Modeling soil respiration based on carbon, nitrogen, and root mass across diverse Great Lake forests

Jonathan G. Martin a, *, Paul V. Bolstad b, Soung-Ryoul Ryu c, Jiquan Chen d

a Oregon State University, Department of Forest Science, 321 Richardson Hall, Corvallis, OR 97331, USA
b Department of Forest Resources, University of Minnesota, 1530 Cleveland Avenue N., St Paul, MN 55108-6112, USA
c Department of Forestry and Natural Resources, Clemson University, Lehotsky Hall, Clemson, SC 29634-0317, USA
d Department of Environmental Sciences, University of Toledo, Toledo, OH 43606-3390, USA

1. Introduction

Linkages between atmospheric carbon dioxide and global thermal properties have forced the examination of biospheric carbon flows and pools. Variability in carbon storage or the net ecosystem exchange of carbon (NEE) in forests and other terrestrial systems can be a considerable source of variability in atmospheric CO₂ (Zeng et al., 2005). Climate change can influence soil properties and therefore drive the microbial and root production of soil CO₂. This study measured soil respiration and soil chemical, biological and physical properties on various types of temperate forest stands in Northern Wisconsin (USA), which included ash elm, aspen, northern hardwood, red pine forest types, clear-cuts, and wetland edges. Soil respiration at each of the 19 locations was measured six times during 1 year from early June to mid-November. These data were combined with two additional data sets from the same landscape that represent two smaller spatial scales. Large spatial variation of soil respiration occurred within and among each forest type, which appeared to be from differences in soil moisture, root mass and the ratio of soil carbon to soil nitrogen (C:N). A soil climate driven model was developed that contained quadratic functions for root mass and the ratio of soil carbon to soil nitrogen. The data from the large range of forest types and site conditions indicated that the range of root mass and C:N on the landscape was also large, and that trends between C:N, root mass, and soil respiration were not linear as previously reported, but rather curvilinear. It should be noted this function appeared to level off and decline at C:N larger than 25. Relationships between soil water and soil C:N, and between soil C:N and root mass were observed indicating an interrelatedness of (1) topographically induced hydrologic patterns and soil chemistry, and (2) soil chemistry and root production. Future models of soil respiration should address multiple spatial and temporal factors as well as their co-dependence.

The variability in the net ecosystem exchange of carbon (NEE) is a major source of uncertainty in quantifying global carbon budget and atmospheric CO₂. Soil respiration, which is a large component of NEE, can be strongly influential to NEE variability. Vegetation type, landscape position, and site history can influence soil properties and therefore drive the microbial and root production of soil CO₂. This study measured soil respiration and soil chemical, biological and physical properties on various types of temperate forest stands in Northern Wisconsin (USA), which included ash elm, aspen, northern hardwood, red pine forest types, clear-cuts, and wetland edges. Soil respiration at each of the 19 locations was measured six times during 1 year from early June to mid-November. These data were combined with two additional data sets from the same landscape that represent two smaller spatial scales. Large spatial variation of soil respiration occurred within and among each forest type, which appeared to be from differences in soil moisture, root mass and the ratio of soil carbon to soil nitrogen (C:N). A soil climate driven model was developed that contained quadratic functions for root mass and the ratio of soil carbon to soil nitrogen. The data from the large range of forest types and site conditions indicated that the range of root mass and C:N on the landscape was also large, and that trends between C:N, root mass, and soil respiration were not linear as previously reported, but rather curvilinear. It should be noted this function appeared to level off and decline at C:N larger than 25. Relationships between soil water and soil C:N, and between soil C:N and root mass were observed indicating an interrelatedness of (1) topographically induced hydrologic patterns and soil chemistry, and (2) soil chemistry and root production. Future models of soil respiration should address multiple spatial and temporal factors as well as their co-dependence.

