



## Carbon pools and productivity in a 1-km<sup>2</sup> heterogeneous forest and peatland mosaic in Minnesota, USA

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### ABSTRACT

Determining the magnitude of carbon (C) storage in forests and peatlands is an important step towards predicting how regional carbon balance will respond to climate change. However, spatial heterogeneity of dominant forest and peatland cover types can inhibit accurate C storage estimates. We evaluated ecosystem C pools and productivity in the Marcell Experimental Forest (MEF), in northern Minnesota, USA, using a network of plots that were evenly spaced across a heterogeneous 1-km<sup>2</sup> mosaic composed of a mix of upland forests and peatlands. Using a nested plot design, we estimated the standing C stock of vegetation, coarse detrital wood and soil pools. We also estimated aboveground net primary production (ANPP) as well as coarse root production. Additionally we evaluated how vegetation cover types within the study area differed in C storage. The total ecosystem C pool did not vary significantly among upland areas dominated by aspen ( $160 \pm 13 \text{ Mg C ha}^{-1}$ ), mixed hardwoods ( $153 \pm 19 \text{ Mg C ha}^{-1}$ ), and conifers ( $197 \pm 23 \text{ Mg C ha}^{-1}$ ). Live vegetation accounted for approximately 50% of the total ecosystem C pool in these upland areas, and soil (including forest floor) accounted for another 35–40%, with remaining C stored as detrital wood. Compared to upland areas, total C stored in peatlands was much greater,  $1286 \pm 125 \text{ Mg C ha}^{-1}$ , with 90–99% of that C found in peat soils that ranged from 1 to 5 m in depth. Forested areas ranged from 2.6 to 2.9 Mg C ha<sup>-1</sup> in ANPP, which was highest in conifer-dominated upland areas. In alder-dominated and black spruce-dominated peatland areas, ANPP averaged 2.8 Mg C ha<sup>-1</sup>, and in open peatlands, ANPP averaged 1.5 Mg C ha<sup>-1</sup>. In treed areas of forest and peatlands, our estimates of coarse root production ranged from 0.1 to 0.2 Mg C ha<sup>-1</sup>. Despite the lower production in open peatlands, all peatlands have acted as long-term C sinks over hundreds to thousands of years and store significantly more C per unit area than is stored in uplands. Despite occupying only 13% of our study area, peatlands store almost 50% of the C contained within it. Because C storage in peatlands depends largely on climatic drivers, the impact of climate changes on peatlands may have important ramifications for C budgets of the western Great Lakes region.

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### 1. Introduction

Terrestrial ecosystems capture and release large amounts of carbon (C) and have the capacity to influence atmospheric carbon dioxide concentrations and climate dynamics. Quantifying C budgets for terrestrial landscapes is an important step in developing predictive climate models and consequently has been the focus of a considerable body of ecological research.

The forest- and peatland-dominated landscapes of the western Great Lakes region of North America contain several different types of ecosystems that have high C densities and are expected to be important to regional C budgets. However, the heterogeneity of these landscapes poses difficulties for scaling C pools and fluxes over large areas. Landscapes of the region are transitional, containing ecosystems that are typical of temperate and boreal areas, including mixed hardwood, aspen, and conifer forests and peatlands (CEC, 1997). These types of ecosystems store large amounts of C globally; temperate and boreal forests store more plant biomass C than all other terrestrial ecosystems except tropical wet forests (Schlesinger, 1997), and peatlands store an estimated one-third of the world's organic soil C (Gorham, 1991). Because of the capacity for these complex landscapes to influence regional patterns of C storage and global climate, overcoming the

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challenges that spatial heterogeneity poses to landscape C accounting is a high priority.

To improve our understanding of C distribution in heterogeneous forest and peatland landscapes in the western Great Lakes region of the United States, we set out to quantify the major C pools and aboveground net primary productivity (ANPP) of a complex forest- and peatland-mosaic in northern Minnesota, USA, using ground-based inventory approaches. We used a regular, grid-based sampling approach designed to relate our ground-based measurements to satellite-based approaches, which should facilitate future efforts to scale C pools and fluxes from landscape to regional scales. For this study, we evaluated C inventories for a 1-km<sup>2</sup> area based on inventory data and the proportional distribution of different vegetation cover types. Our results provide important C estimates for this region that can be used as baseline measurements to assess future C cycle changes.

## 2. Study area

The Marcell Experimental Forest (MEF; 47.23°N, 93.51°W) is located approximately 40 km north of Grand Rapids, MN, USA (Fig. 1a). It encompasses a 900-ha tract reserved for long-term research by the USDA Forest Service and includes multiple small watersheds composed of upland forested areas, peatlands and small lakes. Peatlands at MEF vary with hydrology, ranging from ombrotrophic bogs to minerotrophic fens, and may be forested or non-forested. The forest is within the Laurentian Mixed Forest Province, which is a transitional zone between boreal and broadleaf deciduous forests (McNab and Avers, 1996). Dominant forest species include those common in boreal forests, such as *Populus tremuloides* (aspen), *Pinus banksiana* (jack pine), and *Picea mariana* (black spruce), as well as hardwoods typical of northern temperate forests, including *Acer saccharum* (sugar maple), *Acer rubrum* (red maple), and *Tilia americana* (basswood). Forest stands at MEF are second and third growth forests, i.e., they have been harvested 2–3 times since settlement. The experimental forest currently is managed for timber production (thinning and harvesting) by the Chippewa National Forest, and experimental areas are sometimes managed for research purposes. The specific area of our study has not been subject to experimental manipulations, but has been exposed to timber management operations. In the uplands the predominant soil is Warba fine sandy loam. The peatlands include well-decomposed acidic peat (pH ~4) to varying

depths, overlain by 30–100 cm of less decomposed peat. Mean peat depth is 2.5 m (E.S. Verry, unpublished data). We selected a 1-km<sup>2</sup> study area in the southern unit of MEF for this study (Fig. 1a and b).

