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Managing Wisconsin's Forests for Fiber Production and Carbon Sequestration: A Modeling Approach

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Executive Summary

Ecosystem process models are tools that can be used to examine the long-term effects of different management scenarios on ecosystem dynamics. This issue is particularly important to devising forest management practices and policy to sequester C and still produce wood fiber for biofuel feedstock. The big advantage of ecosystem process models is they provide insight into questions that experimental studies would require decades to centuries to answer.

We used the ecosystem process model Biome-BGC to simulate the effects of harvest and residue removal management scenarios on soil carbon (C), available soil nitrogen (N), net primary production (NPP), and net ecosystem production (NEP) in jack pine (*Pinus banksiana* Lamb.) and sugar maple (*Acer saccharum* Marsh) ecosystems in northern Wisconsin, U.S.A. To assess harvest effects, we simulated short (50-year) and long (100-year) harvest intervals, high (clear-cut) and low (selective) harvest intensities, and three levels of residue retention (15, 25, 35 %) over a 500-year period. Model logic and processes of Biome-BGC and its predecessor, FOREST-BGC, are well described (Running & Coughlan 1988, Running & Gower 1991, Kimball *et al.* 1997, White *et al.* 2000, Thornton *et al.* 2002). We used a modified version of Biome-BGC (version 4.1.2) developed by (Bond-Lamberty *et al.* 2005, Bond-Lamberty *et al.* 2007a, Bond-Lamberty *et al.* 2007b). Biome-BGC simulates multiple, competing vegetation types (Bond-Lamberty *et al.* 2005), as well as disturbance (Bond-Lamberty *et al.* 2007b).

A concerted effort was made to validate the model output of Biome-BGC to determine if the model was providing accurate simulations of vegetation and soil C cycling processes. The model simulation of NPP, soil C accumulation, and NEP agreed reasonably well with biometric and eddy-covariance measurements of these two ecosystems. Simulated NPP for the sugar maple and jack pine stands differed by < 10% from measured NPP for the same two species. Simulated NEP for the base scenario sugar maple stand of 3 tC $ha^{-1}yr^{-1}$ compared favorably to measured annual NEP of 3.8 tC $ha^{-1}yr^{-1}$ for a 70-76 year-old sugar maple-dominated northern hardwood forest (Desai *et al.* 2005). Average NEP for an old growth northern hardwood forest was -0.01 tC $ha^{-1}yr^{-1}$ (Ankur Desai, personal communication), which compares well to modeled NEP of 0.04 tC $ha^{-1}yr^{-1}$ for the sugar maple at an old growth state.

Simulations included clear-cut and selective harvests at 50- and 100-year harvest intervals with varying residue left after harvest from 15-35%. Results of this study indicate that for a given harvest type (clear-cut or selective) and harvest interval, as residue removal increased, mineral soil C losses increased relative to the base scenario. In the sugar maple ecosystem, mineral soil C content increased 0.04 tC ha^{-1} yr^{-1} for the 500-year no harvest management simulation. The largest soil C loss of -0.04 tC ha^{-1} yr^{-1} occurred for 50-year clear-cut scenario with 15% residue retention and represents a 200% decrease from the base scenario. The decline in mineral soil C content is likely due to the reduced amount of C entering the soil pool through decomposition. In general, the more intensive harvest scenarios increased overall net ecosystem production, even though the mineral soil carbon content declined. All the simulated jack pine and sugar maple harvest scenarios decreased mineral soil C and available N content relative to the no-harvest case. Simulations for both the sugar maple and jack pine stands revealed that maximizing carbon storage (i.e. content) in vegetation decreased annual net ecosystem

carbon sequestration rate. These results highlight the complexity of managing forests for carbon sequestration and maintaining long-term soil productivity.

One issue that could not be resolved in this project was which climate data should be used to complete the simulations. There are several climate data sources available, and each has strengths and weaknesses. For example, the NCAR NCEP re-analysis data has a longer record than DayMet. In addition, the documentation to download and acquire DayMet data is out-dated and many links were non-functional. However, some scientists feel the DayMet climate data is of higher quality than NCAR NCEP data. We compared the two climate data sets and observed rather disturbing differences. Moreover, the differences in the climate data result in equally unsettling differences in model results. It is difficult to know which data set is more accurate, but we ended up using the DayMet data. The large differences in the two common climate data sets highlights the need for a collaborative effort among climatologist to evaluate the different climate data and develop one consistent data set.

Introduction

The overall objective of this study was to address several major uncertainties associated with the fate of logging residues, evaluating new forest management approaches that will enhance existing C pools, and use these data to simulate the net effect of different forest management scenarios on the short- and long-term total C accumulation and net C sequestration. Specific objectives were: (1) examine the effects of different forest management practices on net carbon sequestration, (2) quantify trade-offs of different carbon management strategies on net carbon sequestration. To address these objectives we used an ecosystem process model Biome-BGC. Biome-BGC simulates water, carbon, and nitrogen cycles at a daily time step. The required daily climate data are minimum and maximum temperature, total solar irradiance, average vapor pressure deficit, and total precipitation. The daily meteorological data required by Biome-BGC were obtained from the DAYMET database (http://www.daymet.org/). Table 1 summarizes the simulated harvest and residue management scenarios. Below we summarize key findings for each of the two objectives, and highlight a major impediment we encountered related to climate data used to run the model. The research was published in Global Change Biology Bioenergy and a copy of the article is included in the report.

Results

Climate Data Challenge

Biome-BGC, like all other ecosystem process models, requires climate data to simulate the carbon, water, and nitrogen cycles. Biome-BGC requires daily maximum and minimum air temperature, daily total precipitation, average vapor pressure deficit and daily total solar radiation. We evaluated two sources of climate data: NCAR NCEP re-analysis data and the DayMet data. In the past we have the NCAR climate data. We were shocked by the large differences between the two widely used climate data sets. Figure 1 illustrates the large intra-annual differences in vapor pressure deficit and solar radiation for a randomly selected year, 1980. The VPD and SR estimates are consistently lower for the NCAR than DayMet data. A comparison on inter-annual differences in climate variables between the two data sources revealed the observed differences exist for all years, and even the temperature and precipitation data exhibited some differences (Figure 2). The large differences in climate data resulted in significant discrepancies in Biome-BGC simulation outputs (Figure 3). I visited with many climatologists and there was never any consensus which climate data set was better. In the end we ended up using the DayMet, which was a departure from our past efforts. Obtaining the DayMet data also proved to be extremely difficult because the website is out-dated, many links are broken, the user manual was useless, the format of the data is extremely cumbersome, and the lead scientist, responsible for the data was non-communicative.

Table 1. Description of the harvest scenarios simulated using Biome-BGC.

Scenario	Harvest Type	Harvest Interval (years)	Residue Left (%)
Base	-	-	-
C-50-15	Clear-cut	50	15
C-50-25	Clear-cut	50	25
C-50-35	Clear-cut	50	35
S-50-15	Selective	50	15
S-50-25	Selective	50	25
S-50-35	Selective	50	35
C-100-15	Clear-cut	100	15
C-100-25	Clear-cut	100	25
C-100-35	Clear-cut	100	35
S-100-15	Selective	100	15
S-100-25	Selective	100	25
S-100-35	Selective	100	35

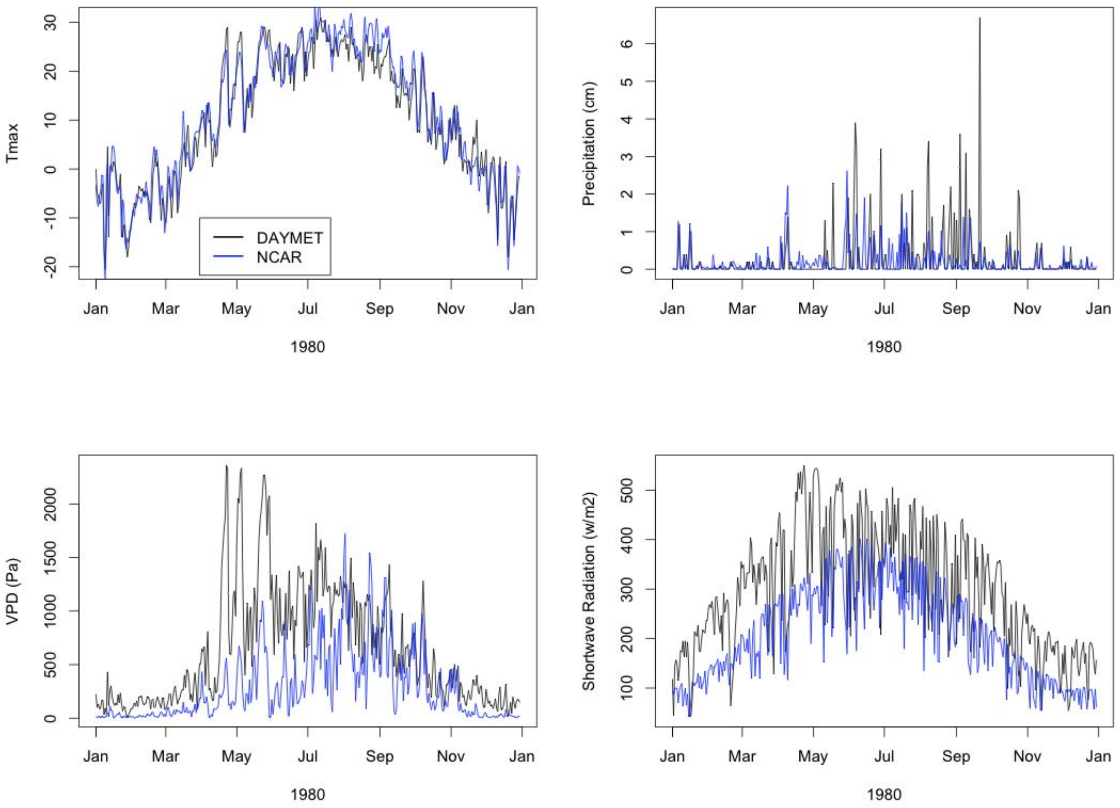

Figure 1. Summary of daily air temperature, precipitation, vapor pressure deficit (VPD), and solar shortwave radiation data from NCAR and DayMet data sources for 1980.

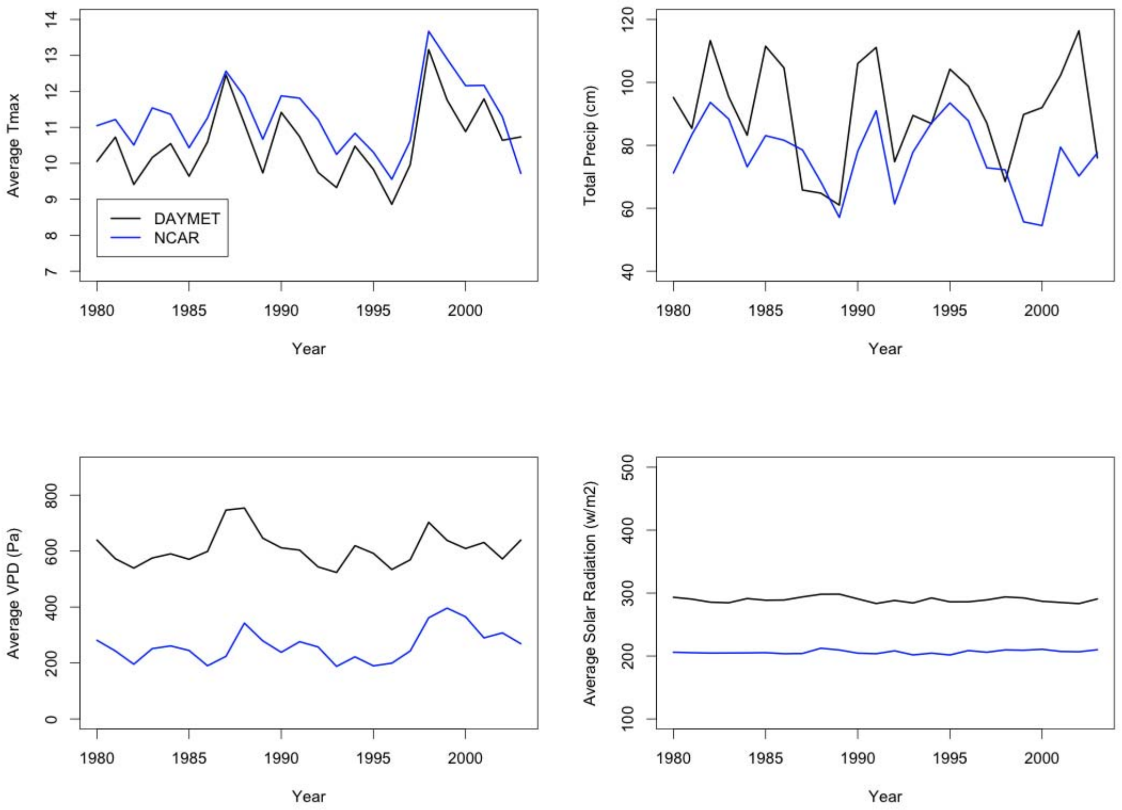

Figure 2. Summary of annual air temperature, precipitation, vapor pressure deficit (VPD), and solar shortwave radiation data from NCAR and DayMet data sources for 1980-2008.

