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Ecosystem Carbon Storage and Flux in Upland/Peatland Watersheds in Northern Minnesota

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CONTENTS

Introduction

Carbon (C) storage (the amount of C in the system at a given time) and fluxes (inputs and outputs of C per unit time) are central issues in global change. Spatial patterns of C storage on the landscape, both that in soil and in biomass, are important from an inventory perspective and for understanding the biophysical processes that affect C fluxes. Regional (e.g., Grigal and Ohmann 1992; Homann et al. 1995; Johnson and Kern 2003; Kulmatiski et al. 2004; Simmons et al. 1996) and national estimates of C storage (Birdsey and Heath 1995; Birdsey and Lewis 2003; Smith et al. 2006) are uncertain because they are based on a specific subset of sites or on extrapolation of broad-based means. The patterns and processes affecting ecosystem C vary considerably among landscapes, limiting extrapolation across broad climatic–geomorphic regions.

Estimates of C storage for specific watersheds or other forested tracts (e.g., Arrouayes et al. 1998; Bell et al. 2000; Thompson and Kolka 2005) provide metrics to evaluate these broader estimates. The catena concept, firmly established in soil science, embodies the view that, in humid regions, hydrologic processes active on hillslopes lead to considerable differences in soil characteristics. Although the concept is firmly established, quantification of changes in soil C with landscape position, especially in forests, is lacking.

This is especially true in more recently glaciated regions such as the northern Great Lakes States, northern New York, and much of south-central Canada, where climate and a poorly developed drainage network have led to abundant peatlands, occupying 10%–30% of most basins. Quantification of the C stored in these immature landscapes, the pools in which it is stored, and the relationship of that storage to landscape features will aid in predicting the magnitude of C response to various scenarios of global change.

Carbon storage is ultimately the summation of the flux of C into and out of ecosystems. Attention has been focused on detailed measurements of net primary productivity, but less attention has been paid to simultaneous C losses. Numerous data relating to C flux in selected ecosystems have been collected over the past several decades, but those empirical data have not been linked. Such a linkage can both provide an estimate of net C flux and indicate where additional research is needed.

Objectives

The primary objective of this work is to better understand the mechanisms responsible for C sequestration at landscape scales. Specific objectives were to

1. Quantify the magnitude and spatial patterns of ecosystem C storage across landscapes at the USDA Forest Service's Marcell Experimental Forest (MEF) in northern Minnesota. Two approaches were used and the results compared; the *categorical* approach extrapolated published estimates of C storage for similar systems and components, and the *continuous* approach used functional relationships developed from an intensive set of plot measurements.
2. Estimate C flux for two common forest types on the MEF: aspen-birch on uplands and black spruce on peatlands. A conceptually simple model/spreadsheet considered C inputs via plant growth and losses via decomposition using functions based wholly on literature data. Results were compared to measures of C storage at various stand ages from the literature and from the MEF.

Carbon Storage

The *categorical* approach to quantify ecosystem C storage was based on categories of vegetation and soils of MEF from conventional mapping (at scales of 1:15,840 and 1:24,000, respectively). Those estimates were applied to all

occurrences of each category on the MEF. The *continuous* approach was based on functional relationships predicting C storage, developed primarily using linear and nonlinear regression with plot measurements, mapping, and landscape attributes, developed from a digital elevation model (DEM) as independent variables. These relationships were then applied to each cell of a GIS database describing the MEF. Although reports of use of the continuous approach to estimate C storage (with different sets of variables than used here) have been optimistic (Mueller and Pierce 2003; Stutter et al. 2009), the categorical approach is much less costly in terms of both time and resources. If results from the two approaches are similar and if the goal is simply estimates of C storage per se, the categorical approach could be applied more widely.

A detailed description of the methods and results of the inventory of ecosystem C at the MEF is available (Grigal 2009). They provide a background for the overview presented here.

Methods

Field

The location and characteristics of the MEF are described elsewhere (Chapter 2). In 1992 and 1993, descriptions and samples of soils, vegetation, and topography were collected at 25 m increments along 20 transects crossing topographic and vegetation boundaries of the MEF. All sample points (596 points) were included in a reconnaissance dataset, and about one-third of those points (219 points) were elected randomly for intensive sampling. In addition, 30 points (including 10 intensively sampled points) were revisited to assess variability in data collection.

The following data were collected at all sample points:

- Topography: slope gradient, aspect, profile curvature (perpendicular to the contour), planar curvature (parallel to contour), and slope position.
- Vegetation: species and dbh (diameter at breast height) for all "in" trees > 2.5 cm dbh using a 10-BAF prism; standing dead trees were also measured and assigned to one of four condition classes (ranging from recently dead to standing bole without branches); percent cover and average height of tall shrubs (SHs); and percent cover of low SHs and forbs.
- Mineral soils (when present): thickness of both forest floor and of the A horizon.
- Organic soils (when present): depth of organic soils (peat) was measured using a McCauley peat auger, and degree of humification was estimated using the von Post method (Malterer et al. 1992; Chapter 5).

At the 219 intensive points, soil samples were collected for laboratory analyses. For mineral soils, samples of the forest floor, a composite sample of the upper 25 cm of mineral soil, and a single sample from the 25–100 cm layer were collected. For peat, samples were collected from the 0–50 cm layer, 50–100 cm layer and from each additional meter thereafter.

The 1992–1993 inventory of the MEF did not include complete sampling of coarse woody debris (CWD); standing dead trees were included but logs (fallen branches and boles) were not. In 2003, logs were inventoried following the methods outlined in Duvall (1997), based in part on techniques described by Van Wagner (1968). Log CWD was sampled at 25 m intervals along 28 transects that roughly followed the same bearings and lengths as the 1992/1993 transects. No attempt was made to relocate sample points from the earlier inventory. Each sample point (n = 546) served as the center of a 10 m line-transect, oriented along the bearing of the overall transect, and logs (≥2.5 cm in diameter at the plane of intersection between the transect and the log) were measured. Stand basal area (BA) was measured with a 10-BAF prism centered at each point. Overall, transect bearings, and hence those of CWD transects, varied across MEF. Because of concern that a single orientation could bias results, about 6% of the points were resampled with transects perpendicular to the original bearing. Paired t-tests indicated no significant differences between log mass from the two sets of data.

Laboratory

All samples of forest floor, mineral soil, and peat were kept cool in the field and sent to the laboratory within 48 h. Upon receipt, mineral and peat samples were frozen until further processing. The moist mass of the forest-floor samples was determined, a subsample was removed to determine water content, and the remainder was frozen. After thawing, subsamples of all materials were analyzed for loss on ignition (LOI) by ashing at 450°C for 12 h. Total C was determined on about 20% of the samples using a LECO CR-12 analyzer (David 1988).

Geospatial Data

A raster GIS database with 10 m cells was developed for MEF, including a DEM, vegetation cover type, and soils from an order II soil survey. The DEM was created from an existing topographic map with 1.2 m elevation contours derived from a ground survey. Cover type was interpreted from 1:15,840 color-infrared airphotos, dated May 1990. Twelve forested types (red pine, jack pine, balsam fir, white spruce, black spruce, tamarack, northern white-cedar, northern hardwoods, lowland hardwoods, black ash, aspen, and birch) and 10 miscellaneous types (upland grass, upland brush, lowland grass, lowland brush, beaver pond, marsh, muskeg, permanent water, stagnant spruce, and stagnant tamarack) were recognized. The forested types were assigned

to one of three dbh size classes. Forested types in the smallest class were further characterized by the percent canopy cover and in the two larger classes by the estimated merchantable volume (in cords per acre). Soil-map unit delineations were digitized from a 1:24,000 Natural Resources Conservation Service (NRCS) order II soil survey for Itasca County, MN (Nyberg 1987). Sixteen soil-mapping units were recognized.

Numerical and Statistical

Categorical C Estimates

Vegetation Type Estimates of aboveground biomass were derived for each cover type. Estimates for the larger dbh classes of the forested types were based on extrapolation of the mapped volume to total biomass by vegetation type, using data from Grigal and Bates (1992). Biomass estimates for the smallest class of the aspen-birch forest type were primarily based on Perala (1972), with comparisons for reasonableness from Silkworth (1980) and Alban and Perala (1992). For the smallest diameter class of the conifer forest types, including pine, spruce-fir, lowland conifers, and black spruce, biomass was estimated with data from Berry (1987) and Methven (1983). Biomass for hardwoods other than aspen-birch was the geometric mean of those for aspen-birch and conifers. Biomass estimates for the nonforest cover types were based on a variety of studies in Minnesota (Bell et al. 1996; Connolly-McCarthy and Grigal 1985; Perala 1972; Swanson and Grigal 1991).

Belowground biomass estimates were simply a ratio of the aboveground estimates. For forested types, the root:shoot was 0.3 (Alban and Perala 1994; Santantonio et al. 1977; Whittaker and Marks 1975). For shrub types (upland brush, lowland brush, and muskeg), it was 1.3 (Alban and Perala 1994; Grigal et al. 1985; Johnston et al. 1996). For the herbaceous types (upland grass, lowland grass, and marsh), the ratio was 2.0 (Abrahamson 1979; Ashmun et al. 1985; Grigal et al. 1985; Gross et al. 1983; Nihlgard 1972; Paavilainen 1980; Remezov and Pogrebnak 1969). In all cases, living biomass was converted to C using a ratio of 1:0.475 (Raich et al. 1991).

Soil-Mapping Unit Soil C was estimated for each soil-map unit. Because tabulated data in the published soil survey report (Nyberg 1987) are relatively general, more detailed data from 73 pedons, representing 16 taxonomic units, were used. Data were primarily collected from the soil characterization database of the NRCS (Soil Survey Staff 1997) and from the University of Minnesota Department of Soil, Water, and Climate. Other sources included Alban and Perala (1990), Balogh (1983), Grigal et al. (1974), and Kolka (1993). Organic C was computed for both the upper 25 cm and the upper meter of these pedons and then extrapolated to the soil-mapping units based on the taxonomic composition of each unit (Nyberg 1987).

Continuous C Estimates

Laboratory The LOI and C data for forest floor, mineral soil, and peat from MEF and similar data gathered from another site in Minnesota in a companion study (Bell et al. 1996, 2000) were combined, and simple linear regressions were developed for each sample type relating LOI (%) and C (%).

Mineral soil bulk density (D_b) was estimated from LOI using the approach of Federer et al. (1993), where soil D_b is a function of the proportion of organic material in the soil and the D_b of the organic (or C) and mineral fractions. The relationship was developed from the data collected in a transect of forested sites across the north-central United States (Ohmann and Grigal 1991). For materials high in organic matter, such as forest floor and peat, soil D_b is simply a function of the organic fraction and its D_b (Gosselink et al. 1984). Using the measured forest-floor thickness, LOI, and mass from the intensively sampled points, the D_b of the organic material was determined using nonlinear least-squares regression (SYSTAT Inc. 2007). The D_b of the organic material in peat was similarly determined using an extensive database of peat LOI and D_b collected in MEF and other peatlands in northern Minnesota (Buttleman 1982).

Vegetation Overstory (tree) biomass was based on the tree dbh collected at each point. For aboveground biomass, we used estimation equations from Alemdag (1983, 1984). Those equations use both dbh and total height as independent variables, so a relationship between dbh and height for trees on the MEF was developed. For belowground biomass, an estimation equation was based on data from Santantonio et al. (1977), Whittaker and Marks (1975), and Alban and Perala (1994).

Although understory strata (below the canopy) are a relatively minor proportion of total stand biomass in closed forest (about 5%; Ohmann and Grigal 1985a; Swanson and Grigal 1991), they may constitute the majority of mass as canopies become more open. Biomass estimation equations for understory strata were developed using data from two comprehensive studies from northern Minnesota, one of uplands (211 stands by Ohmann and Grigal 1985b) and the other of peatlands (235 stands by Swanson, 1988). Because these studies included only data from one mesic hardwood (i.e., northern hardwood) stand, data for seven mesic hardwood stands from east-central Minnesota were added (Suhartoyo 1991). The data were aggregated into three understory groups (ground cover, forbs, and shrubs) and an overstory group (trees) and further grouped into 10 vegetation types (aspen-birch [AB], black spruce [BS], lowland conifers [LC], lowland hardwoods [LH], pine [PI], spruce-fir [SF], upland hardwoods [UH], open bog [OB], shrub [SH], and grass [GR]), based on the majority of overstory biomass (Ohmann and Grigal 1985b) or on the physiognomic group (Swanson 1988).

Vegetation types for points with no or minimal tree cover were based on field notes. For example, residual trees in recently cut areas may not be indicative of the original or regenerating type. Field notes helped assign the appropriate type in those cases and in the shrub, open bog, and grass types.

Understory biomass was estimated by linear regression as a function of the biomass of the conifer and the deciduous overstories, with vegetation type as a dummy variable. Cover of forbs and the cover and height of the tall SHs were used to adjust the estimates.

Aboveground biomass of standing dead trees (snags) was calculated using the same functions as those for live trees, and the resulting mass was adjusted for the decay class. Log volumes were calculated (Van Wagner 1968), and biomass and C content was estimated by using tabulations of density and C concentration as a function of decay class (Duvall 1997). Log CWD for each point in the original (1992/1993) inventory was estimated by extrapolation of the data collected in 2003. Points were placed into vegetation groups, and a regression equation was developed using the continuous variables from each point and with group as a dummy variable.