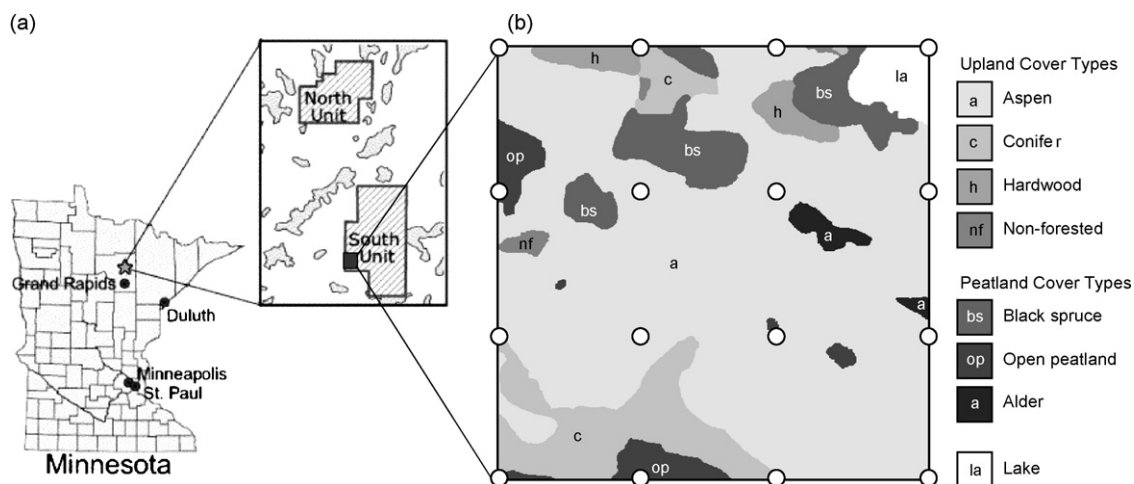
## 3. Methods

### 3.1. Carbon inventory plot establishment

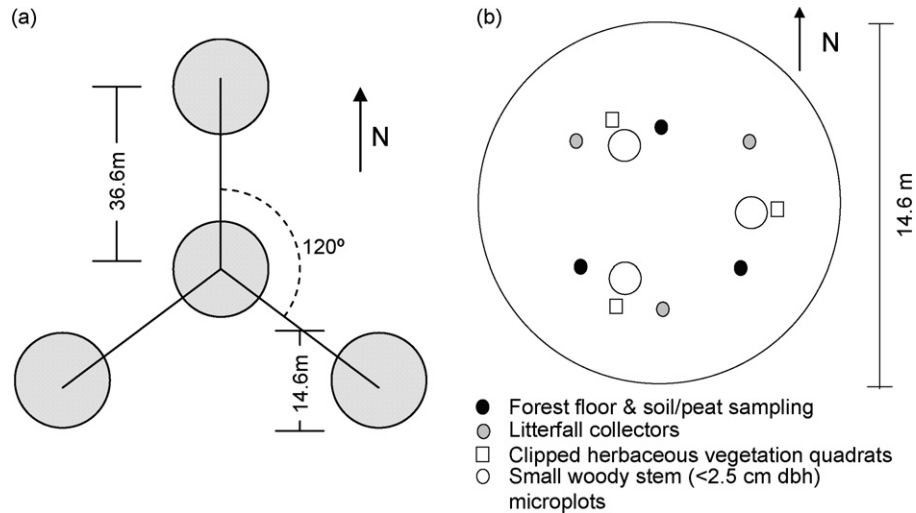
In June 2004, we established 16 plots that were evenly spaced on a grid in the 1-km<sup>2</sup> study area (Fig. 1b). Each plot was divided into four 7.3-m radius subplots, similar to the U.S. Forest Service's Forest Inventory and Analysis (FIA) plot design (USDA, 2005a), with a central subplot surrounded by three subplots located 36.6 m from the central subplot center along 120°, 240°, and 360° bearings (Fig. 2a). These plots were used as the basis for scaling total C storage and net primary productivity (NPP) measurements across the study area. We estimated total C storage as the sum of C stored in aboveground and belowground vegetation, coarse detrital wood, and soils, including forest floor, mineral soil, and peat. We evaluated annual NPP for aboveground components (wood, foliage, understory vegetation, and bryophytes) and coarse roots. Although we recognize that fine roots can contribute significantly to total NPP, a thorough evaluation of fine root production was beyond the scope of this study. Soil pools, detrital wood, and tree biomass data reported in this study were collected in the summers of 2004–2006 from individual subplots. Aboveground woody NPP and coarse root NPP estimates presented represent 5-year mean values for the periods 2001–2005, while foliar NPP represents mean values for 2005–2006. Herbaceous NPP was evaluated in 2005, and *Sphagnum* moss NPP was measured in 2006.