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ABSTRACT

The variability in the net ecosystem exchange of carbon (NEE) is a major source of uncertainty in quantifying global carbon budget and atmospheric CO₂. Soil respiration, which is a large component of NEE, could be strongly influential to NEE variability. Vegetation type, landscape position, and site history can influence soil properties and therefore drive the microbial and root production of soil CO₂. This study measured soil respiration and soil chemical, biological and physical properties on various types of temperate forest stands in Northern Wisconsin (USA), which included ash elm, aspen, northern hardwood, red pine forest types, clear-cuts, and wetland edges. Soil respiration at each of the 19 locations was measured six times during 1 year from early June to mid-November. These data were combined with two additional data sets from the same landscape that represent two smaller spatial scales. Large spatial variation of soil respiration occurred within and among each forest type, which appeared to be from differences in soil moisture, root mass and the ratio of soil carbon to soil nitrogen (C:N). A soil climate driven model was developed that contained quadratic functions for root mass and the ratio of soil carbon to soil nitrogen. The data from the large range of forest types and site conditions indicated that the range of root mass and C:N on the landscape was also large, and that trends between C:N, root mass, and soil respiration were not linear as previously reported, but rather curvilinear. It should be noted this function appeared to level off and decline at C:N larger than 25. Relationships between soil water and soil C:N, and between soil C:N and root mass were observed indicating an interrelatedness of (1) topographically induced hydrologic patterns and soil chemistry, and (2) soil chemistry and root production. Future models of soil respiration should address multiple spatial and temporal factors as well as their co-dependence.

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showed increases in soil respiration (Wan et al., 2005; Hartley et al., 2007) which could transfer portions of the soil carbon pool to the atmosphere. A potential loss of soil carbon could be substantial in the Great Lakes region which has some of the highest stores of soil carbon in the conterminous United States (Guo et al., 2006), but the true fate of soil carbon under a warmer atmosphere is unclear. In order to predict the fate soil carbon and soil fluxes, it is critical to quantify the fluxes spatiotemporally and understand what drivers the variation.

The majority of soil CO₂ production arises from root and microbial tissue; therefore, understanding spatial and temporal changes of these sources will simplify spatiotemporal scaling of soil respiration. Much work has shown that soil respiration is spatially and temporally sensitive to (1) incoming environmental influences such as temperature and moisture, and (2) the current physical state of various site characteristics, above- and below-ground (Vargas and Allen, 2008). The effect of incoming environmental drivers on the respiring tissues of roots and microbes is ultimately dictated by the type, amount and condition of the respiring tissue present; therefore, metrics that represent these tissues is needed in modeling efforts.

Many ecosystem characteristics can be important determinates of soil respiration because of their influence on microbial activity, soil substrates and/or root mass. Characteristics such as leaf area or above-ground production may serve as proxies for scaling soil respiration (Davidson et al., 2002; Hibbard et al., 2005) because of the link between inputs and soil heterotrophic metabolism and/or the link between above-ground and below-ground tissue mass. However, such trends are partially coincidental because below-ground conditions can vary independently from conditions above-ground (Cairns et al., 1997). Direct autotrophic determinants of soil respiration such as root activity and density have been linked to above-ground conditions or structure (Craine et al., 1999; Högberg et al., 2001; Kuzyakov and Cheng, 2001; Irvine et al., 2005, 2008; Nadelhoffer and Raich, 1992), but the relationships are complex. For instance, across forest types, fine root production and total below-ground carbon allocation can increase relative to above-ground production (Nadelhoffer and Raich, 1992), yet the proportion of below-ground allocation may decrease (Raich, 1998). Such patterns arise because the relationships between root mass and above-ground mass can be influenced by many environmental parameters (Cairns et al., 1997). Therefore, while a relationship between above-ground structure and autotrophic soil respiration may exist, it would mostly likely be driven directly by root variability. Since roots provide one of the two sources of soil CO₂, roots should be included directly as an explanatory source of soil respiration variability until robust relationships between above-ground conditions and root mass are quantified.

Above-ground conditions may also influence microbial activity and biomass. Litter inputs have been shown to influence soil fertility and soil carbon pool size, both of which can drive soil respiration (Ladegaard-Pedersen et al., 2005; Vanhala et al., 2005; Conant et al., 2000). However, similar to the role of roots in determining soil respiration rates, soil substrates for microbial consumption may be only casually linked to above-ground structure and status. For instance, species composition may have important controls on NEE and soil respiration (Kutsch et al., 2005; Ahl et al., 2005; Hibbard et al., 2005), yet hidden factors, such as legacy effects from past management history, can be an important consideration (Jiang et al., 2005; Parkin et al., 2005; Zheng et al., 2005). Inputs into the rhizosphere, such as logging residues, can release large fluxes of soil CO₂, while releasing relatively little nitrogen (Palviainen et al., 2004) which may change soil processes through changes in the ratio of carbon to nitrogen in the soil. Soil C:N has been shown to drive soil respiration due to the role of C:N on substrate availability and the subsequent microbial activity (Thomsen et al., 2008); therefore soil chemical characteristics, such as soil C:N ratio, combined with root mass may directly explain soil CO₂ production across a range of forest types in various states.

