest events, then ecosystem C storage would not be maintained in harvested forests and (2) if the intensity of harvest events has a greater effect on forest C balances than the frequency of harvest events, then the C balance of a clear-cut watershed would differ from the C balance of a reference watershed more than the difference in C balances resulting from diameter-limit or single tree selection harvest histories relative to the reference. Component C fluxes (*e.g.* R_a and R_h) and pools (*e.g.* plant C) were calculated to resolve further details about the C balances of harvested forests. Estimates of C sequestration calculated here account for historical development of harvested forestland in a region with high nitrogen (N) availability and can be used to estimate C costs and values of similar forests that may be harvested in the future.

2. Methods

We used an ecosystem process model to simulate harvest events in a deciduous hardwood forest and calculate NEP. To ensure the integrity of these calculations, the model was first validated against long-term measurements of water, carbon, and nitrogen budgets in four watersheds with different harvest histories.

2.1. Study sites

This study was conducted in the Fernow Experimental Forest (FEF), located in the Appalachian Plateau section of the mixed mesophytic forest (Braun, 1950) where extensive logging took place between the years 1903 and 1911 (Trimble, 1977). The FEF has a rainy and cool climate with an average maximum temperature of 15 °C and about 146 cm of annual rainfall (Kochenderfer, 2006). We chose four watersheds in the FEF that have had different harvest histories documented by the USDA Forest Service since the logging event ∼100 years ago. Watershed 13 (WS 13) was subjected to very little disturbance since this logging period and was ∼100 years old at the time of sampling. Watershed 7 (WS 7) was clear-cut in several stages between 1963 and 1969 during which time forest re-growth was suppressed with

herbicide treatments. The herbicide additions were applied to half of the watershed that was clear-cut in 1963, and then to the other half that was clear-cut in 1966. These treatments would have a different effect on subsequent forest C budgets than the effect of a clear-cut without herbicidal treatment, but the general response after 1969 should be similar to other forest responses to clear-cutting. Watershed 2 (WS 2) was subjected to diameter-limit cutting between 1958 and the present (Table 1) with trees over 43 cm in diameter intermittently harvested approximately every 15 years. Watershed 5 (WS 5) underwent single tree selection cutting with trees over 28 cm in diameter harvested periodically in a way that maintained a consistent basal area and stocking density with continued growth of trees in all age classes (a more detailed description can be found in Schuler, 2004). Prior to these harvest events, we assumed that all watersheds were subject to similar disturbances. We estimated that 70% of biomass was removed in 1908 according to Forest Service records of clear-cut practices. About 95% mortality was estimated in response to logging but debris left behind to decompose constituted about 26% of the slashed organic matter, so about 70% of the total biomass was removed with 5% left standing and 25% left to decompose. Mortality from chestnut blight occurred throughout the forest, so we assigned 25% biomass loss to all watersheds in the 1930s (Weitzman, 1949; Hicks, 1998). Harvest histories were simulated with the ecosystem process model PnET-CN$_{sat}$ (described in more detail below; Aber et al., 1997; Davis et al., 2008) by using a percent mortality and percent removal parameter for each harvest event. The percentage of biomass that was removed in each simulated harvest event reflected the assumptions described above (Table 1) and reflected the product of percent mortality and the percent removed to account for the residual debris that remained on the forest floor following disturbance.

2.2. Dendrochronologic estimates of productivity

Six circular 10 m radius plots were randomly located and established in each of the four watersheds. We identified all of the trees in each plot to species, measured the diameter at breast height (DBH), and collected two increment cores from all trees >10 cm DBH within each plot. We also cored all standing dead trees, though only a subset of these cores was suitable for further analysis. Tree increment cores were brought back to the lab where

Table 1
Timeline of biomass removed due to harvest (the product of mortality and removal in PnET-CN$_{sat}$ harvest scenario) in experimental watersheds in the Fernow Experimental Forest.

Year	Reference (WS 13)	Clear-cut (WS 7)	43 cm diameter-limit (WS 2)	Single tree selection cut (WS 5)
1908	70%	70%	70%	70%
1935	25%	25%	25%	25%
1958			32%	21%
1963		49%		
1966		51%		
1968				15%
1969		98%		
1972			11%	
1978			5%	10%
1983				16%
1988			17%	14%
1996			17%	
1998				27%

Column headings denote the harvest treatment with watershed number in parentheses. The initial tree harvest was estimated from Forest Service records of logging practices in 1908 and the chestnut blight in the mid-1930s resulted in approximately 25% removal of biomass from all of these watersheds (Weitzman, 1949).

they were mounted and sanded with increasingly finer grades of sandpaper up to 2000 grit. With the exception of the cores from the clear-cut watershed, all cores were cross-dated using skeleton plots (Stokes and Smiley, 1968) in order to assign biomass estimates to the appropriate year. Following dating, ring widths of all watersheds were measured using a measuring stage and binocular microscope to determine annual growth increments to an accuracy of 0.01 mm. Cross-dating was statistically confirmed using COFECHA (Grissino-Mayer, 2001). For the clear-cut watershed, species means of annual increment changes were dated according to the last year of growth because there were not enough growth anomalies during the subsequent ~35 years to cross-date annual growth with precision.