Soil Forest floor had been quantitatively sampled and LOI determined at each intensive point. Mass per unit area was calculated and converted to C per unit area using the equation relating C to LOI. Extrapolation of the forest-floor C (FFC) mass from the intensive to the reconnaissance points was based on the collected data. The measured aspect was transformed to more closely reflect biological importance, with a maximum of 1 at 225° (SW) and a minimum of 0 at 45° (NE) (Beers et al. 1966). A randomly chosen subsample of 10% of the data from intensive points (15 of the 152 mineral soil points) was used to evaluate the uncertainty of the final estimates.

Determination of C mass of mineral soils requires C concentration, D_b, and horizon thickness. For the intensive points, LOI data were used to estimate C concentration and D_b, and C mass was calculated for the 0–25 cm and the 26–100 cm soil layers. As with forest floor, those data were extrapolated to the reconnaissance points using the same subset of data but including thickness of forest floor and A-horizon as additional independent variables. A subsample of 10% of the data (the same points used for evaluating forest-floor uncertainty) was used to evaluate the uncertainty of the final estimates.

For peat, both C concentration and D_b were expressed as functions of LOI, and C mass was computed as a direct function of LOI and thickness. Depth had been measured at both intensive and reconnaissance points where peat occurred, and C mass was calculated for all those points.

Landscape Attributes The C data from the inventory and landscape attributes were used to estimate C over the entire landscape. The landscape attributes were calculated from the DEM for the 10×10 m cell associated with each inventory point using Arc/Info. Primary attributes included elevation, aspect, flow accumulation, plan/profile curvature, and slope steepness, and secondary attributes included both compound topographic index and stream power index. An aspect code was calculated from aspect (Beers et al. 1966).

The C data for each inventory point, both intensive and reconnaissance, and their map attributes (as categorical variables) were merged with the landscape attributes to create a single database (Table 9.1). Some categorical

TABLE 9.1

Data for Each Inventory Point, Landscape Attributes Calculated from 10 m DEM Interpolation of 1.2 m Contour Data for the MEF

Attribute	Description
POINT	Transect point
NORTHING	Location
EASTING	Location
ELEV	Elevation (m)
ASP	Aspect direction (0°–360°)
CTI	Compound topographic index
PLCURV	Curvature measured in the plan direction
PROCURV	Curvature measured in the profile direction
SCA	Specific catchment area (also known as flow accumulation)
SPI	Stream power index
SLOPE	Slope (degrees)
LEGEND_NUM	Numerical code for combination of overstory, size, and density
OVER_TYPE	Overstory type number
OVER_SIZE	Overstory size
OVER_DENS	Overstory density
SPECIES	Species group or cover type—alpha
MUSYM	Soil-mapping unit symbol
LVL	Level of field sampling; 1 = reconnaissance, 2 = intensive
FFC	Forest floor C
SURFC	Mineral C (0–25 cm)
SUMINC	Mineral C (0–100 cm)
SOILC	Sum FFC + SUMINC
PEATDPTH	Peat depth (cm)
PEATC	Peat C to mineral substrate
PEAT100	Peat C to 100 cm
FF MEAS	Forest floor mass was determined (1) or estimated (0)
MIN MEAS	Mineral soil mass was determined (1) or estimated (0)
COVTYP	Cover type based on measured basal area
C/D	Conifer or deciduous basal area majority?
AGTREC	Aboveground tree C
ROOTC	Belowground tree C
SHRBAGC	Estimated shrub aboveground C
FORBAGC	Estimated forb aboveground C
GRNDC	Estimated ground layer aboveground C
AGVEGC	Sum AGTREC + SHRBAGC + FORBAGC + GRNDC
LOGC	Estimated log CWD C
SNAGC	Standing dead tree C
CWDC	Sum LOGC + SNAGC
ASPCOD	Computed aspect code
LNCTI	Natural log (CTI + 2)

(*continued*)

TABLE 9.1 (continued)

Data for Each Inventory Point, Landscape Attributes Calculated from 10 m DEM Interpolation of 1.2 m Contour Data for the MEF

Attribute	Description
LNSCA	Natural log SCA
LNSPI	Natural log (SPI + 2)
SOILCODE	Coalescence of soil-mapping units into four categories
FORTYP	Coalescence of overstory type into 10 categories
OVSZCOD	Coalescence of overstory size into four categories
OVDNCOD	Coalescence of overstory density into four categories

variables were further grouped. Soil-mapping units were combined into four groups based on a combination of physiography and associated surface soil texture. Cover types were combined into 10 groups based on predominance of overstory biomass as described previously. An additional group, coded as 0 for nonforest types, was added to overstory size; overstory density, based on estimated volume, was combined into four groups, including 0 for nonforest types (Table 9.1).

Because of the continuous vegetation cover at the boundaries of MEF, some inventory points had been established inadvertently outside MEF and had no associated landscape attributes. Those points were eliminated from the analyses, leaving 541 points with a full set of data. Fifty points were chosen randomly to serve as a check, and 491 points were used to develop estimation equations.

Analysis Extensive screening was conducted to determine the best overall set of independent variables to use to estimate C. This screening included analyses of variance (ANOVA) to determine the relative influence of the categorical variables (soil and cover type) on C, stepwise regression to determine the influence of the continuous variables (landscape attributes), and scatterplots. Based on the results, data were separated into peatland and nonpeatland to estimate soil-related C data and into forested and nonforested to estimate vegetation-related C.

Although peatland occurrence should presumably be established by the soil mapping, that occurrence has uncertainty through simple errors or lack of sufficient map resolution (minimum map unit size). Similarly, there is uncertainty in plot locations as determined by GPS. Even without error, these uncertainties can amount to 7–15 m (National Imagery and Mapping Agency, http://www.geocomm.com/channel/gps/news/nimagps2/, accessed February 19, 2010). As a result, mineral-soil data were collected from some plots whose coordinates indicated that they were located on peatland, and peat data were collected on sites mapped as upland. Logistic regression, a mix of categorical and continuous variables used to predict probabilities of a binary response variable, was used to predict the probability that any point was likely to be

peatland (i.e., quantify the uncertainty). Elevation, a continuous variable, and cover type and soil-mapping unit, and categorical variables (Table 9.1) were used as independent variables.

A similar situation occurred with vegetation mapping, and a similar rationale led to the use of logistic regression to estimate the probability that a data point was forested (i.e., had a forest canopy). The criterion for presence or absence of a canopy was approximately 5 m^2 ha^{-1} BA of living trees, equivalent to about 7.5 Mg ha^{-1} of aboveground tree C. Regression was based on the categorical variables overstory dbh class, overstory density class, and soil group.

The final estimation equations for C in vegetation-related ecosystems components—aboveground tree, root, aboveground shrub, aboveground forb, aboveground ground cover, sum of all aboveground vegetation, down log CWD, standing dead CWD, and sum of all CWD—were based on a common set of independent variables; for some dependent variables, the data were divided into nonforested and forested categories. The estimation equations for soil-related C used a different but common set of independent variables following the separation of points into peatland (in which case, peat C to mineral substrate was calculated) or nonpeatland (with calculation of FFC, surface [0–25 cm] mineral soil C, total mineral soil C [0–100 cm], and sum of forest floor plus mineral soil C to 100 cm). Belowground C of SHs was based on a root:shoot = 1.3 and of forbs = 2.0 (sources as described earlier).

The final equations were applied to each cell of the 10 m GIS database (approximately 100,000 cells). Statistical tests were conducted to determine the significance of differences in C estimates among mapped vegetation types and among soil-mapping units.

Results

Categorical C Estimates

Vegetation Type

Total aboveground tree biomass of closed-canopy forested types ranged from about 500–1000 kg m^{-3} of merchantable volume. No estimates of understory biomass were made in closed-canopy types. Total aboveground biomass estimates for the forested size class 1 (<12.5 cm dbh) ranged from 2 to 80 Mg ha^{-1} and from 7 to 35 Mg ha^{-1} for the nonforest vegetation types. After conversion of biomass to C, the results indicated an average of about 51 Mg ha^{-1} of C stored in the vegetation of MEF (Table 9.2). This result has an undefined uncertainty.

Soil-Mapping Unit

As described, data from 73 pedons representing 16 taxonomic units were used to estimate C content of the soil-mapping units on the MEF. Where D_b for a horizon was missing, it was computed using estimates of the mineral (D_{bm}) and the C fractions (D_{bC}) from the remainder of the database

TABLE 9.2

Estimates of Biomass C for Cover Types Mapped on the MEF Based on Categorical Analysis

Cover Type	Area (ha)	C (Mg)	C (Mg ha^{-1})
Aspen	488	32,765	67.1
Balsam fir	3	193	56.0
Birch	26	917	35.3
Black ash	3	51	17.8
Black spruce	76	1,445	19.1
Jack pine	24	1,638	68.3
Lowland brush	17	346	20.2
Lowland grass	2	23	13.5
Lowland hardwoods	18	1,279	69.1
Marsh	18	179	10.0
Muskeg	59	609	10.4
Northern hardwoods	64	5,475	86.1
Northern white-cedar	7	185	27.9
Permanent water	51		
Red pine	36	1,047	29.5
Stagnant spruce	10	194	19.1
Stagnant tamarack	7	151	20.3
Tamarack	28	390	13.9
Upland grass	3	39	13.5
White spruce	26	142	5.5
Sum	966	47,069	51.5[a]

Note: Data include both aboveground and belowground C.

[a] Mass per area-weighted mean, not including area of permanent water.

(Federer et al. 1993). Nonlinear least squares yielded $D_{bm} = 1.73$ Mg m^{-3} and $D_{bC} = 0.100$ Mg m^{-3} ($n = 99$, $R^2 = 0.98$, $s_{y\cdot x} = 0.11$ Mg m^{-3}). For organic soils (C > 15%), $D_{bC} = 0.07$ Mg m^{-3} ($n = 46$, standard error of the mean, SE = 0.004 Mg m^{-3}). Where C data were missing for some subsurface mineral horizons, a general relationship of C to depth was developed using data from Ohmann and Grigal (1991). Mass of organic C was computed for both the upper 25 cm and the upper meter of the pedons and thence for the soil-mapping units (Table 9.3). Uncertainty can be roughly quantified by the pooled SE of estimates for units represented by three or more pedons ($n = 12$). Based on the SEs (13% for the 0–25 cm layer and 11% for the 0–100 cm layer 68 degrees of freedom, d.f.), Fisher's least significant difference (LSD) among units is about 24%.

The estimated C for mapping units tended to be bimodal, as expected in a landscape with a mix of mineral soils and peat (Histosols). Mineral soils generally had less than 50 Mg ha^{-1} C in the surface 25 cm while Histosols had greater than 150 Mg ha^{-1} (Table 9.3). Similarly, mineral soils tended to have about 100 Mg ha^{-1} C in the upper meter while Histosols had greater than

TABLE 9.3

Organic Carbon Content of the Soil-Mapping Units of the MEF Based on Detailed Soil Characterization Data for Individual Taxonomic Units within Mapping Units

Soil-Mapping Unit	Area (ha)	Organic Carbon 0–25 cm (Mg[a])	Organic Carbon 0–100 cm (Mg[a])	Organic Carbon 0–25 cm (Mg ha^{-1})	Organic Carbon 0–100 cm (Mg ha^{-1})
Borosaprists, depressional	51	10,095	38,477	198.9	758.0
Cathro muck	7	1,252	5,295	173.3	733.1
Greenwood peat	48	8,321	29,158	173.5	607.9
Loxely peat	4	1,290	3,338	358.1	926.8
Menahga and Graycalm soils	135	4,193	8,954	31.1	66.4
Menahga loamy sand	71	2,269	5,467	31.9	76.8
Mooselake and Lupton mucky peats	35	5,809	25,505	164.7	722.9
Nashwauk fine sandy loam	159	7,924	17,991	50.1	113.6
Nashwauk–Menahga complex, 1%–10%	45	2,214	5,203	48.9	115.0
Nashwauk–Menahga complex, 10%–25%	96	4,397	9,831	46.1	103.1
Sago and Roscommon soils	8	1,248	3,009	149.9	361.3
Seelyeville–Bowstring association	42	7,996	30,484	188.7	719.2
Warba fine sandy loam, 1%–8%	153	4,576	12,346	30.0	81.0
Warba fine sandy loam, 10%–25%	54	1,644	4,418	30.4	81.7
Sum	964	63,228	199,475	69.7[b]	220.0[b]

[a] Total C mass in each unit.

[b] Mass per area-weighted mean, not including area of permanent water.

600 Mg ha^{-1} in that depth (Table 9.3). A minor exception to this generality was the Sago and Roscommon mapping unit, where the major taxonomic components were Histic and Mollic Aquepts, respectively. These wet mineral soils with surface organic accumulations grouped with the Histosols in the surface 25 cm, but with lower organic matter in deeper horizons fell between mineral and organic soils at 100 cm (Table 9.3).

When the data were extrapolated to the entire landscape of MEF, soil C, even in the 0–25 cm layer (Table 9.3), was higher than that of any vegetation strata, both above- and belowground (Table 9.2). When deeper soil layers were considered, differences were even greater. This demonstrates the importance of soils, especially, peat, in influencing landscape C storage.

Continuous C Estimates

Vegetation

A wide range of species and sizes of trees were used for the height estimation equation. Based on linearized least squares, and including a correction for bias (Beauchamp and Olson 1973), the best-fit relationship was

$$HT = 2.03 * dbh^{0.71}, \quad n = 173, \; r^2 = 0.99, \tag{9.1}$$

where height (HT) is in m and dbh is in cm. The expression relating root mass to tree dbh, an average of the literature sources, was

$$ROOT = 0.031 * dbh^{2.39}, \tag{9.2}$$

where ROOT is root biomass in kg and dbh is in cm. Goodness-of-fit statistics are not relevant for Equation 9.2 because it is simply an average of other relationships.