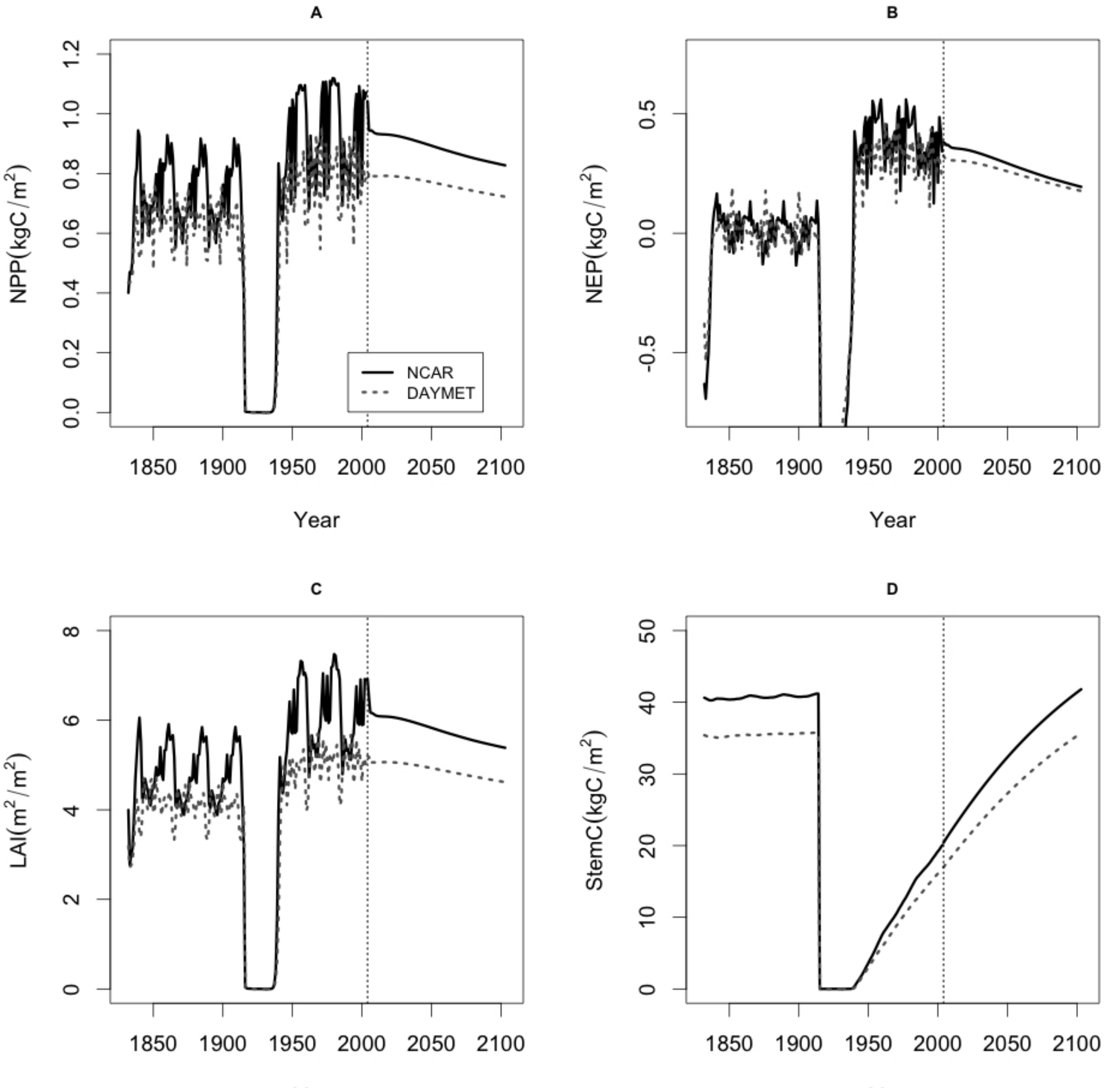

Figure 3. Comparison of Biome-BGC simulations of (a) net primary production (NPP), (b) net ecosystem production (NEP), (c) leaf area index (LAI), and (d) stem carbon content derived from using the NCAR and DayMet climate data.

Objective 1. Examine the effects of different forest management practices on net carbon sequestration.

The harvest scenarios dramatically changed simulated NEP for the sugar maple ecosystem (Figure 4). For the base scenario, cumulative NEP for the 500-year period, was 319 tC ha^{-1}, or 0.64 tC ha^{-1}yr^{-1}. NEP was greater for all harvest scenarios than for the base scenario (Figure 2). The C-50-15 management scenario had the greatest cumulative NEP of 978 tC ha^{-1}, or 1.96 tC ha^{-1}yr^{-1}, while the S-100-35 scenario had the lowest total NEP of 469 tC ha^{-1}, or an average annual NEP of 0.94 tC ha^{-1}yr^{-1}.

Under the various harvest scenarios, despite the large negative shifts in NEP observed in the year following harvest of jack pine, NEP recovered within 15 years to levels higher than the base scenario (Figure 5) and continued at a level above the base scenario for the remainder of the rotation. All harvest scenarios had a higher total NEP than the base scenario (Figure 2). The C-50-15 scenario had the highest NEP and sequestered 473 tC ha^{-1} over 500 years simulation period for an average annual NEP of 0.95 tC ha^{-1}yr^{-1}. Conversely, the least intensive harvest scenario (S-100-35) had the lowest total NEP 138 T ha^{-1} for an average annual NEP of 0.28 tC ha^{-1}yr^{-1}. For comparison, the lowest NEP was 175% greater than the no harvest scenario (50 tC ha^{-1}).

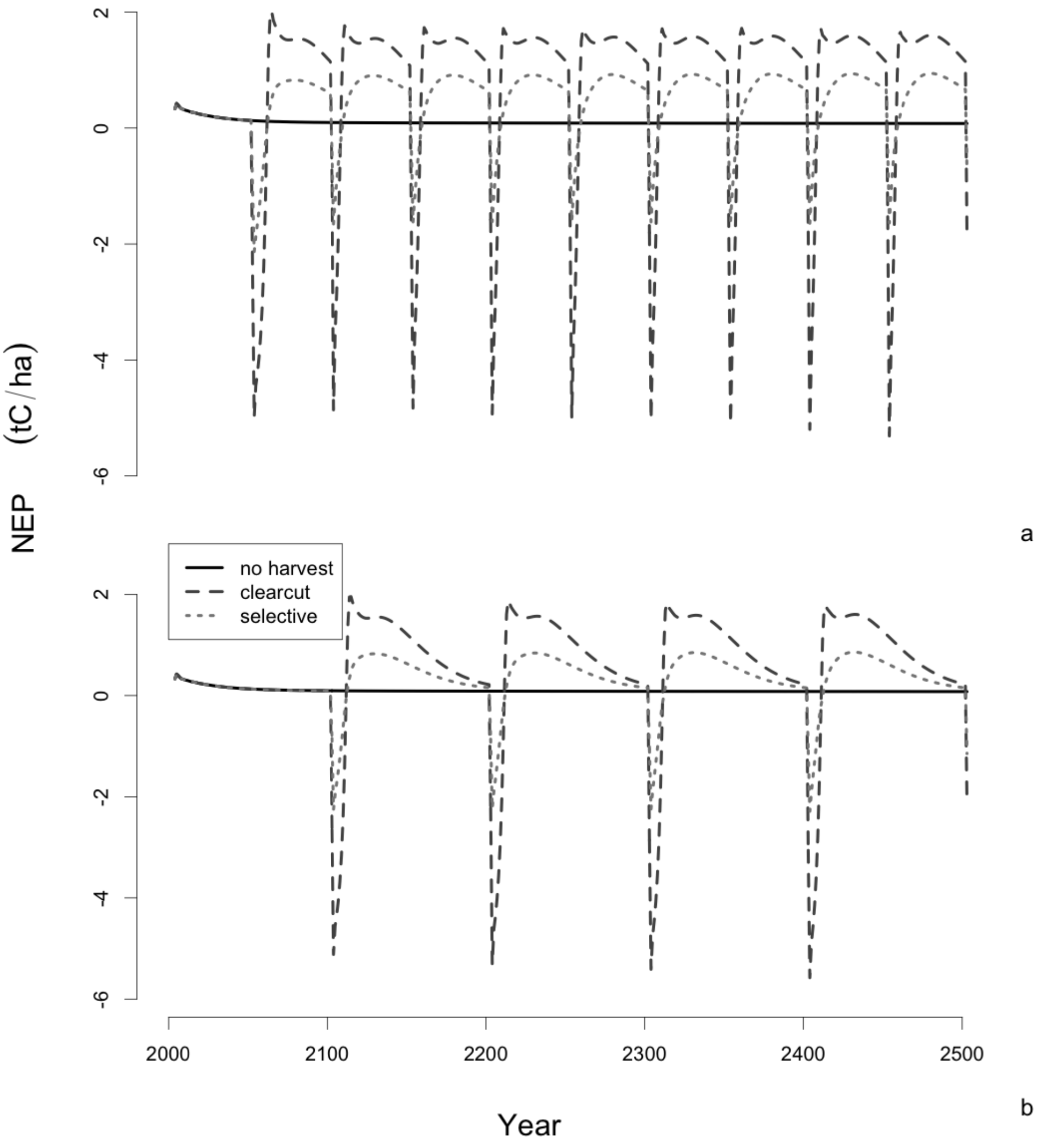

Figure 4. Yearly NEP model output of simulated harvested scenarios for Sugar Maple, a) 50-year interval and b) 100-year interval.

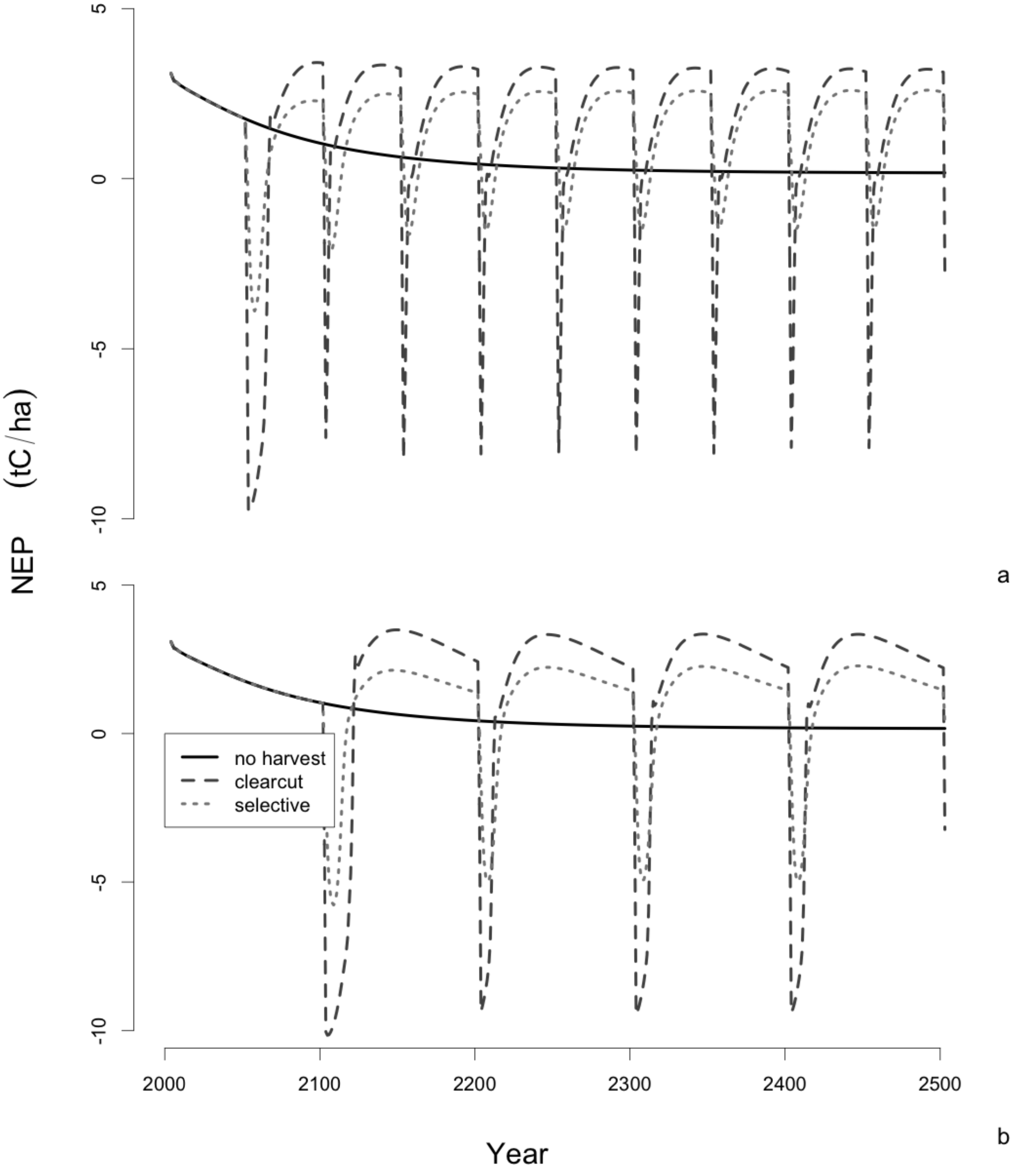

Figure 5. Soil C model output of simulated harvest scenarios for Jack Pine, a) 50-year interval and b) 100-year interval. Only the 25% residue level simulations are shown. The light grey solid line is a no-harvest simulation with both CO_2 and Ndep held at pre-industrial levels.

Objective 2. Quantify trade-offs of different carbon management strategies on net carbon sequestration.

Our model simulations indicate that the more intense harvest scenarios increased total NEP. However, the increase in total NEP was associated with a decrease in mineral soil C content. The results may seem counter-intuitive, but they are reasonable when the different processes (i.e. plant versus soil) and their rates are considered. Net ecosystem production, or NEP, is the difference between net primary production and heterotrophic respiration. The vegetation C dynamics are more variable, non-linear and operate at a faster time scale than soil C dynamics. The NPP decline in forest can range from 4 – 76% (Gower *et al.* 1996) and NEP can range from negative to positive. Conversely mineral soil C dynamics, especially the slow C pools operate on a much slower time scale of 10^2 to 10^3 years.

