Controls on the heterogeneity of soil respiration in a tolerant hardwood forest

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The spatial and temporal distribution of soil respiration (Rs) in forested landscapes and its control by environmental conditions and carbon pools has not been sufficiently investigated. A Rs monitoring strategy targeting different topographic features within a sugar maple forest on the Algoma Highlands on the Canadian Shield revealed that the critical transition zones (transiently wet areas adjacent to wetlands, streams, and lakes) yielded significantly larger Rs than adjacent upland or wetland portions of the catchment. Environmental conditions (soil temperature and soil moisture) explained the majority of variance in Rs. An exponential relationship in which the exponent is a polynomial expression that is linear with respect to temperature (°C) and quadratic with respect to moisture (% by volume) explained 57.0% of the variance in Rs (μmol CO₂ m⁻² s⁻¹). However, inclusion of the quantity of carbon and substrate quality (carbon: nitrogen ratio) in the freshly fallen leaves, and the organic and/or mineral soils into the polynomial regression model explained an additional 15.3% of the variance in Rs (μmol CO₂ m⁻² s⁻¹). This study highlighted the critical transition zone as major sites of Rs because of the synchronicity in optimal temperature and moisture conditions during the growing season and the large pool of high quality substrate that accumulates in topographic depositional areas.


1. Introduction

Forest soils of the Northern Hemisphere are an important reservoir of carbon [Dixon et al., 1994; Schimel et al., 1995]. In Canada, the majority of forests are situated on landscapes composed of a mosaic of topographic features, including upland, critical transition zone (i.e., areas in isolated depressions or adjacent to wetlands, streams, or lakes), and wetlands (i.e., bogs, fens, marshes, and swamps). Major efforts are underway (e.g., Fluxnet Canada) to quantify the CO₂ sinks and sources from ecosystems using eddy covariance methods [Margolis et al., 2006]. Although useful insights into ecosystem respiration rates have been gained using eddy covariance methods [e.g., Coursolle et al., 2006], one cannot assess the heterogeneity in ecosystem respiration rates among topographic features (e.g., uplands and wetlands) within the effective fetch of the eddy covariance sensors [Schmid, 2002; Savage and Davidson, 2003]. Understanding the spatial and temporal heterogeneity in soil respiration (Rs) and the controls on that heterogeneity across the landscape is essential for predicting soil CO₂ efflux in areas where there is substantial complexity of topographic features.

Considerable effort has gone into understanding the importance of environmental conditions and carbon pools on Rs within forests. The importance of soil temperature controls on Rs has been well documented, showing exponential increases in Rs with temperature [Kirschbaum, 2006]. The importance of soil moisture controls on Rs has also been documented [Davidson et al., 1998]. Rs response to soil moisture is uni-modal, oxygen-limited at high soil moisture and limited by diffusion of substrate at low soil moisture. There is less certainty about the importance of the quantity and quality of carbon pools for Rs, despite the fact they are the substrates for decomposition [Kahkonen et al., 2002; Schwendenmann et al., 2003; Janssens and Pilegaard, 2003; Rodeghiero and Cescatti, 2005]. Carbon pools within freshly fallen leaves, the forest floor and organic-rich mineral soils have been identified as important sources of carbon for Rs and differ in their lability and/or availability for decomposition [Bourbonnière and Creed, 2006].

Studies that compare Rs among different topographic features are needed, as topography strongly influences soil environmental conditions and carbon pools within a landscape. As proposed in the catena concept [Milne, 1936], soils develop as a result of the interaction of topographically controlled static and dynamic factors [Young, 1972]. Static factors are controlled by site differences, such as elevation,
slopes and aspect, and influence the radiation, temperature and moisture of the site. Dynamic factors are controlled by the relative position of the site within the catena and reflect the transport of particulate and dissolved materials downslope. Soils formed of the same material may differ because of downslope transport processes that include: (1) differential drainage conditions; (2) differential transport and deposition of suspended materials; and (3) differential leaching, translocation and redeposition of soluble materials [Hall and Olson, 1991]. These catenary processes lead to differences in the concentrations of precursors and products of carbon cycling, the environmental conditions that influence the rate of carbon cycling and the alternative fates of carbon (sequestered or exported to atmospheric and/or aquatic systems).

[5] Research that has focused on Rs from individual topographic features exist but the majority of efforts to quantify Rs from forests have focused on upland areas (see review by Hibbard et al. [2005]). Less is known about Rs from wetlands [Moore and Dalva, 1993; Waddington and Roulet, 1996; Bubier et al., 2003], particularly forested swamps that occur in localized depressions and are difficult to delineate by remote sensing (e.g., aerial photography, satellite imagery) because they are often hidden underneath a forest canopy [e.g., Creed et al., 2003]. Very little is known about Rs from transition zones [Yu et al., 2008], where hydrological flowpaths converge and mix with other redistributitional processes and may represent an important area for carbon cycling [McClain et al., 2003].

[6] Despite the importance of transition zones and recent interest in studying their dynamics there is confusion as to their definition and nomenclature [Yarrow and Marin, 2007]. Under the umbrella classification of transition zone there are numerous subcategories depending on the emphasis on the structure or function of the transition zone. Community ecologists focus on the importance of gradients in community structure have adopted terms such as ecotone and ecocline, while ecosystem scientists typically focus on the functional role of the abiotic entities [Yarrow and Marin, 2007]. Under the category of transition zones, critical transition zones are defined as hybrid ecosystems that serve as conduits for fluxes of material and energy between systems [Ewel et al., 2001]. The term critical transition zone best describes the dynamic hydrologic variability of the transiently saturated upland area which has vegetation and soil structure consistent with the upland areas.

[7] The goal of this study was to develop a predictive model of Rs based on environmental conditions and carbon pools characteristic of topographic features along hillslopes. Topographically driven gradients of environmental conditions and carbon pools were measured and linked between these factors and Rs were explored. The study was established within the Turkey Lakes Watershed (TLW) experimental forest on the Algoma Highlands in central Ontario [Beall et al., 2001; Jeffries and Foster, 2001]. The TLW contains an uneven aged, old-growth sugar maple (Acer saccharum Marsh.) forest on a landscape where the topographic relief creates a mosaic of substrate and environmental conditions which may lead to differential potentials for Rs within the landscape.

[8] Specifically the following questions are addressed: (1) Is there heterogeneity in Rs in a forest where topographically controlled gradients are important? (2) What factors control this heterogeneity? (3) Where and when do optimal conditions in these factors occur? These questions are answered using a combined monitoring-modeling approach with the objective of understanding the physical and substrate controls on the heterogeneity in Rs within a landscape where topography exerts strong controls on the biogeochemical processes.

2. Study Area

[9] The Turkey Lakes Watershed (TLW) is an experimental forest (47°03′00″N and 84°25′00″W) located on the Algoma Highlands on the northern edge of the Great Lakes-St. Lawrence Forest Region, the second largest forest region in Canada that, with the exception of a small gap where the Boreal Forest Region touches the north shore of Lake Superior, extends from southeastern Manitoba to the Gaspé Peninsula.

