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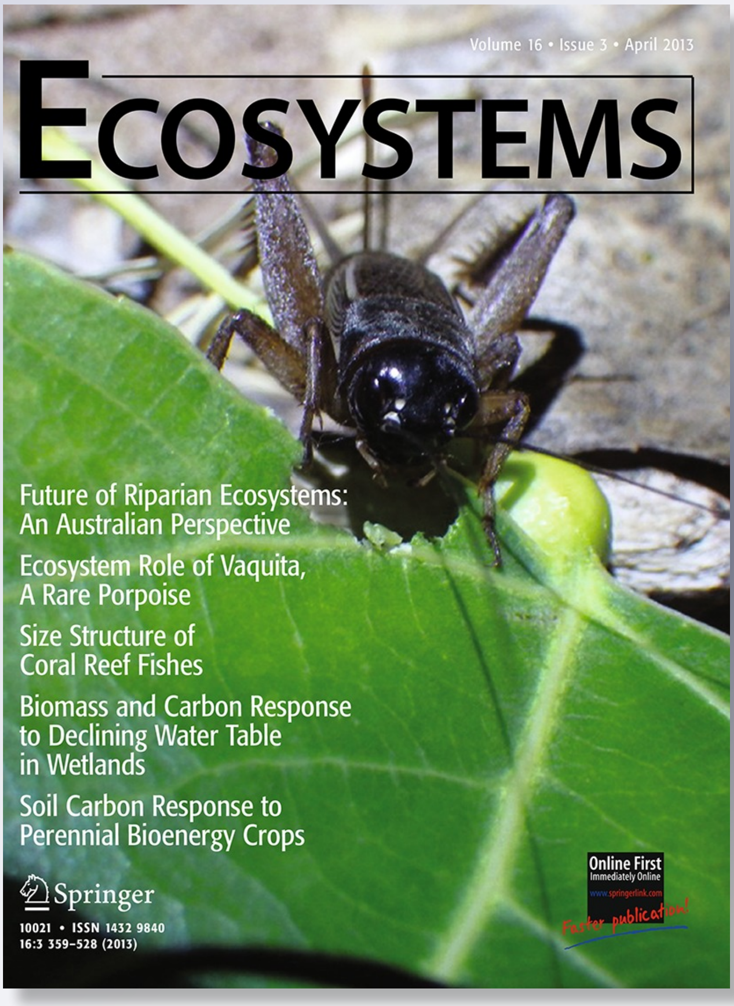

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ECOSYSTEMS

Modeling Soil and Biomass Carbon Responses to Declining Water Table in a Wetland-Rich Landscape

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ABSTRACT

Peatlands and forested wetlands can cover a large fraction of the land area and contain a majority of the regional carbon pool in wet northern temperate landscapes. We used the LANDIS-II forest landscape succession model coupled with a model of plant community and soil carbon responses to water table changes to explore the impacts of declining water table on regional carbon pools in a peatland- and wetland-rich landscape in northern Wisconsin, USA. Simulations indicated that both biomass accumulation and soil decomposition would increase as a consequence of drying. In peatlands, simulated water table declines of 100 cm led to large increases in biomass as well as short-term increases in soil carbon, whereas declines of 40 cm led to continuous declines in soil carbon and smaller increases in biomass, with the net result being a loss of total carbon. In non-peat wetlands, biomass accumulation outweighed soil carbon loss for both scenarios. Long-term carbon cycle responses were not significantly affected by the time scale of water table decline. In general, peatland carbon storage over the first 50–150 years following drainage was neutral or increasing due to increased plant growth, whereas carbon storage over longer time scales decreased due to soil carbon loss. Although the simplicity of the model limits quantitative interpretation, the results show that plant community responses are essential to understanding the full impact of hydrological change on carbon storage in peatland-rich landscapes, and that measurements over long time scales are necessary to adequately constrain landscape carbon pool responses to declining water table.

Key words: wetlands; peatlands; drainage; carbon cycle; hydrological change; plant community succession; LANDIS-II model.

INTRODUCTION

Northern peatlands contain a significant fraction of the global terrestrial carbon pool, and the future evolution of peatland carbon reserves is an important factor in predicting carbon cycle feedbacks to climate change (Gorham 1991; Turunen and others 2002; Mitra and others 2005). In northern temperate regions, peatlands can cover a large fraction of the area, contain significant portions of the carbon pool, and contribute significantly to the regional carbon budget. For example, Weishampel and others (2009)

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found that peatlands in a Minnesota region contained 50% of the regional carbon pool despite occupying only 13% of the area. Similarly, Buffam and others (2011) found that peatlands in a northern Wisconsin region contained 36% of the regional carbon pool while occupying 20% of the area. Lake sediments contained another 38% of the carbon pool, so the combination of peatlands and lakes accounted for 74% of the regional carbon pool. These results suggest that changes in peatland carbon cycling could have disproportionately strong effects on regional carbon budgets compared to their area. These regions also include significant areas of forested wetlands without thick peat layers, which contribute significantly to the regional carbon cycle.

Because peat accumulation and preservation depends on anaerobic soil conditions resulting from high water tables, changes in water table affect CO_2 emissions, and peat decomposition rates (Moore and Knowles 1989; Freeman and others 1992; Junkunst and Fiedler 2007; Yurova and others 2007; Sulman and others 2009; Olivas and others 2010; Flanagan and Syed 2011). Some peatland modeling studies have identified significant positive feedbacks to climate warming due to increased peat decomposition (for example, Tarnocai 2006; Ise and others 2008). However, field and laboratory studies suggest that hydrological change also leads to changes in plant communities (Laine and others 1995; Weltzin and others 2003; Strack and others 2006; Talbot and others 2010), which can significantly affect the net CO_2 budget over the short term (Sulman and others 2009; Flanagan and Syed 2011). Studies of long-term responses to drainage have highlighted the importance of aboveground carbon accumulation, which in some cases can outweigh the loss of carbon from increased peat decomposition (Minkkinen and Laine 1998; Lohila and others 2011). However, most previous studies have considered plant and soil responses separately, with the exception of Frolking and others (2010), which was limited to peatland plant species and did not consider afforestation or spatial interactions. Here, we develop a simplified conceptual model to highlight the relative importance of peatland soil decomposition and plant community succession on total landscape carbon balance.

Climate change may cause declines in water tables at regional scales. Studies using general circulation models (GCMs) predict globally averaged surface warming of 1–2°C by 2050 and up to 3°C by 2100, depending on the future evolution of anthropogenic CO_2 emissions. Northern areas where large areas of boreal peatlands are situated are predicted to warm up to 4°C by mid-century and up to 6°C by 2100, and the incidence of very hot periods and severe droughts is expected to increase (Meehl and others 2007). In addition to direct effects on photosynthesis and soil decomposition rates, increased temperatures will lead to greater rates of evapotranspiration, potentially causing soil drying and drops in the water table (Manabe and Wetherald 1986; Wetherald and Manabe 2002; Erwin 2008), and likely outweighing the effects of predicted increases in precipitation in mid- and high-latitudes. Hydrology can vary coherently at regional scales, as shown by Stow and others (2008). In addition to climatic change, peatland hydrology is often subject to human disturbance. Examples include drainage for forestry (Minkkinen and Laine 1998; Makiranta and others 2010), agriculture (Nieveen and others 2005; Lloyd 2006), or construction and urban development.