Available mineral soil N in jack pine ecosystem tended to increase immediately following harvest, but then decreased during stand re-development. Available N loss was greater for the clear cut than selective tree harvest scenarios (Figure 6). The more intense harvest simulations decreased the available mineral soil N content by up to 10%. For sugar maple, available mineral soil N content decreased for all harvest scenarios relative to the base. The greatest decrease in available soil N occurred for the clear-cut harvest scenarios, with the 50-year interval clear-cut decreasing available mineral soil N by more than 20%.

Understanding the short- and long-term effects of harvesting on soil productivity is a pressing issue because there is growing interest to increase harvest frequency and intensity (in both total amount and removal of harvest residues) to meet the demand for wood fiber and biofuel feedstock. To date most studies are field observations based on short-term measurements after one or two harvests. In a meta-analysis, (Johnson & Curtis 2001) reported no clear trend and found soil C and N both increased and decreased following harvest. Two other studies concluded that harvesting has little effect on soil C in the 10-20 years following harvest (Johnson *et al.* 2002, Powers *et al.* 2005). Based on these meta-analysis studies, the authors concluded that forest type (coniferous or deciduous) and harvest method were important factors that affected soil C and N content. Our modeling results support their conclusion. Whole-tree harvest reduced mineral soil C content while sawlog harvest increased soil C. Our results are reasonably consistent with the short-term results reported from field studies. Selective harvests for the 100-year interval only slightly decreased soil C and available N in the sugar maple ecosystem, relative to the base scenario. Conversely, simulated clear-cuts of sugar maple greatly decreased soil C and available N relative to the base scenario. Our results illustrate the need for field data for several harvest rotations to better evaluate and improve ecosystem process models. Moreover, forest harvest and residue management plans should not be based on total soil nutrient pools, but on available nutrient pools. *The available N pool is a small fraction compared to the total pool, so impacts from management practices could go undetected. In Biome-BGC the available N pool is typically around 0.003% of the total soil N pool. Nadelhoffer et al. (1985) reported annual net mineralizable N comprised only < 5% of total N.*

V. Appendix.   Article published in Global Change Biology Bioenergy, 2010,
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Simulated long-term effects of harvest and biomass residue removal on soil carbon and nitrogen content and productivity for two Upper Great Lakes forest ecosystems

Running title: Residue removal and long term soil productivity

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Abstract

We used the ecosystem process model Biome-BGC to simulate the effects of harvest and residue removal management scenarios on soil carbon (C), available soil nitrogen (N), net primary production (NPP), and net ecosystem production (NEP) in jack pine (*Pinus banksiana* Lamb.) and sugar maple (*Acer saccharum* Marsh) ecosystems in northern

Wisconsin, U.S.A. To assess harvest effects, we simulated short (50-year) and long (100-year) harvest intervals, high (clear-cut) and low (selective) harvest intensities, and three levels of residue retention (15, 25, 35 %) over a 500-year period. The model simulation of NPP, soil C accumulation, and NEP agreed reasonably well with biometric and eddy-covariance measurements of these two ecosystems. The more intensive (50-year rotation clear-cuts with low residue retention) harvest scenarios tended to have the greatest NEP (420 tC ha^{-1} and 678 tC ha^{-1} for the 500-year interval for jack pine and sugar maple, respectively). All the harvest scenarios decreased mineral soil C and available mineral soil N content relative to the no-harvest scenario for jack pine and sugar maple. The rate of change in mineral soil C decreased the greatest in the most intensive biomass removal scenarios (-0.012 and -0.072 tC ha^{-1} yr^{-1} relative to no-harvest for jack pine and sugar maple, respectively) and the smallest decrease was observed in the least intensive biomass removal scenarios (-0.002 and -0.009 tC ha^{-1} yr^{-1} relative to no-harvest for jack pine and sugar maple, respectively). The more intensive biomass removal harvest scenarios in sugar maple significantly decreased peak productivity (NPP) in the simulation period.

1. Introduction

There is growing interest in using biofuels to decrease US's demand for fossil fuel. Many plant species are being considered as feedstock for biofuel production, and each have important ecological, environmental, and economic advantages and disadvantages. Wood fiber, such as roundwood, chips, and harvest residue, are potential source feedstock for biofuels. The Great Lakes States region is a potential source for biofuel feedstock because of its widespread forested landscape, well developed forest industries, and modest forest growth rates. Between 1983 and 1996, Wisconsin produced 986 million board feet of sawtimber annually, making Wisconsin one of the largest producers of sawtimber in the United States (Perry & Everson 2008). The northern part of the state is heavily forested with large tracts of both public and private forest. The Chequamegon-Nicolet National Forest (CNNF), the largest national forest in Wisconsin, harvests about 4,000 hectares annually, or 4% of the total volume harvested from all national forests, making the CNNF the second largest producer of wood fiber of all national forests in 2008 (Benjamin Frater, personal communication).

Understanding the potential impacts of repeated harvests and increased biomass removal is necessary to ensure sustainable management of the forest ecosystems that provide many other ecosystem services. Maintaining soil organic matter (carbon) and nutrients is one of many ecosystem characteristics that comprise sustainable management. However, it is unclear how harvest frequency and intensity (i.e. clear-cut vs. selective tree and varying residue removal rates) will affect the soil carbon and available nitrogen, especially on a time scale greater than several rotations which can be measured in a human lifetime. A decline in soil carbon and nitrogen may lead to decreased forest growth and long-term site productivity (Landsberg & Gower 1997).

Empirical studies have provided useful insight on the short-term effects of harvesting on soil nutrient content and nutrient cycling processes. Powers et al. (2005) reported some C and N loss in the top 20 cm of soil in the first 10 years following harvest, but only when the entire forest floor was removed. Meta-analysis of individual harvest studies provide no real clear pattern, perhaps because of the large variation in harvest regimes (clear-cut, group selection versus single-tree selection) and biomass removal (Johnson & Curtis 2001). A bigger concern is present-day field studies represent one or at most two harvest rotations and the relevance of the results to long-term site productivity is unknown.

As companion to empirical studies, ecosystem process models offer the opportunity to simulate the short- and long-term effects of different harvest regimes for biofuels production on soil fertility, and hence the sustainability of forest management practices. Forest productivity is strongly influenced by soil fertility; therefore, process models can simulate important feedbacks that influence future forest growth. However, ecosystem process models are only as accurate as our understanding of the processes controlling carbon, nutrient and water cycles, and their interactions. Nonetheless, ecosystem process models are valuable tools to explore different scenarios and impacts, and identify key processes that appear to influence soil nutrient dynamics, and soil processes that warrant more empirical field research to improve the models.

Biome-BGC, an ecosystem process model that evolved from the forest ecosystem process model FOREST-BGC (Running & Coughlan 1988, Running & Gower 1991) simulates carbon, nitrogen and water cycles, and their interaction (Thornton *et al.* 2002, Bond-Lamberty *et al.* 2005, Bond-Lamberty *et al.* 2007a). Biome-BGC has been evaluated previously against other models, eddy-covariance data from flux towers, and biometric studies. A full sensitivity analysis of model ecophysiological parameters was published previously by White *et al.* (2000). Biome-BGC performed well in intra-model evaluations of C cycling in a boreal evergreen needleleaf stand (Amthor *et al.* 2001) and a temperate deciduous broadleaf stand (Hanson *et al.* 2004). While not identical to the sites modeled in this study, these two stand types (black spruce and oak) exist within the climate and geographical space considered in this study. Biome-BGC's response to disturbance (both fire and harvest) has been studied previously. Thornton *et al.* (2002) tested Biome-BGC against eddy-covariance data and biometric analyses at seven evergreen needleleaf forests in the United States to assess the model's ability to track NEP following disturbance. Modeled NEP was slightly lower at some sites, but LAI was in good agreement. Merganicova *et al.* (2005) reported good correlation between modeled and observed stem volumes in 36 Norway spruce stands in Europe subjected to three different forest management practices. Cienciala & Tatarinov (2006) reported a positive correlation ($r^2 > 0.85$) between modeled and measured aboveground biomass accumulation for 33 plots of managed beech, oak, and spruce stands. Vetter *et al.* (2005) applied Biome-BGC to managed stands in central Europe to estimate C fluxes and their estimates agreed with other published studies in the region. Biome-BGC has also been successfully tested against chronosequence data in ponderosa pine (Law *et al.* 2003, Law *et al.* 2004) and black spruce (Bond-Lamberty *et al.* 2006). Recently, we have used

Biome-BGC to model the historical C fluxes and assess the impacts of disturbance over 1 x 10^6 ha of boreal forest in North America (Bond-Lamberty *et al.* 2007b).

The objectives of this study were to (i) use the ecosystem process model Biome-BGC to simulate different timber harvest scenarios for two dominant northern temperate forest ecosystems and investigate the long-term impacts on soil C and available N, net primary production (NPP), and net ecosystem production (NEP) and to the extent possible (ii) compare model simulations to field measurements to better understand how the model performed. The second objective is essential, but it was also a major challenge given studies of multiple harvests (and their effects on C and N cycling) have not really occurred in the Upper Great Lakes region. We modeled two forest types that commonly occur in northern Wisconsin and the Upper Great Lakes region and occupy opposite ends of the productivity spectrum. Low productivity jack pine (*Pinus banksiana* Lamb.) ecosystems occur on excessively-drained, nutrient poor, sandy soils, while high productivity sugar maple-dominated northern hardwood stands (*Acer saccharum* Marsh) ecosystems occur on fertile, mesic soils. The model simulations included two harvest frequencies (50 and 100 year), two harvest types (clear-cut and selective tree harvests), and three harvest residue retention rates (15, 25, and 35%). Model outputs of total mineral soil carbon content (soil C), and available mineral soil nitrogen content (soil N), net primary production (NPP) and net ecosystem production (NEP) were compared to a base simulation of no harvest.

2. Materials and Methods

2.1 Site Description

We conducted our simulations on two of the major forest ecosystems in northern Wisconsin, and the Upper Great Lakes region. The topography of this region is flat to gently rolling and the predominant geologic landforms include pitted and unpitted outwash plains, drumlin fields, and moraines. The climate of the study area is characterized by a short growing season and long cold winters. Based on the climate data used to drive the model (1980-2003), air temperatures averaged –9 and +22°C in January and July, respectively. Precipitation falls primarily as rain from May to September and averages 910 mm/yr.

The jack pine and sugar maple-dominated forest ecosystems simulated in this study are represented by the AQV and AViO habitat types (Kotar *et al.* 1988, Fassnacht & Gower 1997); these habitat types are common to north central Wisconsin and occur within the Chequamegon-Nicolet National Forest (CNNF). Typical overstory tree species of the excessively drained, infertile soils jack pine ecosystem include include jack pine, quaking aspen (*Populus tremuloides* Michx.), paper birch (*Betula papyifera* Marsh.), red pine (*Pinus resinosa* Ait.), and to a lesser extent white pine (*Pinus strobus* L.). The dominant over story tree species of the mesic, fertile sugar maple ecosystem of northern Wisconsin include sugar maple (*Acer saccharum* Marsh), red maple (*Acer rubrum* L.), basswood (*Tilia Americana* L.), white ash (*Fraxinus americana* L.), and to a lesser extent, red oak (*Quercus rubra* L.).

2.2 Biome-BGC

Biome-BGC is an ecosystem process model that simulates water, carbon, and nitrogen cycles at a daily time step. The required daily climate data are minimum and maximum temperature, total solar irradiance, average vapor pressure deficit, and total precipitation. The daily meteorological data required by Biome-BGC were obtained from the DAYMET database (http://www.daymet.org/). Biome-BGC partitions plant canopy radiation into sunlit and shaded portions and physiological processes are calculated separately for each. Photosynthesis per unit projected leaf area is simulated using the Farquhar biochemical model (Farquhar *et al.* 1980) and stomatal conductance is calculated as a function of radiation, vapor pressure deficit (VPD), leaf water potential, and minimum nighttime temperature (Running & Coughlan 1988). Both plants and microbes compete for a single pool of available mineral soil N. Potential assimilation and decomposition rates dictate the demand for available N, and the rates of these processes are reduced if demand exceeds the current available N pool. Reduced mineral soil N availability decreases photosynthesis and decomposition and shifts carbon allocation from above- to belowground (Running & Gower 1991). Evapotranspiration is estimated using the Penman-Monteith equation (Monteith 1965). Autotrophic respiration, both growth and maintenance, and heterotrophic respiration (R_H) are calculated individually. Model logic and processes of Biome-BGC and its predecessor, FOREST-BGC, are well described (Running & Coughlan 1988, Running & Gower 1991, Kimball *et al.* 1997, White *et al.* 2000, Thornton *et al.* 2002). We used a modified version of Biome-BGC (version 4.1.2) developed by (Bond-Lamberty *et al.* 2005, Bond-Lamberty *et al.* 2007a, Bond-Lamberty *et al.* 2007b). Biome-BGC simulates multiple, competing vegetation types (Bond-Lamberty *et al.* 2005), as well as disturbance (Bond-Lamberty *et al.* 2007b).

In this study, we simulated only one forest ecosystem type (sugar maple or jack pine) at a time (i.e. we turned off the competing vegetation subroutine because neither forest ecosystem occurs on the other soil type).

