CHAPTER 19

Carbon Cycling in Wetland Forest Soils

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CONTENTS

INTRODUCTION

Wetlands comprise a small proportion (i.e., 2 to 3%) of earth's terrestrial surface, yet they contain a significant proportion of the terrestrial carbon (C) pool. Soils comprise the largest terrestrial C pool (ca. 1550 Pg C in upper 100 cm; Eswaran et al., 1993; Batjes, 1996), and wetlands contain the single largest component, with estimates ranging between 18 and 30% of the total soil C. In addition to being an important C pool, wetlands contribute approximately 22% of the annual global methane emissions (Bartlett and Harris, 1993; Matthews and Fung, 1987). Despite the importance of wetlands in the global C budget, they are typically omitted from large-scale assessments because of scale, inadequate models, and limited information on C turnover and temporal dynamics.

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Forests are recognized for their considerable potential to sequester C and their ability to affect carbon budgets at both the regional and global scales (Birdsey and Heath, 2001). However, the role of forested wetlands is typically not partitioned from upland forests. This distinction is important because of the inherently high plant diversity and productivity and the unique biogeochemistry of forested wetlands, which make them an important C sequestration pathway with a disproportional influence on terrestrial C storage. In the United States, forests comprise approximately 5 1% (20.5 x 10^6 ha) of the total wetland area (Dahl, 2000). These wetland forests comprise approximately 16% of the nonfederal forestland in the United States and are therefore integral to supplying both commodity and noncommodity uses. The forested wetland resource is not static; it is often managed; and while some lands are converted to upland or nonwetland uses, others are restored. Accordingly, soil C pools contained in wetland forests are a function of complex interactions of inherent soil processes, climate, vegetation, time, and disturbance regimes.

Forested wetlands are usually not considered when assessing opportunities for managing ecosystems to enhance terrestrial C storage. It is our hope that this chapter will provide a foundation for new work that is needed to realize the potential for effectively managing C pools in forested wetlands. Our objectives for this chapter are to (1) characterize the C cycle in wetland forests, (2) review the morphological and taxonomic basis for defining soil C status in forested wetlands, (3) summarize soil properties and processes that regulate the soil C cycle in wetland forests, and (4) examine the effects of management and restoration on soil C sequestration in forested wetlands. We focus on forested wetlands in North America while drawing on the international literature when discussing wetland soil processes. For thorough discussions on wetland ecology and hydric soils, the books by Mitch and Gooselink (2000) and Richardson and Vepraskas (2001) are recommended.

CARBON CYCLING IN FORESTED WETLAND SOILS

Conceptually, C cycling in wetland forests is analogous to other terrestrial ecosystems (Figure 19.1). However, hydric soil conditions, active anaerobic microbial populations, and adapted vege-

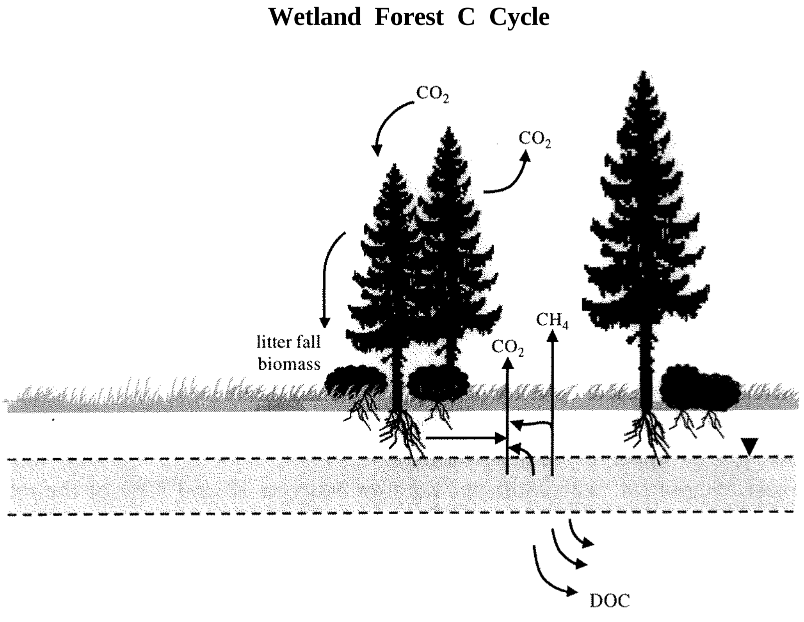

Figure 19.1 Schematic of the carbon cycle in wetland forests.

tation interact to affect the distribution and amount of soil C, the pathways of C fluxes from the soil, and the rates of transfer. The principal difference between wetland and upland forests is the anoxic soil aeration regime during portions of the growing season, which causes plants to adapt to periods of limited soil oxygen (McKee and McKevlin, 1993; McKevlin et al., 1998). Accordingly, hydrology is the fundamental control on biogeochemical processes in wetlands. Forested wetland hydrology differs from upland forests in that hydrologic inputs can come from groundwater, surface water, or precipitation, and the inputs must be of sufficient quantity and duration to cause anoxia. The relative contributions of these sources and the internal drainage conditions influence plant community and soil biogeochemical processes. For discussion purposes, we consider the source of water and its associated influence on fertility (eutrophic vs. ombrotrophic) and the dominant source of water (floodplain, groundwater, precipitation) in combination with geomorphic setting. Comprehensive discussions of wetland hydrology are provided by Boelter and Verry (1977), LaBaugh (1986), Verry (1996), and Winter (1988).

Wetlands are not a homogeneous amalgamation of ecosystems but, rather, a diverse set of ecosystems with the only common denominator being an anoxic aeration regime during the growing season. The interaction of climate, geomorphic setting, soil parent material, and hydrology determine the composition of the wetland forest, which can range from sparsely treed bogs and fens to dense bottomland hardwood swamps. Each of these wetland factors also affects the soil C cycle. We will discuss these interactions on the forested wetland soil C cycle by considering (1) C inputs, (2) soil C pools and interrelationships, and (3) C outputs from wetland forests.

Carbon Fluxes — Inputs

Organic matter, derived from either aboveground or belowground biomass production, is the principal source of soil C. Productivity among wetland forest types varies widely, reflecting differences in climate, hydrology, and vegetation communities (Table 19.1). The effect of climate is evident, with productivity generally being higher in the southern temperate forests as compared with boreal forests. However, within a climatic zone there is also considerable variability, depending on wetland type.

Aboveground Organic Matter Production

Northern wetlands growing on mineral soils associated with riverine systems typically have higher productivity and standing biomass than the fens and bogs, which have organic soils (Campbell et al., 2000). The range in aboveground NPP of temperate wetland forests (ca. 1000 to 1500 g m^{-2} $year^{-1}$ from Table 19.1) is similar among conifer and bottomland hardwood forests and is generally greater than boreal wetland forests (Campbell et al., 2000; Trettin et al., 1995). Conner (1994) reported that the range in aboveground net primary productivity of southeastern U.S. bottomland hardwood forests is 200 to 2000 g m^{-2} year', indicating that the studies shown in Table 19.1, because of belowground data availability, are not representative of the potential range in productivity. Shrub and herbaceous strata are important sources of organic matter in northern wetlands, accounting for 14% of total NPP in wooded swamps and 52 to 65% in bogs and fens (Campbell et al., 2000). The high proportion of aboveground NPP contributed by the understory in bogs is predominantly due to mosses (Grigal, 1985).

