Forest Ecology and Management 262 (2011) 1826–1833

Contents lists available at SciVerse ScienceDirect

Forest Ecology and Management

journal homepage: www.elsevier.com/locate/foreco

Recovery of carbon and nutrient pools in a northern forested wetland 11 years after harvesting and site preparation

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ARTICLE INFO

Article history:
Received 19 May 2011
Received in revised form 24 July 2011
Accepted 26 July 2011
Available online 27 August 2011

Keywords:
Forested wetland
Carbon balance
Harvest and site preparation impacts
Histic mineral soil wetland

ABSTRACT

We measured the change in above- and below-ground carbon and nutrient pools 11 years after the harvesting and site preparation of a histic-mineral soil wetland forest in the Upper Peninsula of Michigan. The original stand of black spruce (*Picea mariana*), jack pine (*Pinus banksiana*) and tamarack (*Larix laricina*) was whole-tree harvested, and three post-harvest treatments (disk trenching, bedding, and none) were randomly assigned to three Latin square blocks ($n = 9$). Nine control plots were also established in an adjoining uncut stand. Carbon and nutrients were measured in three strata of above-ground vegetation, woody debris, roots, forest floor, and mineral soil to a depth of 1.5 m. Eleven years following harvesting, soil C, N, Ca, Mg, and K pools were similar among the three site preparation treatments and the uncut stand. However, there were differences in ecosystem-level nutrient pools because of differences in live biomass. Coarse roots comprised approximately 30% of the tree biomass C in the regenerated stands and 18% in the uncut stand. Nutrient sequestration, in the vegetation since harvesting yielded an average net ecosystem gain of 332 kg N ha^{-1}, 110 kg Ca ha^{-1}, 18 kg Mg ha^{-1}, and 65 kg K ha^{-1}. The likely source for the cations and N is uptake from shallow groundwater, but N additions could also come from non-symbiotic N-fixation and N deposition. These are the only reported findings on long-term effects of harvesting and site preparation on a histic-mineral soil wetland and the results illustrate the importance of understanding the ecohydrology and nutrient dynamics of the wetland forest. This wetland type appears less sensitive to disturbance than upland sites, and is capable of sustained productivity under these silvicultural treatments.

Published by Elsevier B.V.

1. Introduction

Forests comprise a significant proportion of the wetland types in North America and Europe, with approximately 50% of the total wetland area in the United States being forested (Frayer, 1991; Sahagian and Melack, 1998; Dahl, 2000). Forested wetlands are considered to be long-term terrestrial C sinks, so they are very important in global C accounting (Eswaran et al., 1993; Trettin and Jurgensen, 2003; McLaughlin, 2004). These wetlands are a component in many landscapes, and can be very productive under intensive forest management, especially after water management systems are installed (Terry and Hughes, 1975; Paavilainen and Päivänen, 1995). Much information is available on the impact of different forest management practices in drained peatlands, especially in northern Europe, where drainage and timber harvesting typically reduce soil C and nutrient pools (Trettin et al., 1995; Westman and Lasiho, 2003). In contrast, very little research has been conducted on the effects of forest management on C and nutrient pools in undrained wetlands. This was shown by Johnson and Curtis (2001) in a meta-analysis on the effects of timber harvesting and site preparation on mineral soil C and N pools, where only one of the 73 studies was from a wetland – a poorly-drained pine "flatwood" forest in Florida. Only three forested wetlands were among the 75 studies used by Nave et al. (2010) in a similar meta-analysis of harvesting impacts on C pools in both forest floor and mineral soil.

Much information on soil changes following timber harvesting and site preparation in both wetland and upland soils come from short-term (<5 year) studies (Trettin et al., 1995; Johnson and Curtis, 2001; Piirainen et al., 2002; Finér et al., 2003; Nave et al., 2010). However, it is difficult to evaluate potential long-term effects of these forest management practices on wetland soil C and nutrient pools from such short-term studies because of uncertainties in: (a) soil organic matter (OM) decomposition and accumulation rates, (b) stand composition and growth, and (c) the interaction of hydrologic regimes, soil aeration, and nutrient cycling (Fiedler and Sommer, 2002). This was shown by Minkkinen and Laine (1998), who

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0378-1127/$ - see front matter Published by Elsevier B.V.
doi:10.1016/j.foreco.2011.07.031

found both gains and losses in soil C over a 60-year period following drainage and silvicultural treatments on Finnish peatlands with different vegetation types and productivities.

The major impetus for this study was the lack of information on the management of histic-mineral wetland forests, which are important source of wood fiber in the upper Great Lakes region (Trettin et al., 1997). Taxonomically, histic-mineral soils have a thick (5–40 cm) accumulation of OM above the mineral soil, in contrast to Histosols, which have >40 cm of OM within 60 cm of the soil surface (Trettin and Jurgensen, 2003). Collectively, Histosols and histic-mineral soils are often referred to as peatlands or mires, with definitions of peat and mineral soils varying by country. Generally, mires are soils that accumulate OM above a mineral surface. However, the presence of both thick surface organic layers and mineral soil horizons in the rooting zone, which are characteristic of histic mineral soils, could cause these wetlands to respond to management differently than deeper ''peat'' soils. Therefore, in 1988 we established a study to measure the effects of whole-tree harvesting and two site preparation practices (disk trenching, bedding) on soil C and nutrient pools in a histic-mineral soil that is representative of many forested wetlands in the upper Great Lakes Region of the US To our knowledge, this is the only study on the effects of timber harvesting on this type of wetland soil. Earlier results showed that C and nutrient pools declined after harvesting and site preparation (Trettin et al., 1992; McLaughlin et al., 1996; Trettin et al., 1997). In this paper, we report on the status of soil C and nutrient pools 11 years after harvest, and the accumulation of C and nutrients in the regenerating stands during this period.

