The exchange of the important trace gases, methane (CH$_4$), nitrous oxide (N$_2$O), and carbon dioxide (CO$_2$), between forested soils and the atmosphere can show great temporal and spatial variability. We measured the flux of these three gases over 2 years along catenas at two forested sites, to determine the important controls. Well-drained soils consumed atmospheric CH$_4$, while poorly drained swamp soils embedded in depressions were a source. CH$_4$ fluxes could be predicted primarily by temperature and moisture, and tree cover exerted an influence mainly through the creation of large soil porosity, leading to increased consumption rates. In contrast, there were very poor relationships between N$_2$O fluxes and environmental variables, reflecting the complex interactions of microbial, edaphic, and N cycling processes, such as nitrification in well-drained soils and denitrification in poorly drained soils, which led to N$_2$O production (or consumption) in soils and hence larger variability. At the broad temporal and spatial scale, soil C:N ratio was a good predictor of N$_2$O emission rates, through its influence upon N cycling processes. Soil CO$_2$ emission rates showed less spatial and temporal variability, and were controlled by temperature and moisture. The source strength, in global warming potential of CH$_4$ and N$_2$O fluxes in CO$_2$ equivalents, was reduced markedly when trace gas fluxes from 5 to 15% poorly drained soils were included in the net global warming potential calculation of whole forested watersheds. Soils drainage class integrates many of the biogeochemical processes controlling the flux of these gases providing a framework for extrapolating results.

1. Introduction

[2] Biogeochemical functions often show strong spatial and temporal variabilities, termed “hot spots” and “hot moments” [McClain et al., 2003]. They result from environmental heterogeneity, which brings together reactants at specific locations and times, producing fast biogeochemical transformations and large fluxes. Within soils, the movement of reactants in water facilitates these transformations and the products often comprise trace gases, which exchange rapidly with the atmosphere. In forested ecosystems, carbon dioxide (CO$_2$), methane (CH$_4$) and nitrous oxide (N$_2$O) are the major trace gases exchanged between the soil and the atmosphere. All three are important greenhouse gases and the latter two often show large temporal and spatial variability in fluxes [see McClain et al., 2003].

[3] Globally, forest soils are a net sink of atmospheric CH$_4$, with estimates ranging from 1.8 to 11.8 Tg CH$_4$C yr$^{-1}$, while they are a net source of atmospheric N$_2$O estimated to be 2.4 to 5.7 Tg N$_2$O-N yr$^{-1}$ [Bouwman et al., 1995; Intergovernmental Panel on Climate Change (IPCC), 2007]. These large ranges in N$_2$O and CH$_4$ exchange mainly arise from uncertainties associated with limited measurements and their great spatial and temporal variability arising from the influence of topographic heterogeneity, soils drainage class and seasonality on fluxes [e.g., Brumme et al., 1999; Ullah et al., 2008].

[4] The atmospheric exchange of CH$_4$ with forest soils represents a balance between two opposing microbial processes: methanogenesis and methanotrophy. In methanogenesis, methanogens produce CH$_4$ under anoxic soil conditions, while methanotrophy is an aerobic process in which atmospheric CH$_4$ and CH$_4$ produced in situ are oxidized [Moore and Dalva, 1997]. In topographically heterogeneous forests, well-drained soils are generally sinks of atmospheric CH$_4$ [e.g., Brumme and Borken, 1999], while poorly drained soils are sources of CH$_4$ [Ullah et al., 2008].

[5] Nitrous oxide is mainly produced in soils by two microbial processes, nitrification and denitrification. In nitrification,
ammonium (NH₄) is converted to nitrate (NO₃) through sequential enzymatic processes under well-drained, aerobic soil conditions and part of the N is emitted as N₂O [Wragge et al., 2001]. In denitrification (an anaerobic process) denitrifiers utilize NO₃ as a terminal electron acceptor in their respiration and reduce it to N₂O and N₂ gases [Wragge et al., 2001]. The fluxes of CH₄ and N₂O from forest soils are therefore dependent on microbial processes regulated by soils drainage class, through its influence on the extent and distribution of oxic-anoxic conditions in the soil profile. Carbon dioxide is emitted to the atmosphere as a result of heterotrophic and autotrophic respiration and, similarly, fluxes will be dependent on soils drainage class, which influences aerobic and anaerobic decomposition rates, as well as rooting patterns [e.g., Webster et al., 2008].

[6] Both CH₄ and N₂O fluxes can also be affected by the cycling of N in the soil, related to the dominant tree species. Forest soils developed under sugar maple (Acer saccharum) exhibit faster N transformation rates than soils developed under American beech (Fagus grandifolia) and eastern hemlock trees (Tsuga canadensis) [Lovett et al., 2004; Ullah and Moore, 2009]. Faster N mineralization in soils under sugar maple may produce more N₂O than under American beech and hemlock. Forest soils with higher mineral N contents, particularly NH₄, may have smaller CH₄ consumption potentials, as NH₄ competitively inhibits the oxidation of CH₄ by the methane mono-oxygenase enzyme [Amaral and Knowles, 1997]. Bod Elk et al. [2000] reported no inhibition effect due to N fertilization; however, the soils used by the authors were from rice paddies where in situ CH₄ production is higher than in well-drained forest soils.

[7] The temperate deciduous forests in the St. Lawrence River valley in eastern Canada cover ~9 million ha, about half of the total land area in the valley [Bélanger and Grenier, 2002]. These forests are not homogeneous, but rather consist mainly of a mosaic of well-drained and poorly drained soils (hydric soils) defined by topography. Well-drained soils have water which is removed (drained) at rapid to moderate rates that do not lead to excessive wetness of the soil for longer duration, particularly during the growing season, to develop significant anaerobic soil conditions (redox features) [U.S. Army Corps of Engineers, 1987]. Poorly drained soils (hydric soils) are those from which water is removed (drained) at slow to very slow rates resulting in wetness and/or ponding of the soils (hydric soils). The duration of wetness and/or ponding, particularly during the growing season, leads to the development of redoxmorphic features and tends to support the growth of facultative wet or obligate wetland plant species [U.S. Army Corps of Engineers, 1987]. Poorly drained soils are developed mainly in low-elevation areas and are termed forested swamps [Warner and Rubec, 1997]. Unlike wetlands such as bogs, marshes, fens and mires, which have a distinct canopy that can be detected by satellite images of aerial photographs [Creed et al., 2003], forested swamps in deciduous forests are overshadowed by the dominant forests trees and cannot be detected easily. These forested swamps interspersed in temperate deciduous forests are “cryptic” wetlands [Creed et al., 2003]. Since the canopy vegetation of these poorly drained soils is mostly not distinct from those of well-drained soils, the contribution of the poorly drained soils to the net greenhouse gas fluxes is often overlooked [Creed et al., 2003]. It is also not easy to demarcate poorly drained wetland soils in forests through remote sensing or satellite imagery and this could have been the reason for overlooking the role of these wetlands in the overall watershed N and C budgets. In the St. Lawrence River valley, poorly drained soils in low elevation areas range from 0.1 to 12% (0.01 to 1.1 million ha) of the total deciduous forest cover in the valley [Creed et al., 2003; M. Lechowicz, personal communication, 2010]. Owing to their saturation and exposure to surface and subsurface nutrient runoff from well-drained soils, the CH₄, CO₂ and N₂O fluxes from these soils are expected to be different from well-drained soils and could have significant impact on net global warming potential (GWP) of deciduous forests when fluxes from poorly drained soils are included.