In this study, we use a landscape modeling framework to evaluate the responses of peat decomposition and plant community succession to changes in mean water table. We attempt to place peatland and non-peat wetland responses in the context of regional carbon budgets, over multi-century time scales. Because of the relatively large spatial scales, long time periods, and inclusion of plant community responses, we chose to use the LANDIS-II landscape succession model (Scheller and Mladenoff 2004; Scheller and others 2007). Although the design of the LANDIS-II model makes it well suited for studying plant community dynamics at the scales of interest to our study, it does not include explicit hydrology or peatland biogeochemistry. Although numerous peatland-specific ecosystem models exist, they are generally either too computationally intensive for long-term, large-scale studies (for example, Grant and others 2001; Frolking and others 2002; Govind and others 2009), or do not include processes for simulating seed dispersal and long-term plant community changes related to hydrology (for example, Pietsch and others 2003; Belyea and Malmer 2004; Bond-Lamberty and others 2007; St-Hilaire and others 2010). Frolking and others (2010) did present a model including long-term development of peat and associated changes in peatland plant communities, but did not include upland tree species, afforestation of peatlands due to drainage, or landscape heterogeneity, which constitute major features of our analysis.

The major question we addressed was: How does landscape carbon storage respond to declining water table in peatland-rich regions?

To address this question, we focused on building a coupled modeling framework to simulate drying-related changes in peatland and wetland soil and biomass carbon and tested the following hypotheses with the model:

(1) Over short time periods, carbon pool responses to water table change are dominated by plant community changes
(2) Over longer time periods, carbon pool responses to water table change are dominated by changes in soil decomposition rates
(3) Fast declines in water table lead to net decreases in total carbon, whereas slow declines lead to net increases in total carbon
(4) Wetland and peatland responses to hydrological change contribute significantly to the landscape-scale carbon pools of peatland-rich northern temperate regions

Methods

LANDIS-II Model

Landscape succession was modeled using the biomass version of the LANDIS-II model (Scheller and Mladenoff 2004; Scheller and others 2007). The LANDIS-II model was developed based on the LANDIS model (Mladenoff and others 1996; Mladenoff and He 1999). Rather than simulating individual trees, the model uses cohorts divided by species and age class. Aboveground biomass, net primary productivity (NPP), and seed dispersal are simulated for each cohort. The landscape is divided into ecoregions, and growth and establishment parameters are individually defined for each species in each ecoregion. Dynamical factors can be used to modify parameters over the course of the simulation to simulate environmental changes affecting species growth, such as changes in climate or hydrology.

Annual NPP for each cohort is based on a maximum NPP parameter, modified by a number of factors related to cohort biomass and competition:

$$\mathrm{NPP} = \mathrm{NPP}_{\mathrm{Max}} \times \frac{B}{B_{\mathrm{pot}}} \mathrm{e}^{1-\frac{B}{B_{\mathrm{pot}}}} \times \frac{B_{\mathrm{pot}}}{B_{\mathrm{Max}}} \quad (1)$$

where NPP is cohort annual NPP, $\mathrm{NPP}_{\mathrm{max}}$ is cohort maximum NPP, B is cohort biomass, B_{pot} is potential biomass based on available growing space and competition in the grid cell, and B_{max} is cohort maximum biomass. Mortality based on cohort age as a fraction of species maximum age is then subtracted from annual cohort NPP. For more details, see Scheller and Mladenoff (2004).

Seed dispersal occurs between grid cells, and is controlled by effective dispersal radius parameters for each species. Establishment of new cohorts in seeded areas is a function of grid cell shade class (based on total biomass), species shade tolerance, and ecoregion-specific establishment probability for each species. Plant growth, mortality, and soil decomposition are calculated at an annual time step. In our simulations, seed dispersal and reproduction were calculated at a 5-year time step, and carbon pool and flux values are presented at that temporal resolution.

Maximum NPP and establishment probability parameters for tree species were calculated using a version of the PnET model, as described by Xu and others (2009), driven using temperature and precipitation measurements from a nearby meteorological station archived by the National Climate Data Center (NCDC). Maximum NPP for peatland shrub and grass species were based on field measurements from sites in the area (Sulman and others 2009, 2010). Maximum biomass for tree species was based on the values from Thompson and others (2011). Species parameters are shown in Table 1. Shrub and graminoid species were assigned a shade tolerances of 4, because the peatland areas where they grow would generally have open canopies and not be shade limited compared to forests. Mosses were not explicitly included, although they can be important in bog ecosystems.

Belowground carbon cycling was added to the LANDIS-II biomass succession model for this study. In addition to woody and non-woody litter pools, a fast and a slow soil carbon pool were added. When decomposition occurs, carbon flows sequentially between pools (litter to fast to slow), with a fixed fraction respired as CO_2 in each step. This soil pool formulation follows Parton and others (1988). Decomposition rates in the litter pools are determined by species-specific coarse and foliar litter decomposition rates (Scheller and Mladenoff 2004). Decomposition rates in the fast and slow soil carbon pools are determined by a fixed turnover rate parameter, which can be specified for each ecoregion and time step. For these simulations, a fast soil pool turnover rate of 0.15 y^{-1} was used for all ecoregions based on typical literature values (for example, Parton and others 1988; Schimel and others 1994; Bridgham and others 1998). The calculations for slow soil pool turnover rates are described below.

Wetland Simulation Strategy

The LANDIS-II model does not include internal hydrology, so hydrological scenarios were imposed by externally simulating hydrological effects on

Table 1. Species Parameters Used in LANDIS-II Model

Species	Max NPP	Max biomass	SEP	Shade tol	Wetland tol	Longevity
Abies balsamea	565	4,905	0.72	1	Mineral woody	200
Acer rubrum	615	9,405	0.24	4	Wet tolerant	150
Acer saccharum	537	11,205	0.62	5	Upland	300
Betula alleghaniensis	548	9,360	0.92	4	Upland	300
Betula papyrifera	407	9,585	0.92	2	Upland	100
Carya cordiformis	670	11,250	0.83	2	Wet tolerant	200
Fagus grandifolia	329	11,250	0.92	5	Upland	300
Fraxinus americana	495	11,655	0.92	4	Upland	300
Fraxinus nigra	471	5,000	0.92	2	Mineral woody	300
Fraxinus pennsylvanica	412	11,250	0.92	3	Wet tolerant	300
Larix laricina	189	5,500	0.76	1	Peat woody	200
Picea mariana	189	7,000	0.72	3	Peat woody	300
Pinus banksiana	673	11,250	0.85	1	Upland	100
Pinus resinosa	583	11,250	0.86	2	Upland	200
Pinus strobus	411	14,355	0.91	3	Upland	400
Populus deltoides	657	11,250	0.87	1	Upland	250
Populus tremuloides	620	8,370	0.89	1	Upland	120
Quercus rubra	644	10,350	0.86	3	Upland	250
Thuja occidentalis	541	11,250	0.74	2	Wet tolerant	400
Tilia americana	505	11,250	0.93	4	Upland	250
Ulmus americana	582	11,250	0.88	3	Upland	350
Shrubs	286	6,000	0.92	4	Peat woody	40
Graminoids	300	2,400	0.90	4	Peat sedge	10

SEP is species establishment probability, shade tol is shade tolerance, and wetland tol is wetland tolerance. Shade tolerance is a number between 1 and 5, with 5 being the most tolerant of shade. Longevity is species maximum age in years. Max NPP is in gC m^{-2} y^{-1}*and Max biomass is in gC* m^{-2}*. Both of these parameters are aboveground fractions. In wetland areas, maximum NPP, maximum biomass, and SEP were multiplied by the vegetation area fraction for the species wetland tolerance (see Figure 4). ''Upland'' species were limited to ''Upland'' fractions, ''mineral woody'' species were limited to ''Wet woody'' fractions in mineral wetland ecoregions, ''peat woody'' species were limited to ''Wet woody'' fractions in peat wetland ecoregions, and ''wet-tolerant'' species were allowed in both mineral wetland ''Wet woody'' areas and ''Upland'' areas. Graminoids were limited to peat ''sedge'' areas.*

plant growth and soil decomposition for each ecoregion, and then applying the resulting changes to LANDIS-II plant and soil pool parameters over the course of the simulations. Different peatland and wetland types were modeled as different ecoregions. Each ecoregion was assigned an initial water table level, which was then changed over time in different hydrological scenarios. Peatland plant communities and soils can be sensitive to small-scale variations in topography (Waddington and Roulet 1996; Palmer 2005; Strack and others 2006), so sub-grid-scale heterogeneity was included in vegetation and soil decomposition calculations by sampling from a distribution of topography relative to water table. We used a bimodal distribution to reflect the typical hummock/hollow topography of northern peatlands (Eppinga and others 2008), with distribution parameters adjusted to match water table variations observed between two measurement points at the Lost Creek wetland field site in northern Wisconsin, USA (Sulman and others 2009). This strategy made it possible to include hydrology-related carbon cycle changes without implementing a complete hydrological and biogeochemical model within LANDIS-II. The framework's level of complexity matched well with our focus on bulk changes in carbon pools over long periods of time, but it omitted some details of wetland succession that could be important for more focused investigations of plant community and soil property responses to changes in hydrology. Some implications of this approach and possibilities for more sophisticated studies are addressed in the discussion.