2. Methods

2.1. Site description

The study site is a histic-mineral wetland located between two streams on a sandy outwash plain in the Upper Peninsula of Michigan (Fig. 1). The overstory was a 70 year-old mixed stand of jack pine (*Pinus banksiana* Lamb.), black spruce (*Picea mariana* (Mill.) B.S.P.), and tamarack (*Larix laricina* (Du Roi) K. Koch). Understory vegetation was dominated by blueberry (*Vaccinium angustifolium* (Ait.) Gray and *V. myrtiilloides* Michx.), leather leaf (*Chamaedaphne calyculata* (L.) Moench.), Labrador tea (*Ledum groenlandicum*) and *Sphagnum* spp., with minor components of star flower (*Trientalis borealis* [Raf.]), golden rod (*Solidago* spp.), bunch berry (*Cornus canadensis* [L.], and *Carex* spp. The soil is the coarse-textured Kinross series (Typic Haplaquod, sandy, mixed, frigid), which has a histic epipedon overlaying an acid, sandy solum. The soil drainage class is very poorly drained, and is characterized by a seasonal high water table near the surface November through May. The water table fluctuates to a depth of 20–80 cm below the soil surface during the growing season. Mean annual temperature of the site is 5 °C and it receives 840 mm of precipitation, approximately 40% of which is snow.

2.2. Experimental design

Fifteen hectares of the stand were whole-tree harvested (WTH) with feller bunchers and grapple skidders in July 1988. All trees > 5 cm dbh were skidded to a landing outside the study area and chipped. Three 32 x 32 m plots of three site preparation treatments (trenching [TR], bedding [BD], and harvest-only [HO]) were established within each square of a 3 x 3 Latin Square, yielding a total of nine replicates per treatment (Fig. 1). Trenching was done with a TTS-disk trencher, which produced an alternating pattern of furrows and berms over approximately 50% of the soil surface area (Fig. 2). The bedding treatment was a 40–70 cm raised planting bed formed by an Eden Relief bedding plow. The harvest-only treatment had no post-harvest site preparation. Each plot had an 8 m wide buffer strip on each side. Three blocks (nine plots) were also established in the adjacent uncut part of the stand to serve as a reference control. All treatment plots were planted with 1 year old containerized jack pine in August 1988. In 1998, a wildfire destroyed nearly all of the treatment plots in one square, so four replicates of each treatment in the remaining two squares were used in this study.

2.3. Field sampling

2.3.1. Vegetation

2.3.1.1. Overstory. In July 1999 the number, height, and diameter of trees (>2.5 cm at dbh, or at ground line if <2.5 cm at dbh) by species were measured on one 10×10 m subplot centered within each treatment plot. Two increment cores were taken at the base of three dominant trees in each plot and used to determine tree age, diameter increment, and nutrient content. Leaf and branch samples from a branch >30 cm long in the middle of the crown were also collected from six dominant trees in each plot and separated into leaves and branches for nutrient analyses.

2.3.1.2. Sapling layer. Numbers of stems and basal diameter of each shrub and tree <2.5 cm in diameter and >1 m in height were measured on one 4×4 m subplot per treatment plot. Two shrubs and trees of each size class and species were harvested from each treatment, and separated into leaves, branches, and stem.

2.3.1.3. Understory. All plants <1 m in height were clipped from one 0.10 m^2 quadrat located on three adjacent microsite positions (top, side slope, pit) in each plot for a total of three samples per treatment plot. The biomass from these three microsites was composited to give one sample per plot. Bryophytes were cut at ground line at the point where they were no longer considered living (i.e. green) mass.

2.3.2. Woody residue

Four 15.3 m transects were run from the center of each plot in north, east, south, and west directions. The line intercept method described by Brown (1971) was used to measure woody residue amounts in four size classes: 0.6–2.5 cm, 2.5–7.6 cm, >7.6 cm solid, and >7.6 cm rotten. Woody material <0.6 cm was included in the forest floor samples.

2.3.3. Soil

Since some soil redistribution occurs in any mechanical site preparation treatment, the method of soil sampling will affect the interpretation of soil changes. All too frequently, studies addressing site preparation and harvesting impacts fail to consider changes in micro-relief, soil redistribution, and vegetation associated with the treatments in the soil sampling design (Attiwill et al., 1985). Our approach was to ensure that we sampled a soil volume that was comparable among the different site preparation treatments. Since bedding and trenching change soil surface elevation, soil core sampling depths were based on the original mineral soil surface elevation. Since random soil coring would necessarily involve a very large number of samples, we systematically took cores across the range of micro-topographic changes caused by the site preparation treatments. This approach also accommodated irregular surface topography (hummock and hollow relief) present in the HO and uncut stands.

Three sub-plots were located at equal distance along a corner to corner diagonal transect across each plot. At each sub-plot, a reference line was established at a fixed height above the reference elevation which corresponded to the unaltered mineral soil surface

