

Annual soil respiration in broadleaf forests of northern Wisconsin: influence of moisture and site biological, chemical, and physical characteristics

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Abstract. Soil temperature and moisture influence soil respiration at a range of temporal and spatial scales. Although soil temperature and moisture may be seasonally correlated, intra and inter-annual variations in soil moisture do occur. There are few direct observations of the influence of local variation in species composition or other stand/site characteristics on seasonal and annual variations in soil moisture, and on cumulative annual soil carbon release. Soil climate and soil respiration from twelve sites in five different forest types were monitored over a 2-year period (1998–1999). Also measured were stand age, species composition, basal area, litter inputs, total above-ground wood production, leaf area index, forest floor mass, coarse and fine root mass, forest floor carbon and nitrogen concentration, root carbon and nitrogen concentration, soil carbon and nitrogen concentration, coarse fraction mass and volume, and soil texture. General soil respiration models were developed using soil temperature, daily soil moisture, and various site/soil characteristics. Of the site/soil characteristics, above-ground production, soil texture, roots + forest floor mass, roots + forest floor carbon:nitrogen, and soil carbon:nitrogen were significant predictors of soil respiration when used alone in respiration models; all of these site variables were weakly to moderately correlated with mean site soil moisture. Daily soil climate data were used to estimate the annual release of carbon (C) from soil respiration for the period 1998–1999. Mean annual soil temperature did not differ between the 2 years but mean annual soil moisture was approximately 9% lower in 1998 due to a summer drought. Soil C respired during 1998 ranged from 8.57 to 11.43 Mg C ha⁻¹ yr⁻¹ while the same sites released 10.13 and 13.57 Mg C ha⁻¹ yr⁻¹ in 1999; inter-annual differences of 15.41 and 15.73%, respectively. Among the 12 sites studied, we calculated that the depression of soil respiration linked to the drought caused annual differences of soil respiration from 11.00 to 15.78%. Annual estimates of respired soil C decreased with increasing site mean soil moisture. Similarly, the difference of respired carbon between the drought and the non-drought years generally decreased with increasing site mean soil moisture.

Introduction

The influence of atmospheric carbon dioxide on global climate is well documented, and the dynamics of carbon sequestration, storage, and release within and across biotic systems are key to understanding the balance between biospheric and atmospheric carbon. A large amount of carbon enters the world's soils annually through vegetative inputs (75.8 Pg C yr⁻¹, Jenkinson et al. 1991). A substantial amount of this carbon is then lost from the soils to the

atmosphere ($80.4 \text{ Pg C yr}^{-1}$, Raich et al. 2002). The loss of below-ground carbon to the atmosphere is primarily due to heterotrophic and autotrophic metabolism, collectively referred to as soil respiration. In mature temperate forests, global estimates of soil respiration can be as high as $12.9 \text{ Pg C yr}^{-1}$ (Kicklighter et al. 1994). While soil respiration is a poorly understood portion of the terrestrial carbon cycle, it is paramount to understanding the fluxes of carbon dioxide from ecosystems.

Many field studies have shown that soil respiration for an individual site or stand may be controlled by temperature (Lloyd and Taylor 1994; Fang and Moncrieff 2001), moisture (Cook et al. 1985; Gårdenäs 2000), nutrient resources (Zog et al. 1996) and the total mass of respiring tissue (Vose et al. 1995). The link between temperature and soil respiration is well documented (Waksman and Starkey 1924; Reiners 1968; Buchmann 2000; Rustad et al. 2001) but the relationship between soil moisture and respiration is less clear, as the effects may change with temperature (Bowden et al. 1998; Lomander et al. 1998), and may not be discernable during short-term studies.

Soil moisture varies not only within a forest stand, but also among forest types, throughout individual seasons, and substantially among years. Drought conditions have been shown to reduce soil respiration (Davidson et al. 1998; Kaye and Hart 1998; Boriken et al. 1999; Savage and Davidson 2001), yet the true magnitude of a drought-induced reduction of annual soil respiration across a diverse landscape is less certain because few studies have modeled soil respiration for multiple years and for multiple sites. Annual soil respiration has been shown to decline by as much as 40% in well drained, upland sites during severe drought conditions, yet the decrease was less pronounced in wetlands (from Savage and Davidson 2001). It is possible that annual variations in soil climate, such as a decrease in soil moisture, may lead to great differences in the annual release of soil carbon to the atmosphere, and these differences may vary in relation to general site moisture conditions.

