A model of carbon evasion and sedimentation in temperate lakes

PAUL C. HANSON*, AMINA I. POLLARD*, DARREN L. BADE*, KATIE PREDIK†, STEPHEN R. CARPENTER* and JONATHAN A. FOLEY†
*Center for Limnology, University of Wisconsin–Madison, 680 N. Park St., Madison, WI 53706-1492, USA, †Department of Zoology, University of Wisconsin–Madison, 430 Lincoln Dr, Madison, WI 53706, USA, ‡Center for Sustainability and the Global Environment (SAGE), Gaylord Nelson Institute for Environmental Studies, University of Wisconsin–Madison, 1710 University Ave., Madison, WI 53726, USA

Abstract
Lakes process terrigenous carbon. The carbon load processed by lakes may partially offset estimates made for terrestrial net ecosystem exchange (NEE). The balance within lakes between carbon burial and evasion to the atmosphere determines whether lakes are net sinks or net sources of atmospheric carbon. Here we develop a model to study processing of both autochthonous and allochthonous carbon sources in lakes. We run the model over gradients of dissolved organic carbon (DOC) and total phosphorus (TP) concentrations found in the Northern Highlands Lake District of Wisconsin. In our model, lakes processed between 5 and 28 g C m⁻² C₀² yr⁻¹ (watershed) derived from the watershed, which approximates one-tenth of NEE for similar terrestrial systems without lakes. Most lakes were net heterotrophic and had carbon evasion in excess of carbon burial, making them net sources of carbon to the atmosphere. Only lakes low in DOC and moderate to high in TP were net autotrophic and net sinks of carbon from the atmosphere.

Key words: carbon, flux, lake, landscape, metabolism, model, sedimentation

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Introduction
North temperate lakes play an important role in processing organic carbon derived from the landscape as a whole. CO₂ supersaturation (Hope et al., 1996; Striegl et al., 2001; Sobek et al., 2003) and net efflux of CO₂ from lakes to the atmosphere (Cole et al., 1994; Riera et al., 1999) suggest that most lakes vent terrigenous carbon to the atmosphere. Lakes act both as conduits of inorganic carbon to the atmosphere (Riera et al., 1999; Hanson et al., 2003) and as mineralization sites for terrigenous organic carbon (Hessen, 1992; del Giorgio et al., 1999; Jansson et al., 2000). Although the export of dissolved organic carbon (DOC) from terrestrial systems has been well documented (Mulholland, 2003), the view of lakes as ‘hot spots’ for carbon processing is tempered by uncertainties in the magnitude of the carbon load to lakes, the relative contributions of organic and inorganic carbon forms to that load, and the influence of that load on key carbon cycling processes in lakes.

Understanding carbon cycling through lakes may reduce uncertainty in estimates of terrestrial net ecosystem exchange (NEE). For inverse modeling and biometric assessments, omission of processes such as carbon export through aquatic systems could result in biased estimates of carbon sequestration (Curtis et al., 2002; Houghton, 2003). These systematic problems require independent data sources to identify and correct sources of error (Wilson & Baldocchi, 2001). Indeed, a direct comparison of eddy-covariance and ecological inventory estimates of carbon exchange in a midlatitude forest produced discrepancies of about 20% (Ehman et al., 2002). In lake-rich landscapes, such as the Northern Highlands Lake District (NHLD) of Wisconsin, where lakes comprise 13% of the land surface (Peterson et al., 2003), a significant amount of terrestrial carbon may be processed by the lakes. A first-order estimate can be obtained by comparing carbon efflux from lakes (e.g. 1–150 g C m⁻² yr⁻¹) (Hanson, 2003) with NEE in forests (e.g. 70–350 g C m⁻² yr⁻¹) (Curtis et al.,...
2002). By changing net efflux from lakes to watershed areal units (i.e. lake area (LA) = 0.13 watershed area (WA) in the NHLD) and comparing the aforementioned ranges, lakes may mineralize and vent to the atmosphere from <1% to as much as 28% of the NEE from the landscapes in which they are embedded.

Understanding the role lakes play in processing landscape carbon requires quantifying the terrestrial loads as well as the in-lake processing of that carbon. DOC export via rivers and streams from terrestrial systems similar to those in northern Wisconsin range from about 1 to 10 g m\(^{-2}\) yr\(^{-1}\) (Aitkenhead & McDowell, 2000). Streams clearly are an important source of DOC for many drainage lakes. Yet more than half of the lakes in Northern Wisconsin are seepage lakes (Eilers et al., 1988), for which wetlands immediately surrounding the lake may be important DOC sources (Xenopoulos et al., 2003). Although determining the carbon transport informs us of an important component of the lake carbon budget, our appraisal of its fate in lakes requires additional knowledge of lake biological and physicochemical processes. For example, terrigenous DOC can elevate lake respiration (R) (Cole et al., 1994; Riera et al., 1999; Hanson et al., 2003) and suppress primary production (Jackson & Hecky, 1980; Jones, 1992; Carpenter et al., 1998). However, the combined effects of carbon loading on lake metabolism, sedimentation, atmospheric flux, and long-term change remain largely unexplored.

How do terrestrial and aquatic sources of organic carbon interact to determine fates of organic carbon in a lake? The conceptual model needed to address this question is relatively simple. Figure 1 depicts an idealized lake situated in a forested landscape. Black arrows represent fluxes between systems, and the numbered labels adjacent to the arrows indicate the carbon forms. Following are descriptions of the numbered fluxes. (1) Positive net primary production (NPP) in terrestrial systems results in biomass accumulation. (2) Some of that biomass is mineralized and exported as dissolved inorganic carbon (DIC) in groundwater and surface water. (3) Additional biomass is leached through surface water as DOC or translocated as particulate organic carbon (POC). Carbon in the lake cycles through organic and inorganic forms (gray arrow). Primary producers fix DIC to POC and exude DOC in the process. The breakdown of POC produces DIC and DOC. Microbial respiration and photodegradation mineralize DOC to DIC. (4) A portion of the lake POC settles to the sediments. (5) POC in the sediments slowly mineralizes and releases DIC to the water column. (6) The CO\(_2\) partial pressure gradient between the lake and the atmosphere drives net atmospheric flux (NAF) of DIC. (7) All forms of carbon are exported from the lake through surface flow. Although this system is rarely analyzed in an integrated way, many of the fluxes and transformations have been quantified (see Materials and methods for literature values).