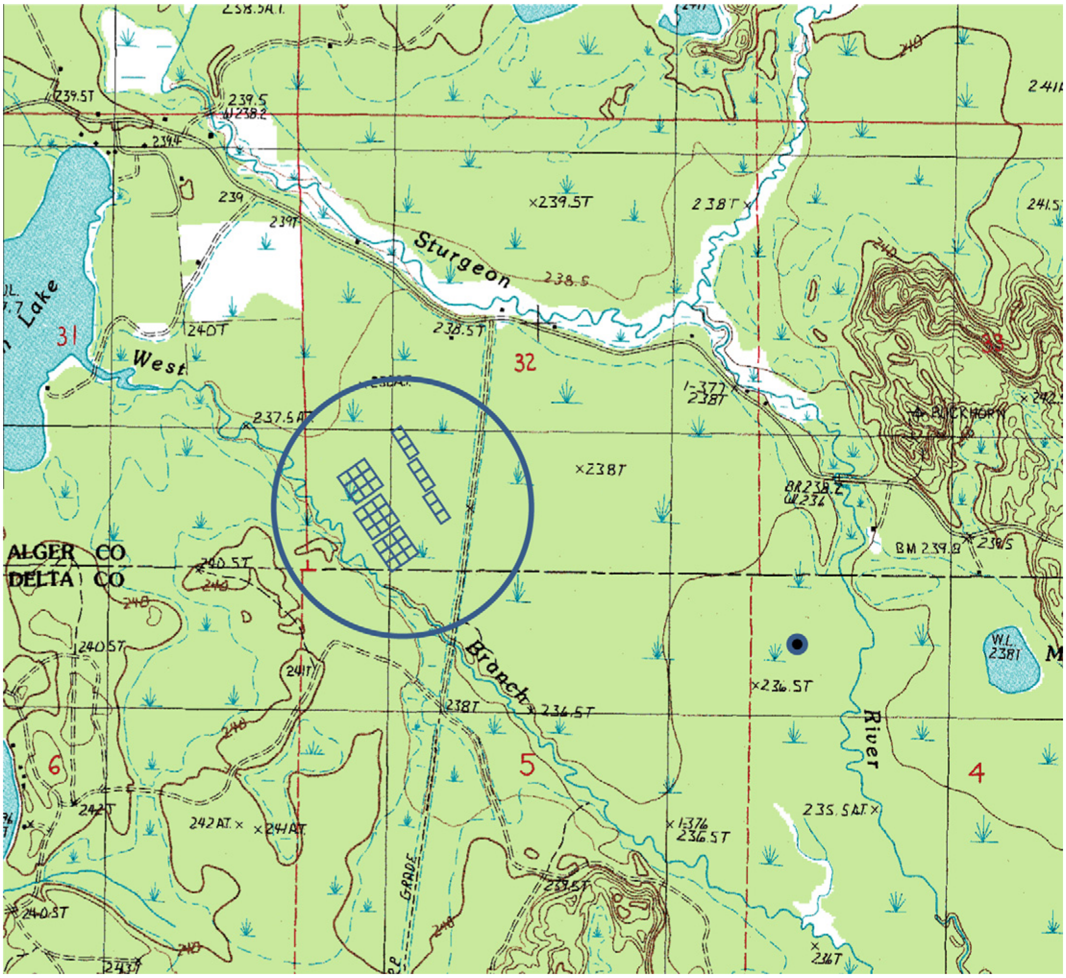

Fig. 1. Location of the study site along the West Branch river in the Upper peninsula of Michigan (46.1609065 N, 86.7153025 W). The imbedded rectangles depict the Latin squares that were harvested and uncut reference plots.

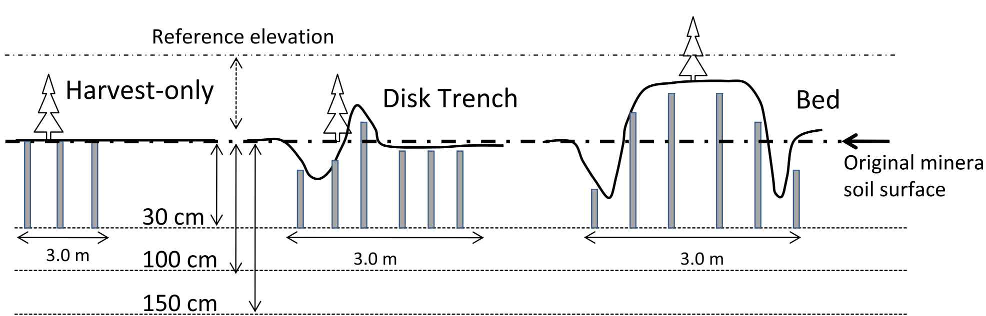

Fig. 2. Cross-section of the site preparation treatments showing how a common soil volume was sampled to account for soil displacement. The common reference elevation was the unaltered mineral soil surface. Allocation of sample cores are illustrated by the shaded bars, they were spaced 50 cm apart. The tree indicates the relative location of the planting line.

and perpendicular to the direction of the bed and trench treatment. Six cores (10 cm diameter) were then taken 50 cm apart to a depth 30 cm below the original mineral soil surface (Fig. 2). In the HO and uncut plots, three cores were taken one meter apart. Additional cores were taken to a depth of 150 cm (30–100, 100–150 cm). The mineral soil from the sample interval in each sub-plot was thoroughly mixed on a tarp and weighed in the field. A subsample was taken by sequential quartering of the composited volume until approximately 2.5 kg of soil remained, which was used for laboratory analyses. Soil bulk density was calculated using the field weight adjusted for moisture content and coarse fragments and total core volume for the respective sampling depth. The forest floor from each sample core was composited into one sample per sub-plot. A total of 72 cores were taken from the BD and TR treatments (4 plots × 3 sub-plots × 6 cores), and 36 from the HO and uncut treatments (4 plots × 3 sub-plots × 3 cores). All samples were taken to the Soil Analytical Laboratory at Michigan Technological University, Houghton, MI for processing and analyses.

2.4. Laboratory Analyses

2.4.1. Vegetation and woody residue samples

Fine roots were separated from air-dried mineral soil that did not pass a 2 mm sieve. All above-ground biomass, woody residue, and root samples were dried at 60 °C, weighed once a constant weight was achieved, ground in a Wiley mill to pass through a #60 mesh screen, and a subsample analyzed for total C and N on a Perkin Elmer CHNS analyzer. A second subsample was ashed in a muffle furnace (600 °C) for 6 h and extracted with 2 N HNO_3 for analyses of total Ca, Mg, and K on a JY-ICP.