[10] The climate is continental and is strongly influenced by the proximity of Lake Superior, with mean annual precipitation and temperature of 1200 mm and 5.0°C, respectively, for the period 1981 to 2006. A snowpack persists from late-November, early December through to late-March, early April. Peak stream discharge occurs during snowmelt and again in October to November during autumn storms.

[11] The landscape is controlled by bedrock and contains rugged slopes terminating abruptly in depressions that may be connected or disconnected from the drainage systems, forming topographic features with distinct physical, chemical, and/or biological properties. These include uplands (frequently dry), critical transition zones (intermittently wet) and wetlands (frequently wet). Glacial till covers the bedrock and Orthic Ferro-Humic and Humo-Ferric podzolic soils have developed with dispersed pockets of highly humified organic deposits (Ferric Humisols) found in bedrock-controlled depressions and adjacent to streams and lakes [Wickware and Cowell, 1985].

[12] TLW is covered by an old-growth (140 years and older), hardwood forest that is tolerant to shade and dominated (90%) by a relatively homogenous canopy of sugar maple (Acer saccharum Marsh.). Upland overstory associates include white pine (Pinus strobus L.), white spruce (Picea glauca Moench Voss.), ironwood (Ostrya virginiana (Mill.) K.Koch.), red oak (Quercus rubra L.) and yellow birch (Betula alleghaniensis Britton). Wetland stands are typically mixtures of black ash (Fraxinus nigra Marsh.), eastern white cedar (Thuja occidentalis L.), red maple (Acer rubrum L.), balsam fir (Abies balsamea (L.) Mill.), yellow birch, and tamarack (Larix laricina [DuRoi] K. Koch.) [Wickware and Cowell, 1985]. Stand density (904 stems ha⁻¹), dominant height (20.5 m), diameter at breast height (15.3 cm), and mean basal area (25.1 m² ha⁻¹) are relatively uniform across vegetation types [Jeffries et al., 1988]. The sparse understories of upland stands are dominated (more than 95%) by saplings and seedlings of sugar maple with a depauperate herb flora dominated by Maianthemum racemosum L. Link, Streptopus roseus Michx., Polygonatum pubescens ([Wild.] Pursh), and a variety of ferns. The wetland understories are composed of the seedlings and saplings of the overstory trees, various
ferns, herbs (e.g., Caltha palustris L., Carex trisperma Dewey., and Impatiens capensis Meerh.) and a mix of feather and sphagnum mosses (e.g., Sphagnum cuspidatum Ehrh. Ex Hoffm. and Ptilium cristacastrensis (Hedw.) De Not.).

3. Methods

3.1. Classification of Topographic Features Along Hillslope Transects

Within the TLW, a 6.3 ha catchment (C38) was chosen as a representative catchment for intense study (Figure 1). Sampling transects were established on three northerly and planar hillslopes, with each sampling transect including upland (crest, backslope) and critical transition zone (footslope, toeslope) positions as defined by Conacher and Dalrymple [1977] and wetland positions (the center of the wetland or “inner wetland” and the perimeter of the wetland or “outer wetland”) and are briefly described here. The crest is a flat area on top of the ridge, characterized by vertical leaching and infiltration processes. The backslope is the steep area near the middle of the hillslope where there is rapid transport of water and materials in lateral flows. The footslope is a moderately sloped area between the steep upland and gentle-sloped lowland where colluvium is deposited from the upslope. The toeslope is the flat to gently sloped area at the base of the hillslope, receiving alluvium from upslope and water flows from both the upland and the wetland. The outer wetland is the concave, saturated and occasionally inundated area around the perimeter of the wetland. The inner wetland is the convex, frequently saturated (although occasionally drying in the surface layers) area in the central portion of the wetland. Topographic features were instrumented for synoptic sampling of Rs and continuous monitoring of soil temperature and soil moisture, with all instruments serviced from a boardwalk to minimize soil disturbance. Topographic features were classified using digital terrain analysis, detailed in Webster [2007] and briefly summarized here.

Catchments C38 was discretized into topographic features using digital terrain analysis performed within the geographical information system software Terrain Analysis System (TAS) 2.0.9 [Lindsay, 2005] using a 2.5 m digital elevation model (DEM). The DEM was derived from spot height data collected by Light Detection and Ranging (LiDAR) technology that was resampled to 5 m resolution using bilinear interpolation.

The topographic classification of hillslopes was achieved through the application of a fuzzy semantic import model based on expert knowledge [MacMillan et al., 2000]. This model uses imprecise and overlapping semantics to describe or classify data [Irwin et al., 1997]. A map was created for each topographic feature with each pixel assigned the probability of belonging to that topographic feature. A final map was produced by comparing all the individual maps and each pixel classified into the topographic feature with the highest probability. Wetlands were identified using a stochastic depression analysis developed by Lindsay and Creed [2006]. This analysis is based on a Monte Carlo procedure [Burrough and McDonnell, 1998; Fisher, 1998] that identifies the probability that a pixel in the DEM is a depression. Probability values used to define outer wetlands were optimized by comparison to the boundaries of ground-truthed wetlands. The inner wetland area was defined as the portion of the wetland with peat depths greater than 70 cm delineated from an interpolated ground-based survey on a 5 m grid within the wetland. This depth represents the extent of “shallow” peat areas, beyond which depths increase rapidly.

Applying this topographic classification of hillslopes to the catchments showed that catchment C38 (6.3 ha) is contains northerly hillslopes composed of uplands (60.2%, with 54.7% backslope and 5.5% crest), critical transition zones (14.8%, with 9.9% toeslope and 4.9% footslope) and wetlands (25.1%, with 14.6% outer wetland and 10.5% inner wetland) (Figure 1).

3.2. Sampling Strategy

3.2.1. Soil Respiration

Rs was determined at a total of 18 collars (at each of the six topographic features on three transects) on all sampling dates in 2005. Sampling was conducted approximately daily during spring melt and autumn storms, weekly during early and late growing season, and every two weeks during the middle of the growing season. Sampling at each plot consisted of three consecutive midday measurements to capture day-to-day changes in peak daily Rs, for a total of 64 sampling events during the April to November period.
[18] Sampling was done using ground-based chamber measurements that have been used successfully in many environments [e.g., Davidson et al., 2002; Pumpanen et al., 2004; Butnor et al., 2005] and have the flexibility to measure Rs in complex terrain. Square aluminum collars, each enclosing a soil area of 0.21 m², were inserted approximately 2 to 10 cm into the soil, depending on the local slope, such that the collar edges were level. Small understory plants and seedlings that grew within the collars between sampling events were clipped to remove the effect of aboveground plant respiration. Clipping occurred at least 24 h prior to sampling to minimize pulses of decomposition resulting from clipping. Mosses, which occurred exclusively at wetland sites during the growing season, were allowed to grow because removing them would result in excessive disturbance of the soil surface. Moss respiration contributes only a minor fraction (estimated to be about 15% based on the moss species present) of the total amount of CO₂ released from the forest floor [Swanson and Flanagan, 2001].