### 3.2. Soil carbon

To estimate C stored in upland subplot soils, we sampled the forest floor and mineral soil following protocols similar to the FIA Phase 3 soil and forest floor sampling protocols (USDA, 2005b). To sample forest floor, we positioned a circular sampling frame (30-cm inside diameter) in three locations in each subplot (Fig. 2b). We removed litter and O-horizon material from within the frame. We dried (70 °C) and weighed these samples in the laboratory. We sampled mineral soil from the same locations that the forest floor samples were taken, using a slide hammer-style sampler that extracted intact cores (6-cm diameter; 40-cm length) inside plastic



**Fig. 1.** (a) Location of the Marcell Experimental Forest. The black square represents the area of our 1-km<sup>2</sup> study grid. (b) Distribution of vegetation cover types within the 1-km<sup>2</sup> study area. Open circles depict plot centers. This map and the proportional representation of different cover types are based on aerial photographs, field surveys, and GIS analyses (Ebrahim Abdela and Josh Gager, unpublished).



**Fig. 2.** (a) Each forest inventory plot consisted of four nested subplots. (b) Location of sampling activities within each subplot.

liners. In the laboratory, we sectioned cores into 0–10, 10–20, and 20–40 cm depth increments. We dried (105 °C), weighed, and passed each section through a 2-mm soil sieve to remove rocks, roots, and other coarse fragments, which we also weighed. We calculated soil weight for each section as total dry weight minus the weight of coarse fractions.

In peatland subplots, we sampled forest floor, if present, as in upland plots, but sampled peat soils to the depth of contact with the hard mineral surface to account for the large organic C stores found in Histosols. We sampled peat with a McCauley peat corer (4-cm diameter; 50-cm length, with multiple 1.5-m extensions), which enabled us to sample with minimal soil compaction. In the laboratory, we dried (70 °C) and weighed peat sections.

We ground dried forest floor, mineral soil and peat samples using a Wiley mill equipped with a 1-mm screen. We placed 15 g of each sample in glass vials and homogenized these subsamples by spinning for 16 h on a vial rotator. We analyzed these subsamples for total C using C–N elemental analyzers (Carlo Erba NA 1500 series; Leco TrueSpec) and determined total C for each pool by averaging the product of C concentration and sample dry weight. These values were expressed per unit of sampling area and then adjusted to units of Mg C ha<sup>-1</sup>.

### 3.3. Live vegetation carbon

In each subplot, we evaluated biomass as the sum of the mass of all woody and herbaceous species. To convert from biomass to C mass, we assumed the commonly adopted convention of 50% C content in plant tissues (Fahey et al., 2005). Although we had the capability to measure plant C content directly, we adopted this convention so that we could devote our instrumental analyses to % C of soil, peat, and forest floor, which vary considerably compared to that of plant tissues (Fahey and Knapp, 2007). We recorded species, diameter at breast height (dbh), and height of woody stems  $\geq 2.5$  cm and estimated aboveground biomass using regionally derived allometric equations (Perala and Alban, 1994). We evaluated saplings  $< 2.5$  cm dbh and  $> 1$  m in height in three 1.2-m radius microplots (Fig. 2b) by recording species and diameter at 15 cm and using regionally derived allometric equations for small trees and shrubs to estimate aboveground biomass (Smith and Brand, 1983). All woody stems  $< 2.5$  cm dbh and  $< 1$  m height and all herbaceous stems were clipped from three 0.5-m<sup>2</sup> quadrats (Fig. 2b). We dried clipped vegetation to a

constant weight in drying ovens set at 60 °C, and used the total dry weight to estimate aboveground biomass for these components.

To estimate belowground biomass, we used a generic allometric relationship for estimating stump and coarse root biomass for stems  $> 2.5$  cm dbh (Perala and Alban, 1994). For smaller stems in upland subplots and coniferous and shrub-dominated peatland plots, we calculated belowground biomass using a root:shoot ratio of 0.3 for woody stems  $< 2.5$  cm dbh and a root:shoot ratio of 0.5 for herbaceous biomass (Whittaker and Marks, 1975). In the open bog and graminoid peatland subplots, belowground biomass for stems  $< 2.5$  cm was estimated using an overall root:shoot ratio of 6.25, which is the root:shoot value reported for herbs and shrubs in a bog and a poor fen in Canada (Moore et al., 2002). Because we made no attempt to separate live bryophytes from peat cores that were sampled as part of the soil pool, we implicitly considered their biomass as part of the peat C pool to avoid double counting.