2.4.2. Soil

Before drying, roots were removed from some forest floor samples, and a subsample of each forest floor was taken for pH determination (1:4 forest floor/water ratio). Due to the large number and volume of forest floor samples, roots were removed by hand from only two sub-plots in each treatment. All forest floor and root samples were then dried at 60 °C, weighed, and ground in a Wiley mill to pass through a 0.5 mm screen, and analyzed for total C, N, K, Mg, and Ca using the same methods as the above-ground biomass. Mineral soil samples were oven-dried at 105 °C until a constant weight was achieved, passed through a 2 mm sieve, and rock and root content determined on the > 2 mm soil fraction. Total C and N were measured on a Perkin Elmer CHNS analyzer (Nelson and Sommers, 1996). Exchangeable Ca, Mg, and K were extracted using the ammonium acetate method (Suarez, 1996), and analyzed on a JY-ICP. Mineral soil pH was determined on a 2:1 (water:soil) paste (Thomas, 1996).

2.5. Biomass and Nutrient Calculations

Allometric equations from Ter-Mikaelian and Korzukhin (1997) and Perala and Alban (1994) were used to estimate above-ground biomass components (bole, branches, foliage) for jack pine, eastern larch, and black spruce in the uncut control plots. Course root biomass of these trees was assumed to be 26% of total above-ground tree biomass (Cairns et al., 1997). Above- and below-ground biomass components of planted and volunteer trees in the harvested treatment plots were calculated from allometric equations developed by Bond-Lamberty et al. (2002). Measured C and nutrient concentrations in the vegetative and soil components were converted to a mass basis using measured soil bulk density and calculated biomass.

2.6. Statistical analyses

Previous statistical analyses of soil data from the Latin square design indicated that a gradient of soil properties across our study site was not present (Trettin et al., 1992). Accordingly, a single-factor ANOVA was conducted incorporating each of the treatments and the uncut plots. Comparisons among treatments were conducted using StatView (Abacus Concepts, Inc.). Differences of treatment means were considered significant at $p < 0.05$ using Fisher's PLSD test.

3. Results

3.1. Tree stocking and understory

Jack pine was planted on each of the harvested plots in 1988 at a density of 1485 seedlings ha^{-1}. In 1999 stocking varied between 2900 and 4600 trees ha^{-1}, reflecting the vigorous natural regeneration of jack pine and the persistence of black spruce saplings following the harvest (Table 1). The trench treatment had the highest stocking level, and regeneration in all cut plots was predominantly jack pine (>98%). Tree growth was greatest on the BD treatment, where jack pine was 1.5 cm larger in diameter and 1 m taller than trees growing in the HO treatment.

Table 1
Average stand stocking characteristics (stems per hectare, average height and diameter) and distribution of biomass among ecosystem components in harvest/site preparation treatments and in an uncut stand. The mean height and diameter for the reference stand represent the dominant trees. The standard error is provided in parenthesis.

	Treatment			
	Harvest-only	Trench	Bed	Uncut*
Stocking and dimensions				
Number of stems ha^{-1}	2921(1.37)^a	4567(18.9)^b	3592 (16.9)^c	2227(10.8)
Height (m)	2.88 (0.05)^a	3.22 (0.04)^b	4.07(0.05)^b	12.5 (0.28)
Diameter (cm)	3.23 (0.11)^a	3.32 (0.08)^a	5.0 (0.12)^b	14.0 (0.38)
Biomass (t ha^{-1})				
Above ground				
Trees	8.4 (0.9)^a	11.2 (3.2)^a	13.0 (2.9)^a	136.7 (44.6)^b
Sapling-shrub	0.3 (1.1)	0.2 (1.1)	0.2 (1.1)	0.2 (1.1)
Ground layer	6.1 (1.1)^a	5.8 (1.1)^a	5.2 (1.1)^a	3.2 (1.1)^b
Below ground				
Roots				
Coarse	2.1 (0.2)^b	3.1 (0.8)^{ab}	5.1 (1.0)^a	35.5 (11.6)^c
Fine	16.8 (4.7)^a	14.8 (1.7)^a	13.7 (1.7)^a	8.5 (1.5)^b
Total	33.6	35.1	37.2	184.1

The same superscript letters represent non-significant differences among means, $p < 0.05$. Differences among means with no letter were non-significant.
* Statistical comparisons among uncut control and harvested treatments were not conducted for tree stocking and dimensions.

3.2. Biomass

Eleven years after clearcutting, the tree biomass of harvested plots was 11 to 13% of that in the uncut stand, and was greatest in the BD plots (Table 1). The corresponding cumulative mean above-ground tree productivity following harvesting ranged from 0.8 (HO) to 1.3 t ha^{-1} yr^{-1} (BD). Understory, in the harvested treatments contributed an additional 5.4–6.4 t ha^{-1}, which was greater than the 3.4 t ha^{-1} in the uncut stand. The harvested treatments had significantly more ground vegetation biomass than the uncut control, but no differences in shrub-saplings. Root biomass averaged 53% of the total plant biomass on the harvested plots (HO = 56%, TR = 51%, BD = 51%) and 24% in the uncut reference. Coarse roots were the predominant below-ground component in the uncut stand, but fine root biomass was greater on the harvested plots. smaller sized trees. Root biomass on the harvested plots averaged 42% of the uncut stand, reflecting important differences in biomass allocation in the early stages of stand development. Average annual total biomass production ranged from 3.1 t $ha^{-1}yr^{-1}$ on the HO to 3.4 t ha^{-1} yr^{-1} on the BD plots. However, these values are underestimates, since fine root turnover is not included.