The model was self-initialized for each forest ecosystem type through a model spin-up (Thornton & Rosenbloom 2005, Pietsch & Hasenauer 2006) using 24 years of historical meteorological data and pre-industrial estimates of atmospheric carbon dioxide (CO_2) concentration and nitrogen deposition (Ndep). Following spin-up, a model run for years 1832-2003 was performed to estimate near-present day C and N pool values in order to initialize all of the harvest simulations in this study. Atmospheric CO_2 concentration and nitrogen deposition varied from pre-industrial (1832) estimates up to near-present day (2004) levels. Carbon dioxide concentrations were obtained from Etheridge (1998). Ndep increased from its pre-industrial value of 1 kg/ha/yr to the 2004 value (7 kg/ha/yr) based on data from National Atmospheric Deposition Program (http://nadp.sws.uiuc.edu/ntn/). Much of northern Wisconsin's forest landscape was clear-cut in the early 1900's; therefore a clear-cut in 1915 was included to accurately simulate past land use history and then we assumed only fire and natural mortality influenced the stands until the simulation end in 2003.

All harvest scenarios were simulated for 500 years, and were started from the end of the 1832-2003 simulation. Atmospheric CO_2 concentration and Ndep were held constant at 2004 levels. We utilized an ensembling method (Thornton *et al.* 2002) to smooth the effects of inter-annual climate variability within the simulations. This approach was selected because the focus of the study was the effect of harvest scenarios on ecosystem C and N dynamics and not the effects of inter-annual variability in the meteorological record.

2.3 Data sources

The physical, hydrological and chemical characteristics of the soil for the sugar maple and jack pine ecosystems were derived from the AViO and AQV habitat types, respectively (Fassnacht & Gower 1998). For the jack pine simulation, the percentages of sand, silt, and clay were 89, 4, and 7, respectively (Fassnacht & Gower 1998). Sand, silt, and clay percentages were 63, 28, and 9, respectively, for sugar maple (Fassnacht & Gower 1998). Soil depth was obtained from the STATSGO database (http://soils.usda.gov/survey/geography/statsgo/). Table 1 summarizes the ecophysiological and ecosystem state variables used for the sugar maple and jack pine model simulations, respectively. The ecophysiological parameters for each species were obtained from White *et al.* (2000). We used species-specific data when available, mean values for broad-leaf deciduous and needle-leaf evergreen species, or as a default, general ecophysiological values.

2.4 Harvest Scenarios

We simulated two harvest types (clear-cut and selective tree harvests) at both 50- and 100-year intervals. A clear-cut consisted of 100% harvest of all trees (all aboveground stem C pools removed from site minus the residue). Leaf and fine root C pools were transferred to litter, and coarse root carbon pool was transferred to coarse woody debris. The selective harvest removed 40% of the stems and the corresponding leaf and root carbon pools were transferred to the litter and CWD pools, while the balance (i.e. 60%) remained unaffected. The biomass removal rates for the selective harvest were based on USFS harvest records (Phil Freeman, CNNF USFS, personal communication). Biome-BGC only simulates live (sapwood) and dead (heartwood) stem C pools (i.e. no size classes or branches), but this simplification has not impeded its ability to simulate C fluxes following disturbance (Thornton *et al.* 2002, Merganicova *et al.* 2005, Bond-Lamberty *et al.* 2007b).

In both clear-cut and selective harvest simulations, we simulated varying the amount of harvest residue left on the site. The three levels of harvest residue retention we used included the high and low limits used by the U.S. Forest Service (Ben Frater, CNNF USFS, personal communication). For each harvest regime and interval, we simulated 15, 25, and 35% of the harvest residue (percent of total harvested C from stem pool) left on site. Table 2 summarizes all the harvest and residue rate scenarios used in this study and their respective abbreviations that are used throughout the study. Although not all of these harvest scenarios are realistic forest management practices (i.e. selective harvest in jack pine), we included all of them for completeness.

2.5 Model evaluation

To confirm the model was accurately simulating the jack pine and sugar maple ecosystem C dynamics and their responses to disturbance, we first compared model outputs to field and eddy-covariance data from regional studies. Following a simulated clear-cut in 1915, each ecosystem was allowed to grow without the presence of fire for 400 years (this simulation was run specifically to compare to field data and is not listed in

Table 2). Model outputs from this simulation were then compared against available site, chronosequence, and flux tower data where stand age (time since disturbance) was known. We assessed the model's performance at tracking ecosystem recovery after harvest. Specifically, the rate of accumulation of soil organic matter (C), NPP, and NEP were compared to other studies.

Modeled total NPP (above- and belowground) were compared to the sum of measurements of above- and belowground (root) NPP for the two ecosystems. Aboveground NPP was estimated over two growing seasons for both jack pine and sugar maple-dominated stands in northern Wisconsin by Fassnacht & Gower (1997) using the sum of woody biomass increment and detritus production. Coarse and fine root production in a red maple-dominated forest in the northeastern U.S. were estimated by McClaugherty *et al.* (1982) from root core samples over two seasons, and their results were added to aboveground NPP to yield total NPP for sugar maple. Total NPP for jack pine was obtained by summing the aboveground data (Fassnacht & Gower 1997) and total root NPP for a jack pine stand in northern Wisconsin from Steele (1998, unpublished data). We also compared the decrease in NPP following simulated selective harvest in sugar maple to a manipulation study where NPP in a sugar maple-dominated hardwood stand was measured before and after a selection harvest (Dyer *et al.* 2010).

Model NEP was compared to eddy-covariance data from three flux towers near CNNF. Our modeled jack pine NEP and its transition from carbon source to sink was compared to observations from flux tower measurements over a young (age 12-14) naturally regenerating jack pine stand in the upper peninsula of Michigan, U.S.A. (Euskirchen *et al.* 2006). Our annual estimates of NEP in the maple ecosystem were compared directly against annual estimates of NEP derived from eddy-covariance measurements (Ankur Desai, personal communication) in mature and old-growth sugar maple-dominated stands located near CNNF (Desai *et al.* 2005).

To assess the model's performance in the accumulation of soil C, we compared model outputs to a chronosequence study located near CNNF that included two sugar maple-dominated stands (Tang *et al.* 2009) where soil C content was measured in the first 60cm of mineral soil. We also compared the model output of soil C (at the beginning of simulation in 2004) for both sugar maple and jack pine to a survey of upland forest C content over the Upper Great Lakes region (Grigal & Ohmann 1992).

3. Results

3.1. Net primary production (NPP)

Total (above- and belowground) NPP during the first 5 simulation years for the jack pine and sugar maple base scenario (equivalent to 85-90 years in stand age) averaged about 4.0 and 8.0 tC $ha^{-1}yr^{-1}$, respectively. Fassnacht and Gower (1997) reported the average aboveground NPP (averaged over two growing seasons) was 3.7 t biomass ha^{-1} yr^{-1} (or 1.8 tC) for four jack pine forests located in northcentral WI, USA, and Steele (1998, unpublished data) estimated root NPP for a jack pine stand in northcentral WI, USA to be 2.6 tC ha^{-1} yr^{-1}. The sum of above- and belowground NPP from these two field studies (4.4 tC ha^{-1} yr^{-1}) compares well to the modeled NPP (4.0) from this study (Figure 1a). For sugar maple, Fassnacht and Gower (1997) reported the average aboveground NPP (averaged over two growing seasons) was 9.2 t biomass ha^{-1} yr^{-1} (or 4.6 tC) for four stands. McClaugherty et al. (1982) estimated fine and coarse root production for a red maple-dominated hardwood stand at 2.7 and 0.7 tC ha^{-1} yr^{-1}. The sum, 8.2 tC ha^{-1} yr^{-1}, compares well to the results in this study (Figure 1a). Simulated NPP was up to 60% lower for the selective harvest (50% biomass/ha removal rate) than base scenario in years following harvest while measured NPP was 10% less for the selective harvest (10% of biomass/ha removal rate) of a sugar maple-dominated northern hardwood forest (Dyer et al. 2010). Collectively these results suggest BIOME-BGC does an adequate job of simulating NPP of these two forest ecosystems and simulating the effects of selective harvest on NPP.

We computed mean absolute NPP (not shown) and the rate of change in peak NPP (linear regression on the NPP peaks following each harvest as a function of time) for each simulation interval and harvest scenario (Figure 2). In the jack pine ecosystem, the C-100-15 scenario had the highest mean NPP of 4.48 tC $ha^{-1}yr^{-1}$. Over the 500-year simulation period, the average NPP was greater for the clear-cut than base and selection harvest scenarios, and ranged from 6.7% for C-50-15 to 11% for C-100-35. Selective harvest had less effect on NPP. The highest rates of increase in peak NPP occured in the 100-year selective harvests.

For sugar maple, NPP averaged 6.84 tC ha^{-1} yr^{-1} for the base scenario. In general, harvesting increased yearly mean NPP compared to the base, except for clear-cut scenarios (data not shown). Peak NPP declined for clear-cuts, but increased for selective harvests (Figure 2). For example, relative to the base scenario, the C-100-35 scenario decreased NPP the greatest (2%), while the S-50-15 increased NPP by 8.2%. All harvests except C-100-15 significantly changed ($p < 0.05$) peak NPP (Figure 2).

3.2 Net ecosystem production (NEP)

Simulated NEP for the base scenario sugar maple stand was 3 tC $ha^{-1}yr^{-1}$ at the beginning of the simulation (85 year-old stand). Estimated annual NEP for a 70-76 year-old sugar maple-dominated northern hardwood forest (Desai *et al.* 2005) was 3.8 tC $ha^{-1}yr^{-1}$ (Ankur Desai, personal communication), but they observed a two-fold variation in growing season (June-August) NEP for the five year measurement period. Based on eddy-covariance flux measurements, average NEP for an old growth northern hardwood forest (Desai *et al.* 2005) was -0.01 tC $ha^{-1}yr^{-1}$ (Ankur Desai, personal communication), which compares well to modeled NEP of 0.04 tC $ha^{-1}yr^{-1}$ for the sugar maple at an old growth state (Figure 1b).

Under the various harvest scenarios, despite the large negative shifts in NEP observed in the year following harvest of jack pine, NEP recovered within 15 years to levels higher than the base scenario (Figure 3) and continued at a level above the base scenario for the remainder of the rotation. All harvest scenarios had a higher total NEP than the base scenario (Figure 2). The C-50-15 scenario had the highest NEP and sequestered 473 tC ha^{-1} over 500 years simulation period for an average annual NEP of 0.95 tC ha^{-1}yr^{-1}. Conversely, the least intensive harvest scenario (S-100-35) had the lowest total NEP 138 T ha^{-1} for an average annual NEP of 0.28 tC ha^{-1}yr^{-1}. For comparison, the lowest NEP was 175% greater than the no harvest scenario (50 tC ha^{-1}).

The harvest scenarios dramatically changed simulated NEP for the sugar maple ecosystem (Figure 4). For the base scenario, cumulative NEP for the 500-year period, was 319 tC ha^{-1}, or 0.64 tC ha^{-1}yr^{-1}. NEP was greater for all harvest scenarios than for the base scenario (Figure 2). The C-50-15 management scenario had the greatest cumulative NEP of 978 tC ha^{-1}, or 1.96 tC ha^{-1}yr^{-1}, while the S-100-35 scenario had the lowest total NEP of 469 tC ha^{-1}, or an average annual NEP of 0.94 tC ha^{-1}yr^{-1}.

3.3 Accumulation of soil organic matter (C)

A key component of NEP and maintaining long-term soil fertility is soil C accumulation. The rate of increase in soil C for the base simulation (0.038 tC ha^{-1} yr^{-1} or 3.8 gC m^{-2} yr^{-1}) was very similar to measured annual soil C accumulation (Figure 1c) of 0.036 tC m^{-2} yr^{-1} , or 3.6 gC m^{-2} yr^{-1} between mature and old growth sugar maple stands reported by Tang *et al.* (2009). The total mineral soil C content at the beginning of the maple simulations of 13.4 kgC m^{-2} (Figure 1c,7) was within the approximate range of 11-

14 kgC m^{-2} for the top 1m of mineral soil for sugar maple-dominated hardwoods (Grigal & Ohmann 1992). Soil C content at the beginning of the jack pine simulation was roughly 80 tC ha^{-1} (8 kgC m^{-2})(Figure 5) which compares well to measured values of 6-8 kgC m^{-2} for the top 1m of mineral soil reported for jack pine in the region (Grigal & Ohmann 1992).

Total mineral soil C accumulated at a rate of 0.04 tC ha^{-1} yr^{-1} (Figure 5,6) over the 500-year simulation for jack pine base scenario. Both 50- and 100-year clear-cut harvest intervals generally accumulated soil C at lower rates than the selective harvest simulations (Figure 6). Annual mineral soil C accumulation rate increased as the amount of residue left increased for all harvest simulations, at a given treatment (selective or clear-cut). The most intensive scenario, C-50-15, exhibited the lowest rate of C accumulation in the soil (0.029 tC ha^{-1} yr^{-1}). Selective harvest scenarios increased total soil C accumulation rate by 15% over the clear-cut harvest for a given harvest interval and residue removal.

In the sugar maple ecosystem, mineral soil C content increased 0.04 tC ha^{-1} yr^{-1} for the 500-year no harvest management simulation. The largest soil C loss of -0.04 tC ha^{-1} yr^{-1} occurred for C-50-15 scenario and represents a 200% decrease from the base scenario (Figure 6). In contrast, the S-100-35 had the highest rate of soil C accumulation (0.03 tC ha^{-1} yr^{-1}) that was a 24% decrease from the base scenario. The other harvest scenarios fell between these two rates. All of the clear-cut harvests decreased mineral soil C content (Figure 6-7).

3.4 Available mineral soil nitrogen (N)

In the jack pine ecosystem, available mineral soil N tended to increase immediately following harvest due to less competition for available N, but then decreased during stand re-development (Figure 8). Available N loss was greater for the clear cut than selective tree harvest scenarios (Figure 6). The more intense harvest simulations decreased the available mineral soil N content by up to 10% (Figure 6,8). The C-50-15 scenario decreased available mineral soil N content by 10% relative to the no-harvest scenario, while the least intensive harvest scenario (S-100-35) decreased available mineral soil N content by only 1% compared to the no harvest scenario.