Plant Communities

Plant community dependence on water table was modeled using a fractional area approach. Land surface area was divided into categories based on distance above the water table, and species were divided into categories based on flood tolerance and typical presence in wetlands as described by Burns and Honkala (1990) (Table 1). ''Underwater'' areas did not support vegetation. Areas very close to the water table were limited to grassy species (''Sedges''). Moderately wet areas were assigned wet-tolerant woody species (''Wet woody''), and areas well above the water table were assigned to upland species (''Upland''). In addition, wetland ecoregions were divided into wet mineral (higher productivity and lower soil carbon) and peatland (lower productivity and higher soil carbon) wetland types. Wetland woody species were designated as either ''Peat woody'' or ''Mineral woody,'' and limited to only those wetland areas. ''Wet-tolerant'' species were allowed in both ''Upland'' and ''Mineral woody'' areas.

Maximum NPP, maximum biomass, and establishment probability for each species were multiplied by the area fraction representing habitat for that species within the grid cell on an ecoregion-specific basis. As area fractions changed in response to changing water table, simulated plant communities responded through the modeled growth, reproduction, and mortality processes. For example, lowering the water table in a wetland area would allow the establishment of upland species through seed dispersal from nearby upland areas, whereas wetland species biomass and growth would decrease as a result of reduced maximum biomass and NPP parameters. Our simulations focused on wetlands and peatlands, and did not include the impact of long-term drought on upland productivity.

Soil Decomposition

Turnover rates for the slow carbon pool in peatlands were calculated using a simplified version of the Frolking and others (2001) peat decomposition model. The underlying model of organic matter decomposition is

$$\frac{\mathrm{d}m(t)}{\mathrm{d}t} = -k_0 m_0 \left(\frac{m(t)}{m_0}\right)^{\alpha} \qquad (2)$$

where $m(t)$ is soil pool mass, k_0 is an initial turnover rate (set to 0.2, following Frolking and others 2001), m_0 is initial mass, and α is a parameter describing the decline in organic matter decomposability with time. The general solution is

$$m(t) = \frac{m_0}{[1 + (\alpha - 1)k_0 t]^{1/(\alpha-1)}} \qquad (3)$$

Using $\alpha = 2$ (following Frolking and others 2001), a turnover rate k can be specified as a function of age t:

$$k(t) = k_0 \frac{m(t)}{m_0} = \frac{k_0}{1 + k_0 t} \qquad (4)$$

Rather than directly simulating peat age cohorts, an age profile was defined as a function of depth ($k_t(z)$) using the results of Frolking and others (2001). Peat age was limited to a minimum of 50 years because additional litter and fast decomposition pools were included in the LANDIS-II model. The age profile is shown in Figure 1. Due to the increasing age of carbon with depth, total decomposition was more sensitive to the upper peat layers than to the lower peat layers. Additions of young carbon to the soil pool over the course of simulations were decomposed using a 50-year turnover time as described below. These simplifications of the model were similar to those previously used by St-Hilaire and others (2010). In addition to the age profile, the depth profile of k depends on the effect of the vertical soil temperature profile ($f_T(z)$) and the effect of water table level ($f_W(z)$). f_W is defined relative to the water table level, allowing the soil decomposition parameter to capture the effect of changing water table. The depth profiles of these functions are shown in Figure 1.

The value of k at each soil depth was the product of these functions:

$$k(z) = k_t(z) f_T(z) f_W(z) \qquad (5)$$

The turnover rate for an individual soil column was calculated by averaging k vertically over the soil profile. This calculation was conducted for 100 soil columns sampled from the soil height distribution, and the mean value was used as the slow carbon pool turnover rate for that ecoregion. The upland and wet forest ecoregions used a single characteristic soil age (50 years for upland and 60 years for wet forest) rather than an age profile, because those ecosystems do not develop thick peat layers over long time periods. Table 2 shows the important soil parameters for each ecoregion.

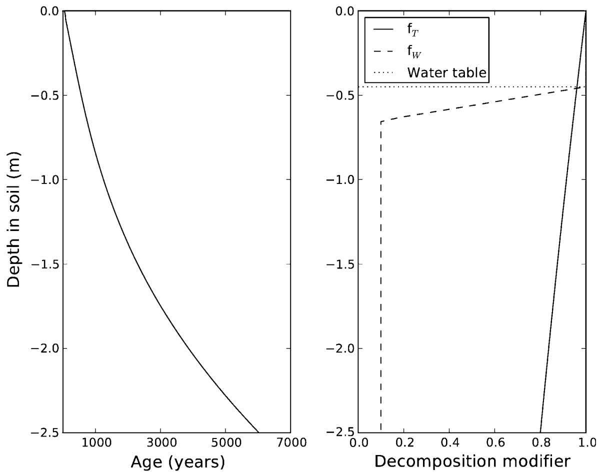

Figure 1. *Left* Peat age profile. *Right* Functions for the effects of soil temperature profile and water table on decomposition rate.

Table 2. Ecoregion Parameters

Ecoregion	WT_0	Pool size (shallow)	Pool size (deep)	Soil depth (shallow)	Soil depth (deep)	Area fraction (%)
Upland	−2.0	9.1	9.1	0.21	0.21	38
Wet forest	−0.45	13.6	13.6	0.62	0.62	27
Shrub peat	−0.30	18.5	100	0.47	2.53	29
Gram peat	−0.15	18.4	100	0.47	2.53	5

WT_0 is water table level (m) at the start of simulation, relative to soil hummock height. Pools are soil C, in kgC m^{-2}, and soil depths are in meters. ''Shallow'' and ''deep'' refer to the shallow and deep peat scenarios. Area fraction refers to the fraction of active grid cells containing that ecoregion. Non-active grid cells include open water, crops, and developed areas.

Annual decomposition for soil pools in the LANDIS-II model was calculated using an exponential dependence on $\bar{k}$:

$$\Delta m = m(1 - e^{-\bar{k}}) \qquad (6)$$

Therefore, the annual soil decomposition for each ecoregion depended on a combination of soil pool size and $\bar{k}$. Peat depth was calculated from peat mass using the bulk density profile from Frolking and others (2001), which was similar in magnitude to local estimates by Buffam and others (2010). This calculation assumed a peat carbon density of 40%. Soil organic layer depth refers to the minimum soil layer thickness, so soil thickness under hummocks is greater than the soil depth parameter. Wet forest and upland soil depths were calculated using the same bulk density profile, but assumed one half the carbon density compared to peat, because these ecosystems had mineral soils with lower concentrations of organic matter. Because the soil carbon pools were much smaller in non-peat ecosystems, those results were not sensitive to the depth calculation. These soil depths represent the area where significant soil carbon is located, and are important for determining the vertical range where water table affects soil decomposition rate.