3.3. Carbon

Total C in plant biomass in the harvested plots ranged from 11% to 15% of the 94 t ha^{-1} in the uncut stand (Table 2). Trees accounted for the majority of vegetative C, with stem wood containing 15–23% of the C in the harvested treatments and 44% in the uncut stand. Above-ground tree C pools were not different among the harvesting treatments. Not surprisingly, C amounts in tree and coarse roots were much higher in the larger diameter

Table 2
Distribution of carbon (C) and nitrogen (N) among above and below-ground ecosystem components within the uncut stand and plots that were harvested and site prepared for regeneration (HO, harvest-only, TR, trench, BD, bed, UC, uncut). The mean with standard error in parenthesis provided.

	Carbon (t ha^{-1})				Nitrogen (kg ha^{-1})			
	HO	TR	BD	UC*	HO	TR	BD	UC*
Vegetation								
Tree								
Needles	1.7 (0.2)	2.4 (0.7)	2.6 (0.6)	8.0 (1.1)	54.3 (6.0)	73.4 (20.7)	87.5 (19.3)	208.1 (29.6)
Branches	1.2 (0.1)	1.7 (0.5)	2.2 (0.5)	21.2 (5.8)	23.9 (2.5)	33.0 (9.3)	37.3 (7.8)	425.7 (116.3)
Stem wood	2.7 (0.2)	3.8 (1.1)	5.0 (1.1)	41.5 (16.1)	16.2 (1.7)	24.3 (6.9)	34.1 (7.3)	256.3 (100.0)
Understory								
Sapling-shrub	0.3 (0.2)	0.15 (.07)	0.09 (.03)	0.09 (.02)	4.7 (3.1)	2.3 (1.1)	1.5 (0.6)	1.6 (4.0)
Ground layer	3.0^{a} (0.3)	2.8^{a} (0.2)	2.5^{a} (0.1)	1.5^{b} (0.3)	87.9 (10.1)^{a}	69.3 (4.2)^{ab}	55.9 (3.0)^{b}	42.4 (8.6)
Roots								
Large	1.1 (0.1)^{a}	1.6 (0.4)^{ab}	2.6 (0.5)^{b}	18.1 (5.9)	6.3 (0.8)^{a}	10.0 (2.7)^{ab}	17.5 (3.4)^{b}	111.9 (35.6)
Small	7.8 (2.0)	6.9 (0.7)	6.5 (0.8)	4.1 (0.7)	129.7 (49.0)	135.0 (31.3)	92.2 (9.2)	65.1 (10.1)
Total	17.8	19.3	21.5	94.5	323.0	347.3	326.0	1111.1
Woody residue	4.6^{a} (1.2)	3.4^{a} (1.0)	3.9^{a} (1.1)	6.8^{b} (1.8)	6 (3)	2 (1)	3 (2)	10 (5)
Soil								
Forest floor	67.8 (10.7)	50.1 (7.4)	64.1 (22.5)	75.9 (13.4)	2122 (380)	1679 (273)	2133 (717)	2020 (268)
Mineral soil								
0–30 cm	25.4 (2.1)	28.8 (1.9	33.7(5.6)	24.7 (1.5)	1383 (109)	1652 (212)	1668 (124)	1391 (73)
30–150 cm	22.0 (2.3)	26.1 (0.9)	22.1 (2.2)	20.8 (5.3)	1802 (348)	1960 (238)	2170 (202)	2135 (335)
Total soil	115.2	105.0	119.9	121.40	5307	5291	5971	5546
Total	137.6	127.7	145.3	222.7	5636.0	5640.3	6300.0	6667.1

The same superscript letters represent non-significant differences among means, $p = 0.05$. Differences between means with no letter were non-significant.
* Statistical comparisons of *C* and *N* pools among uncut control and harvested treatments were not conducted for tree components, large root biomass, and total vegetation, and for the *C* pool of total ecosystem.

uncut stand, but fine root C pools were much larger in the harvest treatments. Ground vegetation biomass C was also significantly greater on all the harvested plots than in the uncut stand. Since the stand was whole-tree harvested, very little logging residue was left on the site. Woody residue C pools were significantly lower on the harvested plots (<5.0 t ha^{-1}), as compared to 6.8 t ha^{-1} in the uncut stand.

Soil, including the forest floor, contained the majority of ecosystem C, ranging from 82% to 84% in the harvested treatments and 54% in the uncut stand (Table 2). Among soil and vegetation components, the forest floor was the largest C pool, ranging from 39% to 49% in the harvested treatments and 34% in the un-cut stand. To our surprise, no significant differences in C content in the forest floor or surface (0–30 cm) mineral soil were found among the harvest treatments and the uncut control stand. The incorporation of the forest floor and harvesting residues into the mineral soil beds 11 years earlier seemed evident, but plot variability in the beds was high, and mineral soil C pools were not different among the harvest treatments and the uncut control. Overall, soil C on the harvested treatments have recovered to pre-harvest levels.

3.4. Nitrogen

As found with C, N pools in above-ground tree components and coarse roots were larger in the BD plots than in the other site treatments (Table 2). Again, the understory and fine roots in the HO treatments contained more N than the uncut stand, but N pools were highest in the HO treatment. This is a result of greater understory growth due to more light beneath the smaller, less dense tree canopy in HO, and to plant community differences among treatments (Anderson et al., 2007). Plant community differences are reflected in C:N ratios of the ground layer, which ranged from 35 in the HO and uncut control plants to 45 in the BD plots. Total aboveground N pools were ∼ 30% of the uncut control stand, which is much higher than the 11–15% difference in C pools. This reflects the proportionally greater accumulation of N in younger trees and understory plants in the harvested plots.

