Interannual variation of soil respiration in two New England forests

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Abstract. Soil respiration is an important component of the annual carbon balance of forests, but few studies have addressed interannual variation in soil respiration. The objectives of this study were to investigate the seasonal and interannual variation in soil respiration, temperature, precipitation, and soil water content in two New England forest soils and to develop and evaluate empirical models for predicting variations in soil respiration using temperature and soil moisture content. We have been measuring soil respiration, using dynamic chambers in well-drained upland sites and poorly drained wetland sites since 1995 at the Harvard Forest, Massachusetts, and since 1996 at the Howland Forest, Maine. The upland sites had consistently greater rates of respiration than wetlands. Prolonged drought periods in 1995, 1998, and 1999 at the Harvard Forest resulted in decreased soil respiration rates in the uplands, particularly once soil moisture contents decreased below about −150 kPa. In contrast, wetland respiration increased upon drying. The interannual variation in soil respiration at the Harvard Forest, 0.23 kg C m⁻² yr⁻¹, exceeds the interannual variation in net ecosystem exchange (NEE), 0.14 kg C m⁻² yr⁻¹ previously measured for this forest, indicating that interannual variation in soil respiration can have an important influence on NEE. Interannual variation was lower at the Howland Forest, and the effects of low soil moisture content on respiration rates were more subtle. The onset of spring was variable among years at both forests, owing to variation in both temperature and precipitation, and contributed to 33–59% of the annual variability in total carbon release. At the upland sites, parameterization of empirical regression models for respiration as a function of soil temperature was inconsistent among years, indicating an important effect of interannual variation in soil water content. The negative residuals of the Harvard Forest temperature regression model were best explained by drought conditions (soil matric potentials ≤−150 kPa). This function was only applicable during severe drought and did not account for less severe dry periods that also reduced soil moisture and soil respiration. An empirical regression model for the wetlands as a function of temperature was significantly improved with the addition of a soil moisture function, which increased respiration rates under dry conditions and decreased it under wet conditions. Climatic changes resulting in drier conditions will likely decrease soil respiration rates in uplands and increase soil respiration in wetlands.

1. Introduction

Interannual variation in temperature and precipitation affects ecosystem processes such as gross primary productivity, aboveground plant respiration, and soil respiration, thus also affecting net ecosystem exchange (NEE) of carbon [Wofsy et al., 1993; Goudzen et al., 1996]. Variation in soil respiration may contribute to interannual anomalies of CO₂ accumulation in the atmosphere [Houghton et al., 1998; Trumbore et al., 1996]. Responses to interannual climatic variability at specific study sites provide information about how soil processes might respond to long-term changes in temperature and precipitation due to expected global warming. Because soils store 2–3 times as much carbon globally as exists in the atmosphere [Batjes, 1996; Esvaran et al., 1993], changes in soil respiration that result in net changes of soil carbon stocks could result in important positive or negative feedbacks to the climate system.

Soil respiration is the sum of root respiration and heterotrophic decomposition of soil organic matter. This biological activity is strongly affected by temperature and moisture [Edwards, 1975; Kowalenko et al., 1978; Oberbauer et al., 1992; Wildung, 1975; Zak et al., 1999]. Respiration rates are positively correlated with soil temperature [Crill, 1991; Davidson et al., 1998; Lloyd and Taylor, 1994; Raich and Potter, 1995] and have generally been expressed as either Q₁₀ or Arrhenius functions. However, temperature responses differ depending on temperature range and type of ecosystem [Kirschbaum, 1995; Lloyd and Taylor, 1994; Winkler et al., 1996]. Root respiration and soil microbial respiration may also respond differently to variation in soil temperature [Boone et al., 1998].

Some of the variability in apparent responses to temperature may be the result of confounding variation in soil water content [Bowden et al., 1998; Davidson et al., 1998; Dorr and Mannick, 1987]. In temperate regions, summers are often warm and dry, while winters are both cool and wet. Under very wet conditions, respiration decreases due to O₂ limitations; under dry conditions, respiration decreases due to moisture stress; field capacity is usually the optimal soil moisture condition for respiration [Linn and Doran, 1984; Grant and Rochette, 1994; Schlenne and Van Cleve, 1985; Skopp et al., 1990; Wildung et al., 1975; Zak et al., 1999]. Orchard and Cook [1983] found that bacterial populations were more susceptible to drought stress than fungi.

The objectives of this study were (1) to investigate seasonal and interannual variation in soil respiration, precipitation, soil temper-
ature, and soil water content in two New England forests and (2) to develop and to evaluate empirical models for predicting variation in soil respiration using temperature and soil moisture. Forests of Massachusetts and Maine were compared to see if empirical models developed for one would be applicable to the other. Within each forest, both moderately well and well-drained uplands and very poorly drained wetlands were studied to investigate how responses to climatic variation might vary according to soil drainage class.

2. Site Description

Soil respiration has been measured for over 5 years, beginning June 1995 at the Prospect Hill tract of the Harvard Forest near Petersham, Massachusetts (42°32'N, 72°11'W). Soils are classified as Typic Distrochrepts. Five sites were selected representing a range of drainage characteristics, from well-drained to very poorly drained peat located along northwest and southwest transects within the footprint of a tower measuring NEE by eddy correlation methods [Goulden et al., 1996; Wofsy et al., 1993]. The soil series for the two well-drained sites is Canton fine sandy loam, the two moderately well drained sites are Scituate fine sandy loam, and the very poorly drained is a hardwood peat swamp. This temperate forest system is comprised of mixed hardwood forest, ranging in age from 50 to 70 years, and is dominated by red oak, red maple, with some hemlock, and white and red pine. Mean annual temperature (MAT) is +8.5°C and mean annual precipitation (MAP) is 1050 mm. See Compton and Boone [2000] for further descriptions of site and soil characteristics.

Over 4 years of soil respiration measurements have been made, beginning June 1996 at the Howland Forest (45°12'N, 68°44'W) near Orono, Maine, which is located ~400 km north-east of Harvard Forest. The Howland Forest is located within International Paper’s Howland Integrated Forest Study Area and has never been cultivated. Soils are formed in coarse-loamy granitic basalt till and are classified as Aquic Haplorthods. Five sites were selected representing a range of soil drainage characteristics from well-drained to very poorly drained. The soil series for the two moderately well drained sites is Skerry fine sandy loam, and the two very poorly drained sites are peat swamp. All sites are located within the footprint of a tower measuring NEE by eddy covariance [Hollinger et al., 2000]. This boreal transition forest is dominated by mixed spruce, hemlock, aspen, and birch stands ranging in age from 45 to 130 years. MAT is +5.5°C, and MAP is 1000 mm. See Fernandez et al. [1993] for further site description and soil characteristics.