Despite the many confounding and complex relationships that exist on the landscape, it is possible that the soil respiration component of net ecosystem carbon exchange may be adequately explained across multiple forest types using simple relationships between soil climate and the precursors of soil CO₂ production. Although vegetation type, landscape position, and past history can influence soil carbon processes (Guo et al., 2007; Webster et al., 2008; Palviainen et al., 2004), these factors should all leave fingerprints on the soil chemistry and root dynamics that ultimately produce soil CO₂. Previous soil respiration studies on a small set of forest types in this area found a strong link between soil biology/chemistry and soil respiration, independent of forest type, as well as a relationship between soil respiration and soil moisture (Martin and Bolstad, 2005; Martin and Bolstad, 2009). The current study expands that work to include additional replicates of similar forest types as well as forest types infrequently measured in this area.

The objectives of this study are to (1) compare soil respiration from many diverse Lake State forests including aspen, ash/elm, clear-cuts, northern hardwoods, red pine, and wetland edges, all of which contain internal variation in age, structure, landscape position, and/or soil properties, and (2) develop a generalized model of soil respiration based on soil biological and chemical variables. We hypothesized that (1) by accounting for spatially variation of root mass and soil chemistry which relate directly to root and microbial respiration, the proposed model will represent the spatial variation of soil fluxes that may be dependent on site history or location, and (2) these variables would supersede forest type as a spatial scalar.

2. Methods

2.1. Study location and site summary

This study was conducted to supplement the existing sites reported on in Martin and Bolstad (2005), and included additional replicates of forest types that were previously sampled. Also included were clear-cuts, red pine, and wetland margins forest types that are often under-sampled and were not monitored during the primary survey of this area. The original locations as well as the new study plots were established in the Chequamegon National Forest of north central Wisconsin. The original sites were established in conjunction with an above-canopy flux tower located near Willow Creek (W90°07', N45°48'); this area is primarily aspen and northern hardwood forest types and contains no clear-cuts, red pine stands or persistent wetland margins. The 30 m tall Willow Creek tower is part of the Chequamegon Ecosystem-Atmosphere Study (CHEAS) and AmeriFlux network, as is the 300 m WLEF eddy flux tower, approximately 40 km to the northwest. The footprint of the WLEF tower is much larger and includes a component comprised of clear-cut stands, plantations of red pine, and wetland margins. For this work, 24 additional sites were added that included 8 aspen, 4 clear-cuts, 4 northern hardwoods, 4 red pine, and 4 wetland edges.

The aspen sites were dominated by Populus tremuloides Michx. and ranged in age from 5 to 20 years old. The clear-cuts had varying degrees of regeneration and site disturbance ranging from minimal to severe; one of the clear-cuts had no residual canopy trees remaining and the others included residual canopy trees of mature white spruce (Picea glauca Voss.) or aspen (P. tremuloides Michx.) at densities of one to ten individuals per hectare. The additional northern hardwood sites were a mix of sugar maple (Acer
saccharum Marsh.), basswood (Tilia americana Marsh.) and green ash (Fraxinus pennsylvanica L.); individual red oaks (Quercus rubra L.) were also present at some of these sites. The red pine sites (Pinus resinosa Ait.) were all mature plantations with similar stocking; understories ranged from sparse herb and ferns to dense hazel ( Corylus spp. L.). The wetland edge sites were located in the transition zone between open water and uplands (typically less than 200 m across) and contained mixed species which varied from black spruce (Picea mariana Mill.) to aspen (P. tremuloides Michx.) overstories with mixed grass species or sphagnum ground cover. These additional sites encompassed a wide range of mean soil moisture conditions due to the heterogeneous terrain and drainage patterns, as well as forest composition, structure, and age.

2.2. Soil respiration and soil carbon, nitrogen and root biomass

Soil respiration was measured at each of the 24 sites six times during the year from early June to mid-November with a LI-COR 6400 (for a complete description of measurement methodology see Martin and Bolstad, 2005). Measurements at each site were made on a series of eight randomly placed PVC collars. The collars were radially arranged between 1 and 10 m from a center stake marking the location of each plot. These data were combined with two additional data sets from the area that represent two smaller scales: (1) data from a survey of sites within the footprint of the Willow Creek eddy flux tower (Martin and Bolstad, 2005) with a spatial scale of approximately 10 km, and (2) data from a topographic sequence at a scale of 500 m (Martin and Bolstad, 2009).