[19] Midday carbon dioxide efflux was determined with a “non-steady state” chamber method [Livingston and Hutchinson, 1995] by inverting a portable acrylic flux chamber over the collars in a water-filled channel to create an air-tight seal. The chambers were painted white on the outside to reflect sun and minimize heat absorption and black on the inside to eliminate any light that gets through the white paint to minimize CO₂ uptake due to photosynthesis. Chambers were also equipped with a mixing fan placed horizontally at the top of the chamber to facilitate mixing without disturbing the air-soil boundary layer. Carbon dioxide concentrations within the chambers were measured with a Vaisala CARBOCAP Carbon Dioxide Probe GMP343 (Vaisala, Helsinki, Finland) infrared gas analyzer (IRGA), logged with a Vaisala MI70 controller. The controller had an internal compensation for humidity (50%), oxygen concentration (20.95%), pressure (101.3 kPa) and temperature (built-in temperature sensor). Fluxes were calculated by linear regression of the slope of increasing CO₂ concentration in the chambers with time. The maximum concentration of CO₂ observed in a chamber was typically in the range of 400 to 650 ppm at the end of a 5-min run. Fluxes were scaled according to the total volume determined by summing the volume of the chamber (dimensions of 49.5 cm × 49.5 cm × 40 cm = 90.2 L) with the volume of each collar, adjusting for the topography of the surface within the collar, and corrected for chamber temperature (Vaisala HM70) and ambient pressure.

3.2.2. Environmental Drivers

[20] Soil temperature and soil moisture were measured at 5 cm below the forest floor. Soil temperature was measured with thermocouples constructed using thermocouple wire (Type T Omega FF-T-24-TWSH) and embedded into a 10 cm by 0.635 cm I.D. copper tube with epoxy. Soil moisture was measured using a Campbell Scientific CS616 Water Content Reflectometer (WCR, Campbell Scientific Canada Corp., Edmonton, AB). Output from the WCRs was converted to relative volumetric water content based on calibration equations provided by the manufacturer for upland soils and provided by Yoshikawa et al. [2004] for the wetland soils. The thermocouples and WCRs were connected to a Campbell Scientific CR10X data logger via an AM16/32 relay multiplexer, and the system was powered by a 30 W solar panel and a 7 Ah battery. Sensors were sampled every 5 min and 30 min means were stored by the data loggers.

3.2.3. Substrate

[21] Substrates were sampled that reflected a range in ages [Bourbonniere and Creed, 2006], including: (1) green leaves (GRL) representing the youngest carbon pool which enters the soil following precipitation events; (2) freshly fallen leaves (FFL) representing a relatively young (<1 year) carbon pool that is available for decomposition at the start of the next growing season; (3) forest floor including the litter (L) layer (1 year old material composed of the partially decomposed leaves from the previous year), the fibric (F) layer (2–3 years old material composed of fragmented leaves collected below the litter), and the humic (H) layer (4+ years old material composed of degraded leaves collected below the fibric layer), as well as fine roots that grew within the LFH [Fahey and Hughes, 1994]; and (4) the organic-rich surface layer of the A-horizon of mineral soil to a maximum depth of 5 cm or peat to a depth of 5 cm (soil).

[22] Green leaves were quantified by measuring leaf area index (LAI) by taking nine radiation measurements at each topographic feature using a Li-Cor LAI-2000 m [Li-Cor, 2004] and corrected with open site radiation measurements from a nearby clearing. To minimize the effects of multiple scattering of light within the canopy on the LAI-2000 measurement, rings 4 and 5 were removed in the postprocessing [Chen et al., 2006]. Five replicates of FFL were collected on a 30 cm × 30 cm mesh placed on the surface of the forest floor prior to leaf fall and collected prior to the development of a snowpack. Six replicates of LFH were collected by cutting 15.5 cm × 15.5 cm blocks into the forest floor during summer. For crest, backslope, footslope and toeslope features, six replicates of soil were collected for chemistry with an open-sided sampler (40 cm × 4.4 cm I.D.) and three replicates of soil were collected for bulk density with a split core sampler (32 cm × 4.8 cm I.D.). Stones greater than 2 mm were removed and weighed to correct for coarse fragment content. In wetland plots, six replicates of soil were collected for chemistry and three replications of soil were collected for bulk density with a split core sampler (32 cm × 4.8 cm I.D.). Stones greater than 2 mm were removed and weighed to correct for coarse fragment content. In wetland plots, six replicates of soil were collected for chemistry and three replications of soil were collected for bulk density with a split core sampler (32 cm × 4.6 cm I.D.).

[23] Carbon in GRL was calculated by multiplying the mean LAI by the specific leaf area for sugar maple (36.3 m² kg⁻¹ C) [White et al., 2000]. Carbon and nitrogen pools (g m⁻²) in FFL were calculated by multiplying carbon and nitrogen concentration (g g⁻¹ litter) by litter mass (g litter m⁻²) (Table 1). Carbon and nitrogen pools in LFH and soil were calculated by multiplying carbon and nitrogen concentration (g g⁻¹ soil or peat) by bulk density (g soil or peat m⁻³) and then by depth (m) (Table 1).

3.3. Model Development

[24] A comparison of models of Rs from the literature [Webster, 2007] identified that Rs could be best explained using an exponential relationship [Tang and Baldocchi, 2005] in which the exponent is a polynomial expression that is linear with respect to temperature (°C), quadratic
with respect to moisture (% by volume) and with linear offsets for carbon quantity and substrate quality. The nonlinear regression was performed using SigmaPlot 7.0 [SPSS Inc., 2001].

### 3.4. Statistical Analyses

Differences in Rs, substrate and soil environmental conditions among topographic positions were examined using one-way analysis of variance (ANOVA) or, if data were not normally distributed, ANOVA on ranks (Kruskall-Wallis). The statistical significance of differences between topographic features were assessed by pair-wise comparison tests (Tukey’s for parametric and Dunn’s for nonparametric data) using SigmaStat 2.03 [SPSS Inc., 1997]. Due to pulses in Rs following rain events [Lee et al., 2002; Yuste et al., 2005], Rs measurements collected within 24 h of precipitation events >10 mm day⁻¹ were removed from all analyses.

### 4. Results

Rs changed over the snowfree period (Figure 2), with low values during snowmelt (median 0.74 μmol CO₂ m⁻² s⁻¹), peaking in summer (median 4.08 μmol CO₂ m⁻² s⁻¹) and then declining throughout the late autumn (median 0.99 μmol CO₂ m⁻² s⁻¹). Rs varied significantly (H = 122.6, d.f. = 5, p < 0.001) among the topographic features during the snow free season (April 1

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**Figure 2.** Soil respiration (μmol CO₂ m⁻² s⁻¹) during April to November 2005 without rain events >10 mm within 24 h of sampling for wetland, critical transition zone, and upland. Individual dots indicate the median Rs for the three consecutive midday measurements of the synoptic sampling event.