Study Region and Spatial Data

The model was run for a 60-by-30 km area within Price county in northern Wisconsin, USA, with a spatial resolution of 100 m (Figure 2). This region was chosen because of the large areas of forests and wetlands, and relatively small areas of urbanization and agriculture. This region has also been the location of several flux tower studies (Cook and others 2004; Desai and others 2005; Sulman and others 2009, 2010) and regional carbon cycle studies (Buffam and others 2010, 2011; Xiao and others 2011), which provided data resources for model parameterization. The landscape was categorized into wetland and upland ecoregions based on a combination of National Landcover Database (NLCD) 2001 remote-sensing-based landcover classification map (Homer and others 2004), and the United State Geological Survey (USGS) Soil Survey Geographic Database (SSURGO) (Natural Resources Conservation Service 2011). NLCD maps were used to distinguish between forest, shrub, and graminoid areas, and SSURGO maps were used to locate areas with hydric or peat soils. Grid cells were categorized as upland, mineral wetland, shrub peatland, or graminoid peatland, with peat and mineral wetland soils distinguished based on the thickness of the organic layer in the SSURGO dataset. A map of ecoregions is shown in Figure 2, and the fraction of the landscape occupied by each ecoregion is shown in Table 2. These fractions exclude areas that were not modeled, such as open water and built-up areas.

Initial plant communities were assigned based on the NLCD map with tree species fractions and ages determined based on area fraction estimates from the United States Department of Agriculture (USDA) Forest Inventory and Analysis (FIA) dataset. The specific tree species shown in Table 1 were inferred based on forest community types from the FIA dataset. Because the analysis was focused on bulk carbon pools and ecosystem types, the results were not sensitive to the individual tree species that were included.

Soil carbon pools and depths for each ecoregion are shown in Table 2. Two peat scenarios were used, one shallow and one deep, to test the effect of peat depth. Values for the upland ecoregion and the shallow peat scenario were determined using measurements from sites in the Chequamegon Ecosystem Atmosphere Study, a network of field sites in northern Wisconsin and the upper peninsula of Michigan. These sites included the Lost Creek shrub wetland (Sulman and others 2009),

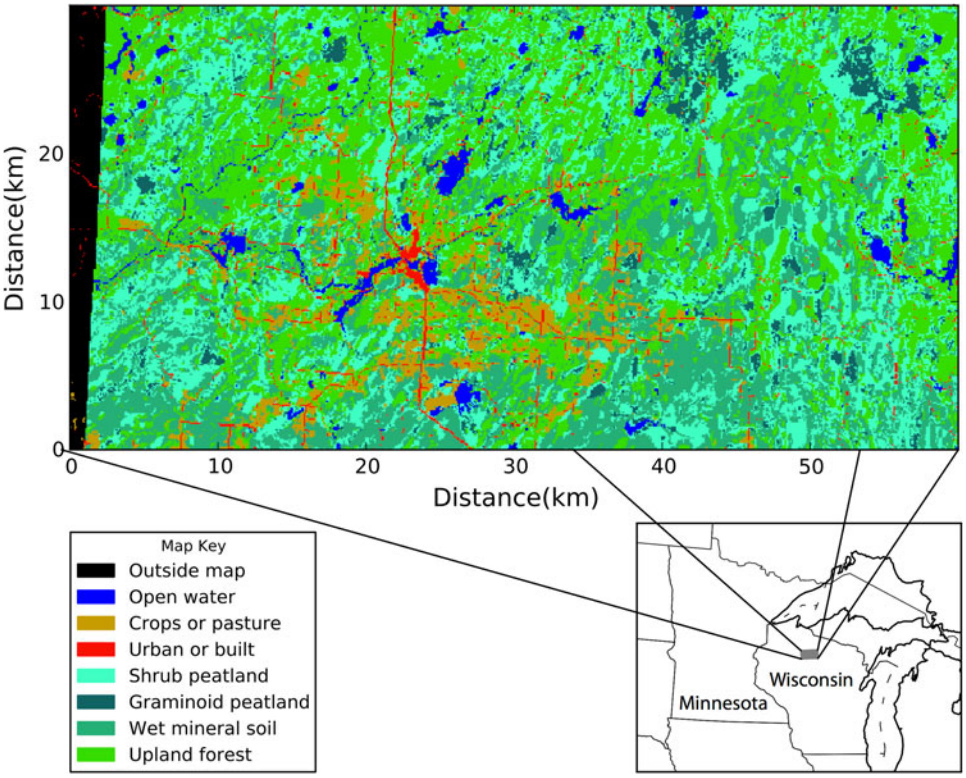

Figure 2. Ecoregion map used to drive simulations. The region was located in Price County in northern Wisconsin, USA. The *gray rectangle* in the regional map shows the location of the modeled area. The built-up area near the center is Philips, WI.

Willow Creek mature hardwood forest (Cook and others 2004), and Sylvania old-growth forest (Desai and others 2005). Soil pools for the deep peat scenario were based on inventories from areas in Wisconsin (Buffam and others 2010) and Minnesota (Weishampel and others 2009). The soil carbon pool size for wet forests was determined using estimates from Bridgham and others (2006). Soil pools for each ecoregion were further tuned from initial values to reach a steady state for initial soil carbon pools.

Simulation Scenarios

We conducted several model simulations to test the hypotheses listed above. Four water table decline scenarios were run: two magnitudes of water table decline (40 cm and 100 cm), and two time periods over which the decline occurred (10 and 40 years). A 40 cm decline was chosen based on an observed decline of that magnitude over 6 years at a peatland in the region (Sulman and others 2009), and a 100 cm decline was simulated to test a more severe scenario such as drainage for forestry. Each water table scenario was initiated after 50 years of model time to avoid transient effects related to the model's initial state. Four model runs were conducted for each scenario to separate soil and vegetation effects. ''Control'' simulations included no water table effects. ''Veg'' and ''soil'' simulations included only water table effects on plant communities or only water table effects on soil decomposition, respectively. The ''both'' simulation included both plant community and soil decomposition responses.

If there are substantial increases in carbon inputs to peatland soils, the age profile used to calculate $\overline{k}$ will no longer reflect the age profile of the soil, and the estimated soil decomposition rate will be too low. To correct for this, additional decomposition with a 50-year characteristic soil age was applied to simulated ''new'' soil carbon in ''Veg'' and ''Both'' scenarios. The size of the new soil carbon pool was determined by subtracting the control simulation soil carbon pool from that of the vegetation effect simulation. Because plant community changes were the same in deep and shallow peat scenarios, equal levels of additional decomposition were applied to both.

RESULTS

Modeled Baseline Carbon Fluxes

Modeled net primary production (NPP) and heterotrophic respiration varied significantly between ecosystem types (Figure 3). Fluxes in upland areas started with substantial carbon uptake, which

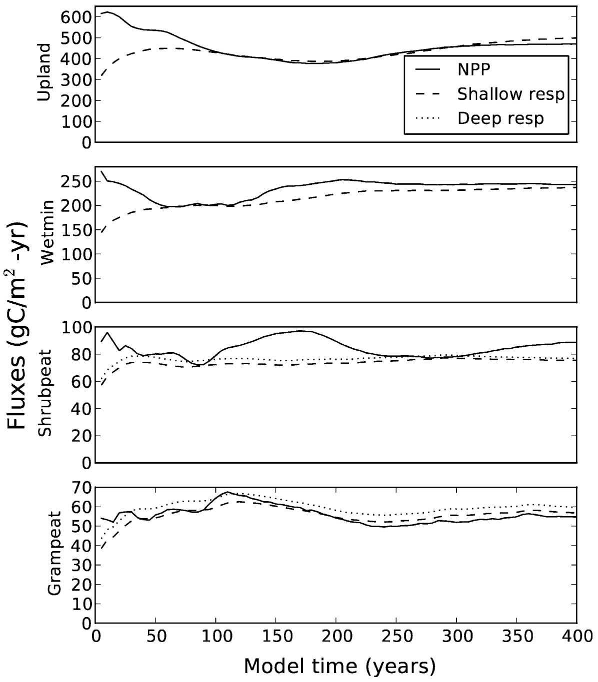

Figure 3. Modeled NPP and heterotrophic respiration for the four ecoregions. Control scenarios are shown. The ecosystem is gaining carbon when NPP is greater than respiration. Respiration in the deep peat scenarios was higher than in the shallow peat scenarios due to larger soil carbon pools.

declined over time until reaching approximate neutrality after 100 years of simulated time. Wet forests showed a similar pattern, but reached neutrality earlier and recovered from the decline in uptake and became a net carbon sink again at approximately 100 years. Shrub peatland areas were net carbon sinks for the duration of the simulation except for a short period. Graminoid peat areas were sinks of carbon in the shallow peat scenario, but the larger carbon pools and higher soil decomposition in the deep peat scenario led to net carbon loss over time. Overall, upland forest areas were the most productive and graminoid peatland areas were the least productive.