As part of a separate study, soil samples were taken from locations next to each collar at the new sites (those listed in Table 1). The soil was sampled to depths of 0–10 and 10–20 cm using a method identical to Martin and Bolstad (2005) but from shallower depths; soil from each depth was combined thorough mixing and each composite sample was sieved to shallower depths; soil from each depth was combined through thorough mixing and each composite sample was sieved to radially arrange between 1 and 10 m from a center stake marking the location of each plot. These data were combined with two additional data sets from the area that represent two smaller scales: (1) data from a survey of sites within the footprint of the Willow Creek eddy flux tower (Martin and Bolstad, 2005) with a spatial scale of approximately 10 km, and (2) data from a topographic sequence at a scale of 500 m (Martin and Bolstad, 2009).

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Because these soil samples were not from the same depth as those taken from the previous study in this area (0–30 cm, Martin and Bolstad, 2005), the values of the earlier study were depth-corrected to be comparable with the new samples. The root mass data from the new study sites indicated that there was no difference between root mass in the layer of soil from 0 to 10 cm and the layer from 10 to 20 cm (t-test of all samples, p-value 0.879; multiple linear regression of root mass by site and depth nested within site, p-values 0.537 and 0.851, respectively; this and all subsequent analyses were done with JMP version 3.2.5, SAS Institute, Cary, NC). Assuming that this trend would hold down to 30 cm, only 2/3 of the root mass for the earlier samples, which integrated root mass down to 30 cm, were used to be comparable to the sum of both layers of root mass data from the newer survey (the 0–10 and 10–20 cm samples).

Soil carbon and nitrogen data did vary with depth in both studies (Fig. 1), but, because the original data consisted of a composite sample that mixed all soil from 0 to 30 cm, the carbon and nitrogen data from the 10 to 20 cm depth were used to represent the soils from the newer survey. The combination of the 0–10, 10–20, 30–60, and the 60–100 cm data from both studies showed that the decline of both elements with depth followed an exponential decay but was approximately linear in the upper portions (Fig. 1). This supported our assumption that the composite samples from 0 to 30 cm had a mean value equal to the carbon or nitrogen concentration at mid-point depth of 15 cm. The 15 cm depth was also the mid-point for the newer 10–20 cm samples; therefore, the two samples could be compared with minimal bias. These data were compared for the two forest types that were sampled during each study, the aspen and northern hardwoods forest types. While there was considerable variation among plots in the newer survey due to the large variation in site condition and location, there were no systematic differences between the older and newer soil data sets for the forest types where sampling overlapped.

Soil surface CO₂ flux data, soil temperature at 10 cm, and volumetric soil water content data at 0–15 cm from both studies

<table>
<thead>
<tr>
<th>Site code</th>
<th>Root mass (g m⁻²)</th>
<th>% C loose soil</th>
<th>% N loose soil</th>
<th>C:N loose soil</th>
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<td>Aspen</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>A15</td>
<td>634.3</td>
<td>2.21</td>
<td>0.12</td>
<td>18.36</td>
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<tr>
<td>A16</td>
<td>561.9</td>
<td>1.88</td>
<td>0.10</td>
<td>18.29</td>
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<tr>
<td>A18</td>
<td>740.1</td>
<td>1.49</td>
<td>0.10</td>
<td>14.49</td>
</tr>
<tr>
<td>A22</td>
<td>1448.7</td>
<td>1.49</td>
<td>0.10</td>
<td>14.85</td>
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<tr>
<td>A23</td>
<td>1855.9</td>
<td>1.49</td>
<td>0.09</td>
<td>16.45</td>
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<tr>
<td>Clear-cut</td>
<td></td>
<td></td>
<td></td>
<td></td>
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<tr>
<td>C01</td>
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<td>0.94</td>
<td>0.05</td>
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<td>626.5</td>
<td>1.32</td>
<td>0.09</td>
<td>14.62</td>
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<td>Northern hardwood</td>
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<td>4.32</td>
<td>0.21</td>
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<td>508.6</td>
<td>1.97</td>
<td>0.10</td>
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<td>N17</td>
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<td>0.20</td>
<td>13.02</td>
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<td>N24</td>
<td>537.6</td>
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<td>10.86</td>
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<td>Red pine</td>
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<td>0.05</td>
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<td>Wetland edge</td>
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<td>1.92</td>
<td>0.10</td>
<td>19.14</td>
</tr>
</tbody>
</table>