The understory estimation equations, where biomass of the understory was a function of the conifer and the deciduous overstory biomass, with vegetation type as a dummy variable, were significant (herbs, $R^2 = 0.67$, $s_{y\cdot x} = 575$ kg ha^{-1}; SHs, $R^2 = 0.32$, $s_{y\cdot x} = 2200$ kg ha^{-1}; ground cover, $R^2 = 0.50$, $s_{y\cdot x} = 1550$ kg ha^{-1}; $n = 436$ for all cases).

There was no need to extrapolate vegetation C estimates from intensive to reconnaissance points, because tree data had been collected on all points. The data indicated a mean biomass C, both above- and belowground, of about 51 Mg ha^{-1} (Table 9.4). This is virtually identical to the areally weighted mean based on the vegetation cover-type map (Table 9.2). The agreement between the results of the two methods increases confidence in those results.

Soil

Laboratory/Statistical Simple linear regressions were developed for forest floor, mineral soil, and peat where x = LOI (%) and y = C (%). Because the y-intercept was only marginally significant for forest floor ($p = .043$) and not significantly different than 0 for peat ($p = .175$), both regressions were rerun forcing the intercept through 0. The final results were

$$\text{Min C (\%)} = 0.50 * \text{LOI (\%)} - 0.15, \; n = 229, \; r^2 = 0.95, \; s_{y\cdot x} = 0.13, \tag{9.3}$$

TABLE 9.4

Estimates of Biomass C for All Sampled Points on the MEF. Biomass Includes Both Aboveground and Belowground Trees, Shrubs, Forbs, and Ground Cover

Vegetation Type	Number of Observations	C, Mean (Mg ha^{-1})	C, Standard Error (Mg ha^{-1})
Aspen-birch	415	53.33	2.03
Black spruce	29	40.68	3.38
Grass	14	6.05	0.21
Lowland conifers	23	35.37	5.61
Lowland hardwoods	22	52.40	7.74
Open bog	16	6.14	0.16
Pine	20	90.21	5.90
Spruce-fir	18	48.67	5.97
Shrub	2	9.72	0.00
Upland hardwoods	36	54.24	5.02
All	595	50.61[a]	1.62

[a] Mean of all observations.

$$\text{FF C (\%)} = 0.484 * \text{LOI (\%)},\ n = 129,\ r^2 = 0.84,\ s_{y\cdot x} = 3.5, \tag{9.4}$$

$$\text{Peat C (\%)} = 0.55 * \text{LOI (\%)},\ n = 82,\ r^2 = 0.91,\ s_{y\cdot x} = 3.2. \tag{9.5}$$

These relationships are similar to others reported for the north-central United States. For the same LOI, however, relationships spanning the North Central States yield higher estimates for both forest floor and mineral soil (about 8% and 0.2% C, respectively, or about 25% of the observed mean) (David 1988). LOI (equivalent to organic matter) apparently is lower in C at MEF than at other locations in the region.

Data collected in a transect of forested sites across the north-central United States (Ohmann and Grigal 1991) yielded D_{bo} of 0.11 Mg m^{-3} and D_{bm} of 1.63 Mg m^{-3} (R^2 between observed and predicted $D_b = 0.70$, n =172). In coarse-textured soils of New England, D_{bo} of 0.10 Mg m^{-3} and D_{bm} ranged from 1.45 to 2.19 Mg m^{-3} (Federer et al. 1993), and, in Quebec, D_{bo} of 0.12 Mg m^{-3} and D_{bm} of 1.40 Mg m^{-3} (Tremblay et al. 2002). For forest floor, D_{bo} of 0.052 Mg m^{-3}, with R^2 between observed and predicted forest-floor mass of 0.46, n of 164. This compares favorably to estimates by Gosselink et al. (1984) (D_{bo} of 0.054 Mg m^{-3} after conversion of C to organic matter). In part, the relatively low-R^2 for D_{bo} of forest floor arose because it was a function of both forest-floor density and thickness and variations in both contributed to uncertainty. Within-plot variation in thickness was high, with a pooled coefficient of variation (CV) of about 42% based on three measurements per point on 164 points.

The estimate of D_{bo} for surface peat (<50 cm depth) was 0.069 Mg m^{-3} with an R^2 of 0.11 for a sample size of 157. For subsurface peat (>50 cm depth), the estimate of D_{bo} was 0.092 Mg m^{-3} with an R^2 of 0.23 for a sample size of 104. The D_{bo} for surface and subsurface peat were significantly different and reflect increasing density of subsurface peats due to compaction, as also noted by Grigal et al. (1989). High variability in the relationship between LOI and peat D_b is commonly observed. For example, Nichols and Boelter (1984) found an r^2 of 0.17 for the relationship between ash (equivalent to 1 – LOI) and D_b for 176 samples of peat from 38 peatlands from the north-central United States.

Forest Floor Based on the quantitative sampling and the LOI and C data, the mean C mass of forest floor on the intensively sampled points was 5.3 Mg ha^{-1} (Table 9.5). In the preliminary analysis of the extrapolation of the FFC mass from the intensive to the reconnaissance points, planar curvature (prob. = 0.97), position on slope (prob. = 0.22), and deciduous tree BA (prob. = 0.16) were not significant predictor variables. The remaining variables were significant, and the final regression had an R^2 of 0.64 (Table 9.5). The correlation between the observed and predicted C for the subsample used to evaluate uncertainty was $r^2 = 0.30$ (Table 9.5). A paired t-test indicated no significant difference between the observed and predicted FFC of that subsample (prob. = 0.45, n = 15).

TABLE 9.5

C Mass of Soil Variables from Intensive Points and Basis of Extrapolation to Reconnaissance Points Sampled on the MEF

Descriptor	Units	Forest Floor	Mineral C, 0–25 cm	Mineral C, 0–100 cm	Peat[a]
All points					
n		152	161	161	113
Mean	Mg ha^{-1}	5.31	34.36	115.23	962.60
Standard deviation	Mg ha^{-1}	3.75	9.62	35.99	751.57
Basis of equations					
n		137	146	146	
Mean	Mg ha^{-1}	5.27	34.56	116.70	
Standard deviation	Mg ha^{-1}	3.64	9.58	36.16	
r^2		0.64	0.42	0.29	
$s_{y \cdot x}$	Mg ha^{-1}	2.23	7.41	31.12	
Check of equations					
n		15	15	15	
Mean	Mg ha^{-1}	5.72	32.43	100.94	
Standard deviation	Mg ha^{-1}	4.80	10.22	31.93	
r^2		0.30	0.60	0.45	
$s_{y \cdot x}$	Mg ha^{-1}	4.17	6.68	24.55	

[a] No extrapolation was made for peat; all points were sampled to mineral soil.

Based on the extrapolation, forest-floor mass increased with an increase in conifer tree BA and with a decrease in slope gradient. Less expected, warmer aspects (toward the southwest) had greater forest-floor mass; the greatest mass was found where profile curvature was convex, less where flat, and least where it was concave. Although some of these relationships are contrary to accepted paradigms, they may have rational explanations. For example, the decline of forest floor-mass as the profile curvature becomes more concave may be associated with increased incorporation of C into the surface mineral soil at those positions.

Mineral Soil Measured mineral soil C to 100 cm from the intensive points was 115 Mg C ha^{-1} (Table 9.5). The extrapolation of the mineral soil C mass from the intensive to the reconnaissance points was based on the same variables used for extrapolation of FFC. In the preliminary analysis, profile curvature (prob. = 0.25 for surface soil and prob. = 0.51 for 0–100 cm), planar curvature (prob. = 0.16 for surface and prob. = 0.11 for 0–100 cm), deciduous tree BA (prob. = 0.47 for surface and prob. = 0.92 for 0–100 cm), aspect code (prob. = 0.69 for surface and prob. = 0.72 for 0–100 cm), and slope gradient (prob. = 0.11 for surface and prob. = 0.82 for 0–100 cm) were not significant predictor variables. The remaining variables were significant, and the final regression for surface soil had an R^2 of 0.42 (Table 9.5). For the subsample used to evaluate uncertainty, the correlation between the observed and predicted C was $r^2 = 0.60$ (Table 9.5); a paired t-test indicated no significant difference between the observed and predicted C (prob. = 0.51, n = 15). For the sum of mineral C to 100 cm, the final regression had an R^2 of 0.29 (Table 9.5), the correlation between the observed and predicted C for the subsample was $r^2 = 0.45$ (Table 9.5), and a paired t-test again indicated no significant difference between the subsample observed and predicted C (prob. = 0.15, n = 15).

Mineral C mass increased with A thickness and was lowest in upper slope positions, increasing downslope. Mineral-soil C mass also increased with forest-floor thickness and decreased with increase in conifer-tree BA. The increase with forest-floor thickness is interesting because there was no relationship between forest-floor thickness and A thickness ($r^2 = 0.01$). The decrease in mineral C mass with increase in conifer BA may be related to a general tendency for conifers to occur on coarser-textured soils than broadleaf deciduous trees.

Peat As described, C content was a function of LOI and thickness. Carbon mass of surface peat (<50 cm depth) was 3.80 Mg ha^{-1} cm^{-1} and of subsurface peat (>50 cm depth) was 5.06 Mg ha^{-1} cm^{-1}. Because depth had been determined at all points where peat occurred, both intensive and reconnaissance, there was no need to extrapolate data (Table 9.5).

CWD

Points from the CWD inventory were aggregated into one of nine groups (CWD groups) based on the plurality of live-tree BA. These groups were nearly identical to the 10 vegetation types used to develop estimation equations for understory biomass, but the open CWD group (O) included the grass and open bog types; neither had live-tree BA. Log biomass was statistically significant among the groups [F(8537) = 3.689, prob. < 0.001]. Although differences were significant, mean separation tests indicated considerable overlap. In addition, relatively high-log mass in the open and shrub groups indicated that many of those points had been recently forested.

A subset of 25 points was removed randomly from the data to test the uncertainty of the final equation used to extrapolate measured log CWD to the points in the original inventory. The final equation for that extrapolation used CWD group as a dummy variable and a set of continuous variables including standing dead-tree BA and density, total and deciduous live-tree BA, live-tree density, and average live-tree diameter. The resulting equation ($R^2 = 0.21$, $n = 521$, $s_{y\cdot x} = 17.4\,Mg\ ha^{-1}$) had relatively high uncertainty. Points with high observed mass were especially underpredicted because of the weighting of the equation by a large number of points with minimal CWD. To accommodate some of that underprediction, a simple quadratic equation with 0 intercept was fitted with predicted CWD as the independent variable and observed CWD as the dependent variable. The relationship was not a major improvement ($R^2 = 0.24$, $n = 521$, $s_{y\cdot x} = 16.9\,Mg\ ha^{-1}$), but it reduced some of the error in the high estimates and explained 33% of the variation in the 25 observation test dataset.

The resulting estimates of log C mass for the original MEF inventory points, when summarized by vegetation type, ranged from 5 to 20 Mg ha^{-1} (Table 9.6). Those estimates are also similar to the measured C from the 2003 inventory summarized by CWD group (Figure 9.1).

Landscape Attributes

Peatland Probability The parameters in the logistic model for predicting the probability that a point was peatland (elevation, presence of a wetland vegetation type, and presence of an organic soil-mapping unit) were significant (prob. < 0.03), and the model was significantly different than using a constant to predict peat occurrence (Chi-square = 198, 3 d.f., and prob. < 0.001). A point was considered to be peatland if the predicted probability was >0.5. Cohen's kappa (Rosenfield and Fitzpatrick-Lins 1986) was used to measure agreement between the observed and predicted occurrences. Values range from 0 (when agreement is no better than chance) to 1.0 (when agreement is perfect), with >0.75, indicating strong and <0.40 indicating poor agreement (SYSTAT Inc. 2007). Kappa was 0.64 for the data used to develop the model and 0.56 for the 50 observation test dataset.

Forested Probability The parameters in the logistic model predicting probability of a point being forested (overstory dbh class, overstory density class,

TABLE 9.6

Estimated C Mass of CWD from Inventory Points on Marcell Experimental Forest

Vegetation Type	Number of Observations	Snag, Mean (Mg ha^{-1})	Snag, Standard Error (Mg ha^{-1})	Log, Mean (Mg ha^{-1})	Log, Standard Error (Mg ha^{-1})
Aspen-birch	415	10.3	0.6	12.2	0.5
Black spruce	29	11.7	2.4	9.3	2.7
Grass	14	0.7	0.4	6.4	0.1
Lowland conifers	23	6.9	1.9	5.2	1.4
Lowland hardwoods	22	12.2	3.6	19.0	3.5
Open bog	16	1.5	1.1	7.4	0.7
Pine	20	15.0	2.7	10.7	2.1
Spruce-fir	18	13.4	3.3	10.4	2.4
Shrub	2	0.0	0.0	6.4	0.0
Upland hardwoods	36	13.4	1.6	11.9	1.5
ALL	595	10.3[a]	0.5	11.6[a]	0.4

[a] Mean of all observations.