As expected, soil had the greatest amount of N, but surprising was the apparent recovery of soil N to pre-harvest levels on all the harvested treatments. No significant differences in N pools were found in the forest floor, mineral soil, and total soil among the three post-harvest treatments and the uncut stand. Compared to the uncut stand, total N pools in the 11 year-old harvest treatments ranged from 84% in the HO and TR to 94% in the BD plots.

3.5. Cations

Similar to N, the understory and fine root pools of Ca, Mg, K were considerably higher in all the harvested treatments than in the uncut stand (Table 3). Again, BD plots had the lowest aboveground cation content of the three harvest treatments, which reflect less understory growth and a different plant community beneath a denser canopy. Ca and Mg contents of the forest floor, surface mineral, and total soil in the uncut control were generally lower than the harvested plots.

4. Discussion

Results from our earlier studies on this histic-mineral wetland showed that soil C and nutrient pools declined after harvesting and site preparation (Trettin et al., 1992; McLaughlin et al., 1996; Trettin et al., 1997). However, results from this study show a recovery of soil C, N, and cation levels within an 11 year period after harvesting, especially in the forest floor. This is in contrast to upland forests, where forest floor C pools are thought to decrease until 20 years after timber harvesting (Yanai et al., 2003; Nave et al., 2010). As shown below, these C and nutrient gains in the forest floor are a function of changes in the understory plant community after harvesting, and the presence of a water table in the rooting zone which is characteristic of these histic-mineral soil wetlands.

Table 3
Distribution of cations (Ca, Mg, K) among above and below-ground ecosystem components within the uncut stand and plots that were harvested and site prepared for regeneration (HO, harvest-only, TR, trench, BD, bed; UC, uncut). The mean with standard error in parenthesis provided.

	Calcium (kg ha^{-1})				Magnesium (kg ha^{-1})				Potassium (kg ha^{-1})			
	HO	TR	BD	UC*	HO	TR	BD	UC*	HO	TR	BD	UC*
Vegetation												
Tree												
Needles	9.7 (1.1)	13.8 (3.9)	11.8 (2.6)	52.7 (7.5)	2.9 (0.3)	4.9 (1.3)	4.6 (1.0)	13.1 (1.9)	14.2 (1.6)	19.5 (5.5)	20.4 (4.5)	50.3 (7.1)
Branches	5.5 (0.6)	7.2 (2.0)	7.4 (1.5)	117.1 (31.9)	1.9 (0.2)	2.6 (0.7)	3.3 (0.7)	40.0 (10.9)	7.0 (0.7)	9.8 (2.7)	12.7 (2.7)	116.6 (31.9)
Stem wood	10.1 (1.1)	11.8 (3.4)	18.6 (3.9)	140.2 (54.6)	1.6 (0.2)	2.1 (0.6)	2.8 (0.6)	23.5 (9.1)	4.1 (0.4)[a]	6.8 (1.9)[ab]	9.4 (2.0)[b]	68.7 (26.8)
Understory												
Sapling-shrub	1.2 (0.8)	0.6 (0.3)	0.8 (0.3)	1.3 (0.3)	0.3 (0.2)	0.2 (0.1)	0.1 (0.04)	0.2 (0.1)	1.3 (0.8)	0.6 (0.3)	0.5 (0.2)	0.8 (0.2)
Ground layer	21.3 (2.4)	20.6 (1.2)	16.2 (0.9)	11.9 (2.4)	4.1 (0.5)[ab]	4.5 (0.3)[a]	3.4 (0.2)[b]	2.5 (0.5)	16.6 (1.7)[ab]	18.6 (1.1)[a]	13.1 (0.7)[b]	10.5 (2.1)
Roots												
Large	3.9 (0.5)[b]	4.9 (1.3)[b]	9.5 (1.9)[a]	61.1 (19.9)	0.6 (0.1)[a]	0.8 (0.2)[ab]	1.4 (0.3)[b]	10.2 (3.3)	1.6 (0.2)[a]	2.8 (0.8)[ab]	4.8 (0.9)[b]	29.9 (9.8)
Small	22.1 (4.6)	20.1 (4.0)	18.9 (3.1)	12.3 (2.5)	4.5 (1.5)	4.9 (0.9)	4.3 (0.6)	2.2 (0.4)	11.3 (3.4)	9.9 (0.7)	9.3 (1.2)	4.4 (0.7)
Total	73.7	80.0	83.3	396.6	15.8	20.0	19.9	91.7	56.1	68.0	70.2	281.2
Woody Residue	17.5 (4.6)	13.0 (3.8)	14.7 (4.0)	25.7 (6.8)	7.4 (2.0)	5.5 (1.6)	6.2 (1.7)	10.9 (2.9)	6.0 (1.6)	4.5 (1.3)	5.1 (1.4)	8.8 (2.3)
Soil												
Forest floor	364.3 (49.8)[b]	231.0 (39.4)[ab]	240.5 (61.0)[ab]	207.6 (49.2)[a]	78.9 (13.0)	55.9 (10.1)	62.8 (23.1)	57.9 (13.3)	122.7 (19.4)	87.1 (12.7)	92.4 (26.6)	110.9 (16.3)
Mineral soil#												
0–30 cm	129.8 (9.6)[b]	162.1 (5.0)[ab]	157.7 (19.5)[b]	99.3 (11.1)[a]	25.3 (2.9)[ab]	28.9 (0.6)[a]	28.3 (3.8)[b]	19.2 (1.1)[a]	54.0 (8.2)[a]	85.9 (6.3)[b]	79.3 (3.4)[b]	78.9 (4.9)[b]
30–150 cm	365.7 (24.8)	349.6 (30.9)	422.6 (51.1)	363.3 (63.7)	72.7 (5.8)	57.5 (6.7)	75.9 (9.7)	73.3 (16.2)	152.8 (5.6)[ab]	191.5 (20.7)[abc]	221.9 (30.0)[c]	105.0 (13.9)[a]
Total soil	859.8	742.7	833.6	670.2	176.9	142.3	167.0	150.4	329.5	364.5	393.6	294.8
Total	948.6	835.0	931.6	1092.5	200.1	167.8	193.1	253.1	391.6	437.0	468.0	584.8

The same superscript letters represent non-significant differences among means, $p = 0.05$. Differences between means with no letter were non-significant.
* Statistical comparisons of cation pools among harvested treatments and uncut control were not conducted for tree components, large root biomass, and total vegetation.
\# Cation pools in the forest floor are "total"; cation pools in the mineral soil are "exchangeable".

