Multimodel simulations of forest harvesting effects on long-term productivity and CN cycling in aspen forests

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Abstract. The effects of forest management on soil carbon (C) and nitrogen (N) dynamics vary by harvest type and species. We simulated long-term effects of bole-only harvesting of aspen (*Populus tremuloides*) on stand productivity and interaction of CN cycles with a multiple model approach. Five models, Biome-BGC, CENTURY, FORECAST, LANDIS-II with Century-based soil dynamics, and PnET-CN, were run for 350 yr with seven harvesting events on nutrient-poor, sandy soils representing northwestern Wisconsin, United States. Twenty CN state and flux variables were summarized from the models' outputs and statistically analyzed using ordination and variance analysis methods. The multiple models' averages suggest that bole-only harvest would not significantly affect long-term site productivity of aspen, though declines in soil organic matter and soil N were significant. Along with direct N removal by harvesting, extensive leaching after harvesting before canopy closure was another major cause of N depletion. These five models were notably different in output values of the 20 variables examined, although there were some similarities for certain variables. PnET-CN produced unique results for every variable, and CENTURY showed fewer outliers and similar temporal patterns to the mean of all models. In general, we demonstrated that when there are no site-specific data for fine-scale calibration and evaluation of a single model, the multiple model approach may be a more robust approach for long-term simulations. In addition, multimodeling may also improve the calibration and evaluation of an individual model.

Key words: aspen forest ecosystem; biogeochemical cycles; bole-only harvest; multiple model simulation; nitrogen depletion; soil carbon and nitrogen dynamics; Wisconsin, USA.

Introduction

Forest productivity is determined by potential growth rate, climate, site quality, and management practices (Dyck and Cole 1994). Forest management may alter long-term forest productivity through changes in available resources (e.g., soil N, available water) and stand composition (Johnson 1994, Stone 2002, Nave et al. 2010). These changes often differ with harvesting practices (e.g., whole tree vs. conventional bole-only), timing (e.g., month), type of equipment used for harvesting, and period and number of harvest rotations. As a result, differing amounts and types of biomass residues with varying chemistry (e.g., lignin content) are left on site (Johnson and Curtis 2001), and many soil physical properties, such as bulk density and cation exchange capacity, are affected to various degrees (Jurgensen et al. 1997). Consequently, the harvest regime will influence soil C and N (CN) dynamics and

the potential availability of nutrients for subsequent forest growth (Olsson et al. 1996, Johnson et al. 2002, Walmsley et al. 2009, Nave et al. 2010, Jones et al. 2011). Nutrient-poor sites that are initially low in soil organic matter (SOM) have been found to be especially vulnerable to the removal of organic matter resulting in lower site productivity (Morrison and Foster 1979, Morrison et al. 1993).

Effects of harvesting on site productivity and soil CN dynamics have been studied for over 100 years (Johnson 1994, Tiarks et al. 1997). A recent review by Nave et al. (2010) showed that harvesting reduced soil C by an average of 8% ± 3% (mean ± SD; 95% CI) and forest floor C by a remarkably consistent 30% ± 6% in temperate forests around the world. Variations among the impacts were due to species composition (hardwood vs. coniferous/mixed), soil taxonomic order, and time since harvest. Another review by Thiffault et al. (2011) revealed that negative impacts of biomass harvesting on soil N are more frequent in the forest floor than in the mineral soil. Harvesting had the greatest potential to influence tree survival and growth for at least 20 years in some stands. These reviews show that existing investi-

gations on harvesting effects are specific to certain ecosystem CN states and fluxes but lack a quantitative analysis of interactions between CN cycling following harvesting events, in particular, the long-term mechanism of N cycling and its feedback on C dynamics.

Time since harvest is an important variable when determining potential long-term effects of harvesting on forest productivity, since productivity responses to harvesting may exist beyond the duration of a single rotation, or an observed change in one rotation may not necessarily continue in perpetuity (Eisenbies 2006). Therefore, one-time measurements, lack of long-term trials, and inappropriate sampling frequency (e.g., annual or once over multiple years) may not be sufficient for making general conclusions regarding long-term harvesting effects on productivity (Eisenbies 2006). Chronosequences and retrospective methods have been used to overcome time limitations in studies of the long-term effects of harvesting, but there are shortcomings to this approach (Dyck and Cole 1994). Long-term field trials or experiments have been established to produce controlled, experimental results, but many of these experiments are too early in their establishment to provide long-term results.

Ecosystem modeling may be one of the most feasible ways of estimating the long-lived effects of harvest on forest CN cycles (Wei et al. 2003). Yet application of an individual model may be limited by data availability for calibration, especially when observations of long-term effects of harvesting on forest productivity and CN cycles are in short supply. Even if independent data are available, calibration and recalibration may not be able to reduce the difference between model outputs and the data (Zhang et al. 2008). It may be unwise to use results from only one ecosystem model while simulating effects of environmental changes on ecosystem dynamics (Parton 1996). Alternatively, a multiple model approach can reduce uncertainty where sufficient data for calibration and evaluation do not exist for every process and state. The mean value of the output from multiple models may have the best fit to empirical observations and provide an acceptable reference point for the evaluation of individual model performance (Hanson et al. 2004). For example, the International Panel on Climate Change (IPCC) has employed outputs of 18 models for assessment of climate change in the future (IPCC 2007), and Knutti et al. (2010) suggested that an average of the models' simulations of different emission scenarios compared better to observations than a single model. In addition, the average of multiple models supplies a practical opportunity to evaluate mechanism of CN interactions because no individual model is designed to simulate all CN cycles.

We used a multiple model approach to simulate the effects of bole-only harvesting on productivity, C, and N cycling in an aspen (*Populus tremuloides*) forest in the northern U.S. Lake States. Specifically, our project was designed to answer three questions: (1) what are the short- and long-term effects of harvesting on forest productivity on sandy, nutrient poor soil? (2) How does harvesting affect N dynamics and interactions between N and C? (3) How and why do the models agree and disagree in simulating CN cycles when no site-calibration is performed and parameters representing the same processes/states across the models share the same values? We used five models: CENTURY (Parton et al. 1987, 1988, Sanford et al. 1991); LANDIS-II (Scheller and Mladenoff 2004, Scheller et al. 2007) with a Century-derived soil dynamics extension (hereafter LANDIS-II-Century; Scheller et al. 2011); Biome-BGC (Running and Hunt 1993, Thornton 1998, White et al. 2000, Thornton et al. 2002); FORECAST (Kimmins et al. 1990, 1999, Seely et al. 2002); and PnET-CN (Aber and Federer 1992, Aber and Driscoll 1997, Aber et al. 1997). Our primary purpose is not model comparison per se, but to describe overall changes in productivity and nutrient cycling among a group of well used, but different, modeling approaches.

Methods

Study area

The aspen site was located in northwest Wisconsin, USA (between 90°35′ W and 92°58′ W, and 45°04′ N and 47°06′ N; Fig. 1). Surface elevation ranges from 232 to 390 m. The site has nutrient-poor, sandy soils on glacial outwash and is considered vulnerable to C depletion. We selected aspen for our simulation because it has the highest volume among forest types on these soils, is the most harvested, and has the most available published data for model parameters. Though precipitation is sufficient, low annual temperature (average 5°C) and a short growing season (98–145 d) limit plant growth (Wisconsin Department of Natural Resources 1999).

Modeling approach

Model descriptions and comparison.—Biome-BGC, CENTURY, FORECAST, LANDIS-II-Century, and PnET-CN have lineages of from less than a decade to 30 years, and most have evolved over time. These models have been widely used to simulate forest ecosystem growth and CN dynamics under various disturbances and management activities, as well as divergent climate change scenarios. Fundamentally, the models are different in that Biome-BGC, CENTURY, and PnET-CN are stand-level, process-based biogeochemical models, while FORECAST is a hybrid, empirically based stand growth model with partial process dynamics. LANDIS-II-Century is a spatially explicit, process-based model that is also a spatially dynamic landscape model, but here is used only in single-cell mode. We provide a brief introduction of each model, but a more detailed comparison of the processes in each model is provided in Appendix A.