[8] Temperate deciduous forest soils have been reported as sinks of atmospheric CH₄ and sources of N₂O [e.g., McHale et al., 1998; Bowden et al., 2000; Ambus and Robertson, 2006; Groffman et al., 2006], but, to our knowledge, there are few studies elucidating the influence of soils drainage class on CH₄ and N₂O fluxes in deciduous forests [Corre et al., 1999; Goossens et al., 2001; von Arnold et al., 2005] to be able to account not only for fluxes from well but also from poorly drained soils in these forests. This hampers our ability to accurately estimate net greenhouse gas exchanges at the watershed scale [Lessard et al., 1994]. The aerial extent of poorly drained soils in forested landscapes may be reported as small, but the occurrence of these wetlands, as shown by Creed et al. [2003] in central Ontario forests, may cover a significant portion of the landscape, acting as “hot spots” leading to biogeochemical transformations of CH₄ and N₂O and atmospheric exchange with significant implications for net GWP and forest restoration for atmospheric C sequestration.

[9] Here, we examine the patterns of CH₄, N₂O and CO₂ fluxes between soils and the atmosphere along a catena, ranging from well to poorly drained soils, at two deciduous forest sites in southern Quebec, Canada. One site is located in an old-growth forest and the other in a semimanaged forest. Our objectives were twofold: first to determine the seasonal and spatial pattern of fluxes, identifying “hot spots” and “hot moments”; and second to establish the influence of soils drainage class and dominant trees species on the fluxes. We hypothesized that soils drainage class (well- versus poorly drained) and dominant vegetation in the canopy significantly influence soil CH₄, N₂O and CO₂ fluxes through their influence on aerobic and anaerobic biogeochemical transformations, such as greater denitrification in poorly drained and nitrification in well-drained soils driving N₂O fluxes. Thicker O horizons under American beech tree results in larger soil porosity leading to enhanced CH₄ consumption, compared to thinner O horizons developed under sugar maple trees with smaller porosity. We also hypothesized that saturated soil conditions in poorly drained soils result in lower CO₂ emissions, offsetting larger CH₄ and N₂O emissions from poorly drained soils in terms of net GWP, compared to well-drained soils.

2. Methods

2.1. Study Sites

[10] The two sites were located in an old-growth forest (OGF) at Mont St. Hilaire and a semimanaged forest (SMF) at Morgan Arboretum. The OGF is located about 32 km east
of Montreal on a Monteregian Hill and has never been logged or used for any commercial purposes with trees being from 140 to >400 years old [Takahashi and Lechowicz, 2008]. Mean annual precipitation at the OGF is 1046 mm and the daily mean air temperature is 5.8°C for the period 1961–1990, measured at a nearby weather station. The SMF is located about 30 km west of Montreal with tree age ranging from 60 to 120 years [Côté and Fyles, 1994]. Mean annual precipitation measured at the nearby Trudeau Airport is 979 mm and daily mean temperature is 6.2°C for the period 1961–1990. Soils at the SMF are of glacial origin, while those at the SMF are of fluvial and marine sediment origin, which is typical of the Great Lakes-St. Lawrence forest region in Canada [Côté and Fyles, 1994].

[11] Plots for greenhouse gas and soil sampling were located along a transect running from well to poorly drained locations in both OGF and SMF sites [Ullah and Moore, 2009]. Four sampling plots, upland, slope, riparian and hemlock, were located along the OGF transect. Upland and slope plots represent locations which are well-drained loamy sands, while those of riparian and hemlock plots represent poorly drained silt loams. Upland, slope and riparian plots at OGF are dominated by American beech and eastern hemlock. The riparian and hemlock plots also have scattered trees of yellow birch (Betula alleghaniensis).

[12] Four plots, upland and slope (well-drained, loamy sand), wetland A and wetland B (poorly drained, silt loam) were located along the SMF transect. Upland and slope plots at SMF are dominated by sugar maple with a few scattered yellow birch trees. The wetland A and B plots have a tree layer dominated by sugar maple with scattered trees of bitternut hickory (Carya cordiformis), white ash (Fraxinus americana) and red maple (Acer rubrum).

[13] The upland and slope plots in OGF had an O horizon about 5 cm thick, while the average thickness of the O horizon in upland and slope plots in the SMF was 0.5–1.5 cm. Poorly drained soils in both OGF and SMF sites had an O horizon ranging from 5 to 10 cm thick, overlying mineral A horizons. Well-drained soils in OGF are Orthic Dystric Brunisols while those in SMF are Melanic Brunisols. Poorly drained soils in OGF and SMF sites are Humic Gleysols [Agriculture Canada Expert Committee on Soil Survey, 1987]. The average groundwater table depth in the upland and slope plots at the OGF and SMF sites was more than 1 m. Soils in the riparian and hemlock plots of OGF and wetland A and B plots in SMF remained saturated or ponded, with 85–100% water–filled pore space (WFPS), in spring (March–May) and fall (October and November), and the WFPS dropped to an average of 70% in the summer months (June–September). Soil saturation and ponding, particularly in spring, result in redoximorphic features in A horizons, characteristic of hydric soils.

2.2. Gas Flux Measurements

[14] Four soil gas flux measurement collars (472 cm²) were randomly installed in April 2006 in each plot (4 plots along each transect in the two forest sites), perpendicular to the slope of transects in OGF and SMF (total of 16 collars along each transect, 4 in each plot). While inserting the collars to a depth of 10–12 cm, an effort was made to minimize disturbance of the soils including the O horizon. Gas sampling followed the closed chamber technique [Hutchinson and Mosier, 1981]. The collars had a continuous circular groove filled with water to create a seal between the collar and the chamber (headspace enclosure) during gas sampling. The volume of the chamber was 8 L and the average volume-to-area ratio of the chamber was 17 cm, which met the minimum required without influencing gas diffusion patterns that would prevail under normal atmospheric pressure [Hutchinson and Mosier, 1981]. The chambers were wrapped with aluminum foil to minimize heating the enclosed air during sampling.

[15] Gas sampling started in May 2006 and continued until May 2008 at biweekly intervals except in the winter months (monthly intervals in the winter of 2006–2007 and no sampling in the winter of 2008). Upon enclosure of the collars with cover chambers (starting between 9 and 11 am), gas samples were collected at 0, 30, 60 and 90 min intervals via a sampling port attached to the top of the chamber. The gas samples (25 cm³) were transferred to preevacuated, crimped glass vials fitted with gray Supelco septa (13 cm³) and analyzed within 1–4 d of collection on a Shimadzu 14-A gas chromatograph (GC) equipped with an ECD detector for N₂O analysis, and on a Shimadzu Mini-GC equipped with an FID detector for CH₄ and CO₂ analysis, using a methanizer column to determine CO₂ concentration. Porapak Q columns were used for the separation of gases in both GCs, where the column for N₂O separation was 6 m long while for CH₄ separation the column was 2 m long. The column leading to ECD detector was fitted with an automated four-way Valco-Valve for purging out eluted O₂ before the sample gas was directed towards ECD for N₂O determination. The ECD was operated at 310°C while the FID was operated at 100°C. The flux of each gas was determined based on a linear change in gas concentration over the 90 min incubation period. Gas concentrations with no consistent increase or decrease over the 90 min incubation period were considered as zero flux, provided the coefficient of variation of the flux pattern was not greater than that of known, repeatedly injected gas standards [Lessard et al., 1994]. Zero fluxes were more frequently observed during the winter sampling period when soils were fully or partially frozen. Travel blanks of oxygen-free N₂ gas and known standards of N₂O, CO₂, and CH₄ in the crimped vials were taken to the field and brought back with the collected samples to ensure and account for any diffusion related losses of trace gases during sampling, transport and analysis. Analysis of the control standards within 1 week of transfer to the crimped vials did not result in a significant change in the concentration of the standards.