In this study, we develop a process-based model of a simple landscape with an idealized north temperate lake that has gross biogeochemical characteristics of lakes found in the Upper Midwest of the USA. This

![Fig. 1 A simplified diagram of carbon cycling through a landscape with one lake.](https://example.com/fig1.png)
model accounts for internal lake carbon cycling, as well as carbon fluxes with terrestrial and atmosphere systems. We consider broad ranges in carbon loading and internal production in lakes, and explore model sensitivity to parameters. We identify areas of future research with implications for land use, spatial and temporal variability in carbon loading, and food web structures. Ultimately, we seek to understand the roles lakes play in processing terrestrial carbon and the implications for carbon flux to the atmosphere.

We use the model to address ecosystem questions that would be expensive to address by direct measurements in thousands of lakes on a landscape. What is the fate of terrigenous carbon in lakes? How does exogenous carbon loading alter key carbon cycling processes in lakes? At what carbon loads do lakes become net sources of carbon to the atmosphere? And how are these phenomena likely to be affected by other ecosystem drivers not explicitly included in the model, such as food webs?

Materials and methods

The biogeochemical characteristics of the modeled lake were consistent with lakes in the NHLD of northern Wisconsin. The watershed area ($a$) was 250 $\times$ 10$^3$ m$^2$, and the LA to WA ratio ($\text{lw} = 0.13$) was set to the open water ratio for the NHLD (Peterson et al., 2003). WA was used to scale areal rates of carbon loading and the water budget to the landscape. We did not explicitly account for land use or land cover, and we assumed that these lakes were located in carbonate-poor soils, based on the generally low carbonate alkalinity for lakes in this region (Eilers et al., 1988). We included sufficient detail in the water budget for estimating carbon loading and lake turnover rate. Our goal in this paper was a steady-state model driven by annual carbon loads, the data most commonly reported in the literature. Thus, annual loads were prorated to daily values. Lake total phosphorus (TP) concentrations were fixed at the beginning of any given model run. Because we consider the lake to be a homogeneous mixed reactor, we did not vary lake morphometry nor did we separate littoral and pelagic habitats. For simplicity, we assumed a cylindrical lake with mean depth ($z$) of 10 m in a circular watershed.

The model computes mass balances of carbon species at dynamic steady state (Fig. 2). We group carbon into three pools, DIC, DOC, and POC, resulting in the differential equations listed in Table 1. These were solved by an adaptive-step-size Runge–Kutta algorithm in modeling software (Matlab, v. 6.0, Mathsoft, Inc. 2000). The time-step is daily and all parameters and variables are described as daily values. All changes due to seasonality, such as water temperature, light, stratification and ice cover occur at discrete times. The model reaches annual dynamic equilibrium in less than 20 years, after which time we track pools and fluxes for 1 year. The model was run for 60 lakes that represented discrete points in TP and DOC gradients, as shown in Fig. 3 and as described below. Many parameters for this model were borrowed from the carbon cycling literature, in which it is important to distinguish between LA and WA (Table 2).

The number of days the lake was not covered in ice ($c = 224$ days) or was stratified ($h = 120$ days) was set to values typical of lakes in northern Wisconsin (NTL-LTER data set, http://lter.limnology.wisc.edu). We fixed water temperature at 4°C during the winter, and 12°C during spring and autumn. During summer stratification, we set the epilimnion to 20°C and the hypolimnion to 12°C. The sediment temperature was set to the same value as the water immediately above it. Complete stratification occurred on the first day of the stratified period, and the thermocline depth ($Z_l$) was set as a function of DOC concentration (Snucins & Gunn, 2000). Each stratum was assumed to be well mixed.

A water budget was created within the model to assess whether terrestrial loading rates gave reasonable values for ground- and surface-water carbon concentrations. The water input was modeled as precipitation ($p$) on the watershed and lake. Excess water, precipitation ($p$) – evapotranspiration ($v$), from the watershed was partitioned into groundwater (25%) and surface water (75%). Water was lost from the lake via
Table 1  Model differential equations and intermediate equations describing parameter implementation

<table>
<thead>
<tr>
<th>Differential equations</th>
<th>No.</th>
</tr>
</thead>
<tbody>
<tr>
<td>( \frac{d\text{DOC}}{dt} = \text{DOC}<em>{\text{Gin}} + \text{DOC}</em>{\text{Qin}} + \text{DOC}<em>{\text{Pin}} + \text{GPP}</em>{\text{exudate}} - R_{\text{DOCE}} - \text{DOC}_{\text{Qout}} )</td>
<td>(1)</td>
</tr>
<tr>
<td>( \frac{d\text{DOCH}}{dt} = \text{DOC}<em>{\text{Gin}} + \text{DOC}</em>{\text{Qin}} - R_{\text{DOCH}} - \text{DOC}_{\text{Qout}} )</td>
<td>(2)</td>
</tr>
<tr>
<td>( \frac{d\text{DIC}}{dt} = \text{DIC}<em>{\text{Gin}} + \text{DIC}</em>{\text{Qin}} + \text{DIC}<em>{\text{Pin}} + R</em>{\text{A}} + R_{\text{DOCE}} + R_{\text{POCE}} + R_{\text{S}} - \text{GPP} - \text{DIC}<em>{\text{Qout}} - \text{DIC}</em>{\text{V}} - \text{Flux}_{\text{atm}} )</td>
<td>(3)</td>
</tr>
<tr>
<td>( \frac{d\text{POC}}{dt} = \text{POC}<em>{\text{Gin}} + \text{POC}</em>{\text{Qin}} + \text{POC}<em>{\text{Pin}} + R</em>{\text{DOCE}} + R_{\text{POCE}} + R_{\text{S}} - \text{POC}_{\text{Qout}} )</td>
<td>(4)</td>
</tr>
<tr>
<td>( \frac{d\text{Sed}}{dt} = \text{Sed}<em>{\text{LE}} + \text{Sed}</em>{\text{LH}} - \text{Death}<em>{\text{LE}} - \text{Death}</em>{\text{LH}} - \text{POC}_{\text{Qout}} )</td>
<td>(5)</td>
</tr>
<tr>
<td>( \frac{d\text{DE}}{dt} = \text{POC}<em>{\text{DE}} + \text{POC}</em>{\text{DEH}} - \text{POC}_{\text{Qout}} )</td>
<td>(6)</td>
</tr>
<tr>
<td>( \frac{d\text{DHE}}{dt} = \text{POC}<em>{\text{DEH}} + \text{POC}</em>{\text{DEH}} - \text{POC}_{\text{Qout}} )</td>
<td>(7)</td>
</tr>
<tr>
<td>( \frac{d\text{DEH}}{dt} = \text{POC}<em>{\text{DEH}} + \text{POC}</em>{\text{DEH}} - \text{POC}_{\text{Qout}} )</td>
<td>(8)</td>
</tr>
<tr>
<td>( \frac{d\text{H}}{dt} = \text{Sed}<em>{\text{H}} + \text{Sed}</em>{\text{LH}} - R_{\text{S}} )</td>
<td>(9)</td>
</tr>
</tbody>
</table>