Biome-BGC is an ecosystem process model that simulates water, C, and N cycles at a daily time step.
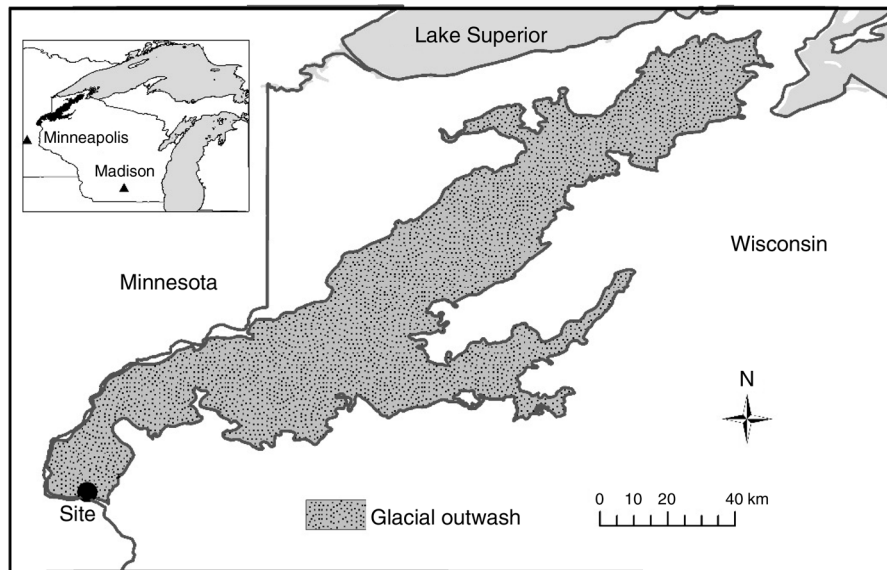
Fig. 1. The sandy Pine Barrens and simulation site in Wisconsin, USA.

The version used in this study (Bond-Lamberty et al. 2005, 2007) was updated from earlier versions (Running and Hunt 1993, Thornton 1998, White et al. 2000, Thornton et al. 2002) to allow simulation of multiple, competing vegetation types and for poorly drained sites. Biome-BGC incorporates minimal species-specific data, which allows it to be used for regional-scale, woody and herbaceous vegetation research. Dynamics are not spatial, but the model operates in cells over a gridded landscape or region. Daily weather conditions, leaf C:N, and specific leaf area index (SLA) are variables with substantial control over ecosystem processes, including canopy interception, transpiration, respiration, photosynthesis, C allocation, and litterfall (Running and Coughlan 1988, White et al. 2000).

CENTURY was initially developed to analyze SOM dynamics in grassland, agricultural lands, and savanna ecosystems in response to changes in management and climate (Parton et al. 1987, 1988). Sanford et al. (1991) developed a forest submodel for CENTURY to examine impacts of hurricanes on soil nutrient availability and pool sizes, as well as forest productivity. The model simulates the flow of C, N, phosphorus (P), and sulfur (S) through plant litter and the different inorganic and organic soil pools. We applied CENTURY version 4.5 (C. Keough and W. Parton, *unpublished program*). This version includes several recent improvements. For example, two parameters, maximum annual net primary production (NPP) and biomass, are no longer needed as user-supplied inputs.

PnET-CN (Aber and Driscoll 1997, Aber et al. 1997) is a simple, lumped parameter model simulating the CN cycles of temperate and boreal forest ecosystems at the stand level. It is a successor to PnET-II (Aber and Federer 1992) with additional litter and SOM compartments, state N variables to all compartments, and N dynamics including mineralization, nitrification, uptake, and leaching. The soil compartment has a simple structure, with a single soil layer that turns over at a moderate rate. The model assumes that maximum photosynthetic rate is a function of foliar N concentration. As compared to PnET-II, foliage nitrogen in PnET-CN varies annually, depending on availability, which consequently enables PnET-CN to simulate a dynamic maximum photosynthetic rate and the effects of N cycling on forest productivity.

FORECAST combines empirical and processed-based growth models and simulates production with historical raw field data, which are then modified by simulated light and nutrient availabilities (Kimmins et al. 1999). It uses historical yield data, stand density, and mortality rate combined with other data and algorithms to estimate annual NPP (Kimmins et al. 1999). The model does not account directly for the effect of moisture and temperature limitations on forest growth (Seely et al. 2002), but it estimates light (shade) effects on production of foliage and foliage N content; consequently, foliage N use efficiency is corrected for shade and is the major driving force for simulating potential growth of a given species in the ecosystem. As compared to other models described above, FORECAST provides extra options for users to supply N inputs from weathering and slope seepage, and enables simulating the internal N cycle from not only foliage but also other tree components, such as wood.

LANDIS-II (Scheller and Mladenoff 2005), a successor of LANDIS (Mladenoff et al. 1996, He and Mladenoff 1999, Mladenoff and He 1999), is a spatially explicit and stochastic forest landscape model that simulates broad scale spatial processes and interactions

of forest succession, seed dispersal, and disturbances (e.g., fire, wind, management activities) and climate change. LANDIS-II simulates these processes on a gridded landscape of cells. Cell size is flexible and chosen by the user. Trees or shrubs are represented as cohorts defined by species and age. Each cell can contain multiple species-age cohorts, and each cohort can be differentially affected by a disturbance. We used LANDIS-II v3 (Scheller et al. 2012) with the Century extension; it is a combination of the LANDIS-II Biomass Succession extension v2.1 and soil CN dynamics based on CENTURY v4.5 (Scheller et al. 2011). LANDIS-II-Century uses species-age cohorts with wood and leaf biomass as the basis for succession and differential disturbance mortality.

Model input and parameterization.—Climate inputs drive environmental variables in all models except FORECAST. In order to compare the harvesting-only effect on aspen long-term productivity, we utilized monthly mean climate data (1970–2000) simulated by parameter–elevation regressions on independent slopes model (PRISM; *available online*)[7] for CENTURY, PnET-CN, and LANDIS-II-Century. Biome-BGC runs on a daily time step and is very sensitive to climate input. Therefore, we used 24 yr (1980–2003) of daily climate data estimated from the mountain climate simulator (MT-CLIM; Thornton and Running 1999). We ran Biome-BGC 24 times with each year of the climate data and averaged the 24 sets of outputs as the final of the model simulation. Atmospheric N deposition was extracted from a data set of N deposition in the United States, from annual deposition data interpolated from wet deposition and dry, ambient air concentration monitoring networks in the United States (Holland et al. 2005). For our model initializations, N deposition was 0.509 g $N \cdot m^{-2} \cdot yr^{-1}$, the sum of the average of wet deposition collected during 1978–1994 (0.47 g $N \cdot m^{-2} \cdot yr^{-1}$) and of dry deposition during 1989–1994 (0.04 g $N \cdot m^{-2} \cdot yr^{-1}$). The wet deposition was identical to the mean value obtained from the closest National Atmospheric Deposition Program monitoring site with measurements from 1980–2010. Nonsymbiotic N fixation was set to a constant of 0.23 g $N \cdot m^{-2} \cdot yr^{-1}$, an average from two studies by Alban et al. (1991) and Son (2001).

Values for the models' parameters and site conditions are derived from multiple sources: peer-reviewed literature, the U.S. Forest Service Forest Inventory and Analysis (FIA) database (Forest Inventory and Analysis Program 2010), SSURGO (Soil Survey Geographic database, *available online*)[8] soil data, and a tree chemical database (Hessl et al. 2004). To parameterize the model we (1) located species-specific values for our target species, aspen, whenever possible, (2) selected published values from similar site conditions, (3) searched for

multiple sources when a parameter range was required, (4) replicated a parameter value across the five models, and (5) did not perform a site calibration because we lacked site-specific data for all parameters. Because Biome-BGC, CENTURY, PnET-CN, and LANDIS-II-Century have several parameters representing the same ecological process (e.g., carbon allocation), only parameters unique to individual models are listed in Appendices B–E.