In addition to estimating the size of the live vegetation C pool, we also estimated annual ANPP as the sum of growth in trees, shrubs, herbaceous vegetation, and *Sphagnum* moss. Additionally, we estimated coarse root production. We estimated wood production from annual growth rings measured on cores of three individuals of the dominant species and 1–3 individuals of subdominant species in each of the 63 subplots. Trees were sampled randomly to help ensure that sampling represented species composition and size distribution of our overall tree inventory. The total number of trees for which annual growth increments were evaluated was 260. We mounted and sanded cores to help visualize growth rings and determined the mean annual growth for the most recent 5 years using a dissecting microscope and micrometer. For these cored trees, we estimated woody aboveground and coarse root productivity using allometric relationships (Perala and Alban, 1994). We then developed regression relationships by species between dbh and aboveground woody production and coarse root production, which we used to estimate woody production in all measured (non-cored) trees. The regressions followed the model

$$G = a (\text{dbh})^b \quad (1)$$

where  $G$  is mean annual growth for a 5-year period, dbh is breast height diameter, and  $a$  and  $b$  are constants. For species in which we did not have sufficient data to establish dbh-productivity relationships (approximately 3% of all trees surveyed), we based

productivity estimates on a mean annual increment measured in cored trees of those species. Because we do not have allometric relationships that predict fine root production and we made no direct measurements, our productivity estimates do not include fine root contributions.

We collected litterfall to estimate foliar production. In each subplot, we placed three 38-cm diameter plastic baskets, with mesh liners (Fig. 2b). Litter was removed twice during the growing season and once after senescence. Litter was dried (70 °C), weighed and analyzed for C content using an elemental analyzer. We estimated foliar production for each subplot based on the total litter weight and the C content.

We used the herbaceous biomass from the clipped quadrats to estimate aboveground annual production of herbaceous forest understory and peatland vegetation. In peatland subplots, we also estimated aboveground production of ericaceous shrubs and *Sphagnum* mosses. For the ericaceous shrubs, which included *Chamaedaphne calyculata*, *Vaccinium oxycoccus*, and *Ledum groenlandicum*, new growth segments were identified on branches of plants harvested from the clipped plots. These segments were clipped, dried, and weighed, and weights were incorporated into estimates of ANPP. We made no attempt at estimating below-ground productivity contributions for ericaceous shrubs and herbs.

We estimated annual growth of *Sphagnum* mosses using a cranked wire approach (Clymo, 1970; Vitt, 2007). We set up two 0.5 m<sup>2</sup> arrays of 50 cranked wires each in peatland subplots in the spring of 2006 after snow melt (late April), and we measured vertical growth of *Sphagnum* along the wires at the end of the growing season (mid October). Two 10 cm × 10 cm × 10 cm sections of peat associated with each array were cut from each subplot. From these sections, we determined the *Sphagnum* stem density (number of stems per unit area) and the mean mass per unit length of stem, which was determined by weighing 2-cm sections obtained immediately below the capitula of 100 *Sphagnum* stems. Our estimate of *Sphagnum* production was obtained by multiplying the mean vertical growth times mass per unit length of stem times the density of the moss layer.

### 3.4. Detrital wood carbon

We considered two types of detrital wood in our C storage assessment: down (fallen) coarse woody debris (CWD), and standing dead biomass (snags). To estimate CWD, we used a line-intercept sampling approach that previously has been used to describe coarse woody debris in FIA plots (Chojnacky et al., 2004). On each subplot, three 7.3-m transects (total transect length, 21.9 m) were surveyed and all intersections with woody pieces >7.6 cm diameter were recorded. At each intersection, we identified the tree species of the woody piece and recorded its diameter and decay class (Woodall and Williams, 2005). We computed CWD using the following equation, based on the single-diameter equation in Chojnacky et al. (2004):

$$\text{CWD} = \sum_{i=1}^n \frac{f \text{diam}_i^2 \rho_d}{L}, \quad (2)$$

where CWD (Mg ha<sup>-1</sup>) is down coarse woody debris mass for a subplot,  $n$  is the number of pieces of wood per transect,  $\text{diam}_i$  is the diameter of an individual piece of wood,  $\rho_d$  is the density for the wood type's decay class,  $f$  is a unit conversion factor, and  $L$  is the sum of the length of the three transects on the subplot (21.9 m). For wood density,  $\rho_d$ , we used regionally derived values for different tree species of different decay classes (Duvall and Grigal, 1999), rather than the more generic values published in Chojnacky et al. (2004). To convert from mass units to mass-C units, we used

regionally derived detrital wood carbon concentrations that ranged from 53 to 58%, depending on decay class (Duvall, 1997).

To estimate snag biomass in each subplot, we recorded the species and dbh of snags >2.5 cm dbh. To reflect different stages of decomposition, snags were assigned one of three condition classes and one of four decay classes using criteria established by Duvall and Grigal (1999) for snags in the Great Lakes states. The condition classes account for structural losses from trees (e.g., loss of twigs, loss of limbs, and loss of bark), while the decay classes account for changes in wood density with decomposition. From the snag diameters, we estimated the biomass for the snag at the time of mortality using allometric equations (Perala and Alban, 1994). The biomass was adjusted by multiplying by condition class constants to account for structural losses, and by density constants to account for changes in density with decay (Duvall and Grigal, 1999). As with CWD, we used regionally derived detrital wood carbon concentrations to convert from mass to mass-C units (Duvall, 1997).

### 3.5. Stand characterization

Based on dominant species present, each subplot was assigned to one of seven vegetation cover types (Fig. 1b), including four upland cover types (aspen, hardwood, conifer, and non-forested) and three peatland cover types (open peatland, alder peatland, and black spruce peatland). We made cover type designations at the subplot level rather than the plot level because plots often straddled obvious transitions in vegetation, such as those occurring along a peatland–upland boundary. When a subplot straddled such a boundary, we designated it as transitional. To further characterize each different cover type, we calculated mean stem height, dbh, and basal area from our vegetation inventory.