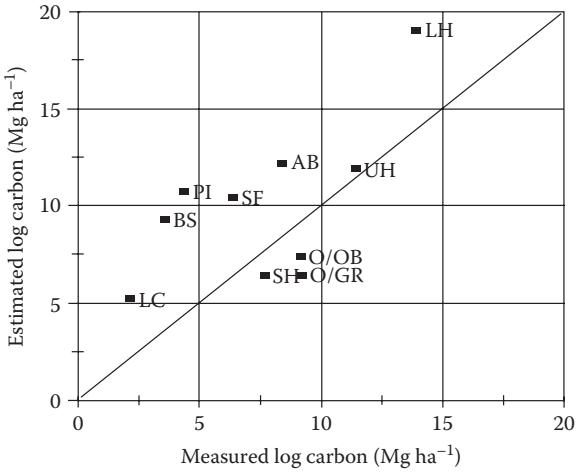

FIGURE 9.1

Mean measured C mass of logs by CWD group (x axis), based on a 2003 survey of 546 plots, compared to mean estimated C mass by vegetation type (y axis) based on application of estimation equations to data from 595 other plots. Vegetation groups/types are AB, aspen-birch; BS, black spruce; LC, lowland conifers; LH, lowland hardwoods; O/GR, open/grass; O/OB, open/open bog; PI, pine; SF, spruce-fir; SH, shrubs; and UH, upland hardwoods. The generally good relationship between the two variables is indicated by the 1:1 line.

and soil group) were significant (prob. < 0.06), and the model was significantly different than no prediction (Chi-square = 147, 9 d.f., prob. < 0.001). Kappa for the data used for the model was 0.51 and for the 50 observation test dataset was 0.35.

Estimation Equations The C data from the inventory, used to extrapolate ecosystem C over the entire MEF, were highly variable (Table 9.7). For the 443 nonpeat points, the CV was nearly 80% for FFC and about 25% for mineral soil C (SUMINC). For the 98 peat points, the CV for peat C to mineral substrate (PEATC) was similar to that for FFC, about 80%. Vegetation-related C was similarly highly variable. For all sample points (n = 541, with n = 443 for mineral soil and n = 98 for peat), the CV was nearly 100% for CWD and 80% for vegetation C (Table 9.7).

A limited number of variables was used in the final estimation equations (equations in Grigal 2009, at http://www.nrs.fs.fed.us/ef/marcell/pubs/proceedings/accessed August 13, 2009). These included the categorical variables from the vegetation and soil mapping, and the landscape variables of slope, aspect (coded from NE to SW), elevation, specific catchment area (the number of cells contributing flow to a specific cell), and compound topographic index (wetness index, a function of both slope, and catchment area). In general, the relationships used to predict soil-related C did not have high-explanatory power (Table 9.7), explaining only about 15% of the variation in both FFC and mineral-soil C, and about 38% of that in peat C (n = 401 for mineral points and n = 90 for peat points). The relationships only explained about 7% of the variation in both FFC and mineral-soil C for the check data, but about 55% of that in peat C (n = 42 for mineral points, n = 8 for peat points) (Table 9.7). It is clear that soil C is not easily predictable over the MEF despite the large suite of variables we had measured (Table 9.1).

The continuous relationships had a higher explanatory power for vegetation-related C than for soil C (Table 9.7). Relationships explained about 61% of the variation in aboveground tree C and root C, 24% of the variation in aboveground shrub C, 43% in aboveground forb C, and 51% in ground layer C (n = 491). Using the check data, the relationships explained about 65% of the variation in aboveground-tree C and root C, 16% of the variation in aboveground-shrub C, 37% in aboveground-forb C, and 23% in ground-layer C. The sum of aboveground-vegetation C had 58% of the variation explained in the estimation dataset and 66% in the check data (Table 9.7). Vegetation-related C is better predicted than is soil C. As with soil C, CWD C generally was not well predicted by the estimation equations. Relationships explained about 28% of the variation in snag C, 13% of the variation in log C, and 24% of the variation in their sum (n = 491; Table 9.7). Using the check data, the relationships explained about 37% of the variation in snag C, less than 1% of the variation in log C, and 14% of the variation in their sum (Table 9.7).

TABLE 9.7

Descriptive Statistics and Details of Estimation Equations

	All Points			Basis of Equations					Check of Equations				
C Pool	n	Mean (Mg ha^{-1})	Standard Deviation (Mg ha^{-1})	n	Mean (Mg ha^{-1})	Standard Deviation (Mg ha^{-1})	R^2	$s_{y\cdot x}$	n	Mean (Mg ha^{-1})	Standard Deviation (Mg ha^{-1})	R^2	$s_{y\cdot x}$
Forest floor	443	4.00	3.19	401	4.08	3.27	0.146	3.10	42	3.24	2.24	0.069	2.18
Mineral, 0–25 cm	443	34.10	10.55	401	34.35	10.85	0.146	10.29	42	31.78	6.72	0.060	6.60
Mineral, 0–100 cm	443	112.52	28.96	401	112.79	29.48	0.174	27.47	42	109.89	23.65	0.067	50.44
Forest floor + 100 cm mineral	443	116.52	29.13	401	116.87	29.66	0.161	27.65	42	113.13	23.76	0.039	50.49
Peat	98	966.60	785.39	90	977.50	804.70	0.379	709.74	8	843.80	544.80	0.549	395.36
Aboveground tree	541	38.43	33.05	491	39.19	32.93	0.613	20.50	50	31.01	33.60	0.660	19.80
Belowground tree	541	9.57	7.56	491	9.74	7.47	0.606	4.70	50	7.96	8.27	0.653	4.92
Aboveground shrub	541	1.03	0.38	491	1.04	0.38	0.242	0.34	50	1.00	0.39	0.163	0.36
Aboveground forb	541	0.34	0.24	491	0.33	0.23	0.429	0.18	50	0.39	0.30	0.374	0.24
Aboveground ground layer	541	0.64	0.53	491	0.64	0.54	0.505	0.39	50	0.65	0.42	0.230	0.37
Sum vegetation aboveground	541	40.45	32.66	491	41.20	32.54	0.612	20.30	50	33.03	33.26	0.660	19.60
Log CWD	541	11.75	9.83	491	11.75	9.91	0.127	9.46	50	11.79	9.13	0.006	9.19
Standing dead tree	541	10.46	11.64	491	10.64	11.84	0.267	10.14	50	8.75	9.47	0.367	7.62
Log + standing dead	541	22.21	20.65	491	22.39	20.98	0.213	18.64	50	20.54	17.17	0.144	16.05

Application to MEF

The estimation equations were applied to the approximately 100,000 10 m cells in the MEF GIS database. ANOVA invariably indicated that differences in C among categories of soils or vegetation exceeded those arising by chance, due in part to the large number of cells in each class. The significance of the differences among estimates was evaluated by Fisher's LSD (at prob. = 0.05). Nearly, all the vegetation types differed from one another in live-vegetation C, with highest C in the pine type (Figure 9.2). This is consistent with the categorical estimates of vegetation C (Table 9.2). Most of the pine types on the MEF are plantations, and their uniform stocking apparently leads to high vegetation C. Ironically, the lowest vegetation C also was in conifer plantations in the upland spruce-fir type (Figure 9.2). Nearly, all these plantations were young when sampled with associated low tree C. However, the soil was the largest contributor to ecosystem C differences among vegetation types (Figure 9.2). Types on peat, including lowland conifers and hardwoods, open, SHs, and black spruce, all had high C (Figure 9.2).

When viewed at a landscape scale, the distribution of vegetation C at the MEF shows expected spatial variation (Figure 9.3). However, this variation

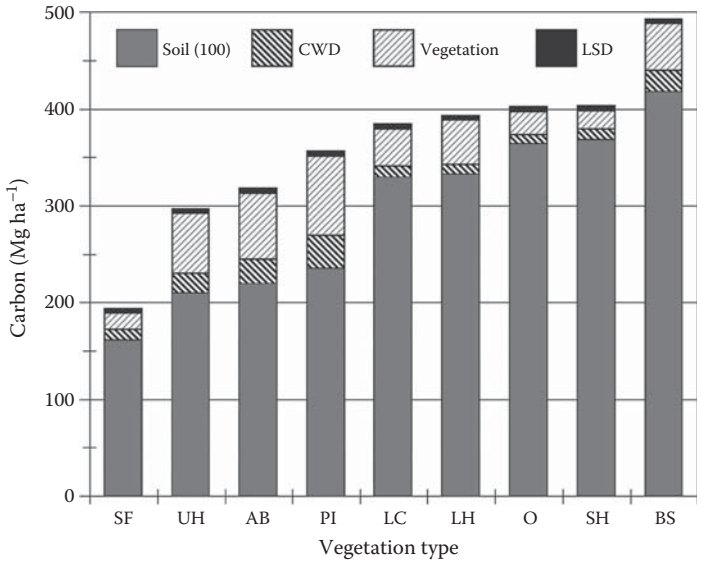

FIGURE 9.2
Estimates of ecosystem C mass for MEF, categorized by vegetation type. Types are AB, aspen-birch; BS, black spruce; LC, lowland conifers; LH, lowland hardwoods; O, open; PI, pine; SF, spruce-fir; SH, shrubs; and UH, upland hardwoods. "Soil (100)" includes sum of forest floor and mineral soil or organic soil (peat) to 100 cm depth, "Vegetation" includes above- and belowground living vegetation, and "CWD" includes both snags and logs. Fisher's least significant difference (prob. = 0.05), based on sum of components, indicated (LSD). With the exception of young SF plantations, the major difference is between peatland (LC, LH, O, SH, and BS) and upland ecosystems.

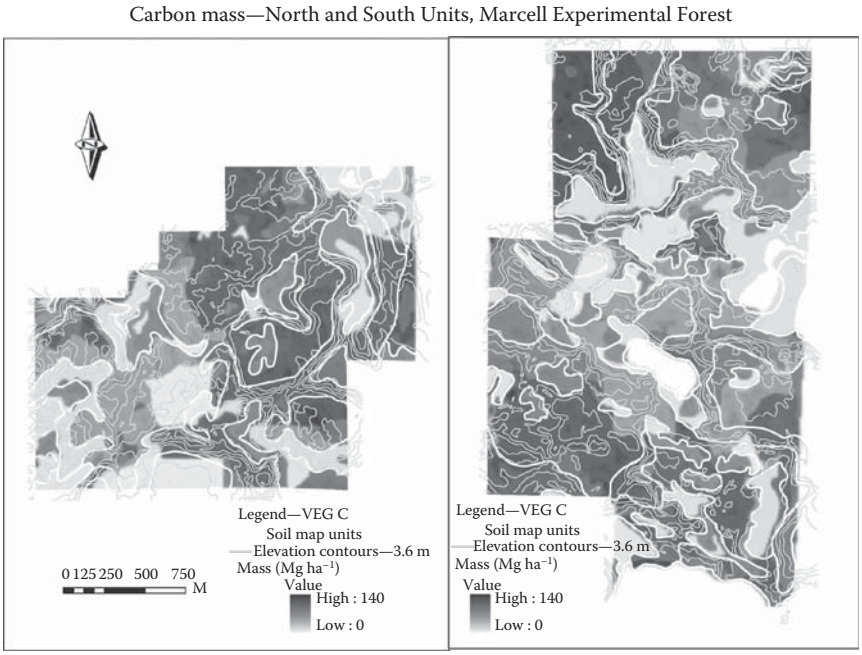

FIGURE 9.3
Landscape distribution of above- and belowground vegetation C at MEF. Distribution based on estimation equations using mapped and landscape variables that were applied to individual cells of a GIS database with 10 m resolution. Left panel, North Unit; right panel, South Unit. Note the continuous gradation from low-C open peatlands and recently cut areas to fully stocked forests. Scale from 0 to 140 Mg ha^{-1}.

becomes a simple nuance when the C content of the entire ecosystem, either to a depth of 100 cm or to the entire peat depth, is considered. The resulting map is nearly "black and white," with much higher C in peatland ecosystems than in upland systems (Figure 9.4); contrast is even greater when the entire depth of peat is included. As shown here and in other studies, peatlands are important C reservoirs in northern landscapes (Bell et al. 2000; Gorham 1991; Johnston et al. 1996).

Comparisons

With Other Studies

As described earlier, the categorical and continuous C estimates for vegetation (mean for total aboveground and belowground) are similar (51 Mg ha^{-1}; Tables 9.2 and 9.4, respectively). Because these means include nonforested types, they are lower than reports for forests. As a point of comparison, the continuous estimate for aspen-birch, the dominant cover type on MEF (53 Mg ha^{-1}; Table 9.4), can be compared to other estimates for aspen-birch, including 67 Mg ha^{-1} (Smith et al. 2006), 69 Mg ha^{-1} (Grigal and Ohmann

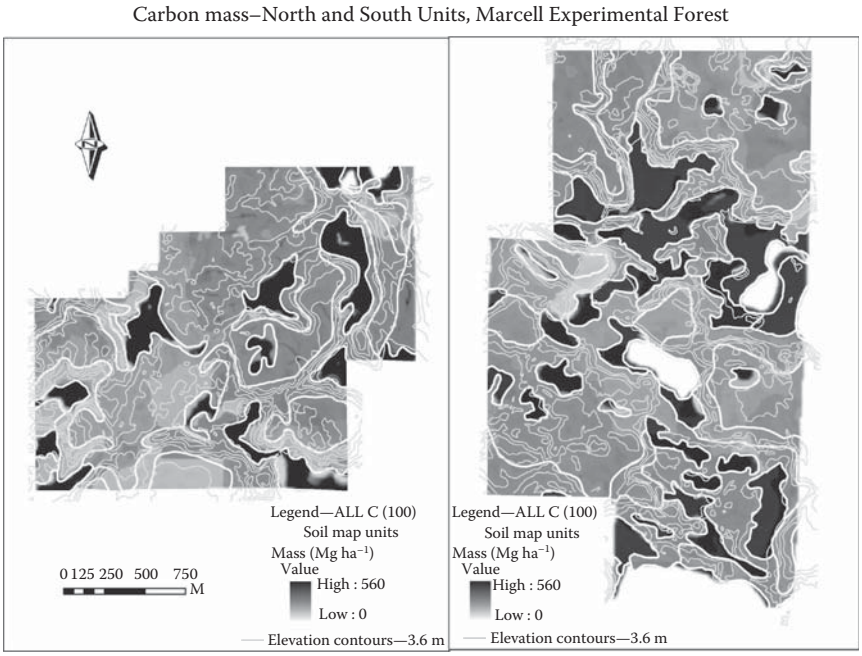

FIGURE 9.4
Landscape distribution of ecosystem C, including vegetation, CWD, and soil to 100 cm depth at MEF. Distribution based on estimation equations using mapped and landscape variables that were applied to individual cells of a GIS database with 10 m resolution. Left panel, North Unit; right panel, South Unit. Note the sharp contrast between high C peatlands and uplands. Scale from 0 to 560 Mg ha^{-1}.