### Intermediate equations

- \( R_{\text{A}} = \text{GPP} \times \text{ra} \)
- \( \text{GPP}_{\text{exudate}} = \text{GPP} \times \text{e} \)
- \( R_{\text{DOCE}} = \text{DOC}_{\text{E}} \times \text{g} \)
- \( R_{\text{DOCH}} = \text{DOC}_{\text{H}} \times \text{h} \)
- \( R_{\text{POCE}} = \text{POC}_{\text{DE}} \times \text{f} \)
- \( R_{\text{POCH}} = \text{POC}_{\text{DEH}} \times \text{h} \)
- \( R_{\text{S}} = \text{CS} \times \text{sf} \)
- \( \text{Sed}_{\text{LE}} = \text{POC}_{\text{LE}} \times 0.0188 \times (d/2)^{2}/z \)
- \( \text{Sed}_{\text{LH}} = \text{POC}_{\text{LH}} \times 0.0188 \times (d/2)^{2}/z \)
- \( \text{Sed}_{\text{DE}} = \text{POC}_{\text{DE}} \times 0.0188 \times (d/2)^{2}/z \)
- \( \text{Sed}_{\text{DEH}} = \text{POC}_{\text{DEH}} \times 0.0188 \times (d/2)^{2}/z \)
- \( \text{Death}_{\text{LE}} = \text{POC}_{\text{LE}} \times \text{ed} \)
- \( \text{Death}_{\text{LH}} = \text{POC}_{\text{LH}} \times \text{hd} \)

Subscript definitions are: G, groundwater; Q, surface water; P, precipitation; V, evaporation; E, epilimnion; H, hypolimnion; S, sediments; D, dead; and L, living.

Evaporation, and outflow was calculated as inflow – evaporation, which assumed a steady-state lake volume. For carbon loading from surface and groundwater, we assumed that during stratification, both surface and groundwater carbon was distributed between the hypolimnion and epilimnion according to the ratio of the particular stratum volume to whole-lake volume.

The areal rate of DOC loading from the terrestrial system (\( \text{DOC}_{\text{Q}} \)) was varied from 2 to 20 g C m\(^{-2}\) WA yr\(^{-1}\) to represent export ranges from a variety of land covers (Mulholland, 2003). Lake TP concentration was varied from 5 to 100 \( \mu \)g L\(^{-1}\) to represent a broad range of productivity (Hanson et al., 2003). DIC load from the terrestrial system through groundwater (\( \text{DIC}_{\text{C}} \)) was set to 3 g C m\(^{-2}\) WA yr\(^{-1}\) or 0.3 \( \text{DOC}_{\text{Q}} \) whichever was larger. The minimum value ensured that groundwater DIC concentrations were consistent with concentrations typical of the region (NTL-LTER data), and the higher values followed a relationship described by Dillon & Molot (1997). DOC and POC in groundwater were considered negligible, and DIC in fluvial input was set to 10 times atmospheric equilibrium (P. C. Hanson, unpublished data). Carbon outflow was the product of the daily epilimnetic concentrations of the carbon pools and the daily volumetric outflow of water. The parameter space for in-lake DOC and TP concentrations included combinations normally found in northern Wisconsin (Hanson et al., 2003) (Fig. 3). We did not represent the relative frequency of occurrences of the combinations, but included six lakes for every 2 g C m\(^{-2}\) WA yr\(^{-1}\) increment in \( \text{DOC}_{\text{Q}} \). Acid-neutralizing capacity (ANC) was set for each lake according to measured values from the data set used for DOC and
However, DIC does not pass between the hypolimnion and epilimnion, stratification. During stratification, strata, which include epilimnion and sediments for the total carbon load (watershed area (WA) units) and total phosphorus (TP) concentration lake space used for simulations in this model. For each C load, six lakes spanning a TP gradient were simulated.

TP distributions. In general, ANC was directly related to TP and inversely related to DOC. To fill the complete DOC and TP space used in this model, ANC data were linearly interpolated between measured values. Maximum ANC (1000 μEq L⁻¹) was in the low DOC, high TP lake, and minimum ANC (11 μEq L⁻¹) was in the low TP, high DOC lake. pH and carbonate speciation (Stumm & Morgan, 1981) were calculated daily as a function of the dynamic DIC concentration and the fixed ANC.

Carbon is modeled within the lake in three pools – DOC, DIC and POC. Pools are separated according to strata, which include epilimnion and sediments for the entire year, plus the hypolimnion during summer stratification. During stratification, DIC and DOC do not pass between the hypolimnion and epilimnion, however, DIC fluxes to the atmosphere (Flux atm) as a function of the concentration gradient and an assumed diffusion coefficient (k) (Cole et al., 2002). POC settles from the epilimnion, through the hypolimnion and into the sediments. DIC in the sediments is released to the stratum immediately above. Carbon is either converted between pools via gross primary production (GPP) and R, or is lost from the active carbon pool in the lake due to sedimentation, NAF to the atmosphere, or export in lake outflow.