Soil climate directly and indirectly influences soil respiration rates through chemical and physical processes; however, soil respiration is also driven by biological factors, most notably at regional and global scales. Studies have shown that, across a range of forested ecosystems, soil respiration is positively correlated to primary production (Raich and Nadelhoffer 1989) and litter production (Raich and Tufekcioglu 2000). These above-ground trends may be difficult to separate, as both are similarly related to nutrient inputs, landscape position, and climate.

Recent studies, focusing on smaller spatial and temporal scales, have identified a proportion of soil respiration that may be due to autotrophic activity, and that short-term variation in soil respiration is related to root and rhizosphere activity associated with diurnal patterns of production and seasonal phenology (Högberg et al. 2001; Curiel Yuste et al. 2004). While these and related experimental studies substantially improve our understanding of the

mechanisms and pathways of carbon through the soil system, they should be paired with larger scale studies. This can allow the estimation of differences in annual respiration rates across broader landscapes and provide estimates of the changes in soil respiration due to climatic variation among years or across the variation of stand conditions found in most regions.

At the stand scale, many studies have compared differences in soil respiration rates from a wide variety of systems and conditions. Among these studies, there have been comparisons of soil respiration from different ecosystems sharing similar spaces, from similar systems at different ages, and from similar systems changed in different ways (Lessard et al. 1994; Striegel and Wickland 1998; Griffiths and Swanson 2001). Specifically, it has been shown that soil respiration was lower in agricultural systems than in adjacent forests (Lessard et al. 1994), higher in older vs. younger stands of Douglas fir (Griffiths and Swanson 2001), and lower when a forest was clear-cut (Striegel and Wickland 1998). Despite the conclusions drawn from these studies, little knowledge exists concerning what causes the smaller differences seen in soil respiration among neighboring forest stands that do not differ greatly in climate, species composition, disturbance regime, nutrient availability and/or topographic position (Garnett and Cox 1973).

Three objectives were addressed in this study. The first was to quantify soil surface CO₂ fluxes for a number of Lake States forest ecosystems and examine differences in the flux rates as a function of soil climate and site/soil biological, chemical and physical properties. We expected that:

- (i) Intra-annual differences in soil flux are influenced by soil temperature and soil moisture.
- (ii) Inter-spatial differences in soil flux would be a function of site/soil biological, chemical and physical properties.

The second objective was to develop a model of soil respiration based on soil climate as well as site and soil properties. The third objective was to use this model to estimate annual soil respiration from the various forested systems included in this study for a 2-year measurement period (1998–1999). This period included a drought that occurred during the summer of 1998 where volumetric soil moisture was below the 2-year average for 81 continuous days. Additional expectations included:

- (iii) Annual carbon released by soil respiration will generally be less during a drought year because of the suppression of plant and microbial activity in response to reduced soil water.
- (iv) Annual carbon release will vary more among the sites during the drought year due to the differential effect of the drought on relative soil moisture. Wetter sites may have sufficient soil water to resist a depression of soil respiration during a drought, while drier sites would not. Soil respiration rates at wetter sites may actually increase during dry periods due to the reduction of anaerobic soil conditions.

Materials and methods

Study location and site summary

Twelve measurement plots were established in conjunction with an above-canopy flux tower located near Willow Creek, in the Chequamegon National Forest of north central Wisconsin (W 45°48', N 90°07'). The Willow Creek tower is part of the Chequamegon Ecosystem-Atmosphere Study (ChEAS) and AmeriFlux network, and consists of mature, second growth northern hardwood forests. Plots were selected to represent common deciduous forest types of the Lake States (Table 1). There were six aspen sites (*Populus tremuloides* Michx.), two in each of three age groups. There were also four northern hardwood sites [sugar maple (*Acer saccharum* Marsh.), basswood (*Tilia americana* Marsh.) and green ash (*Fraxinus pennsylvanica* L.)], and two ash/elm sites [black ash (*Fraxinus nigra* Marsh.), elm species (*Ulmus* spp.) and red maple (*Acer rubrum* L.)]. These 12 sites encompassed a wide range of mean soil moistures, from moderately dry (aspen sites) through mesic (northern hardwoods) to moist (ash/elm sites). A subset of these sites was examined by Bolstad et al. (2004).