The FORECAST model was previously calibrated with aspen data from Canada (Seely et al. 2002, Welham et al. 2007). In our simulations, we changed only the parameters for our site conditions and available aspen parameters listed for the other four models. Other parameters, such as site index and stand density by age, were derived from FIA data in 1983, 1996, and 2001–2008. We defined three site conditions in the model to simulate a range of conditions that exist on the sand plain. The maximum, minimum, and average of the values at all FIA plots within the sand plain were set to correspond to the good, moderate, and poor sites accordingly. In this paper, we present simulation results for the moderate site only.

Model initializations and simulations.—For initializing ecosystem models, it is common to run a model for hundreds or thousands of years to bring the model into equilibrium to ensure that there is a balance between input and output fluxes and that the system has equilibrated to the environmental and site factors (Thornton and Rosenbloom 2005). This is a typical approach of steady-state solutions and requires a threshold (e.g., <1 g/cm^2) to determine if a state variable reaches a steady state (McGuire et al. 1992). The steady state can be interpreted as the state at a certain time of an undisturbed ecosystem (Law et al. 2001). However, forests on our landscape have experienced at least some degree of disturbance from fire, wind, harvesting, and climate change (Radeloff et al. 1999, Grossmann and Mladenoff 2008). Therefore, a question arises whether the stable state at equilibrium can represent the forest and site conditions we intend to simulate. In addition, standard self-initialization towards a steady state may produce biased and inconsistent predictions resulting in systematically overestimated CN pools vs. observations (Pietsch and Hasenauer 2006). Besides the steady-state approach, another approach for initialization is to use observed values of plant, litter, and SOM pools as initial conditions (Running and Coughlan 1988). This approach is only applicable to sites where the necessary state variables have been measured (Thornton and Rosenbloom 2005), and therefore, not for large-scale applications where the information for every site is not commonly available.

Therefore, we took a combination approach of spin-up and setting initial values. We applied one particular variable, soil C, as the indicator of initial conditions of our ecosystem (Seely et al. 2010). The quantity of SOM established a baseline for the rate and amount of net N

TABLE 1.　Summarized C and N state and flux variables from the models' outputs for an aspen forest ecosystem on glacial outwash plains in Wisconsin, USA.

Variable	Abbreviation	Definition
Net primary production (g C·m^{-2}·yr^{-1})	NPP†	Annual net primary production
Live-wood biomass C, N (g CN m^{-2})	BiomC†, VegN†	C and N in living above- and belowground aspen compartments at year end, thus no foliage biomass included
Stem biomass (g C/m^2)	StemC†	C in stem pool in CENTURY and FORECAST, and 70% of the large wood component in Biome-BGC and LANDIS-II, and 80% of the woody component in PnET-CN
Soil organic matter/soil C, N (g CN m^{-2})	SoilC†, SoilN†	Soil C and N summarized from all soil C and N pools
Litter C, N (g C/N m^{-2})	LitC, LitN	C and N in two litter pools of foliage and fine roots
Coarse woody debris C, N (g CN m^{-2})	CwdC†, CwdN†	C and N in dead branch, stem, and coarse root
Net N mineralization (g N·m^{-2}·yr^{-1})	Nnetmin†	Annual N net released from the litter, wood detritus, and soil pools
N immobilization (g N·m^{-2}·yr^{-1})	Nimmob	Annual N immobilized to litter, wood detritus, and soil pools
N uptake (g N·m^{-2}·yr^{-1})	Nuptake	Annual N uptake by aspen forests
N leaching (g N·m^{-2}·yr^{-1})	Nleach†	Annual N leaching losses through water drainage
N volatilization (g N·m^{-2}·yr^{-1})	Nvol	Annual N losses through volatilization
N fixation (g N·m^{-2}·yr^{-1})	Nfix	Annual N fixation through nonsymbiotic process
Photosynthesis (g C·m^{-2}·yr^{-1})		C fixed by photosynthesis
Plant respiration (g C·m^{-2}·yr^{-1})		C losses through respiration, including maintenance and growth respiration
Heterotrophic respiration (g C·m^{-2}·yr^{-1})		C losses through respiration of microbes in litter, wood detritus, and soil organic matter pools
N use efficiency (g CN·m^{-2}·yr^{-1})	NUE†	A division of NPP by N uptake; the ratio C:N, each measured as g·m^{-2}·yr^{-1}
Harvested C, N (g CN/m^2)		C and N removed through harvesting

† Variables used in PCA ordination analysis.

release and N available to forest growth in the subsequent simulations. In order to have an initial SOM of 7400 g/m^2 (derived from SSURGO) over the entire vertical profile (1.5 m), we ran the models for several hundred years until equilibrium for Biome-BGC and PnET-CN and input initial conditions for LANDIS-II-Century. In the case of PnET-CN, we were unable to attain our desired initial values due to two main reasons: (1) we were not performing site calibrations as part of our premise in using a multimodel, averaging approach, due to a lack of site-specific data, and (2) the disturbance parameters were unable to be changed within a scenario (i.e., after a spin-up period to reach desired levels of SOM). We also used the fire disturbance routines available for CENTURY and FORECAST to accumulate SOM to the initial amount.

After initialization, we ran the models for 350 yr with a 50-yr forest harvest rotation period, based on the typical age at economic maturity in this region (Alban et al. 1991). For the bole-only harvest scenario, we harvested stem CN pools in CENTURY and FORE-CAST. The other three models lacked an explicit stem component, so instead the bole component is harvested using a biomass fraction derived from FIA, 70% of the large wood component in Biome-BGC and LANDIS-II-Century, and 80% of the woody component in PnET-CN.

Model outputs and analysis.—Twenty CN state and flux variables, representing the main CN dynamics and processes in the forest ecosystem, were summarized from the models' output (Table 1). Though ideally we would be able to compare output of every variable from each

model, the unique conceptual design and processes included in each model restricted our options. For each variable, we calculated the average of the models' outputs, which was employed to examine the long-term effects of harvesting on forest productivity and CN states and fluxes. In order to compare how much C was removed over the six rotations, the harvested biomass CN was also computed by the models. Effects of harvesting on N dynamics were determined by evaluating whole amounts of N by states and fluxes during an entire or half rotation period.

Model performance was compared by principal components analysis (PCA) ordination in PC-ORD v.6 and ANOVA in SAS v.9.2 (Peck 2010, SAS Institute 2010). Ordination is the method most often used in ecology to seek and describe patterns among multivariate data (McCune et al. 2002). We applied PCA because the data have approximately linear relationships among variables. In the PCA data matrix, rows represented 30 harvest rotations of the five models (six rotations per model). Columns were mean values of the 11 variables (footnoted abbreviations in Table 1). Each column was relativized to make the units of the attributes comparable. Dissimilarity of the matrix was calculated by Euclidean distance. Joint plots were generated by loading the data matrix in both main and secondary matrices. From the plots, the spatial locations of each rotation of every model not only revealed how different the five models were in multivariate variable space but also how the model's positions changed through time (rotations).

TABLE 2. Summary of the multimodel mean values across six bole-only harvest rotations in an aspen forest ecosystem.