Primary production is assumed to occur only in the epilimnion. GPP in mmol m⁻³ day⁻¹ is calculated from an empirical relationship with TP, according to data from Hanson et al. (2003) as:

\[ \ln GPP = 0.883 \ln TP, \]

where \( \ln TP \) is the natural log of the TP concentration in μg L⁻¹. Total grams of production is the product of \( e^{\ln GPP} \) in mass units and the epilimnion volume. GPP is returned to the DIC pool, exuded as DOC, or accumulated as POC, as follows. About 80% is quickly returned to DIC through autotrophic respiration, planktivory and mineralization of highly labile autotrophic products (ra). Rapid POC turnover (Cole et al., 2002) suggests that 85–90% of GPP may be respired in short order. Quay et al. (1986) suggest a lower range of 54–88%. A value of 0.80 day⁻¹ appears to be reasonable for ra, but we explore uncertainty in this parameter through sensitivity analysis. Three percent of GPP is exuded as refractory DOC (a). Literature-based estimates of extracellular release of DOC are around 10% of phytoplankton production (Baines & Pace, 1991). We assume that about one-third of this DOC is refractory, based on similar estimates from marine phytoplankton experiments (Biddanda & Benner, 1997). The impact of this assumption on the model is explored through sensitivity analysis of the a parameter. The remainder of GPP enters the POC pool. The rate (ed = 0.03 day⁻¹) at which living POC (POCₐ) in the epilimnion converts to dead POC (POCₒₐ) was taken from Connolly & Coffin (1995). Conversion of POCₐ to POCₒₐ in the hypolimnion (hd) was assumed to be rapid, and all POC entering sediments was assumed to be dead. POCₐ and POCₒₐ sedimentation rate is calculated after Carpenter (1992), who used a modified Stoke’s equation to model settling as a function of particle size (d). Particle size was estimated for combined pools of pico- and microplankton (Wetzel, 2001). Permanent burial in the sediments is a function of the sediment decay rate constant (sf) acting on accumulated sediments.

Whole-lake respiration is the sum of three first-order decay processes that occur independently of each other on a daily time-step. These rate constants represent fast, moderate and slow mineralization. The fast rate is conversion of GPP to DIC, which is ra as described above. The moderate rate is the mineralization of POC to DIC (sf for the epilimnion, hf for the hypolimnion, and sf for the sediments), which represents processes such as consumption and subsequent respiration of particles by higher orders in the food chain and mineralization of labile particulate substrates by
Table 2  Parameter values, state variables, drivers and their associated units as used in the model

<table>
<thead>
<tr>
<th>Symbol</th>
<th>Name</th>
<th>Units</th>
<th>Value</th>
<th>Source</th>
</tr>
</thead>
<tbody>
<tr>
<td>c</td>
<td>Ice-free days</td>
<td>day</td>
<td>224</td>
<td>NTL-LTER</td>
</tr>
<tr>
<td>h</td>
<td>Stratified days</td>
<td>day</td>
<td>120</td>
<td>NTL-LTER</td>
</tr>
<tr>
<td>w</td>
<td>Watershed area</td>
<td>m²</td>
<td>$250 \times 10^4$ *</td>
<td></td>
</tr>
<tr>
<td>lw</td>
<td>Lake area to watershed area ratio</td>
<td></td>
<td>0.13</td>
<td>Peterson et al. (2003)</td>
</tr>
<tr>
<td>z</td>
<td>Mean depth</td>
<td>m</td>
<td>10</td>
<td>*</td>
</tr>
<tr>
<td>v</td>
<td>Evapotranspiration</td>
<td>m·day⁻¹</td>
<td>0.556/365</td>
<td>Webster et al. (2000)</td>
</tr>
<tr>
<td>p</td>
<td>Precipitation</td>
<td>m·day⁻¹</td>
<td>0.831/365</td>
<td>Webster et al. (2000)</td>
</tr>
<tr>
<td>k</td>
<td>NAF piston velocity</td>
<td>m·day⁻¹</td>
<td>0.5</td>
<td>Cole et al. (2002)</td>
</tr>
<tr>
<td>d</td>
<td>Diameter of particles</td>
<td>μm</td>
<td>5.0</td>
<td>Wetzel (2001)</td>
</tr>
<tr>
<td>t</td>
<td>Base temperature</td>
<td>°C</td>
<td>20</td>
<td>*</td>
</tr>
<tr>
<td>a</td>
<td>GPP that becomes exudate</td>
<td></td>
<td>0.03</td>
<td>Biddanda &amp; Benner (1997)</td>
</tr>
<tr>
<td>ra</td>
<td>GPP that is respired</td>
<td></td>
<td>0.80</td>
<td>Quay et al. (1996); Cole et al. (2002)</td>
</tr>
<tr>
<td>ed</td>
<td>Death of algae rate constant (epi)</td>
<td>day⁻¹</td>
<td>0.03</td>
<td>Connolly &amp; Coffin (1995)</td>
</tr>
<tr>
<td>ef</td>
<td>Conversion of POC to DIC (epi)</td>
<td>day⁻¹</td>
<td>0.05</td>
<td>*</td>
</tr>
<tr>
<td>eg</td>
<td>Conversion of DOC to DIC (epi)</td>
<td>day⁻¹</td>
<td>0.005</td>
<td>Houser (2001)</td>
</tr>
<tr>
<td>ld</td>
<td>Death of algae (hypo)</td>
<td>day⁻¹</td>
<td>0.90</td>
<td>*</td>
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<tr>
<td>hf</td>
<td>Conversion of POC to DIC (hypo)</td>
<td>day⁻¹</td>
<td>0.05</td>
<td>*</td>
</tr>
<tr>
<td>hg</td>
<td>Conversion of DOC to DIC (hypo)</td>
<td>day⁻¹</td>
<td>0.005</td>
<td>*</td>
</tr>
<tr>
<td>sf</td>
<td>Conversion of POC to DOC in sediments</td>
<td>day⁻¹</td>
<td>0.005</td>
<td>*</td>
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Lake state variables

<table>
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<th>Symbol</th>
<th>Name</th>
<th>Units</th>
<th>Value</th>
<th>Source</th>
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<tr>
<td>Zt</td>
<td>Thermocline depth</td>
<td>m</td>
<td></td>
<td>Snucins &amp; Gunn (2000)</td>
</tr>
<tr>
<td>DIC</td>
<td>Dissolved inorganic carbon</td>
<td>g·C·m⁻²·LA</td>
<td>Output</td>
<td></td>
</tr>
<tr>
<td>DOC</td>
<td>Dissolved organic carbon</td>
<td>g·C·m⁻²·LA</td>
<td>Output</td>
<td></td>
</tr>
<tr>
<td>POC_D</td>
<td>Dead POC</td>
<td>g·C·m⁻²·LA</td>
<td>Output</td>
<td></td>
</tr>
<tr>
<td>POC_L</td>
<td>Living POC</td>
<td>g·C·m⁻²·LA</td>
<td>Output</td>
<td></td>
</tr>
<tr>
<td>NAF</td>
<td>Net atmospheric flux</td>
<td>g·C·m⁻²·LA</td>
<td>Output</td>
<td></td>
</tr>
<tr>
<td>S</td>
<td>Sediments</td>
<td>g·C·m⁻²·LA</td>
<td>Output</td>
<td></td>
</tr>
<tr>
<td>GPP</td>
<td>Gross primary production</td>
<td>g·C·m⁻²·LA·day⁻¹</td>
<td>Hanson et al. (2003)</td>
<td></td>
</tr>
<tr>
<td>R</td>
<td>Respiration</td>
<td>g·C·m⁻²·LA·day⁻¹</td>
<td>Output</td>
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Drivers