3. Methodology

3.1. Soil Respiration Measurements

Soil respiration was measured with dynamic chambers and a portable infrared gas analyzer (IRGA) as described by Davidson et al. [1998]. Flux measurements were made weekly during the spring and summer months and once or twice per month during the fall and winter. Collars, made from 25-cm diameter polyvinylchloride (PVC) tubing cut to 10 cm lengths, were placed into the ground to a depth of 2–4 cm. There were six collars per site at the Harvard Forest and eight collars per site at the Howland Forest. For each flux measurement a vented chamber top was placed over the collar, and a Licor 6252 IRGA was used to measure CO2 concentration within the chamber headspace. The IRGA was calibrated each sampling day with CO2-free air and a 523 µL L⁻¹ (±2%) CO2 certified standard. Air was circulated between the chamber and the IRGA, with a small pump, at a rate of 0.5 L min⁻¹ over a 5-min period. Pressure differences between the chamber headspace over the soil and the ambient air outside the chamber were below detection limits (0.1 Pa measured by an Infiltec micromanomter). Varying the flow rate from 0.1 to 0.9 L min⁻¹ had no effect on the measured fluxes. A linear regression was applied to the straightest increasing portion of CO2 concentration ~1 min. after the chamber top had been placed on the collar to determine a flux rate. Fluxes were corrected for atmospheric pressure and air temperature. Winter fluxes were measured only when the collars were exposed or when the snow cover was continuous enough that the chamber top could be inserted 1–2 cm directly into the snow. At each date, the individual chamber flux measurements were averaged per site. Mean site flux rates were interpolated linearly between sampling dates.

Several steps were taken to maintain consistency throughout the study years. Two research assistants have been responsible for overseeing the fieldwork, and their tenures overlapped. Summer interns collected much of the data, but their results were carefully and frequently checked by the research assistants. Chamber collar heights were measured each spring to correct for possible changes in collar volume from one year to the next. At the Harvard Forest, new collars were installed less than 1 m from the original collar locations in the spring of 1998 because of compaction near the original positions. Mean fluxes from the old and new collars were then compared for 2 weeks before measurements of the old ones were terminated. Similarly, the concentrations of new cylinders of calibration gas were compared to old ones before the old ones ran out.

3.2. Soil Temperature

Temperature was measured at 10 cm depth at the same time respiration was being measured. Studies of soil respiration often give an empirical relationship with temperature in the form of a Q₁₀ value [Davidson et al., 1998; Raich and Schlesinger, 1992; Raich and Potter, 1995]. However, it has been observed that the response of respiration is often greater at lower temperatures than at warmer temperatures [Kirschbaum, 1995; Lloyd and Taylor, 1994]. An empirical regression model for soil respiration at the Harvard and Howland Forest sites was derived based on the function given by Lloyd and Taylor [1994]:

\[ R = A\{\exp\left(-E_o/(T - T_o)\right)\}, \]

where \( R \) represents the soil respiration (mg C m⁻² hr⁻¹), \( E_o \) is a fitted parameter (°K) which is similar to an activation energy, \( T_o \) is a fitted temperature value (°K), and \( T \) is the measured soil temperature (°K) at 10 cm soil depth. The \( A \) parameter is a site-specific factor which accounts for intersite variation not attributed to seasonal variation in temperature. The \( A \) values are in units of mg C m⁻² hr⁻¹ and were set to the average annual flux. Although \( E_o \) in this formulation is not meant to be a true activation energy, we multiplied our \( E_o \) values by 1000 in order to obtain \( E_o \) values that are close to expected activation energies. This modification did not alter our regression model results. We used the Lloyd and Taylor [1994] function because it allows the temperature response to vary within the range of observed temperatures and it provided a more unbiased fit to the data at lower soil temperatures (<10°C) while maintaining a similar fit at warmer soil temperatures (10°–18°C) compared to a simple exponential fit (Figure 1).

3.3. Soil Moisture

Soil water content was measured using time domain reflectometry (TDR). At the Harvard Forest upland sites, the \( O \) horizon was carefully removed, a 15-cm three-pronged unbalanced probe [Zegelin et al., 1989] was inserted vertically into the mineral soil, and the \( O \) horizon was then replaced (\( n = 3–4 \) probes per site). In
the very poorly drained swamp site the probes were entirely in an organic horizon. A two-phase mixing model was used to derive a calibration curve to convert the soil dielectric constant to a measure of soil moisture content on soils at the Harvard Forest [Newkirk et al., 1994]. This model was applied to the determined dielectric constants for conversion to soil moisture content at all sites. Although the absolute values of soil moisture for the swamp may be less certain because no specific calibration for that site was conducted, the relative seasonal and annual soil moisture trends are still reliably detected.

A different TDR system was installed at the Howland Forest. Two-pronged TDR probes were inserted horizontally into different soil horizons of moderately well drained soil pits. Each probe was positioned horizontally within a soil horizon. Data from the probes installed at 5 cm depth are reported here. The Moisture Point system (a product of Environmental Sensors Inc.) determines soil dielectric constant and automatically converts to soil moisture content (conversion equation from Hook and Livingston [1996]).

Duplicate intact soil cores from each site at the Harvard Forest and four cores per site at the Howland Forest (excluding the very poorly drained sites) were collected and sent to Keith Cassel at North Carolina State University for measuring soil water retention curves using pressure cells [Reginato and van Bavel, 1962]. To these data we applied the equation of Papendick and Campbell [1980]:

$$\Psi = a \theta^b$$

where $\Psi$ is the matric potential (kPa), $\theta$ is the soil moisture content ($cm^3 H_2O cm^{-3} soil$), and $a$ and $b$ are site-specific parameters. Examples of two water retention curves for a well-drained soil at the Harvard and Howland Forests are presented in Figure 2a and 2b. Because of swelling and shrinking of cores of organic material, water retention curves could not be generated for the swamp soils.