Variable	Rotation					
	1	2	3	4	5	6
NPP (g C·m^{-2}·yr^{-1})	362.46	350.77	341.65	337.01	333.81	331.67
BiomC (g/m^2)	3903.46	3879.63	3779.47	3777.75	3695	3751.72
StemC (g/m^2)	2070.36	2054.06	2003.16	2000.35	1958.49	1983.83
SoilC (g/m^2)	6025.36[a]	5918.11[b]	5814.29[c]	5745.95[d]	5700.57[e]	5664.9[f]
LitC (g/m^2)	206.91[a]	188[b]	188.45[b]	187.24[b]	186.54[b]	186.46[b]
CwdC (g/m^2)	2463.39[a]	2034.09[ab]	1922.57[b]	1872.21[b]	1840.98[b]	1815.57[b]
VegN (g/m^2)	19.22	19.38	18.94	18.84	18.48	18.66
SoilN (g/m^2)	327.1[a]	320.38[b]	316.03[c]	313.39[d]	311.96[e]	310.92[e]
LitN (g/m^2)	2.6	2.4	2.43	2.42	2.41	2.41
CwdN (g/m^{22})	10.67	9.29	9	8.84	8.77	8.72
Nnetmin (g·m^{-2}·yr^{-1})	4.19[a]	3.89[b]	3.71[c]	3.6[d]	3.53[de]	3.48[e]
Nimmob (g·m^{-2}·yr^{-1})	7.96[a]	7.17[ab]	6.98[b]	6.86[b]	6.71[b]	6.66[b]
Nuptake (g·m^{-2}·yr^{-1})	5.16	4.99	4.82	4.72	4.65	4.64
Nleach (g·m^{-2}·yr^{-1})	0.28	0.3	0.25	0.23	0.22	0.21
Nvol (g·m^{-2}·yr^{-1})	0.35[a]	0.3[b]	0.29[b]	0.28[b]	0.28[b]	0.27[b]
Nfix (g·m^{-2}·yr^{-1})	0.28	0.27	0.27	0.27	0.27	0.27
Plant respiration (g C·m^{-2}·yr^{-1})	214.81	220.96	212.03	207.75	204.45	201.57
Photosynthesis (g C·m^{-2}·yr^{-1})	571.23	581.71	557.11	544.84	535.64	527.9
Heterotrophic respiration (g C·m^{-2}·yr^{-1})	311.3[a]	284.14[b]	273.55[bc]	266.85[bc]	262.87[bc]	255.33[c]
NUE (g CN·m^{-2}·yr^{-1})	74.56	75.95	75.83	76.1	76.67	76.35

Notes: Within a row, different superscript letters a–e indicate means that differ significantly among the rotations ($P < 0.05$ for Tukey pairwise comparison test). Absence of letters indicates no significant differences between rotations. Abbreviations are defined in Table 1.

ANOVA and Tukey post hoc tests were also applied to the variables to determine the models' differences from each other, from multimodel averages, and to distinguish the long-term effects of the harvesting scenario on aspen productivity. Significant differences were evaluated with $\acute{\alpha} = 0.05$.

RESULTS

Effects of harvesting on CN pools and fluxes

Effects of harvesting on productivity and CN dynamics were assessed by calculating the mean values of output variables from the five models. Aspen ecosystem productivity, represented by mean NPP, live wood biomass C (BiomC), and stem biomass C (StemC), was not significantly different among the six harvest rotations (Table 2, Fig. 2a, b). NPP gradually decreased between rotations, with an overall 9% decline between the first and last rotation (Fig. 2a). Within a rotation, mean annual NPP increased rapidly in the first couple of years, reached a maximum around year 20, and then declined gradually until the next harvest. Total mean annual BiomC and StemC (Appendix F) showed similar patterns, increasing almost linearly within a rotation. BiomC did not show any significant trends but fluctuated over the rotations (Fig. 2b).

Overall soil organic matter C (SoilC) and N (SoilN) showed significant differences among the rotations (Table 2, Figs. 2c and 3b). SoilC decreased by 67%, from 6025 ± 1327 g/m^2 (mean ± SD) at the end year of the first rotation to 5664 ± 1767 g/m^2 in the last year of the simulation. During the same time period, SoilN decreased by 5%, from 327 ± 209 g/m^2 to 311 ± 194 g/m^2. Within each rotation, mean annual SoilC and SoilN

accumulated to a peak around the third year as litter and coarse woody debris (CWD) from harvesting was incorporated into the soil and then declined quickly due to decomposition and less inputs from the live components until CN stabilized at about year 15.

Across the rotations, litter C (LitC) was higher in the first rotation (207 g·m^{-2}·rotation^{-1}) than the other rotations (186–188 g·m^{-2}·rotation^{-1}), which indicated an effect of initialization on LitC (Table 2, Fig. 2c, d). As with C, litter N (LitN) showed a narrow range from 2.4 to 2.6 g·m^{-2}·rotation^{-1} across the rotations (Fig. 3c). The CN variation in litter within a rotation reflected a dynamic interaction among litter inputs from harvesting, annual litterfall, fine root turnover, and decomposition processes.

Overall coarse woody debris C (CwdC) showed a significant difference with a range of 2463–1816 g·m^{-2}·rotation^{-1} between the first and the last four rotations, which was mainly caused by an elevated CWD value in PnET-CN and Biome-BGC (Table 2, Fig. 2e). However, coarse woody debris N (CwdN) was similar among the rotations with a range of 11–9 g·m^{-2}·rotation^{-1} (Table 2, Fig. 3d). The CwdC and CwdN patterns over the rotations were similar to each other with a rapid increase after harvest, followed by a decline to about year 28, and another increase until harvest. This pattern differed from the temporal pattern of LitC, indicating divergent dynamics of decomposition and input between litter and wood detritus.

Among the N fluxes, even though N mineralization (Nnetmin) in some rotations was significantly different from other rotations, the mean values over the rotations changed only slightly from 3.5 to 4.2 g·m^{-2}·rotation^{-1}. Of the 4.3 g·m^{-2}·rotation^{-1} available N, (sum of Nnetmin,
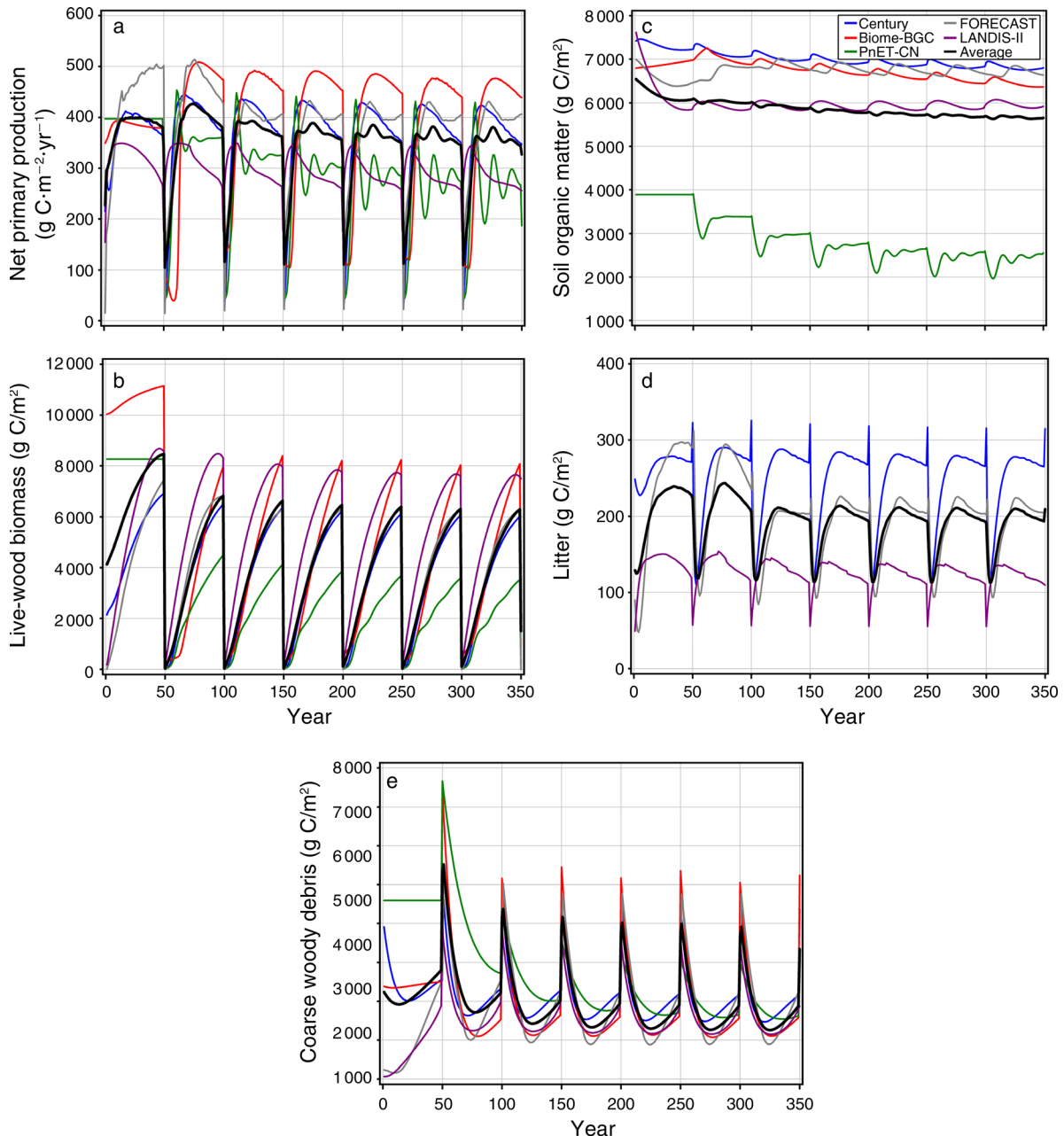
Fig. 2. Carbon pools and fluxes of an aspen forest ecosystem on glacial outwash plains in Wisconsin managed by bole-only harvesting every 50 yr. Colored lines represent the results of simulations of the five models Biome-BGC, CENTURY, FORECAST, LANDIS-II-Century, and PnET-CN. The black line is the average of all models.