Site/soil biological, chemical and physical measurements

Above-ground and below-ground measurements were made for each of the sites (Tables 2–4). Circular, 20 m radius plots were randomly placed within each forest type 50 m from any edge. We measured diameter at breast height (DBH, 1.37 m above the ground) and noted species of each tree greater than 1 cm. Total tree height, height to canopy bottom, and increment cores were taken for every 10th tree. Increment cores were extracted and measured to determine 5 and 10 years of growth rings. Litter production was measured for 1998, 1999, 2000, and 2002 with 14 litter traps per site; each was 15 cm deep and had a footprint of 0.092 m².

We used a hand held 10.16 cm diameter bucket auger to extract 14 cores from each site to a depth of 30 cm; of those, four were continued to a depth of 60 cm, and of those, two were continued to 100 cm (Tables 3 and 4). The soil from each depth was kept at 0 °C until it was dried, and sieved with a 1 mm mesh screen. The soil that passed through the sieve was sub-sampled for chemical and textural analysis, and the remaining organic matter was sorted into fine roots (<2 mm), coarse roots (>2 mm), coarse fraction, and forest floor. Forest floor was considered to be any organic material that was not a root. The root samples were rinsed, and both the roots and forest floor were weighed, ground and analyzed for carbon and nitrogen concentrations. These samples were ground with a Wiley mill (0.5 mm² screen, size 40) and analyzed with a combustion elemental analyzer (2400CHN, Perkin Elmer, Norwalk, CT, USA). To compute coarse fraction volume, a sub-sample of 10 rocks, ranging

Table 1. Site data and descriptions.

Site name (code)	Plot	Age (yrs)	Dominant species (in order of relative abundance)	Description	% Sand	% Silt	% Clay
Ash/elm (AE)	1	71	<i>Fraxinus nigra</i> Marsh., <i>Ulmus</i> spp., <i>Acer rubrum</i> L.	Prominent low area with periodic standing water. Relatively flat	64.00 (2.94)	27.75 (2.86)	8.25 (0.5)
	2	78	<i>Fraxinus nigra</i> Marsh., <i>Ulmus</i> spp., <i>Acer rubrum</i> L.	Prominent low area with periodic standing water. Relatively flat	72.25 (1.08)	20.50 (1.79)	7.25 (0.92)
Aspen/fir (AF)	1	60	<i>Abies balsamea</i> (L.) Mill., <i>Populus tremuloides</i> Michx., <i>Acer rubrum</i> L., <i>Acer saccharum</i> Marsh.	Rolling topography with dense balsam fir under-story	75.25 (2.72)	19.25 (2.26)	5.50 (0.64)
	2	54	<i>Abies balsamea</i> (L.) Mill., <i>Populus tremuloides</i> Michx., <i>Acer rubrum</i> L., <i>Acer saccharum</i> Marsh.	Rolling topography with dense balsam fir under-story	72.5 (1.85)	21.50 (1.55)	6.00 (0.47)
Intermediate aspen (IA) ^a	1	23	<i>Populus tremuloides</i> Michx., <i>Ostrya virginiana</i> (Mill.) K. Koch, <i>Acer saccharum</i> Marsh.	Gentle rolling topography	69.50	18.10	12.4
	2	26	<i>Populus tremuloides</i> Michx., <i>Ostrya virginiana</i> (Mill.) K. Koch, <i>Acer saccharum</i> Marsh.	Prominent low area with periodic standing water. Relatively flat	63.50 (4.91)	27.75 (5.21)	8.75 (1.43)
Northern hardwoods (NH)	1	64	<i>Acer saccharum</i> Marsh., <i>Tilia americana</i> L., <i>Fraxinus pennsylvanica</i> Marsh.	Gentle rolling topography, sparse under-story	66.25 (3.26)	27.25 (2.83)	6.50 (0.83)
	2	Same	<i>Acer saccharum</i> Marsh., <i>Tilia americana</i> L., <i>Fraxinus pennsylvanica</i> Marsh.	Gentle rolling topography, sparse under-story	60.50 (2.08)	33.00 (1.66)	6.50 (0.61)
	3	Same	<i>Acer saccharum</i> Marsh., <i>Tilia americana</i> L., <i>Fraxinus pennsylvanica</i> Marsh.	Gentle rolling topography, sparse under-story	55.25 (2.81)	38.75 (2.98)	5.75 (0.5)
	4	Same	<i>Acer saccharum</i> Marsh., <i>Tilia americana</i> L., <i>Fraxinus pennsylvanica</i> Marsh.	Gentle rolling topography, sparse under-story	55.25 (1.6)	37.00 (1.29)	7.75 (0.47)
Young aspen (YA)	1	13	<i>Populus tremuloides</i> Michx., <i>Acer rubrum</i> L.	Relatively flat. Dense aspen	67.50 (0.88)	25.75 (0.75)	6.75 (0.31)
	2	8	<i>Populus tremuloides</i> Michx., <i>Acer rubrum</i> L.	Relatively flat. Dense aspen	72.00 (1.22)	22.30 (0.87)	5.50 (0.31)

Note: NH1-4 are located within the same continuous stand. The remaining sites are all located in separate distinct forest stands.