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**Table 1.** Summary of Physical and Chemical Properties of Soil From Plots on Transects Within Catchment C38

<table>
<thead>
<tr>
<th>Pool</th>
<th>N</th>
<th>Statistic</th>
<th>Inner Wetland</th>
<th>Outer Wetland</th>
<th>Toeslope</th>
<th>Footslope</th>
<th>Backslope</th>
<th>Crest</th>
</tr>
</thead>
<tbody>
<tr>
<td>Freshly fallen leaves (FFL)</td>
<td>90</td>
<td>Depth (g cm⁻³)</td>
<td>0.03</td>
<td>0.03</td>
<td>0.04</td>
<td>0.04</td>
<td>0.03</td>
<td>0.03</td>
</tr>
<tr>
<td></td>
<td></td>
<td>mean % C</td>
<td>47.45</td>
<td>46.25</td>
<td>46.38</td>
<td>46.24</td>
<td>47.55</td>
<td>47.57</td>
</tr>
<tr>
<td></td>
<td></td>
<td>(SD)</td>
<td>(0.77)</td>
<td>(1.14)</td>
<td>(1.32)</td>
<td>(1.19)</td>
<td>(1.20)</td>
<td>(0.87)</td>
</tr>
<tr>
<td></td>
<td></td>
<td>mean % N</td>
<td>1.33</td>
<td>1.26</td>
<td>1.06</td>
<td>0.99</td>
<td>1.04</td>
<td>0.93</td>
</tr>
<tr>
<td></td>
<td></td>
<td>(SD)</td>
<td>(0.23)</td>
<td>(0.19)</td>
<td>(0.12)</td>
<td>(0.15)</td>
<td>(0.18)</td>
<td>(0.11)</td>
</tr>
<tr>
<td>Forest floor (LFH)</td>
<td>108</td>
<td>Depth (g cm⁻³)</td>
<td>0.79</td>
<td>0.91</td>
<td>4.21</td>
<td>5.20</td>
<td>4.31</td>
<td>4.42</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Bulk density</td>
<td>0.11</td>
<td>0.12</td>
<td>0.09</td>
<td>0.08</td>
<td>0.08</td>
<td>0.09</td>
</tr>
<tr>
<td></td>
<td></td>
<td>mean % C</td>
<td>39.14</td>
<td>39.98</td>
<td>38.55</td>
<td>38.48</td>
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<td>39.69</td>
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<td></td>
<td></td>
<td>(SD)</td>
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<td>(2.12)</td>
<td>(5.78)</td>
<td>(7.58)</td>
<td>(6.65)</td>
<td>(5.22)</td>
</tr>
<tr>
<td></td>
<td></td>
<td>mean % N</td>
<td>2.27</td>
<td>2.32</td>
<td>1.85</td>
<td>1.88</td>
<td>1.83</td>
<td>1.85</td>
</tr>
<tr>
<td></td>
<td></td>
<td>(SD)</td>
<td>(0.15)</td>
<td>(0.29)</td>
<td>(0.26)</td>
<td>(0.33)</td>
<td>(0.28)</td>
<td>(0.13)</td>
</tr>
<tr>
<td>A- horizon or peat below forest floor to max 5 cm depth (soil)</td>
<td>108</td>
<td>Depth (g cm⁻³)</td>
<td>5.00</td>
<td>5.00</td>
<td>4.71</td>
<td>3.90</td>
<td>4.29</td>
<td>4.39</td>
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<tr>
<td></td>
<td></td>
<td>Bulk density</td>
<td>0.10</td>
<td>0.12</td>
<td>0.35</td>
<td>0.31</td>
<td>0.35</td>
<td>0.46</td>
</tr>
<tr>
<td></td>
<td></td>
<td>mean % C</td>
<td>39.50</td>
<td>36.44</td>
<td>21.16</td>
<td>19.37</td>
<td>17.32</td>
<td>19.47</td>
</tr>
<tr>
<td></td>
<td></td>
<td>(SD)</td>
<td>(2.84)</td>
<td>(7.07)</td>
<td>(10.94)</td>
<td>(8.39)</td>
<td>(8.62)</td>
<td>(10.80)</td>
</tr>
<tr>
<td></td>
<td></td>
<td>mean % N</td>
<td>2.33</td>
<td>2.17</td>
<td>1.23</td>
<td>1.18</td>
<td>0.97</td>
<td>1.10</td>
</tr>
<tr>
<td></td>
<td></td>
<td>(SD)</td>
<td>(0.20)</td>
<td>(0.38)</td>
<td>(0.47)</td>
<td>(0.42)</td>
<td>(0.35)</td>
<td>(0.36)</td>
</tr>
</tbody>
</table>
to November 30) (Figure 3, ‘All seasons’). Median midday Rs rates were highest in the footslope (3.07 \(\mu\)mol CO\(_2\) m\(^{-2}\) s\(^{-1}\)) and toeslope (2.98 \(\mu\)mol m\(^{-2}\) s\(^{-1}\)) features of the critical transition zone, lowest in the inner wetland (1.30 \(\mu\)mol CO\(_2\) m\(^{-2}\) s\(^{-1}\)) and outer wetland (0.82 \(\mu\)mol CO\(_2\) m\(^{-2}\) s\(^{-1}\)) features, and intermediate in the backslope (2.35 \(\mu\)mol CO\(_2\) m\(^{-2}\) s\(^{-1}\)) and crest (1.55 \(\mu\)mol CO\(_2\) m\(^{-2}\) s\(^{-1}\)) features of the upland.

The trend among topographic features was consistent. The wetland had low Rs, the upland had moderate Rs and the critical transition zone had high Rs (Figure 3). During the late summer period there is a distinct change in the pattern in Rs, with high production in the critical transition zone and inner wetland and lower rates from the upland and outer wetland. During the autumn storm period Rs in the inner wetland decreases and the backslope Rs increases, returning to the general pattern of critical transition zone > upland > wetland.

Figure 3. Box plots of soil respiration (\(\mu\)mol CO\(_2\) m\(^{-2}\) s\(^{-1}\)) for each topographic feature during different seasons and across all sampling dates (April to November 2005) without rain events >10 mm depth within 24 h of sampling. ANOVA on ranks (\(H = 122.6\), d.f. = 5) is significant at \(p < 0.001\). Features with different letters are significant at \(p < 0.05\) using Dunn’s method. The box represents the bounds of 25th, 50th (median), and 75th percentiles, and the bars indicate the 10th and 90th percentiles. Dots indicate extreme values outside the 10th and 90th percentiles.
4.1. Environmental Conditions Versus Rs

Temperature (T, °C) and moisture (M, %) conditions changed over the snowfree period (Figure 4). Soil temperatures were coolest during snowmelt (median 3.1 °C), peaking in the summer (median 14.8 °C) and then cooled through late autumn (median 4.7 °C). Soil moisture was wettest during snowmelt (median 51.8%) and dried to lowest levels during the summer (median 14.5%) and rewetted in the late autumn (median 34.0%).