Species-specific allometric equations (Tritton and Hornbeck, 1982; Brenneman et al., 1978) were used to estimate woody biomass from stem diameters of living and dead trees (equations do not include foliage because foliage mass was measured separately). Estimates of annual wood production dating back to 1971 were calculated by subtracting the diameter increment of the subsequent year and applying the species-specific allometric equations. Some trees (~16%) were too rotten to either core or measure and, in these cases, a neighboring tree of the same species and similar size (±10 cm) was used as a substitute for that tree in plot level productivity calculations. Mortality of trees that were no longer standing could not be included in dendrochronological estimates; this likely increased the error of wood NPP estimates during periods of self-thinning.

Litterfall collections were combined with tree-ring data to estimate aboveground biomass and ANPP (Clark et al., 2001). Two litter baskets (0.23 m^2) located at random positions in each plot were sampled at monthly intervals for 1 year. Litter was sorted by species into leaf, wood, and germinal parts, then dried and weighed. Litterfall mass measurements in the clear-cut watershed were also available from US Forest Service datasets for the years 1997–2001 (Adams, 2008). Total litterfall estimates were added to annual wood productivity estimates to calculate ANPP. We used a 5-year record of litterfall from the clear-cut watershed to reconstruct ANPP over the 20-year period for which we estimated wood NPP. The same approach was used to estimate ANPP for the reference (un-harvested) watershed after scaling litterfall to account for the 11% greater average annual difference (based on the 1-year plot means of litterfall measurements in WS 13). In the case of the diameter-limit and single tree selection cut watersheds, where stems were removed at repeated intervals, we estimated the proportional stem mass that would have been harvested over time and added the estimated wood biomass removed at each harvest to the original dendrochronologic estimate.

2.3. Additional site measurements

Site-specific measurements of canopy foliar C and N, litter N, and stream flow were made in the four watersheds for model validation in July of 2006. We sampled upper-canopy leaves from dominant canopy tree species, included *Acer rubrum*, *Acer saccharum*, *Betula lenta*, *Fagus grandifolia*, *Liriodendron tulipifera*, *Prunus serotina*, and *Quercus rubra*, in each watershed (N = 120). Leaf area of each leaf was measured using an LI-3100C Area Meter (LI-COR Biosciences, Lincoln, NE) within 5 h of sampling and then leaf samples were dried for 48 h (65 °C) and weighed so that specific leaf weight (SLW) could be calculated. Litter samples were also collected from six plots in each watershed by randomly locating three subsamples in each plot that were then compiled and dried for 48 h (65 °C). Carbon and N concentrations of dried leaf and litter samples were measured with a Carlo Erba CN autoanalyzer (Fison Inst., Milan, Italy). Stream flow records starting in 1957 were compiled for each watershed from datasets maintained by the USDA Forest Service Northern Research Station (Fernow Experimental Forest, 2003). Records of stream flow in the reference watershed were only available starting in 1989, so we also used stream flow data from a near-by reference watershed that had a similar management history (WS 4); this provided a more long-term and robust test against modeled stream flow for the un-harvested reference case.

2.4. Validation of PnET-CN$_{sat}$

An ecosystem productivity model, PnET-CN$_{sat}$ (Davis et al., 2008), was parameterized for each watershed to more completely describe the effects of different harvest strategies on forest C balances, including net ecosystem productivity (NEP), R_h, R_a, and the plant C pool. Modeled NEP estimates were derived from calculations that include empirically derived process descriptions of belowground biomass allocation, turnover, and respiration (Aber et al., 1997; Ollinger et al., 2002). PnET-CN$_{sat}$ is a revised version of the PnET-CN model (Aber et al., 1997; Ollinger et al., 2002) that has formerly been validated in the reference watershed (WS 13) in the FEF (Davis et al., 2008). Physiological process-based submodels include C, N, and water budgets as well as subroutines to describe the biomass removal associated with harvest or disturbance (Aber et al., 1997; Ollinger et al., 2002). Site-specific parameters were described in Davis et al. (2008) and included AmaxA, AmaxB, SLW$_{max}$, GDDFolStart, GDDFolEnd, GDDWood-Start, GDDWoodEnd, FLPctN, WLPctN, MaxNStore, FolNRetrans, NReten, Nitr, Lat, WHC, NRatio, SnowPack, and HON (defined in Table 2). Local climate files were constructed based on climate records from a weather station in the FEF that has been maintained by the USDA Forest Service Northern Research Station Timber and Watershed lab since 1952. Climate was reconstructed for the time period before 1952 using monthly averages of precipitation and temperature during the time for which climate data was available.

While PnET-CN$_{sat}$ predictions have been validated in the un-harvested watershed (Davis et al., 2008), the model structure was designed to reflect a closed-canopy (Aber and Federer, 1992) and has less frequently been applied to young forests prior to canopy closure. In order to apply PnET-CN$_{sat}$ to regenerating forests, such as WS 7 that was clear-cut ~40 years ago, we modified the equation that allocates biomass to foliar growth. The new equation limits foliar growth to a percentage of the standing wood mass in any particular year so that a mature forest canopy is not assumed by the model until the wood mass is comparable to that of a mature forest. The percentage of foliar mass relative to wood mass was based on a comprehensive description of biomass pools in the FEF (Adams et al., 2004).