3.4. Regression Model Parameterization and Evaluation

The model parameters $E_o$ and $T_o$ from (1) were derived using a nonlinear regression model in Systat 7.0, with soil respiration and temperature data collected from the Harvard and Howland Forest sites. The estimation method was Gauss-Newton, and the loss function was least squares. Soil moisture models were derived using a linear regression model in Systat 7.0. The $R^2$ values for the temperature regression models represent the proportion of variance accounted for by the model and were determined by subtracting from 1 the ratio of model variance to total variance. Significant differences between the temperature
and the temperature-soil moisture regression models were determined by stepwise regression procedures using the 99% confidence level.

4. Results and Discussion

4.1. Stratification by Soil Drainage Class

The well and moderately well drained sites had the greatest rates of respiration, and the very poorly drained sites consistently showed the lowest fluxes at both Harvard and Howland Forests (Table 1, Figure 3). The only exception occurred in 1995 at the Harvard Forest, where a prolonged summer drought caused the very poorly drained site to dry out and to respire almost as much CO₂ as the better drained sites (Figure 3a). Significant differences among years (as indicated by 95% confidence intervals of means in Figure 3) were also observed for the mean summertime respiration (June, July, August) in the well and moderately well drained sites of both the Harvard and Howland Forests. Mean summertime respiration rates were not different among years at the wetlands at Howland Forest (Figure 3b).

Within each year, differences between well and moderately well drained sites generally were not significant (Figure 3). Owing to the similarity in magnitude and annual pattern of respiration rates between the well and moderately well drained sites, they were grouped and categorized as "upland." Further statistics derived from this category are the mean among these four upland sites at the Harvard Forest (n = 24 flux measurements per date) and three upland sites at the Howland Forest (n = 24). Similarly, the very poorly drained sites are categorized separately as the Harvard "wetland" (one site, n = 6) and the Howland "wetland" (mean of two sites, n = 16).

The annual respiration rates observed at both the Harvard (0.64–0.86 kg C m⁻² yr⁻¹) and Howland (0.66–0.80 kg C m⁻² yr⁻¹) upland sites are within the range observed in other temperate and boreal forests: 0.73–0.93 kg C m⁻² yr⁻¹ [Hanson et al., 1993], 0.68 kg C m⁻² yr⁻¹ [Law et al., 1999], 0.93–1.07 kg C m⁻² yr⁻¹ [Andrews, 1999; Andrews and Schlesinger, 2001], and 0.81–0.91 kg C m⁻² yr⁻¹ [Russell and Voroney, 1998]. The annual estimates for the wetlands at Harvard (0.37–0.40 kg C m⁻² yr⁻¹) and Howland (0.42–0.48 kg C m⁻² yr⁻¹) Forests are larger than those observed by Alm et al. [1999] of 0.22–0.32 kg C m⁻² yr⁻¹ and Silvola et al. [1996] of 0.05–0.62 kg C m⁻² yr⁻¹ in boreal bogs in Finland and by Moore [1986] of 0.08–0.18 kg C m⁻² yr⁻¹ in a subarctic peatland.

4.2. Effects of Drought: Uplands

The seasonal pattern of soil respiration for all upland sites followed the seasonal temperature cycle, with peak respiration occurring during the warm summer months (Figures 4a, 4b, 5a, and 5b). Extended periods of low precipitation resulted in decreased soil water content and soil respiration rates at the Harvard upland sites (Figures 4a, 4c, and 4d). This was particularly evident between August 15 through September 18, 1995, when an extended period of drought caused soil moisture contents to decrease below 0.12 cm³ H₂O cm⁻³ soil and caused a concurrent decrease in soil respiration rates (see also Davidson et al., 1998). During the generally wet summer of 1996, there was a brief dry period in August corresponding to a lowering of soil moisture values but not to levels that caused a decrease in respiration rates. Below-average precipitation fell during the summer of 1997 at both Harvard and Howland Forests, and respiration rates were low compared to other years, but there was no severe drought episode in which soil moisture contents decreased below

<table>
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<tr>
<th>Harvard Forest</th>
<th>Well-Drained 1, kg C m⁻² yr⁻¹</th>
<th>Well-Drained 2, kg C m⁻² yr⁻¹</th>
<th>Moderately Well- Drained 1, kg C m⁻²</th>
<th>Moderately Well- Drained 2, kg C m⁻²</th>
<th>Very Poorly Drained, kg C m⁻² yr⁻¹</th>
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<tr>
<td>1995b</td>
<td>0.75</td>
<td>0.71</td>
<td>0.71</td>
<td>0.67</td>
<td>0.55</td>
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<td>1996</td>
<td>0.79</td>
<td>0.79</td>
<td>0.75</td>
<td>0.78</td>
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<td>1997</td>
<td>0.64</td>
<td>0.63</td>
<td>0.70</td>
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<td>1998</td>
<td>0.94</td>
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<td>0.81</td>
<td>0.71</td>
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<td>1999</td>
<td>0.62</td>
<td>0.44</td>
<td>0.46</td>
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Howland Forest

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<th>Well-Drained, kg C m⁻² yr⁻¹</th>
<th>Moderately Well- Drained 1, kg C m⁻²</th>
<th>Moderately Well- Drained 2, kg C m⁻²</th>
<th>Very Poorly Drained 1, kg C m⁻² yr⁻¹</th>
<th>Very Poorly Drained 2, kg C m⁻² yr⁻¹</th>
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<tr>
<td>1996b</td>
<td>no data</td>
<td>0.82</td>
<td>0.74</td>
<td>0.50</td>
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<tr>
<td>1997</td>
<td>0.80²</td>
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<td>0.47</td>
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<tr>
<td>1998</td>
<td>0.89</td>
<td>0.84</td>
<td>0.68</td>
<td>0.55</td>
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<tr>
<td>1999</td>
<td>0.90</td>
<td>0.83</td>
<td>0.66</td>
<td>0.54</td>
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²During winter months (December 1 through April 1), at the Howland forest, respiration measurements could not always be taken (see Figures 3 and 4 for frequency of sampling). The average wintertime fluxes for uplands (14.7 mg C m⁻² h⁻¹) and wetlands (10.2 mg C m⁻² h⁻¹) were used to fill in missing flux values falling between December 1 and April 1.