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**Fig. 1.** Soil chemistry as a function of soil sampling depth for aspen and hardwood forest types. Error bars represent one standard deviation. Soil depth refers to the lowest depth reached for a particular sample (i.e., 0–10, 10–20, 30–60, and 60–100 cm).
were pooled along with root mass, soil carbon concentration, and soil nitrogen concentration data. The soil respiration data were transformed by the natural log to homogenize variance. The following model, developed from the earlier survey, was used as a starting point to develop a new model in attempts to explain the variation among sites:

\[
\ln(R_s) = b_0 + b_1(T_{soil}) + b_2(T_{soil}^2) + b_3(\theta) + b_4(\theta^2) + b_5(T_{soil} \times \theta)
\]

where \( R_s \) is the measured soil respiration rate in \( \mu \text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1} \) when the soil temperature is \( T_{soil} \) in °C at 10 cm depth, and the volumetric soil water content is \( \theta \) in % or m³ water 100 m² soil at 0–15 cm depth. The term “f(soil characteristics)” is the function or functions that relates a soil characteristic or characteristics to soil respiration, and could include soil carbon concentration, soil nitrogen concentration, C:N of the bulk soil, and/or root biomass. The terms “\( b_0\)–\( b_5 \)” are estimated coefficients.

Soil carbon and nitrogen, soil C:N, and root biomass were chosen because all were shown to be potential predictors of soil respiration at multiple scales (Martin and Bolstad, 2005; Martin and Bolstad, 2009). For a wide range of sites and site conditions, these variables should covary with soil respiration because substrate availability and quality will drive microbial activity and the resultant heterotrophic CO₂ flux, and the remaining root CO₂ flux should be directly related to the mass of respiring root tissue. A potential complication arises because substrate availability/quality and root mass are not independent, as root mass should respond to soil fertility to compensate for limitations or surpluses.

3. Results and discussion

3.1. Soil respiration across soil climate gradients

Fig. 2 shows the relationship between soil respiration and soil climate (soil temperature and volumetric soil moisture) for the new sites added to the pooled data set. Across a wide range of soil moisture and temperatures, all sites exhibited the typical exponential increase with temperature that is commonly seen. The trends between soil respiration, soil temperature, and soil moisture are in agreement with previous studies similar to trends seen in other studies and the flux rates are comparable to those measured in other hardwood forests (Davidson et al., 1998), aspen forests (Russel and Voroney, 1998), and pine forests (Striegl and Wickland, 2001; Wiseman and Seiler, 2004). The trend appears to level off when soil temperatures exceed 20 °C, which occurred in the clear-cuts sites only.

Despite only using the five to six measurement dates from the new sites, pooling the data by forest type showed a strong curvilinear relationship between soil respiration and soil moisture (Fig. 2). This relationship is most apparent for the forest types that exist on a wide range of soil moisture conditions (e.g., the aspen, clear-cut, and northern hardwood sites). The red pine sites were generally found on drier upland soils, while the wetland edges were inherently found on wetter soils; both situations are apparent in Fig. 2. Because of the positions of these sites on the unimodal response of soil respiration to soil moisture, soil respiration at the red pine sites had a positive relationship with soil moisture while the wetland edges had a negative relationship, similar to Webster et al. (2008). These opposite findings are both valid but illustrate the need to quantify the controls of soil hydrologic processes on soil respiration at larger scales.

We also found large variation associated with sites within each forest type (Fig. 2). Some of this variation appears to be from consistent differences in soil moisture (i.e., certain sites are consistently wet or dry). However, certain sites that span similar soil moistures have noticeably different soil respiration rates. This is most evident in the aspen and northern hardwood sites in Fig. 2 which exhibit considerable site-wide variability during mesic conditions. From the patterns between forest types and from the large variation within forest types it can be concluded that (1) although forest type may covary with soil moisture, soil moisture can have important effects on the rates of measured soil respiration independent of forest type as shown by the function in Fig. 2, and (2) due to the remaining site to site variability, there may exist potential controls, other than soil moisture, that influence soil respiration independent of forest type.

3.2. Site contributions to soil respiration spatial variability

In previous work from this region that included a portion of these sites, root mass and C:N was shown to be important in driving soil respiration within a given site, between sites on a landscape continuum, and across broad leaf forest sites at distances of up to 20 km (Martin and Bolstad, 2005; Martin and Bolstad, 2009). To explore the independence of soil respiration from forest type on the larger data set presented here, Eq. (1) was fit to the pooled data set without the function of forest type, but including solely the site specific soil variables. Fig. 3 shows the residuals from the fit of Eq. (1) to the pooled data set in relation to both root mass and C:N. Both functions followed a quadratic relationship with all terms significant at α = 0.05. In the prior analysis of the broad leaf forests used in this pooled data set (Martin and Bolstad, 2005), both root mass and C:N were positively related to soil respiration. Root mass in that data set ranged from 139 to 1154 g m⁻² when the samples from 0 to 30 cm were corrected to represent a soil profile from 0 to 20 cm, which was the sampling depth of the new study. This small range would lead to the positive relationship reported in the earlier analysis (Fig. 3). The addition of the new sites, with a range of root mass from 295 to 1855 g m⁻² (Table 1), extends the data set and provides evidence for a curvilinear function. The polynomial relationship (Fig. 3a) may explain why other studies have seen both positive and flat relationships between root mass and soil respiration (Fang et al., 1998; Samuelson et al., 2004).