2.3. Soil Pore Air Measurements

[16] Soil pore air was sampled biweekly in well-drained plots of OGF and SMF through stainless steel tubes. Soil pits (one per plot, ∼50 × 80 cm) were dug to allow insertion of 3 stainless steel tubes (2 mm diameter, 20 cm long) sideways into O, A, AB and B horizons. The tubes were attached to 4 mm diameter PVC tubes, extending to the soil surface, and the soil pits were filled. The free ends of the PVC tubes were fitted with three-way stopcocks so that the tubes could be locked to avoid any diffusion of surface air into the soil horizons through the tubes. The three replicate pore air sampling tubes in each horizon were separated
2.4. Soil Sampling and Analysis

Soil samples (0–10 cm, including Oe and Oa horizons) were collected from 3 locations within each plot at monthly intervals from spring to fall in 2006 and 2007. Soils were sampled with an aluminum tube of 5.3 cm diameter and stored at 4°C until analyzed. The soil samples were transferred to 10 mL crimped vials for transport and analysis into the pore space three times. The air samples were transferred to 10 mL crimped vials for transport and analysis. Field gas samples were collected through a syringe by attaching it to the stopcock after mixing the air in the tubes slowly (through pumping about 1 ml sample back into the vials). Soil samples collected in October 2006 were used for determination of potential denitrification rates following 

Table 1. Properties (Mean ± Standard Error of the Mean) of the 0–10 cm Depth of Soils of the Four Plots at the Two Sites

<table>
<thead>
<tr>
<th>Soil Property</th>
<th>Upland</th>
<th>Slope</th>
<th>Riparian</th>
<th>Hemlock</th>
<th>Upland</th>
<th>Slope</th>
<th>Wetland A</th>
<th>Wetland B</th>
</tr>
</thead>
<tbody>
<tr>
<td>Dominant canopy tree species</td>
<td>American beech</td>
<td>American beech</td>
<td>American beech</td>
<td>Eastern hemlock</td>
<td>Sugar maple</td>
<td>Sugar maple</td>
<td>Sugar maple</td>
<td>Sugar maple</td>
</tr>
<tr>
<td>Bulk density (g cm⁻³)</td>
<td>0.67 ± 0.01</td>
<td>0.78 ± 0.1</td>
<td>0.42 ± 0.2</td>
<td>0.48 ± 0.1</td>
<td>1.19 ± 0.04</td>
<td>1.14 ± 0.02</td>
<td>0.61 ± 0.03</td>
<td>0.52 ± 0.03</td>
</tr>
<tr>
<td>Total porosity (cm³ cm⁻³)</td>
<td>0.75</td>
<td>0.71</td>
<td>0.84</td>
<td>0.82</td>
<td>0.55</td>
<td>0.57</td>
<td>0.77</td>
<td>0.81</td>
</tr>
<tr>
<td>Average volumetric water content (%)</td>
<td>24 ± 1</td>
<td>43 ± 2</td>
<td>87 ± 2</td>
<td>66 ± 2</td>
<td>27 ± 2</td>
<td>23 ± 1</td>
<td>85 ± 3</td>
<td>79 ± 5</td>
</tr>
<tr>
<td>Average water-filled pore space (%)</td>
<td>33 ± 1</td>
<td>63 ± 3</td>
<td>96 ± 1</td>
<td>79 ± 3</td>
<td>51 ± 3</td>
<td>40 ± 2</td>
<td>96 ± 2</td>
<td>88 ± 3</td>
</tr>
<tr>
<td>Sand (%)</td>
<td>67 ± 8</td>
<td>83 ± 2</td>
<td>17 ± 5</td>
<td>14 ± 3</td>
<td>72 ± 5</td>
<td>40 ± 4</td>
<td>44 ± 2</td>
<td>33 ± 8</td>
</tr>
<tr>
<td>Silt (%)</td>
<td>33 ± 8</td>
<td>17 ± 2</td>
<td>81 ± 5</td>
<td>84 ± 3</td>
<td>28 ± 5</td>
<td>60 ± 4</td>
<td>56 ± 2</td>
<td>67 ± 8</td>
</tr>
<tr>
<td>Soil texture</td>
<td>Sandy loam</td>
<td>Loamy sand</td>
<td>Silt loam</td>
<td>Silt loam</td>
<td>Sandy loam</td>
<td>Loamy sand</td>
<td>Silt loam</td>
<td>Silt loam</td>
</tr>
<tr>
<td>pH</td>
<td>4.7 ± 0.5</td>
<td>4.6 ± 0.31</td>
<td>5.0 ± 0.31</td>
<td>4.8 ± 0.39</td>
<td>5.1 ± 0.05</td>
<td>5.9 ± 0.13</td>
<td>5.6 ± 0.03</td>
<td>5.8 ± 0.08</td>
</tr>
<tr>
<td>C:N ratio</td>
<td>26 ± 1.3</td>
<td>25 ± 3.5</td>
<td>20 ± 1.3</td>
<td>25 ± 1.5</td>
<td>16 ± 0.7</td>
<td>15 ± 0.7</td>
<td>16 ± 0.3</td>
<td>17 ± 1.0</td>
</tr>
<tr>
<td>NO₃ (mg N m⁻²)</td>
<td>53 ± 4</td>
<td>66 ± 9</td>
<td>43 ± 5</td>
<td>25 ± 2</td>
<td>145 ± 14</td>
<td>179 ± 12</td>
<td>65 ± 5</td>
<td>64 ± 5</td>
</tr>
<tr>
<td>NH₄ (mg N m⁻²)</td>
<td>632 ± 37</td>
<td>975 ± 117</td>
<td>213 ± 23</td>
<td>162 ± 19</td>
<td>683 ± 59</td>
<td>602 ± 62</td>
<td>296 ± 34</td>
<td>146 ± 9</td>
</tr>
<tr>
<td>Leaf litter fall (g m⁻²)</td>
<td>513 ± 106</td>
<td>448 ± 105</td>
<td>424 ± 115</td>
<td>254 ± 32</td>
<td>507 ± 22</td>
<td>620 ± 64</td>
<td>366 ± 17</td>
<td>438 ± 33</td>
</tr>
<tr>
<td>Leaf litter N input (g m⁻²)</td>
<td>4.6 ± 1.4</td>
<td>3.7 ± 0.9</td>
<td>3.3 ± 1.0</td>
<td>1.9 ± 0.3</td>
<td>4.9 ± 0.1</td>
<td>5.6 ± 0.5</td>
<td>3.2 ± 0.2</td>
<td>4.0 ± 0.3</td>
</tr>
<tr>
<td>Leaf litter fall C:N ratio</td>
<td>61 ± 6</td>
<td>64 ± 1</td>
<td>70 ± 6</td>
<td>71 ± 3</td>
<td>52 ± 0</td>
<td>55 ± 2</td>
<td>60 ± 5</td>
<td>58 ± 1</td>
</tr>
<tr>
<td>Total soil N (0–10 cm depth, g N m⁻²)</td>
<td>248 ± 34</td>
<td>354 ± 31</td>
<td>876 ± 77</td>
<td>339 ± 60</td>
<td>283 ± 30</td>
<td>326 ± 35</td>
<td>476 ± 27</td>
<td>608 ± 43</td>
</tr>
</tbody>
</table>

*Values in mass per area basis (mass m⁻²) were based on a 10 cm depth. Sample size (n) per plot per variable: bulk density 3, porosity 3, VWC 33, WFPS 33, soil particle size 3, pH 3, C:N ratio 3, NO₃ 15, NH₄ 15, litter fall 3, litter N input and C:N ratio 3.