3.5 g·m^{-2}·rotation^{-1}; deposition, 0.5 g·m^{-2}·rotation^{-1}; and fixation, 0.3 g·m^{-2}·rotation^{-1}), 4.6 g·m^{-2}·rotation^{-1} N were taken up by aspen, 0.24 g·m^{-2}·rotation^{-1} were leached, and 0.3 g·m^{-2}·rotation^{-1} were volatilized. Temporally, Nnetmin within a rotation was high initially, declined quickly to a minimum in about the second year, increased gradually for 20 yr, and then declined slightly (Fig. 3e). Nitrogen leaching peaked in the first two years, then gradually decreased to about 0 at year 30 (Fig. 3f).

The models' average showed that the C and N removed by harvesting were high at the first harvesting rotation and gradually decreased through subsequent harvest events (Appendix G). Harvested C and N at the first cut were 24% and 17% higher than the average harvested C (3518 g/m^2) and N (15 g/m^2) across the remaining rotations. In subsequent harvests, harvested C and N were only −3% to 5% for C, and −3% to 3% for N. These differences may imply an effect of initial conditions on the subsequent CN cycles, in particular, for Biome-
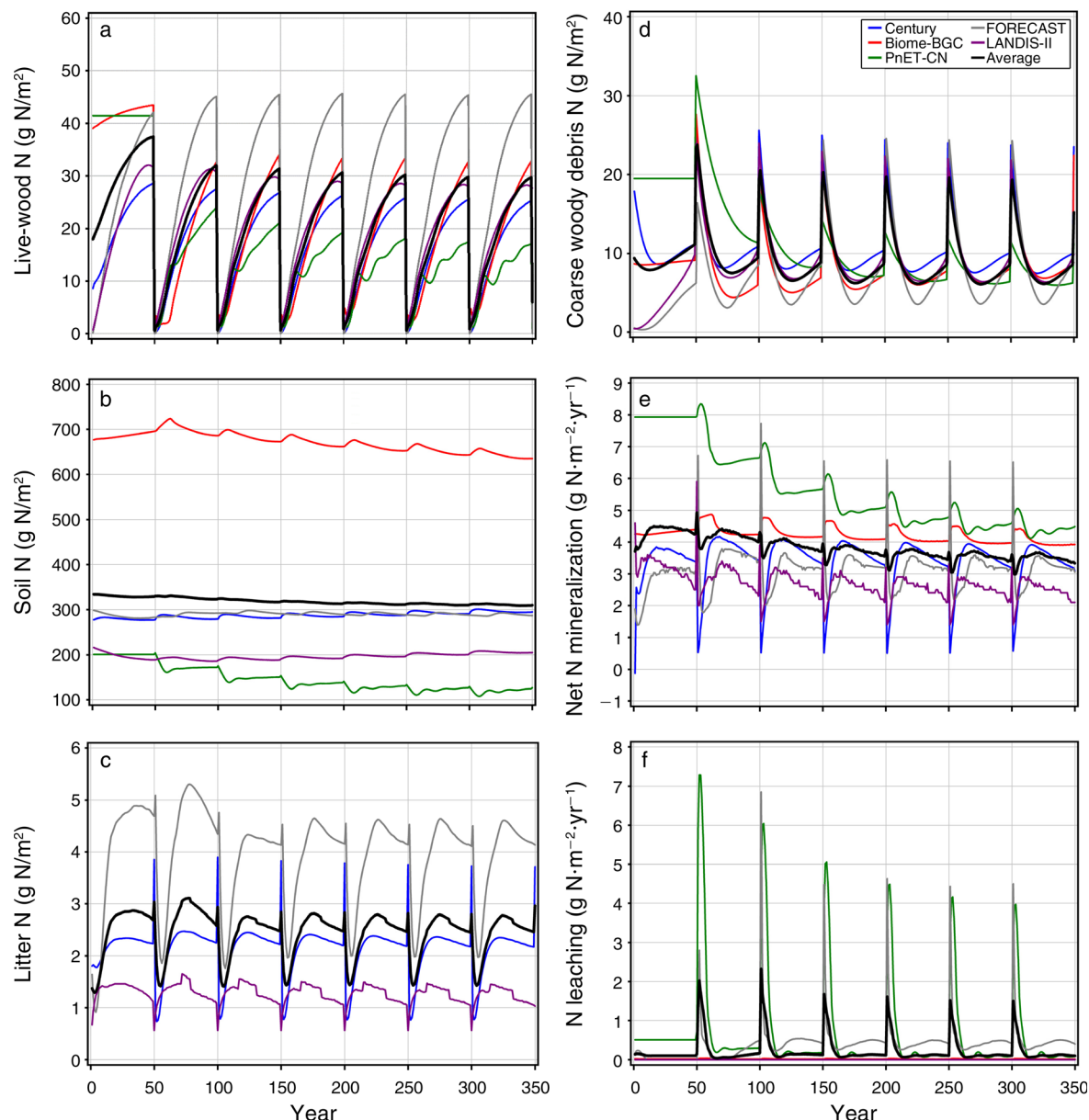
FIG. 3. Nitrogen pools and fluxes and CN interaction of an aspen forest ecosystem on glacial outwash plains in Wisconsin disturbed by bole-only harvesting every 50 yr. Colored lines represent the results of simulations of the five models Biome-BGC, CENTURY, FORECAST, LANDIS-II-Century, and PnET-CN. The black line is the average of all models.

BGC and PnET-CN. Temporal patterns of the remaining CN states and fluxes are described in Appendix F.