³Respiration sampling at the Harvard Forest did not begin until June 1, 1995. In order to obtain an annual respiration for each site, fluxes during the period of January 1 to May 31 were summed for each site for 1996, 1997, and 1998. An average of these 5-month totals per site was added to 7 months of measurements in 1995 for that site. Owing to difficulties in wintertime respiration measurements between December 1995 and April 1996, the average flux during this period in subsequent years was used for the period December 8, 1995, through April 5, 1996.

⁴Respiration sampling at the Howland Forest began May 1, 1996. In order to determine an annual respiration rate for each site in 1996, fluxes during January 1 to April 30 were summed for each site for 1997 and 1998. An average of these 4-month totals per site was added to the 8 months of measurements in 1996 for that site.

⁵Respiration sampling for the well-drained site did not begin until May 15, 1997. To obtain a 1997 annual respiration for this site, fluxes between January 1 and May 15 of 1998 and 1999 were summed then averaged. This average of a 4.5-month period was added to the 8.5 months of measurements in 1997 for
0.12 cm$^3$ H$_2$O cm$^{-3}$ soil. Soil moisture contents also decreased due to a period of drought late in the summer of 1998 following a very wet spring (Figure 4c and 4d). Soil respiration rates declined during this 1998 drought, presumably owing to storage of soil water from the wet spring, but not until very late in the summer (Figures 4a and 5a). Not until September 1998 did soil water content fall below 0.12 cm$^3$ H$_2$O cm$^{-3}$ soil at the Harvard Forest, and at that time, both soil respiration and temperature also began to decrease. The late summer drought in 1998 continued into the spring and summer months of 1999, resulting in the lowest summertime fluxes yet observed in the upland sites at the Harvard Forest (Figure 4a). Other teams measuring soil respiration at various locations at the Harvard Forest also found unusually low fluxes in 1999. Soil respiration increased sharply following a drought-breaking large storm in late September 1999 (Figure 4), but then rates declined with declining temperatures in the autumn. Preliminary results from the wet summer of 2000 (data not shown) indicate that carbon dioxide fluxes returned to normal rates.

Matric potential is a measure of the energy of the water that is in contact with soil particles relative to free water. Matric potential is a good index of drought stress to microorganisms and roots and is comparable across soils of different texture. In the Harvard Forest soils the matric potential values decrease sharply (i.e., become larger negative numbers) once soil moisture content values decrease below ~0.12 cm$^3$ H$_2$O cm$^{-3}$ soil (Figure 2a). This water content, which is between −100 and −250 kPa matric potential (Figure 2a), appears to be the threshold for obvious effects of moisture stress on soil respiration in the mineral soil. The exponential fit to the water retention curve is poorest in this range of water content, so it is difficult to estimate this threshold matric potential with confidence. In a laboratory study, using upland taiga soils collected in Alaska, Gulledge and Schimel [1998] found CO$_2$ production dramatically declined once soil matric potentials fell below approximately −150 kPa.

The effects of low water content appear to be more subtle at the Howland Forest compared to the Harvard Forest. In 1997, at the Howland Forest, peak respiration rates did not occur until August, probably because of a significant drought in July of 1997 that prevented soil respiration from peaking when temperature did. In 1998, respiration rates peaked on July 6, when soil temperature also peaked, then began to decline concurrently with declining soil moisture content (Figure 5a and 5e). The spring and summer of 1999 were also relatively dry, but soil respiration rates did not decline with decreasing soil moisture content.

Unlike the Harvard Forest, a clear threshold effect of low soil moisture content on soil respiration was never observed at Howland. Interannual variation of NEE at the Howland site has been low, perhaps because the nearness of the water table to the surface buffers this system from drought [Hollinger et al., 1999; D. Y. Hollinger, personal communication, 1999].

4.3. Effects of Drought: Wetlands

The response of the wetlands to precipitation patterns differed from that of the uplands. During the prolonged summer dry periods of 1995 and 1999, respiration rates at the Harvard Forest wetland did not decrease as dramatically as was observed at the uplands and even briefly exceeded fluxes at upland sites (Figure 4a). Beaver activity in the Harvard wetland in 1999 prevented that site from drying out, despite the intense summer drought. Indeed, we were forced to stop measurements there in the late summer when the beaver dam completely flooded the wetland site. At Howland, respiration increased in the wetlands during the relatively dry summer of 1999.

Respiration has been observed to increase in wetland environments as water tables drop and peat begins to dry out [Alm et al., 1999; Funk et al., 1994; Oberbauer et al., 1992; Silvola et al., 1996]. An O$_2$ limited environment when wet, the wetlands at both Harvard and Howland Forests partially dry throughout the summer, and respiration rates continued to increase until September. Temperatures peaked at the same time in both uplands and wetlands, but the continued drying of excess water in the wetlands is more important than declining temperature late in the summer, resulting in late summer peaks in wetland respiration (Figures 4a–4c and 5a–5c).

4.4. Importance of Springtime Soil Respiration

In addition to summer drought, the onset of spring was also variable among years. During the spring of 1996 and 1998, at the Harvard Forest, respiration rates began to increase sharply in late May, whereas rates did not begin to increase until mid-May in 1997 (Figure 6a). Although temperatures were warmer during the spring (May 1 to June 31) of 1996 and 1998 compared to 1997 (Figure 6b), there was also a noticeable difference in soil moisture content (Figure 6c) and precipitation. The precipitation totals for May and June of 1996 and 1998 were 236 and 250 mm, respectively, whereas the totals for May and June of 1997 and 1999 were 112 and 113 mm, respectively. The warm and moist soil conditions during the...
1996 and 1998 springs promoted an earlier increase in respiration and subsequently an earlier peak in respiration during the summer months (Figure 6a). Bud break (J. O’Keefe, Harvard Forest, personal communication, 1999) also occurred earlier in 1996, 1998 and 1999 than 1997 (Figure 6a). The earlier bud break in 1996 and 1998 may be due to the warm wet spring, prompting both root and microbial respiration to “turn on” early.

The spring of 1999 was unlike the other years because it was warm but dry. The low moisture values in 1999 correspond to the lowest spring respiration rates sampled, even though soil temperatures were greater than any other year sampled at the Harvard Forest. One brief peak in respiration measured on June 3, 1999, closely followed a rain event, but then the soils quickly dried and respiration rates decreased. Bud break in 1999 occurred at about the same time as the warm and wet spring of 1996, presumably due to early spring warmth, but persistently low soil moisture content appears to have depressed root and/or microbial activity.