Environmental conditions also varied significantly among topographic features (Figure 5). Temperature differences between topographic features were muted (median temperature ranged from 11.1 °C to 12.3 °C). A one-way ANOVA on ranks for soil temperature (H = 37.46, d.f. = 5, p < 0.001) showed a gradual decrease in median temperature from the crest (12.3 °C) and backslope (11.9 °C) in the upland to the footslope (11.1 °C) and toeslope (11.3 °C) of the critical transition zone, followed by a gradual increase from the critical transition zone to the outer and inner wetland (11.6 °C and 12.1 °C respectively). In contrast, there were dramatic differences in soil moisture among topographic features (median soil moisture ranged from 22.3% to 69.4%). A one-way ANOVA on ranks for soil moisture (H = 37.46, d.f. = 5, p < 0.001) showed a gradual decrease in median moisture from the crest (22.3%) and backslope (22.6%) in the upland to the footslope (30.0%) and toeslope (39.7%) of the critical transition zone, which were significantly drier than the outer (66.1%) and inner (69.4%) wetland.

The exponential function of Rs, whose exponent is a linear relationship to soil temperature and a quadratic function of soil moisture (% by volume) is presented in equation (1):

\[ Rs(n) = \exp(a_1 + a_2 \cdot T(n) + a_3 \cdot M(n) + a_4 \cdot M^2(n) + \varepsilon(n)) \]

where T is soil temperature in °C, M is soil moisture in % volume, \( a_i \) are fitted parameters and \( \varepsilon \) is the error term [Tang and Baldocchi, 2005]. Fifty-seven percent of variance in Rs could be explained by this model (p < 0.001, equation (2), Figure 6):

\[ Rs = \exp(-0.6826 + 0.1292 \cdot T + 0.0349 \cdot M - 0.0006 \cdot M^2) \]

The majority of the variance (48.1%) was explained by an exponential response to temperature (Q10 = e^0.1292 = 3.64). The remainder of the variance (8.9%) could be explained by a quadratic response to moisture, with optimal Rs, calculated from equation (2), to be at 29% soil moisture. Mean residual variation in the overall model of Rs was centered on zero, with slight positive anomalies during June and July, and slight negative anomalies in April, October and November. There was large variation in the magnitude of the residuals among topographic features which was most pronounced during the summer months of July and August. In the wetlands, residuals were small and centered at zero, thus modeled and observed data closely matched. In the toeslope and footslope, residuals were larger and biased to the positive and indicated observed Rs was greater than modeled Rs. In contrast, the residuals of the backslope and crest were biased to the negative and indicated that Rs was lower than predicted by the model.

4.2. Environmental Conditions and Substrate Versus Rs

Significant spatial heterogeneity in the C quantity was observed in FFL, LFH and soil (Table 2) whereas carbon concentrations were relatively uniform in the FFL and LFH but varied in the soil (Table 1). Despite the relative homogeneity in forest canopy, there appeared to be redistribution of FFL (Table 2). There was significant heterogeneity in mean carbon pools of FFL (p < 0.001), with larger
inputs in the footslope area (197 g m^{-2}), moderate inputs in the toeslope and crest (163 and 147 g m^{-2}) and the smallest litter inputs in the backslope and wetland areas (range of 122 to 127 g m^{-2}). There was also significant spatial heterogeneity in the LFH carbon pool, although the pattern is not consistent with FFL. Larger median carbon pools were recorded in the wetland features (2850 and 3250 g m^{-2}) due to greater depths and bulk density than the upland features (range of 1260 to 1360 g m^{-2}). Carbon pools contained within the soil were variable within features and there was a significant (p = 0.005) trend in median carbon between features, with the pattern different from all the other horizons. Within the soil, the largest carbon pool occurred at the crest (3350 g C m^{-2}) due to moderate carbon concentrations and high bulk density and the smallest pool at the inner wetland (1930 g C m^{-2}) having high carbon concentration but low bulk density, and the intermediate positions were not significantly different from either of the extreme positions (range of 2260 to 2790 g C m^{-2}).

[33] Significant spatial heterogeneity in substrate quality was found in FFL and LFH, but not in soil (Table 3). The C:N of FFL decreased significantly going down the slope (p < 0.001). Mean C:N of FFL was highest at the crest (52), moderate in backslope, footslope and toeslope (range 44 to 47) and lowest in wetland FFL (37). There was a similar spatial trend in the LFH quality (p < 0.001), with higher mean C:N in the upland features (range of 20 to 21) compared to the wetland (17 and 18). There was no significant difference in the mean C:N of the soil (range of 16 to 17, p = 0.963).

[34] Inclusion of the quantity of carbon in substrate as offset parameters to the environmental model significantly increased the variance explained by an additional 5.6% (r^2 = 0.626, p < 0.0001) over the model that included only environmental drivers (Table 3). The addition of the size of the carbon pool within FFL had a positive effect (p < 0.0001), the size of the carbon pool within LFH had no effect (p = 0.4899) and the size of the carbon pool within the soil had a negative effect (p < 0.0003). Inclusion of substrate quality, as measured by C:N of FFL (p < 0.0001), LFH (p < 0.0002) and soil (p < 0.0193), had a significant effect on modeled Rs and increased the variance explained by an additional 3.1% (r^2 = 0.601, p < 0.0001) over the model that included only environmental drivers. The C:N of the FFL had a negative effect on Rs while C:N of LFH and the soil had positive effects on Rs.

[35] There was a synergistic effect of including both carbon quantity and substrate quality terms together,

![Figure 5](image.png)

Figure 5. Box plots of daily environmental conditions for each topographic feature (April to November 2005): (a) Soil temperature (°C) (H = 37.46, d.f. = 5), and (b) soil moisture (volume %) (H = 2532, d.f. = 5). ANOVA on ranks for soil temperature and soil moisture is significant at p < 0.001. Features with different letters are significant at p < 0.05 using Dunn’s method. The box represents the bounds of 25th, 50th (median), and 75th percentiles, while the bars indicate the 10th and 90th percentiles. Dots indicate extreme values outside the 10th and 90th percentiles.
Table 2. Summary of ANOVA Results for Carbon Pools