1992), 80 Mg ha^{-1} (Weishampel et al. 2009), and an average of 51 Mg ha^{-1} for a chronosequence and 81 Mg ha^{-1} for a 63-year-old stand (Ruark and Bockheim 1988). The MEF estimate included recently harvested stands with low C. The estimate for pine on MEF, 90 Mg ha^{-1}, falls between other reports for pine in the Northern Lake States, 65 Mg ha^{-1} (Grigal and Ohmann 1992) and 107 Mg ha^{-1} (Smith et al. 2006).

The estimates of CWD, about 22 Mg C ha^{-1} evenly divided between snags and logs (Table 9.6), fall within the broad range of literature values. On the basis of the data from 778 plots, Chojnacky et al. (2004) estimated log CWD in the North Central States at 7.3 Mg ha^{-1}; C yield tables estimate a CWD mass of 19.6 Mg ha^{-1} for upland forest types in the Northern Lake States (Smith et al. 2006). Another study on MEF estimated 9.3 Mg C ha^{-1} CWD in aspen-birch and 23.1 Mg ha^{-1} in upland conifers (Weishampel et al. 2009). Other studies have similar estimates of about 9 Mg C ha^{-1} in aspen-birch stands (Alban and Perala 1992; Gower et al. 1997; Ruark and Bockheim 1988).

The FFC (slightly more than 5 Mg ha^{-1}) (Table 9.5) is lower than other reports from similar systems. For example, Smith and Heath (2002) indicated an average FFC mass of about 20 Mg ha^{-1} for northern upland forests,

including aspen-birch, pine, and northern hardwoods. They also reported a C:mass of 0.38. At MEF, the C:mass was 0.33 (SE = 0.006 and n = 152); the MEF forest floor is less C-rich than average northern forests. Grigal and Ohmann (1992), reporting on five upland-forest cover-types across the Great Lakes States, found average FFC mass of about 16 Mg ha^{-1}. Although average LOI was higher in the MEF data (68%) than in their dataset (55%), the ratio of C:LOI was lower for the MEF data (0.48 versus 0.61). This led to slightly less C per unit mass of forest floor at MEF than in the broader dataset. The most important reason for the difference in C mass between the two datasets is that the average forest-floor thickness across the Great Lakes States was about 40 mm (Ohmann and Grigal 1991) compared to 17 mm for the MEF.

There are other reports of lower FFC mass for northern forests. The average FFC mass at the MEF is slightly lower than those for forested sites from a similar study in east-central Minnesota (8.0 Mg ha^{-1}, Bell et al. 1996) and from a study using a different sampling design at the MEF (8.2 Mg ha^{-1}, Weishampel et al. 2009) and is similar to that for a chronosequence of aspen forests in northern Wisconsin (4.8 Mg ha^{-1}, Ruark and Bockheim 1988).

A comparison of the estimates of mineral soil C at the MEF with data from the literature is constrained by differences in depth of reporting, though a common denominator for many reports is C to 100 cm. The mean C content of the soil orders that are areally most important on the MEF, Alfisols and Entisols (85 Mg ha^{-1}, based on the categorical approach), is similar to that based on large databases (56 Mg ha^{-1}, Guo et al. 2006; 70 Mg ha^{-1}, Kern 1994; 87 Mg ha^{-1}, Johnson and Kern 2003). The mean of all intensive sampling points on mineral soils (115 Mg ha^{-1}; Table 9.5) is near that estimated for all cells of the 10 m GIS database that fell on Alfisols or Entisols mapping units (110 Mg ha^{-1}). This is consistent with the mean from five upland forest cover types across the Great Lakes States (106 Mg ha^{-1}, Grigal and Ohmann 1992), for Entisols and Inceptisols in hardwood forests in Rhode Island (144 Mg ha^{-1}, Davis et al. 2004) or north-central New York (135 Mg ha^{-1}, Galbraith et al. 2003), and Alfisols, Entisols, and Inceptisols in Danish forest soils (105 Mg ha^{-1}, Vejre et al. 2003). These values are considerably higher than mineral soil C for forested sites from a similar study in east-central Minnesota (46 Mg ha^{-1}, Bell et al. 1996), but those soils were almost exclusively sandy Entisols. In general, our estimates fall well within the range of other estimates from the literature.

The C mass in peat at the MEF (about 960 Mg ha^{-1}, the mean of sampling points falling on peat; Table 9.5) is similar to that for Histosols from large databases (975 Mg ha^{-1}, Guo et al. 2006; 843 Mg ha^{-1}, Kern 1994; 832 Mg ha^{-1}, Johnson and Kern 2003). However, the estimate for the MEF is for mass from the surface to contact with the mineral substrate, which averaged about 200 cm, whereas the estimates from large databases were to a 100 cm depth. At the MEF, peat to 100 cm contained approximately 445 Mg C ha^{-1}, less than that from a companion study in east-central Minnesota (630 Mg ha^{-1} to 100 cm, Bell et al. 1996) and lower than the mean of the organic soil-mapping

units on the MEF based on the categorical estimate (745 Mg ha^{-1} to 100 cm; Table 9.3). Average D_b and C content of peat from an extensive review of the literature (Gorham 1991) yields an estimate of 580 Mg ha^{-1} to 100 cm. It appears that the peatlands at MEF contain relatively less decomposed peat than other sites in the literature, resulting in a combination of lower C concentration and D_b, both of which result in lower C mass per unit depth or area. The lower estimate for the MEF is similar to that from a comprehensive study of 10 northern Minnesota peatlands, evenly divided between bogs and fens, with organic material ranging from hemic to fibric (Grigal and Nord 1983). The average C mass in the surface 100 cm of those peatlands was 470 Mg ha^{-1}, with Fisher's LSD based on within-peatland variance of 68 Mg ha^{-1}. The continuous estimate for MEF peatlands is not different from this average, though the categorical estimate is higher. Uncertainty in the C content of peatlands in the MEF is important because of their dominance in the overall C inventory.

Between the Two Estimates

A relevant question is whether the machinations described here were worth it. In other words, did the data collection and statistical manipulations that produced the continuous estimates of C, as described here, provide better estimates than the much less intensive categorical mapping and application of existing data?

The categorical estimates of C were about 15% greater than those using continuous variables. The areally weighted estimates of vegetation C were nearly identical; the difference between the two approaches was due to the difference in soil C (to 100 cm), primarily related to the estimates of peat C. The categorical estimate of peat C (745 Mg ha^{-1} to 100 cm) was more than 1.5 times the continuous estimate (445 Mg C ha^{-1}). Within-stand variation reported or computed from studies of mature aspen-birch and black spruce stands can be used to calculate Fisher's LSD and evaluate the significance of the difference in the estimates from the two approaches. For vegetation C, the difference between estimates from the two approaches (0.9 Mg ha^{-1}) is much less than the LSD (51 Mg ha^{-1}). Even in the case of soil C, the difference between estimates is less than the LSD (42 Mg ha^{-1} versus 68 Mg ha^{-1}, respectively). Statistically, the two approaches to estimating ecosystem C do not differ.

It appears that landscape-level estimates of ecosystem C might be economically feasible using literature data and vegetation and soil mapping, which exists for most systems in the north-central United States. Any ecosystem sampling should be concentrated on peatlands because of both their large C mass and the variation in that mass as reported in the literature. This comparison via overall averages and LSDs does not speak to landscape patterns of C. No attempt was made in this study to develop landscape patterns of C mass based on the categorical approach, but a spatial integration of the vegetation and soil mapping almost certainly would yield patterns similar to those from the continuous approach.

Carbon Flux

Quantification of the C storage at the MEF is one step in understanding the C budget of its ecosystems, but C storage is the summation of C fluxes into and out of ecosystems. A simple spreadsheet/model (Carbon FLuX—CFLX) was developed to describe C fluxes for two common forest types on MEF: aspen-birch on uplands and black spruce on peatlands (70% of the inventory points were assigned to the aspen-birch type and 5% to black spruce). CFLX annually computes the size of major C pools by tracking the annual cohort of each pool over the simulation period. Some pools change as a function of time (stand development) and others as a function of inputs and outputs. CFLX is simply an accounting tool for even-aged stands; it does not attempt to mechanistically simulate growth processes, interactions among pools, effects of climate, or other factors important to forest development. Although it is a spreadsheet, CFLX is coded in FORTRAN. It was not calibrated for a specific stand or site; rather, it generically describes average stand behavior. The functional forms are embedded in the coding, but CFLX was designed, so that the constants can be easily altered to produce alternative scenarios or application to specific sites or conditions.

Major Pools and Central Relationships

The major C pools considered by CFLX differed between the two forest types (Table 9.8). Carbon flux was estimated by quantifying a number of central

TABLE 9.8

Major C Pools Used to Estimate C Flux in the Aspen-Birch and Black Spruce Forest Types at the MEF

C Pool	Aspen-Birch	Black Spruce
Overstory foliage	X	X
Overstory wood	X	X
Fine woody debris	X	X
Coarse woody debris	X	X
Understory herbs	X	
Tall shrubs	X	
Tree seedlings	X	X
Forest floor	X	
Mineral soil to 50 cm	X	
Low shrubs		X
Moss		X
Roots		X
Peat accretion		X
Residual peat		X

relationships using data from the literature. The data sources and the general approaches used to define key relationships are described in Appendix 9.1 at the end of this chapter. In nearly all cases, nonlinear regression was used to estimate constants (SYSTAT Inc. 2007).

Basal Area versus Time

The fundamental basis of CFLX is a logistic function describing BA change over time,

$$BA = a/\left(1+\exp(b*(T-c))\right), \tag{9.6}$$

where
BA is stand basal area (BA) in $m^2\ ha^{-1}$
T is stand age in years
a, b, and c are constants

The constant a is the maximum BA at infinite time, b is the rate at which the function approaches maximum BA (a), and c can be considered a lag term related to time to establishment of a new stand. Constants were derived from a set of empirical yield tables for Minnesota. Results indicated that a tended to increase with site quality, b nominally decreased (becoming more negative, but not a strong trend), and c decreased (Tables 9.9 and 9.10). The increase in the asymptote with site quality is logical, and the decrease in the lag may be related to a quicker occupancy of a site following disturbance. More negative values of b are associated with more rapid rise toward near asymptotic values.

Biomass versus Basal Area

The relationship between biomass (or C) and BA was expressed as the power function

$$BIOM = a*BA^{b}, \tag{9.7}$$

where
BIOM is stand aboveground biomass in $kg\ ha^{-1}$
BA is stand basal area (BA) in $m^2\ ha^{-1}$
a and b are constants

Constants were estimated using data from about 450 aspen-birch stands (Table 9.9) and more than 100 black spruce stands (Table 9.10).

Diameter versus Time

The change in average stand diameter over time also is described by the logistic relationship (Equation 9.6), with diameter as the dependent variable.