### 3.6. Data analyses

We used ANOVA and least significant difference tests to evaluate differences in C pools and production among cover types, excluding transitional areas. To avoid pseudoreplication (Hurlbert, 1984), data from subplots of the same cover type within a given plot were pooled to form a single unit rather than treated as independent replicates. To meet ANOVA assumptions of normality and homogeneity of variance, data were log-transformed as necessary. Because there was no true replication within the black spruce and non-forested upland cover classes, these were excluded from statistical analyses.

We evaluated C storage and productivity in the entire 1-km<sup>2</sup> study area using the results for the different cover types. A Minnesota Department of Natural Resources Land Cover Map (Fig. 1b) was used to determine the total area of different cover types in the 1-km<sup>2</sup> area. We summed the cover-type means, proportionally weighted by area, to develop inventory estimates for the entire study area.

## 4. Results

Our nested plot design imposed on a grid in our 1-km<sup>2</sup> study area included 16 nested plots, with 64 subplots. Of those subplots, 59 were classified into vegetation cover types. Four of the remaining subplots were located in transitional areas and one was located in a lake. Among the forested upland cover types, forest age and tree size are similar, on average (Table 1). Stem density and basal area are highest in conifer and lowest in the hardwood subplots, while aspen subplots encompass a wide range of stem density and basal area. Structural characteristics of plant communities in the peatland cover types cover a broad range, with



**Table 1**

Selected characteristics of different cover types (means across all plots within a cover type, with ranges in italics).

Cover type	# of plots	# of subplots	Major species <sup>a</sup>	Forest age <sup>b</sup> (years)	Tree height <sup>b</sup> (m)	dbh <sup>b</sup> (cm)	Stem density <sup>b</sup> (ha <sup>-1</sup> )	Basal area <sup>b</sup> (m <sup>2</sup> ha <sup>-1</sup> )	Basal area (shrubs) <sup>c</sup> (m <sup>2</sup> ha <sup>-1</sup> )
<b>Uplands</b>									
Aspen	15	36	Pt, Pg, Bp	40, 20–58	15, 8–22	19, 8–31	966, 237–1764	21.8, 6–40	1.1, 0–5
Hardwood	5	5	Ar, Ta, As	46, 24–63	15, 9–21	19, 11–27	654, 416–1071	19.9, 4.4–31.7	0.8, 0–2.7
Conifers	3	5	Pb, Pr, Ab	44, 36–52	16, 13–19	18, 13–21	1288, 921–1487	30.6, 21–38	0.8, 0–1.4
Non-forested	1	2	Cc, Sa	–	–	–	–	–	0.2
<b>Peatlands</b>									
Open	3	8	Sp, es, Ca	–	–	–	10, 0–30	0.1, 0–0.3	0
Alder <sup>d</sup>	2	2	Ai, Ab	–	10, 5–17	9, 6–14	594	3.7	8.3, 5–12
Black spruce <sup>e</sup>	1	1	Pm, Ab	53, 27–88	11, 5–22	12, 6–23	2022	23.6	2.8

<sup>a</sup> Abbreviations: Ab, *Abies balsamea*; Ai, *Alnus incana*; Ar, *Acer rubrum*; As, *Acer saccharum*; Bp, *Betula papyrifera*; Ca, *Carex* species; Cc, *Corylus cornuta*; es, ericaceous shrubs; Pm, *Picea mariana*; Pb, *Pinus banksiana*; Pr, *Pinus resinosa*; Pg, *Populus grandidentata*; Pt, *Populus tremuloides*; Sa, *Salix* species; Sp, *Sphagnum* species; Ta, *Tilia americana*.

<sup>b</sup> Based on stems with dbh  $\geq$  6.35 cm.

<sup>c</sup> Based on stems with dbh  $\geq$  2.5 cm and  $<$  6.35 cm.

<sup>d</sup> Only one subplot contained stems  $>$  6.35 cm dbh. Reported ranges for tree height and dbh are based on individual trees instead of subplot means.

<sup>e</sup> Reported ranges are based on individual trees instead of subplot means.

**Table 2**Carbon pool sizes (means, with S.E. indicated in parentheses) in different vegetation cover types at MEF (Mg C ha<sup>-1</sup>). Significant differences evaluated by ANOVA ( $P < 0.05$ ), and Fisher's Least Significant Difference test, with letters denoting differences among cover types. Black spruce and non-forested cover types were omitted from analyses because of low sample sizes.