For each of the experimental watersheds studied here, modeled aboveground predictions were verified against the detailed site measurements described above. After parameterizing PnET-CN$_{sat}$ for the four watersheds, we tested model predictions against the dendrochronologic estimates of wood NPP, ANPP, historical records of stream flow, and on-site measurements of foliar C, foliar N, and woody litter N. We used regression analyses (α = 0.1) to determine the degree to which modeled estimates of wood NPP, ANPP, and stream flow predict measured values over time (SAS-JMP software version 5.1, SAS Institute, Cary, NC, USA). We used a t-test (SAS-JMP software version 5.1, SAS Institute, Cary, NC, USA) to compare foliar C, foliar N, and woody litter N predictions to independent on-site measurements.

2.5. Watershed carbon balance estimates

Using the validated PnET-CN$_{sat}$ model, we estimated ecosystem C fluxes that included net changes in soil and root biomass and

Table 2
Parameters specified according to on-site characteristics of the Fernow Experimental Forest.

| Parameter	Definition
AmaxA	Intercept of the relationship between foliar N and saturated photosynthesis (A_{max})
AmaxB	Slope of the relationship between foliar N and saturated photosynthesis
FLPctN	Minimum N concentration in foliar litter
FolNCon	Concentration of foliar N
FolNRetrans	Proportion of foliar N that is retranslocated
GDDFolStart	Sum of all daily average temperature degrees above zero from Jan 1 to the start of foliage production
GDDFolEnd	Sum of all daily average temperature degrees above zero from Jan 1 to the end of foliage production
GDDWoodStart	Sum of all daily average temperature degrees above zero from Jan 1 to the start of wood production
GDDWoodEnd	Sum of all daily average temperature degrees above zero from Jan 1 to the end of wood production
HON	Proportion of N in humus organic matter
HalfSat	Light level at which photosynthesis is half saturated
k	Canopy light attenuation constant (a property of the leaves)
Lat	Latitude of site
MaxNStore	Maximum N in plant pool
Nitr	Nitrification rate
NReten	Proportion of N input retained in soil
NRatio	Mobile N as a percentage of maximum plant N
SLW_{max}	Specific leaf weight at the top of the canopy (same as leaf mass per area)
SnowPack	Average depth of standing snow (0)
WHC	Water holding capacity: maximum amount of water that can be retained in soil
WLPctN	Minimum N concentration in woody litter

Parameters and definitions were all originally published in Aber et al. (1995, 1997).

then compared average C stocks and storage rate predictions for the four watersheds from 1958 to the present using an ANOVA (SAS-JMP software version 5.1, SAS Institute, Cary, NC, USA). We simulated harvest history effects on annual net ecosystem productivity (NEP), monthly net C balance (NetCBal), and monthly plant C (PlantC). We also compiled annual averages of modeled ecosystem gross primary productivity (GPP), ecosystem net primary productivity (NPP), autotrophic respiration, and heterotrophic respiration over the entire harvest treatment history (starting in 1958). To determine how the response of ecosystem C pools to harvest events varied over time with repeated harvests, we compared the average annual ecosystem C sequestration since 1958 to average annual ecosystem C sequestration in the short-term between the first and second harvest events. These long- and short-term estimates provide two different temporal perspectives of the effect of harvest on components in the ecosystem C budget.

3. Results

3.1. Validation of PnET-CN$_{sat}$ for four watersheds in the FEF

Modeled estimates of ANPP, wood NPP, and stream flow were generally verified by comparisons with measurements. Measured and modeled estimates of ANPP were significantly correlated for both watersheds ($p_{WS13} = 0.0235$; $p_{WS7} < 0.0001$) and measured wood NPP was significantly correlated with modeled wood NPP estimates for all four watersheds ($p_{WS13} = 0.0714$; $p_{WS7} < 0.0001$; $p_{WS2} = 0.0029$; $p_{WS5} = 0.0163$). The verification of modeled estimates of wood NPP against measurements in the clear-cut watershed (WS 7) indicated that the changes made to relative growth equations in the model were sufficient to reflect growth of a young regenerating forest. Modeled estimates of ANPP (Fig. 1) and wood NPP (Fig. 2) in the clear-cut watershed were 5% and 12% lower on average annually than estimates from the last 20 years of
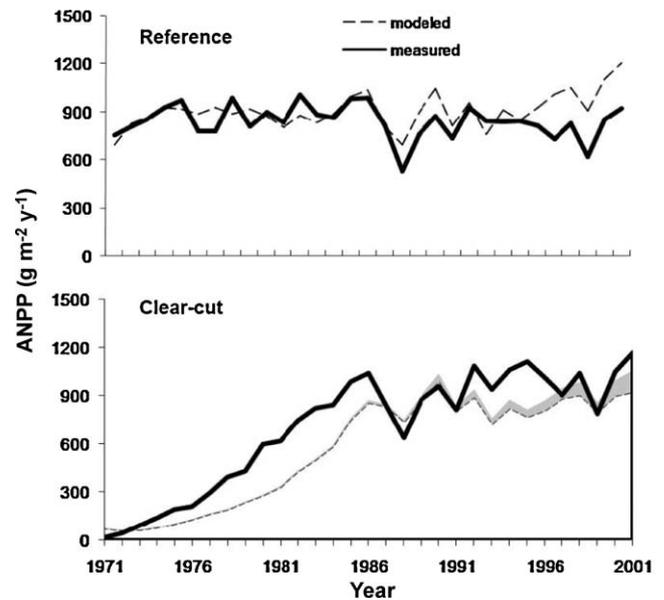