Trends in available soil mineral N content were similar to those observed in mineral soil C (Figure 6,9) simulations for sugar maple. Available mineral soil N content decreased for all harvest scenarios relative to the base. The greatest decrease in available soil N occurred for the clear-cut harvest scenarios, with the 50-year interval clear-cut decreasing available mineral soil N by more than 20%. Selective harvests reduced available mineral soil N content by 10% or less in all simulations (Figure 6).

3.5 Disturbance recovery

Another key consideration of forest ecosystem models is whether they can simulate the well-documented changes in NPP and NEP during stand redevelopment following stand-killing disturbance (i.e. clear-cut, wildfire, etc). NPP is initially low for several years after disturbance, reaches a maximum at canopy closure (10-30 years) and then declines as the stand matures (Gower *et al.* 1996, Ryan *et al.* 1997). NEP is typically negative for several years after stand-killing disturbance, reaches a peak around canopy closure and then declines to near zero for many forests (Bond-Lamberty et al.

2004). For sugar maple, BIOME-BGC simulated the negative NEP immediately after harvest, peak NEP around canopy closure and a 74% decline (Figure 1b). Desai *et al*. (2008) reported NEP decreased by 71% between the 75-year-old and the 200-year old growth northern hardwood forest. In jack pine, the stand transitioned between a C source and a C sink about 10 years after harvest (Figure 1b). Euskirchen *et al.* (2006), using eddy covariance towers, reported a young jack pine stand in northern Wisconsin transitioned from C source to a C sink between 10 and 20 years following disturbance.

Based on these comparisons we conclude that Biome-BGC is doing an adequate job simulating the C dynamics of jack pine and sugar maple over a typical rotation, and capturing the C dynamics associated with harvest. We acknowledge the uncertainty of the model at simulating multiple harvest rotations and suggest these data be viewed as general patterns. Nonetheless, these data are the only way to begin to explore the effects of different harvest scenarios on long-term C dynamics.

4. Discussion

4.1 Comparison of model simulations to field measurements

Ecosystem process models are tools that can be used to examine the long-term effects of different management scenarios on ecosystem dynamics. We examined the effects of different harvest and residue removal rates on key components of ecosystem C dynamics and available mineral soil N content – an important factor influencing forest productivity (Landsberg & Gower 1997). This issue is particularly important to devising forest management practices and policy to sequester C and still produce wood fiber for biofuel feedstock. The big advantage of ecosystem process models is they provide insight into questions that experimental studies would require decades to centuries to answer. Model simulations are the only short-term approach to determining if forest management scenarios will maintain the long-term soil productivity. The disadvantage to using ecosystem process models is they are analytical algorithms of how scientists perceive ecosystem function; therefore, it is important to understand if the models are providing realistic estimates of easily measured components of the C cycle.

Based on previous applications of Biome-BGC to both natural and managed ecosystems and our comparison of model outputs for the sugar maple and jack pine ecosystems, we conclude that Biome-BGC is doing a respectable job simulating the C dynamics of these forest ecosystems.

4.2 Effects of harvest on soil C and N

Understanding the short- and long-term effects of harvesting on soil productivity is a pressing issue because there is growing interest to increase harvest frequency and intensity (in both total amount and removal of harvest residues) to meet the demand for wood fiber and biofuel feedstock. To date most studies are field observations based on short-term measurements after one or two harvests. In a meta-analysis, (Johnson & Curtis 2001) reported no clear trend and found soil C and N both increased and decreased following harvest. Two other studies concluded that harvesting has little effect on soil C in the 10-20 years following harvest (Johnson *et al.* 2002, Powers *et al.* 2005). Based on these meta-analysis studies, the authors concluded that forest type (coniferous or deciduous) and harvest method were important factors that affected soil C and N content. Our modeling results support their conclusion. Whole-tree harvest reduced mineral soil C content while sawlog harvest increased soil C. Our results are reasonably consistent with the short-term results reported from field studies. We observed soil C and available mineral soil N content increased slightly in the decade following harvest (Figure 5, 7), but decreased thereafter for most scenarios. Similar trends were observed in post-harvest simulations using Biome-BGC for forests in Europe (Merganicova *et al.* 2005). Aber *et al.* (1982) performed one of the first model simulations of the effects of harvest options on soil fertility and they concluded that short rotations (i.e. 3 x 30-year or 2 x 45-year rotations versus 1 90-year) increased nutrient removal and decreased yield by as much as 66%. Duchesne and Houle (2008) concluded that whole-tree harvesting of boreal balsam fir forests increased K removal over conventional (i.e. stem-only) harvests by 60%, and therefore should be avoided for these forests. Selective harvests for the 100-year interval only slightly decreased soil C and available N in the sugar maple ecosystem, relative to the base scenario. Conversely, simulated clear-cuts of sugar maple greatly decreased soil C and available N relative to the base scenario. Our results illustrate the need for field data for several harvest rotations to better evaluate and improve ecosystem process models. Moreover, forest harvest and residue management plans should not be based on total soil nutrient pools, but on available nutrient pools. *The available N pool is a small fraction compared to the total pool, so impacts from management practices could go undetected. In Biome-BGC the available N pool is typically around 0.003% of the total soil N pool. Nadelhoffer et al. (1985) reported annual net mineralizable N comprised only 0.xx -0. xx% of total N.*

Soil N losses following harvest have been reported for sugar maple ecosystems (Holmes & Zak 1999). Although the effects of harvest were only observed for one year following a clear-cut harvest, increased rates of net N-mineralization and losses of mineral N due to leaching were reported. BIOME-BGC does not have a rigorous N leaching subroutine and therefore it may be unwise to compare simulation results to field measurements; however, the higher mineral N loss in the sugar maple than jack pine ecosystem is consistent with Vitousek et al. (1982), who reported higher N losses in nutrient-rich northern hardwood forests than nutrient-poor coniferous forests.

4.3 Impacts of increased harvest residue removal

Many state and federal forest management agencies are contemplating removing harvest residue or slash left on the site for biofuel feedstock and as a result are developing biomass harvest guidelines. Typically stems comprise 65% of the total aboveground biomass so the residual slash (i.e. branches, cull trees, etc.) represents a significant biomass pool. Results of this study indicate that for a given harvest type (clear-cut or selective) and harvest interval, as residue removal increased, mineral soil C losses increased relative to the base scenario. The decline in mineral soil C content is likely due to the reduced amount of C entering the soil pool through decomposition. While mineral soil C and available N content generally decreased with increasing residue removal, total NEP increased. This result is likely due to the reduction in litter and coarse woody debris that is available for decomposition and subsequent heterotrophic respiration. The decreased nutrient availability caused by greater removal of residual biomass decreased modeled NPP in some simulations, but only for sugar maple. Decreased nitrogen availability decreases (i) leaf level photosynthetic rates, (ii) canopy-level leaf area index, and allocation to woody biomass in favor of fine root NPP (Gower *et al.* 1995). Although NPP is positively related to plant-available N in both deciduous broadleaf and evergreen needleleaf forests in Wisconsin (Nadelhoffer et al. 1985), we did not observe a significant linear decline in peak productivity with declines in available N. These results suggest that there may be a threshold of harvest frequency, type, and residue removal rate where N begins to limit productivity. Average NPP for selective harvest scenarios with lower amounts of residue left on site did not decline as much in the harvest year as those with higher amounts of residue removal. In the clear-cut simulations, scenarios with the lower residue recovered to maximum NPP more quickly than those with higher amounts of residue left, likely due to the reduced competition for available N between growth and decomposition. These results highlight the potential opportunity to improve the model's ability to simulate soil N dynamics; however, the model logic should be based on fundamental understanding of harvest effects on the different soil C and N pools – and this is lacking (Holmes & Zak 1999, Idol *et al.* 2003, Stoffel *et al.* 2010).

4.4 Maximizing carbon sequestration and long-term soil productivity

Our model simulations indicate that the more intense harvest scenarios increased total NEP. However, the increase in total NEP was associated with a decrease in mineral soil C content (Figure 10a-b). The results may seem counter-intuitive, but they are reasonable when the different processes (i.e. plant versus soil) and their rates are considered. Net ecosystem production, or NEP, is the difference between net primary production and heterotrophic respiration. The vegetation C dynamics are more variable, non-linear and operate at a faster time scale than soil C dynamics (Figure 5 versus Figure 3). The NPP decline in forest can range from 4 – 76% (Gower *et al.* 1996) and NEP can range from negative to positive. Conversely mineral soil C dynamics, especially the slow C pools operate on a much slower time scale of 10^2 to 10^3 years. NEP is negative immediately following fire in black spruce and timber harvest of jack pine for roughly the first 10-15 years (Bond-Lamberty *et al.* 2004, Howard *et al.* 2004), then increases to a maximum within 50 years of disturbance, and then declines to near zero. Similar patterns have been reported for sugar maple (Desai et al. 2008). Conversely, the soil C pools change less because of the slow turnover rates, especially the recalcitrant pool. We acknowledge that the results of the model are very sensitive to the approach of modeling the different carbon pools, which does not differ from most other ecosystem process models (i.e. Century, BIOMASS, PNET, etc.). Admittedly our understanding of the effects of land use and management activities on the various mineral soil C pools is rudimentary compared to our understanding of vegetation C processes of photosynthesis and respiration. However, our pre-simulation initialization of the soil C pool follows other published studies (Pietsch & Hasenauer 2002, Thornton *et al.* 2002, Thornton &

Rosenbloom 2005) and seems to provide accurate estimates of annual soil C accumulation rates (see model evaluation section).

Assuming the model is a reasonable approximation of the vegetation and soil C dynamics, the data can be used to determine which management scenario would provide the greatest amount of biomass for biofuel feedstock and minimize reduction of long-term soil productivity. Maximum C storage in the soil occurs when no harvesting occurs; however, maximum C sequestration in the vegetation occurs for shorter harvest intervals because the forest rotation spends a greater amount of time near maximum NEP, even though more frequent harvest regimes increase mineral soil C loss.

Long-term simulation of different management scenarios provides the opportunity to assess the effects of different harvest regimes on soil carbon and nitrogen cycles, as well as to assess their sustainability. In this study we used the ecosystem process model Biome-BGC to simulate harvests for two common forest types in the Great Lakes states. Simulations included clear-cut and selective harvests at 50- and 100-year harvest intervals with varying residue left after harvest from 15-35%. While more intensive harvest scenarios tended to increase overall net ecosystem production, mineral soil carbon and nitrogen declined. All the simulated jack pine and sugar maple harvest scenarios decreased mineral soil C and available N content relative to the no-harvest case. Certain harvest scenarios in sugar maple increased net ecosystem production over no-harvest, and increased soil C content. The fate of harvested C was not included in this study and should be the focus of future research in order to determine overall system C balance.

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Zak DR, Host GE, Pregitzer KS (1989) Regional variability in nitrogen mineralization, nitrification, and overstory biomass in Northern Lower Michigan. *Canadian Journal of Forest Research,* **19**, 1521-1526.

Table 1. Ecophysiological values used to parameterize Biome-BGC. All values were selected or calculated from White *et al.* (2000). The superscripts denote species-specific (γ), general evergreen needleleaf or deciduous broadleaf (φ), or all biome (ζ) values. Values used only during model initialization (and set to 0 otherwise) are denoted by (*).

Parameter	Jack pine	Sugar maple
Turnover and mortality		
Leaf mortality (year^{-1})	0.29^{γ}	1.0^{φ}
Live wood mortality (year^{-1})	0.70^{ζ}	0.70^{ζ}
Whole-plant mortality (year^{-1})	0.005^{φ}	0.005^{φ}
Fire mortality (year^{-1})	0.015^{*}	$0.0025^{\varphi *}$
Allocation and N requirements		
Fine root C:leaf C	1.0^{γ}	1.55^{γ}
Stem C:leaf C	2.2^{γ}	2.3^{γ}
Live wood C:total wood C	0.07^{φ}	0.179^{φ}
Coarse root C: stem C	0.3^{φ}	0.22^{φ}
Growth C:storage C	0.5^{φ}	0.5^{φ}
Leaf C:leaf N	40.3^{γ}	25.0^{γ}
Leaf litter C:leaf litter N	103.0^{γ}	55.0^{γ}

Fine root C:fine root N	58.0^{φ}	48.0^{γ}
Live wood C:live wood N	60.0^{φ}	50.0^{γ}
Dead wood C:dead wood N	730.0^{φ}	556.0^{γ}
Leaf litter labile:cellulose:lignin (%)	$29{:}42{:}29^{\gamma}$	$45{:}43{:}12^{\gamma}$
Fine root labile:cellulose:lignin (%)	$34{:}44{:}22^{\varphi}$	$18{:}48{:}34^{\gamma}$
Dead wood cellulose:lignin (%)	$72{:}28^{\gamma}$	$75{:}25^{\gamma}$
Canopy parameters		
Water interception ($LAI^{-1} day^{-1}$)	0.052^{γ}	0.04^{φ}
Light extinction	0.51^{φ}	0.54^{φ}
SLA (projected area basis) ($m^2 kg^{-1} C$)	8.2^{γ}	36.3^{γ}
Shaded/sunlit SLA	2.0^{ζ}	2.0^{ζ}
All sided:projected leaf area	2.6^{φ}	2.0^{φ}
Leaf N in Rubisco (%)	4.0^{γ}	9.0^{γ}
Maximum g_s ($m s^{-1}$)	0.006^{ζ}	0.006^{ζ}
Cuticular conductance ($m s^{-1}$)	0.00006^{ζ}	0.00006^{ζ}
Boundary layer conductance ($mm s^{-1}$)	0.09^{φ}	0.01^{φ}

Ψ_L start of g_s reduction (MPa)	-1.0^{γ}	-0.2^{γ}
Ψ_L complete g_s reduction (MPa)	-2.8^{γ}	-1.3^{γ}
VPD start of g_s reduction (kPa)	0.8^{γ}	1.2^{γ}
VPD complete g_s reduction (kPa)	3.8^{γ}	3.4^{γ}

Table 2. Description of the harvest scenarios simulated using Biome-BGC.