<table>
<thead>
<tr>
<th>Pool</th>
<th>N</th>
<th>Statistic</th>
<th>Inner Wetland</th>
<th>Outer Wetland</th>
<th>Toeslope</th>
<th>Footslope</th>
<th>Backslope</th>
<th>Crest</th>
</tr>
</thead>
<tbody>
<tr>
<td>Carbon (g m(^{-2}))</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Freshly fallen leaves (FFL)</td>
<td>90</td>
<td>Mean</td>
<td>127</td>
<td>122</td>
<td>163</td>
<td>197</td>
<td>123</td>
<td>147</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Sig. Diff.</td>
<td>a</td>
<td>a</td>
<td>ab</td>
<td>b</td>
<td>a</td>
<td>ab</td>
</tr>
<tr>
<td>Forest floor (LFH)</td>
<td>108</td>
<td>Median</td>
<td>2850</td>
<td>3250</td>
<td>1360</td>
<td>1360</td>
<td>1340</td>
<td>1260</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Sig. Diff.</td>
<td>b</td>
<td>b</td>
<td>a</td>
<td>a</td>
<td>a</td>
<td>a</td>
</tr>
<tr>
<td>A-horizon or peat below forest floor to max 5 cm depth (soil)</td>
<td>108</td>
<td>Median</td>
<td>1930</td>
<td>2260</td>
<td>2790</td>
<td>2070</td>
<td>2440</td>
<td>3350</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Sig. Diff.</td>
<td>a</td>
<td>ab</td>
<td>ab</td>
<td>ab</td>
<td>ab</td>
<td>b</td>
</tr>
<tr>
<td>C:N</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Freshly fallen leaves (FFL)</td>
<td>90</td>
<td>Mean</td>
<td>37</td>
<td>37</td>
<td>44</td>
<td>47</td>
<td>47</td>
<td>52</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Sig. Diff.</td>
<td>a</td>
<td>a</td>
<td>b</td>
<td>bc</td>
<td>bc</td>
<td>c</td>
</tr>
<tr>
<td>Forest floor (LFH)</td>
<td>108</td>
<td>Mean</td>
<td>17</td>
<td>18</td>
<td>21</td>
<td>20</td>
<td>21</td>
<td>21</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Sig. Diff.</td>
<td>a</td>
<td>a</td>
<td>b</td>
<td>b</td>
<td>b</td>
<td>b</td>
</tr>
<tr>
<td>A-horizon or peat below forest floor to max 5 cm depth (soil)</td>
<td>108</td>
<td>Mean</td>
<td>17</td>
<td>17</td>
<td>17</td>
<td>16</td>
<td>17</td>
<td>17</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Sig. Diff.</td>
<td>a</td>
<td>a</td>
<td>a</td>
<td>a</td>
<td>a</td>
<td>a</td>
</tr>
</tbody>
</table>

\(^{a}\)Carbon in freshly fallen leaves based on ANOVA and carbon in forest floor and A-horizon or peat to maximum depth of 5 cm are ANOVA on ranks due to nonparametric nature of the data. Features with different letters are significant at \(p < 0.05\) using Tukey’s test for parametric data and Dunn’s method for nonparametric data.

Figure 6. Observed soil respiration for all plots (points) and soil respiration modeled as a function of soil temperature and moisture (surface, \(F = 365.6,\) d.f. = 3, \(p < 0.001, r^2 = 0.57, SE = 1.40\)).
increasing the variance explained by an additional 15.3% ($r^2 = 0.723$, $p < 0.0001$) over the model that only included environmental drivers. Carbon in LFH had no effect when included with only the carbon quantity terms, but did have a significant negative effect when it was included with the carbon quality terms. A forward stepwise regression (Table 4) indicated that carbon quantity in FFL ($\Delta r^2 = 0.723$) explained most of the additional 15.3% of variance explained over environment alone.

### 5. Discussion

[36] Rs from forest soil is important to forest carbon budgets as it is a significant component of ecosystem carbon exchange. Quantifying the heterogeneity in Rs and controls on that heterogeneity is the first step in understanding its effect at the landscape scale. This study sampled topographically driven gradients of environmental conditions and carbon pools and explored links among these factors to heterogeneity in Rs.

[37] Median rates of Rs across all features ranged from near zero in the wetlands following the spring snowmelt to 17.4 μmol CO$_2$ m$^{-2}$ s$^{-1}$ during the late summer period in the footslope. These rates of Rs were comparable to previous studies in north-temperate hardwood forests (see review in the work of Hibbard et al. [2005]). What was unique was the magnitude of spatial heterogeneity in Rs within the catchment. Median Rs in the critical transition zone were 1.6 times the median magnitude in the upland and 2.8 times the median magnitude in the wetland. Two studies that investigated the spatial heterogeneity in forest Rs along a topographic gradient reported a decrease in Rs from ridge to valley bottom [Hanson et al., 1993; Epron et al., 2006]. However, they did not identify (or monitor) high rates of Rs in the biogeochemically dynamic interface between the upland and lowland that we observed. The “effect” within the critical transition zone was similar to Saiz et al. [2006] who observed increases in Rs in small depressions or “furrows” and Yu et al. [2008] who observed increases in Rs in transition areas. This study highlights the importance of the critical transition zone as a “hot spot” [McClain et al., 2003] of Rs on the landscape.

#### 5.1. Environmental Conditions Versus Rs

[38] Previous studies have demonstrated the importance of environmental conditions in determining the rate of Rs [e.g., Davidson et al., 1998; Xu and Qi, 2001; Scott-Denton et al., 2003; Reichstein et al., 2005; Tang and Baldocchi, 2005; Yuste et al., 2005]. This study presented a general empirical model that incorporated a wide range of environmental conditions driven by topographic gradients. The amount of landscape-level variation in Rs due to variation in environmental conditions (57.0%) was comparable to other studies [e.g., Hanson et al., 1993; Kane et al., 2003; Rodeghiero and Cescatti, 2005; Tang et al., 2006]. The temperature sensitivity of the model ($Q_{10}$) of 3.64, was higher than expected given the enzyme dependency of ~2.5 [Davidson et al., 2006], but was comparable to other studies in cool temperate and boreal regions, ranging from 2 to 6 [Davidson et al., 1998; Janssens and Pilegaard, 2003]. The model predicted optimal Rs at soil moisture of 29%. This is higher than the optimal soil moisture of 12% identified by Davidson et al.

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**Table 3.** Additive Model of Soil Respiration as a Function of Environment [exp(a + bT + cM + dM$^2$)], Carbon Quantity (Carbon in Freshly Fallen Leaves, Forest Floor, A, or Peat to 5 cm) and Substrate Quality (C:N of Freshly Fallen Leaves, Forest Floor, A, or Peat to 5 cm) for All 18 Positions