Fig. 1. Aboveground annual net primary productivity (ANPP) in a 100-year-old reference forest (WS 13) and a forest clear-cut in the 1960s (WS 7), measured as the summation of litterfall (measured over 5 years) and annual woody increments. An estimate of ANPP with higher nitrogen retention is shown in gray for the clear-cut watershed.

the dendrochronologic records (1971–2001). Model predictions of ANPP and wood NPP in the reference watershed were overestimated by 9% and 26% on average, respectively (Figs. 1 and 2) over a 20-year period. All model predictions for ANPP and wood NPP fell within a 90% confidence interval of measurements.

The difference between measured and modeled estimates of wood NPP in both the diameter-limit and single tree selection cut watersheds was greatest in the years prior to 1990 (Fig. 2). This difference was due to the trees that were removed during the diameter-limit and single tree selection cuts that were not included in the dendrochronology sampling. With the back-calculated estimates of wood NPP that included removed stem mass (gray region in Fig. 2), the measured estimates were improved, with 30% and 3% lower wood NPP than modeled wood NPP estimates in the diameter-limit cut and single tree selection cut watersheds, respectively.

Stream flow measurements in each of the four watersheds were highly correlated with model predictions ($p < 0.0001$ for all watersheds). Modeled estimates were very similar to measured estimates over time; the largest difference occurred prior to 1985 in the single tree selection watershed (Fig. 3) where modeled stream flow was 18% less on average than measurements. Modeled stream flow estimates were only 0.2% higher than measurements in the diameter-limit cut watershed and 2.5% lower than measurements in the clear-cut watershed. Stream flow predictions for the reference watershed were 14% higher on average than measurements in the reference watershed with a longer data record (WS 4) and 16% lower than measurements in the other reference watershed (WS 13).