Effects of Water Table on Soil Decomposition and Plant Communities

Sensitivity of soil decomposition rate to water table (Figure 4, top panel) was highest in the upper soil layers due to the increase in age and resulting decrease in maximum decomposition rate at lower depths. The shallow peat simulations were insensitive to water table levels below approximately 1 m, because water tables below this level were below the bottom of the peat layer. Deep peat simulations continued to respond to water table at lower levels, leading to moderately higher decomposition rates at low water tables. However, the difference in total emissions between shallow and deep peat was minor due to the age of peat at low levels in the soil profile.

Upland and wet mineral soil decomposition rates were both higher and more sensitive to water table level because of lower soil age. However, simulated water tables in upland areas were always well below the soil depth, so upland soil decomposition did not vary between hydrological scenarios.

Modeled plant communities were also sensitive to water table level (Figure 4, middle panel). When water tables were close to the surface, a substantial fraction of landscape area was underwater and nonproductive, and the rest was dominated by sedge species. With deeper water tables, wet-tolerant woody species occupied more area, and dry upland communities became well established when water table was below approximately 1 m. The effect of hummock and hollow topography can be seen clearly in the pattern of sedge area, as sedges occupy hummock or hollow areas at 10 and 45 cm water table depths, respectively. Dashed lines show the initial water table positions for each wetland ecoregion. Upland ecoregions were assigned an initial water table of −2.0 m, placing them entirely in the upland species range.

Plant community responses to water table led to a pattern of increased biomass with lower water table (Figure 4, bottom panel). Model maximum biomass rose with lowering water table as more area became available to high-biomass shrubs and trees. Biomass measurements (shown in numbers on the plot and summarized in Table 3) were generally close to the model maximum biomass for wetlands, although the model maximum biomass was higher than measured biomass in forests.

Effects of Water Table Decline on Landscape Carbon Balance

Separating the water table effects on vegetation and soil carbon shows the importance of offsetting responses (Figure 5). Water table decline led to immediate and continued loss of soil carbon in ''Soil'' simulations, relative to control simulations. All wetland ecosystems experienced large increases in biomass relative to control for approximately 100 years following water table decline. The net effect on soil carbon and total carbon was an increase in carbon over the first 100 years after water table decline, followed by a loss of carbon over the next 250 years in peatland ecoregions, and

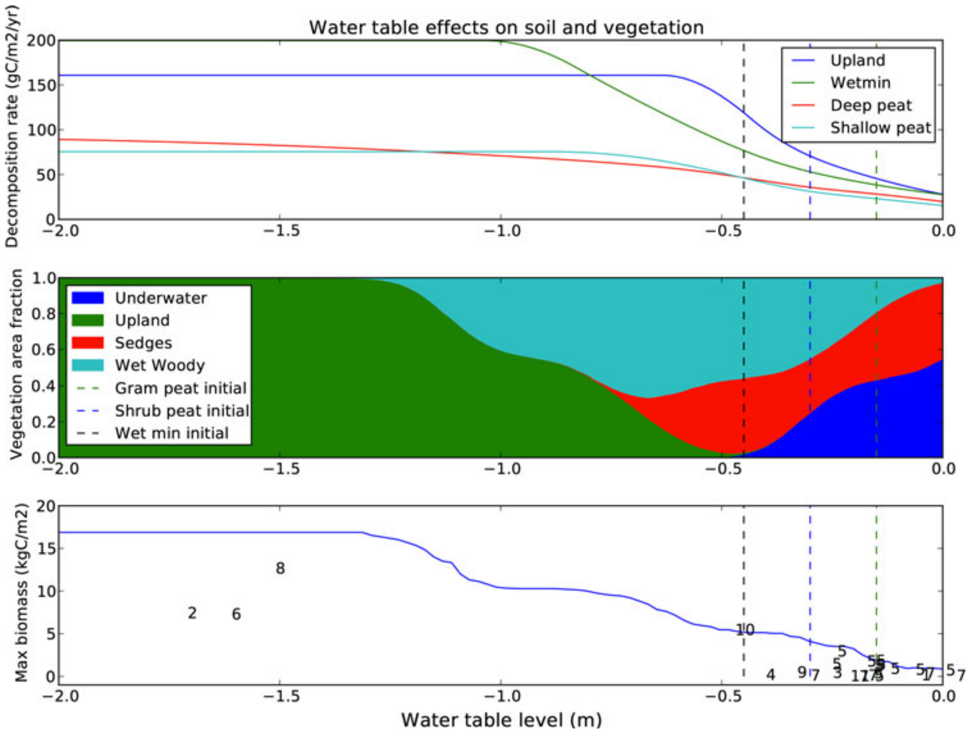

Figure 4. Effects of water table level on modeled soil decomposition, vegetation fractions, and maximum biomass. *Top panel* shows annual soil carbon decomposition for each ecoregion. Deep peat and shallow peat scenarios used different peat depths and carbon pools (see Table 2). Shrub and graminoid peat decomposition profiles were identical. *Middle panel* shows the area fraction occupied by each vegetation type as a function of water table. Species growth and biomass parameters were multiplied by this area fraction at each time step. *Dashed lines* show the initial water table positions for the three wetland ecosystems. *Bottom panel* shows model maximum biomass (*line*) and measured aboveground biomass (*numbers*) as a function of mean water table for a number of field sites. The numbers identify the data sources in Table 3. Forest sites without measured water table (numbers *2*, *6*, and *8*) were assigned water table values in the range of 1.5–1.7 m below the surface for ease of comparison, and the mean forested wetland biomass estimate (number *10*) was plotted with the same water table as the initial value for forested wetlands used in the model.

Table 3. Field Sites Shown in Figure 4

Number	Ecosystem type	Data source
1	Sedge fen	Sulman and others (2010)
2	Mature hardwood forest	Ameriflux biometric data
3	Shrub fen	Sulman and others (2009)
4	Bog	Moore and others (2002)
5	Set of drained, road-impacted, and undrained bogs and fens	Miller (2011)
6	Mature mixed northern forest	Gough and others (2008)
7	Set of northern fens and bogs	Humphreys and others (2006)
8	Old-growth hemlock-hardwood forest	Desai and others (2005)
9	Treed fen	Syed and others (2006)
10	Estimated mean biomass of forested wetlands in the United States	Bridgham and others (2006)
11	Bog	Sulman and others (2010)

relatively constant carbon relative to control for wet mineral ecoregions. The difference between soil-only and net effect scenarios shows the importance of including vegetation effects in the carbon balance. Simulations that only included water table effects on soil decomposition predicted a net loss of carbon over the entire simulation, whereas simulations including vegetation effects predicted initial net carbon gain resulting from water table decline. At the end of the 400-year