Cover type	Aboveground vegetation	Belowground vegetation	Forest floor	Soil	Snags	Coarse woody debris <sup>a</sup>	Total ecosystem C
<b>Uplands</b>							
Aspen	67.9 <sup>ab</sup> (10.5)	12.5 <sup>a</sup> (1.5)	6.8 <sup>b</sup> (0.6)	59.7 <sup>c</sup> (2.5)	5.6 <sup>b</sup> (1.3)	3.7 <sup>ns</sup> (2.5–5.2)	160 <sup>c</sup> (13)
Hardwood	68.9 <sup>ab</sup> (14.5)	11.8 <sup>a</sup> (2.4)	7.3 <sup>b</sup> (0.7)	57.2 <sup>c</sup> (3.3)	5.4 <sup>bc</sup> (4.7)	1.2 (0.3–2.5)	153 <sup>c</sup> (19)
Conifers	88.2 <sup>a</sup> (17)	15.4 <sup>a</sup> (2.3)	10.5 <sup>a</sup> (1.7)	59.7 <sup>c</sup> (3.1)	19.5 <sup>a</sup> (7.2)	3.6 (2.5–5.2)	197 <sup>c</sup> (23)
Non-forested	10.8	3.1	3.7	57.6	0	0.3	76
<b>Peatlands</b>							
Open	1.9 <sup>c</sup> (0.1)	10.6 <sup>a</sup> (0.9)	0.1 <sup>c</sup> (0.01)	1506 <sup>a</sup> (99)	0.1 <sup>c</sup> (0.1)	0	1518 <sup>a</sup> (98)
Alder	14.3 <sup>bc</sup> (1.3)	3.6 <sup>b</sup> (0.3)	0.6 <sup>c</sup> (0.5)	1199 <sup>b</sup> (11)	0 <sup>c</sup>	1.7 (1.7–4.7)	1221 <sup>b</sup> (13)
Black spruce	59.8	13.5	1.4	641	3.1	0	718

Letters differentiating significant results are be super-scripted.

<sup>a</sup> Error values represent asymmetrical standard error range around back-transformed mean.

open peatland subplots lacking woody stems  $>$  2.5 cm dbh and alder peatland subplots having few woody stems  $>$  6.35 cm dbh, while the black spruce peatland subplot had a higher density of woody stems  $>$  6.35 cm dbh.

In upland forested areas, approximately 50% of the total C was stored in vegetation with another 30–35% stored in the forest floor and the top 40 cm of mineral soil (Table 2). In peatland areas, 99% of the total C was stored as peat. We found the deepest peat in open peatlands, where some cores were 5 m deep. Peat depth averaged  $2.83 \pm 0.47$  m (mean  $\pm$  S.E.) in open peatlands and  $1.83 \pm 0.23$  m in alder peatlands. In the single black spruce peatland subplot, peat depth was 1.00 m. Because of these deep peat deposits, peatlands stored significantly more soil C ( $P \ll 0.001$ ) and more total C ( $P \ll 0.001$ ) than upland cover types (Table 2). Open peatlands stored more soil C and

total C than did alder peatlands. The mean total carbon content across all peatland plots was  $1286 \pm 125$  Mg C ha<sup>-1</sup>. Total C and C in mineral soil did not differ among upland cover types; however, conifer-dominated areas stored more C as forest floor ( $P \ll 0.001$ ) and as snags ( $P = 0.02$ ) than was found in other cover types. Aboveground C in live vegetation did not vary significantly among upland cover types, but upland cover types did store significantly greater C in aboveground pools than peatland cover types ( $P = 0.02$ ). Aboveground vegetation C in alder peatlands was significantly greater than that of open peatlands. Coarse woody debris did not vary significantly among cover types ( $P = 0.56$ ). Differences among cover types in belowground plant C (coarse roots, as estimated by allometric relationships) were marginally significant ( $P = 0.10$ ); the alder cover type had lower belowground plant C than all other cover types.

**Table 3**Components of NPP (means, with S.E. indicated in parentheses) in different cover types at MEF (Mg C ha<sup>-1</sup>). Significant differences evaluated by ANOVA ( $P < 0.05$ ), and Fisher's Least Significant Difference test, with superscripted letters denoting differences among cover types. Black spruce and non-forested cover types omitted from analyses because of low sample sizes.

Cover type	Aboveground wood	Canopy tree/shrub foliage	Herbs	Ericaceous shrubs	Sphagnum	ANPP total	Coarse tree roots
<b>Uplands</b>							
Aspen	0.84 <sup>a</sup> (0.08)	1.52 <sup>a</sup> (0.08)	0.22 <sup>b</sup> (0.03)	0 <sup>a</sup>	0 <sup>b</sup>	2.58 <sup>a</sup> (0.11)	0.13 <sup>b</sup> (0.01)
Hardwood	0.88 <sup>a</sup> (0.18)	1.71 <sup>a</sup> (0.11)	0.18 <sup>b</sup> (0.07)	0 <sup>a</sup>	0 <sup>b</sup>	2.77 <sup>a</sup> (0.24)	0.12 <sup>b</sup> (0.03)
Conifers	0.69 <sup>a</sup> (0.03)	1.67 <sup>a</sup> (0.32)	0.53 <sup>ab</sup> (0.40)	0 <sup>a</sup>	0 <sup>b</sup>	2.88 <sup>a</sup> (0.53)	0.17 <sup>ab</sup> (0.02)
Non-forested	0.12	0.49	0.46	0	0	1.07	0.02
<b>Peatlands</b>							
Open	0 <sup>b</sup>	0 <sup>b</sup>	0.88 <sup>a</sup> (0.27)	0.16 <sup>b</sup> (0.06)	0.45 <sup>a</sup> (0.17)	1.50 <sup>b</sup>	0 <sup>c</sup>
Alder	0.53 <sup>ab</sup> (0.15)	1.23 <sup>a</sup> (0.24)	0.23 <sup>b</sup> (0.13)	0.005 <sup>a</sup> (0.001)	0.77 <sup>a</sup> (0.48)	2.77 <sup>a</sup> (1.00)	0.24 <sup>a</sup> (0.07)
Black spruce	0.82	1.53	0.16	0.01	0.23	2.76	0.20

**Table 4**  
Areal estimates of total C and total NPP for different cover types in the entire 1-km<sup>2</sup> study area.