TABLE 9.9

Functional Relationships Used in the Aspen-Birch Version of CFLX

Dependent Variable	Independent Variable	Function	Constant, a	Constant, b or k	Constant, c or p	R^2	n	$S_{y,x}$	Notes
Basal area	Time	Logistic	24.962	−0.055	14.206		5,019		Mean of six site classes
Biomass	Basal area	Power	2,185.073	1.223		0.765	447	33,198.042	
Diameter	Time	Logistic	22.232	−0.064	31.305		920		Mean of six site classes
ln Herb mass	Ln overstory mass	Linearized power	12.899	−0.580		0.515	348	0.788	Plus a dummy variable for type
ln Shrub mass	Ln overstory mass	Linearized power	9.688	−0.240		0.243	313	1.077	Plus a dummy variable for type
Herb mass	Overstory mass	Power	270,410	−0.580					Exponentiation of ln herb
Shrub mass	Overstory mass	Power	27,351	−0.240					Exponentiation of ln shrub
Litterfall	Basal area/ latitude	Modified power	80,984	0.443	−1.246	0.458	33	523.000	With latitude
Litterfall	Basal area	Power	661.758	0.443					At 47.3° N
Tall shrub density	Age	Neg. exponential		−0.202	0.950		34		
Herb decay rate	Time	Mod. neg. exponential	1	−1.811	1	0.996	4	0.047	
Leaf decay rate	Time	Mod. neg. exponential	1	−0.492	0.722	0.906	20	0.060	
Fine wood decay rate	Time	Mod. neg. exponential	1	−0.208	1				Duvall and Grigal (1999)
Residual forest floor decay rate	Time	Mod. neg. exponential	1	−0.078	1				Alban and Perala (1982)
Standing snags	Time	Neg. exponential	1	−0.145			62		
Snag decay rate	Time	Mod. neg. exponential	1	−0.037	1	0.829	3	0.114	
Log decay	Time	Neg. exponential	1	−0.070	1	0.984	6	0.058	

TABLE 9.10

Functional Relationships Used in the Black Spruce Version of CFLX

Dependent Variable	Independent Variable	Function	Constant, a	Constant, b or k	Constant, c or p	r^2	n	$S_{y,x}$	Notes
Basal area	Time	Logistic	22.254	−0.056	21.243	0.980	651	20.929	
Biomass	Basal area	Power	3,795.365	1.015		0.644	117	30,083.731	
Diameter	Time	Logistic	18	−0.020	60				
Moss mass	Overstory mass	Power	13,473	−0.082		0.622	6	394.757	
Low shrub plus herb mass	Overstory mass	Power	203,041	−0.409		0.645	6	1,047.291	
Low shrub mass	Overstory mass	Power	283,755	−0.447		0.643	6	1,098.919	
Tree seedling mass	Overstory mass	Power	263,747	−0.667		0.812	6	108.097	
Litterfall	Basal area / latitude	Modified power	1.036E + 12	1.826	−6.736	0.927	18	476.398	With latitude
Litterfall	Basal area	Power	5.417	1.826					At 47.3° N
Accumulating peat decay	Time	Mod. neg. exponential	1	−0.286	0.723	0.765	28	0.057	
Decay peat 0–25 cm	Time	Mod. neg. exponential	1	−0.0005000	1				
Decay peat 25–50 cm	Time	Mod. neg. exponential	1	−0.0001000	1				
Decay peat 50–100 cm	Time	Mod. neg. exponential	1	−0.0000500	1				
Decay peat 100–200 cm	Time	Mod. neg. exponential	1	−0.0000100	1				
Decay peat 200–300 cm	Time	Mod. neg. exponential	1	−0.0000010	1				
Standing snags	Time	Neg. exponential	1	−0.106					
Snag decay rate	Time	Mod. neg. exponential	1	−0.010	1	0.899	3	0.062	
Log decay	Time	Mod. neg. exponential	1	−0.071	0.774	0.953	6	0.073	

For aspen-birch, the constants tended to change less with site class than was the case with BA. Although average diameter increased with site quality, the asymptotes a and c changed little, and there was a small increase in b (less negative) (Table 9.9). For black spruce, constants resulted in a slowly increasing diameter to about 15 cm at 150 years (Table 9.10).

Stand Density versus Time

The change in stand density over time, as trees per hectare, is important to stand dynamics; however, no separate function was developed to describe it. Stand density is computed within CFLX from changes in BA and stand diameter with time.

Understory Mass

Mass of understory strata was based on the nonlinear function

$$\text{UBIOM} = a * \text{BIOM}^{b}, \tag{9.8}$$

where
UBIOM is aboveground biomass for a vegetation stratum in kg ha^{-1}
BIOM is aboveground tree biomass in kg ha^{-1}
a and b are constants

The relatively low-explanatory power for aspen-birch (Table 9.9) is tolerable, because understory C pools are relatively small; less than 2% of aboveground biomass for stands in the database. Over half of the variation in black spruce understory strata was explained (Table 9.10).

Substrate

A major difference between the application of CFLX to aspen-birch compared to black spruce is the treatment of the substrate. The substrate for aspen-birch is the forest floor and mineral soil, and for black spruce it is peat. In both cases, substrate C over time is the sum of initial conditions and inputs (positive) and losses (negative). The forest floor (aspen-birch) or peat (black spruce) existing before the simulation begins is carried as subpools without inputs, only losses, whereas forest floor or peat produced during the simulation has both inputs and losses. Although CFLX includes a C pool for mineral soil, the size of that pool does not change.

Inputs

Inputs to forest floor or accumulating peat include litterfall from overstory and SHs, annual herb turnover, and coarse and fine woody debris. Inputs to peat also include moss growth and root turnover and mortality.

Overstory and Shrub Litterfall

Although overstory foliar mass can be estimated by biomass estimation equations, crown size and thus foliage mass are affected by stand density (Grigal and Kernik 1984). Because of the centrality of BA change over time in CFLX, estimates of overstory litterfall were based on a relationship with stand BA,

$$\text{LIT} = a * \text{BA}^{b}, \tag{9.9}$$

where
LIT is litterfall in kg ha^{-1}
BA is stand BA in m^2 ha^{-1}
a and b are constants

The relationship for aspen-birch indicates that overstory litterfall increases with BA at a much slower rate (b = 0.44) than total overstory biomass (b = 1.22) (Table 9.9), reflecting the proportionally decreasing leaf mass with stand development. Conversely, black spruce overstory litterfall increases at a more rapid rate with BA (b = 1.83) than total overstory biomass (b = 1.02) (Table 9.10). Because black spruce stocking often is low on ombrotrophic peatlands, as BA increases, the trees may develop proportionally larger crowns with greater litterfall.

For both aspen-birch and black spruce, litterfall from SHs and tree seedlings was based on foliage:total biomass and foliage turnover (Equation 9.8; Table 9.11). Herb biomass (C) (from Equation 9.8) also was added to the substrate annually.

TABLE 9.11

Ratios Used in Black Spruce Version of CFLX to Convert among Biomass Components

Component	Ratio	Multiplier
Low shrub leaves	0.3	Low shrub biomass
Low shrub litter	0.5	Low shrub leaves
Herb litter	1	Herb biomass
Seedling needles	0.5	Seedling biomass
Seedling litter	0.15	Seedling needles
Low shrub turnover	0.4	Low shrub wood mass
Seedling turnover	0.2	Seedling wood mass
Moss production	1.750	Mg C ha^{-1} $year^{-1}$
Fine root turnover	1.75	Litterfall
Tree root mortality	0.3	Aboveground mortality
Seedling root mortality	0.3	Aboveground mortality
Low shrub root mortality	1.85	Aboveground mortality

Fine Woody Debris

The fine woody inputs to the substrate have three sources: overstory litterfall and mortality of SHs and young trees. The proportion of woody twigs in aspen-birch litterfall is relatively uniform (20.2%, SE = 1.5%; Grigal and Homann 1994; Grigal and McColl 1975; Van Cleve and Noonan 1975) and similar to that in black spruce litterfall (17%, SE = 1.9%; Grigal et al. 1985). Therefore, annual inputs of fine woody debris via litterfall were considered to be those proportions.

For aspen-birch, estimates of additions to forest floor by the woody fraction of shrub mortality were based on shrub demography as described by a negative exponential function

$$\text{STEMS} = a * \exp(-b * A), \tag{9.10}$$

where
STEMS is tall shrub density in stems per hectare
A is shrub age in years
a and b are constants (Balogh and Grigal 1987) (Table 9.9)

In the case of black spruce stands, data from a detailed study of low shrub and tree seedling mortality in black spruce (Grigal et al. 1985) were used to estimate additions to peat (Table 9.11).

Moss and Roots

Growth and accumulation of moss, predominantly *Sphagnum*, is a significant part of the C cycle in peatland black spruce forests, and growth was assumed to be 1.75 Mg C ha^{-1} $year^{-1}$ (Table 9.11). Root turnover and mortality are also major inputs to accumulating peat (Table 9.11).

CWD

Tree mortality is the source of CWD. In CFLX, mortality is assumed to be chronic, not episodic, and is described by changes in stand BA and tree diameter with time (i.e., self-thinning). Mortality first creates standing dead trees (snags; Tables 9.9 and 9.10), and those snags subsequently transfer to the ground surface (fall) based on a simple negative exponential (Gore et al. 1985),

$$Y = \exp(-k * T), \tag{9.11}$$

where Y is the proportion of dead snags remaining at time T in years (Tables 9.9 and 9.10).

Losses

After materials reach the substrate, decomposition (mass loss) begins. The classic functional expression of loss of biomass (or C) is a negative exponential (Equation 9.11; Wieder and Lang 1982), where, in this case, Y is the decimal fraction of mass remaining, T is time in years, and k is a constant. In CFLX, that expression is modified as

$$Y = \exp(k * T^{p}), \tag{9.12}$$

where
variables are as in Equation 9.11
p is an additional constant (Kelly and Beauchamp 1987)

When $p = 1$, this form is identical to the classic expression (Equation 9.11); alternatively, rate of mass loss increases ($p > 1$) or decreases ($p < 1$) with time. Most decomposition data in the literature simply report k from Equation 9.11, but Equation 9.12 is used in CFLX to allow the functional form to conform more closely to some observations.

Litter Losses

In the aspen-birch version of CFLX, decomposition of each kind of input (herbs, foliar litterfall, and fine woody debris) is considered separately and their losses summed. In the black spruce version, all inputs are aggregated and treated by a single decomposition function for accumulating peat. In both cases, decomposition of preexisting forest floor or peat has unique functions. Herb-mass loss is relatively rapid ($k = -1.8$; Equation 9.11; Table 9.9). Rates of mass loss of overstory leaves decline with time ($k = -0.49$ and $p = 0.72$; Equation 9.12), consistent with an increase in the recalcitrance of the remaining material (Table 9.9). Decomposition of fine woody debris is even slower ($k = -0.208$, with $p = 1$; Equation 9.12).

Measures of decomposition rates in peat are rare in the literature, and most are not easily adapted to either Equation 9.11 or 9.12. Data-based rates for accumulating peat were near those for fine woody debris ($k = -0.286$ and $p = 0.72$; Equation 9.12). For residual peat, low rates decreasing with depth were set (Table 9.10). In preliminary runs of CFLX, these low rates resulted in minimal C loss.

CWD Losses

The mass loss of standing dead trees (snags) is assumed to follow Equation 9.12 (Tables 9.9 and 9.10). When a snag reaches the ground (becomes a log), it continues to lose mass but the constants in Equation 9.12 change. The rate

of mass loss of logs should be more rapid than that of snags because of log contact with the moist ground (Tables 9.9 and 9.10).

Initial Conditions

Initial conditions of the system must be specified, including the size of the major C pools and the stand age in years. Initial conditions may be at stand initiation following a harvest or fire or may be in mid to late rotation. The model initially was constructed on the basis of biomass because the literature contains more data on biomass and organic matter than on C. Outputs were modified by conversion from biomass or organic matter to C (biomass, including litterfall, C = 48%, Alban and Perala 1990 and Raich et al. 1991; fine woody debris and residual forest floor, C = 50%, Alban and Perala 1982; snags, C = 50%, Alban and Pastor 1993; CWD, C = 54%, Duvall and Grigal 1999; 0–25 cm and 25–50 cm peat, C = 50%, 50–100 cm peat, C = 49%, and 100–200 cm and 200–300 cm peat, C = 48%, data from the MEF).

Notes/Caveats

There are important caveats associated with CFLX. First, it is simply an accounting tool; it does not attempt to mechanistically simulate forest stand development. Second, the fundamental drivers of CFLX are the temporal changes in BA and diameter described by the logistic function, which increases with time. As even-aged stands surpass maturity, evidence indicates that mortality increases and BA and biomass decrease, but those changes are not included in CFLX. It is designed to represent systems to the time that stands begin to decline. CFLX deals with even-aged stands and does not incorporate succession to another forest type.

Another caveat is associated with the uncertainty of the constants in the model. Each is derived from or based on one or a few studies. Changes in the parameters, through improved data or professional judgment, may better represent reality. For example, change in BA with time was based on midpoint ages from the empirical yield tables (e.g., midpoint from 10 to 20 years was 15 years). Although, for most age classes, this may be reasonable for the 0–10 year age class (midpoint = 5 years), a better assumption may have been the geometric mean or the final year of the age class. CFLX was designed to allow easy changes in the constants for virtually all functions.

Evaluation

The functions and constants used in CFLX were derived from the literature, albeit from a multitude of studies separated in time and space. After their derivation, the constants *were not* manipulated to achieve a better fit to any existing data. The selection of constants for rates of decomposition of deep

peat required some preliminary runs of CFLX, but no other constants were manipulated. Iterative runs of CFLX, with adjustment of constants, are likely to better match observed data, but those iterations were not conducted. CFLX was evaluated by comparing its estimates with observations of C pools during early stand development (for aspen-birch) and with observations from mature stands (for both aspen-birch and spruce).

Initial Conditions

The aspen-birch version of CFLX was run using initial conditions from two studies that followed aspen stand development after whole-tree harvesting (Alban and Perala 1990; Silkworth and Grigal 1982). Average values for forest floor, CWD, and soil for the growing season following harvest were used as inputs. Neither study measured standing snags, but they were likely to be nearly absent after the harvest. CWD log data were available only from Alban and Perala (1990). Initial stand BA was set to 0 m^2 ha^{-1}, and the simulation was carried for 75 years. In the case of black spruce, there were no measures of recently disturbed stands, so initial conditions were set arbitrarily with no trees or CWD and with a generic peat mass (~550 Mg ha^{-1} C to 100 cm).

Early Stand Development

To evaluate CFLX with respect to early stand development, the C pools from the model were compared to those reported by Alban and Perala (1990) and Silkworth (1980). Alban and Perala (1990) graphically presented changes in C pools of biomass, forest floor, CWD, and soil to 50 cm for three sites for up to 8 years following whole-tree harvest, and the data were extracted from those graphs. Silkworth (1980) reported biomass in trees, SHs, and herbs; forest-floor organic matter; and soil properties, including horizon depths, bulk densities, gravel content, and C and N concentrations for three sites at 2, 3, and 5 years after whole-tree harvest. From those data, C in biomass, forest floor, and soil to 50 cm was computed.