^aOnly two soil cores were taken because of the large amount of rocks at this site that were greater in size than the auger diameter. Summary data is followed by standard error when applicable (SE).

in size, were measured using a volumetric displacement method (Heinrichs and Lassen 1970) yielding a rock density of 2.70 g cm^{-3} with a standard error of 0.05.

Site/soil biological, chemical and physical estimations

To estimate leaf area index (LAI), leaves from the litter traps were separated by species, dried and weighed. A random subset of leaves for each species was re-hydrated and the area was measured using a flatbed scanner and image analysis software (Sigma Scan Pro version 4, SPSS Inc., Chicago, IL). Wood production was estimated using per year growth-data measured from the increment cores, which was then regressed upon DBH (JMP version 3.2.5, SAS Institute, Cary, NC). In this model, *tree species* was not a significant effect within *site*, but *site* was significant across all measurements (see Appendix). Using this model, per year growth was predicted for each un-cored tree and then used to predict tree diameter for the previous year. Species-specific allometric equations were used to predict total wood mass from the current diameter and the previous year's diameter (allometric equations from Ter-Mikaelian and Korzukhin 1997). The difference between successive years was considered to be net wood production by each tree. Wood production per tree was summed by plot; the mass increase was summed over ground area, and added to the measured litter production to yield total above-ground net primary productivity or ANPP (Table 2). Soil biomass was estimated by summing the mean fine root mass, mean coarse root mass and forest floor mass. The ratio of carbon to nitrogen of the sieved soil was calculated, as was the ratio of carbon to nitrogen of the total mass of soil tissues (roots + forest floor).

Soil respiration measurements

Soil respiration was measured with a LICOR 6400 portable photosynthesis system fitted with a LICOR 6000-9 soil respiration chamber (LICOR, Inc., Lincoln NE). The accuracy of soil respiration measurements was verified using a custom-testing device that produces known flux rates (Martin et al. 2004). All measurements were taken within fixed circular plots with a 20-m radius. Plots were measured during approximately 18 periods over the 2-year study. The 96, 5 cm long collars that held the soil respiration chamber were made from 10 cm (4 in.) thin walled PVC pipe. Eight collars were placed in each of the 12 plots with new, random locations for each of the 18 measurement periods. Randomization between measurement periods avoided the effects that a permanently installed collar might have on soil gas flow, soil water and soil temperature, and the randomized collars provided a large area of combined sample space (11.3 m^2 for each plot over the two year period, 3.6% of the total plot area). The collars were inserted through the existing forest floor

Table 2. Above-ground plot biological and physical characteristics.

Site code	Trees sampled	% of trees <10 cm	Mean DBH (cm)	Height top of canopy (m)	Height bottom of canopy (m)	Basal area (m ² ha ⁻¹)	Trees ha ⁻¹	LAI	Litter production (g m ⁻² yr ⁻¹)	Wood production (g m ⁻² yr ⁻¹)	ANPP (g m ⁻² yr ⁻¹)
AE1	161	32	14.7 (0.70)	14.3 (0.79)	6.5 (0.56)	29.7	1281	5.44	295.66	537.95	833.61
AE2	161	51	11.7 (0.80)	12.1 (1.30)	6.8 (0.95)	27.4	1997	4.61	293.48	328.60	622.08
AF1	152	80	7.5 (0.73)	7.0 (1.27)	2.5 (0.93)	30.0	2761	5.62	320.97	335.29	656.27
AF2	165	53	11.7 (0.89)	12.3 (1.67)	6.0 (1.40)	30.9	2061	4.65	302.94	245.09	548.04
IA1	96	71	8.0 (0.34)	10.4 (0.94)	6.0 (1.08)	27.1	4584	4.40	300.35	238.11	538.46
IA2	102	75	7.7 (0.35)	9.3 (1.17)	5.5 (0.80)	27.0	4870	4.28	274.91	231.13	506.04
NH1	137	22	17.6 (0.65)	17.9 (0.90)	10.6 (0.77)	31.3	1090	4.98	259.70	261.59	521.29
NH2	122	25	18.0 (0.81)	17.7 (0.97)	9.8 (0.73)	30.7	971	5.79	302.44	299.22	601.66
NH3	105	10	20.5 (0.71)	19.9 (0.86)	10.4 (0.82)	31.1	836	6.05	297.57	242.80	540.38
NH4	111	29	18.2 (1.02)	16.9 (1.10)	8.9 (0.71)	30.9	883	4.62	261.53	190.80	452.33
YA1	150	91	4.8 (0.25)	7.2 (0.65)	3.7 (0.38)	27.6	10,743	4.70	306.19	345.26	651.45
YA2	93	100	2.2 (0.08)	4.4 (0.29)	1.7 (0.13)	5.8	13,321	4.30	222.92	150.55	373.47