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<tbody>
<tr>
<td>TP</td>
<td>Total phosphorus</td>
<td>μg·L⁻¹</td>
<td>5–100</td>
<td>Input</td>
</tr>
<tr>
<td>DOC_Q</td>
<td>DOC loading from surface water</td>
<td>g·C·m⁻²·W·yr⁻¹</td>
<td>2–16</td>
<td>Input</td>
</tr>
<tr>
<td>DIC_G</td>
<td>DIC loading from groundwater</td>
<td>g·C·m⁻²·W·yr⁻¹</td>
<td>0.3·DOC_Q</td>
<td>Input</td>
</tr>
<tr>
<td>ANC</td>
<td>Acid-neutralizing capacity</td>
<td>μEq·L⁻¹</td>
<td>1–1000</td>
<td>Input</td>
</tr>
</tbody>
</table>

The ‘Source’ column are parameter value references. Annual rates were converted to daily rates in the model by dividing by 365. Source fields that have asterisks are either inferred or derived from other sources, and are explained in the methods.

NAF, net atmospheric flux; POC, particulate organic carbon; DIC, dissolved inorganic carbon; WA, watershed area; LA, lake area.

Microbes. Connolly & Coffin (1995) model POC mineralization, in part, as relatively rapid conversion (0.1–0.3 day⁻¹) of POC to labile DOC, which is then mineralized by bacteria. We chose to combine those two steps in our POC to DIC rate constants for the epilimnion and hypolimnion (ef = hf = 0.05 day⁻¹), because we assume that DOC in our model is relatively refractory. Cole et al. (2002) found POC turnover rates to be an order of magnitude faster than DOC turnover rates, further supporting our assumption. In this model, we assume that particles reaching the sediments are relatively refractory; thus, sf is an order of magnitude smaller than ef and hf. The third and slowest rate constants are for the epilimnetic (eg) and hypolimnetic (hg) mineralization of recalcitrant DOC originating from loading and from primary production. In a study of north temperate lakes, Houser (2001) found the mean rate constant for DOC decay to be about 0.005 day⁻¹. Each respiration value, except ra, is adjusted for temperature using a form of the Arrhenius equation:

$$R_t = R_0 \times e^{Q_{10} \times (\text{current temperature} - t)/10},$$  \hspace{1cm} (2)$$

where t is the base temperature, $R_0$ is respiration unadjusted for temperature, $Q_{10}$ is the temperature coefficient (assumed to be 2), and $R_t$ is the temperature-adjusted respiration.
Model calibration and sensitivity analysis

The model was calibrated to three relatively conservative lake indices – concentrations of DIC, DOC and POC. We calibrated the model to summer conditions reported in Hanson et al. (2003) for epilimnetic DIC and DOC concentrations. We calibrated hypolimnetic values, as well as autumn, winter and spring conditions for the above variables to data from the NTL-LTER data set. Water budgets were adjusted so that a given lake’s mean residence time in years equaled its average mean depth in meters (Michaels, 1995).

We expected our dynamic carbon pools to fall within measured ranges for the region (Table 3). Although there is more uncertainty in measured values of GPP and R than of carbon pools, we expected our model to approximate literature values for GPP and R as well. We expected our values for sedimentation and NAF to fall within the range found in the literature. Most importantly, we compared NAF with the accumulation of carbon in the sediment pool (S) in our model to determine the extent to which terrigenous carbon is buried in the sediments or fluxed to the atmosphere.

Sensitivity analysis was performed on the model by assessing the magnitude of change in state variables in response to changes in parameter values. The default simulation against which all others were compared had parameter values set according to Table 2, and driver variables set as follows: \( TP = 15 \mu g L^{-1} \), \( DOCQ = 4 g m^{-2} yr^{-1} \), and \( ANC = 200 \mu Eq L^{-1} \). These \( TP \) and \( ANC \) values, as well as the resulting lake DOC concentration, typify low to moderately productive lakes for the region, and produce NAF and S of the same magnitude in this model. To test model sensitivity, we increased the value by 10% for a given parameter while keeping the remaining parameters at their default values, and recorded the change in NAF and S. We repeated this procedure for each parameter, thus running 19 simulations. The model was considered sensitive to a parameter if the change in NAF or S exceeded 10% of the value in the default simulation.

Results

We varied total carbon loads from about 4 to 26 g C m\(^{-2}\) W A yr\(^{-1}\), which resulted in mean lake DOC concentrations ranging from about 2 to 20 mg L\(^{-1}\). Lakes with low DOC concentrations had received the lowest ratio of organic carbon to inorganic carbon in the loads (OC:IC). Over the first four loads, OC:IC increased from 0.75 to 2.85 and stabilized at about 3.17 thereafter. This model behavior resulted from our algorithm for DIC load as a function of DOC load, coupled with the high DIC concentration in surface waters.

The model showed expected annual carbon cycling dynamics with respect to DIC, DOC and POC concentrations across a range of DOC loads and TP concentrations. Annual dynamics for an oligotrophic lake are depicted in Fig. 4. During the stratified season, there was a slight drawdown of epilimnetic DOC (~1 mg L\(^{-1}\)), and a slight increase in hypolimnetic DOC (~0.1 mg L\(^{-1}\)). From autumn through spring, there was an increase in DOC, due to temperature-suppressed ecosystem respiration (R). Epilimnetic DIC remained relatively low during the stratified season (~1.5 mg L\(^{-1}\)), whereas hypolimnetic DIC increased slightly to ~3 mg L\(^{-1}\). During spring and autumn, DIC fell in response to the concurrent processes of primary production and temperature suppressed respiration. POC remained low (~0.3 mg L\(^{-1}\)) year round, but with moderate net increases during the spring and fall. Although most lakes followed expected patterns in carbon concentrations, high DOC lakes showed unusually high annual variation in epilimnetic DOC. For example, DOC drawdown in our model was about 11 mg L\(^{-1}\) in a lake with mean annual DOC ~25 mg L\(^{-1}\), whereas the epilimnetic drawdown in DOC from a similar lake in our calibration data set was only 6.5 mg L\(^{-1}\). Mean annual surface water carbon concentrations matched our expectations, with the exception of DOC and POC in the mesotrophic lake being slightly high. Table 3 shows mean annual surface water values