Effects of harvesting on nitrogen budget

In our simulations, N inputs to the forest ecosystems occurred through N deposition and nonsymbiotic N fixations; N exports included N leaching, volatilization, and harvesting (Fig. 4). Across the initial 50 yr (labeled as 0 in Fig. 4) and the six harvest rotations, N input from atmospheric wet and dry deposition and N nonsymbiotic fixation (deposition + fixation; Fig. 4a) were a constant of 39 g/m^2 within each rotation. Together with N minerali-

zation from litter, CWD, and soil, total available mineral N in soil (Fig. 4a) was the highest (250 g·m^{-2}·rotation^{-1}) before the first harvest and then decreased gradually to 210 g·m^{-2}·rotation^{-1} in the last rotation. N depletion through harvest and volatilization varied slightly across the rotations, with a range of 14–18 g·m^{-2}·rotation^{-1}, and of 13–17 g·m^{-2}·rotation^{-1}, respectively. In contrast, N leaching showed a dramatic increase from 5.4 g·m^{-2}·rotation^{-1} in the initial rotation to the highest (14.7 g·m^{-2}·rotation^{-1}) in the second rotation, implying significant N depletion through leaching due to harvesting.
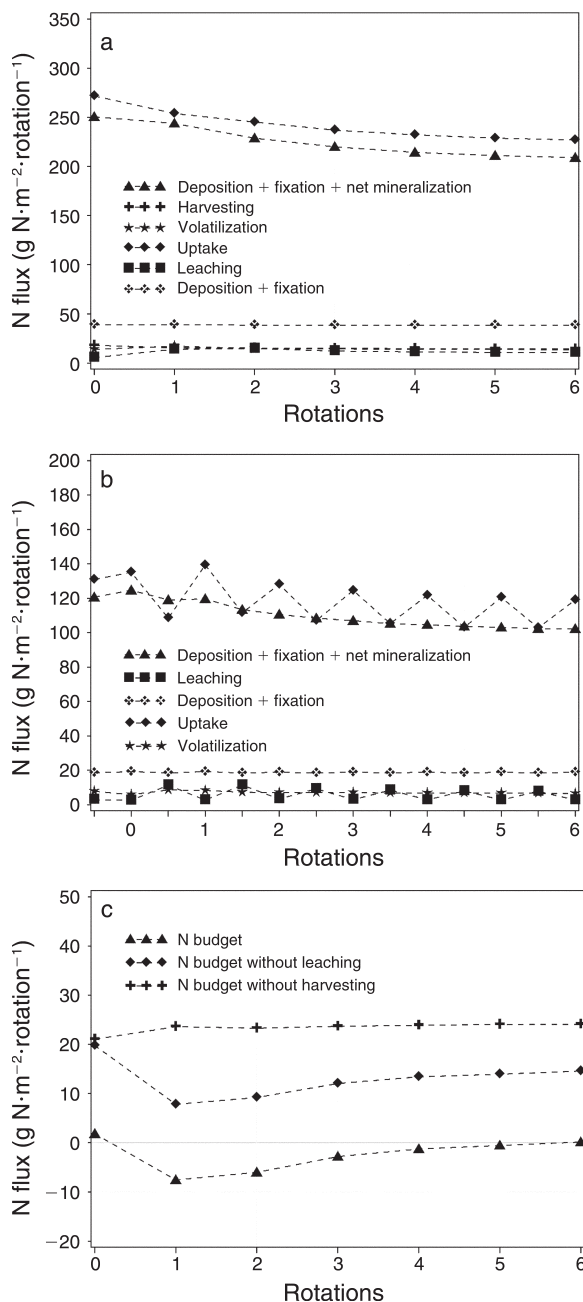
FIG. 4. Effects of harvesting on N fluxes by (a) rotation every 50 yr, (b) rotation every 25 yr, and (c) effects of leaching and harvesting on N geochemical cycle (budget) in the aspen forest ecosystem. N budget is the difference of N input (deposition and fixation) and outputs (volatilization, leaching, and harvesting).

If we divide the N cycle into two 25-yr periods within a rotation (Fig. 4b), N input, Nnetmin, and volatilization do not noticeably differ between any two periods. In contrast, N leaching in the first 25 yr in the initial rotations was 1.1 times (0.4–0.7 g/m^2) higher than the subsequent 25-yr period, but harvesting caused a pulse

that increased N leaching by 2.8- to 4.3-fold in the subsequent rotations.

We observed a net N depletion in the aspen ecosystem across four rotations (Fig. 4c). Nitrogen loss peaked at the initial rotation and then decreased until the last two harvests when the losses balanced the inputs. The reduction was caused by both bole removal and N leaching. If no harvesting occurred, a positive balance of N would remain in the ecosystem as the initial rotation indicated (Fig. 4c). Apparently, leaching contributed to more N diminution than the removal of boles alone in this coarse soil system (Fig. 4c).

Model comparison

PnET-CN was unique among the models we compared (ANOVA, $P = 0.05$). Among the 20 compared variables, only five variables simulated by PnET-CN were similar to other models (i.e., LANDIS-II-Century, CENTURY, and Biome-BGC). For the remaining simulations, PnET-CN did not show any significant similarity with the other four models (Table 3). The other four models possessed similarities in some of the variables, but not all. Three of the four models showed nonsignificant differences among BiomC, StemC, and Nleach; two of them presented similarities in seven variables including NPP, CwdC, live wood biomass N (VegN), SoilN, and CwdN.

Like ANOVA, locations of the models (e.g., B and C) within the PCA ordination (Fig. 5) also revealed the unique nature of the models. The PCA reduced the 12 variables to two primary principle components or axes (Axes 1 and 2) with 71% and 16% variance explained. For the five C state and flux variables, four (SoilC, NPP, BiomC, and StemC) were strongly negatively, and one (CwdC) positively correlated with Axis 1. Therefore, Axis 1 could be described as a C or productivity axis, indicating that models except for PnET-CN simulated higher productivity but low CWD accumulation on the forest floor and C in soil. In addition, N leaching was most strongly related to Axis 1, indicating less N leaching was correlated with higher productivity. In contrast, Axis 2 could be described as an N axis because of its strongly positive relation to SoilN, Netmin, and N uptake (Nuptake), and negative relation to N use efficiency (NUE). Though Biome-BGC, CENTURY, and LANDIS-II-Century simulated similar higher productivity as indicated by Axis 1, Axis 2 showed that the higher productivity by Biome-BGC was a result of high SoilN and N supply (Nnetmin and Nuptake). In contrast, for LANDIS-II-Century, the higher productivity was caused by high NUE. The NUE also played a strong role in locating FORECAST on the PCA ordination graph.

The time change vectors, connecting rotations of each model in ordination space (Fig. 5), provide a visual comparison of the direction and magnitude of the CN changes by rotations within a model and among the models. Overall the vectors indicated that relatively little

TABLE 3. Predicted values of the variables across the six rotations by the five models.

Variable	Biome-BGC	CENTURY	FORECAST	LANDIS-II	PnET-CN
NPP (g C·m^{-2}·yr^{-1})	394.76[a]	366.44[b]	376.66[ab]	295.04[c]	281.57[c]
BiomC (g/m^2)	4002.27[b]	3562.03[b]	3887.34[b]	5410.98[a]	2126.57[c]
StemC (g/m^2)	1987.14[b]	2134.53[ab]	2316.18[a]	2365.35[a]	1255.33[c]
SoilC (g/m^2)	6711.54[c]	6952.43[a]	6758.48[b]	5935.14[d]	2700.06[e]
LitC (g/m^2)	0	250.4[a]	196.15[b]	125.25[c]	
CwdC (g/m^2)	1869.47[c]	2080.84[b]	1935.68[bc]	1644.43[d]	2426.92[a]
VegN (g/m^2)	17.56[c]	16.21[c]	28.35[a]	19.99[b]	12.5[d]
SoilN (g/m^2)	669.44[a]	288.93[b]	290.57[b]	196.9[c]	137.32[d]
LitN (g/m^2)		2.12[b]	3.95[a]	1.26[c]	
CwdN (g/m^{22})	8.47[c]	10.55[a]	7.81[c]	9.42[b]	9.82[ab]
Nnetmin (g·m^{-2}·yr^{-1})	4.21[b]	3.41[c]	3.19[d]	2.6[e]	5.28[a]
Nimmob (g·m^{-2}·yr^{-1})	8.76[a]				5.35[b]
Nuptake (g·m^{-2}·yr^{-1})	7.36[a]	4.95[bc]	3.48[de]	3.28[de]	5.08[bc]
Nleach (g·m^{-2}·yr^{-1})	0.02[c]	0[c]	0.51[b]	0[c]	0.7[a]
Nvol (g·m^{-2}·yr^{-1})	0.46[a]	0.41[b]		0.02[c]	
Nfix (g·m^{-2}·yr^{-1})	0.23[b]	0.2[c]	0.37[a]		
Plant respiration (g C·m^{-2}·yr^{-1})	282.28[a]				138.25[b]
Photosynthesis (g C·m^{-2}·yr^{-1})	676.92[a]				575.67[b]
Heterotrophic respiration (g C·m^{-2}·yr^{-1})	315.43[a]	291.45[b]		241.79[c]	254.02[c]
NUE (g CN·m^{-2}·yr^{-1})	53.62[d]	73.81[c]	106.81[a]	91.01[b]	54.31[d]

Note: Within a row, different superscript letters a–e indicate means that differ significantly among the the models ($P < 0.05$ for Tukey pairwise comparison test). Abbreviations are defined in Table 1.

change occurred through multiple harvest rotations simulated by CENTURY, LANDIS-II-Century, and Biome-BGC. Differences between the first two rotations simulated by both FORECAST and PnET-CN were related to large changes in CwdC and N leaching. PnET-CN had the most variation between rotations, with decreases in NuseEff and biomass C through time.