Similar variation at the onset of spring was observed at the Howland Forest. The spring of 1997 at Howland had lower total precipitation, (May plus June equals 130 mm) than 1998, (May plus June equals 211 mm). Respiration rates began to increase in early May of 1998 in conjunction with increased soil temperature (Figure 7b) and moist soils (Figure 7c), whereas respiration did not begin to increase until mid-June in 1997.

Spring played an important role in the total annual variation in carbon respired in both forests. At the Harvard and Howland Forests, the early increase in respiration rates during the springs of 1996 and 1998 (Figures 6a and 7a) accounted for 33 to 69% of the interannual variability in total carbon release from the upland sites (Table 2). Warm wet springs caused respiration to increase earlier in the season and subsequently peak earlier in the year, whereas dry springs delayed peak respiration, and these differences

Figure 4. Harvard Forest mean daily rates of (a) soil respiration (with standard error bars), (b) soil temperature, (c) soil moisture content, and (d) daily precipitation total beginning June 1995 and continuing to August 2000. The horizontal line at 0.12 cm$^3$ H$_2$O cm$^{-3}$ soil indicates the apparent threshold where the matric potential empirical model becomes effective.
play a significant role in the interannual variation in carbon release from upland soils.

4.5. Interannual Variation in Soil Respiration Relative to NEE and Soil Sinks of C

Using tower-based eddy covariance measurements at the Harvard Forest, Goulden et al. [1996] found that the annual ecosystem respiration during the period 1991–1995 ranged between 0.93 and 1.14 kg C m$^{-2}$ yr$^{-1}$. For the same years, NEE ranged from $-0.14$ to $-0.28$ kg C m$^{-2}$ yr$^{-1}$ (negative values indicating a net C sink in the terrestrial ecosystem). During our study of 1995–1999, mean annual soil respiration for the upland sites ranged between 0.64 and 0.87 kg C m$^{-2}$ yr$^{-1}$ (Table 2). This interannual variation of 0.23 kg C m$^{-2}$ yr$^{-1}$ is similar to the range of 0.21 kg C m$^{-2}$ yr$^{-1}$ of total ecosystem respiration and greater than the range of 0.14 kg C m$^{-2}$ yr$^{-1}$ of NEE estimated by Goulden et al. [1996]. Hence interannual variation in soil respiration can significantly influence the NEE of an ecosystem. Moreover, we found interannual variation of soil respiration in both forests, located 400 km apart in New England. If similar regional responses were continental in scale, an effect on the global interannual anomaly of atmospheric CO$_2$ would be plausible [Fan et al., 1998].

Goulden et al. [1996] estimated that ecosystem respiration decreased by 30% during the 1995 summer drought at the Harvard Forest but that photosynthesis decreased by only 10%, perhaps because of mycorrhizal uptake of water in surface horizons and/or because roots had access to water deep in the soil profile. Because respiration declined more than photosynthesis during the 1995 drought, the NEE for the year was $-0.27$ kg C m$^{-2}$ yr$^{-1}$, the second largest annual sink estimate reported. However, this C sink during dry years may be transitory. We measured above average respiration during the following wet summer of 1996 (Figure 4a). If drought stress limits decomposition during dry years, we speculate that undecomposed labile litter and soil C may be released as above average CO$_2$ flux in the subsequent wet year.
4.6. Empirical Regression Models of Soil Respiration

Both temperature and soil moisture affected soil respiration rates. Soil temperatures at 10 cm depth and soil moisture were used to derive empirical regression models of respiration rates. In the uplands, matric potential was used as an indicator of soil moisture available to plants in unsaturated environments. In the organic soils of the swamp sites, it was not possible to obtain water retention curves for estimating matric potential, and soil volumetric water content may also be a better indicator of the effects of excess water in restricting aeration in seasonally saturated environments [Linn and Dotart, 1984].

Regressions derived using the Harvard Forest data are denoted “Har,” whereas those derived using the Howland Forest data begin with “How.” Upland regressions are symbolized by U, and wetlands are symbolized by W. Regressions using temperature are denoted by T, matric potential is denoted by MP, and soil water content is denoted by WC. Table 3 presents a summary of temperature regression names, data ranges, parameter values, and correlation coefficients, and Table 4 presents the summary of the matric potential and soil moisture regressions.

4.6.1. Temperature Regression Model for the Uplands. A temperature function for predicting soil respiration was derived based on (1) for the first 2 years of the Harvard Forest study, June 1995 through May 1997 (Table 3). This Har_U_T1 regression accounted for 73% of the variation in respiration measurements (June 1995 through May 1997), primarily representing the seasonal changes in soil respiration at the sites. The Har_U_T1 regression was then tested with data from the last 2 years of the study (June 1997 through August 1999), for which the $R^2$ was 0.59. In contrast, the regression that was derived specifically from the June 1997 through August 1999 data, Har_U_T2, had a higher $R^2$ value of 0.64 and different $E_o$ and $T_o$ values (Table 3). We combined all data for the 4 year study to...
produce a third temperature model, called Har U Temp (shown in Figure 1 as the Lloyd and Taylor function), which had an $R^2$ value of 0.67, and the $E_o$ and $T_o$ values were intermediate between the other two regression models (Table 3).

The Har U Temp regression was then applied to the Howland upland data set and compared to a regression derived using the Howland data set (How U Temp). The $R^2$ for the Har U Temp regression, 0.76, was lower than the one derived specifically from

**Table 2. Relative Contribution of Springtime Fluxes to the Annual Respiration Rates at the Harvard and Howland Forest Upland and Wetland Sites**

<table>
<thead>
<tr>
<th></th>
<th>Annual Respiration, kg C m$^{-2}$ yr$^{-1}$</th>
<th>Difference Between Years, kg C m$^{-2}$ yr$^{-1}$</th>
<th>Spring Respiration, kg C m$^{-2}$ 61d$^{-1}$</th>
<th>Differences Between Springs, kg C m$^{-2}$ 61d$^{-1}$</th>
<th>Spring Difference as a Percentage of the Annual Difference, %</th>
</tr>
</thead>
<tbody>
<tr>
<td>Upland</td>
<td>0.76</td>
<td>0.64</td>
<td>0.87</td>
<td>-0.12</td>
<td>0.23</td>
</tr>
<tr>
<td>Wetland</td>
<td>0.41</td>
<td>0.37</td>
<td>0.40</td>
<td>-0.03</td>
<td>0.03</td>
</tr>
</tbody>
</table>