Estimates for years 2 through 8 from CFLX and the data from Alban and Perala (1990) and Silkworth (1980) were compared using ANOVA, where individual studies were considered factors, and year after harvest was a covariate. Results indicated that the size of C pools differed among studies, with the significance of differences in soil (prob. = 0.056) and CWD (prob. = 0.097) less than those for biomass (prob. = 0.001) and forest floor (prob. = 0.012). Year-to year differences were not significant for forest floor or for soil. Although C pools differed among studies, the estimates from CFLX were not uniformly higher or lower than observations (Figure 9.5). Baysian least significant difference (BLSD) (Smith 1978) indicated no differences between the estimates from CFLX and the observations from one or the other study. In other words, the estimates were within the range of the observations. Although modeled biomass C was at the high end of the data, a small change (decrease) in c

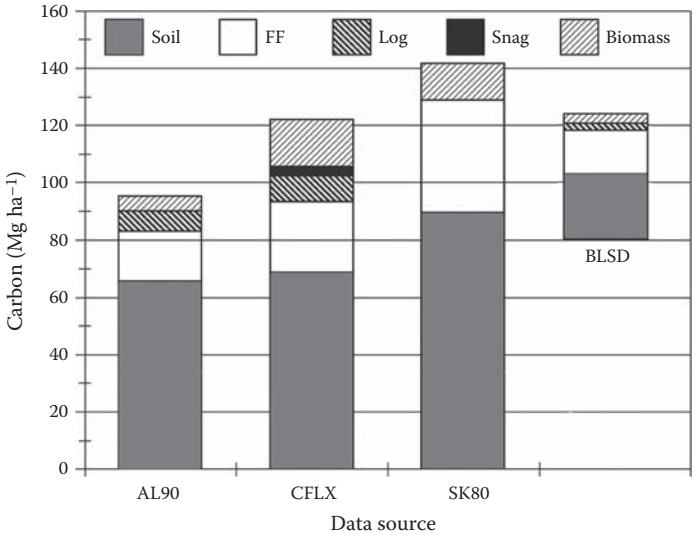

FIGURE 9.5
Comparison of ecosystem C estimates from model/spreadsheet for period of first 10 years following aspen harvest with literature measurements (AL90, Alban and Perala 1990; CFLX, model/spreadsheet; and SK80, Silkworth 1980). Based on Baysian least significant difference (BLSD), the estimates did not differ from the range of measurements.

in Equation 9.6 would lead to slower initial BA and biomass accretion and would more closely match the observations.

Mature Stands

The estimated C pools for mature aspen-birch stands from CFLX were compared to observations from a variety of detailed assessments of C pools reported by Alban et al. (1991), Ohmann et al. (1994), Alban and Perala (1990), Perala et al. (1995), Silkworth (1980), and data from the MEF. All data were from mature aspen stands, though in some cases, actual ages were not reported. Sample sizes varied widely, from 3 (Alban and Perala 1990) to 415 (MEF data). The mean and variation of each dataset were compared to the estimates from CFLX at 60 years with initial conditions as described previously.

For black spruce, the estimated C pools from CFLX were compared to data collected and/or reported by Grigal et al. (1985), Moore et al. (2002), Swanson (1988), Weishampel et al. (2009), the MEF, and in the case of peat, on five Histosols from the NRCS. Data were primarily from peatlands dominated by black spruce except those from Moore et al. (2002), which were not forested, and those from the NRCS, where vegetation type was not reported. Sample sizes varied from 1 (Weishampel et al. 2009) to 63 (Swanson 1988). The mean and variation of each dataset were compared with the estimates from CFLX at 110 years with initial conditions as described earlier.

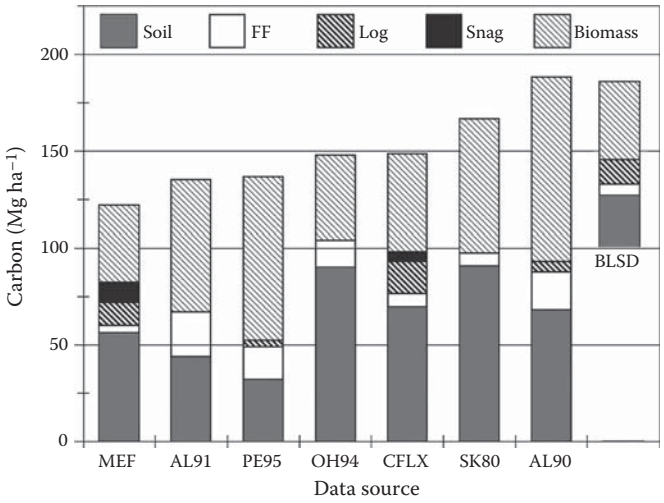

FIGURE 9.6
Comparison of ecosystem C estimates from model/spreadsheet for mature aspen stands with literature measurements (CFLX, model/spreadsheet; AL91, Alban et al. 1991; OH94, Ohmann et al. 1994; SK80, Silkworth 1980; MEF, inventory of Marcell Experimental Forest; AL90, Alban and Perala 1990; and PE95, Perala et al. 1995). Based on BLSD, the estimates did not differ from the range of measurements.

A one-way ANOVA was constructed using published means, variances, and numbers of observations. Data from an individual study were considered to be a treatment, including the estimates from CFLX (these latter data have no measure of variation). Due in part to the large number of within-treatment degrees of freedom for aspen-birch, differences in size of C pools among treatments (studies) were highly significant. However, there were no patterns in the ranking of any of the C pools by size; estimates from CFLX were not uniformly higher or lower than the observations (Figure 9.6), and BLSD indicated overlapping of means. For black spruce, differences among treatments were significant only for a few of the subpools (low SHs; herbs including low SHs, forbs, and sedges; overstory and peat to 100 cm). As was the case with aspen-birch, there were no patterns in the ranking of any of the C pools by size; CFLX estimates were not uniformly higher or lower than the observations (Figure 9.7), and where differences were significant, BLSD indicated overlapping of means. For both aspen-birch and black spruce, the estimates from CFLX were indistinguishable from means developed from detailed stand measurements.

Net Carbon Flux

The objective of the development of CFLX was to determine net C flux (also termed net ecosystem production [NEP] the net difference between C inputs

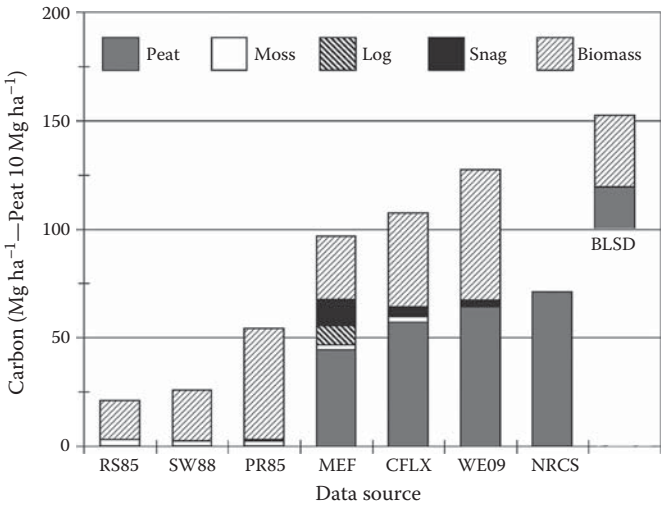

FIGURE 9.7
Comparison of ecosystem C estimates from model/spreadsheet for mature black spruce stands on peatlands with literature measurements (RS85, data for raised bogs from Grigal et al. 1985; SW88, Swanson 1988; PR85, data for perched bogs from Grigal et al. 1985; MEF, inventory of Marcell Experimental Forest; CFLX, model/spreadsheet; WE09, Weishampel et al. (2009); and NRCS, data from National Resource Conservation Service). Based on BLSD, the estimates did not differ from the range of measurements.

and losses from an ecosystem; Odum 1969). Annual NEP indicates whether an ecosystem is a source or sink to the atmosphere. In the case of aspen-birch, ecosystem C (including forest floor but excluding mineral soil) decreased annually for about 5 years following disturbance from harvest, increased, and peaked at about 1 Mg ha year^{-1} at 25–30 years after stand establishment, and declined and became negative at about 50 years. At 75 years, NEP was −0.4 Mg C ha year^{-1}. Aboveground, net primary production (ANPP) was about 2.3 Mg C ha year^{-1} at 25 years and 2.1 Mg C ha year^{-1} at 50 years. Other reports of ANPP for aspen-birch include 2.6 Mg C ha year^{-1} at MEF (Weishampel et al. 2009), 2.2 Mg ha year^{-1} in northeastern Minnesota (Reich et al. 2001), 3.5 Mg ha year^{-1} in boreal Canada (Gower et al. 1997), and 3.9 Mg ha year^{-1} (Burrows et al. 2003) and 5.1 Mg ha year^{-1} (Ruark and Bockheim 1988) in northern Wisconsin. To reiterate, CFLX was constructed to generically describe average stand behavior not to predict C fluxes at specific sites.

In the case of black spruce, NEP, including aboveground and belowground vegetation and peat to 100 cm, peaked at about 0.7 Mg ha year^{-1} at 30–40 years after stand establishment and declined to negative values at about 90 years, reaching −0.15 Mg C ha year^{-1} at 150 years. O'Connell et al. (2003) estimated NEP of −1.28 Mg ha year^{-1} for a 120 year old black spruce-*Sphagnum* forest in Saskatchewan. CFLX estimated ANPP of about 1.5 Mg C ha year^{-1} during a period of 30–50 years, excluding *Sphagnum* growth, or 3.3 Mg ha

year^{-1} including *Sphagnum*, declining slightly to 3.1 Mg ha year^{-1} at 100 years. This can be compared to 2.8 Mg ha year^{-1} (including *Sphagnum*) at the MEF (Weishampel et al. 2009), 1.0 Mg ha year^{-1} (excluding *Sphagnum*) in northeastern Minnesota (Reich et al. 2001), and 3.4 Mg ha year^{-1} (including *Sphagnum*) in northern Minnesota (Grigal et al. 1985). These rates can be compared to other similar sites (all including *Sphagnum*), 1.5 Mg ha year^{-1} in Alberta (Szumigalski and Bayley 1996) and for Canadian boreal sites (Gower et al. 1997), and 1.8 Mg ha year^{-1} for a bog and muskeg in Manitoba (Reader and Stewart 1972). These wider ranges in ANPP for black spruce compared to aspen-birch are caused by wider variations in stand density, affecting both overstory and understory NPP.

Conclusions

Several conclusions can be drawn from this interlinked C inventory and model/spreadsheet. First, to emphasize what has been repeated by many, peatlands are important C pools in the northern landscape. The relative size of the C pool in forest vegetation is surprisingly uniform across the landscape, with apparent compensation by mixes of species yielding roughly similar masses among vegetation types. The mineral-soil C pool, at least in the morainic landscape of MEF, is also relatively uniform. Topographic variation does not play a strong role in creating major differences in C storage in mineral soil. As a result, prediction equations based on topographic variables have low explanatory power. However, the topographic variation that gives rise to peatlands has a profound effect on landscape C storage. In this area on the western edge of the mid-continental forests, both forest floor and peat have lower C than more northerly and easterly sites.

It also appears that there are nearly sufficient data in the literature with which to make reasonable predictions about landscape C storage without resorting to detailed measurements. Even a large suite of detailed measurements (Table 9.1) does not eliminate uncertainty (Table 9.7). Finding and accessing existing data can provide relatively inexpensive assessments of landscape C storage via categorical mapping and development of C estimates for categories.

There are many data on C flux in the literature, though often not under that rubric. The simple spreadsheet described here demonstrates that those data can be linked to provide realistic estimates of ecosystem C change with time. The same problem of finding and accessing relevant data also is true for estimates of C flux.

Two major points emerge from this work, carried out in a landscape with a poorly developed drainage network:

- C storage in vegetation and CWD did not differ appreciably among soils and differed little among mineral soils. The major difference in ecosystem C storage was related to differences between peatlands and other systems.
- Annual net C flux for both the most common upland (aspen-birch) and peatland (black spruce) forest types peaked at between 25 and 35 years after establishment, though C continued to accumulate with time.

The ramifications of these points with respect to potential climate change are that

- Climate-induced changes in peatland area will have profound effects on C storage.
- Manipulation of vegetation types by management will only marginally affect landscape C storage. Maintenance of maximum rates of C sequestration would best be achieved by management to maintain the forest in relatively young age classes.

Appendix 9.1

The data sources and rationale used to develop functional relationships describing C fluxes in aspen-birch and black spruce forest types at the MEF:

Basal Area versus Time

$$BA = a / \left(1 + \exp(b * (T - c))\right), \tag{9.6a}$$

The data used to quantify the constants were from empirical yield tables for Minnesota collected by the USDA Forest Service Forest Inventory and Analysis (FIA) program (Hahn and Raile 1982). The tables provide the average BA and the number of observations by stand-age and site-quality class for 14 forest types. Inputs to CFLX for aspen were simple arithmetic averages of a, b, and c over six site classes (Table 9.9), inputs for black spruce, with only two site classes, were from all data (Table 9.10). Observed and predicted BA were strongly correlated; all r^2s were greater than 0.95 except for the highest aspen site class (28–30 m at 50 years).

Biomass versus Basal Area

$$BIOM = a * BA^b, \tag{9.7}$$

For aspen-birch, the constants were developed from a database of about 1000 forest stands (from Bell et al. 1996, Ohmann and Grigal 1985b, Swanson 1988, Wilson 1994, and the C inventory of MEF) spanning a range of vegetation types, including 447 aspen-birch stands (Table 9.9). The database for black spruce contained 117 spruce stands (from Grigal et al. 1985; Moore 1984; Swanson 1988; the MEF inventory, and tabulated data from a number of studies; Grigal and Brooks 1997; Table 9.10).