<table>
<thead>
<tr>
<th></th>
<th>Intercept</th>
<th>$T$</th>
<th>$M$</th>
<th>$M^2$</th>
<th>C in FFL</th>
<th>C in LFH</th>
<th>C in Peat or Soil</th>
<th>C:N in FFL</th>
<th>C:N in LFH</th>
<th>C:N in Peat or Soil</th>
<th>$r^2$</th>
<th>$p$</th>
</tr>
</thead>
<tbody>
<tr>
<td>Environment</td>
<td>Coefficient</td>
<td>-0.6826</td>
<td>0.1292</td>
<td>0.0349</td>
<td>-0.0006</td>
<td>0.570</td>
<td>&lt;0.0001</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>Std. Error</td>
<td>0.1078</td>
<td>0.0057</td>
<td>0.0041</td>
<td>0.0001</td>
<td>0.0001</td>
<td>&lt;0.0001</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>p</td>
<td>&lt;0.0001</td>
<td>&lt;0.0001</td>
<td>&lt;0.0001</td>
<td>&lt;0.0001</td>
<td>&lt;0.0001</td>
<td>&lt;0.0001</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Environment +</td>
<td>Coefficient</td>
<td>-1.3565</td>
<td>0.1324</td>
<td>0.0333</td>
<td>-0.0006</td>
<td>0.0050</td>
<td>0.626</td>
<td>&lt;0.0001</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>C quantity</td>
<td>Std. Error</td>
<td>0.1412</td>
<td>0.0058</td>
<td>0.0038</td>
<td>0.0001</td>
<td>0.0004</td>
<td>0.0000</td>
<td>0.0000</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>p</td>
<td>&lt;0.0001</td>
<td>&lt;0.0001</td>
<td>&lt;0.0001</td>
<td>&lt;0.0001</td>
<td>&lt;0.0001</td>
<td>&lt;0.0001</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Environment +</td>
<td>Coefficient</td>
<td>-1.3244</td>
<td>0.1327</td>
<td>0.0378</td>
<td>-0.0006</td>
<td>0.0102</td>
<td>0.4899</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>substrate quality</td>
<td>Std. Error</td>
<td>0.3497</td>
<td>0.0063</td>
<td>0.0043</td>
<td>0.0001</td>
<td>0.0031</td>
<td>0.0000</td>
<td>0.0000</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>p</td>
<td>&lt;0.0001</td>
<td>&lt;0.0001</td>
<td>&lt;0.0001</td>
<td>&lt;0.0001</td>
<td>&lt;0.0001</td>
<td>&lt;0.0001</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Environment +</td>
<td>Coefficient</td>
<td>-4.2304</td>
<td>0.1486</td>
<td>0.0456</td>
<td>-0.0007</td>
<td>0.0048</td>
<td>0.723</td>
<td>&lt;0.0001</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>C quantity and</td>
<td>Std. Error</td>
<td>0.3599</td>
<td>0.0054</td>
<td>0.0036</td>
<td>0.0001</td>
<td>0.0030</td>
<td>0.0000</td>
<td>0.0000</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>substrate quality</td>
<td>p</td>
<td>&lt;0.0001</td>
<td>&lt;0.0001</td>
<td>&lt;0.0001</td>
<td>&lt;0.0001</td>
<td>&lt;0.0001</td>
<td>&lt;0.0001</td>
<td></td>
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</tr>
</tbody>
</table>

This table lists the coefficients, standard errors, and significance levels for the additive model of soil respiration as a function of environment, carbon quantity, and substrate quality. The model includes terms for temperature ($T$), moisture ($M$), moisture squared ($M^2$), carbon in freshly fallen leaves (FFL), carbon in the forest floor (LFH), carbon in peat or soil, C:N ratio in freshly fallen leaves (FFL), C:N ratio in the forest floor (LFH), C:N ratio in peat or soil, and the interaction between C:N and moisture ($M^2$). The table shows how each variable contributes to the explained variance ($r^2$) and the significance level ($p$) for the model. The model is significant at $r^2 = 0.723$ ($p < 0.0001$).

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**Table 4.** Forward Stepwise Regression Analysis for Prediction of Soil Respiration From Environmental, Carbon Quantity, and Substrate Quality Variables

<table>
<thead>
<tr>
<th>Step</th>
<th>Variable Added to Model</th>
<th>$r^2$</th>
<th>$\Delta r^2$</th>
<th>$p$</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>$T$</td>
<td>0.481</td>
<td>0.481</td>
<td>&lt;0.0001</td>
</tr>
<tr>
<td>2</td>
<td>$M^2$</td>
<td>0.527</td>
<td>0.046</td>
<td>&lt;0.0001</td>
</tr>
<tr>
<td>3</td>
<td>$M$</td>
<td>0.570</td>
<td>0.043</td>
<td>&lt;0.0001</td>
</tr>
<tr>
<td>4</td>
<td>C in FFL</td>
<td>0.620</td>
<td>0.050</td>
<td>&lt;0.0001</td>
</tr>
<tr>
<td>5</td>
<td>C:N in FFL</td>
<td>0.629</td>
<td>0.009</td>
<td>&lt;0.0001</td>
</tr>
<tr>
<td>6</td>
<td>C in soil</td>
<td>0.634</td>
<td>0.005</td>
<td>&lt;0.0001</td>
</tr>
<tr>
<td>7</td>
<td>C:N in soil</td>
<td>0.690</td>
<td>0.056</td>
<td>&lt;0.0001</td>
</tr>
<tr>
<td>9</td>
<td>C in LFH</td>
<td>0.714</td>
<td>0.024</td>
<td>&lt;0.0001</td>
</tr>
<tr>
<td>10</td>
<td>C:N in LFH</td>
<td>0.723</td>
<td>0.009</td>
<td>&lt;0.0001</td>
</tr>
</tbody>
</table>

*Here $p < 0.001$, SE = 1.123.*
Figure 7. Observed soil respiration at each plot within a topographic feature (points) and soil respiration modeled as a function of soil temperature and moisture (surface, $F = 365.6$, d.f. = 3, $p < 0.001$, $r^2 = 0.57$, SE = 1.40).
pools were large, suggesting the saturated and reducing wetland, despite small FFL carbon pools the LFH carbon leaves was rapidly metabolized (or leached). This further age (i.e., LFH) suggested that carbon in the freshly fallen zone did not result in larger carbon pools of >1 year accumulation of freshly fallen leaves in the critical transition 

5.2. Environmental Conditions and Substrate Versus Rs

The distribution of the residuals from the environment versus Rs model showed large deviations from predicted response, particularly during mid growing season, with pronounced positive residuals in critical transition zone and negative residuals in the upland features. Given the depth the collars were inserted, roots and rhizosphere respiration would be a component of the Rs, thus the pattern in the residual Rs and a $Q_{10}$ $\geq$ 2.5 suggests that controls on root respiration or some unidentified component that covaries with soil temperature (e.g., substrate supply, seasonal changes in allocation of photosynthate and root biomass, or activity of rhizosphere microbes) confounded the observed temperature variation [Davidson et al., 2006].