The variance from Eq. (1) also appeared to be attributed to C:N at the various sites (Fig. 3). Similar to the effect of root mass, C:N follows a unimodal quadratic function. From the original analysis of the broad leaf forests used in this pooled data set (Martin and Bolstad, 2005), soil respiration was determined to be strongly and positively influenced by the ratio of soil carbon to soil nitrogen. Again, the range of C:N for those sites was small when compared to a broader range of sites and forest types used in this newer analysis. The C:N of the soils from the original analysis ranged from 12.2 to 19.7; over that range, there was a positive relationship between C:N and soil respiration. The addition of the supplemental sites indicates that the range of C:N on the landscape was much larger, from 10.9 to over 40 (Table 1), and that the trend between C:N and soil respiration was not linear, but rather curvilinear. It should be noted this function appears to level off and decline at C:N larger than 30 (Fig. 3); a C:N of 25–30 indicates the approximate value where microbial nitrogen immobilization can change the nutrient status of a given soil (Gundersen et al., 1998). Soil substrates with C:N lower than approximately 25 will provide ample nitrogen for microbial growth leading to volatile free nitrogen for root uptake. Soil substrates with a C:N above 25–30 will have less available nitrogen due to microbial immobilization (Gundersen et al., 1998). Although microbial respiration should be higher at sites with higher quality substrate (low C:N), the higher available
nitrogen may decrease the root mass needed to support aboveground production which would decrease the root contribution to total soil respiration. This decrease would need to be disproportionately larger than the increase of microbial respiration to cause an overall decrease in soil respiration. Unfortunately, no measurements were made of the separate autotrophic and heterotrophic respiration components across all of the sites; therefore, any conclusions concerning changes in the proportionality of root/microbial respiration to total soil respiration are speculative. Further analyses are needed to examine this hypothesis.

3.3. Developing a generalized model for soil respiration

The residual analysis of Eq. (1) by root mass and C:N indicates that these variables explain much of the site to site variability of soil respiration. A multiple linear regression of the pooled data set using Eq. (1) with polynomial functions for both root mass and C:N resulted in the formation of a generalized model for the most common forest types in this portion of the Chequamegon National Forest of north central Wisconsin:

$$\ln(R_s) = b_0 + b_1(T_{soil}) + b_2(T_{soil}^2) + b_3(\theta) + b_4(\theta^2) + b_5(M_{roots})$$
$$+ b_6(M_{roots}^2) + b_7(C : N) + b_8(C : N)^2$$

(2)

This model is identical to Eq. (1) except the term to express an interaction between soil temperature and soil moisture was insignificant, and this model contains the quadratic functions for root mass ($M_{roots}$ in g m$^{-2}$), and the ratio of soil carbon to soil nitrogen (C:N). Table 2 contains the estimates for this fit which explained 87.4% of the variation for the pooled data set (adjusted $R^2 = 0.872$). Models fit with soil C or N individually resulted in these terms being insignificant, perhaps due to the large variation among sites. Additionally, the interaction between soil C and N is important for determining soil organic matter quality which drives

![Fig. 2. Soil respiration as a function of soil temperature and soil moisture for each site grouped by forest type. Each site is labeled with a different symbol, and the general data trend and fitted function for temperature and soil moisture are shown with arrows. The range and magnitudes of soil moistures indicate both positive and negative responses of soil respiration at the wetland and red pine sites, respectively, as denoted by arrows.](image-url)
measurements. In both forest types, rates of soil respiration and hardwood sites, the forest types with the majority of magnitude of fluxes is rare and may be related to unseen bias in the to the overall annual amount of carbon respired from the soil, this 3.5 m more variable than lower rates. A soil respiration rate of 8 m 8 over-predicts. Additionally, the aspen and northern hardwood dent use of soil C and N would miss this important process.

The relationships between the residuals from a model (with soil temperature and soil moisture only) and the root mass (a) and soil C:N (b) for each site. Open symbols are the data from the original study. Noted are the ranges of values obtained in the earlier analysis that included only intact broad leaf forests (Martin and Bolstad, 2005).