Modeled estimates of woody litter N concentrations were not significantly different from on-site measurements in the reference, clear-cut, and single tree selection watersheds (Table 3, $p > 0.1$), but were significantly different than on-site measurements in the diameter-limit cut watershed (Table 3, $p = 0.0393$). Differences between modeled and measured foliar N and C also varied. Average foliar N estimates modeled over the last 5 years were similar to on-site measurements in both the single tree selection cut and clear-cut watersheds ($p > 0.1$) but model estimates of foliar N were significantly different from on-site estimates in the diameter-limit
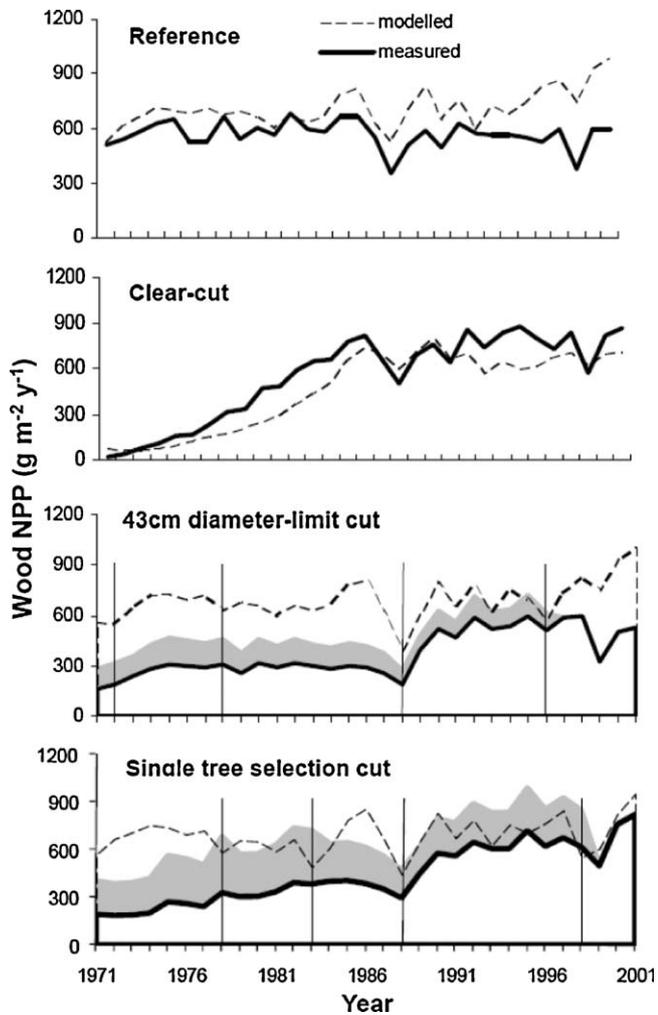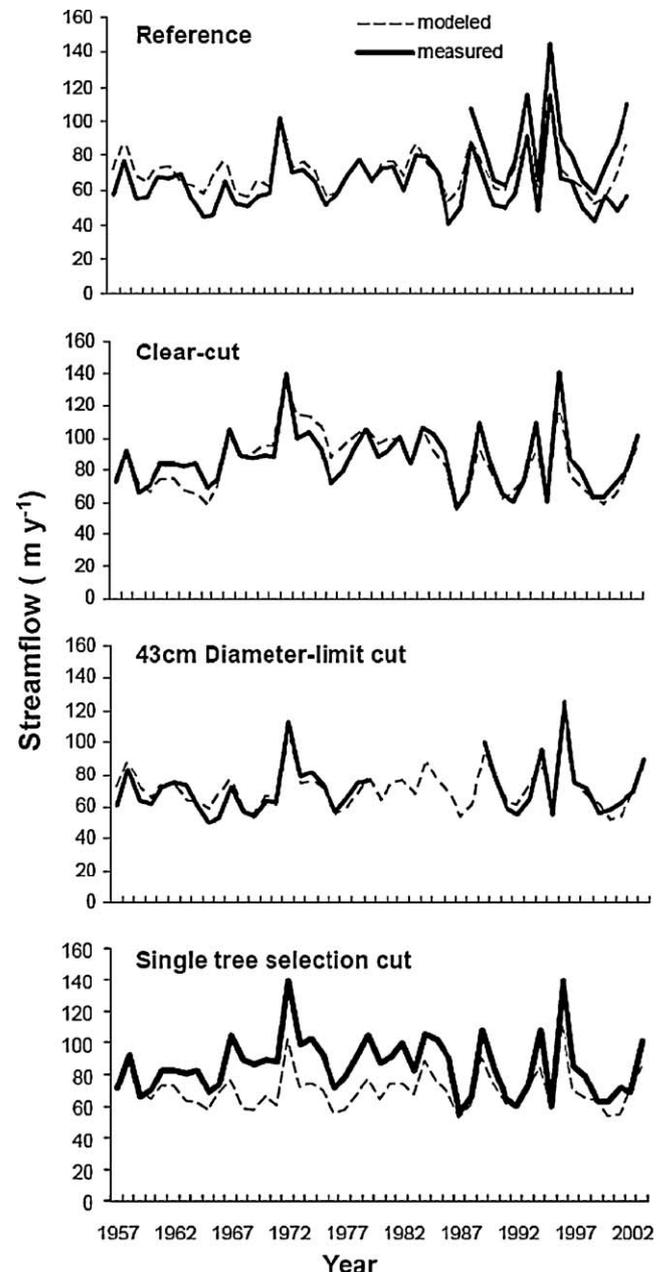
Fig. 2. Twenty-year record of annual wood net primary productivity (NPP) in each treatment watershed compared to modeled estimates for the same time period. All modeled estimates were generated with PnET-CN$_{sat}$ (Davis et al., 2008). Vertical lines in the bottom two panels mark the years that correspond to diameter-limit cutting events. The accuracy of woody increment estimations declines in earlier years when representative stems would have been removed from the dendrochronologic samples. An estimate of wood productivity that includes wood that was removed during harvests is shown in gray.
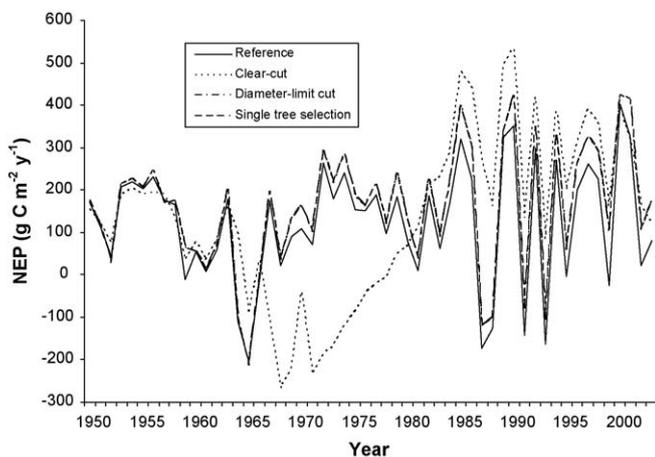

Fig. 3. Historical record of annual stream flow measured since 1957 in the four experimental watersheds (WS 7: clear-cut in 1960s; WS 13 and 4: reference watersheds; WS 2: 43 cm diameter-limit cut; WS 5: single tree selection cut) by the USDA Forest Service Northern Research Station compared with modeled estimates from PnET-CN$_{sat}$.

cut and reference watersheds ($p < 0.1$). Modeled predictions of foliar C during the last 5 years were significantly lower than measurements made in all of the watersheds ($p < 0.05$), but the difference was consistently only 6–7% and there was less than 1% difference in foliar C among watersheds.