Cover type	Cover type area (ha)	Total C (Mg)	% of total C	Total NPP (Mg C)	% of total NPP
<b>Uplands</b>					
Aspen	73.2	11,640	42.4	198	73.0
Hardwood	2.1	320	1.2	6.0	2.2
Conifers	10.8	2,130	7.7	33.0	12.2
Non-forested	0.5	40	<1	0.5	<1
<b>Peatlands</b>					
Open	4.1	6,220	22.6	6.2	2.2
Alder	1.0	1,220	4.4	3.0	1.0
Black spruce	8.2	5,890	21.4	24.3	8.9
<b>Total for 1-km<sup>2</sup> study area</b>	<b>100</b>	<b>27,530</b>	<b>100.0</b>	<b>272</b>	<b>100.0</b>

Our estimates of productivity differed among vegetation cover types at MEF (Table 3). Forested cover types (including alder-dominated plots) did not vary in ANPP; however, ANPP was greater in these cover types than in open peatlands, which lacked woody and foliar inputs from trees. Foliar production was similar among conifer, aspen, hardwood, and alder areas. Our estimates of coarse tree root production in alder did not differ from that for conifers, but was greater than coarse root production in aspen or hardwoods. As we based coarse root estimates on tree allometry, no coarse root production was estimated for the open peatland cover type. Open peatland ANPP was dominated by the productivity of herbaceous vegetation, which was greater in open peatlands than in alder, aspen, and hardwood cover types ( $P = 0.007$ ,  $F = 4.5$ ).

Stored carbon is distributed unevenly among the different cover types at MEF (Table 4). Peatlands, which occupy 13% of the landscape, account for 48% of total C stored. Aspen cover, because of its abundance (73% of total area), accounts for 42% of C stored. In contrast, the distribution of production across cover types is approximately commensurate with the proportional area of cover types.

## 5. Discussion

### 5.1. C storage and productivity in uplands

Smith et al. (2006) evaluated C storage for Great Lakes region FIA plots as a function of stand composition and age. Our estimate of C stored in aspen at MEF is approximately 25% greater than the regional values Smith et al. (2006) reported for aspen-dominated stands of comparable age. Carbon storage in live biomass accounts for most of this difference. In contrast to aspen, our estimate of C storage in pine-dominated plots at MEF is only 7% greater than the regional average for comparably aged stands and our estimate of C stored in maple-dominated stands at MEF is 15% lower than the regional average for comparably aged stands. The forest floor C reported for maple stands by Smith et al. (2006) is approximately three times greater than the forest floor C pool that we found at MEF and explains most of the difference between the MEF and regional estimates of C in maple.

Our estimates of mineral soil C in upland forested cover types (Table 2), which are based on a sampling depth of 40 cm, are comparable to estimates of 52.3 and 63 Mg C ha<sup>-1</sup> made for similar soils (Warba fine sandy loams) elsewhere in Minnesota (Alban and Perala, 1992). We recognize that some soil C exists below our 40 cm sampling depth. For example, in their survey of upland forest carbon soils in Great Lakes states, Grigal and Ohmann (1992) reported that soil C at 50–100 cm depth contained 20–60 Mg C ha<sup>-1</sup>. In an independent study at MEF, soil to a depth of

100 cm (including forest floor) was estimated to contain approximately 100 Mg C ha<sup>-1</sup> (D. Grigal, unpublished).

Our estimates of ANPP in aspen and hardwood cover types (Table 3) are 30 and 20% lower, respectively, than ANPP values reported by Burrows et al. (2003) for those forest covers in northern Wisconsin, assuming a 50% C content in the Wisconsin biomass pools. Differences in wood biomass between the MEF and Wisconsin stands account for most of this difference.

Estimates in the literature of ANPP in conifer stands dominated by jack pine and red pine vary considerably, ranging from 1.1 to 2.9 Mg C ha<sup>-1</sup>, assuming 50% C content in vegetation for studies that report biomass only (Pastor et al., 1984; Fassnacht and Gower, 1997; Gower et al., 1997). Our estimates of ANPP in MEF conifers (Table 3) fall within this range.

### 5.2. C storage and productivity in peatlands

Peatlands represent the largest C pool in the MEF study area, a consequence of their deep organic-rich soils. Our estimate of total C in peatlands at MEF is on par with C estimates for non-permafrost peatlands across the coterminous United States (Bridgman et al., 2006) and global averages (Gorham, 1991). Although peatlands represent only 13% of the MEF 1-km<sup>2</sup> study area, they contain approximately 50% of the C stored therein (Table 4). Roughly 90–99% of this C is stored as peat, making any estimate of total C stored in the MEF study area highly sensitive to estimates of C in peat.

Literature estimates of live vegetation biomass in peatlands range widely, from <1 to nearly 70 Mg C ha<sup>-1</sup> (Dyck and Shay, 1999; Grigal et al., 1985). Our estimate of C stored as biomass in open peatland and alder peatlands is comparable to estimates made in similar peatlands of the Great Lakes region (Moore et al., 2002; Dyck and Shay, 1999) and biomass in our only black spruce subplot is within the range reported for perched and raised black spruce bogs within MEF and elsewhere in northern Minnesota (Grigal et al., 1985).