Only a portion of aboveground NPP is allocated to perennial live tissues; the balance is allocated to foliage, small branches, and fine roots that, in turn, comprise the annual litter input. The litter production in bottomland hardwood forests typically ranges between 44 to 62% of aboveground NPP (Burke et al., 1999; Megonigal et al., 1997). Unfortunately, similar data for boreal wetlands are not available, but assuming that biomass is 50% C and that litter production is 50% of aboveground NPP, the annual aboveground C inputs to the soil in forested wetlands range from 89 to 400 g C m^{-2} year-‘. North-south climate differences account for most of this

Table **19.1 Allocation of Biomass and Organic Matter Production between Above- and Belowground Components of Broad Forest Types on Organic and Mineral Wetland Soils in North America**

	Aboveground			Belowground				
	Biomass (g m^{-2})	**NPP** (g m^{-2} year^{-1})	**Litter** (g m^{-2} year^{-1})	**Biomass** (g m^{-2})	**NPP** (g m^{-2} year^{-1})	**Root Turnover [Litter]** (g m^{-2} year^{-1})	**Note**	**Reference**
				Boreal				
Organic soils								
Bogs	1768	449			224		a	Campbell et al., 2000
Fens	1860	358			179		a	Campbell et al., 2000
Wet mineral soils								
Swamps	2482-5882	654-I 232			196–370		b	Campbell et al., 2000
				Temperate				
Organic soils								
Coniferous swamps	21,857– 34,503	1097-1176	678-758	892-I 091	992-I 221	999-I 221	d	Megonigal and Day, 1988
Wet mineral soils								
Pine flats	21,722	1490					c	Clark et al., 1999
Bottomland hardwoods	15,400–45,000	830-I 600	250–758	40–736	59-632	829	d, e	Megonigal and Day, 1988 Baker et al., 2001 Burke et al., 1999 Jones et al., 1996 Powell and Day, 1991 Mitch and Gooselink, 2000

[a] Belowground productivity calculated as 50% of aboveground productivity.

[b] Belowground productivity calculated as 30% of aboveground productivity.

[c] Aboveground productivity calculated as net ecosystem exchange.

[d] Root productivity estimated based on fine-root biomass and a fine-root biomass:productivity ratio of 1.12.

[e] Belowground biomass and productivity as fine roots only.

range in litter C inputs. Litter variability among southern wetland forests alone was smaller (207 to 400 g C m^{-2} year’).

Belowground Organic Matter Production

Belowground organic matter inputs are considered to be an important source of soil C. Unfortunately, there are few direct measures of belowground productivity in wetland forests. Belowground NPP is reported to range from 25 to 90% of the total NPP in northern wetlands to 8 to 110% of aboveground NPP in southern wetland forests (Table 19.1). Belowground production, expressed as a proportion of aboveground NPP, provides little insight into differences among climatic zones or forest types, because assumptions for the proportional estimates vary. Direct measures of fine-root productivity in bottomland hardwood forests have shown that belowground productivity is a smaller proportion (8 to 14%) of aboveground NPP (Baker et al. 2001), yielding net belowground production levels comparable with estimates from the northern forests. Megonigal and Day’s (1988) root-production values are higher based on total root biomass than those of Baker et al. (2001). Other reports of high fine-root productivity reflect the influence of sampling methods and the forest type on the estimate (Table 19.1).

Fine-root biomass and productivity in bottomland hardwood forests are sensitive to depth and duration of saturated soil conditions (Persson, 1992). Comparing bottomland hardwood sites with different drainage classes in South Carolina, Baker et al. (2001) reported that well-drained sites had higher belowground biomass and productivity than poorly drained sites, but each site had approximately 75% of the fine-root biomass in the upper 15 cm of soil. Results from other studies in both mesocosms (Megonigal and Day, 1992) and forest communities in the Dismal Swamp (Day and Megonigal, 1993) have suggested that the lower root biomass in flooded soils is a result of more-efficient nutrient and water acquisition; hence fewer resources are allocated to the root system.

Although the focus of belowground studies is typically on the fine-root component, stump and coarse-root biomass may account for as much as 90% of the belowground biomass (Laiho and Finer, 1996). Another important wetland soil component is mycorrhizal fungi. Jurgensen et al. (1997) found that bottomland hardwoods on poorly drained soils had significantly higher rates of mycorrhizal fungal infection and a greater belowground allocation of C, compared with roots growing in better-drained soils. Both of these wetland soil C pools are typically not measured in soil C studies.

The paucity of belowground biomass and NPP data is a serious impediment to assessing the C dynamics in wetland forests. Interpretation of available data is further complicated by inconsistent definitions of root size classes and variable sampling and analytical methods. Accordingly, estimating belowground C inputs is tenuous. Using data from Table 19.1 as an illustration and assuming that roots contain 50% C, belowground NPP may contribute 44 to 610 g C m^{-2} year’ to the soil. These relatively high rates of C input from roots are determined by the proportion of fine roots and their turnover rate, which have been reported to range from approximately 3 to 0.5 of belowground NPP (Baker et al., 2001; Finer and Laine, 1998; Megonigal and Day, 1988). Root biomass and production should be higher in soils with fluctuating water table as compared with those that are saturated to near the surface for prolonged periods during the growing season (Day and Megonigal, 1993).

Soil C Pools in Wetland Forests

Once organic matter is deposited on the soil surface or in the mineral soil, it becomes part of a heterotrophic food web that, together with soil properties, hydrology, and land-use activities, induces biogeochemical processes that regulate soil C fluxes and storage. As a result, soil layers or horizons in forested wetlands have distinct properties that reflect the distribution of soil C within the profile and provide insights into the characteristics of the soil C pool. Correspondingly, clas-

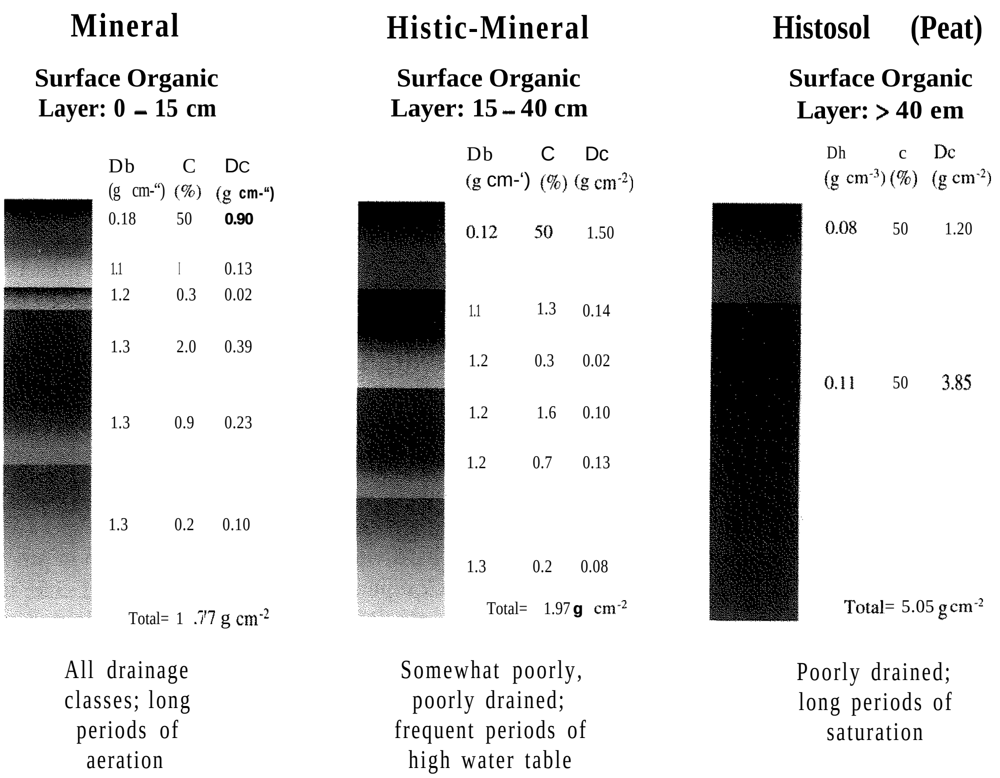

Figure 19.2 Morphological characteristics and representation of the carbon distribution in mineral, histic-mineral, and organic soils using data from the Spodosol and Histosol Orders. (Db = bulk density, Dc = carbon density.)

sifying wetland soils according to the distribution of organic matter in a soil profile provides a useful basis for categorizing soil C cycling.

Morphology and Distribution

Soil horizon morphology provides a basis for classifying soils according to features and properties that reflect the distribution, characteristics, and transformations of soil organic matter. In wetland soils, surface organic matter accumulation is an obvious indicator of soil C storage, and it is indicative of conditions affecting organic-matter turnover (Collins and Kuehl 2001). Three categories of surface soil organic-matter accumulation are used to define the distribution of soil C in wetlands: (1) Histosols, (2) histic-mineral soils, and (3) mineral soils (Figure 19.2).