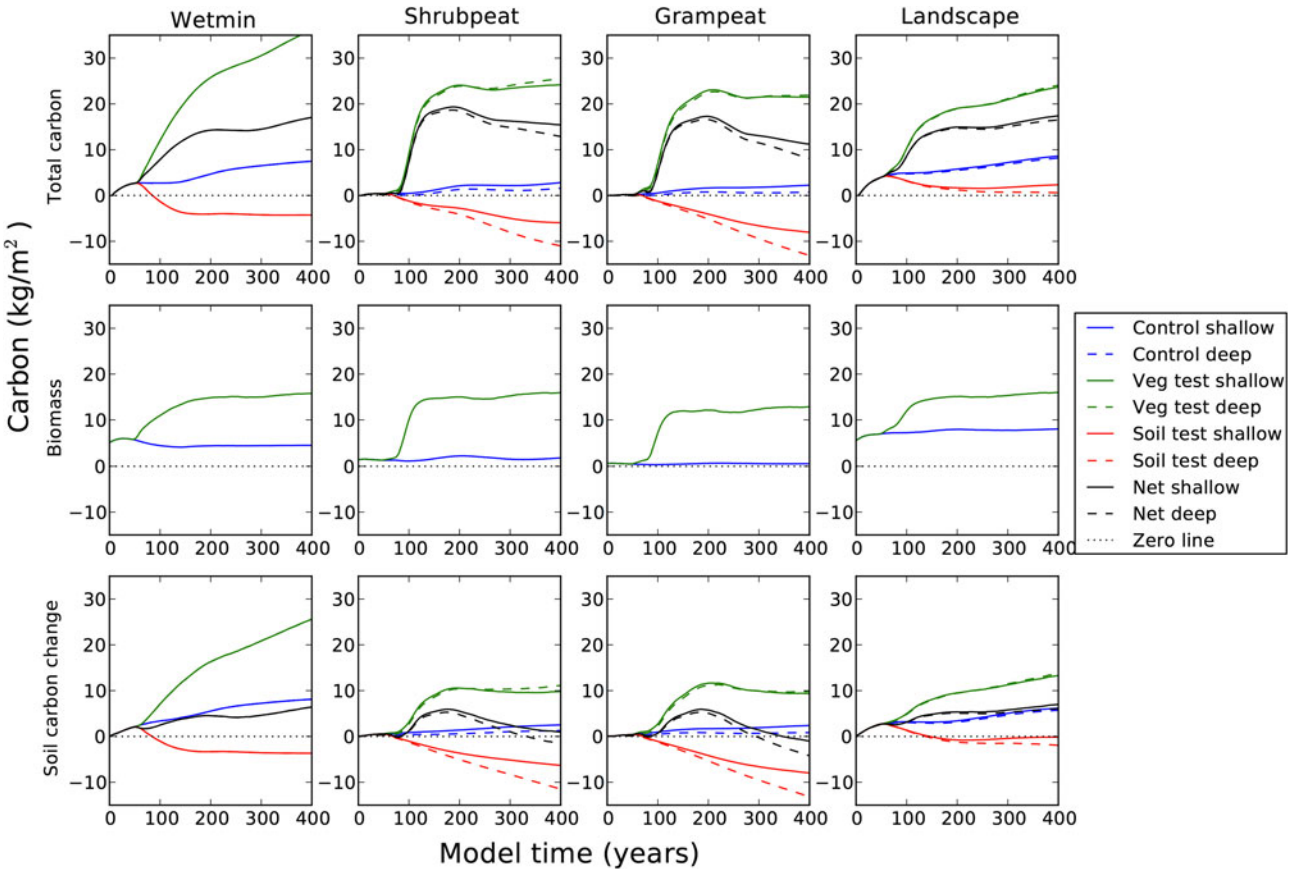

Figure 5. Effects of water table decline on ecosystem carbon balance for 100-cm water table decline over 40 years. Water table decline was initiated at the 50-year point. Control simulation (*blue*), separated effects of water table on vegetation (*green*) and soil (*red*), and the net effect (*black*) are shown. *Solid lines* show results from the shallow peat simulation and *dashed lines* show the deep peat scenario. *Columns* show results for the three included wetland ecosystem types (wet mineral soil forest, shrub peatland, and graminoid peatland), and the entire landscape, which also included upland regions. Results for the upland ecoregion are omitted because they did not vary between water table scenarios. *Rows* show total carbon, biomass, and soil carbon. Total carbon and soil carbon are plotted relative to their initial values.

simulation, ''Both'' simulations had somewhat more total carbon than ''Control'' simulations, whereas ''Soil'' simulations had substantially less. The larger deeper peat carbon pools in the deep peat scenarios led to increased carbon loss relative to shallow peat scenarios, but the temporal pattern of effects was similar. The total landscape simulations included upland areas, which were not sensitive to water table changes. However, the changes in carbon pools were still significant at the landscape scale.

All four scenarios of water table decline resulted in initial increases in aboveground biomass for the three wetland ecosystems (Figure 6). Biomass reached a maximum approximately 50–100 years following the water table decline, and remained relatively constant afterward. Declines of 100 cm led to much more biomass accumulation than declines of 40 cm. The time scale of decline (occurring over 10 or 40 years) caused differences in the initial rate of biomass accumulation, but there was little difference by about 50 years following water table decline.

Water table declines of 40 cm led to continuous net loss of soil carbon in the peatland ecosystems, but soil carbon in the wet mineral ecosystem showed little sensitivity to water table decline. Declines of 100 cm resulted in increases in soil carbon in peatlands over approximately 100 years following water table decline, because increased carbon inputs from vegetation growth outweighed losses from increased decomposition. However, after biomass accumulation leveled off after about 100 years, soil carbon began to decline, and by the end of the simulations soil carbon was at or below the control simulation. Additions of new carbon from increased plant growth were largely transient due to faster decomposition compared to old carbon in peat.