Summary data is followed by standard error when applicable (SE).

approximately 3.5 cm deep; insertion was at least 1 h but less than 12 h from the start of each measurement to reduce a disturbance-induced CO₂ flux.

Time of day or non-temperature related diurnal fluctuations of soil respiration linked to photosynthate production seen in shallow rooted plant species (see Craine et al. 1999) were ignored as Eklad and Höberg (2001) found that carbon assimilated in the canopy of boreal conifers took one to four days to appear as carbon respired by the soil. Also, periodic diurnal measurements at our sites indicated no strong diurnal pattern in soil surface respiration independent of soil temperature at 10 cm. We concluded that, in these forested systems with complex below-ground structures, any diurnal patterns in root respiration driven by above-ground activity would likely be buffered by finer textured soils and deeper rooting.

Soil respiration measurements were taken periodically starting in the spring of 1998 and continued through the fall of 1999 for a total of approximately 144 measurements per site (eight samples per site for each of the ~ 18 sampling periods). The eight soil respiration measurements per site were averaged for each of the 18 sampling periods; this average was used for all subsequent analyses. Measurements spanned a range of seasonal soil temperatures and soil moistures, which resulted in a wide range of soil respiration fluxes.

Soil climate: point and continuous measurements

We used the integrated temperature probe on the LiCor 6400 (steel-embedded, copper-Constantan thermocouple, type T) to record soil temperature (°C) down to 10 cm for each soil respiration collar. Volumetric soil moisture (g water 100 cm³ soil) down to 15 cm was determined for each of the eight collars per site by time domain reflectometry using a portable soil moisture probe (CS615 Water Content Reflectometer and CR21X data-logger, Campbell Scientific, Logan UT). Both sensors were longer than the desired measurement depth so each was inserted completely through the forest floor at an angle so that the resultant depth would be 10 or 15 cm. The CS615 soil moisture probe was calibrated for a silt loam, the major soil type common for all of the 12 sites (see Table 1 for particle distribution). The eight soil temperature measurements and the eight soil moisture measurements from the 12 sites were averaged by site for each of the 18 measurement periods.

Hourly soil temperature (°C) at 10 cm and hourly soil moisture (g water/cm³ soil) at 15 cm were recorded by buried sensors at a micro-meteorology station located at an aspen/fir site [site code = AF1, N 45°56.53', W 90°16.48', copper-Constantan thermocouple (type T) and CS615 probe with a CR10X data logger, Campbell Scientific, Logan UT]. An analysis of the spatially distinct, point soil temperature measurements, which were made in conjunction with soil respiration measurements, indicated that the spatial variability of soil temperatures within a plot was minimal (SE ranged from 0.02 to 0.50 °C with mean SE of 0.15 °C). Despite this, we felt that using a single spatial

measurement of soil temperature to represent soil temperature at all sites could introduce unnecessary and systematic error. To create site-specific continuous records of soil temperature, the individual point measurements of temperature, taken during each of the soil respiration measurements, were matched by day and hour to the continuous record of hourly soil temperature from the meteorological station at AF1. Using linear regression, the 2-year record of daily mean temperatures from the station (January 1, 1998 to December 31, 1999) was compared by date to the site-specific data to develop correction equations for each site (this and all subsequent analyses were done with JMP version 3.2.5, SAS Institute, Cary, NC; see Appendix for equation coefficients). *Site* was not a significant factor in the model, indicating that soil temperature did not differ greatly between sites. The data were pooled and a single site-specific correction equation was then applied to the continuous temperature record to create a continuous, site-specific record, which was used for all sites.