[17] Soil samples (0–10 cm, including Oe and Oa horizons) were collected from 3 locations within each plot at monthly intervals from spring to fall in 2006 and 2007. Soils were sampled with an aluminum tube of 5.3 cm diameter and stored at 4°C until analyzed. The soil samples were homogenized manually and a subsample of 5 g dry equivalent was weighed into 250 mL acid-washed plastic bottles for KCl-extractable NO₃ and NH₄ contents, by adding 50 mL of 2M KCl solution, shaken gently for 1 h, filtered through No. 42 Whatman filter paper and analyzed for NH₄ and NO₃ concentrations on a flow injection analyzer. Field-based monthly N mineralization rates (monthly), potential N mineralization and nitrification enzyme assays were also determined, as reported by Ullah and Moore [2009]. At least 3 blanks were run during mineral nitrogen extraction for blank correction and limit of detection determination for the individual monthly runs.

[18] Total soil C and N on the 0–10 cm depth soil samples were determined using finely ground soil samples collected in June 2007 from each plot and analyzed on an an Elemental Analyzer Carlo Erba™ (instrument model NC2500). Bulk density, pH and soil particle size distribution was determined as by Ullah and Zinati [2006]. Soil temperature (0–10 cm soil depth) and volumetric water content (VWC; 0–12 cm soil depth) were measured next to each collar during gas flux sampling, using a portable soil temperature probe (10 cm long) and a HydroSense CS620 soil moisture probe (12 cm long) (Campbell Scientific, Edmonton, Alberta, Canada). Soil temperature and moisture probes integrate measurements over the length of the probes inserted into the soil. Using the soil porosity parameter and VWC, water-filled pore spaces (WFPS) were calculated. Mean values of VWC and WFPS were calculated for each plot by taking the mean of all the plot scale data values measured during gas sampling. The associated error of the means integrates temporal variability of these variables.

[19] Leaf litter was collected from September to December in 2006 in 3 round plastic trays in each plot, dried at 65°C for 48 h and weighed. A 20 g subsample was milled to a powder and analyzed on an Elemental Analyzer Carlo Erba™ (instrument model NC2500) for total leaf litter N and C contents.

2.5. Potential Denitrification Rates

[20] Soil samples collected in October 2006 were used for the determination of potential denitrification rates following Tiedje [1982]. Soil were taken out of the fridge (~4°C) and left on the bench top for 1 h to allow the soil microbes to adjust to room temperature. The equivalent of 10 g dry soil...
was weighed into duplicate 150 mL serum bottles and to one bottle we added 20 mL KNO₃ solution (delivering 15 μg NO₃ N g⁻¹ dry soil), while the other bottle received 20 mL of deionized (DI) water. The bottles were wrapped in aluminum foil, capped with an air-tight septa and purged with O₂-free N₂ gas for 30 min to induce anaerobic conditions. After purging the bottles, 15 mL of the headspace of the bottles was replaced with acetylene (C₂H₂) gas to block the conversion of N₂O to N₂ gas. The bottles were shaken for 6 h, headspace samples were collected at 0, 2, 4 and 6 h duration and analyzed for N₂O concentration as described above. Linear regression of N₂O concentration increase over the 6 h incubation time was used to estimate denitrification rate. Corrections were made for dissolved N₂O in the slurries by using Bunsen absorption coefficient of 0.54. Denitrification potential rates are reported as μg N₂O-N g⁻¹h⁻¹.

2.6. Statistical Analyses

Descriptive statistics (mean and measures of spread) of gas flux data at each plot (n = 4) for each sampling date at the two sites was determined using Excel. An average daily mean of trace gases at plot scale was calculated by taking the mean of the data from each plot. Standard deviations and standard error of the means were calculated to represent the temporal error of fluxes at each plot. Soil variables such as NO₃ and NH₄, which were measured monthly in 2006 and 2007, were averaged with standard error of the mean calculated to represent temporal variability.

**Table 2.** Soil Fluxes of CH₄, N₂O, and CO₂ as Mean ± Standard Error and Sample Size (n)a

<table>
<thead>
<tr>
<th>Gas</th>
<th>Old-Growth Forest</th>
<th></th>
<th>Semimanged Forest</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Upland</td>
<td>Slope</td>
<td>Riparian</td>
</tr>
<tr>
<td>CH₄ flux (mg CH₄-C m⁻² d⁻¹)</td>
<td>-1.7 ± 0.1 (39)</td>
<td>-0.9 ± 0.1 (39)</td>
<td>1.6 ± 0.4 (36)</td>
</tr>
<tr>
<td>N₂O flux (μg N m⁻² d⁻¹)</td>
<td>71 ± 23 (33)</td>
<td>96 ± 21 (33)</td>
<td>171 ± 27 (30)</td>
</tr>
<tr>
<td>CO₂ flux (g CO₂-C m⁻² d⁻¹)</td>
<td>1.4 ± 0.2 (39)</td>
<td>1.8 ± 0.2 (39)</td>
<td>1.2 ± 0.1 (37)</td>
</tr>
</tbody>
</table>

aPositive values indicate emissions, and negative values indicate consumption.
for the period of measurement during the snow-free period. CH₄ and N₂O data from well- and poorly drained soils were not distributed normally, based on both Shapiro-Wilk and KS tests. Thus, the CH₄ and N₂O flux data were log-transformed before statistical analysis using SAS version 9.1 (SAS 2003). A constant value was added to the trace gas data to convert the largest negative flux to a positive value before log transformation. Stepwise multiple linear regression models were run using mean CH₄, N₂O and CO₂ fluxes pooled together based on soils drainage class in both sites (well- and poorly drained) as dependent variables and various soil and environmental variables as predictor variables (soil moisture, temperature, NO₃, NH₄, bulk density, DOC, TDN, C:N ratio, litter fall N content and N mineralization). Stepwise regression was chosen to develop a model with predictor variables that are not collinear. The proc-univariate procedure in SAS was also run to check that the residuals of the regression analysis were normally distributed according to the Shapiro-Wilk test of normality. Pearson’s correlations among various variables were also determined using SAS. Plot scale CO₂ and CH₄ fluxes from well- and poorly drained soils were log transformed and then a CO₂:CH₄ flux ratio was calculated and regressed against %WFPS. A two-sample pooled variance t test was used to compare means of the denitrification potentials of NO₃-amended and unamended soil samples within each plot. The criterion of significance for all the statistical tests was 5%. GWP potential of well- and poorly drained soils was calculated as CO₂ equivalent by multiplying N₂O and CH₄ fluxes with factors of 310 and 23, respectively [IPCC, 2007]. Net GWP of the deciduous forest soils with varying percent area under poorly drained soils (5–15%) out of the total land area on a hectare basis was estimated.