Histosols

Histosols is an Order within the U.S. soil classification system for soils having a thick (>40 cm) accumulation of surface organic matter within 60 cm of the soil surface (Soil Survey Staff, 1999). These organic horizons must contain a minimum of 12 to 18% organic C, depending on subsurface mineral soil texture, but usually contain 35 to 55% C. Histosols, also called peat, are a consequence of organic-matter inputs exceeding decomposition outputs and are more decomposed and recalcitrant than fresh litter (Craft, 2001).

Three states of decomposition are used to characterize Histosol organic horizons, which reflect nominal (fibric), intermediate (hemic), and extensive (sapric) states of decomposition. These states of decay influence physical and hydrologic properties of the soil (Boelter and Verry, 1977; Bridgham et al., 2001). The mineral content (ash) of the organic horizons depends on the age and degree of decomposition within the profile. Typically, the highly decomposed (sapric) layers located above the mineral soil will have higher ash contents as compared with fibric or hemic layers, which are closer to the soil surface. The bulk density of organic horizons varies between 0.03 and 0.40 $g\,cm^{-3}$. The nutrient and acidity regimes of histosols varies considerably, depending on the dominant source of water (Bridgham et al., 2001). Traditionally, bogs are nutrient poor and acidic because water is derived primarily from precipitation. In contrast, fens receive groundwater and tend to be oligotrophic and circum-neutral.

Histic-Mineral Soils

Histic-mineral soils are soils with a thick (20 to 40 cm) accumulation of organic matter above the mineral soil. The surface organic layer has the same characteristics as in Histosols. In the U.S. classification system they are recognized taxonomically as having a histic epipedon, which is a diagnostic criterion within mineral soil Orders. Collectively, Histosols and histic-mineral soils are often referred to as peat soils, with definitions of peat and mineral soils varying by country. In Europe these soils are called mires, i.e., soils that accumulate organic matter above a mineral surface.

Mineral soils

Wet mineral soils are typically poorly drained and have a thin (<20 cm) organic forest floor overlying a mineral-soil horizon sequence. Wet mineral soils occur in each of the soil Orders except Aridisols (Soil Survey Staff, 1999). The A and B horizons in mineral wetlands are usually enriched in organic matter relative to upland soils in the same soil Order. Carbon concentrations in mineral wetlands are low (0.2 to 3.5%) and are predominantly complex humic substances. However, because soil bulk densities are higher (1.1 to 1.6 $g\,cm^{-3}$), the carbon density (D_C) may approach that found in organic soils. The C content in mineral wetlands is greatest in the surface horizons and declines to near zero in the subsoil. However, the subsoil in wet Spodosols may contain a significant amount of soil C due to accumulations in spodic Bh or Bhs horizons (Figure 19.2).

Forest-Soil C Pool Calculations

The amount of C contained in the soil of a wetland forest depends on the type of vegetation, geomorphic setting, hydrology, and disturbance regimes. Although there are few studies characterizing the C content in forest wetland soils, organic soils have considerable more C per unit area than mineral soils due to the accumulation of carbon-rich surface organic matter (Figure 19.3). The

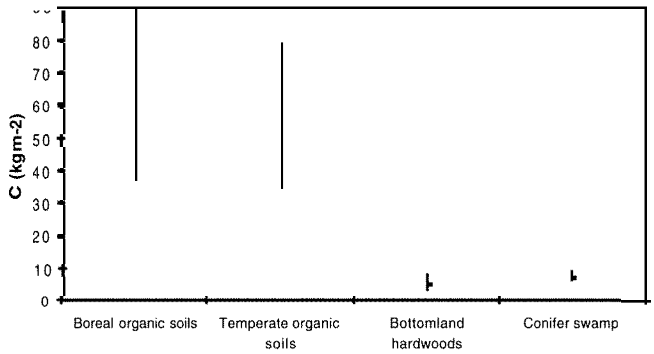

Figure 19.3 Soil carbon pools in representative wetland forests (bars indicate range, point is the mean).

amount of C within a forest soil profile is a function of the C density (DC) and thickness of the soil horizons or layers (Equation 19.1, Figure 19.2).

$$\text{Soil profile C } (\text{g/cm}^2) = \text{D}_\text{C}, * t_h \qquad (19.1)$$

where

DC = coarse-fragment-free soil bulk density (g/cm^3) x C concentration (%) of each horizon
t = horizon thickness (cm)

A significant source of uncertainty in estimating soil C pool size, particularly in Histosols, is the depth of the soil profile. Too often information is only available for the surface meter, and rarely is information available below 2 meters, even though the rooting zone of many species is below that depth (Canadell et al., 1996). Accordingly, soil depth and peat and horizon thickness can have tremendous effects on the estimate of the soil C pool (Maltby and Immirzi, 1993). Another source of uncertainty in estimating C pools in peatlands is that the underlying mineral soil is usually not considered. Prior to accumulating a thick surface organic layer, C often accumulated in the mineral matrix. Subsequently, the mineral soil was buried by the peat and further enriched in C by water leaching through the peat. Turunen et al. (1999) reported an additional 2 kg C m^{-2} in the mineral subsoil beneath several peatlands in Finland compared with adjacent nonpaludal mineral soils.

Another source of uncertainty is the assumption that organic matter occurs in uniform horizons that can be represented conceptually as a series of boxes (e.g., Equation 19.1). In many types of wetland forests, this simplified model does not provide an accurate representation because soil microtopography affects the distribution and estimates of soil carbon. Microtopography is known as hummock-hollow relief and is usually associated with peat soils, but it is also common in wet mineral soils. The undulating surface profile associated with the hummock-hollow relief influences the distribution of soil carbon and estimates of the pool size. Usually estimates of soil C assume a planar soil surface, so failure to consider the volume of soil contained in the irregular elevations (i.e., hummocks) will result in an underestimation of the soil C pool. Studying Histosols and histic-mineral soils in coastal North Carolina pocosins, we found that the mass of organic matter contained in the hummocks adds an additional 12 to 26% to the estimate of the total soil C pool.

Large-scale Estimates of Forested Wetland Soil C pools

In order to scale measurements from an individual pedon to a stand, watershed, or region, information is needed about the area and variability of the soil. All too often, estimates are scaled from limited data in order to provide a perspective, usually without consideration for the uncertainties associated with the estimate. This is the case with forest wetland soils, because they are usually considered synonymous with peatlands. Since organic soils (e.g., peatlands) are recognized at the highest level of soil classification systems worldwide, that data is usually available and convenient. Unfortunately, wet mineral soils (e.g., hydric) and histic-mineral soils, depending on the soil classification system and inventory, are usually included as mineral soils, where it is very difficult to discern drainage class differences in large-scale inventories. Eswaran et al. (1995) provide the only global estimate of wet mineral soils (108 Pg C; 8808 x 10^3 km^2) and Histosols (390 Pg C; 1745 x 10^3 km^2). Their statistics demonstrate the importance of wet mineral soils, because they comprise five times the area of Histosols and 22% of the total wetland soil C pool.

In an attempt to estimate the area of wet mineral soils and Histosols in the North America continent, we have combined survey data from several sources (Table 19.2). In North America, wet mineral soils contain approximately Il.5 Pg C, or 6% of the total wetland soil C pool. Unfortunately, statistics to partition the C content of forested wetland soils from wetlands in general, at large scales, are not available. To provide some perspective U.S. statistics, forested wetlands contain approximately 50% of the total soil C in forests while comprising only 16% of the forestland area wetland soils are not flooded all year but instead have saturated hydroperiods that vary seasonally or episodically. These alternating periods of wetting and drying stimulate decomposition as compared with unflooded soils (Lockaby et al., 1996a). Soil aeration is also influenced by microtopography in peat soils. Hummocks are typically aerated for longer periods than hollows, which results in faster organic matter decomposition in the hummocks (Farrish and Grigal, 1985 and 1988; Hogg, 1993; Hogg et al., 1992).

Bacteria, fungi, actinomycetes, and soil fauna are all involved in organic-matter decomposition in aerated soils, while anaerobic bacteria are the primary decomposers when soils are waterlogged and anoxic (Craft, 2001). Anaerobic respiration is less efficient, so the decomposition rates are slower than under aerobic conditions, which is the main reason why organic matter accumulates in wetland soils (Chamie and Richardson, 1978; Craft, 2001). However, Freeman et al. (2001b) suggest that organic-matter decomposition in peatlands is inhibited by an accumulation of phenols under low-oxygen conditions rather than by the direct effect of oxygen limitation on microbial processes.