<p>| Table 3: Mean annual surface water concentrations for four representative lake types |
|--------------------------------------|----------------|----------------|----------------|</p>
<table>
<thead>
<tr>
<th>Lake type</th>
<th>TP</th>
<th>DOC</th>
<th>DIC</th>
<th>POC</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Cal</td>
<td>Sim</td>
<td>Cal</td>
<td>Sim</td>
</tr>
<tr>
<td>Oligotrophic</td>
<td>5</td>
<td>1.4–3.9</td>
<td>2.4</td>
<td>0.2–11.5</td>
</tr>
<tr>
<td>Mesotrophic</td>
<td>35</td>
<td>3.6–5.3</td>
<td>5.7</td>
<td>7.0–11.2</td>
</tr>
<tr>
<td>Eutrophic</td>
<td>100</td>
<td>2.8–10.5</td>
<td>5.4</td>
<td>9.0–13.0</td>
</tr>
<tr>
<td>Dystrophic</td>
<td>17</td>
<td>8.8–21.8</td>
<td>20.6</td>
<td>0.1–1.2</td>
</tr>
</tbody>
</table>

Columns are calibration values (Cal) and simulation results (Sim) for the selected lake types. Total phosphorus (TP) is in \( \mu g L^{-1} \), and dissolved organic carbon (DOC), dissolved inorganic carbon (DIC) and particulate organic carbon (POC) are in mg L\(^{-1}\).

for lake carbon concentrations from our simulations for typical categories of lakes.

We compared modeled results for lake GPP, R, and net ecosystem production (NEP) with estimates from another study. Figure 5 compares metabolism over a gradient in DOC, where the direct measurements were made using data sondes (Hanson et al., 2003). The model results for GPP agreed well with direct measurements (Fig. 5a). The results for R (Fig. 5b) and NEP (Fig. 5c) occupied roughly the same lake space as literature values, but diverged somewhat at higher DOC concentrations. The high DOC lakes from the literature are surrounded by bog mats, in which the interstitial waters have extremely high DIC concentrations (Kratz TK, unpublished data). This DIC may be transported to the lake at a rate high enough to artificially elevate R as measured by sondes (Hanson et al., 2003). Figure 6 compares model results and literature values over a TP gradient. Once again, model results for GPP agreed well with direct measurements (Fig. 6a), but model results for R were consistently lower than direct measurements (Fig. 6b). For NEP, model results were directly related with TP, but direct measurements showed considerable scatter at TP concentrations below 40 μg L⁻¹.

**Sedimentation, NAF and metabolism**

The influence of terrestrial carbon on the lake carbon budget was a function of the carbon load as well as the lake TP concentration. We gauged the contributions of autochthonous and allochthonous carbon sources to the lake carbon cycle by plotting carbon accumulation in the sediment pool (S) and NAF against the ratio of GPP to total (inorganic + organic) carbon loading from the watershed (C_load) (Fig. 7). As GPP : C_load increased, S increased and NAF decreased. At low GPP : C_load, NAF
was greater than \( S \), and lakes were net sources of carbon to the atmosphere. When \( \text{GPP}:\text{C load} \) exceeded 2.5, \( S \) exceeded \( \text{NAF} \) and lakes became net sinks of atmospheric carbon.

Calculating the balance between contrasting ecosystem processes can provide convenient metrics for classifying net trophic level and fluxes in lakes. Net ecosystem production (\( \text{NEP} = \text{GPP} - R \)) describes the metabolic balance of the aquatic system, such that negative \( \text{NEP} \) equals heterotrophy and positive \( \text{NEP} \) equals autotrophy. Heterotrophy implies that an external source of organic carbon is fueling \( R \) in excess of \( \text{GPP} \). Net carbon flux (\( \text{Flux}_{\text{net}} = \text{NAF} - S \)) describes the lake as a net source (positive (\( +\))\( \text{Flux}_{\text{net}} \)) of carbon to the atmosphere or a net sink (negative (\( -\))\( \text{Flux}_{\text{net}} \)) of carbon from the atmosphere.

\( \text{NEP} \) and \( \text{Flux}_{\text{net}} \) showed similar but opposite responses over \( TP \) and \( \text{C load} \) gradients. As \( \text{C load} \) increased, \( \text{NEP} \) decreased (Fig. 5c) and \( \text{Flux}_{\text{net}} \) increased (Fig. 8a). Above \( \text{C load} \) load of 10 g m\(^{-2}\) WA yr\(^{-1}\), almost all lakes had negative \( \text{NEP} \) and positive \( \text{Flux}_{\text{net}} \), regardless of \( TP \) concentration. Below \( \text{C load} \) of 10 g m\(^{-2}\) WA yr\(^{-1}\), results were mixed. About one-fourth of the lakes showed heterotrophy and positive \( \text{Flux}_{\text{net}} \), whereas others showed the opposite trend. Those lakes with positive \( \text{NEP} \) and negative \( \text{Flux}_{\text{net}} \) were highest in \( TP \). As \( TP \) concentration increased, \( \text{NEP} \) increased and \( \text{Flux}_{\text{net}} \) decreased (Fig. 8b). When \( TP \) was above 35 \( \mu \text{g L}^{-1} \), lakes had positive \( \text{NEP} \) and negative \( \text{Flux}_{\text{net}} \), but at or below 35 \( \mu \text{g L}^{-1} \); only three lakes with moderately high \( TP \) and low DOC showed this balance. \( \text{Flux}_{\text{net}} \) and \( \text{NEP} \) were inversely related (Fig. 9).

**Model sensitivity analysis**

Model sensitivity to parameter changes was indicated by changes in \( \text{NAF} \) and \( S \) from their values calculated under default conditions (22.7 g C m\(^{-2}\) LA yr\(^{-1}\) for \( \text{NAF} \) and 13.7 g C m\(^{-2}\) LA yr\(^{-1}\) for \( S \)). The model was slightly sensitive to changes in five parameters. A 10% increase in ice-free days (\( c \)) led to a 10.2% increase in \( S \). Increasing \( LA \) to \( WA \) ratio (\( lw \)), precipitation (\( p \)), and base temperature (\( t \)) led to decreases in \( \text{NAF} \) of 15.4%, 15.9%, and 12.8%, respectively. Increasing evapotranspiration (\( v \)) increased \( \text{NAF} \) by 12%. The model was very sensitive to \( ra \), the term that represents rapid mineralization of \( \text{GPP} \) products. An increase of 10% in \( ra \) led to a 41.6% decrease in \( S \) and a 26.4% increase in \( \text{NAF} \).