**Harvard Forest**

<table>
<thead>
<tr>
<th></th>
<th>0.66</th>
<th>0.80</th>
<th>0.15</th>
<th>0.11</th>
<th>0.21</th>
<th>0.10</th>
<th>0.13</th>
<th>0.03</th>
<th>69</th>
</tr>
</thead>
<tbody>
<tr>
<td>Wetland</td>
<td>0.42</td>
<td>0.49</td>
<td>0.06</td>
<td>0.10</td>
<td>0.13</td>
<td>0.03</td>
<td>0.13</td>
<td>0.03</td>
<td>52</td>
</tr>
</tbody>
</table>

*Spring totals are from May 1st to June 30th.*
the Howland data ($R^2 = 0.82$). This indicates that while the Harvard-derived temperature model accounted for 76% of the seasonal variation in soil respiration at Howland, it was not as good as one derived from the Howland upland data set.

Interestingly, the Har_U_Temp model had a better $R^2$ (0.76) when applied to the Howland data than when applied to all of the Harvard data (0.67). In general, the temperature functions had better fits at the Howland Forest than at the Harvard Forest.

Several field studies have derived site-specific empirical models of soil respiration and temperature [Hanson et al., 1993; Pinol et al., 1995; Russell and Voroney, 1998]. The temperature function most commonly cited, the $Q_{10}$ value, has been found to be both temperature dependent [Kirschbaum, 1995], depth dependent [Winkler et al., 1996], and independent of soil moisture [Davidson et al., 1998; Dorr and Munnich, 1987]. The Lloyd and Taylor function (equation (1)) is more applicable over differing temperature ranges, but parameterization of $E_o$ and $T_o$ in this function is also likely to be site-specific and variable in time, depending on the depth where temperature is measured relative to where CO$_2$ is produced within the soil, as well as other confounding factors like soil water content.

### 4.6.2. Temperature regression model for the wetlands

A similar comparison was made for the wetlands. The Har_W_T3 regression model accounted for 75% of the variation in respiration for 1995 through May 1997 at the wetland site (Figure 8). When applied to the 1997–1999 data, however, the Har_W_T3 regression model was not significant (Table 3). Because the Har_W_T3 regression was derived utilizing data collected during an unusually dry period in 1995, which had a large effect on the wetland respiration, this regression was biased by the higher than normal flux rates due to drying of the wetland soils (Figure 8b).

Hence a temperature function based on only 1 or 2 years of data may be inadequate because of confounding effects, such as a drought, experienced during that particular period. A temperature function based on all the wetland data (Har_W_Temp) accounted for 64% of the variation in respiration (Table 3). As was the case for uplands, the best temperature regression models were site-specific and had different values for $E_o$ and $T_o$ (Har_W_Temp and How_W_Temp in Table 3).

### Table 3. Parameters for All Empirical Temperature Models (Equation (1)) From Harvard and Howland Forest

<table>
<thead>
<tr>
<th>Upland Model Name</th>
<th>Data Range That the Model was Derived From</th>
<th>Data Range That the Model was Applied To</th>
<th>$E_o$, °K</th>
<th>$T_o$, °K</th>
<th>$R^2$</th>
</tr>
</thead>
<tbody>
<tr>
<td>Har_U_T1</td>
<td>June 1, 1995, to May 31, 1997</td>
<td>June 1, 1995, to May 31, 1997</td>
<td>350.6</td>
<td>213.2</td>
<td>0.73</td>
</tr>
<tr>
<td>Har_U_T2</td>
<td>June 1, 1995, to May 31, 1997</td>
<td>June 1, 1995, to Aug. 31, 1999</td>
<td>333.9</td>
<td>235.1</td>
<td>0.68</td>
</tr>
<tr>
<td>Har_U_T3</td>
<td>June 1, 1995, to Aug. 31, 1999</td>
<td>June 1, 1995, to Aug. 31, 1999</td>
<td>333.9</td>
<td>235.1</td>
<td>0.64</td>
</tr>
<tr>
<td>Har_U_T4</td>
<td>June 1, 1995, to May 31, 1997</td>
<td>June 1, 1995, to Aug. 31, 1999</td>
<td>350.6</td>
<td>213.2</td>
<td>0.65</td>
</tr>
<tr>
<td>Har_U_T5</td>
<td>June 1, 1995, to Jan. 1, 1999</td>
<td>June 1, 1995, to Aug. 31, 1999</td>
<td>333.9</td>
<td>235.1</td>
<td>0.66</td>
</tr>
<tr>
<td>Har_U_T6</td>
<td>June 1, 1995, to Aug. 31, 1999</td>
<td>June 1, 1995, to Aug. 31, 1999</td>
<td>346.8</td>
<td>232.5</td>
<td>0.67</td>
</tr>
<tr>
<td>How_U_Temp</td>
<td>June 1, 1995, to Aug. 31, 1999</td>
<td>June 1, 1995, to Aug. 31, 1999</td>
<td>346.8</td>
<td>225.5</td>
<td>0.76</td>
</tr>
<tr>
<td>How_W_Temp</td>
<td>Howland; Sept. 1, 1996, to June 30, 1999</td>
<td>Howland; Sept. 1, 1996, to June 3, 1999</td>
<td>415.1</td>
<td>220.8</td>
<td>0.82</td>
</tr>
<tr>
<td>Har_W_T1</td>
<td>June 1, 1995, to May 31, 1997</td>
<td>June 1, 1995, to May 31, 1997</td>
<td>296.3</td>
<td>238.1</td>
<td>0.75</td>
</tr>
<tr>
<td>Har_W_T2</td>
<td>June 1, 1995, to Aug. 31, 1999</td>
<td>June 1, 1995, to Aug. 31, 1999</td>
<td>296.3</td>
<td>238.1</td>
<td>0.75</td>
</tr>
<tr>
<td>Har_W_T3</td>
<td>June 1, 1995, to Aug. 31, 1999</td>
<td>June 1, 1995, to Aug. 31, 1999</td>
<td>345.4</td>
<td>233.2</td>
<td>0.44</td>
</tr>
<tr>
<td>Har_W_T4</td>
<td>June 1, 1995, to Aug. 31, 1999</td>
<td>June 1, 1995, to Aug. 31, 1999</td>
<td>345.4</td>
<td>233.2</td>
<td>0.71</td>
</tr>
<tr>
<td>Har_W_T5</td>
<td>June 1, 1995, to Aug. 31, 1999</td>
<td>June 1, 1995, to Aug. 31, 1999</td>
<td>345.4</td>
<td>233.2</td>
<td>0.71</td>
</tr>
<tr>
<td>Har_W_T6</td>
<td>June 1, 1995, to Aug. 31, 1999</td>
<td>June 1, 1995, to Aug. 31, 1999</td>
<td>345.4</td>
<td>233.2</td>
<td>0.71</td>
</tr>
<tr>
<td>Har_W_T7</td>
<td>June 1, 1995, to Aug. 31, 1999</td>
<td>June 1, 1995, to Aug. 31, 1999</td>
<td>345.4</td>
<td>233.2</td>
<td>0.71</td>
</tr>
<tr>
<td>Har_W_T8</td>
<td>June 1, 1995, to Aug. 31, 1999</td>
<td>June 1, 1995, to Aug. 31, 1999</td>
<td>345.4</td>
<td>233.2</td>
<td>0.71</td>
</tr>
<tr>
<td>Har_W_T9</td>
<td>June 1, 1995, to Aug. 31, 1999</td>
<td>June 1, 1995, to Aug. 31, 1999</td>
<td>345.4</td>
<td>233.2</td>
<td>0.71</td>
</tr>
<tr>
<td>Har_W_T10</td>
<td>June 1, 1995, to Aug. 31, 1999</td>
<td>June 1, 1995, to Aug. 31, 1999</td>
<td>345.4</td>
<td>233.2</td>
<td>0.71</td>
</tr>
<tr>
<td>How_W_Temp</td>
<td>Howland; Sept. 1, 1996, to June 30, 1999</td>
<td>Howland; Sept. 1, 1996, to June 3, 1999</td>
<td>391.0</td>
<td>225.6</td>
<td>0.81</td>
</tr>
</tbody>
</table>