Adding carbon quantity and substrate quality to the environment versus Rs model further increased the amount of variance explained (72.3%). The carbon pool in freshly fallen leaves had the single greatest effect on reducing the unexplained variance. Despite a relatively homogenous canopy cover (Table 2) and homogeneity in the density of understory saplings within the upland and critical transition zone ($p = 0.55$, K. L. Webster, unpublished data), there is a pattern of higher accumulation of FFL in the depositional areas within the critical transition zone and lower accumulation in erosional areas of the backslope. This redistribution of the freshly fallen leaves, with their low mass and large surface area, is likely promoted by wind [Orndorff and Lang, 1981]. This pool was collected in the fall following the autumnal measurements of Rs and while there may be some inter-annual variation in the size of the pool, it can be considered indicative of what likely was available at the beginning of the growing season from the previous year leaf litter fall. Previous studies have demonstrated the importance of fresh litter carbon pools to Rs [e.g., Martin and Bolstad, 2005; Yuste et al., 2005; Cisneros-Dozal et al., 2006; Davidson et al., 2006; Sotta et al., 2006]. Isotope studies have also indicated the importance of this pool as respired carbon signatures reflect that of recently fixed carbon [Fessenden and Ehleringer, 2003; Certini et al., 2003].

Surprisingly, the contribution of the forest floor (LFH) pool to Rs was small. The observation that increased accumulation of freshly fallen leaves in the critical transition zone did not result in larger carbon pools of >1 year age (i.e., LFH) suggested that carbon in the freshly fallen leaves was rapidly metabolized (or leached). This further supports the importance of the fresh litter pool to Rs. In the wetland, despite small FFL carbon pools the LFH carbon pools were large, suggesting the saturated and reducing conditions that occur for most of the year limit decomposition [Laiho, 2006].

There has been ambiguity in the literature as to the importance of the mineral soil carbon pool to Rs [Kahkonen et al., 2002; Janssens and Pilegaard, 2003; Schwendenmann et al., 2003; Rodeghiero and Cescatti, 2005]. The analysis presented here suggested that there was a negative contribution of carbon in the soil to Rs possibly due to its recalcitrance and sorption on to the mineral surfaces [Kalbitz et al., 2005]. The pattern within this soil carbon pool was likely influenced by infiltration but also by deeper, subsurface lateral flows from upslope contributing areas [Rosenbloom et al., 2006]. In crest areas, with minimal inputs from lateral transport, infiltration processes would result in leaching of material from organic surface layers and carbon accumulation in the upper mineral horizons. Backslope and footslope areas would have greater lateral flows through the organic horizons, limiting deeper infiltration and explaining their smaller soil pools. Toeslope areas had the greatest variability in their pools (25th to 75th percentile range of 2100 to 5100 g C m$^{-2}$). This is a region on the hillslope where differences in flow length and contributing area would be most pronounced and may explain the variability within this feature. The outer wetland, which is hydrologically connected to the hillslope, had similar pools to its critical transition zone and upland neighbors than the inner wetland which is disconnected from the hillslope flowpaths. Other studies have shown that A-horizon or soil rooting depth increases in downslope positions [Pennock et al., 1987; Park et al., 2001; Schmidt and Hewitt, 2004; Martin and Timmer, 2006] due to coupled erosion and deposition processes [Yoo et al., 2005]. Despite the patterns with depth, patterns in A-horizon organic matter have been found to be less distinct. For example, Martin and Timmer [2006] found a gradual pattern in soil organic matter (SOM) within the A-horizon, with larger pools in level features than shoulder and footslope features.

Including spatial heterogeneity in substrate quality (C:N) also reduced unexplained variance in the model. The relatively high C:N of freshly fallen leaves was negatively related to Rs, while low C:N in LFH and soil was positively related to Rs. This suggests optimal C:N ratios for Rs is between the values observed for FFL (36 to 52) and the LFH or soil (16 to 21). At higher C:N, decomposition slowed due to limited availability of N for assimilation by microbes for metabolic needs (immobilized), and at low values decomposition slowed due to poor substrate quality (refractory). Martin and Bolstad [2005] also observed a positive relationship of C:N in the forest floor and SOM to Rs, while Khomik et al. [2006] observed an inverse relationship between C:N of LFH and Rs. Differences in upland and wetland C:N in FFL and LFH can be explained by differences in vegetation. Palik et al. [2006] also observed decreased C:N transitioning from upland to wetland due to lower litter C:N in wetland species of black ash than upland species of sugar maple. The pattern in substrate quality of FFL within the upland, where sugar maple dominates, may be explained by the degree of shading. Exposure to sunlight in upland features would result in higher rates of photosynthesis, higher rates of carbon fixation and higher C:N ratios than more shaded leaves in
the footslope, toeslope and wetland features [Niinemets and Tenhunen, 1997]. Confounding these patterns may be selective decomposition, incomplete decomposition or different decomposition by-products from decomposition of the same substrate under anaerobic conditions within the wetland [Kalbitz et al., 2000].

[45] There was a synergistic effect of including both carbon quantity and substrate quality terms to predict Rs. This effect may reflect the proportion of labile carbon within the pool. If a higher proportion of the total carbon is refractory in these pools (e.g., lignin) then it may be protected from decomposition or have been further altered through humification [Bourbonniere and Creed, 2006; Michel et al., 2006]. Further work is required to clearly understand the mechanisms relating carbon quantity and substrate quality to Rs.

[46] There remained 27.2% of the variance in Rs that was not explained. This study examined the carbon contained within ‘static’ substrates differing in their age and composition, but did not consider the ‘dynamic’ pool of substrate found dissolved within the soil pore water. Dissolved organic matter is thought to be a labile source of carbon to microbes [e.g., Kalbitz et al., 2000] and the importance of this dynamic pool in controlling Rs and is the focus of a future study. Other factors that were not measured that could explain the remainder of the variation include: (1) the influence of other nutrients (e.g., phosphorus or base cations) limiting microbial activity; (2) factors that control availability of carbon (e.g., sorption, recalcitrance, and solubility); (3) heterogeneity in microbial and rhizosphere communities [Stenrod et al., 2006], (4) factors that control autotrophic respiration (e.g., fine root density, distribution, and phenology), which comprise approximately 50–60% of total Rs [Pregitzer et al., 1998], and (5) seasonal changes in the allocation of carbon between aboveground and belowground components.

6. Conclusions

[47] Topographic control on environmental conditions and carbon pools resulted in heterogeneity of Rs within a forest that had a homogeneous canopy. Overall the critical transition zone was a hot spot of respiration because there was synchrony in optimal soil moisture conditions (29%) during the warm summer months plus large pools of good quality carbon substrate, particularly freshly fallen leaves. This large pool of freshly fallen leaves was also very soluble. The FFL pool has been shown to produce eight times more leachate than one year old litter within the LFH [Bourbonniere and Creed, 2006], resulting in a labile C pool readily available for decomposition. The critical transition zone is hydrologically dynamic due to both hydrologic inputs from upland areas and due to expansion of neighboring source areas in the wetland. This timing of the hydrologic connection and disconnection along with the large, labile pool of substrate resulted in the critical transition zone being a large source of Rs during the summer. Our findings are based on data collected during the driest year on record (2005). We expect with wetter conditions, the critical transition zone would shift into the upland, while further drying would shift the critical transition zone into the wetland. Thus the location, size and strength of the areas with peak Rs production will likely change with different climate conditions. A future study will explore the spatial and temporal dynamics of environmental conditions captured in the topographic features and establish their importance in estimating Rs from the entire landscape.

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