Soil Temperature

Temperature regulates organic-matter turnover in wetland soils, particularly when soil aeration conditions are altered (Hogg et al., 1992). However, the interactions between temperature and aeration have not been determined for forested wetland soils. Trettin et al. (1996) showed that increased soil temperature following several timber-harvesting and site-preparation treatments was associated with increased cellulose decomposition in a histic-mineral soil from a northern swamp. Higher soil temperatures following tree removal have also been associated with increased organic-matter decomposition in Histosols (Bridgham et al., 1991). The possible effects of phenol toxicity on organic-matter decomposition may also be sensitive to soil temperature, which could provide a negative feedback on decay processes (Freeman et al., 2001a).

Organic Matter Quality

The quality or structural composition of soil organic matter is also an important factor in organic-matter decomposition (Howard-Williams et al., 1988). Soil organic-matter quality is primarily determined by organic chemical content and structure, which is a function of plant species and soil properties in which the plants were growing (Finer, 1996; Wieder and Yavitt, 1991). The length of previous exposure to decomposition also has a great affect on organic-matter composition, hence its value as an energy source. Organic matter from a highly decayed, subsurface peat horizon will decompose more slowly than fresh organic matter when exposed to the same environments (Yavitt et al., 1987). However, bulk-density differences among peat layers and across peatland sites may account for some of these results (Bridgham et al., 1998).

Nutrients

In comparison with other soil factors, nutrient availability has a smaller influence on organic-matter turnover in hydric forest soils. However, fertilization of some peatland soils in Finland increased litter decomposition, especially on the hummock microtopographic positions (Braekke and Finer, 1990). Litter transplant experiments have also shown that site nutrient conditions may affect organic-matter turnover (Yavitt et al., 1987).

Carbon Losses as CO,

An important loss of soil C from forest wetlands is gas as CO,, primarily to the atmosphere but also dissolved in the soil-water column. Gas emission rates of CO, from forested wetlands range from 75 to 400 g C m^{-2} year’, which reflect variations in hydrology, temperature, and fertility

Table 19.5 Soil Carbon Pool and Fluxes from the Soil Surface and Shallow Groundwater from Organic and Mineral Soils in Representative Wetland Forests

		Flux in Air		Flux in Groundwater
	Soil C Pool (kg m^{-2})	CO_2 (g C m^{-2} $year^{-1}$)	CH_4 (g C m^{-2} $year^{-1}$)	DOC (g C m^{-2} year-‘)
		Boreal		
Organic soils (bogs and fens)	37-81	—	—	20-80
Bogs	—	170	2.5	—
Fens	—	198	30-83	—
Mineral soils				
		Temperate		
Organic soils (bogs and fens)	35-79	—	—	lo-43
Wet mineral soils				
Bottomland hardwoods	3-8	313	42-144	72
Conifer swamp	6-9	—	—	—

Note: Flux values represent a net release to the atmosphere

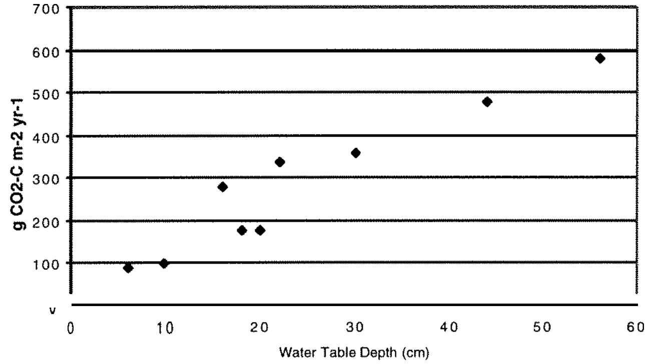

Figure 19.4 Average annual CO_2-C emissions from boreal peat soils related to average water table depth; points represent different peatland sites. (Adapted from Silvola, J. et al., *J. Ecol.*, 84: 219-228, 1996a. With permission.)

regimes (Table 19.5). The water table is the principal factor affecting CO, fluxes from boreal wetlands (Carroll and Crill, 1997; Silvola et al., 1996a; Jarvis et al., 1997), which have consistently shown a strong positive relationship between CO, fluxes and water-table depth (Figure 19.4). Similar conclusions have not been documented for southern wetland forests. Although water-table position is a dominant factor controlling soil CO, flux from wetland soils, temperature is also important, particularly in the boreal zone (Goulden et al., 1998).

An important consideration in estimating losses of gaseous CO, from soil C pools is partitioning soil microbial respiration from root respiration. There are a few such measurements from forested peatlands, which gave root respiration estimates of between 10 and 45% (Silvola et al., 1992, 1996b). These ranges are similar to values reported from upland forests (Höberg et al., 2001). However, no information is available as to whether this ratio would apply to histic-mineral or mineral wetland soils. Another uncertainty in estimating the CO, loss is the paucity of measurements of dissolved gases in the groundwater and their fate.

Carbon Losses as CH_4

Methane is the other source of gaseous loss of C from wetland soils. The factors controlling CH, emissions are soil redox conditions, the availability of readily mineralizable substrate, and temperature. Other than the difference in CH, fluxes between bogs and fens, there is little indication that soil nutrients affect CH, production (Hutchin et al., 1996). Methane emissions from forested wetlands are much less than CO,, with rates varying between 2 and 144 g C m^{-2} year' (Table 19.5) and rates in boreal peatlands usually below 10 g C m^{-2} $year^{-1}$ (Moore and Roulet, 1995). Since CH, is not produced by plant roots, all C lost as CH, comes from microbial activity. Methane flux rates vary considerably over the year, with summer exhibiting the greatest losses (Pulliam, 1993). Snowpack and cold temperatures had been assumed to preclude CH, and CO, losses in northern wetlands, but recent studies indicate that winter fluxes of both CH, and CO, may be significant (Roulet, 2000). Similar to CO,, CH, emissions from bogs and fens are also sensitive to water-table depth (Baker-Blocker et al., 1977; Crill et al., 1988; Roulet et al., 1992). When the water table is below 15 to 30 cm depth, CH, diffuses through unsaturated soil, where it is oxidized to CO, (Bergman et al., 1998; Sundh et al., 1994, 1995; Svensson and Sundy, 1992).

While the data are limited, there does not appear to be a systematic difference in CH, release between northern and southern wetlands. Bogs appear to have much lower CH, emission rates than other wetlands. The presence of graminoid vegetation is positively correlated with CH, fluxes in northern wetlands and has been attributed as the basis for CH, differences between bogs and fens (Johnson et al., 1996). Greater production of graminoid vegetation may enhance CH, losses by increased gas diffusion through arenchema and greater microbial utilization of root exudates (Bellisario et al., 1999). It is not known whether this graminoid relationship is prominent in southern forested wetlands, but it is unlikely, since these forests typically do not have a dense herbaceous understory.

Dissolved Organic Carbon

Dissolved organic carbon (DOC) is the principal pathway for hydrologic losses of soil C (Wetzel, 1992), and losses through the water column are second only to soil CO, flux (Table 19.5). There is very little data on DOC losses from forested wetlands, but Moore (1998) indicated the importance of terrestrial sources of DOC to aquatic ecosystems. The hydrologic flux through wetland soils is the most critical factor affecting DOC output (Laine et al., 1995), but higher temperatures have been reported to increase DOC fluxes, presumably by increasing organic-matter decomposition rates (Freeman et al., 2001a). DOC flux through mineral wetland soils is also affected by high Fe or Al levels, which remove DOC from solution by forming stable organo-Fe or Al complexes (McLaughlin et al., 1994). In contrast, Fe and Al concentrations are generally low in organic soils, and DOC retention in these soils is minimal (Moore, 1998).