DISCUSSION

Effects of harvesting on productivity and CN interactions

Conventional bole-only harvesting did not significantly affect long-term productivity (NPP, BiomC, and StemC) of aspen across the six rotation periods after the first cut. Since climate is held constant in the simulations, the main factor affecting C assimilation rate and aspen growth is N dynamics. Mineral N in forest soils has been recognized to retain greater importance in predicting the performance of tree crops on very infertile sites, where NO_3^- levels are usually very low (Wilson et al., 2005) and sites with higher mineral N in soil would have a greater site index (Alban et al. 1991). Our simulations indicate that after six harvest rotations, 15–17 g·m^{-2}·rotation^{-1} of N, or 4% of the N capital in the ecosystem, was depleted through harvesting, leaching, and volatilization. The 4% is comparable to an average of 5% removed by bole wood harvested in the forests of
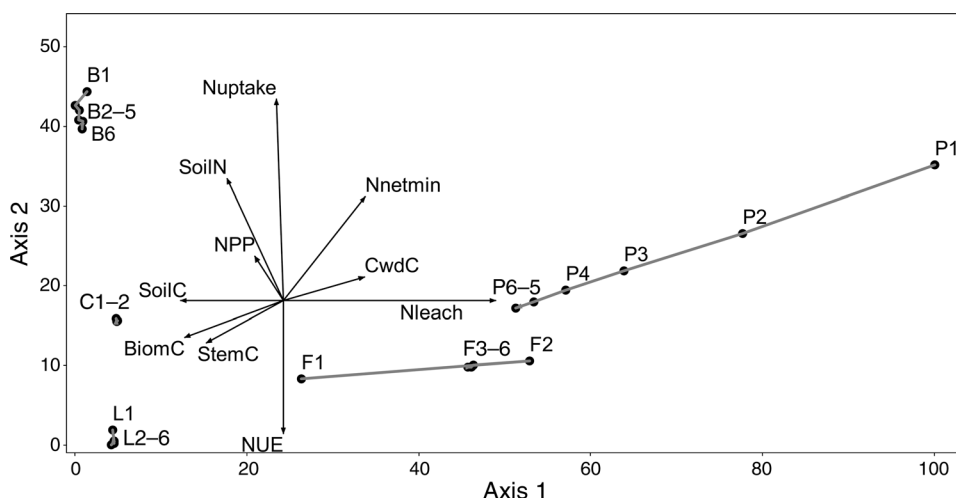
FIG. 5. Model comparison using PCA ordination. The variance explained by Axis 1 and Axis 2 is 71% and 16%, respectively. Labels B1–B6, C1–C6, F1–F6, L1–L6, and P1–P6 represent the six rotations (1–6) simulated by Biome-BGC, CENTURY, FORECAST, LANDIS-II-Century, and PnET-CN. Eleven out of 12 variables are displayed with an R^2 cutoff of 0.2. NPP is net primary production; BiomC is live wood biomass C; StemC is stem biomass C; SoilC/SoilN is soil organic matter C/soil N; CwdC is coarse woody debris C; Nnetmin is net N mineralization; Nleach is N leaching; NUE is N use efficiency; and Nuptake is N uptake.

the Pacific Northwest of the United States (Edmonds et al. 1989). Because most nutrient loss can be compensated for by atmospheric inputs, mineral weathering, and N fixation (Keenan and Kimmins 1993), the bole-only harvest practice may be inconsequential for aspen productivity through the rotations. This finding is consistent with a previous simulation that high N leaching (80% NO_3^- and 71% NH_4^+) during the three years following a bole-only harvest did not affect a mixed hardwood site productivity over the long term (Zhu et al. 2003). Titus et al. (2006) reported that both N removed in boles and N leaching within five years after harvesting old-growth forest dominated by Pacific silver fir (*Abies amabilis*) and western hemlock (*Tsuga heterophylla*) in the coastal mountains of British Columbia did not have a major impact on site productivity. Even increases in soil N availability after harvesting only slightly increased seedling foliar N concentrations for two to four years after logging before decreasing to below deficiency thresholds (Titus et al. 2006).

In addition, our simulations imply that if a moderate reduction of N deposition occurs in the future, the variation would not undermine our findings for bole-only harvesting impacts on aspen production. The reason is that N wet and dry depositions constitute only 13% of available N, but N net mineralization in SOM and litter pools supplies 80% of available N in the aspen forest ecosystem. The remaining 7% is from nonsymbiotic N fixation.

Soil CN dynamics vs. model structure

SoilC and SoilN storage significantly decreased across the rotations (Table 2). Heterotrophic respiration also declined across the rotations, indicating that soil microbial activity was significantly lower after the initial two rotations. The diminution could be because of dwindling organic matter input, fast decomposition, or the models' structure in representing SOM (Appendix A). SOM is composed of a variety of pools with different decomposition rates, and nutrient and C contents (Pineiro et al., 2006), however, PnET-CN represents soil as a single layer containing a single organic matter compartment that turns over at a moderate rate. In contrast, the other models partition SOM into different CN pools, which then decompose at various rates. For instance, in CENTURY, turnover rates of SOM in fast, slow, and passive pools were hypothesized as 2–5 years, 50 years, and 2000 years. The slow rate of C turnover in the passive pool apparently made the model less sensitive than PnET-CN. In addition, the current models hypothesize that allocation of SOM to the various pools is based on chemical properties of input substrates (e.g., lignin vs. nonlignin or C:N), and SOM decay rate is controlled by maximum decomposition rate and affected by soil temperature, moisture, and texture (Appendix A). However, recently, some of these assumptions have been questioned because molecular structure of plant

inputs and SOM are recognized to play a secondary role in determining SOM residence times. The complex interactions between organic matter and its environment, such as climate and the presence of potential degraders in the immediate microenvironment, may be the most important determinants of decomposition rates (Schmidt et al. 2011).

For the four models with multiple SOM pools (Appendix A), simulated SoilC is not significantly different between Biome-BGC and FORECAST, but is different from those simulated by the other two models (Table 2). The soil N modeled by CENTURY and FORECAST are similar but significantly different from those of Biome-BGC and LANDIS-II-Century. The four models also produced significantly different rates of heterotrophic respiration, with values ranging from 242–315 g $C \cdot m^{-2} \cdot yr^{-1}$. Biome-BGC and CENTURY have the highest values of soil N and heterotrophic respiration among the models. Structurally, this could be because of various algorithms describing decomposition rate, C:N ratio, and flow paths of litter and CWD to the soil pools (Appendix B, C, and E). CENTURY and LANDIS-II-Century have the same SOM pools, but simulated SoilC differed, indicating a different relative contribution of litter and CWD input to soil. The high SoilN accumulation simulated by Biome-BGC could be because of higher N immobilization (Appendix F) in the two soil pools with low decomposition rates (0.0014 and 0.0001), as compared to CENTURY's passive pool (0.0009).