\[
\Psi \leq -150 \text{ kPa}
\]

then

\[
R = \{A \exp[-350.6^0K/(T - 231.2^0K)]\} - [7.044 + 0.103(\Psi)]
\]

Figure 8. Temperature models for the Harvard Forest wetland. Table 3 describes the model names, parameters, and $R^2$ values.
Table 4. Parameters of All Empirical Soil Moisture Models (Equations (3) and (4)) for Harvard Forest

<table>
<thead>
<tr>
<th>Model Name</th>
<th>Data Range That the Model was Derived From</th>
<th>Data Range That the Model was Applied To</th>
<th>$a$</th>
<th>$b$</th>
<th>$R^2$</th>
</tr>
</thead>
<tbody>
<tr>
<td>Har_U_MP</td>
<td>June 1, 1995, to May 31, 1997</td>
<td>June 1, 1995, to May 31, 1997</td>
<td>-7.044</td>
<td>0.103</td>
<td>0.78</td>
</tr>
<tr>
<td>Har_U_MP</td>
<td>June 1, 1995, to May 31, 1997</td>
<td>June 1, 1997, to Aug. 31, 1999</td>
<td>-7.044</td>
<td>0.103</td>
<td>0.61</td>
</tr>
<tr>
<td>Har_U_MP</td>
<td>June 1, 1995, to May 31, 1997</td>
<td>June 1, 1995, to Aug. 31, 1999</td>
<td>-7.044</td>
<td>0.103</td>
<td>0.69</td>
</tr>
<tr>
<td>Har_W_WC</td>
<td>June 1, 1995, to Aug. 31, 1999</td>
<td>June 1, 1995, to Aug. 31, 1999</td>
<td>40.9</td>
<td>-58.9</td>
<td>0.70</td>
</tr>
</tbody>
</table>

else

$$R = A \{ \text{exp}\left[-350.6^\circ K/(T - 231.2^\circ K)\right]\}$$  \hspace{1cm} (3)

The addition of this matric potential function significantly increased the predictive ability of the Har_U_T1 regression model during the 1995–1997 period, increasing the $R^2$ from 0.73 to 0.78. Likewise, applying this regression model to the entire Harvard Forest data set significantly increased the $R^2$ values from 0.67 to 0.69 of the regressions (Table 3). Owing to TDR equipment failure that created gaps in the soil moisture data for the Howland Forest, the Har_U_MP function was not applied to the Howland upland sites. Examination of the residuals of the How_U_Temp regression model with the available soil matric potential data showed no distinct pattern (data not shown). The absence of a clear effect of soil water content in the Howland Forest upland regressions is consistent with Howland sites having higher $R^2$ values than the Harvard sites for functions of temperature alone.

4.6.4. Temperature and soil moisture model for the wetlands. A soil moisture function (Har_W_WC) was also applied to the residuals of the Har_W_Temp regression model (Figure 9b, Table 4):

$$R = \{A \{ \text{exp}\left(-338.2^\circ K/(T - 329.2^\circ K)\right)\} + [40.7 - 58.9 \text{ soil moisture}]\}, \hspace{1cm} (4)$$

where “soil moisture” is the percent volumetric water content. As was the case for uplands, the addition of a soil moisture function to the temperature-only model significantly increased the predictive power ($R^2 = 0.64$ for Har_W_Temp and $R^2 = 0.70$ for Har_W_Temp + Har_W_WC; Table 4). Similarly, Alm et al. [1999] found that an empirical model utilizing both temperature and depth to water table to explained 59–71% of the variation in respiration rates in a Finnish bog.

Unlike the regression model for uplands, however, our wetland function applies across the entire range of water contents. Also, unlike the upland model, water content is negatively correlated with respiration in the wetlands, indicating that water is often in excess and that drying of wetlands enhances respiration. This finding is consistent with observations of C loss from wetlands following drainage [Carroll and Crill, 1997; Waddington and Roulet, 1996]. Significant loss of carbon could result from climatic changes that reduce mean annual precipitation, causing wetlands to become drier.

4.7. Importance of Interannual Variation in New England

The relatively modest increases in $R^2$ values when the soil water functions are added to the temperature-only regression models (Tables 3 and 4) belies the importance of interannual variation in soil moisture. The temperature functions alone account for the huge variation in respiration rates between winter and summer, thus inflating the $R^2$ value of the temperature function fit. The summer drought effect is small relative to large winter-summer differences in soil respiration, but, nevertheless, soil water content is important for explaining interannual variation. Hence models of soil respiration in temperate forests based only on temperature are likely to make good predictions of seasonal variation of soil respiration but are unlikely to predict interannual variation well.