[22] The total number of observations used in regression and correlation analysis of various variables in the well- and poorly drained soils was not the same. This was due to missing data for a specific variable in the analysis (e.g., soil moisture probe and temperature probe broken at times resulting in data gaps for these variables against trace gas flux data). Similarly, occasional inaccessibility to gas measurement collars in the poorly drained soils during the snow cover period resulted in data gaps.

3. Results

3.1. Soil Properties

[23] The mean bulk densities of well-drained soils (0–10 cm depth) in OGF and SMF were larger than those of poorly drained soils (Table 1). Well-drained soils under sugar maple in the SMF site were denser (1.14–1.19 g cm⁻³) than in well-drained soils under American beech in the OGF site (0.67–0.78 g cm⁻³). Soil pH ranged from 4.8 to 5.8 and WFPS averaged 56% in well-drained and 90% in poorly drained soils. Soil C:N ratios (0–10 cm depth) were larger under American beech and eastern hemlock in the OGF site (20:1–26:1) than under sugar maple in the SMF site (15:1–17:1). Soil NO₃ content under different trees species in well- and poorly drained soils ranked: sugar maple > American beech > eastern hemlock. Soil NH₄ content did not differ significantly among well- and poorly drained soils. Litter fall did not differ significantly among well- and poorly drained soils; however, litter C:N ratios were smaller in well- and poorly drained soils under sugar maple in the SMF than under American beech in the OGF site (Table 1).

3.2. CH₄ Fluxes

[24] Well-drained soils were net sinks of atmospheric CH₄ (mean –1.1 mg CH₄·C m⁻² d⁻¹) while poorly drained soils were net sources of CH₄ (mean 7.8 mg CH₄·C m⁻² d⁻¹) (Figure 1 and Table 2). CH₄ consumption rates in well-drained soils were larger in the summer months (June–September) than in the fall/winter months (October–March) (Figure 1). Well-drained soils produced CH₄ during the spring thaw season (March and April) in 2007 and 2008, reaching a maximum of 3 mg CH₄·C m⁻² d⁻¹ at OGF and 1.7 mg CH₄·C m⁻² d⁻¹ at SMF (Figure 1). CH₄ emissions from poorly drained soils were large in May and June and

### Table 3. Relationships Between CH₄, N₂O, and CO₂ Fluxes and Environmental Variables, Based on Pearson Correlation, With Those Significant at p < 0.05 Shown and Sample Size (n)

<table>
<thead>
<tr>
<th>Gas Flux and Soils</th>
<th>Drainage Class</th>
<th>WFPS (%)</th>
<th>Soil Temperature</th>
<th>CO₂ Flux</th>
<th>NO₃ Content</th>
<th>NH₄ Content</th>
<th>Soil C:N Ratio</th>
</tr>
</thead>
<tbody>
<tr>
<td>Ln CH₄ flux, well-drained</td>
<td>0.56 (126)</td>
<td>-0.43 (145)</td>
<td>-0.39 (151)</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Ln CH₄ flux, poorly drained</td>
<td>0.22 (118)</td>
<td>0.21 (128)</td>
<td>-0.21 (136)</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Ln N₂O flux, well-drained</td>
<td>-0.22 (122)</td>
<td>-0.20 (128)</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Ln N₂O flux, poorly drained</td>
<td>0.25 (104)</td>
<td>0.21 (104)</td>
<td>-0.15 (130)</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>CO₂ flux, well-drained</td>
<td>-0.31 (126)</td>
<td>0.36 (143)</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>CO₂ flux, poorly drained</td>
<td>-0.62 (122)</td>
<td>0.64 (132)</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

*Ln, natural logarithm.

### Table 4. Stepwise Regression Between CH₄, N₂O, and CO₂ Fluxes and Environmental Variables

<table>
<thead>
<tr>
<th>Gas Flux</th>
<th>Well-Drained Soils</th>
<th>Poorly Drained Soils</th>
</tr>
</thead>
<tbody>
<tr>
<td>CH₄ (mg CH₄·C m⁻² d⁻¹)</td>
<td>Ln CH₄ flux = 2.0 + 0.003 WFPS − 0.003 T</td>
<td>Ln CH₄ flux = 0.16 + 0.01 WFPS − 0.40 CO₂ emission + 0.12 T</td>
</tr>
<tr>
<td>NO₃ (µg N₂O·N m⁻² d⁻¹)</td>
<td>Ln N₂O flux = 3.5 − 0.02 T − 0.02 C:N ratio</td>
<td>Ln N₂O = 3.04 + 0.003 NO₃</td>
</tr>
<tr>
<td>CO₂ (µg CO₂·C m⁻² d⁻¹)</td>
<td>CO₂ flux = -0.84 + 0.01 WFPS + 0.20 T</td>
<td>CO₂ flux = 3.5 − 0.04 WFPS + 0.09 T</td>
</tr>
</tbody>
</table>

WFPS, water-filled pore space (%); T, soil temperature (°C); NO₃, nitrate content (mg N m⁻²).
declined with a decrease in WFPS (<70%) in the summer months, particularly July and August (Figure 1), often switching to minor sinks ranging from $-1.0$ to $-1.9$ mg CH$_4$-C m$^{-2}$ d$^{-1}$. No significant difference was observed in CH$_4$ consumption rates between years (2006–2008) in well-drained and poorly drained soils. On average, well-drained soils consumed $-409$ mg CH$_4$-C m$^{-2}$ yr$^{-1}$, while poorly drained soils emitted 2874 mg CH$_4$-C m$^{-2}$ yr$^{-1}$.

Figure 2. Relationship of soil percent water-filled pore space (WFPS) and temperature with mean daily CH$_4$ fluxes from well-drained ($n = 128$) and poorly drained soils ($n = 122$).
Stepwise multiple linear regression of CH$_4$ consumption rates at the plot scale (i.e., averaged in the plot at each sampling date) in well-drained soils showed that soil temperature and WFPS could explain 34% of the variability (Table 4 and Figure 2). CH$_4$ consumption rates were larger when soil temperatures were high and WFPS low. In the spring thaw season with larger WFPS (Figure 2), well-drained soils were smaller sources of CH$_4$ (Figures 1 and 2).

In poorly drained soils, WFPS, soil temperature and CO$_2$ emission rates could explain 30% of the variability in CH$_4$ emissions at the plot scale (Table 4). CH$_4$ emissions increased with an increase in soil temperature, when WFPS was high, and declined with a decrease in soil temperature (Figure 2). Average CH$_4$ consumption rates in the upland plot soils under American beech (OGF) were 1.6 times larger than in upland plot soils under sugar maple (SMF). Average soil pore air CH$_4$ concentration declined more markedly from the O to B horizons in the upland plot of the OGF than in the SMF site (Figure 3), supporting a faster CH$_4$ consumption rate in soils under American beech than under sugar maple.

Ratios of log transformed CO$_2$:CH$_4$ showed that an increase in WFPS in poorly drained soils result in linear decrease in the emission ratios thus the contribution of CH$_4$ efflux to the total C efflux increases (Figure 4). On the other hand, with an increase in WFPS in well-drained soils, the log-transformed CO$_2$:CH$_4$ ratio decreases thus leading to smaller CH$_4$ consumption and smaller CO$_2$ emissions into the atmosphere (Figure 4).