Multiple model simulation and evaluation

Simulation.—The multimodel approach provides a way to evaluate uncertainties in model predictions and individual model structures (Li and Wu 2006, Knutti et al. 2010). This approach is particularly useful when the predictions cannot be validated (Oreskes et al. 1994), as when we do deductive modeling without historical data (Beven 2009). A large benefit of a multimodel approach is seen when the performance of all aspects (variables) of the simulation are considered. The benefit is caused not only by error compensation but in particular by the greater consistency and reliability of multiple models (Hagedorn et al. 2005). A multimodel approach may cancel or reduce the influences related to model structure, as different models have different structures. Each of the five models we used has been widely evaluated, and all are recognized as reliable models in simulating forest ecosystem CN dynamics (Blanco et al. 2007, Johnson et al. 2010, Peckham and Gower 2011). A simulation with these models and indirect evidence of the advantage of using a multimodel approach over individual models raises our confidence in using the models' averages to evaluate effects of harvesting on CN dynamics.

Model comparison.—Differences in the models' output variables have revealed important consequences of model algorithms and structures, such as the PnET-

CN simulation of SoilC, the Biome-BGC and LANDIS-II-Century simulations of SoilN, and the LANDIS-II-Century simulation of CN interactions (Figs. 2c and 3b, Appendix F: Fig. F1h). As mentioned in *Methods*, our inability to perform a model spin-up to the desired initial conditions for SOM due to limited disturbance parameters resulted in very different starting conditions for the PnET-CN simulation that had sustained consequences throughout the harvest scenario. This is less an evaluation of the accuracy and usefulness of the PnET-CN model than a consequence of some operational inflexibility in the model. In our case, one point of the study was to use a group of well-validated models without detailed calibration of each. One point being that to do such calibration on a suite of models, the required time and resources needed collectively would make the multimodel approach infeasible.

Forests are conceptually represented by different CN pools in each model (Appendix A). Since tree components (branches, stems, coarse roots) differ in N concentration and rates of decomposition, the amount of net N released will vary based on how the components are allocated to pools in each model (Abbott and Crossley 1982, Silver and Miya 2001, Rytter 2002, Shorohova et al. 2008, Melin et al. 2009). Therefore, the combination of branch with stem (e.g., LANDIS-II-Century and Biome-BGC) and with coarse roots (PnET-CN) into one component would affect the N cycle and subsequent forest productivity. FORE-CAST separates stem wood from bark, branches, and foliage, three pools with high N concentrations; this structure could explain why FORECAST has the highest values of VegN and LitN (Fig. 3a, c).

The allocation scheme is not only a process to allocate photosynthesis carbohydrate to the tree components but also to allocate N, depending on C:N ratio. In response to increasing water and nutrient stress in forests, trees have been observed to decrease the proportional allocation of C to foliage and stems while greatly increasing the absolute allocation of C to fine roots (Makela et al. 2008, Ryan et al. 2010, Dybzinski et al. 2011). Among the models we used, PnET-CN and LANDIS-II-Century allocate C to the components at fixed rates, regardless of water or temperature stress. In contrast, the allocations in CENTURY and Biome-BGC are dynamic processes in response to water or nutrient availability. For our nutrient-poor and well-drained soil, water stress and nutrient limitations are possible. Therefore, CENTURY and Biome-BGC will incorporate and reflect the effects of site conditions on productivity and consequently other CN states and dynamics of the system.

Except for C:N ratio dependence, carbon allocation to different components varies by age (Ericsson et al. 1996). Aspen forests sprout after cutting and grow quickly during the first couple of years after harvesting (Peterson and Peterson 1992) by root suckering from lateral roots. Usually, 20 000 suckers/ha is a modest density in the first year; but there is a very rapid reduction (e.g., 80%) in the density in the first five years (Peterson and Peterson 1992). As early as five years postharvest, diameter at breast height (dbh) of the suckers could surpass 2.5 cm (Alban et al. 1991). Along with the root sprouting, a high NPP is expected in the first couple of years and in the first/second year leaf area index of aspen could reach half of the maximum (E. Kruger, *personal communication*). Among these models, dynamic C allocation against stand age, similar to CENTURY, caught aspens' fast growth property in the early years. In contrast, PnET-CN's allocation approach (requiring a minimum wood production) apparently contributes to the low productivity in the same period of time.

CWD and SOM are the other major source of available N in forest ecosystems besides N input from atmospheric deposition and fixation and N mineralization from litter decomposition. Decomposition and N release from these pools are determined by initial chemical composition (e.g., lignin) or C:N ratio and environmental condition of temperature, humidity, and soil temperature and water content (Cisneros-Dozal et al. 2007, Manzoni et al. 2008, Karhu et al. 2010). In modeling the decomposition process in our study (Appendix A), even for the same type of litter, different models employ various approaches to determine how the litter and detritus decompose, which could be one of the reasons why the models are different in LitC, LitN, and N availability to aspen growth. In addition, Biome-BGC was initially designed for simulating general forest types. For simulation at the species level, an adjustable decomposition rate would be preferable as used in the other four models.

There are limitations to our simulations, such as that the versions of the models we used are unable to simulate reproduction by sprouting. Only the KLAI parameter in CENTURY and LANDIS-Century, large wood mass (g C/m^2) at which half of theoretical maximum leaf area is achieved, can partially simulate the sprouting process. In addition, we did not address other nutrients (e.g., P), climate change, rotation period, or equipment utilization (Keenan and Kimmins 1993, Stone and Elioff 2000, Brais 2001, Miller et al. 2004, Bockheim et al. 2005). Interactions among different species may also affect the short- and long-term CN cycles in forest ecosystem and deserve to be explored further.

Conclusions

Impacts of harvesting on long-term forest productivity and CN interactions have been extensively studied for decades. Simulation modeling is recognized as a flexible approach in exploring how harvesting affects forest floor and soil CN states and fluxes and then how these in turn interact with forest growth over long time periods. Through multimodel simulations, we did not

find significant impacts of conventional bole-only harvesting with a 50-yr rotation period on long-term productivity of aspen. This could be because N removals from timber extraction (4% of the capital) and increased N leaching caused by harvesting were not significant enough to decrease long-term productivity. Site productivity was maintained even though harvesting reduced soil CN. The fraction of N loss caused by harvesting could be replenished by geochemical N input including deposition and nonsymboitic N fixation and due to all branch compartment wood being retained on site.

In our multimodel approach, outputs generally differed among models. Some model outputs were noticeable outliers compared to the mean values of the five model outputs and their temporal patterns. Each model simulates ecosystem CN processes differently. CENTURY was most similar to the multimodel mean, while FORECAST and PnET-CN differed more from the multimodel mean than the other models evaluated. A multimodel approach is a robust option when sufficient long-term field observations of all CN processes for calibration and evaluation for an individual model are lacking. In addition, a multimodel comparison provides a way to evaluate individual models, how and why they agree or disagree, through which to amend the models and improve their performance.

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SUPPLEMENTAL MATERIAL

Appendix A

Comparisons of states and processes simulated by CENTURY, Biome-BGC, and PnET-CN, LANDIS-II-Century extension (LANDIS-Century), and FORECAST (*Ecological Archives* A024-082-A1).

Appendix B

CENTURY parameters (*Ecological Archives* A024-082-A2).

Appendix C

LANDIS-II with Century Succession extension parameters (*Ecological Archives* A024-082-A3).

Appendix D

PnET-CN parameters (*Ecological Archives* A024-082-A4).

Appendix E

Biome-BGC parameters (*Ecological Archives* A024-082-A5).

Appendix F

CN states and cycles in an aspen forest ecosystem on glacial outwash plains in Wisconsin disturbed by bole-only harvesting every 50 yr (*Ecological Archives* A024-082-A6).

Appendix G

(a) Harvested C and (b) N simulated by the five models. Bars illustrate average of the five models (A), Biome-BGC (B), CENTURY (C), FORECAST (F), LANDIS-II-Century (L), and PnET-CN (P) (*Ecological Archives* A024-082-A7).