**Discussion**

**Lakes process terrestrial carbon**

Our results suggest that lakes can process and vent to the atmosphere a significant proportion of carbon fixed in terrestrial systems. In our model, terrestrial carbon export was about 5–28 g C m\(^{-2}\) WA yr\(^{-1}\). As much as
60% of that carbon was returned to the atmosphere. By comparing lake NAF with NEE estimates for northern hardwood forests (160 gC m⁻² yr⁻¹) (Barford et al., 2001), we find that a single lake in a watershed may process and vent as much as 3–9% of terrestrial NEE. Much of the remaining terrigenous carbon was exported from the lake as DOC and POC. Because most of the exported C is in a form that will not be sedimented, we speculate that it, too, may be destined for mineralization and vented to the atmosphere. By combining NAF and export numbers, we raise the percentage of terrigenous carbon fluxed to the atmosphere to as much as 90% of the carbon load. This flux equates to 3–14% of terrestrial NEE. The upper end of this range is of the same magnitude as error associated with eddy-covariance estimates of terrestrial NEE (Baldocchi, 2003), as well as disturbance effects on terrestrial NEP, such as nitrogen deposition, climate change, and CO₂ fertilization (Chen et al., 2000).

The influence of autochthonous and allochthonous carbon on lake carbon cycling

Terrigenous sources can contribute as much as GPP to lake carbon pools. Though direct measurements of loads and aquatic ecosystem production are difficult to make in real ecosystems, estimates exist. Biddanda & Cotner (2002) found that allochthonous contributions to Lake Michigan were as much as 0.1 GPP, which would be equivalent to our GPP : C₇ load result of 10 (Fig. 7). Based on our model, oligotrophic and mesotrophic lakes have much lower GPP : C₇ load ratios of about 0.7 and 3, depending on TP concentration. Our lower estimates may reflect shorter water residence times in our lakes, which are an order of magnitude lower than that of Lake Michigan. The contribution of allochthonous carbon to lake metabolism also can be evaluated in terms of its subsidy to aquatic ecosystem R. Cole et al. (2002) found that 52% of R was supported by allochthonous DOC. A lake of similar nutrient concentrations in our model showed that allochthonous C subsidized at least 40% of R. Though all DOC in our model was pooled, making it impossible to determine which source was mineralized vs. exported, we can only balance R in excess of GPP through mineralization of allochthonous sources. In high C₇ load lakes, allochthonous C may subsidize as much as 85% of R.

Carbon loading influenced lake productivity through its effects on DOC concentration. In our model, shading did not limit light, and volumetric productivity was the same for all lakes of a given TP concentration. It was the effect of DOC on thermocline depth that indirectly limited productivity. As DOC concentration increased, thermocline depth decreased, and the biologically active volume of the lake decreased. Given two morphometrically equivalent lakes, one with a DOC concentration of 3 mg L⁻¹ would have nearly five times the phototrophic volume of a lake with 25 mg L⁻¹ of DOC.

Lakes often are categorized by trophic status, which is associated with TP and DOC concentrations (Kalff, 2002). In Fig. 10, we display the carbon budgets of four selected lake types from our model: oligotrophic (low TP, low DOC), eutrophic (high TP, low DOC), mesotrophic (moderate TP, low DOC) and dystrophic (low-to-moderate TP, high DOC). The oligotrophic lake had...
NAF in excess of S. Its carbon load (43 g C m\(^{-2}\) LAyr\(^{-1}\)) was similar to estimates for Mirror Lake (as high as 40 g C m\(^{-2}\) LAyr\(^{-1}\)) (Likens, 1985), as well as Canadian shield lakes (1-52 g C m\(^{-2}\) LAyr\(^{-1}\)) (Dillon & Molot, 1997). The modeled S values (7 g C m\(^{-2}\) LAyr\(^{-1}\)) also were similar to those for Mirror Lake (less than 12 g C m\(^{-2}\) LAyr\(^{-1}\)) (Cole \textit{et al.}, 1989). NAF in the oligotrophic lake (28 g C m\(^{-2}\) LAyr\(^{-1}\)) was higher than a value of 13.8 estimated by Riera \textit{et al.} (1999) for an oligotrophic lake in the same region. The eutrophic lake had the strongest NAF into the lake, and it also had the highest S. The eutrophic and mesotrophic lakes had S exceeding NAF. The dystrophic lake was qualitatively different from the others in that its load was roughly four times that of the others. Such a high load could represent carbon export from abundant surrounding wetlands, which can contribute as much as 500 g C m\(^{-2}\) LAyr\(^{-1}\) (Kortelainen, 1993; del Giorgio & Peters, 1994). The high load to the dystrophic lake forces NAF to exceed S by a great margin, even though S was moderate (17 g C m\(^{-2}\) LAyr\(^{-1}\)) and comparable with that of a similar lake (18 g C m\(^{-2}\) LAyr\(^{-1}\)) (Jonsson \textit{et al.}, 2001). NAF in the modeled dystrophic lake (141 g C m\(^{-2}\) LAyr\(^{-1}\)) was somewhat higher than a value estimated for a dystrophic lake in the same region (120 g C m\(^{-2}\) LAyr\(^{-1}\)) (Riera \textit{et al.}, 1999). Sedimentation values for all four lakes lie within reported estimates for organic carbon burial in temperate lakes (5-72 g C m\(^{-2}\) LAyr\(^{-1}\)) (Dean & Gorham, 1998).