Soil C Balance in Managed and Restored Wetland Forests

Our consideration here is those wetland forests that are in some form of management or those that have been perturbed as a result of land-use changes. While data to characterize the extent of these activities are not available, the status and trends for the continental United States provide some perspective (Dahl, 2000). Of the 1.5 x 10^6 ha loss in forested wetlands between 1986 and 1997, only 176 x 10^3 ha were lost to nonwetland categories (Table 19.6). Most of the loss in forested wetlands was caused by converting forests to other wetland types as a result of forest management practices (i.e., harvested wetland forests can be categorized as shrub wetlands). The establishment of plantations was considered to be a conversion to a nonwetland, even though wetland hydrologic functions can persist in plantations. Accordingly, soil C loss is not implicit in conversions of forest-cover types on hydric soils. The gain in forested wetlands from the freshwater-shrub wetland category reflects the reestablishment of a forest on prior cutover land. Accordingly, 64% of the forested wetland loss represents a change in wetland community type (e.g., stage of succession) that will retain inherent wetland C cycling properties. Exempting the plantations, the balance (176

Table 19.6 Change in Continental U.S. Forested Wetland Area, 1966-l 997

	Area (10^3 ha)		
Wetland Type	Loss	Change to Nonwetland	Long-Term Soil C Loss[a]
Freshwater shrub	171.4	N	U
Freshwater emergent	222.5	N	U
Upland land uses			
Urban	55.5	55.5	Y
Agriculture	56.3	56.3	Y
Plantations	43.3	U	U
Other	21.6	21.6	Y
Ponds	31.6	31.6	U
Lakes and rivers	11.2	11.2	U
Total	613.4	176.2	

Note: Categories indicate the wetland type or land use effecting the change; the presented categories do not sum to the total because minor categories excluded.

[a] The prospects for long-term soil C loss reflect assumption about changes in the soil C pool (U = uncertain, Y = yes, N = no).

Source: From Dahl, T.E., Status and Trends of Wetlands in the Conterminous United States 1986-1997, U.S. Dept. of Interior, Fish and Wildlife Service, Washington, DC., 2000.

x 10^3 ha) represents a change from wetland C cycling and a likely loss of soil C from conversions to agriculture and urban use.

Silviculture

Harvesting, site preparation, and water management systems have been reported to reduce soil C pool in forested wetlands (Trettin et al., 1995). This loss of soil C results from increased organic-matter mineralization caused by management-induced changes in soil temperature, moisture, and aeration. However, recent studies in Finland have indicated that soil C can be maintained or even increased on some managed peatland forests (Minkkinen and Laine, 1998). Most reports of management impacts on forested wetlands have also come from peatlands in northern Europe. Consequently, organic soils will be discussed separately from the much-less-studied histic-mineral and mineral wetland soils.

Histosols

Water management or drainage is the single biggest factor contributing to the loss of C in peatland soils. Drainage increases the aerated soil volume, thereby improving conditions for organic-matter decomposition (Lähde, 1969). This is shown by increased soil CO, respiration (Silvola et al., 1996a) and reduced soil C (Laine et al., 1995; Laine and Minkkinen, 1996) in drained peat soils. The primary pathway for soil C loss from these managed organic soils is thought to be CO,, since little differences were found in DOC export between drained and undrained peatlands (Laine et al., 1995). Because of results such as these, enhancing C sequestration by managed peatlands has been discounted (Batjes, 1998). However, almost all of these studies on forest-management-induced changes in wetland soil C pools are based on short-term (<5 years) assessments. Results from recent studies in Finland found net gains in soil C over a 60-year period following drainage, despite increased organic-matter decomposition rates (Minkkinen et al., 1999; Minkkinen and Laine, 1998; Silvola et al., 1996a). The long-term impact of different management regimes on soil C pools is difficult to project because of uncertainties associated with (a) biotic and abiotic influences on timber-harvesting residues and existing soil C pools, and (b) the interaction between the soil and new plant community.

Soil C balance is thought to be a function of overall site productivity; hence any changes in soil productivity would affect soil C pools (Vompersky et al., 1992). Consequently, measuring changes in C pools over long time periods would provide a means to integrate site-productivity changes associated with both soil and vegetation processes. In their assessment of management-induced changes on soil C in hundreds of peatlands across Finland, Minkkinen and Laine (1998) found that more-productive sites exhibited C gains both above and below ground, while poorer sites lost soil C even when sizeable C gains occurred in the aboveground stands. These results show the importance of understanding the interactions between forest management practice and inherent site productivity when considering the soil C balance.

Mineral Soils

Histic-mineral and mineral wetlands are important components of forestlands in North America and are often intensively managed in both the northern and southern regions. Extensive analyses of silvicultural impacts on soil C pools in upland mineral soils have shown that harvesting usually does not cause long-term (>5 years) soil C losses (Johnson, 1992; Johnson and Curtis, 2001). However, silvicultural practices on wet mineral soils affect water-table dynamics and the hydric soil-water regime (Xu et al., 2002), which in turn will interact with C cycling, as previously discussed. Unfortunately, these interactions on hydric mineral soils have been studied little. In addition to harvesting, mechanical site preparation designed to provide an elevated planting site and reduce vegetative competition is a major impact in forested wetlands. The development of planting beds has the benefit of concentrating nutrients and increasing the volume of aerated rooting zone, but the combination of these factors also increases organic-matter decomposition (Trettin et al., 1996). In a study we conducted on a histic-mineral soil in northern Michigan, both harvesting and site preparation caused a significant reduction in soil C within the first 5 years after disturbance (Trettin et al., 1992; 1997). Long-term assessments are needed to determine the extent of the C loss and recovery rates.

Restoration

Restoring wetland forests from other nonwetland land uses, including previously converted lands, is an attractive concept to mitigate rising atmospheric CO, concentrations, given that wetlands are a major terrestrial C sink and that wetland conversions to other uses are usually associated with soil C losses. Unfortunately, very little information is available on C balances in restored wetlands, hence an all-too-common perspective is that upland soils should be the focus of restoration efforts (Batjes, 1998). A prerequisite of any wetland restoration project is the reestablishment of the hydrologic regime. However, depending on the reconstructed hydrologic regime, it may drive soil processes differently than in the original wetland. Wetland restoration may also involve reconstructing a soil from fill or other spoil material, which would give much-different properties than the original wetland soil. Accordingly, these uncertainties make predictions about the efficacy of wetland restoration as a mechanism for enhancing C storage questionable. However, the few examples available suggest that the concept is viable in some situations.

Histosols

Organic soils have been cleared and drained for agriculture and peat harvesting, and poorly stocked peatlands have also been drained in order to enhance tree production. In the case of cleared peatlands, restoration involves reestablishing the hydrology and reintroducing native vegetation. In the early stages of restoration, the focus is on vegetation that is known to be an effective builder

Table 19.7 Carbon Gain and Methane Losses on Restored Forested Wetland Sites

Site	C Gains[a] (g C m^{-2} year^{-1})	CI-I, Losses[b] (g CH, m^{-2} year^{-1})	Time[c] (years)	Reference
		Organic soils — Finland		
Harvested peat	+64.5	-2 to -4	3	Tuittila et al., 1999, 2000
Drained forest fen	+162 to +283	-0.1 to -2.1	2	Komulainen et al., 1998, 1999
Drained forest bog	+54 to +101	-0.8 to -4.6	2	Komulainen et al., 1998, 1999
		Mineral soils — southern U.S.		
Floodplain	+125 to +480	—	9-I 1	Wiggington et al., 2000

[a] Positive C values indicate a net sink.

[b] Negative C values indicate a net source.

[c] Time indicates years since restoration.

of organic soils, typically sedges *(e.g., Eriophorum vaginatum* L.) and *Sphagnum* spp. Restoration of organic soils can be effective in establishing a positive C balance, but there is also an associated increase in CH, production (Table 19.7). Tuittila et al. (1999) reported that soil respiration was reduced once wetland hydrology had been reestablished on a partially harvested peat soil, and the soil became a C sink within 3 years. On both fen and bog sites that had been drained and restored by closing ditches and removing the tree canopy, a positive C balance was measured after 2 years. This was in contrast to drained reference soils that had either a near-zero (3 g m^{-2}, bog site) or negative (-183 g m^{-2}, fen site) C balance.