3.2. Forest carbon balance estimates

We used model estimates of C balances, including soil and belowground C pools, in each watershed to simulate the effect of the four different harvest histories on NEP of Central Appalachian hardwood forests. Because of the high year to year variability, annual average NEP (g C m^{-2} year^{-1}) since 1958 was not significantly different among watersheds ($F = 0.73$, $p = 0.5381$). Averages by decade revealed a significant difference in NEP among harvest treatments in the 1970s when NEP of the clear-cut watershed (WS 7) was lower than that of the watersheds with diameter-limit cutting (WS 2), selective cutting (WS 5), and no harvest (WS 13) (interactive effect of harvest history and decade: $F = 2.84$, $p = 0.0006$). Total C sequestered (or ∫NEP) in the clear-cut watershed since 1958 was about 12% higher than the total C

sequestered in the reference watershed (Fig. 4). Both the diameter-limit and selectively harvested watersheds had 37% higher total C stored than that estimated for the reference. Average monthly C balance (g C m^{-2}) (NetCBal) estimates were similar to NEP results, with no significant difference in the annual average NetCBal among watersheds ($F = 0.93$, $p = 0.4275$). However, plant C (g C m^{-2}) estimates since 1958 were not similar among all watersheds ($F = 164.21$, $p < 0.0001$). According to a post hoc Tukey HSD test, average monthly plant C of the clear-cut watershed (WS 7) was significantly lower than the average plant C estimated in the other three watersheds ($\alpha = 0.05$). Plant C in the clear-cut watershed was especially low in the 1970s following the clear-cut, but remained somewhat lower in the most recent decade as well (Fig. 5). Average plant C since 1958 was 33% lower in the clear-cut watershed than

Table 3

Modeled estimates (predicted) versus on-site measurements (observed) of nitrogen (N) and carbon (C) concentrations (% of biomass) in the four experimental watersheds at the Fernow Experimental Forest.
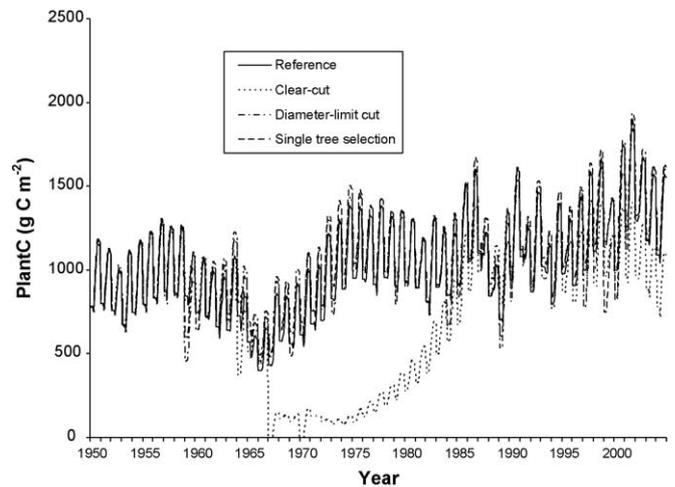
	Predicted	Observed	p
Foliar N			
Reference	2.99	2.51	0.0328
Clear-cut	2.51	2.61	0.2551
Diameter-limit cut	3.03	2.36	<0.0001
Single tree selection cut	3.08	2.88	0.3952
Foliar C			
Reference	45.07	48.21	<0.0001
Clear-cut	45.14	48.73	<0.0001
Diameter-limit cut	45.14	48.16	<0.0001
Single tree selection cut	45.13	48.59	<0.0001
Wood litter N			
Reference	1.24	1.40	0.0974
Clear-cut	1.27	1.38	0.4642
Diameter-limit cut	1.29	1.03	0.0393
Single tree selection cut	1.29	1.13	0.1986

Fig. 5. Modeled estimates (PnET-CN$_{sat}$) of monthly plant C (PlantC) since 1950 in the four experimental watersheds (WS 7: clear-cut in 1960s; WS 13: reference; WS 2: 43 cm diameter-limit cut; WS 5: single tree selection cut).

Fig. 4. Modeled estimates (PnET-CN$_{sat}$) of annual net ecosystem productivity (NEP) since 1950 in the four experimental watersheds (WS 7: clear-cut in 1960s; WS 13: reference; WS 2: 43 cm diameter-limit cut; WS 5: single tree selection cut).

plant C in the reference watershed, while modeled plant C in both the diameter-limit cut and single tree selection watersheds was only 1% greater than plant C in the reference watershed.

The long-term C balances of the four watersheds were similar except in the case of the clear-cut watershed (Table 4). Gross primary productivity (GPP) of the clear-cut watershed was about 35% lower than GPP of the other three watersheds (ANOVA: $F = 19.84$, $p < 0.0001$; Tukey HSD: $\alpha = 0.05$, $Q = 2.5932$). Before the

clear-cut event (before 1963), GPP in the clear-cut watershed was only about 17% lower than the long-term average in the other watersheds, so clear-cutting appears to correspond to a 22% decline in GPP (after 1969). The clear-cut harvest induced a decline in both NPP and respiration, but declines in respiration were much greater so that the average postharvest NEP of the clear-cut watershed was 138% greater than average NEP preharvest and 51% greater than the long-term average NEP of the reference watershed (Table 4).