Diameter versus Time

$$\mathrm{DIAM} = a / \left(1 + \exp(b * (T - c))\right), \tag{9.6b}$$

For aspen-birch, a dataset from FIA plots measured between 2002 and 2006 in the aspen cover type in six northern Minnesota counties (M. Hatfield, USDA Forest Service, 2008, pers. commun.) was used. Because of minimal observations, stands with site quality <12 and >28 m at 50 years or with ages <10 and >100 years were removed, and constants were determined for each of the remaining six site-quality classes. The r^2s were greater than 0.90 for the four site classes with more than 100 observations and dropped to 0.76 (site class 28 m, n = 25) and 0.55 (site class 12 m, n = 39). The simple arithmetic average of a, b, and c over the six site classes was used (Table 9.9). There were no readily available age-diameter data for black spruce. Therefore, constants were estimated using both the results of the analysis with aspen-birch and several age-diameter data (Table 9.10).

Understory Mass

$$\mathrm{UBIOM} = a * \mathrm{BIOM}^{b}, \tag{9.8}$$

For aspen-birch, data were from the same database used for the continuous estimates of C storage (n = 453). Constants were determined for the linearized form of Equation 9.8 including a dummy variable determined by vegetation type; the solution was converted to the nonlinear form.

For black spruce, data were from a study of black spruce peatlands in northern Minnesota (Grigal et al. 1985). Tall woody SHs constitute a small proportion of biomass and were excluded. Because the herb stratum had low mass and high variability, Equation 9.8 was solved for low SHs and for the sum of low SHs and herbs, and herb mass was determined by difference.

Substrate

Mineral-soil C does not change based on both the lack of documentation of such change following aspen harvest and the difficulty of detecting

measurable changes; belowground C inputs via root turnover and mortality are assumed to be in approximate equilibrium with C losses via decomposition. Following an extensive study, Alban and Perala (1990) stated that harvesting "…did not affect total soil carbon." An ANOVA of their table 4 indicated that differences related to time after harvest in forest floor plus soil C to 50 cm were not significant (prob. = 0.464). Similarly, analysis indicated that their mineral soil data and that from Silkworth (1980), who also sampled soils following aspen harvest, had virtually identical means (80.5 Mg ha^{-1}, prob. = 0.999) and that time after harvest again had no effect (prob. = 0.910). The pooled variance indicated that detection of a 5% change in soil C would require about 100 samples per stand (Freese 1962), demonstrating the difficulty of such detection.

In the case of the black spruce on peatland soils, inputs to peat via *Sphagnum* growth and vascular root turnover and mortality and their losses via decomposition are considered. In addition to the subpool of peat produced during the simulation, five subpools of preexisting peat, with only losses, are included (0–25, 25–50, 50–100, 100–200, and 200–300 cm). Because of the slow loss rates, especially in the lower layers (100–200 and 200–300 cm), their inclusion has little effect on net C flux.

Overstory and Shrub Litterfall Inputs

$$LIT = a * BA^{b}, \tag{9.9a}$$

Determination of a and b for aspen-birch was based on measured litterfall or foliage mass in a variety of aspen and other deciduous stands in Minnesota and Wisconsin, Alaska, and Canada (Alban et al. 1991; Alban and Perala 1982; Bernier et al. 2007; Lee et al. 2002; Pastor and Bockheim 1984; Reich et al. 2001; Ruark and Bockheim 1988; Steele et al. 1997; Van Cleve and Noonan 1975; Weishampel et al. 2009). Because of the wide geographic range, an additional explanatory variable, latitude (Lonsdale 1988) was used in the initial relationship,

$$LIT = a * BA^{b} * LAT^{c} \tag{9.9b}$$

where variables are as in Equation 9.9 and LAT is degrees (north) latitude. The solution was a significant improvement over the relationship without latitude ($r^2 = 0.46$ and 0.09, respectively; Table 9.9). In the case of black spruce, measured litterfall in stands in Minnesota, Wisconsin, Alaska, and Canada was used (Alban and Perala 1982; Reich et al. 2001; Steele et al. 1997; Van Cleve and Noonan 1975; Weishampel et al. 2009). Equation 9.9a had higher explanatory power for black spruce ($r^2 = 0.93$) than for aspen-birch (Tables 9.9 and 9.10). The annual contribution of overstory litterfall to

forest floor or accumulating peat was estimated by substituting an appropriate latitude, which is 47.3° N for the MEF into Equation 9.9a (Tables 9.9 and 9.10).

In aspen-birch, foliage as 20% of aboveground tall shrub biomass from Equation 9.8 (Table 9.9) was annually added to forest floor (Grigal et al. 1976). Similarly, for black spruce, half of low shrub foliage as 30% of biomass from Equation 9.8 (Table 9.10) was added annually to accumulating peat (Grigal et al. 1985; Table 9.11). About half of tree seedling mass is in needles, and one-seventh (about 15%) of that was included as litterfall (Table 9.11). For both aspen-birch and black spruce, herb biomass (C) (from Equation 9.8) was also added to the substrate annually.

Fine Woody Debris Inputs

$$\text{STEMS} = a * \exp(-b * A), \tag{9.10}$$

Estimates of fine-wood additions to aspen-birch forest floor by tall shrub mortality were based on shrub demography described by a negative exponential function where initial stem density (a) declines annually at a rate of b (Equation 9.10; Balogh and Grigal 1987). The pooled value of b did not differ significantly among shrub populations in closed upland aspen and conifer stands in northern Minnesota ($b = -0.202$, $n = 34$ stands; Balogh and Grigal 1987), implying that mortality rates are independent of shrub density and overstory and soil characteristics. Ideally, Equation 9.10 can be used to estimate annual shrub turnover as the reciprocal of the time required to reach 100% mortality, but, because it is exponential, there is no solution. It can be solved to 99% (time = 23 years and turnover = 0.04 year^{-1}) or 90% mortality (e.g., time = 11 years and turnover = 0.09 year^{-1}), with lesser mortality leading to faster turnover. A uniform b assumes a steady state; there are no significant changes in the age-class distribution. Although this may be the case for stands with closed canopies, it probably is not for recently disturbed stands. There, an initial burst of SHs is reduced by competition with the developing overstory, and mortality rates probably are higher than in stands with fully developed overstories. Because the pooled value of b in Equation 9.10 was from closed-canopy stands, and faster turnover is more reasonable for stands during canopy closure, time to 95% mortality was used to estimate shrub turnover rates over a spectrum of stand ages (Table 9.9). Dead stems (80% of tall shrub mass) were included as inputs of fine woody debris to the forest floor.

A study of demographics in black spruce stands in Minnesota indicated that about 40% of low SHs and 20% of tree seedlings turn over annually (Grigal et al. 1985), and those data were used to determine inputs of fine woody debris to peat (Table 9.10).

Moss and Root Inputs

Annual *Sphagnum* production in peatland black spruce forests of about 1.75 Mg C ha^{-1} $year^{-1}$ was measured in Minnesota (Grigal 1985). That measure was consistent with literature values at similar latitudes in North America. Additional work, since then, including Chapin et al. (2004) and Moore et al. (2002), also is in agreement. Weishampel et al. (2009) measured *Sphagnum* productivity at MEF as only about a 15% of that value, but their study was carried out during an unusually dry growing season, which adversely affected *Sphagnum* growth.

Fine root turnover was estimated as 1.75 times litterfall (Table 9.11) based on data from a variety of boreal forests, including black spruce (Steele et al. 1997). Additions of roots to peat also include both overstory and shrub mortality. Woody roots constitute about 30% of tree and seedling and about 185% of low shrub aboveground biomass in Minnesota black spruce stands (Grigal et al. 1985). Those ratios were used to compute mortality-based additions (Table 9.11).

CWD Inputs

$$Y = \exp(-k * T) \tag{9.11}$$

In addition to self-thinning, mortality has been described by a simple rate per year, with estimated mortality in forests in the North Central States from 0.0146 to 0.0149 $year^{-1}$ for aspen-birch stands and from 0.0070 to 0.0130 $year^{-1}$ for upland spruce-fir (and no estimate for peatland black spruce—Harmon 1993). A sophisticated model of mortality for Lake States' trees also has been developed based on current diameter and past diameter growth (Buchman 1983) that predicted that smaller, slower growing trees have higher mortality rates than larger, faster growing trees. The self-thinning mortality rates in CFLX decline with tree size, spanning the values suggested by Harmon (1993) and tending to be lower than those tabulated by Buchman (1983).

There are limited data on the longevity of snags in north-central U.S. forests. Snags were monitored after the Little Sioux Fire in northeastern Minnesota (Ohmann and Grigal 1979; Slaughter et al. 1998), and the rate of an aspen-birch snag falling (k in Equation 9.11) was = −0.145 (n = 62), implying a half-life of 4.8 years, with 99% of snags down in about 21 years. That rate was used in the aspen-birch version of CFLX (Table 9.9). The rate of a black spruce or jack pine snag (as a surrogate for black spruce) falling was similar (k = −0.149, n = 154). Monitoring of snags during an intensive bog study (Grigal et al. 1985) showed that k = −0.063, with a half-life 11 years. The average of these two rates, k = −0.106, was used in the black spruce version CFLX (Table 9.10).

Litter Losses

Decomposition of herb leaves (*Aster* spp.) from northeastern Minnesota is relatively rapid (k = –1.8, Grigal and McColl 1977; –1.3, Ohmann and Grigal 1979, following Equation 9.11). The former figure, from a wider variety of sites, was used for herb litter (Table 9.9).

Mass loss of aspen leaves over 3 years, with additional cohorts added every year (data from Grigal and McColl 1977, yielded k = –0.49 and p = 0.72; Equation 9.12; Table 9.9). The rate of decomposition of fine woody debris was that from managed red pine stands (k = –0.208, with p = 1; Equation 9.12; Duvall and Grigal 1999). These stands were thinned continuously, and so the decomposing material was primarily branches and twigs. The annual rate of mass loss of residual forest floor is difficult to estimate, because most studies have determined rates of loss of fresh material, not of the multiple-aged residues in forest floor. The rate of loss of residual forest floor was considered to be that based on "turnover" of forest floor in aspen stands in northern Minnesota (k = –0.078, with p = 1; Equation 9.12; Alban and Perala 1982; Table 9.9).

Decomposition rates in peat are not easily adapted to Equation 9.11 or 9.12. Gorham et al. (2003) measured the age/mass relationship of the S2 bog on the MEF and reported a linear rate of peat accretion of 56.5 g m^{-2} $year^{-1}$ over 9200 years. This is equivalent to an accretion rate of 0.65 mm $year^{-1}$, but there is no data indicating whether this rate also is linear with time. Near-surface peat has lower D_b than deeper peat, and a linear rate of mass accretion makes a linear rate of depth accretion unlikely. Farrish and Grigal (1985) measured annual rates of mass loss of both cellulose strips and of peat returned to its point of origin within the surface 100 cm of the S2 bog. The data showed significant linear reductions in rates of decomposition with depth within the upper 35 cm of peat (measured from the top of hummocks; $r^2 = 0.83$, n = 8, and prob. = 0.001), while, at greater depths, the slope was barely significant ($r^2 = 0.16$, n = 12, and prob. = 0.11). At those greater depths (ages), decomposition rate changed little. Both these studies provided useful background information, including a limit on cumulative mass losses through time (Gorham et al. 2003) and marked reductions in rates of mass loss with depth per time (Farrish and Grigal 1985). However, rates of decomposition for peat from Farrish and Grigal (1985) were much higher than indicated by data from Gorham et al. (2003). Removing the peat, placing it in litter bags, and replacing it apparently increased rates. The overall decomposition function for accumulating peat was based on data from Moore (1984), who monitored black spruce needles and *Ledum* leaves on two substrates (burned and unburned) for more than 2 years. Decomposition was well described by Equation 9.12 (k = –0.286 and p = 0.72, $r^2 = 0.76$; Table 9.10). Low rates, decreasing with depth, were set for residual peat (following Equation 9.11, 0–25 cm, k = –0.000500; 25–50 cm, k = –0.000100; 50–100 cm, k = –0.000050; 100–200 cm, k = –0.000010; and 200–300 cm, and k = –0.00000; Table 9.10).

CWD Losses

The mass loss of standing dead trees (snags) is assumed to follow Equation 9.12. Reports of decomposition rates of snags are rare. Duvall and Grigal (1999) measured density of snags in three decay classes, ranging from recently dead to a condition with most large branches missing and "unsound" wood. An empirical decomposition rate can be computed if the three classes of decay are assumed to represent time = 1 year (class 1), the half-life of standing snags (class 2), and the time when 90% of the snags have fallen (class 3), respectively. Following this approach, the result for aspen-birch snags was $k = -0.037$ and for "softwood" snags (not including red pine) was $k = -0.0096$ (with p assumed to be equal to 1; Tables 9.9 and 9.10). There are some data on log decay for aspen, none for black spruce, and a limited amount for jack pine (as a surrogate for black spruce), and most are one-time observations. The rate of decomposition of aspen-birch logs was based on data at 1 and 5 years from Miller (1983), at 14 and 17 years from Alban and Pastor (1993), at 50 years using Harmon's (1993) rate in aspen-birch forests, and at 100 years using the rate from Duvall and Grigal (1999). The resulting analysis yielded $k = -0.0699$ (Equation 9.11; Table 9.9). In the case of jack pine, data at 11 and 17 years from Alban and Pastor (1993), at 50 years using Harmon's (1993) rate in pine and spruce-fir forests, and at 100 years using the rate from Duvall and Grigal (1999) were used. The result yielded $k = -0.0713$, $p = 0.774$ (Equation 9.12; Table 9.10).

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