Scenario	Harvest Type	Harvest Interval (years)	Residue Left (%)
Base	-	-	-
C-50-15	Clear-cut	50	15
C-50-25	Clear-cut	50	25
C-50-35	Clear-cut	50	35
S-50-15	Selective	50	15
S-50-25	Selective	50	25
S-50-35	Selective	50	35
C-100-15	Clear-cut	100	15
C-100-25	Clear-cut	100	25
C-100-35	Clear-cut	100	35
S-100-15	Selective	100	15
S-100-25	Selective	100	25
S-100-35	Selective	100	35

Figure Legends

Figure 1. Comparison of model outputs to regional measurements. All model outputs are plotted versus time (in years) since disturbance. a) Modeled NPP for both jack pine and sugar maple are compared to the sum of aboveground NPP from Fassnacht & Gower (1997) and root NPP for jack pine from Steele (unpublished data) and sugar maple from McClaugherty *et al.* (1982). b) Modeled NEP for sugar maple is compared to eddy-covariance data for two sugar maple-dominated stands (Ankur Desai, personal communication). c) Soil C accumulation in sugar maple is compared to measurements made in the first 60cm of mineral soil in sugar maple stands (Tang *et al.* 2009).

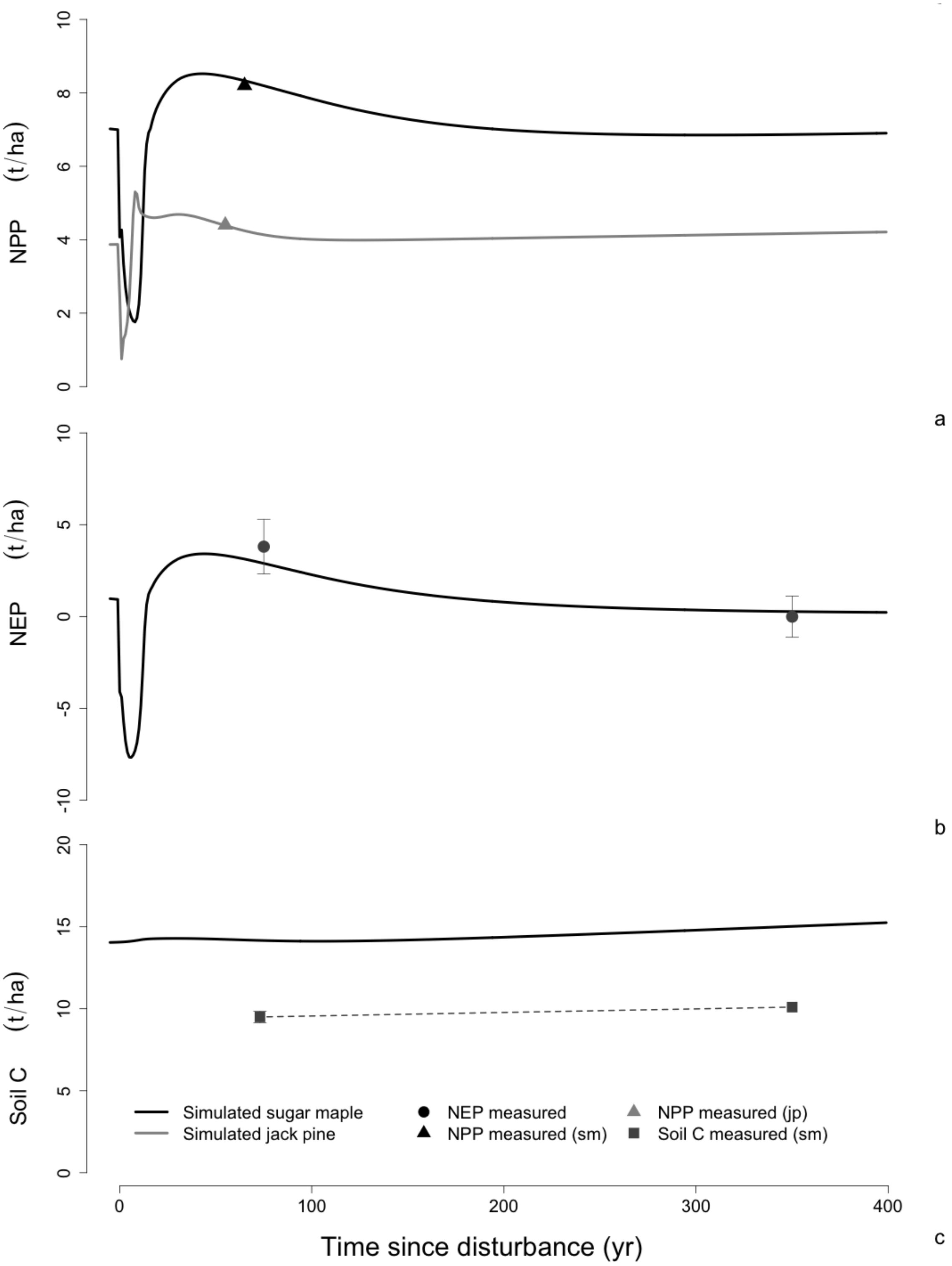

NPP (t/ha)
10
8
6
4
2
0
a
NEP (t/ha)
10
5
0
-5
-10
b
Soil C (t/ha)
20
15
10
5
0
Simulated sugar maple
Simulated jack pine
● NEP measured
▲ NPP measured (sm)
▲ NPP measured (jp)
■ Soil C measured (sm)
0
100
200
300
400
Time since disturbance (yr)
c

Figure 2. Change in peak NPP plotted versus total NEP. Open symbols denote sugar maple simulations while solid symbols denote jack pine. Triangles denote clear-cut and circles the selective harvests. Square symbols represent no harvest simulations.

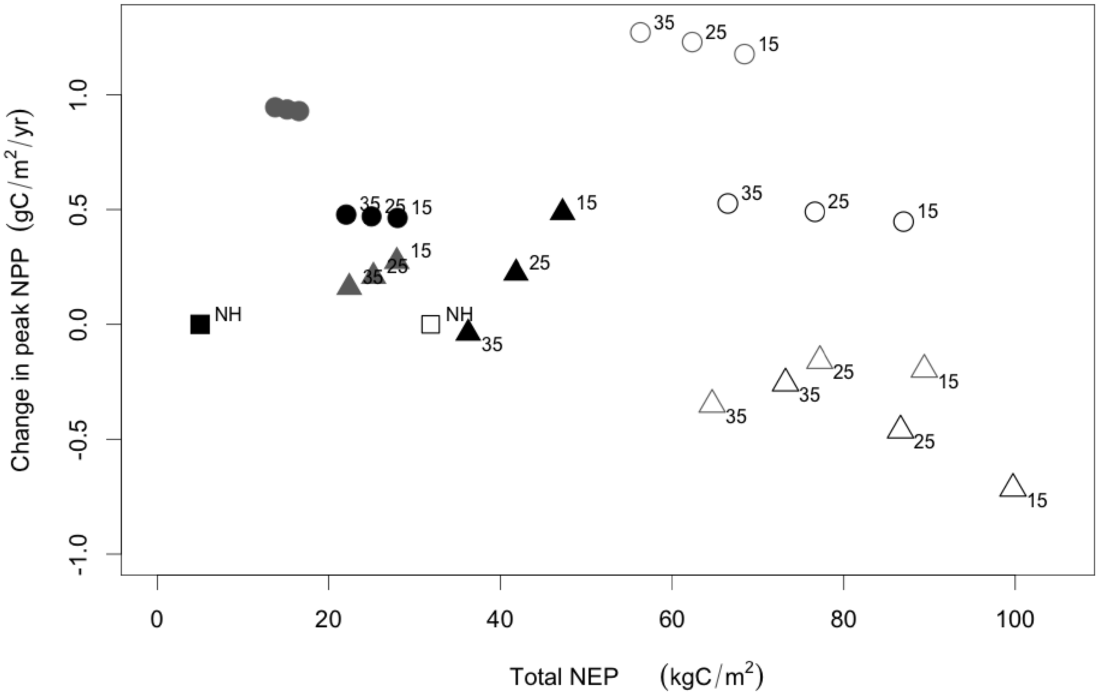


Figure 3. Yearly NEP model output of simulated harvested scenarios for Jack Pine, a) 50-year interval and b) 100-year interval.

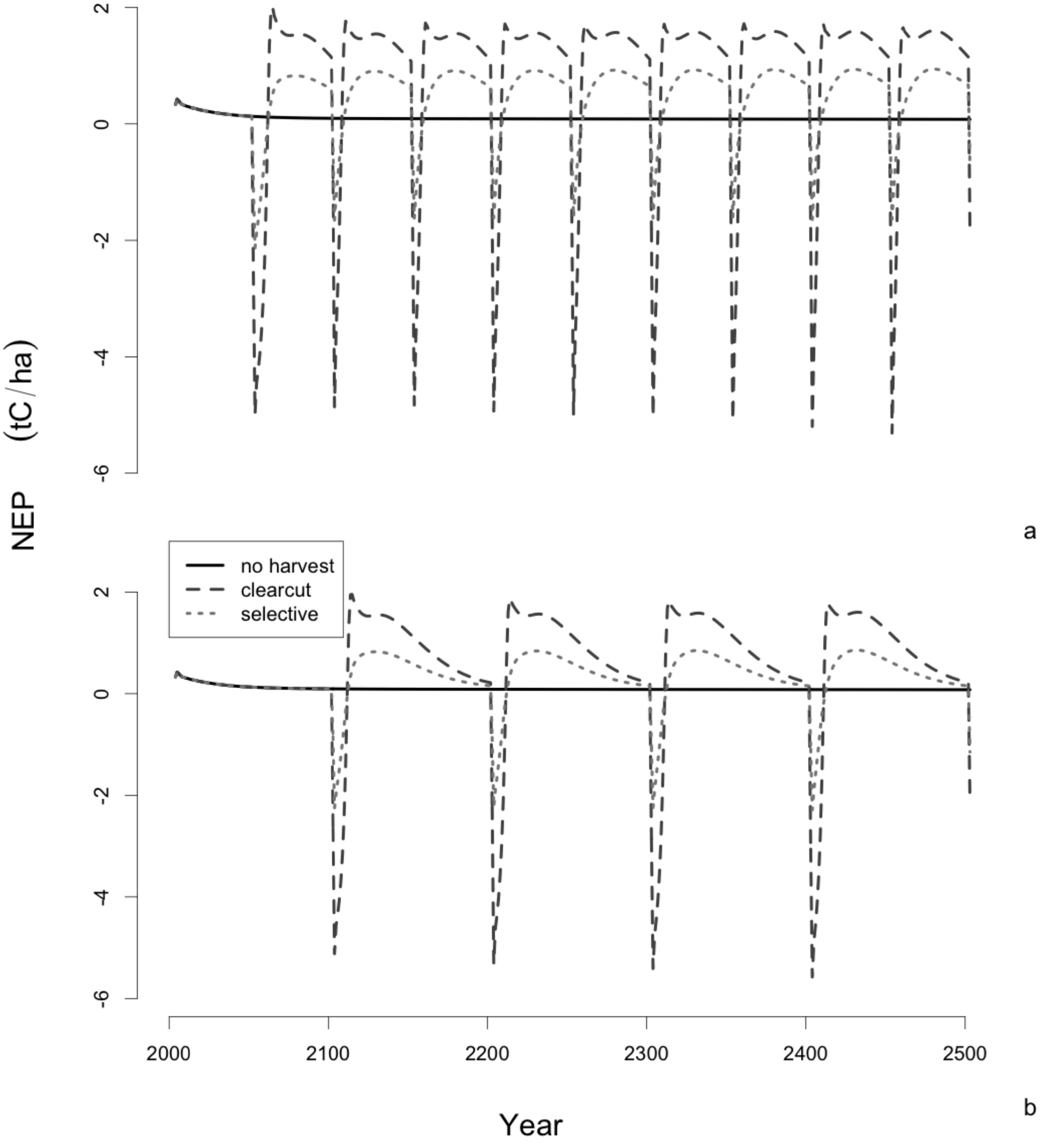


Figure 4. Yearly NEP model output of simulated harvested scenarios for Sugar Maple, a) 50-year interval and b) 100-year interval.