The diameter-limit cut and selective cut watersheds both had stimulated productivity over the long-term, including increases in GPP, NPP, and NEP. However, short-term productivity responses to harvest (in the years between the first and second harvest) were negative so that NEP of the single tree selection and diameter-limit cut watersheds was 70% and 45% lower than the control watershed NEP, respectively (Table 4). Over time, the recovery periods following each harvest offset the short-term reduction in C sequestration.

4. Discussion

Harvest events had a significant effect on short-term forest C storage rates, but the average annual rate of ecosystem C sequestration (NEP) over 55 years was similar in harvested and un-harvested forests (Fig. 4). NPP declined over the short-term following harvest events, but R_a and R_h also both declined (Table 4) resulting in a net C sink in the ecosystem following harvests. Respiration decreased more dramatically after clear-cutting

Table 4

Carbon balances over the long-term (since 1958) and short-term (time between harvest intervals) (g C m^{-2} year^{-1}) in four watersheds subject to different harvest histories.

WS	Reference	Clear-cut			43 cm diameter-limit cut		Single tree selection cut	
	Long-term	Long-term	Preharvest	Postharvest	Long-term	Short-term	Long-term	Short-term
GPP	733 ± 177	478 ± 270	619 ± 33	484 ± 285	745 ± 172	609 ± 130	754 ± 177	589 ± 151
NPP	462 ± 163	313 ± 183	369 ± 31	322 ± 195	483 ± 160	388 ± 125	491 ± 165	363 ± 143
ANPP	377 ± 72	241 ± 147	342 ± 24	246 ± 153	371 ± 74	292 ± 45	369 ± 74	292 ± 46
CUE	0.61 ± 0.10	0.64 ± 0.15	0.60 ± 0.03	0.66 ± 0.16	0.63 ± 0.10	0.62 ± 0.11	0.63 ± 0.10	0.59 ± 0.13
R_a	271 ± 33	165 ± 100	249 ± 18	161 ± 104	262 ± 35	221 ± 20	263 ± 35	226 ± 27
R_h	347 ± 29	185 ± 72	296 ± 12	149 ± 42	326 ± 24	326 ± 34	334 ± 21	332 ± 28
NEP	115 ± 150	128 ± 208	73 ± 40	174 ± 211	157 ± 152	63 ± 114	157 ± 157	32 ± 132

Only long-term values are shown for the reference watershed (WS 13). Pre- and postharvest time periods were included for short-term estimates of carbon balances in the clear-cut watershed (WS 7). Short-term estimates for the diameter-limit cut and single tree selection watersheds (WS 5 and WS 2) represent the years between the first and second harvest. Term are defined as follows: GPP ≡ gross primary productivity; NPP ≡ net primary productivity; ANPP ≡ aboveground NPP only; CUE ≡ carbon use efficiency; R_a ≡ autotrophic respiration; R_h ≡ heterotrophic respiration; NEP ≡ net ecosystem productivity.

relative to the other harvest treatments. Despite the eventual stimulation of NEP following the clear-cut, there was a net decline in the plant C component because all aboveground biomass was removed. Without recovery and maintenance of plant C, repeated clear-cutting, even 45 years later, would lead to a decline in the future growth potential. Intense harvests, like clear-cuts, have a greater effect on ecosystem C balances than less intense, but more frequent, harvests like diameter-limit cuts and single tree selection. There was no sustained decline in plant C following diameter-limit and single tree selection cuts (Fig. 5), suggesting that these lower intensity harvest techniques may be a more sustainable way to cut timber and minimally impact C sequestration in managed forests.

Carbon sequestration changes with frequent harvests were striking in the case of diameter-limit cut and selectively cut forests because repetitive periods of released growth in the understory after harvests resulted in a 37% greater total C storage after 55 years relative to the reference watershed. This increase was explained by the increased available light through the canopy after harvest. Despite this increase in total C over the long-, short-term NEP rates after the first harvest in these treatments were 80% (single tree selection) and 60% (diameter-limit cut) lower than long-term average NEP with repeated harvests. Thus, the frequency at which these lower intensity harvest treatments were applied was an important determinant of C storage. Schuler (2004) also found that the interval of harvest was important for sustaining annual woody increment growth, but changes in wood production were partially mediated by changes in species composition. In another recent study, we found that the interaction of species and N availability has important implications for the sustainability of forest C stores in mature West Virginia forests (Davis et al., 2009). Here, we estimated C storage at the ecosystem scale, but it should be noted that biased timber species selections would influence the effect of harvests reported here.