### 3.3. N$_2$O Fluxes

Both well- and poorly drained soils were sources of N$_2$O, with well-drained soils emitting 3 times less N$_2$O than poorly drained soils (Figure 5). When averaged, N$_2$O emissions from well-drained soils ranged from 71 to 130 µg N$_2$O-N m$^{-2}$ d$^{-1}$, while those from poorly drained soils ranged from 124 to 737 µg N$_2$O-N m$^{-2}$ d$^{-1}$ (Table 2). On certain sampling dates, particularly in June and July of 2006, atmospheric N$_2$O was consumed, being more pronounced in the well-drained soils of the OGF (Figure 5), reaching a maximum of $-528$ µg N$_2$O-N m$^{-2}$ d$^{-1}$.

N$_2$O fluxes were highly variable, particularly where background and larger, event-based emission occurred and no significant difference in emission rates between years (2006–2008) was observed. Background fluxes were interrupted by event-based fluxes in the summer months following rainfall. In July 2007, N$_2$O emissions from soils in the wetland A plot in SMF after a rainfall reached a maximum of 14.3 mg N$_2$O-N m$^{-2}$ d$^{-1}$. Well-drained soils under sugar maple in the SMF emitted 1.4 times more N$_2$O than well-drained soils under American beech in the OGF; however the differences were not significant. In poorly drained plots, soils under sugar maple emitted 3 and 4 times more N$_2$O than soils under American beech and eastern hemlock trees. When averaged, well-drained and poorly drained soils produced 37 and 115 mg N$_2$O-N m$^{-2}$ yr$^{-1}$, respectively.

N$_2$O fluxes from well-drained soils correlated significantly with CO$_2$ emission rates, soil C:N ratio and soil temperature, while N$_2$O fluxes from poorly drained soils correlated with soil C:N ratio, NO$_3$ and NH$_4$ contents (Table 3). Soil temperature and soil C:N ratios explained 10% of the variability in N$_2$O fluxes averaged at plot scale for each sampling date in well-drained soils, while soil NO$_3$ content explained 6% of the variability in N$_2$O fluxes from poorly drained soils (Table 4). However, mean annual N$_2$O fluxes from well- and poorly drained soils in deciduous forests and
boreal forest soils in northern Quebec [Ullah et al., 2009] showed a significant exponential relationship ($r^2 = 0.39; p < 0.05$) with soil C:N ratios, where an increase in soil C:N ratio accompanied a decrease in N$_2$O emissions (Figure 6).

[30] Potential denitrification rates of NO$_3$-amended soils were significantly higher in poorly drained soils than unamended soils, while we observed no significant response to NO$_3$ amendment in terms of increased denitrification potential in well-drained soils (Figure 7). A significant response to NO$_3$ amendment shows stronger N limitation of denitrifiers in poorly drained soils than in well-drained soils.

3.4. CO$_2$ Fluxes

[31] CO$_2$ emissions from well-drained soils were 1.3 times larger than from poorly drained soils, ranging from 1.4 to 2.9 g CO$_2$-C m$^{-2}$ d$^{-1}$ and 0.9 to 1.9 g CO$_2$-C m$^{-2}$ d$^{-1}$, respectively (Table 2). CO$_2$ emissions were larger in summer months than in spring, autumn and winter (data not shown). Both WFPS and temperature significantly correlated with CO$_2$ emissions, explaining 63 and 56% of the variability in CO$_2$ emission rates from well- and poorly drained soils, respectively (Tables 3 and 4).

3.5. Global Warming Potential

[32] When fluxes from poorly drained soils (5–15% of the total area of the watershed) were included in the GWP calculation of forested watersheds, the source strength of GWP was reduced with an increase area under poorly drained soils (Figure 8). Forested watersheds at ~12% poorly drained soils, become CH$_4$ neutral where consumption in the 88% well-drained soils balances emissions from the poorly drained soils. The source strength of GWP of forest soils was reduced by ~560 Kg CO$_2$ equivalent ha$^{-1}$ yr$^{-1}$ when trace gas fluxes from 15% of poorly drained soils was included in the GWP calculation (Figure 8).

4. Discussion

4.1. CH$_4$ Fluxes

[33] CH$_4$ flux from poorly drained soils followed a close correlation with soil moisture and temperature: in early summer, larger WFPS and warmer temperature led to larger CH$_4$ emissions with a lower CO$_2$:CH$_4$ emission ratio. With a decline in WFPS later in summer (July–September in 2006–2007), poorly drained soils switched to minor CH$_4$ sinks or sources with most of the C efflux in the form of CO$_2$ (Figure 4). This result has implications for net CH$_4$ fluxes from poorly drained soils in forested watersheds where a significant change in soil WFPS under climate change scenarios could potentially alter net CH$_4$ fluxes from poorly drained soils in forested watersheds [Yu et al., 2008]. Net nitrification rates (an aerobic process) in poorly drained soils

![Figure 4. Relationship between mean log-transformed CO$_2$:CH$_4$ ratio and mean percent water-filled pore space (WFPS) in well-drained and poorly drained soils in the OGF and SMF sites.](image-url)
were significantly smaller than in well‐drained soils [Ullah and Moore, 2009] resulting in the likelihood of an increase in redox potential promoting larger CH4 production (Figure 7). This was the case where larger CH4 emission rates were observed in early summer with larger WFPS in poorly drained soils (Table 1). Our results show that changes in soil temperature and moisture can have substantial influence on CH4 fluxes from forest soils often resulting in “hot moments,” such as peak emissions from poorly drained soils in early summer when WFPS is high with lower CO2:CH4 emission ratios. Our biweekly measurements may have missed many more such “hot moments” of CH4 fluxes and more detailed sampling, for example through automatic chambers, could improve the quantification of fluxes [Wu et al., 2010]. Our results cover two transects in two watersheds with 32 permanent gas measurement collars integrating the effect of both soil heterogeneity (drainage class) and vegetation differences on gas fluxes.

Well‐drained soils under American beech in upland plots in the OGF exhibited 1.6 times larger CH4 consumption rates than similar soils under sugar maple in the SMF. Potential CH4 consumption rates determined in the laboratory also showed significantly larger methanotrophic activity in soils under American beech in the OGF than in soils under sugar maple in the SMF [Ullah et al., 2008]. Mean soil air CH4 concentration was smaller in the OGF soil horizons than at the SMF site (Figure 3), also suggesting with an average of 7.8 ± 1.9 mg CH4·C·m−2·d−1, similar to fluxes observed in a forested swamp in the OGF (7.5 to 15 mg CH4·C·m−2·d−1 [Moore and Knowles, 1990]) and poorly drained soils in Nova Scotia (5.3 mg CH4·C·m−2·d−1 [Clair et al., 2002]) and larger than poorly drained boreal forest soils in central Quebec (0.36 mg CH4·C·m−2·d−1 [Ullah et al., 2009]). These poorly drained “hot spots” of CH4 emission have a significant influence on net CH4 flux at the watershed scale, even though their coverage is <12%. For example, taking average well‐drained and poorly drained soil CH4 exchange rates of −5 and 38 mg CH4 ha−1 yr−1, respectively, results in a landscape having zero net CH4 exchange with the atmosphere, when poorly drained soils occupy 12% of the landscape. Many forested landscapes contain a similar proportion of poorly drained soils [Creed et al., 2003].