It is important to recognize that the short-term C balance calculations do not reflect long-term accumulation rates. The C inputs in these restored Finnish peatlands appear to be sufficient to sustain the development of an organic soil, a rate that Alm et al. (1998) estimated to be 64 to 76 g m^{-2} year^{-1}. However, the added organic matter will continue to degrade over time, which is the reason that long-term C accumulation rates in peat soils are estimated to be lower (13 g m^{-2} year^{-1} in bogs and 18 g m^{-2} year^{-1} in fens (Clymo et al., 1998). The C balance in restored wetlands is subject to the same factors as natural wetlands (Alm et al., 1998), and so annual variations in C sequestration should be expected.

Mineral soils

Floodplains represent an attractive setting for restoring wetland forests. Many of these wet-mineral-soil sites have been cleared for agriculture, which caused a large reduction in soil C content. In the Mississippi delta, restoring bottomland hardwood forests is seen as an opportunity to reverse the loss of important habitat and water-storage functions and to sequester C for energy credits. Establishing hardwood plantations on abandoned agricultural land may be a means to further enhance soil C sequestration. Understory vegetation has an important role in the early successional stages of restored floodplain forests (Giese et al., 2000). In one study, understory vegetation on a wet mineral soil comprised 94% of the aboveground biomass and was the main source of litter production on the site. As a result, 675 g m^{-2} accumulated in the forest floor after 7 years, and the mineral soil also exhibited organic-matter gains (Wiggington et al., 2000).

PERSPECTIVES

Wetlands are acknowledged to comprise a significant proportion of the global terrestrial C pool. Although current inventories of wetlands and forests are inadequate to assess the role of forested wetlands in the terrestrial C budget, their importance in the United States is implicit, since 60%

of the wetlands are forested. Given the diversity of wetland forests and the management opportunities for affecting C sequestration in these soils, improved inventory and analysis procedures are desperately needed. Inventories could provide the basis for developing management, restoration, and conservation strategies that enhance terrestrial C sequestration while sustaining other important wetland functions.

In addition to resource inventory and modeling tools for assessing the C balance in forested wetlands, there is a need to better understand the processes controlling the C cycle. Recent studies indicate that the old paradigm that wetland disturbance will cause a loss in soil C is too simplistic. Vompersky's (1992) idea that increasing site productivity potential can also increase C storage both above and below ground has been substantiated for organic soils (Minkkinen and Laine, 1998). Similar studies on the highly productive wet mineral soils in the southeastern United States have not been conducted, but it seems likely that changes in soil C should also reflect productivity gains in these forests. However, increased aboveground productivity does not necessarily imply gains in the soil C pool, since the soil response is dependent on the interaction of both soil and plant functions, many of which are not clearly understood.

More information on the factors controlling C cycling in forested wetlands is needed to effectively manage the overall C balance in forested wetlands. Our perspective has been shaped by the general principals of temperature, aeration, and acidity affects on organic-matter turnover. The recent reports by Freeman et al. (2001a, 2001b) suggest an enzymatic control on organic-matter turnover that has not been widely considered. Other work has recognized the important role of soil minerals in sequestering humic substances in mineral soils. These findings suggest a more intricate system of interactions among abiotic conditions, especially redox, vegetation, and microbiology that regulate C dynamics in wetland forests. Focused efforts to understand these interactions are needed in order to provide a basis for managing C dynamics and possible C sequestration in wetland forests.

Enhancing terrestrial C storage through forested wetland restoration involves the development of surface organic horizons, organic-matter accumulation in the mineral soil, or both. The surface organic horizons of forested wetlands should be expected to form following establishment of hydric soil conditions, yielding 9 to 15 kg C m^{-2} in a mature forest if estimates from undisturbed soils are applicable. However, we could not find any reports of long-term studies that confirmed an increase in soil C content following wetland restoration. Given the large soil C pool in forested wetlands, utilizing gas-exchange measurements would be more sensitive than soil-C-balance studies to detect relatively small changes. While there are examples of long-term soil C gains following afforestation in uplands (e.g., Lal, 2001), there are others that fail to detect a change in the mineral soil (e.g., Richter et al., 1999). Also, an increase in C accumulation in aboveground biomass does not necessarily mean a long-term gain in soil C pools. These inconsistencies reinforce caution regarding assumptions about soil C response following wetland restoration. It is also disconcerting that the more widely used soil C models are not appropriate for simulating C dynamics in forested wetlands (Trettin et al., 2001). However, given the decomposition environment of wetland forests, their C sequestration potential should exceed that of uplands. It is hoped that simulation tools and experiments will be developed soon to test this idea.

The annual C balance in wetlands is sensitive to minor changes in climatic conditions that alter the hydrologic regime (Alm et al., 1998). In the short term, wetlands can be expected to be either sources or sinks for C. However, over the long term, hydrologic conditions must be sufficiently stable to sustain the vegetation community that sequesters C, and the soil environment must be sufficiently low in oxygen to constrain organic-matter decomposition rates. Although this critical role of hydrology in wetland functions is widely acknowledged, hydrologic considerations are inadequate in assessing C dynamics in wetlands and virtually absent from soil models (Trettin et al., 2001). Hydrology must be a fundamental tenet of future research on C cycling in forested wetlands.

REFERENCES

Alm, J. et al., Carbon balance of a boreal bog during a year with an exceptionally dry summer, *Ecology, 80:* 161-174, 1998.

Baker, T.T., III et al., Fine root productivity and dynamics on a forested floodplain in South Carolina, *Soil Sci. Soc. Am. J., 6.5:* 545–556, 2001.

Baker-Blocker, A., Donaheu, T.M., and Mancy, K.H., Methane flux from wetlands, *Tellus, 29: 245-250,* 1977.

Bartlett, K.B. and Harris, R.C., Review and assessment of methane emissions from wetlands, *Chemosphere,* 26: 261-320, 1993.

Batjes, N.H., Total carbon and nitrogen in the soils of the world, *Eur. J. Soil Sci.,* 47: 151-163, 1996.

Batjes, N.H., Mitigation of atmospheric CO, concentrations by increased carbon sequestration in the soil, *Biol. Fert. Soils, 27: 230-235,* 1998.

Bellisario, L.M. et al., Controls on CH, emissions from a northern peatland, *J. Geophys. Res.,* 13: 81, 1999.

Bergman, I., Svensson, B.H., and Nilsson, M., Regulation of methane production in a Swedish acid mire by pH, temperature, and substrate, *Soil Biol. Biochem., 30:* 729-741, 1998.

Birdsey, R. and Heath, L.S., Forest inventory data, models, and assumptions for monitoring carbon flux, in *Soil Carbon Sequestration and the Greenhouse Effect,* Lal, R., Ed., Soil Science Society of America, Madison, WI, 2001, p. 137-154.

Boelter, D.H. and Verry, E.S., Peatland and Water in the Northern Lake States, Gen. Tech. Rep. NC-31, USDA Forest Service, St. Paul, MN, 1977.

Braekke, F.H. and Finer, L., Decomposition of cellulose in litter layer and surface peat of low-shrub bogs, *Scand. J. For: Res.,* 5: 297-310, 1990.

Bridgham, SD. et al., Soils of northern peatlands: Histosols and Gelisols, in *Wetland Soils,* Richardson, J.L. and Vepraskas, M.J., Eds., Lewis Publishers, Boca Raton, FL, 2001, p. 343–370.

Bridgham, S.D. et al., Cellulose decay in natural and disturbed peatlands in North Carolina, *J. Environ. Qual.,* 20: 695–701, 1991.

Bridgham, SD., Updegraff, K., and Pastor, J., Carbon, nitrogen, and phosphorus mineralization in northern wetlands, *Ecology, 79:* 1545–1561, 1998.

Burke, M.K., Lockaby, B.G., and Conner, W.H., Aboveground production and nutrient circulation along a gradient in a South Carolina Coastal Plain forest, *Can. J. For. Res.,* 29: 1402-1418, 1999.

Campbell, C. et al., Net primary production and standing biomass in northern continental wetlands, Inf. Rep. NOR-X-369, Natural Resources Canada, Canadian Forest Service, Northern Forestry Center, Edmonton, Alberta, 2000.

Canadell, J. et al., Maximum rooting depth of vegetation types at the global scale, *Oecologia,* 108: 583–595, 1996.

Carroll, P. and Crill, P., Carbon balance of a temperate poor fen, *Global Biogeochemical Cycles,* 11: 349-356, 1997.