The architectural complexity of a forest community enhances the variation in plant responses to disturbance and climate over time. The effect of wood harvest and forest regeneration on C accumulation has long been debated due to uncertainty about C budget changes with forest age and disturbance (Dixon et al., 1994; Houghton, 2003b). Here, we synthesized the process-level responses to harvest over a long time sequence that was atypical of physiological ecosystem models; thus the prediction error in some cases was higher than some published model predictions that are only validated against a single year or a few years. There was increasing error with time, but PnET-CN$_{sat}$ predicted wood productivity very well in recent years. While litter N concentration estimates were also verified against measurements, live foliar N concentration predictions were more inconsistent; this is probably indicative of the more variable light environment introduced by canopy gaps after harvest events. Following harvest events, the chronological changes in light regimes, nutrient dynamics, and metabolism affect C pools and can have long-lasting effects on the architecture and physiology of a forest ecosystem (Goodale and Aber, 2001; Foster et al., 2003; Yanai et al., 2003; Latty et al., 2004). Latty et al. (2004) described the lasting effects that a period of high light can have on canopy physiology; foliar N could be stimulated for many years after high light conditions were present. PnET-CN$_{sat}$ includes mathematical simulations of canopy architecture and light attenuation (Aber and Federer, 1992) that are more sophisticated than many other ecosystem process models, but some of the more subtle long-lasting responses to light were likely overlooked.

Changes in climatic conditions over time can induce temporal differences in ecosystem growth responses to harvest. For example, growth stimulation by atmospheric CO_2 may be more pronounced for a young aggrading forest (DeLucia et al., 1999; Norby et al., 2002) like the clear-cut watershed in recent years than

it was for the reference watershed at an earlier age (when atmospheric CO_2 was much lower). This climate change effect was included in the PnET-CN$_{sat}$ model estimates because we included a routine for ramping CO_2 over time (Aber et al., 1995). Perhaps more important for C storage differences was the timing of drought events relative to harvest events as both influenced C sequestration rates. In some years, C accumulation in the reference watershed declined more in response to drought than the decline in response to harvest events in the other watersheds. For example, both measured and modeled productivity noticeably declined in all watersheds following the droughts in 1988 and 1999; the average Palmer Drought Severity Index (PDSI: Palmer, 1965; Dai et al., 2004) for these years was −2.41 and −2.71, respectively. The most severe drought period recorded in this region over the last century was in 1966 (PDSI = −3.85), which coincides exactly with the clear-cutting event in WS 7. Because most of the plant biomass was removed with the clear-cut (a C loss not accounted for in NEP), there was a lower respiration cost due to drought stress in this watershed relative to the other watersheds that had greater plant water demands. Productivity responses to the single intense harvest (clear-cutting) would be much greater relative to the other watersheds if precipitation patterns were more moderate during that time period.

Soil C changes that were simulated with PnET-CN$_{sat}$ played an important role in the total ecosystem C budgets. Empirical evidence indicates that this role varies with time and land use change (Post and Kwon, 2000; Guo and Gifford, 2002; Rillig et al., 2003; Yanai et al., 2003; Beedlow et al., 2004). The high NEP predicted in the clear-cut watershed after 1980 is largely explained by the soil C budget because the plant C pool during this period was not higher than that of the other watersheds, but respiration rates were lower and more C was retained overall in the ecosystem. This means that accumulation of C in the forest floor was greater in the early successional stage, a trend that is consistent with observations from other studies (Post and Kwon, 2000; Guo and Gifford, 2002; Yanai et al., 2003). Not all studies agree, however, because Seely et al. (2002) found that soil C declined up to 20% in boreal spruce forests with frequent harvest rotations and still other studies have reported that forest harvest has no significant effect on the overall soil C budget (Johnson and Curtis, 2001). Some soil erosion can occur following a major harvest disturbance, but residues of biomass left behind after harvests contribute to soil C sequestration. Troendle et al. (1974) found that soil losses immediately following the clear-cut in WS 7 were insignificant. Despite no effect on total soil C, temporary growth suppression with herbicides did affect the new organic matter additions to the soil immediately after harvest (Troendle et al., 1974), and thus the overall ecosystem C sequestration changes estimated in this study could be lower than those resulting after typical clear-cut events. In any case, the clear-cut harvest resulted in greater loss of organic matter (even after herbicide treatments ended) that would otherwise have been used as nutrients in future growing seasons. Thus, the plant C following the clear-cut treatment remained lower than the amount estimated in the other management treatments and may indicate a reduction of site quality.

The results of this study must be considered in combination with results from other studies that quantify the residence time of C in harvested wood (e.g. Glover et al., 2002; Perez-Garcia et al., 2005). The model results presented here do not take this carbon into consideration. If the wood removed from the watersheds was converted to long-standing wood products like furniture or structural materials, then the wood removed would be an additive contribution to carbon storage (C sink). On the other hand, wood that is burned or converted to short-lived products represents a negative contribution to the carbon budget (C source). If forested ecosystems are to be managed with carbon sequestration in mind,

then wood product market fluctuations must be considered in addition to ecosystem responses to harvest.

5. Conclusion

Carefully managed harvests affect short-term forest C budgets, but do not significantly impact average annual C sequestration rates over the long-term ($\geq$55 years). Total C sequestered over a 55-year period was stimulated ~37% by both diameter-limit cutting and selective cutting relative to the reference watershed. There was a stimulation of C storage following clear-cutting that offset C losses due to harvest, but repeated clear-cuts would not be sustainable because there was also a significant decline in plant C.

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