Our range of CH4 consumption in well‐drained soils was in agreement with those reported in temperate deciduous forest soils elsewhere in North America and Europe [e.g., Crill, 1991; McHale et al., 1998; Bowden et al., 2000; Ambus and Robertson, 2006; Borken and Beece, 2006; Groffman et al., 2006]. Owing to their saturated soil moisture conditions (Figure 1), poorly drained soils emitted CH4, Figure 5. Seasonal variation in N2O fluxes from well‐drained and poorly drained soils in OGF and SMF sites, with standard error of the means (n = 4). On the x axis, Julian days of sampling dates are only shown for each year.
faster consumption rates in soils under American beech in the OGF. Well-drained soils under American beech in the OGF had higher total soil porosity than soils under sugar maple in the SMF (Table 1), and the effect of dominant tree species on CH$_4$ consumption rates may be due to the differences in soil bulk density, as sugar maple trees prefer coarse-textured soils, while American beech prefers fine textured soils. McHale et al. [1998] also suggested that soil porosity influenced diffusion of CH$_4$ into consumption zones, and Ambus and Robertson [2006] reported 1.8 times larger CH$_4$ consumption in an old-growth deciduous forest with a thicker litter layer than coniferous forest soils in Pennsylvania. Furthermore, well-drained soils in OGF responded more significantly to changes in %WFPS in terms of CO$_2$:CH$_4$ emission ratios (Figure 4) than similar soils in the SMF signifying the role of porosity and soil moisture content in diffusion limitation of CH$_4$ into consumption zones. These findings show that soils under American beech with a thicker O horizon have a larger porosity facilitating faster atmospheric CH$_4$ and O$_2$ diffusion into zones of CH$_4$ consumption in soils [Amaral and Knowles, 1997] compared to soils under sugar maple with a thinner O horizon.

4.2. N$_2$O Fluxes

[36] Given the high spatial and temporal variability in N$_2$O fluxes from well- and poorly drained soils, no significant influence of soils drainage class on net N$_2$O fluxes was observed, though net fluxes from poorly drained soils were 3 times larger than those from well-drained soils (Table 2). Mean N$_2$O emission rates from well-drained soils were in the wide range for deciduous forests in the northeastern USA reported by McHale et al. [1998] and Bowden et al. [2000], but smaller than those measured by Groffman et al. [2006]. Even though the difference was statistically nonsignificant, mean N$_2$O emissions were 1.4 times lower from well-drained soils under American beech in the OGF than from sugar maple in the SMF. Net N mineralization rates were also 1.5 times slower in well-drained soils under American beech in the OGF than from sugar maple in the SMF [Ullah and Moore, 2009] and net nitrification rates in these sites showed a significant linear relationship with average N$_2$O emission rates ($r^2 = 0.80$, $n = 4$, data not shown), which suggests a coherent dependence of N$_2$O emissions on N mineralization rates in well-drained soils [Ambus et al., 2006].

[37] N$_2$O emissions from poorly drained soils were variable and ranged from $-0.7$ mg N m$^{-2}$ d$^{-1}$ (consumption) to 14.3 mg N m$^{-2}$ d$^{-1}$ (emission) signifying background, event and seasonal fluxes [Brumme et al., 1999]. The larger N$_2$O emissions occurred in summer months with warmer soil temperatures following rainfall events and after the lowering of water table from the surface to about 10 cm below the surface. The falling water level may have led to larger N mineralization rates in the surface layers enhancing N$_2$O emissions and at the same time poising the redox potential at a higher level resulting in minor CH$_4$ emissions and/or consumption in poorly drained soils. These event-based larger N$_2$O fluxes may be frequent and missed by biweekly flux measurement campaigns, requiring a more temporally intensive sampling scheme. In poorly drained plots, soils under sugar maple produced 3 and 4 times more N$_2$O than soils under American beech and eastern hemlock trees suggesting that N$_2$O fluxes may have been influenced by the litter N input (Table 1) produced by the dominant trees in the plots (Table 1). Mean N$_2$O fluxes from poorly drained soils in our study sites were in the broader range of N$_2$O fluxes reported from temperate riparian forest soils [Ullah and Zinati, 2006] but smaller than from the Lower Mississippi River floodplain forest soils [Yu et al., 2008].

[38] The larger N$_2$O emission observed from poorly than well-drained soils appears to be associated with greater denitrifier activity (Figure 7). NH$_4$NO$_3$ amendments of
repacked soils cores collected from these plots showed significantly larger net N₂O emission responses from poorly drained than from well-drained soils [Ullah et al., 2008]. The significant response of poorly drained soils to NO₃ addition through larger total N₂O emissions determined through C₂H₂ block techniques showed that denitrifier activity was limited by available mineral N content. Nitriﬁcation enzyme activity was signiﬁcantly smaller in poorly drained soils than well-drained soils [Ullah and Moore, 2009]. Thus it appears that denitrification is the major source of N₂O emission from poorly drained soils and both NO₃ and NH₄ contents signiﬁcantly correlated with N₂O emission (Table 3). Nitrifier enzyme activity and net nitriﬁcation rates were signiﬁcantly larger in well-drained than poorly drained soils [Ullah and Moore, 2009], suggesting that nitrifiﬁcation is probably the major source of N₂O emissions from well-drained soils. This finding is further supported by the correlation of net N mineralization rates with N₂O emissions from well-drained soils.

[39] Occasional atmospheric N₂O consumption was also observed (Figure 5), a feature that has often been ignored or poorly understood [Clough et al., 2005; Chapuis-Lardy et al., 2007; Frasier et al., 2010]. N₂O consumption was more pronounced in the summer of 2006 than in 2007, with higher annual precipitation in 2006 (1343 mm) than in 2007 (999 mm), which may have led to higher soil moisture and the creation of anoxic microsites consuming atmospheric N₂O. Wetter soil conditions led to lower net nitrification rates in well- and poorly drained soils (15 and 7 mg N m⁻² d⁻¹, respectively) in 2006 than in 2007 (29 and...
22 mg N m$^{-2}$ d$^{-1}$, respectively) creating NO$_3$ limitation for denitrification [Ullah and Moore, 2009]. Potential N$_2$O consumption rate in soils collected from well-drained plots in OGF and SMF was mainly driven by wetter soil conditions, amount of organic matter and soil NO$_3$ limitation [Frasier et al., 2010] suggesting that wetter conditions in the summer of 2006 may have been responsible for N$_2$O consumption. Frasier et al. [2010] showed that thicker organic soil layer under American beech and eastern hemlock trees in the OGF maintained a faster N$_2$O consumption potential than soils under sugar maple in the SMF. This is in agreement with the faster in situ rates of N$_2$O consumption observed in well-drained soils under American beech in the OGF compared to well-drained soils in the SMF (Figure 5). Both denitrifier and nitrifier denitrification may have been responsible for atmospheric N$_2$O consumption [Wrage et al., 2001; Vieten et al., 2008] and Castro et al. [1993] also reported N$_2$O consumption in spruce-fir forest soils under condition of low soil NO$_3$ concentration and high soil moisture. Dong et al. [1998], Goossens et al. [2001] and Peichle et al. [2010] also observed consumption of N$_2$O in temperate deciduous forest soils ranging from $-14$ to $-1584$ g N $\mu$g m$^{-2}$ d$^{-1}$. Net N$_2$O fluxes from well drained soils under American beech and sugar maple averaged $72 \pm 17$ and $130 \pm 7$ $\mu$g N m$^{-2}$ d$^{-1}$, respectively, when N$_2$O consumption rates were included in the calculation of mean daily N$_2$O fluxes; however, net fluxes averaged $132 \pm 12$ and $156 \pm 15$ $\mu$g N m$^{-2}$ d$^{-1}$ when consumption rates were excluded from the calculation. Therefore, it is critical to account for N$_2$O consumption in the overall net flux calculation.