Literature reports of ANPP in open peatlands range widely from as low as 0.7 to nearly 4 Mg C ha<sup>-1</sup> (Moore et al., 2002); our estimate of ANPP in open peatlands at MEF falls within this range. The relative contribution of herbs, bryophytes, and shrubs to ANPP in open peatlands appears to be rather plastic. For example, Chapin et al. (2004) found *Sphagnum* production to be approximately 70–90% of ANPP in a northern Minnesota bog, while Moore et al. (2002) reported that *Sphagnum* contributed 50% of ANPP in the Mer Bleu peatland in Ontario. In our study *Sphagnum* accounted for only 30% of ANPP. Relative production in peatland bryophytes, shrubs, and herbs varies with water chemistry; for example, minerotrophic fens tend to have greater herb contributions than bogs while bogs tend to have greater bryophyte contributions than fens (Chapin et al., 2004). Additionally, interannual variation in water table may influence relative production of these vegetation types; *Sphagnum*

production is highest when water tables are closest to the peat surface (Weltzin et al., 2000, 2001). During 2006, northern Minnesota experienced severe to extreme drought conditions for much of the summer (National Drought Mitigation Center, 2006). The *Sphagnum* production that we measured at MEF falls within the low end of the range of 0.1–1.9 Mg C ha<sup>-1</sup> found across 22 bogs and poor fens, summarized by Moore et al. (2002). Our estimate is also considerably lower than estimates of 1.6 Mg C ha<sup>-1</sup> obtained from cranked wire measurements in a forested bog at MEF 20 years earlier (Grigal, 1985). The low *Sphagnum* production that we measured at MEF may reflect dry conditions experienced during the period of measurement. Our estimates of ANPP in black spruce peatlands are approximately 25% greater than earlier estimates made for black spruce at MEF (Grigal et al., 1985; Grigal, 1985), with most of this difference accounted for by woody growth.

The large amounts of C stored in peatlands and the low productivity underscore the potential of peatlands to impact regional C cycling with changes in climate (Gorham, 1991; Bridgman et al., 1995). Over time scales of hundred to thousands of years, peatlands have acted as carbon sinks through peat accretion at rates of approximately 0.2–0.3 Mg C ha<sup>-1</sup> (Roulet et al., 2007). Peat accretion depends upon a positive balance of C inputs and losses, e.g., productivity, autotrophic and heterotrophic respiration, and DOC export, which in turn depend upon climatic drivers. Respiration losses near peat surfaces (i.e., the acrotelm) are sensitive to temperature and generally increase with warmer soils (Updegraff et al., 2001; Blodau et al., 2007). Decomposition of deeper peat, i.e., the catotelm, is slower because of anaerobic conditions imposed by water level, but in a warmer, drier climate, declines in water level may make this peat more vulnerable to C loss (Bridgman et al., 1995). While a warmer, drier climate may cause productivity patterns to shift, it is not clear whether total net productivity will increase, decrease, or remain unchanged, as occurred in a mesocosm scale climate manipulation study of Minnesota peatlands (Weltzin et al., 2000). Increases in peatland respiration with no change or a decline in production would reduce the strength of these historical C sinks, possibly changing them to net C sources. In addition to influencing the regional net balance between production and respiration, changes in peatland disturbance regimes could impact regional C budgets. For example, a moderate increase in fire frequency and intensity, which is predicted under warmer and drier climate scenarios, could turn northern and temperate peatlands into a net source of C to the atmosphere (Turetsky et al., 2002; Poulter et al., 2006).

### 5.3. Importance of fine root contributions

In our study, we estimated belowground biomass and productivity using generalized allometric equations (Perala and Alban, 1994). Those equations related the biomass of 15 cm high excavated stumps with attached coarse roots (>5 mm diameter) to tree diameter. Therefore, our study does not consider the contributions of fine roots to C pools and total net primary production. While fine roots typically do not account for a substantial portion of total C in most ecosystems (e.g., 2% or less in mature forests; Kalyn and Van Rees, 2006), they can be a considerable component of total productivity in forests. Kalyn and Van Rees (2006) reported that fine roots accounted for 42 and 62%, respectively, of NPP in boreal aspen and jack pine. Fine root productivity was the largest component of NPP in these ecosystems. Across a range of experimentally imposed temperature and water table conditions, fine roots accounted for 18–42% of total NPP in peatlands (Weltzin et al., 2000). In light of these studies, total ecosystem NPP at MEF is likely to be substantially

higher than the sum of NPP measurements that we report for both upland forest and peatlands (Table 3), highlighting a continued need for improved understanding of fine root dynamics.

## 6. Conclusion

The distribution of C at MEF illustrates the importance of peatlands to understanding C cycling in heterogeneous landscapes of the western Great Lakes region. Carbon in the region is unevenly distributed, with peatlands having C densities that are up to 10 times greater than upland forest ecosystems. Carbon storage in peatlands is a consequence of long-term climate trends in which a positive water balance enables accretion of peat. The dependence of peatland development and stability on climate underscores the potential vulnerability of stored peatland C to climate changes and the importance of this stored C to the regional C balance.

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