Therefore, understanding the soil hydrologic setting is essential when evaluating the effects of management of harvesting forested wetlands.

4.1. Carbon

Many studies have been conducted on timber harvesting impacts on C changes in drained peatlands of northern Europe (Trettin et al., 1995; Westman and Lasiho, 2003). However, little is known on the effects of forest management on C pools in undrained wetlands. Histic-mineral wetlands are common to many forest landscapes in North America (Bridgham et al., 2006), but other than our earlier studies, we could not find any information in the literature on timber harvesting and site preparation impacts on soil C in these wetlands. Moroni et al. (2009) reported that soil respiration from a riparian black spruce forest in Canada was lower after harvesting and no change was measured in a harvested balsam fir stand, both mineral soils; unfortunately, they did not report on changes in soil C pools.

Since clearcutting removed the overstory trees on our study site, understory plants were the major source of C additions to the forest floor. Understory biomass in all harvested treatments was double that in the uncut stand. Fine root C pools in both the forest floor and mineral soil were also much higher in the harvested treatments, most of which were from understory plants (Trettin et al., 1997; Gale et al., 1998). Plant species composition also changed after harvesting, as the number of *Sphagnum* and other bryophytes were reduced, while graminoid and herbaceous species increased (Fig. 3), which was reflected in higher understory biomass and nutrient pools than in the uncut stand. These new post-harvest plant communities would undergo a more rapid turnover of above- and below-ground OM pools. The importance of understory vegetation for the recovery of C pools following harvesting and site preparation of peatlands was also reported by Hargreaves et al. (2003). Assessing the change in C stocks among several silvicultural treatments, Arevalo et al. (2009) also reported that differences in C recovery were attributable to plant biomass rather than soil C. However, Laiho et al. (2003) reported C gains in the absence of an understory five years after the clear-cut harvest of a mineral soil wetland in North Carolina.

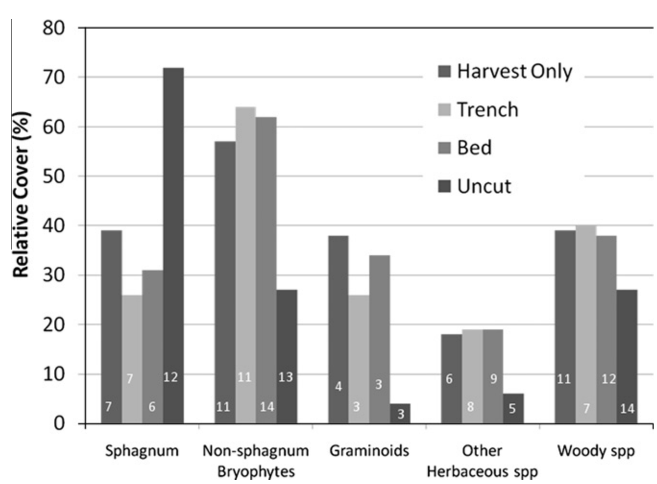

Fig. 3. Relative cover of understory groups occurring on the harvested treatments and uncut reference stand. The total number of species within groups for each treatment is presented as the imbedded number within the coverage bar. Developed from Anderson et al. (2007).

4.2. Nitrogen

While the rapid recovery of the forest floor C on our study site following timber harvesting and site preparation was unexpected, a similar accumulation of N was even more surprising. Approximately 720 kg N ha^{-1} were removed in biomass during the whole-tree harvest, plus additional soil N losses associated with the oxidation of the forest floor in the first few years after harvesting (Trettin et al., 1992). The soil is very coarse-textured and susceptible to leaching loss, especially during periodic high water levels. This was demonstrated during a small-scale fertilization trial that was conducted in the buffer strips between treatment plots on our site, which showed elevated N leaching in the first year following fertilizer additions (McLaughlin et al., 2000). Considering only the N accumulation in biomass, and if we assume that N gains were linear since the harvest (an unlikely occurrence), an average of 29 kg N ha^{-1} yr^{-1} were added to the harvested plots. Nitrogen accumulation in the tree above-ground biomass alone on the harvested plots ranged from 8.5 to 14.4 kg N ha^{-1} yr^{-1}, highlighting the large gains in ecosystem N. Atmospheric deposition could only account for 3–5 kg ha^{-1} yr^{-1} (http://nadp.sws.uiuc.edu). Symbiotic and non-symbiotic fixation of atmospheric N is another possible source. Nitrogen fixation rates for northern fens and bogs have been reported to range from 0.3 to 119 kg N ha^{-1} yr^{-1} (Bowden, 1987), but rates in histic-mineral wetlands have not been measured. Alder (*Alnus rugosa- now called Alnus incana*) does occur in the area, but very few were found in the study plots. Nitrogen additions of 1–2 kg ha^{-1} yr^{-1} have been reported for *N*-fixing cyanobacteria in association with feather mosses (*Hylocomium splendens and Pleurozium schreberi*) in boreal forests (Zackrisson et al., 2009). *P. schreberi* was very common in the uncut stand, but coverage was <5% in all harvested treatments (Anderson et al., 2007). Nitrogen fixation by heterotrophic soil bacteria is also likely very low, at most 2–3 kg N ha^{-1} yr^{-1} (Son, 2001).