Chamie, J.P.M. and Richardson, C.J., Decomposition in northern wetlands, in *Freshwater Wetlands,* Academic Press, New York, 1978, p. 115-130.

Clark, K.L. et al., Environmental controls over net exchanges of carbon dioxide from contrasting Florida ecosystems, *Ecol. Applic., 9: 936-948,* 1999.

Clymo, R.S. et al., Carbon accumulation in peatlands, *Oikos,* 81: 368-388, 1998.

Collins, M.E. and Kuehl, R.J., Organic matter accumulation and organic soils, in *Wetland Soils,* Richardson, J.L. and Vepraskas, M.J., Eds., Lewis Publishers, Boca Raton, FL, 2001, p. 137-162.

Conner, W.H., Effect of forest management practices on southern forested wetland productivity, *Wetlands,* 14: 27-40, 1994.

Craft, C.B., Biology of wetland soils, in *Wetland Soils,* Richardson, J.L. and Vepraskas, M.J., Eds., Lewis Publishers, Boca Raton, FL, 2001, p. 107-135.

Crill, P.M. et al., Methane flux from Minnesota peatlands, *Global Biogeochemical Cycles, 2:* 371-384, 1988.

Dahl, T.E., Status and Trends of Wetlands in the Conterminous United States 1986-1997, U.S. Dept. of Interior, Fish and Wildlife Service, Washington, D.C., 2000.

Day, F.P., Jr. and Megonigal, J.P., The relationship between variable hydroperiod, production allocation, and belowground organic turnover in forested wetlands, *Wetlands,* 13: 115-121, 1993.

Eijsackers, H. and Zehnder, A.J.B., Litter decomposition: a Russian matrochaka doll, *Biogeochemistry, 11:* 153–174, 1990.

Eswaran, H., van der Berg, E., and Reich, P., Organic carbon in soils of the world, *Soil Sci. Soc. Am. J., 57:* 192-194, 1993.

Eswaran, H. et al., Global soil carbon resources, in *Soils* and *Global* Change, Lal, R. et al., Eds., Lewis Publishers, Boca Raton, FL, 1995, p. 22-27.

Farrish, K.W. and Grigal, D.F., Mass loss in a forested bog: relation to hummock and hollow microrelief, *Can. J. Soil Sci., 65: 37.5-378,* 1985.

Farrish, K.W. and Grigal, D.F., Decomposition in an ombrotrophic bog and minerotrophic fen in Minnesota, *Soil Sci.,* 145: 353-3.58, 1988.

Finer, L. and Laine, J., Root dynamics at drained peatland sites of different fertility in southern Finland, *Plant Soil,* 210: 27-36, 1998.

Finer, L., Variation in the amount and quality of litterfall in a *Pinus sylvestris* L. stand growing on a bog, *For. Ecol. Manage., 80:* l-l 1, 1996.

Freeman, C. et al., Export of organic carbon from peat soils, *Nature,* 412: 785, 2001 a.

Freeman, C., Ostle, N., and Kang, H., An enzymic "latch" on a global carbon store, *Nature, 409:* 149, 2001b.

Giese, L. et al., Spatial and temporal patterns of carbon storage and species richness in three South Carolina coastal plain riparian forests, *Ecol. Eng.,* 15: S157–S170, 2000.

Goulden, M.L. et al., Sensitivity of boreal forest carbon balance to soil thaw, *Science, 279:* 214-217, 1998.

Grigal, D.F., Sphagnum production in forested bogs in northern Minnesota, *Can. J. Bot., 63:* 1204-1207, 1985.

Höberg, P. et al., Large scale forest girdling shows that current photosynthesis drives respiration, *Nature,* 111: 789-792, 2001.

Hogg, E.H., Decay potential of hummock and hollow sphagnum peats at different depths in a Swedish raised bog, *Oikos, 66: 269-278, 1993.*

Hogg, E.H., Lieffers, V.J., and Wein, R.W., Potential carbon losses from peat profiles: effects of temperature, drought cycles, and fire, *Ecol. Applic., 2: 298-306,* 1992.

Howard-Williams, C., Pickmere, S., and Davies, J., The effect of nutrients on aquatic plant decomposition rates, *Verh. Internat. Verein. Limmol., 23:* 1973-1978, 1988.

Hutchin, P.R. et al., Methane emission rates from an ombrotrophic mire show marked seasonality which is independent of nitrogen supply and soil temperature, *Atmos. Environ., 30:* 301 l-3015, 1996.

Jarvis, P.G. et al., Seasonal variation of carbon dioxide, water vapor, and energy exchanges of a boreal black spruce swamp forest, *J. Geophys. Res., 102: 253-289,* 1997.

Johnson, D.W., Effects of forest management of soil carbon storage, *Water Air Soil Poll., 64:* X3-120, 1992.

Johnson, D.W. and Curtis, P.S., Effects of forest management on soil C and N storage: meta analysis, *For. Ecol. Manage.,* 140: 227-238, 2001.

Johnson, L.C. et al., Effects of drainage and temperature on carbon balance of tussock tundra microcosms, *Oecologia,* 108: 737-748, 1996.

Jones, R.H., Locakaby, B.G., and Somers, G.L., Effects of microtopography and distribution on fine root dynamics in wetland forests of low-order stream floodplains, *Am. Midland Nut.,* 136: 57-7 1, 1996.

Jurgensen, M.F. et al., Mycorrhizal relationships in bottomland hardwood forests of the southern Unites States, *Wetlands Ecol. Manage., 4: 223-233,* 1997.

Komulainen, V-M. et al., Restoration of drained peatlands in southern Finland: initial effects on vegetation change and CO, balance, *J. App. Ecol., 36: 634-648,* 1999.

Komulainen, V-M. et al., Short-term effect of restoration on vegetation change and methane emissions from peatlands drained for forestry in southern Finland, *Can. J. For: Res., 28:* 402–41 1, 1998.

LaBaugh, J.W., Wetland ecosystem studies from a hydrologic perspective, *Water Res. Bull., 22:* I-10, 1986.

Lähde, E., Biological activity in some natural and drain peat soils with special reference to oxidation-reduction conditions, *Acta For. Fenn., 94:* l-94, 1969.

Laiho, R. and Finer, L., Changes in root biomass after water-level drawdown on pine mires in southern Finland, *Scand. J. For. Res.,* 11: 25 l-260, 1996.

Laine, J. and Minkkinen, K., Effect of forest drainage on the carbon balance of a mire: a case study, *Scand. J. For. Rex, I 1:* 307-312, 1996.

Laine, J., Vasander, H., and Sallantaus, T., Ecological effects of peatland drainage for forestry, *Environ. Rev.,* 3: 286–303, 1995.

Lal, R., The potential of soil carbon sequestration in forest ecosystems to mitigate the greenhouse effect, in *Soil Carbon Sequestration and the Greenhouse Effect,* Lal, R., Ed., Soil Science Society of America, Madison, WI, 2001, p. 137-154.

Latter, PM. et al., Long-term study of litter decomposition on a Pennine peat bog: which regression? *Oecologia,* 113: 94-113, 1998.

Lockaby, B.G., Wheat, R.S., and Clawson, R.G., Influence of hydroperiod on litter conversion to soil organic matter in a floodplain forest, *Soil Sci. Soc. Am. J., 60:* 1989-1993, 1996a.

Lockaby, B.G., Murphy, A.L., and Somers, G.L., Hydroperiod influences on nutrient dynamics in decomposing litter of a floodplain forest, *Soil Sci. Soc. Am. J., 60:* 1267-1272, 1996b.

Maltby, E. and Immirzi, P., Carbon dynamics in peatlands and other wetland soils: regional and global perspectives, *Chemosphere, 27:* 999-1023, 1993.

Matthews, E. and Fung, I., Methane emissions from natural wetlands: global distribution, area, and environmental characteristics of sources, *Global Biogeochemical Cycles,* 1: 61-86, 1987.

Mausbach, M.J. and Richardson, J.L., Biogeochemical processes in hydric soil formation, *Cur,: Top. Wetland Biogeochemistry,* 1: 68-127, 1994.

McKee, W.H., Jr. and McKevlin, M.R., Geochemical processes and nutrient uptake by plants in hydric soils, *Environ. Tox. Chem.,* 12: 2197-2207, 1993.