The complex interactions of soil C and N content and availability, season and environmental conditions led to poor correlations between individual N$_2$O fluxes and environmental variables. Averaged plot-scale N$_2$O fluxes from well-drained soils correlated negatively with soil temperature, CO$_2$ emissions and soil C:N ratio and plot-scale N$_2$O emissions from poorly drained soils correlated positively with NO$_3$, NH$_4$ concentrations and negatively with soil C:N ratios (Table 3). Given the large spatial and temporal variability in N$_2$O fluxes and the interaction of various soil and microbial processes controls, our data set did not identify strong predictive relationships of N$_2$O fluxes with plot scale variables such as soil moisture, temperature, NO$_3$, NH$_4$, DOC, total dissolved nitrogen, litter fall N content and N mineralization, a pattern encountered by other researchers [e.g., Groffman et al., 2000]. However, the estimated annual N$_2$O flux showed a negative relationship with soil C:N ratio both in well- and poorly drained soils (Figure 6). Similar relationships between soils C:N ratios and N$_2$O fluxes from forest soils has been reported [Klemetsdsson et al., 2005; Pilegaard et al., 2006; Ernfors et al., 2008] suggesting that this may be an integrating soil variable to predict broad variations in N$_2$O flux at annual timescales. When annual N$_2$O fluxes from both well- and poorly drained soils were combined with those from boreal forest soils and regressed on soil C:N ratios, an exponential relationship ($r^2 = 0.39$) was observed (Figure 6). Klemetsdsson et al. [2005] and Ernfors et al. [2008] reported a similar exponential relationship between N$_2$O fluxes and C:N ratios in deciduous and coniferous forest soils in Sweden. The link is between soils C:N ratio and net N mineralization and nitrification rates [Ullah and Moore, 2009; Ullah et al., 2009].

### 4.3. CO$_2$ Fluxes

Soil temperature and moisture explained 63 and 56% of the variability in CO$_2$ emission from well- and poorly drained soils, which is consistent with the findings of Crill [1991], Raich and Schlesinger [1992], Peterjohn et al. [1994], Davidson et al. [1998], Bowden et al. [2000], Risk et al. [2002] and Wu et al. [2010]. In the regression models, the standardized regression coefficients for soil temperature and moisture were 0.86 and 0.14, respectively, in
well-drained soils, while in poorly drained soils the coefficients were 0.45 and −0.42, respectively. This observation shows that soil temperature is more critical in explaining CO₂ fluxes than soil moisture in well-drained soils, while soil moisture is more important in regulating CO₂ emission from poorly drained soils, as seen in the CO₂:CH₄ emission ratios. Crill [1991] and Lessard et al. [1994] also observed a similar response of CO₂ emissions from well-drained soils to soil temperature in deciduous forest soils and our data suggest that soils drainage class is important when estimating CO₂ emissions from forested landscapes. This is important because calculation of net GWP of trace gas fluxes from forest soils could be greatly under or overestimated from deciduous forest soils in Eastern Canada if the impact of soils drainage class on CO₂ fluxes is not accounted for in the calculation.

4.4. Net Global Warming Potential

[42] Poorly drained soils in deciduous forests contribute significantly to reduction in net GWP when their net fluxes of CH₄, N₂O and CO₂ are included in the calculations. Even though N₂O and CH₄ fluxes are larger from poorly drained soils than from well drained soils, a 1.3 times reduction in CO₂ emissions from poorly drained soils resulted in reduced source strength of GWP from forest soil when fluxes from the wetlands (5–15% of the total area) were included in the GWP calculation (Figure 8). This result shows that it is critical to account for the fluxes of greenhouse gases from poorly drained soils and include it in net C flux budgets of temperate deciduous forest soils [Yu et al., 2008]. Forest restoration for C sequestration in the region may be likely to benefit from techniques that would retain a relatively larger proportion of (10–20%) of poorly drained soils in the restored forest to optimize C sequestration credits on mole per mole basis relative to net CO₂, N₂O and CH₄ fluxes. Total soil C averaged 8% in well-drained and 16% in poorly drained soils in the top 10 cm in these forests. This observation supports the general conclusion that restoration of forests with 10–20% of land maintained under poorly drained soils would not only lead to lower net GWP but would also increase sequestration of C in soils.

5. Conclusions and Implications

[43] Soils drainage class significantly influenced CH₄ fluxes from forest soils, with consumption in well-drained soils and emission from poorly drained soils. Our data suggest that temperate deciduous forests with 10–12% poorly drained soils out of the total land area would have a net zero flux of CH₄, when emissions from poorly drained soils are included in the overall CH₄ flux from these forests. Within each soils drainage class, soil moisture and temperature can be used to extrapolate plot scale fluxes to larger spatial units. Larger CH₄ consumption rates in well-drained soils under American beech appear to result from faster diffusion of atmospheric CH₄ into consumption sites through the porous upper soil profile, compared to less porous soils developed under sugar maple.

[44] Soils drainage class also significantly influenced microbial sources of N₂O production through denitrification and nitrification rates; our data suggest that denitrification is a major source of N₂O in poorly drained soils, while it is nitrification in well-drained soils. Poorly drained soils produced 3 times more N₂O than well-drained soils; however, this difference is not significant given the larger variability of fluxes driven by baseline and event-based fluxes ("hot moments") in both well- and poorly drained soils. N₂O emissions were higher from soils developed under sugar maple than those under American beech trees in well-drained soils and eastern hemlock trees in poorly drained soils, associated with differences in rates of N cycling. The predictive relationship of hourly N₂O fluxes with climate and soil variables was weak but annual N₂O fluxes correlated significantly with soil C:N ratio. Atmospheric N₂O consumption in forest soils was mainly driven by high soil moisture, and low nitrification rates and thus it is important to account for N₂O consumption when calculating net N₂O fluxes from forest soils.

[45] Our results suggest that poorly drained soils developed in low-elevation areas of temperate deciduous forests in the St. Lawrence River valley can have significant bearing on net greenhouse gas fluxes and GWP from these forests and inclusion of these wetlands in greenhouse gas models is recommended for improved prediction of fluxes; and calculation of C sequestration credits as part of forest restoration.

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References


Bélanger, L., and M. Grenier (2002), Agriculture intensification and forest fragmentation in St. Lawrence Valley, Quebec, Canada, Landscape Ecol., 17, 495–507.


Corre, M. D., J. D. Pennock, C. V. Kessel, and D. K. Elliot (1999), Estimation of annual nitrous oxide emissions from a transitional grassland-forest region in Saskatchewan, Canada, Biogeochemistry, 44, 29–49.


McClain, M. E., et al. (2003), Biogeochemical hot spots and hot moments at the interface of terrestrial and aquatic ecosystems, Ecosystems, 6, 301–312.


Pilegaard, K., et al. (2006), Factors controlling regional differences in forest soil emission of nitrogen oxides (NO and N2O), Biogeoosciences, 3, 651–661.