Most lakes were heterotrophic on an annual basis, and only under low DOC and moderate-to-high TP were lakes autotrophic. This result is consistent with previous work describing heterotrophy as the dominant condition in north temperate lakes during stratified periods (del Giorgio & Peters, 1994; Hanson \textit{et al.}, 2003; but see also Carignan \textit{et al.}, 2000). We also found that when DOC concentration in lakes exceeded 8 mg L\(^{-1}\) (DOC loading of about 8 g m\(^{-2}\) WA yr\(^{-1}\)), lakes were consistently heterotrophic, but below that DOC concentration the trophic statuses varied, depending on the DOC and TP concentrations (Fig. 5c). In some ways, it was not surprising that this result was consistent with those of Hanson \textit{et al.} (2003), because the GPP relationship in this study was derived empirically from TP and GPP data in theirs. However, the mechanisms for respiration were different between the two studies. Measured R was estimated from changes in gas concentration, whereas we modeled R as first-order decay rates from multiple carbon pools. The influence of DOC concentration on NEP has been reported in

\begin{figure}
\centering
\includegraphics[width=\textwidth]{fig10.png}
\caption{Carbon loading (input), accumulation of carbon in the sediment pool (S), net atmospheric flux (NAF) and output (as labeled in the upper left lake) from four lakes representing the classical categories of lake trophic status. Units for the values adjacent to arrows are g C m\(^{-2}\) LAyr\(^{-1}\). Dissolved organic carbon (DOC) and total phosphorus (TP) concentrations are mean annual values. Numbers below the input arrows are the relative percentages of the different carbon species in the input.}
\end{figure}
other research as well. Prairie et al. (2002) suggest that as DOC concentration exceeds about 6 mg L\(^{-1}\), lakes become net heterotrophic.

**Lakes as net sinks or net sources of carbon**

The combined influences of TP concentration and carbon load on NAF and S are highlighted in Fig. 11. Using the results of the simulations for each carbon load, we determined the TP concentration at which NAF equaled S and plotted it as the solid line. We performed a similar calculation for R and GPP and plotted it as the dashed line. Filled circles representing lakes in this study were plotted on the graph according to their assumed carbon loads and TP concentrations. About 75% of the lake space in this study was in the regions of heterotrophy and net sources of carbon to the atmosphere. Only those lakes low in carbon load and moderate-to-high in TP fell into the autotrophic and net sink regions.

Although our model did not address the frequency distribution of lake DOC and TP concentrations, many of the lakes in this region of Wisconsin are oligotrophic, or similar in nutrient concentrations to those lakes in the lower left corner of the figure. Because these lakes are close to the trophic threshold line, we felt the model warranted closer inspection of the most influential parameter at these nutrient concentrations. The following analysis investigates the positions of those lines as a function of \(r_a\), the proportion of GPP respired quickly.

The value of \(r_a\) influenced the amount of lake space that fell into the heterotrophic and net source classifications. When \(r_a\) was set to 0.88, about 90% of the total lake space was heterotrophic and the threshold for lakes with the least carbon load rose to about 22 \(\mu\)g TP L\(^{-1}\). When \(r_a\) was 0.72, about 65% of the total lake space was heterotrophic and the autotrophic threshold for oligotrophic lakes dropped to about 5 \(\mu\)g TP L\(^{-1}\). Only by reducing \(r_a\) to values below about 0.7 could we force the autotrophic threshold below 5 \(\mu\)g TP L\(^{-1}\) for the lowest DOC lakes. However, when \(r_a\) was this low, carbon burial in lakes with TP > 80 \(\mu\)g L\(^{-1}\) was well above 100 g C m\(^{-2}\) LA yr\(^{-1}\), which exceeded literature values for eutrophic lakes (Rea et al., 1981). The mechanism by which changes in \(r_a\) propagate through the model is by the inverse relationship of \(r_a\) with POC\(_L\), which could also be thought of as algal biomass. The uncertainty in \(r_a\) may reflect scatter in relationships between TP and algal biomass in real systems. Although the range in summer epilimnetic POC\(_L\) in our model falls within reported algal biomass values for lakes with similar TP concentrations (Wetzel, 2001), algal biomass in real lakes can be influenced by factors other than TP, including aquatic food webs. Experiments on lakes have demonstrated that food webs can alter primary productivity, which in turn can alter carbon NAF with the atmosphere (Schindler et al., 1997). The abundance of zooplankton can either increase or decrease C flux out of the mix layer, depending on plankton concentrations (Sarnelle, 1999).

A simple approach to evaluating the effect of consumers on NAF and S in this model is to adjust

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**Fig. 11**  Lakes from the simulation are plotted in a lake space with gradients of total C loading and total phosphorus (TP) concentration. The dashed line represents the dissolved organic carbon (DOC) and TP combinations that produce net ecosystem production (NEP) of zero (gross primary production (GPP) = R). Lakes above this line are autotrophic, and lakes below are heterotrophic. The solid line represents DOC and TP combinations in which S equals net atmospheric flux (NAF). Lakes above this line are net sinks of atmospheric carbon and lakes below this line are net sources of atmospheric carbon.

the parameter \( (ed) \) that converts \( \text{POC}_L \) to \( \text{POC}_D \). If we assume that consumers ingest \( \text{POC}_L \) and excrete \( \text{POC}_D \), which is subject to sedimentation and bacterial respiration, then the effect of consumers on the system is analogous to that of \( ed \). Evaluating the model’s sensitivity to consumers was accomplished by evaluating its sensitivity to changes in \( ed \). A decrease in \( S \) of 10% required a doubling of \( ed \). To increase \( NAF \) by 10%, \( ed \) was increased 18-fold. The greater sensitivity of \( S \) to \( ed \) may be the result of excluding consumer respiration in this analysis. Although adding the consumer pool would allow for partitioning between consumer excretion and respiration, the simplicity of the present model seems justified by its lack of sensitivity to \( ed \).

Conclusions

This model of a lake in a landscape is perhaps the simplest representation that could be used to address our questions about the contributions of lakes to processing, sequestration, and atmospheric flux of carbon. Despite its simplicity, the patterns predicted by the model are consistent with the available literature and our field measurements. It is somewhat surprising that a steady-state model was generally consistent with measurements of dynamic ecosystem processes. Nevertheless, further modeling and empirical work on temporal change in carbon processing is needed to determine the conditions under which steady-state assumptions may be important, and understand the patterns of change in carbon processing over time.

The model suggests that carbon processing by lakes is significant and worthy of exploration as an important component of carbon processing on landscapes rich in lakes. What spatial patterns of carbon processing emerge from the topographic, hydrologic, and biotic heterogeneity of real landscapes? How does the variable morphometry of real lakes affect the magnitude of \( NAF \) and carbon sequestration? As landscapes become drier or wetter over long-time scales, how do changes in lake dimensions affect carbon processing, \( CO_2 \) flux, and carbon sequestration at the landscape scale? These are among the questions that suggest the need for modeling and observational approaches that address landscapes and the lakes they contain in integrated ways.

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