McKevlin, M.R., Hook, D.H., and Rozelle, A.A., Adaptations of plants to flooding and soil waterlogging, in *Southern Forested Wetlands: Ecology and Management,* Messina, M.G. and Conner, W.H., Eds., Lewis Publishers, Boca Raton, FL, 1998, p. 173-204.

McLaughlin, J.W. et al., Soil factors related to dissolved organic carbon concentrations in a black spruce swamp, Michigan, USA, *Soil Sci.,* 1.58: 4.54-464, 1994.

Megonigal, J.P. and Day, F.P., Jr., Organic matter dynamics in four seasonally flooded forest communities of the dismal swamp, *Am. J. Bot., 75:* 1334-1343, 1988.

Megonigal, J.P. and Day, F.P., Jr., Effects of flooding on root and shoot production of bald cypress in large experimental enclosures, *Ecology, 73:* 1182-1193, 1992.

Megonigal, J.P. et al., Aboveground production in southeastern floodplain forests: a test of the subsidy-stress hypothesis, *Ecology, 78: 370-384,* 1997.

Minkkinen, K. and Laine, J., Long-term effect of forest drainage on the peat carbon stores of pine mires in Finland, Can. *J. For. Res., 28:* 1267-1275, 1998.

Minkkinen, K. et al., Post-drainage changes in vegetation composition and carbon balance in Lakkasuo mire, Central Finland, *Plant Soil, 207:* 107-120, 1999.

Mitch, W.J. and Gooselink, J.G., *Wetlands,* Van Nostrand Reinhold, New York, 2000.

Moore, T.R., Dissolved organic carbon: sources, sinks and fluxes and role in the soil carbon cycle, in *Soil Processes and the Carbon Cycle,* Lal, R. et al., Eds., CRC Press, Boca Raton, FL, 1998, p. 281-292.

Moore, T.R. and Roulet, N.T., Methane emissions from Canadian peatlands, in *Soils and Global Change,* Lal, R. et al., Eds., CRC-Lewis Publishers, Boca Raton, FL, 1995, p. 153-164.

Persson, H., Factors affecting fine root dynamics of trees, Sun, 43: 163-172, 1992.

Powell, S.W. and Day, El?, Root production in four communities in the Great Dismal Swamp, *Am. J. Bot.,* 78: 288-297, 1991.

Pulliam, W.M., Carbon dioxide and methane exports from a southeastern floodplain swamp, *Ecol. Monogr.,* 63: 29-53, 1993.

Rice, M.D. et al., Woody debris decomposition in the Atchafalaya River basin of Louisiana following hurricane disturbance, *Soil Sci. Soc. Am. J.,* 61: 1264-1274, 1997.

Richardson, J.L. and Vepraskas, M.J., Eds., *Wetland Soils,* Lewis Publishers, Boca Raton, FL, 2001.

Richter, D.D. et al., Rapid accumulation and turnover of soil carbon in a re-establishing forest, *Nature, 400:* 56-58, 1999.

Roulet, N.T., Peatlands, carbon storage, greenhouse gases, and the Kyoto protocol: prospects and significance for Canada, *Wetlands, 20:* 605-615, 2000.

Roulet, N.T., Ash, R., and Moore, T.R., Low boreal wetlands as a source of atmospheric methane, *J. Geophys. Res., 97: 3739-3749,* 1992.

Silvola, J., Alm, J., and Ahlholm, U., The effect of plant roots on CO, release from peat soil, *Suo,* 43: 259-262, 1992.

Silvola, J. et al., CO, fluxes from peat in boreal mires under varying temperature and moisture conditions, *J. Ecol., 84:* 219-228, 1996a.

Silvola, J. et al., The contribution of plant roots to CO, fluxes from organic soils, *Biol. Fert. Soils, 23:* 126-131, 1996b.

Soil Survey Staff, Soil Taxonomy, Agriculture Handbook 436, USDA NRCS, U.S. Government Printing Office, Washington, D.C., 1999.

Sundh, I. et al., Depth distribution of microbial production and oxidation of methane in northern boreal peatlands, *Microhiol. Ecol., 27: 253-265,* 1994.

Sundh, 1. et al., Potential aerobic methane oxidation in a sphagnum-dominated peatland — controlling factors and relation to methane emissions, *Soil Biol. Biochem., 27: 829-837,* 1995.

Svensson, B.H. and Sundy, I., Factors affecting methane production in peat soils, *Suo,* 43: 183-190, 1992.

Tarnocai, D., The amount of organic carbon in various soil orders and ecological provinces in Canada, in *Soil Processes and* the *Carbon Cycle,* Lal, R. et al., Eds., CRC Press, Boca Raton, FL, 1998, p. 81-92.

Tolonen, J. and Turunen, J., Accumulation rates of carbon in mires in Finland and implications for climate change, *Holocene, 6:* 171-178, 1996.

Trettin, C.C. et al., Carbon storage response to harvesting and site preparation in a forested mire in northern Michigan, U.S.A., Suo, 43: 281-284, 1992.

Trettin, C.C. et al., Soil carbon in northern forested wetlands: impacts of silvicultural practices, in *Carbon Forms and Functions in Forest Soils,* McFee, W.W. and Kelly, J.M., Eds., Soil Science Society of America, Madison, WI, 1995, p. 437–461.

Trettin, C.C. et al., Organic matter decomposition following harvesting and site preparation of a forested wetland, *Soil Sci. Soc. Am. J., 60:* 1994–2003, 1996.

Trettin, C.C. et al., Effects of forest management on wetland functions in a sub-boreal swamp, in *Northern Forested Wetlands: Ecology and Management,* Trettin, C.C. et al., Eds., Lewis Publishers, Boca Raton, FL, 1997, p. 41 l-428.

Trettin, C.C. et al., Existing Soil Carbon Models Do Not Apply to Forested Wetlands, Gen. Tech. Rep. SRS-46, USDA Forest Service, Southern Research Station, Asheville, NC, 2001.

Tuittila, E-S. et al., Methane dynamics of a restored cut-away peatland, *Global Change Biol., 6:* 569–581, 2000.

Tuittila, E-S. et al., Restored cut-away peatland as a sink for atmospheric CO,, *Oecologia,* 120: 563-574, 1999.

Turunen, J. et al., Carbon accumulation in the mineral subsoil of mires, *Global Biogeochemical Cycles,* 13: 71-79, 1999.

Verry, ES., Hydrological processes of natural, northern forested wetlands, in *Northern Forested Wetlands: Ecology and Management,* Trettin, C.C. et al., Eds., Lewis Publishers, Boca Raton, FL, 1996, p. 163-188.

Vompersky, S.E. et al., The effect of forest drainage on the balance of organic matter in forest mires, in *Peatland Ecosystems and Man: An Impact Assessment,* Bragg, O.M. et al., Eds., Dept. of Biological Sciences, The University, Dundee, U.K., 1992, p. 12-22.

Wetzel, R.G., Gradient-dominated ecosystems: sources and regulatory functions of dissolved organic matter in freshwater ecosystems, *Hydrobiologia, 229:* 18 l-l 98, 1992.

Wiggington, J.D., Lockaby, B.G., and Trettin, C.C., Soil organic matter formation and sequestration across a forested floodplain chronosequence, *Ecol. Eng.,* 15: S 14 1-S 155, 2000.

Wieder, R.K. and Yavitt, J.B., Assessment of site differences in anaerobic carbon mineralization using reciprocal peat transplants, *Soil Biol. Biochem., 23:* 1093-l 095, 1991.

Winter, T.C., A conceptual framework for assessing cumulative impacts on the hydrology of nontidal wetlands, *Environ. Manage.,* 12: 605–620, 1988.

Xu, Y-J. et al., Changes in surface water table depth and soil physical properties after harvesting and establishment of loblolly pine (*Pinus taeda* L.) in Atlantic coastal plain wetlands of South Carolina, *For. Ecol. Manage., 63:* 109– 12 1, 2002.

Yavitt, J.B., Lang, G.E., and Wieder, R.K., Control of carbon mineralization to CH, and CO, in anaerobic Sphagnum-derived peat from Big Run Bog, West Virginia, *Biogeochemistry, 4:* 141–157, 1987.