Fig. 3. The relationships between the residuals from a model (with soil temperature and soil moisture only) and the root mass (a) and soil C:N (b) for each site. Open symbols are the data from the original study. Noted are the ranges of values obtained in the earlier analysis that included only intact broad leaf forests (Martin and Bolstad, 2005).

Microbial respiration (Thomsen et al., 2008); therefore, independent use of soil C and N would miss this important process.

The model performed well for all sites (Fig. 4) with the exception of the clear-cut sites for which the model consistently over-predicts. Additionally, the aspen and northern hardwood sites are under-predicted at high flux rates indicating a lack of fit at high soil temperatures. While soil respiration rates, as high as 8 μmol CO₂ m⁻² s⁻¹, were observed and would contribute greatly to the overall annual amount of carbon respired from the soil, this magnitude of fluxes is rare and may be related to unseen bias in the measurement protocol.

Fig. 4 also shows a trend in the variability of fluxes at the aspen and hardwood sites, the forest types with the majority of measurements. In both forest types, rates of soil respiration greater than approximately 3.5 μmol CO₂ m⁻² s⁻¹ are consistently more variable than lower rates. A soil respiration rate of 3.5 μmol CO₂ m⁻² s⁻¹ would roughly correspond to a soil temperature of approximately 10–11 °C. In the spring, the onset of leaf out generally occurs when soils reach this temperature (Martin et al., unpublished data); therefore, measurements of soil respiration taken at temperatures above 10 °C are generally made in the presence of an active canopy. These data may support previous studies which have implicated active foliage as a driver of soil respiration (Craine et al., 1999; Högberg et al., 2001; Kuzyakov and Cheng, 2001; Irvine et al., 2005). Because the spatial variability of roots can be high (mean standard deviation was 36% of plot means, Martin and Bolstad, 2005), it is possible that changes in root activity influenced by photosynthesis would translate into greater spatial variability of soil respiration.

3.4. The relationship between soil conditions and root mass

Root mass and the ratio of soil carbon to soil nitrogen can influence the rates of soil respiration across the sites measured in this study (Fig. 3), but root mass and soil C:N are not wholly independent, and both are potentially governed by soil moisture (Fig. 5 and Callesen et al., 2007). Soil water content can influence not only microbial activity, which will dictate decomposition rates, but also potentially root turn-over and above-ground production (Tateno et al., 2004). For this data set, the ratio of soil carbon to soil nitrogen declined with mean annual soil water content (Fig. 5a). This decline trend follows an exponential decay function, with the majority of sites ranging from 30 to 55% mean annual volumetric soil moisture (for 2004 data only). Soils that were routinely drier than 30% appear to have a much higher C:N, although there was considerable variation and three of the four red pine sites seem to leverage the relationship. Evergreen coniferous foliage generally has a higher C:N than broadleaf foliage (McGroddy et al., 2004) which indicates a relationship between soil C:N and soil water content, soil water content, soil C:N ratio, and root mass, respectively.

Table 2

<table>
<thead>
<tr>
<th>Model coefficient</th>
<th>Estimate</th>
<th>Std error</th>
<th>p-Value</th>
</tr>
</thead>
<tbody>
<tr>
<td>b₀</td>
<td>-2.3611</td>
<td>0.1750</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>b₁ &quot;Tsoil&quot;</td>
<td>0.2882</td>
<td>0.0137</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>b₂ &quot;Tsoil²&quot;</td>
<td>-0.0069</td>
<td>0.0006</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>b₃ &quot;Qp&quot;</td>
<td>0.0048</td>
<td>0.0001</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>b₄ &quot;Qp²&quot;</td>
<td>-0.0006</td>
<td>0.0001</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>b₅ &quot;C:N&quot;</td>
<td>0.0480</td>
<td>0.0117</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>b₆ &quot;C:N²&quot;</td>
<td>-0.0008</td>
<td>0.0002</td>
<td>0.001</td>
</tr>
<tr>
<td>b₇ &quot;Mroots&quot;</td>
<td>0.0004</td>
<td>0.0001</td>
<td>0.005</td>
</tr>
<tr>
<td>b₈ &quot;Mroots²&quot;</td>
<td>-2.10E-07</td>
<td>7.19E-08</td>
<td>0.004</td>
</tr>
</tbody>
</table>

Model df 8
Error df 387
MSE 0.053
adj R² 0.382
Model p-value <0.001

* Parameters for use with Eq. (2): \( \ln(R_s) = b_0 + b_1(T_{soil}) + b_2(T_{soil}^2) + b_3(Q_p) + b_4(Q_p^2) + b_5(M_{roots}) + b_6(C:N) + b_7(C:N)^2 \), where \( T_{soil}, Q_p, C:N, \) and \( M_{roots} \) represent soil temperature, soil water content, soil C:N ratio, and root mass, respectively.