Figure 9. Harvard Forest soil moisture models: (a) the matric potential model for uplands and (b) the soil moisture model for wetlands.
potential function visibly reduces the predicted respiration rates in 1995, as was observed. The matric potential function was less important in 1996, 1997, and 1998 but was important in 1999 when severe drought conditions again caused substantially lower soil respiration rates.

How important then is the matric potential function for predicting soil respiration in New England forests, and how important are drought conditions? Periods of low precipitation are common in New England. After June of 1998, there was no precipitation event >20 mm for 96 consecutive days. The total precipitation during this 96-day period was 105.4 mm, averaging 1.1 mm per day. Similarly, there was an extended dry period in 1999, with 63 consecutive days with no precipitation event >20 mm and averaging to 1.6 mm per day. There were seven incidences during the summer months at Harvard Forest between 1964 and 1994 when there were 60–101 consecutive days with precipitation not exceeding 20 mm and when the average precipitation during these dry periods ranged from 0.7 to 2.5 mm d⁻¹. Hence the extended dry periods observed in 1995, 1998, and 1999 are not unusual events, as their duration and low precipitation rates occurred 7 times in 30 years between 1964 and 1994. Severe droughts that would probably cause the soil matric potential to fall below the apparent threshold value of about −150 kPa are probably important for about one drought event per 4 years averaged over the three decades. However, the fact that three such droughts occurred in the last 5 years may be unusual, although a longer precipitation record may be necessary to properly evaluate this temporal variability.

Laboratory incubations have consistently shown a relationship between soil moisture content and respiration rates [Howard and Howard, 1993; Orchard and Cook, 1983], but field results are more variable. Hanson et al. [1993] found that including water content increased the predictive power of their model at four of their five sampling sites ($R^2$ from 0.49 to 0.60 increased to 0.67–0.73). Pinol et al. [1995] found soil moisture to be significant at one of their sites. These empirical models are site specific, and few attempts have been made to apply them to other locations.

Similarly, we were only able to develop a significant soil moisture component to the temperature model under very dry conditions at the Harvard Forest, and this same pattern was not evident at the Howland Forest, nor were we able to derive a soil moisture function that included the effects of very wet conditions and above average precipitation observed at the Harvard Forest upland sites during the summer of 1996 and the spring of 1998. The temperature and matric potential models under predicted the summertime peak fluxes in 1996 and 1998 (Figure 10). The regression models do not account for this apparent positive effect of high precipitation on summertime CO₂ fluxes.

Figure 10. Predicted respiration rates from the Har_U_T1 model and the Har_U_T1+Har_U_MP model compared to observed rates for respiration for one representative upland site.
Despite this shortcoming of the regression models, interannual variation in precipitation clearly affects soil respiration, as is evidenced by the differences in emissions among wet and dry years. The limited applicability of the matric potential model may be due to the use of TDR measurements of water content of the top 15 cm of mineral soil, which do not provide a good empirical index of drought stress in the litter layer and the top few millimeters of mineral soil. Rapid increases in soil respiration have been observed at the Harvard Forest following wet-up of the litter layer during small rain events (G. Winston, personal communication, 1999). Laboratory studies have also observed a rapid increase in respiration following wet-up events, particularly after dry periods [Orchard and Cook, 1983; Bottner, 1985]. We suspect that some of the higher-than-predicted respiration rates that we measured are related to small precipitation events, which wet the topsoil layers but which are not measured by the TDR probes that integrate water content over the top 15 cm of mineral soil. Similarly, the TDR measurements of the mineral soil do not reveal dry conditions that may develop in the litter layer during less severe periods of below average precipitation, thus missing the effects of moderate drying on soil.

As already discussed in section 4.5, another plausible speculative explanation for high summertime respiration rates in 1996 and 1998 (Figure 10) is that significant amounts of readily decomposable organic matter remained from the previous dry years, when the full capacity of decomposition was limited by dry conditions. Hence the effects of soil water content may be confounded with availability of fresh, readily decomposable C substrates. We need to sample two consecutive wet years to determine if high respiration rates persist during both years or if they are high only during the first wet year after a dry year. Our on-going measurements may yield this and other opportunities to investigate a wide range of interannual variability.

5. Summary and Conclusions

Interannual variation in soil respiration is significant relative to interannual variation in net ecosystem exchange of carbon. The major sources of interannual variation in soil respiration identified in this study were the occurrence of spring and summer droughts and the onset of the springtime increase in respiration. In the Harvard Forest of Massachusetts and, to a lesser extent, in the Howland Forest of Maine, dry periods reduced soil respiration rates in upland sites and increased respiration in wetlands. The extent to which drought affected soil respiration was dependent on its duration and severity. Springtime variation at the upland sites accounted for one-third to two-thirds of this interannual variation.

The parameterization of an empirical model for respiration at the upland sites as a function of soil temperature varied among years at the Harvard Forest, indicating that interannual variation in precipitation was also affecting soil respiration. The temperature model derived for the Harvard Forest was also a good predictor at the Howland Forest, although not as good as a model derived specifically for Howland data. Parameterization of temperature functions is likely to be site specific and to be confounded by other effects, such as interactions with water content and depth of temperature measurements. Positive residuals of the Harvard upland temperature model were best explained by drought conditions (matric potential \(-150 \text{kPa}\)). However, the matric potential function was applicable only during severe droughts and did not account for less severe, but still important, dry periods that reduced soil respiration.

An empirical temperature model for wetlands was derived that was applicable to both the Harvard and Howland locations. There was a strong negative correlation with soil moisture content in the wetlands; the addition of a soil moisture term significantly increased the predictive power of the regression model. For both uplands and wetlands, temperature functions predicted seasonal variation in soil respiration fairly well, but variation in precipitation and soil water content was key to understanding interannual variation. Climatic change resulting in drier summertime conditions will probably reduce soil respiration in uplands and increase respiration in wetlands. Decreases in soil respiration in uplands during dry years probably result in only a transient C sink, but increased respiration in wetlands could cause significant losses of C from wetlands to the atmosphere.

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References