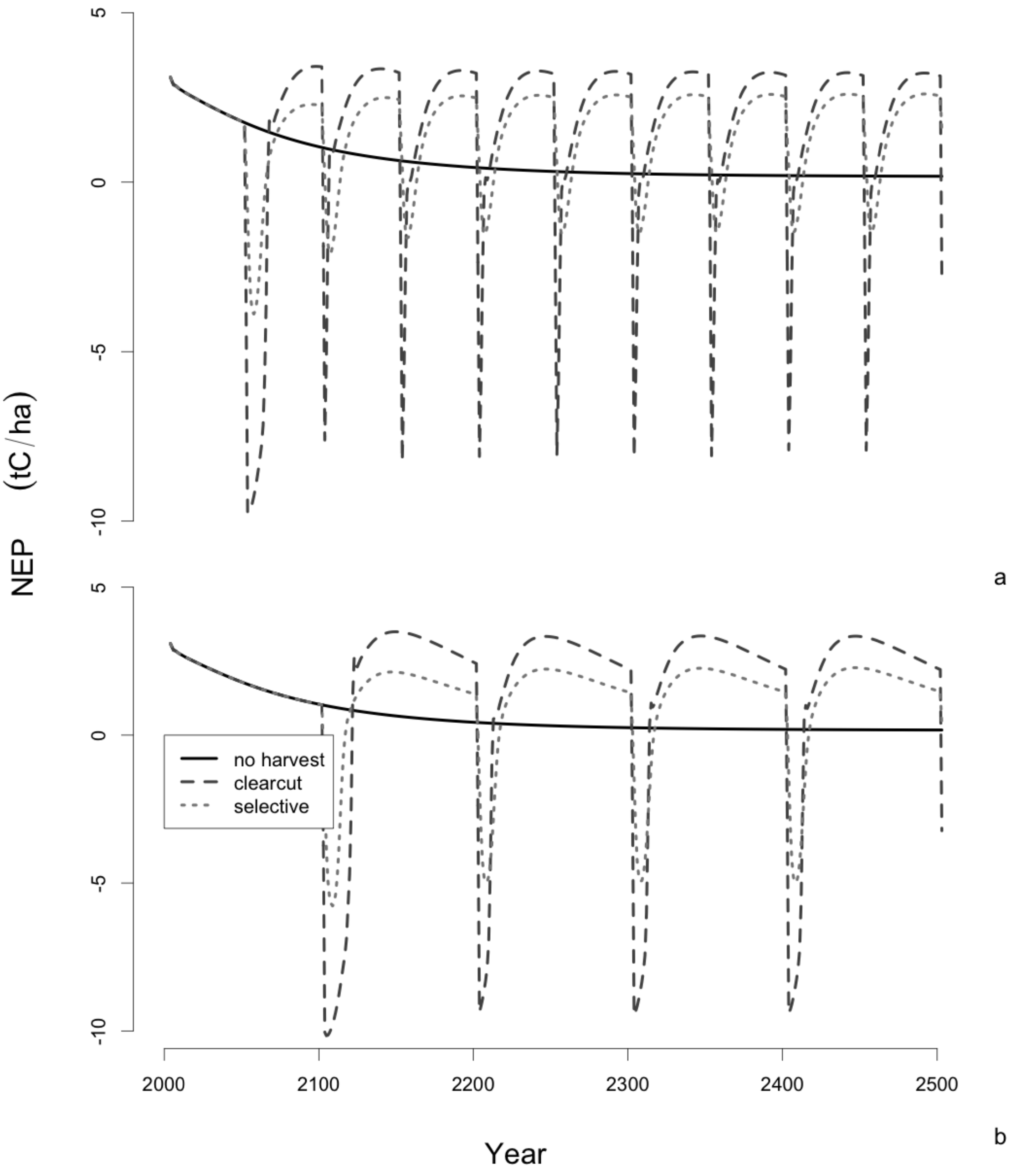


Figure 5. Soil C model output of simulated harvest scenarios for Jack Pine, a) 50-year interval and b) 100-year interval. Only the 25% residue level simulations are shown. The light grey solid line is a no-harvest simulation with both CO_2 and Ndep held at pre-industrial levels.

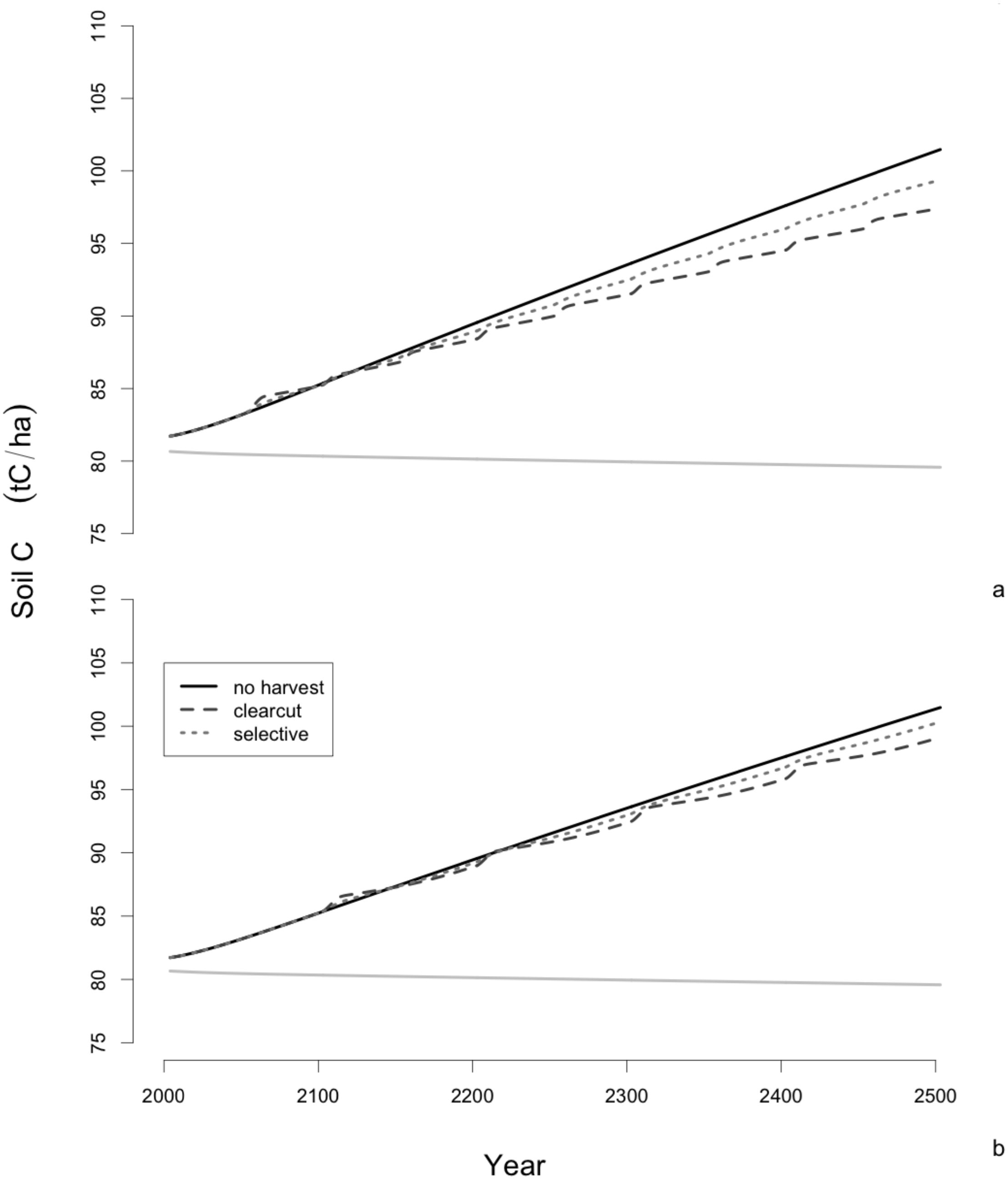


Figure 6. Soil C accumulation rate plotted versus the decrease in available soil N. Open symbols denote sugar maple simulations while solid symbols denote jack pine. Triangles denote clear-cut and circles the selective harvests. Square symbols represent no harvest simulations.

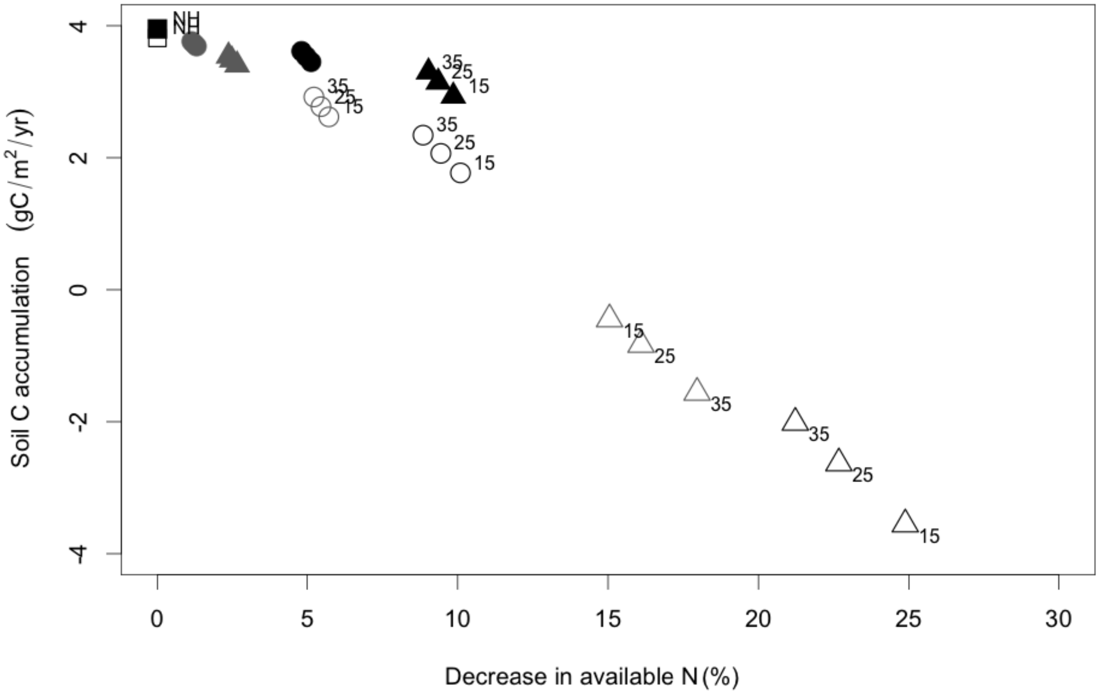


Figure 7. Soil C model output of simulated harvest scenarios for ssugar maple, a) 50-year interval and b) 100-year interval. The light grey solid line shows the result had the no harvest simulation been conducted with pre-industrial CO_2 and Ndep.

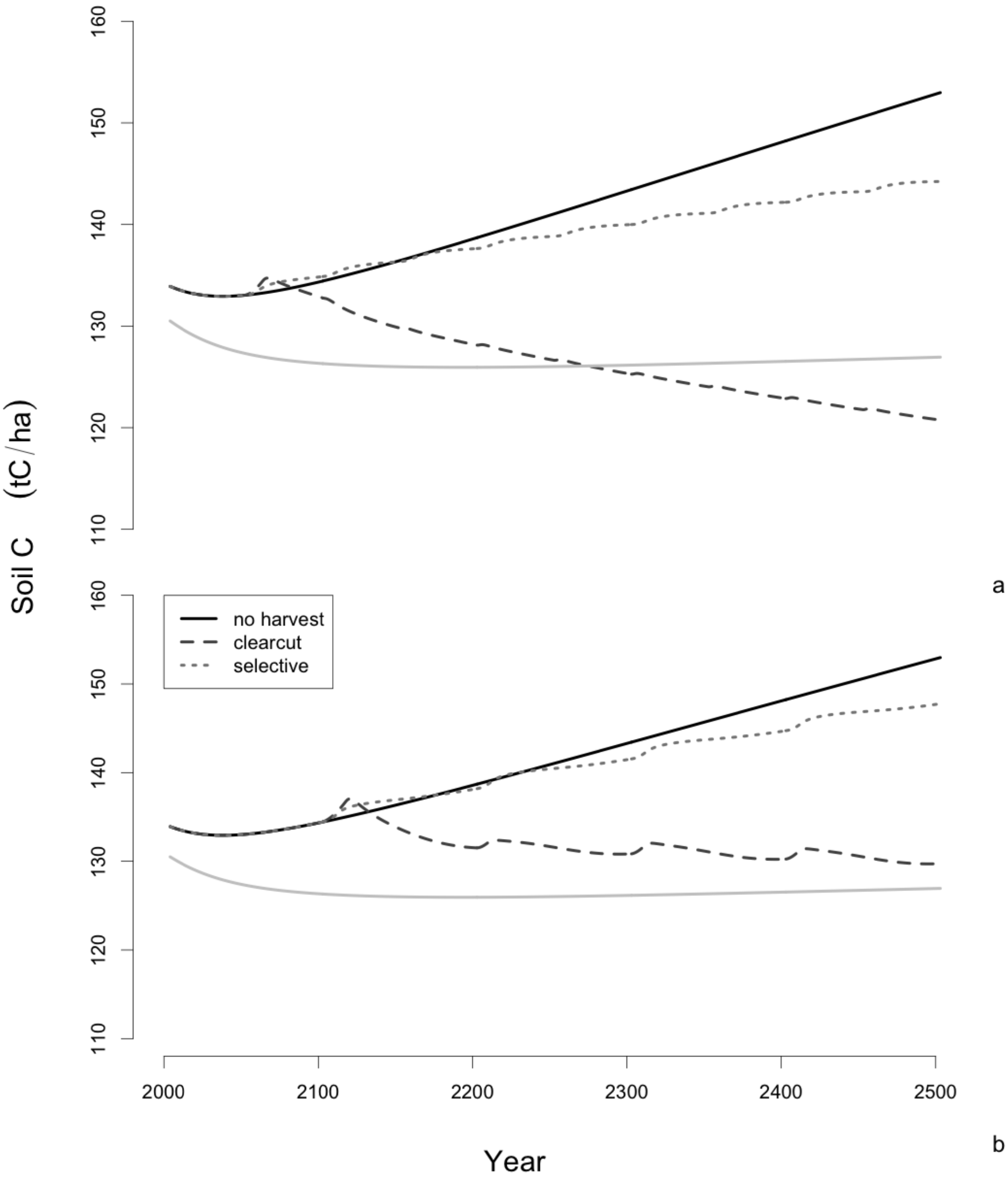


Figure 8. Available mineral soil N model output of simulated harvest scenarios for jack pine, a) 50-year interval and b) 100-year interval.