This study (Fig. 3), but root mass and soil C:N are not wholly independent, and both are potentially governed by soil moisture (Fig. 5 and Callesen et al., 2007). Soil water content can influence not only microbial activity, which will dictate decomposition rates, but also potentially root turn-over and above-ground production (Tateno et al., 2004). For this data set, the ratio of soil carbon to soil nitrogen declined with mean annual soil water content (Fig. 5a). This decline trend follows an exponential decay function, with the majority of sites ranging from 30 to 55% mean annual volumetric soil moisture (for 2004 data only). Soils that were routinely drier than 30% appear to have a much higher C:N, although there was considerable variation and three of the four red pine sites seem to leverage the relationship. Evergreen coniferous foliage generally has a higher C:N than broadleaf foliage (McGroddy et al., 2004) which would substantially alter the soil C:N, and red pine forests are generally planted on drier sites. If the three red pine sites are removed from this analysis, no significant trend exists between soil water and soil C:N (simple linear regression, slope p-value = 0.107). Soil moisture could differentially drive the decomposition of organic matter, thereby enriching carbon relative to nitrogen in the drier soils while maintaining the low C:N ratio of litter inputs to the soil at the wetter sites that experience periodic anoxic conditions and lower decomposition rates. The data shown here only weakly indicate a relationship between soil C:N and soil water. With the exclusion of the three red pine sites, there appears to be no forest type effect on soil C:N and no relationship between soil water and soil C:N. However, one of the four red pine sites had a low soil C:N which suggests that soil C:N may be influenced by factors beyond soil water and species type. Finally, we found, while species composition may strongly drive soil chemistry and species composition can be influenced by the availability of soil water, soil water may partially dictate whether microbial activity at a particular site is limited by carbon or nitrogen (Fig. 5a). Further experimentation on this topic is required.
We also detected a relationship between root mass and the ratio of soil carbon to soil nitrogen for the sites (Fig. 5b). Similar to the trend between soil water and soil C:N, a weak relationship was observed between soil C:N and root mass. Again, three of the four red pine sites seem to leverage the relationship and the removal of these three sites resulted in no significant trend (simple linear regression, slope $p$-value = 0.633). As noted in the relationship between soil water and soil C:N (Fig. 5a), one of the four red pine sites had a low soil C:N. The low soil C:N of the one red pine site, coupled with the low root mass, suggests that the influence of species composition on soil properties may be masked by additional factors such as previous land use or differences in parent material that would affect soil chemistry.

The amount of carbon relative to the amount of nitrogen present in the soil can ultimately determine the availability of free nitrogen for plant uptake (Eichhorn and Hütttermann, 1994) and, therefore, should influence the roots. It appears that, for soils with a C:N below 25, decreasing the amount of soil nitrogen relative to soil carbon (increasing the C:N) may increase root mass, perhaps to compensate for resource limitation (Fig. 5). Beyond a C:N of 17 root mass appears to decrease, which may be due to overall resource limitations on growth. As reported earlier, the relationship between C:N and soil respiration was a polynomial; this is possibly because, as C:N increases, root mass increases which may increase soil respiration. However, at a C:N greater than 25–30, nitrogen could be limiting (Eichhorn and Hütttermann, 1994) which may limit overall stand productivity and root mass, subsequently reducing overall soil respiration rates. It should be noted that these trends are weak, and further analysis of the relationships between soil C:N, root mass, and soil respiration is warranted.

These relationships between root mass, soil C:N and soil respiration appear useful for explaining the variations in carbon fluxes from soils across many forest types, and similar trends should be examined in other systems. However, from a modeling standpoint, the soil data used in this analysis would be hard to obtain on large area basis because soil analyses are difficult to accomplish and expensive to support. Future attempts to map soil respiration over large areas will need to build on additional analyses based on the ecophysiological relationships between soil nutrients or water status, and their subsequent effects on root production (Zheng et al., 2005). Also needed is an understanding of the relationships between below-ground production and more easily measured above-ground characteristics (e.g., leaf area index or site index) as well as the influence of soil nutrients and water status on both. With continued attempts to quantify sources of variation of carbon movement across space and through time; local, regional, continental, and global models will need to evolve to reduce errors. Soil respiration models that can be applied spatially will help reduce uncertainty in one aspect of terrestrial carbon modeling.
Acknowledgements

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References