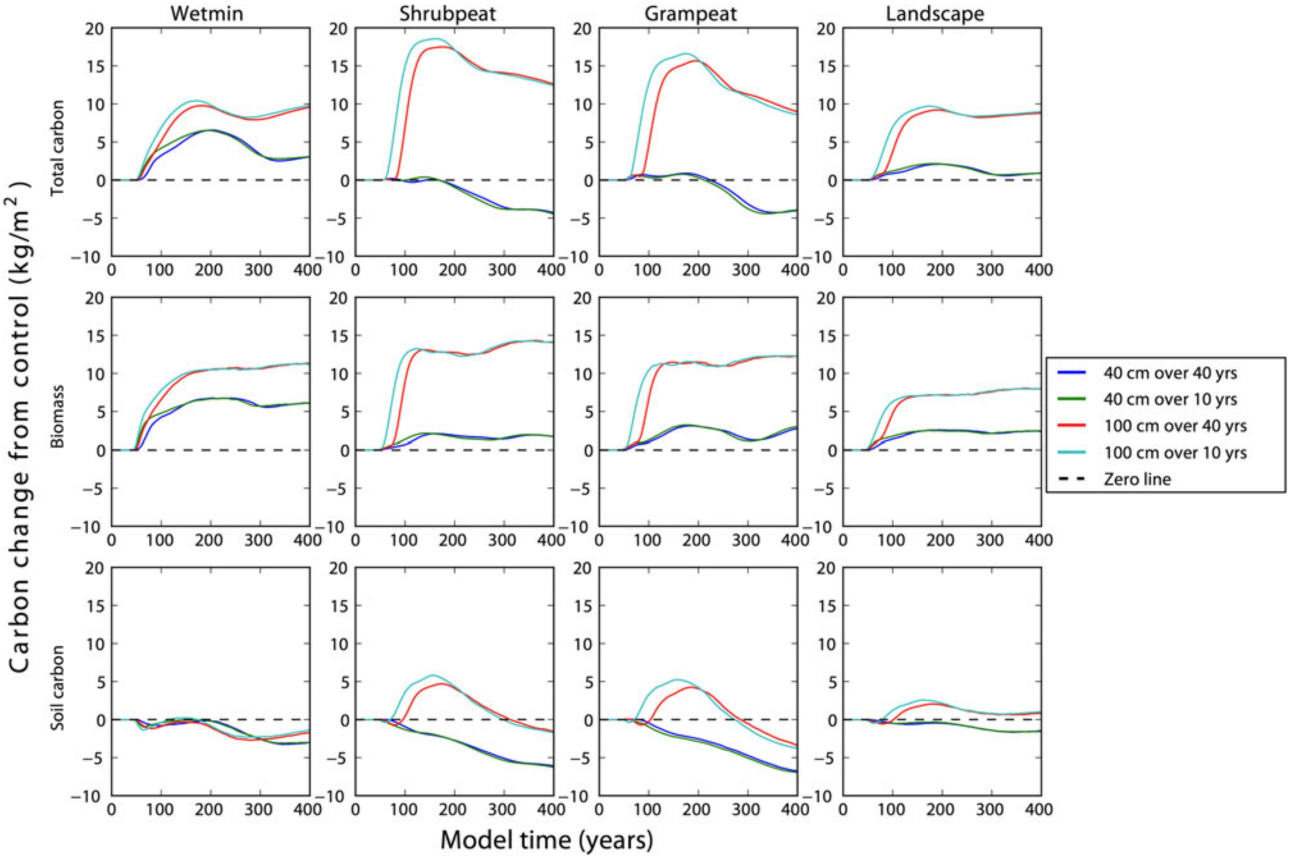

Figure 6. Effects of water table decline on ecosystem carbon balance. This plot shows results from the shallow peat scenarios. Each plot shows the difference between both scenario results and control run results. Water table decline was initiated at the 50-year point. *Columns* show results for the three wetland ecosystem types (wet mineral soil forest, shrub peatland, and graminoid peatland), and the entire landscape. *Rows* show total carbon, biomass, and soil carbon.

For 100 cm declines, the net effect of changes in biomass and soil carbon in peatland ecosystems was a substantial increase in total carbon for about 100 years after the water table decline, followed by a gradual loss of carbon over the remainder of the simulation. At the end of the simulations, all wetland ecosystems and the whole landscape retained additional carbon compared to control simulations, although peatland ecosystems were continuing to lose carbon. Declines of 40 cm led to net loss of peatland carbon, although the carbon balance was neutral for approximately 100 years after water table decline. Upland carbon cycles did not respond to decreases in water table because initial water tables were already too low to affect vegetation or soil.

The changes in carbon pools resulting from water table decline were still significant when averaged over the entire landscape, confirming our initial hypothesis. Total carbon increased at the landscape scale in all scenarios, and total carbon appeared to be stable at the end of the simulations, due to cancelation between continuing losses in peatlands and gains in mineral wetlands.

DISCUSSION

In 100-cm water table decline scenarios, simulated carbon pool responses over time periods of up to 150 years were dominated by increases in biomass confirming Hypothesis 1. However, for 40 cm declines, the magnitudes of biomass increase and soil carbon loss in peatlands were approximately equal over the first 150 years, resulting in no net carbon response to drying. There was little difference between scenarios in which water table declined over 10 or 40 years, contradicting Hypothesis 3. The initial net gain in soil carbon modeled in the 100-cm water table decline scenarios contradicted the implications of short-term studies that focused on soil effects and found substantial losses of carbon following soil drying, such as Moore and Knowles (1989), Freeman and others (1992), Silvola and others (1996), and Bubier and others (2003). However, the steady state of total carbon for the first 100 years following 40-cm water table decline was consistent with Sulman and others (2009) and Flanagan and Syed (2011), who observed no change in NEE over short time scales following drainage of that magnitude in peatlands. In simulations that included only soil effects, the model did predict substantial losses of carbon for both depths of water table decline, indicating that the major difference between our simulations and short-term, soil-focused studies was the inclusion of plant community changes. These results highlight the importance of plant community changes in the net carbon budget response of peatlands to hydrological change.

Increased plant growth resulting from declining water table has been observed in field studies over inter-annual time scales (Sulman and others 2009; Flanagan and Syed 2011), although Strack and others (2006) observed variations in the response between hummock, hollow, and lawn microforms. Wetland succession studies over decadal time scales have observed large increases in biomass as sedge, shrub, or moss-dominated wetland landscapes are converted to forest (Laine and others 1995; Laiho and others 2003). Minkkinen and Laine (1998) observed a net increase in wetland soil carbon after 60 years of drainage and afforestation. The results of our 100 cm decline simulations agreed well with these field studies, indicating that large declines in water table could cause a net increase in stored carbon in wetland-rich landscapes over time scales of about 100 years. This effect was significant at the landscape scale, confirming Hypothesis 4, but was partially driven by the non-peat wetland fraction of the landscape, indicating that mapping of peat reserves is important for quantifying landscape-scale carbon cycle responses to hydrological change. The trajectory of total peatland carbon at the end of our simulations suggests that over time scales of several centuries to millenia, peatland drainage could eventually result in net carbon loss, confirming Hypothesis 2. This would be consistent with the results of Ise and others (2008), who identified a large positive climate feedback from wetland drying, although their results did not include an initial increase in carbon following drainage. Because several decades were necessary for the net results to become clear in some scenarios, and because several centuries of simulation time were required to see the long-term trajectory, our results suggest that longer measurement periods are necessary to accurately represent wetland responses to hydrological change, and that short-term measurements should not be interpreted as predictive of the long-term carbon cycle response.

In peatlands, the magnitudes of changes in soil and total carbon over the course of the simulations were somewhat dependent on the method used to account for additions of new carbon to the soil profile, revealing a potential weakness of the model. However, because new carbon had an inherently faster turnover time than peat carbon, much of the additional soil carbon in ''Both'' simulations should decompose, and the total will eventually reach a steady state where soil carbon is equal to that of the ''Soil'' simulations plus the additional inputs from continuing plant growth. As soil carbon continues to decline while biomass remains constant, we expect that total carbon would eventually reach a steady state value lower than the initial value before drainage, representing a net loss of carbon. However, based on our simulations, it could take 400 years or more to reach this steady state depending on model boundary conditions.

The peatland decomposition model used in this study predicted an increase in CO_2 emissions from soil decomposition of approximately 100% resulting from a 40 cm decrease in water table level (Figure 4). Sensitivity of the overall soil decomposition rate to water table declined at lower levels due to the effect of increasing carbon age in deeper peat. The magnitude of the soil respiration increase is consistent with the dependence observed in soil columns by Moore and Knowles (1989) and Freeman and others (1992), and in field observations by Oechel and others (1998) and Silvola and others (1996). The decline in water table effect on soil respiration at lower water table levels is consistent with the observations of Silvola and others (1996), Sulman and others (2009), and Lafleur and others (2005). However, those studies observed a drop-off of water table dependence at 30 cm below the surface, closer to the surface than predicted by our model. Furthermore, severe drying could suppress soil respiration, an effect that was not included in our model. This suggests that our model may have overestimated the increase in soil respiration resulting from lowering of the water table.

There are several additional factors that need to be considered in assessing the applicability of these simulations, including the role of the nitrogen cycle, anthropogenic influences to succession, climate trends, and fire. Peatland type and nutrient levels likely determine whether biomass accumulation following drainage would be nitrogen limited. A comparison of wetland plant community responses to drainage by Laine and others (1995) found that forest development was much faster on nutrient-rich sites than on poorer sites, and that poorer sites gained less biomass overall. Vasander (1982) found little increase in biomass at all following drainage of an ombrotrophic bog, and Talbot and others (2010) identified a shift in shrub species and only moderate increase in biomass related to declining water table at a dry bog. These findings suggest that the results of our simulations may not be applicable to very nutrient-poor peatlands, although the time scale of our simulations was significantly longer than that of these studies. Unfortunately, we were unable to find spatial data distinguishing between rich and poor peatlands in our study region, so we could not estimate what fraction of peatlands in our study area would be constrained by these nutrient limitations. Our simulations also assume a conversion from peatland to forest following drainage. If drained peatlands were instead converted to cropland, pasture, or built areas, biomass accumulation would be much less, and the net change in landscape carbon would likely be negative rather than positive over century time scales.