We could only find one other study on the impact of timber harvesting on N pools in an undrained wetland soil. Lockaby et al. (1999) showed N gains of 300–900 kg N ha^{-1} over 8 years from OM and sediment deposition after periodic flooding of a bottomland hardwood swamp in Alabama. Since over-bank flooding was not a factor in our study site, the most likely source of N was root uptake of inorganic N from the shallow groundwater. Periodic chemical analysis of ground water on the study site found NO_3 + NH_4-N concentrations typically ranging from 1–2 mg l^{-1} (McLaughlin et al., 2000). While we could not determine the contribution of groundwater derived N to the soil or biomass pools, McLaughlin et al. (2011) estimated the flux from groundwater at 7 kg N ha^{-1} yr^{-1} for a single growing season on this site. Given the relatively shallow depth of the water table during the growing season, which was well within the active rooting zone, and the permeable soil, the conditions do suggest the potential for nutrient supply from the shallow groundwater. Lisuzzo et al. (2008) documented that capillary rise and rooting within the hyporeic zone can supply a large proportion (25–55%) of the plant N demand in an Alaska riparian willow site, which is geomorphologically similar to our site. In a study on scrub oak woodland in Florida, McKinley et al. (2009) found that NH_4 supplied by the water table at 2.5 m depth in an N-limited coarse-textured soil sustained increased stand growth at elevated CO_2 levels. Hinkle et al. (2001) also reported that N supplied from the hyporheic zone of the Willamette River, Oregon was an important source for plants growing in a large river floodplain.

4.3. Cation balance

As seen with C and N, eleven years after harvest Ca, Mg, and K pools in the forest floor of the harvested plots were comparable to the uncut stand, and the amounts mineral soil exchangeable cations were generally higher than in the uncut stand. Again, this was unexpected due to the large amounts of cations removed in the timber harvest (300 kg Ca ha^{-1}, 110 kg Mg ha^{-1} and 260 kg K ha^{-1}), and subsequent leaching losses from post-harvest decomposition of the forest floor. Accumulation of Ca, Mg and K in biomass on the harvested plots ranged from 1.7 to 7.2 kg ha^{-1} yr^{-1}. Mineral weathering is an unlikely source of cation gains in our coarse-textured, acid outwash soil (Zabowski, 1990; Kolka et al., 1996). Deep-rooted trees can take up nutrients from deep fine-textured lenses in sandy soils (e.g. Buxbaum et al., 2005), but such lenses are not present in our soil. Pine trees are able to take up K from water tables > 2 meters in depth (Jurgensen and Leaf, 1965) even when O_2 is limited by water table fluctuations (Fisher and Stone, 1990). Consequently, similar to N, the rapid cation accumulation in our soil is likely due to root uptake of cations present in the water table (Trettin et al., 1997). McLaughlin et al. (2011) measured the cation flux in the shallow groundwater across this study site for one growing season, confirming fluxes of available Ca, Mg, and K. This supply of cations from shallow ground water is identical to the mechanism supplying nutrients in fen peatlands. Cation input associated with sediment deposition is a buffer against nutrient removals from whole-tree harvesting bottomland hardwood swamps in floodplains (Lockaby et al., 1999), but this mechanism is not applicable to our site.

5. Management perspectives and conclusion

Histic-mineral wetlands are important for the ecosystem services common to most forested wetlands, and also are an important source of wood biomass. When this study was established in 1988, the principal environmental concern was the potential consequences of harvesting and plantation silviculture on site productivity and stand composition. Earlier studies on this wetland showed rapid losses of soil C and nutrients after harvesting, and we speculated these losses might decrease site productivity (Trettin et al., 1992; McLaughlin et al., 1996, 2000). However, results from this study have shown a rapid recovery of C and nutrients in the forest floor and soil, and at age eleven, the number of trees far exceeds initial planting density. While species composition of the understory showed a shift to gramminoids following harvest, the eventual return to a sphagnum-dominated forest floor is expected (Anderson et al., 2007). Stand growth in all three post-harvest site preparation treatments was similar to expected norms for the region (Guo and Wang, 2006). The net ecosystem productivity (NEP) of tree regeneration on the HO, TR and BD treatments at age 11 was 1.55, 1.73, and 1.91 t C ha^{-1} yr^{-1}, respectively. This is greater than the productivity of jack pine on boreal upland soils in Canada, which ranged from 0.2 t C ha^{-1} yr^{-1} ten years following harvest, to 0.7 t C ha^{-1} yr^{-1} after 30 years (Zha et al., 2009). If these results are confirmed in future studies, it appears that histic-mineral wetlands can be intensively managed sustainably for timber production without impacting site productivity and plant community composition and structure. Future consideration of C and cation pools on this site will provide additional perspective on sustainability questions and an important benchmark for managed histic mineral soil forested wetlands.

Our study also shows that the hydro-geomorphic setting is an important factor when assessing nutrient cycling and growth responses of histic-mineral soil forested wetlands to management. While this is routinely considered in peatlands (i.e. fen vs. bog), shallow ground water is generally not recognized as a nutrient source in histic-mineral or mineral wetlands, except in active floodplains. Linking site hydro-geomorphology with soil processes and plant community dynamics in managed wetland forests is necessary to provide the basis for ensuring sustained productivity and other ecosystem functions.

Acknowledgements

This experiment was established with support from the National Council of the Paper Industry for Air and Stream Improvement (NCASI), and MeadWestvaco, Inc. Plum Creek Inc. provided access to the site for re-measurements and sampling. The maintenance of the long-term monitoring has been supported by the US Forest Service and Michigan Technological University. We appreciate the helpful comments and suggestions by two anonymous reviewers.

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