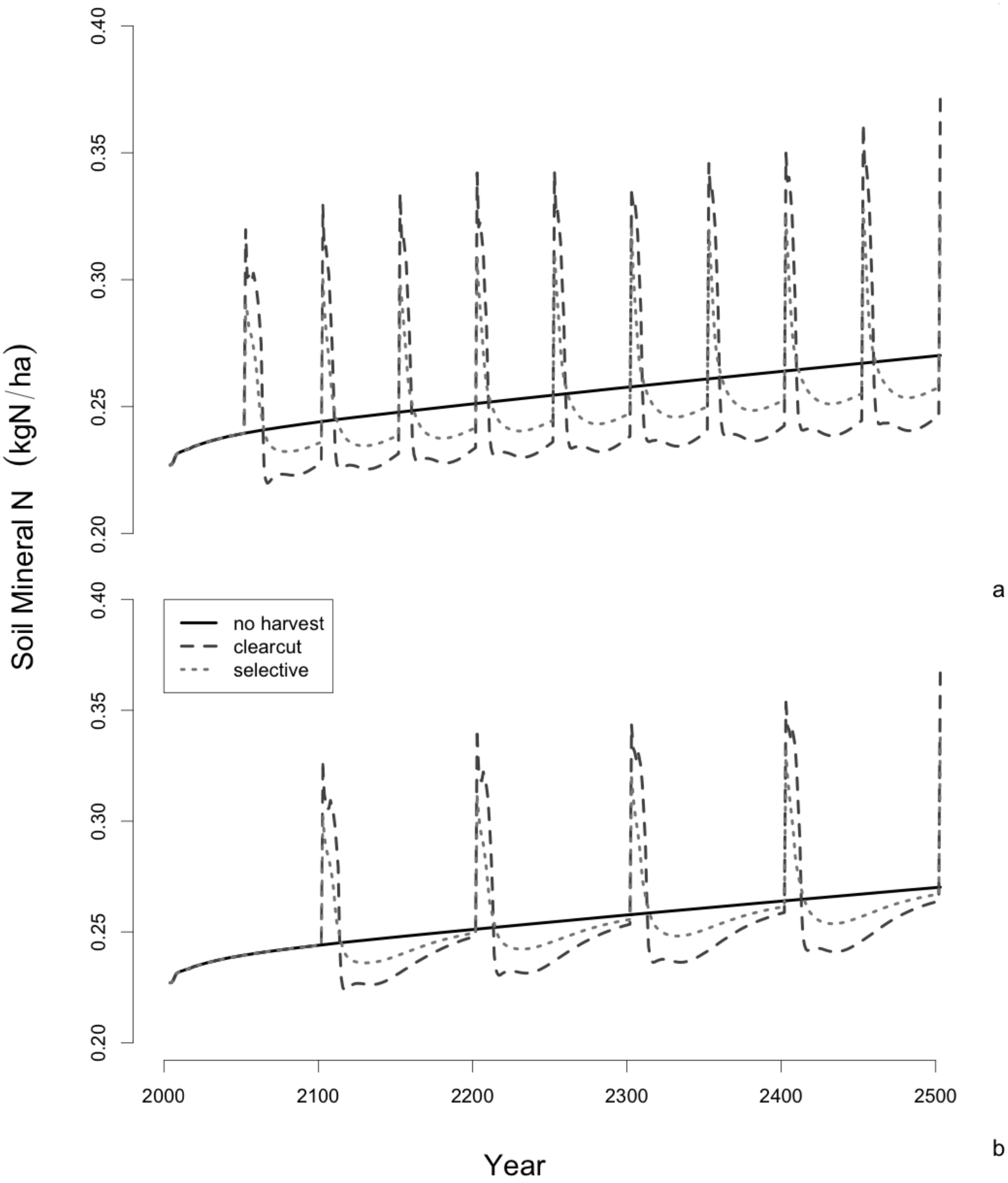


Figure 9. Available mineral soil N model output of simulated harvest scenarios for sugar maple, a) 50-year interval and b) 100-year interval.

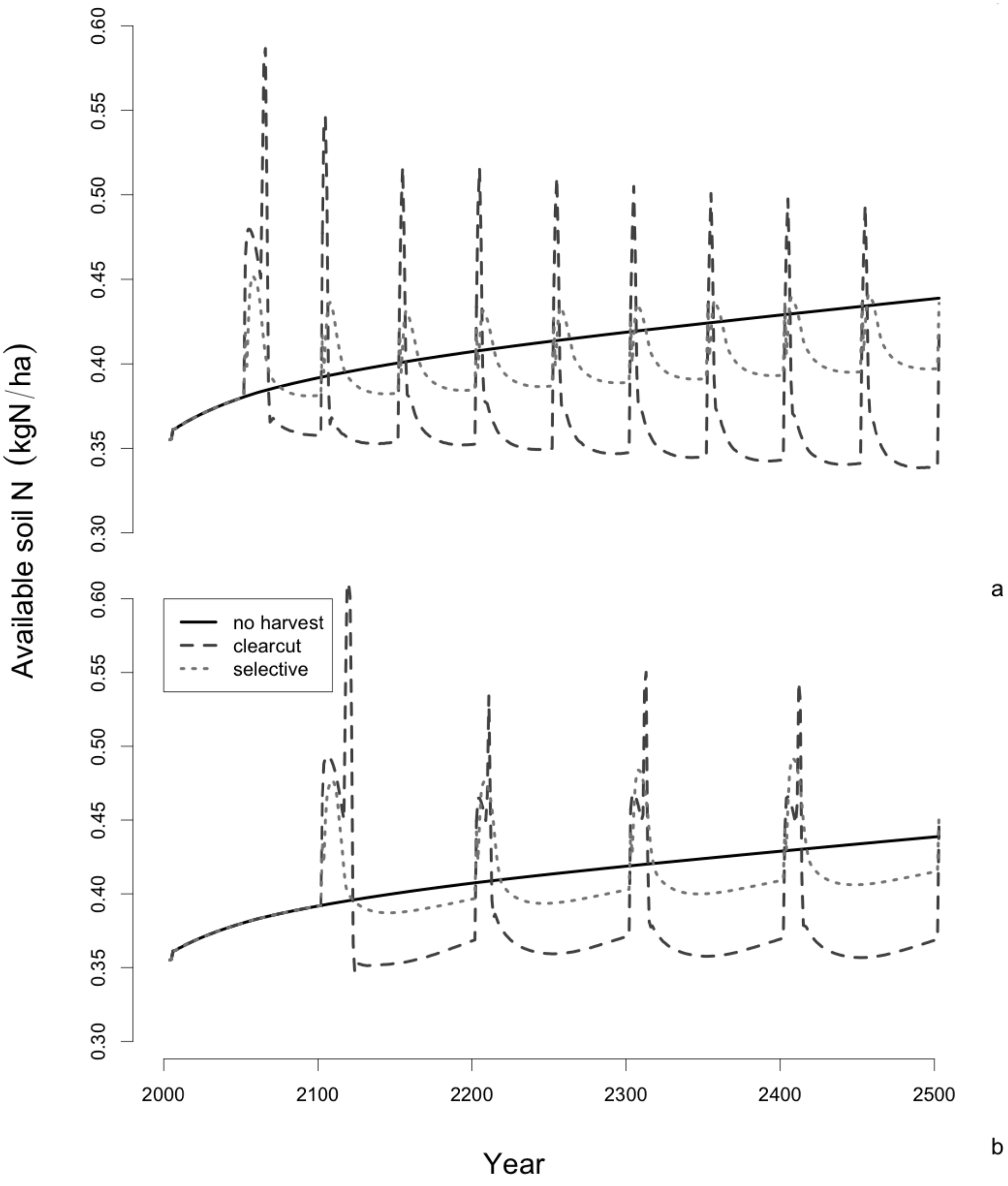
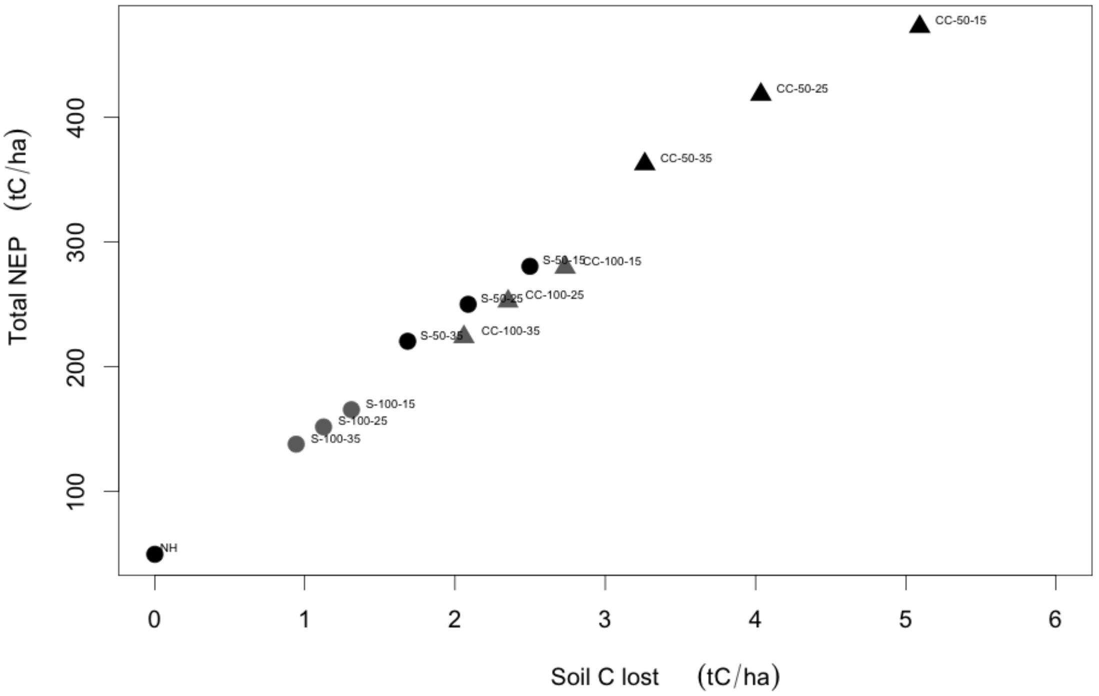
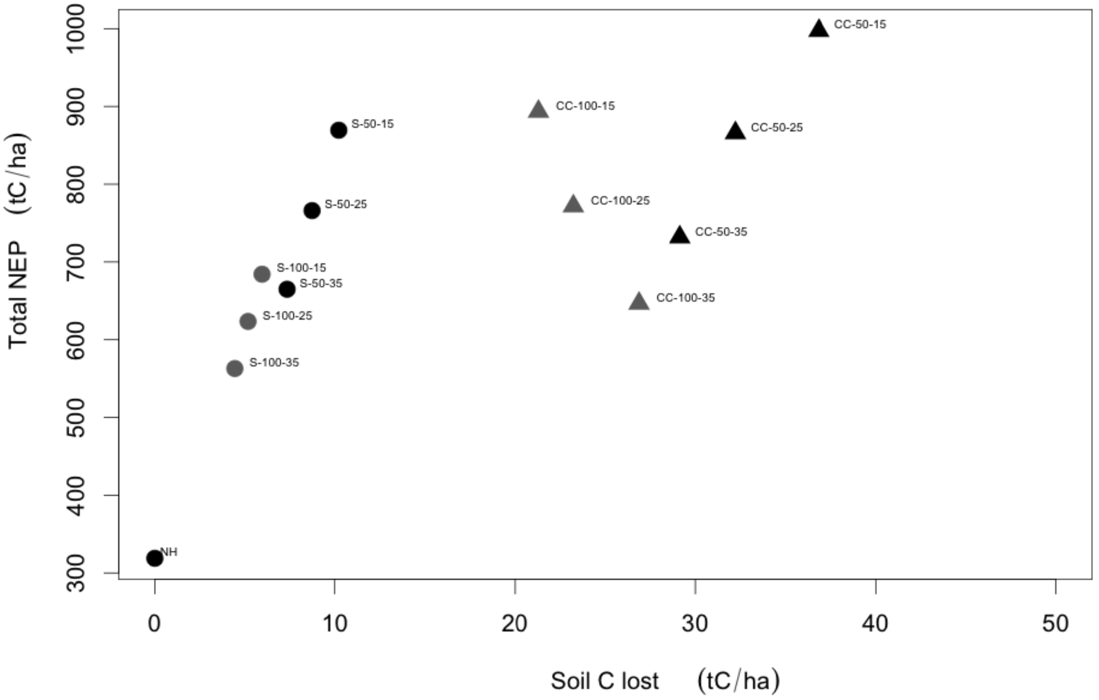


Figure 10. NEP vs. soil C lost for all model simulations, a) jack pine and b) sugar maple. Circles denote selective harvests and triangles the clear-cut scenarios. 50-year interval simulations are represented by black-colored symbols and 100-year interval by grey-colored symbols. Each simulation is labeled with its respective residue level. No harvest simulations are marked with a square.


CC-50-15
CC-50-25
CC-50-35
S-50-15
CC-100-15
S-50-25
CC-100-25
S-50-35
CC-100-35
S-100-15
S-100-25
S-100-35
NH
Total NEP (tC/ha)
100
200
300
400
Soil C lost (tC/ha)
0
1
2
3
4
5
6

a


Total NEP (tC/ha)
Soil C lost (tC/ha)
300
400
500
600
700
800
900
1000
0
10
20
30
40
50
NH
S-50-15
S-50-25
S-50-35
S-100-15
S-100-25
S-100-35
CC-50-15
CC-50-25
CC-50-35
CC-100-15
CC-100-25
CC-100-35

b