The omission of mosses as a distinct species type was a potential weakness of this study. Mosses can represent a significant portion of biomass and productivity in poor fens and bogs, and the physical and chemical properties of moss biomass can lead to different peat properties compared to vascular plant litter (Dorrepaal and others 2005). In nutrient-poor peatlands where mosses effectively compete with vascular plants, ignoring mosses could lead to overestimates of productivity gains following drainage. Moss litter is more recalcitrant than vascular plant litter, which could cause overestimates of soil decomposition. However, we believe that several factors mitigated the impact of this omission on our results. First, the simulated plant community response to water table decline was dominated by tree growth. Because moss biomass is typically small compared to woody biomass, we do not believe that including moss productivity would have made a large difference in the total biomass response. Second, our approach to soil decomposition should address the change in litter quality connected with the transition from mosses to vascular plants. Simulated peat decomposition was based on the parameters of Frolking and others (2001), which were derived from measurements of moss-dominated peatlands. The effect of moss litter is therefore included in the modeled peat decomposition rate. The model used a faster decomposition rate for new soil carbon inputs than for existing peat, which should help to account for the greater recalcitrance of moss-derived litter compared to vascular plant detritus. Even with these corrections, our simulations may have missed changes in soil respiration and carbon balance due to changes in litter properties, and future simulations would benefit from including mosses as a distinct species and litter type. For poor fens and bogs, this means that our results would be more appropriately interpreted as a reasonable upper limit rather than a precise prediction of carbon pool responses to drying.

Changes in species composition and litter properties could also lead to hydrological feedbacks, such as increased evapotranspiration with increased woody plant growth or declines in soil height due to subsidence. Furthermore, differences in peat hydrological properties between bogs and fens and between moss and vascular plant litter could lead to different hydrological responses to climatic forcings. These effects were not included in the model. We chose to use prescribed scenarios of water table change rather than modeling hydrological responses to changes in precipitation and temperature to maintain the focus on direct links between carbon storage and hydrology. Although this makes the results more difficult to relate to climatic forcings, it does make them applicable to hydrological change caused by processes such as drainage for agriculture and road development in addition to climate-related declines in water table.

Our landscape simulations did not include any interaction between declining water tables and upland forest productivity. In actuality, declines in water table due to climatic change would likely be accompanied by drought stresses on tree growth, which could cause declines in forest productivity and reduce the carbon gains at the landscape scale. Alternatively, CO_2 fertilization and extension of the growing season could increase forest productivity (Pastor and Post 1988). Falge and others (2002) estimated that extending growing season length would increase NPP by 5–8 g m^{-2} day^{-1} for temperate forests. Our simulations predicted increases in landscape mean NPP of around 200 g m^{-2} y^{-1} following a water table decline of 100 cm, equivalent to a growing season increase of 26–40 days according to these estimates. Increases in growing season length could also increase autumn soil respiration, partially offsetting carbon gains from increased production (Piao and others 2008). Landscape-scale water table responses would therefore be important even in the context of more direct climate effects.

Our simulations did not include the effects of changes in temperature, which could increase soil decomposition rates and offset carbon gains (Updegraff and others 2001; Dorrepaal and others 2009). Christensen and others (2007) predicted an average surface warming of 4–6°C in boreal regions. For a Q_{10} of 2.0, this is equivalent to an increase in respiration of 30–50%. Using a Q_{10} of 2.9, as measured by Silvola and others (1996) for a peatland under high water table conditions, this is equivalent to an increase of 50–90%. These estimates place the effect of warming on soil decomposition in the same order of magnitude as the increase in respiration following a 40 cm decline in water table using our model.

Rather than declining, water tables could rise due to increased precipitation resulting from climate change (Meehl and others 2007) or due to wetland creation activities (Roulet, 2000). Within the framework of our model, rising water tables would result in decreased productivity as productive upland and shrub species occupy less area. This seems like a plausible outcome for wetland-rich regions, where precipitation is not a major limiting factor to forest growth. Increased flooding could kill less flood-tolerant species in upland areas, and drive succession toward lower biomass grassy species in wetlands. Although higher water tables can reduce soil decomposition rates and begin to drive long-term peat accumulation, biomass, and productivity loss would likely cause reduced carbon uptake or carbon loss over the short term. This is consistent with the results of Frolking and others (2006), who found that wetland creation did not have a net climate cooling impact until hundreds of years after flooding occurred.

The soil model used in this study predicted that carbon contained in deep peat was stable due to its age, and would decompose slowly even when the water table was substantially lowered. However, soil carbon losses resulting from fires could be much more rapid. Fire can be an important factor in the net carbon balance of northern peatlands (Kuhry 1994; Pitkänen and others 1999), and individual events can lead to large losses of soil carbon (Turetsky and others 2011). Greater fire incidence is a likely consequence of climatic warming and wetland drying, and could be a crucial factor in future peatland carbon accumulation and retention rates, especially in fire-prone boreal regions (Turetsky and others 2010; Grosse and others 2011).

This study did not distinguish between types of wetland soil carbon loss. In fact, how soil carbon loss is partitioned between CO_2, CH_4, and dissolved organic carbon (DOC) can have important implications for both carbon balance and climate impacts. DOC fluxes of carbon can be important components in wetland carbon budgets (Billett and others 2004; Roulet and others 2007; Buffam and others 2011). Anaerobic respiration will primarily produce CH_4 rather than CO_2 (Clymo 1984), and as a result decomposition in inundated peat soils is a major source of methane (Harriss and others 1985; Matthews and Fung 1987; Frolking and others 2006). The climate effects of increasing CO_2 emissions following wetland drainage could therefore be counteracted by decreases in methane emissions (Moore and Knowles 1989; Strack and others 2004).

CONCLUSIONS

This study introduced a novel method for modeling peatland succession and peat decomposition within a landscape succession model originally intended for forests. Peatlands have not been previously simulated using the LANDIS-II model, and plant community succession has not historically been a focus in peatland modeling studies. The strategies introduced here simplified or omitted some potentially important processes, but the results were plausible and consistent with previous field and modeling studies. We hope our strategy will inform future implementations of peatland biogeochemistry within landscape succession models to improve understanding of these important processes.

Despite the simplifications described above, it is clear that regional drying would have substantial impacts on the future of landscape carbon pools and the carbon cycle in boreal and subarctic regions that are rich in wetlands and peatlands, and that plant community responses are as important as changes in soil decomposition. Overall, our results suggest that declining water tables can lead to increases in total carbon over time scales of a few hundred years, but that the longer term effect is potential loss of carbon as biomass accumulation reaches a maximum while soil carbon loss continues. These long time scales proved more important than the time scale of the initial water table decline. The depth of drainage was the most important factor with 40 cm water table declines leading to net carbon loss in peatlands and 100 cm declines leading to net carbon gain. These results highlight the importance of hydrology in maintaining long-term carbon storage in peatlands. Plant community responses were integral to the net carbon cycle response, suggesting that both peat and plant community responses must be considered in any complete assessment of peatland carbon storage and its response to climate change. The magnitude of changes in peatland and landscape carbon pools would be of global significance if scaled by the estimated total boreal and subarctic wetland area of 2–4 × 10^{12} m^2 (Mitra and others 2005).

Our results should encourage caution when interpreting the results of short-term studies, because they could suggest very different conclusions depending on the time scale being considered. Over 5–10-year time scales, simulations indicated net loss or only a small increase in peatland total carbon. Time scales of 50–100 years indicated large increases in carbon following 100-cm water table decline and neutral carbon balance following 40 cm decline, whereas the results over longer time scales suggested eventual net losses of carbon. In terms of climate change mitigation, although there may be a short-term climate benefit to peatland drainage in the form of increased NPP, this comes at the expense of the long-term ecosystem service of carbon storage and retention that makes peatlands a unique and important component of the global carbon cycle.

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