Mean soil moisture measurements that were measured at each site during the soil respiration measurements (mean for each site from each measurement date) were matched to concurrent measurements at the meteorological station by date and time. An analysis of the spatially distinct, point soil moisture measurements, which were made in conjunction with soil respiration measurements, indicated that the spatial variability of soil moisture within a plot was moderate (SE ranged from 0.08 to 6.85 g water/100 cm³ soil with mean SE of 1.43 g water/100 cm³ soil). As with soil temperature, we felt that using a single spatial measurement of soil moisture could introduce unnecessary and systematic error. Site-specific equations were developed through linear regression between continuous soil moisture measurements from the meteorological station and soil moisture at each site (see Appendix). *Site* was a significant factor in the model, indicating that soil moisture differed between sites. Each site-specific correction equation was then applied to the continuous moisture record to produce 12 continuous, site-specific records. Missing values in the continuous record of soil moisture were estimated from linear regression based on the last known values before and after the gap.

Modeling soil respiration and annual carbon release

We used multiple linear and non-linear regression (SigmaPlot version 5.05, SPSS Inc, Chicago, IL) to fit three soil respiration models for each site; one with and two without a soil moisture term. We chose a linear model (Eq. (1)), the Lloyd and Taylor equation (1994, Eq. (2)), and a natural log-linear quadratic model, similar to Azzalini and Diggle (1994, Eq. (3)):

$$R_s = b_0 + b_1(\text{soil } T) + b_2(\text{site code}) \quad (1)$$

$$R_s = R_{10} * e^{E_0 * \left(\frac{1}{56.02} - \frac{1}{\text{soil } T} + 46.02 \right)} \quad (2)$$

$$\ln(R_s) = b_0 + b_1(\text{soil}T) + b_2(\text{soil}T^2) + b_3(SWC) + b_4(SWC^2) \\ + b_5(\text{soil}T * SWC) + b_6(\text{site code or site/soil characteristics}) \quad (3)$$

where *soil*T is soil temperature (°C, at 10 cm); *SWC* is soil moisture (volumetric soil water content, g water 100 g soil⁻¹, at 15 cm); *site code* is the nominal term used to designate sites, *site/soil characteristics* is any of the site/soil characteristics (Tables 2–4), and *b*₀–*b*₆ are estimated coefficients.

Eq. (2) is widely used (Subke et al. 2003) although many equations can perform comparably (Fang and Moncrieff 2001). The choice of the more complex model form of Eq. (3) was based on trends observed in previous work (Bowden et al. 1998; Bouma et al. 1997). In this equation, the response of soil respiration to soil temperature and soil moisture appears to be unimodal, with an optimum from which respiration decreases as temperature and/or moisture become too high or too low (Doran et al. 1990; Bowden et al. 1998). Also, the natural logarithm transformation of the soil respiration data eliminates problems of non-constant variance. Eq. (3) was chosen to represent our data and was fit to the individual sites. Daily mean soil temperature and daily mean soil moisture from the corrected, continuous records for each site were used with Eq. (3) to calculate daily mean soil respiration (μmol CO₂ m⁻² s⁻¹). To develop an annual estimate of respired soil carbon, these daily estimates were converted to g C m⁻² day⁻¹, summed for 1998 and 1999.

Results

Seasonal and annual soil climate

Daily soil temperature (Figure 1) showed strong seasonal patterns that followed seasonal air temperature. Mean annual soil temperature for 1998 and 1999 were compared using a repeated measures analysis (*n* = 730). Mean annual soil temperature was not significantly different between 1998 and 1999 (*p* = 0.69). The point temperature measurements at each site fit closely with continuous record (Figure 1); however, discrepancies between the two data sets do exist. The continuous records reported are composed of daily means, while the point measurements were taken during daylight hours when soil temperatures were much higher. The daily range between minimum and maximum soil temperatures was as high as 3.5 °C and averaged 1.5 °C for the months of April through September. Because the instantaneous soil climate measurements were not equal to the daily means of soil climate, the instantaneous measurements were used only in developing the models, not as model inputs for continuous predictions.

Seasonal and annual soil moisture trends were more variable than soil temperature trends because soil moisture responds to isolated precipitation events and can be differentially modified by canopy interception and root uptake. The

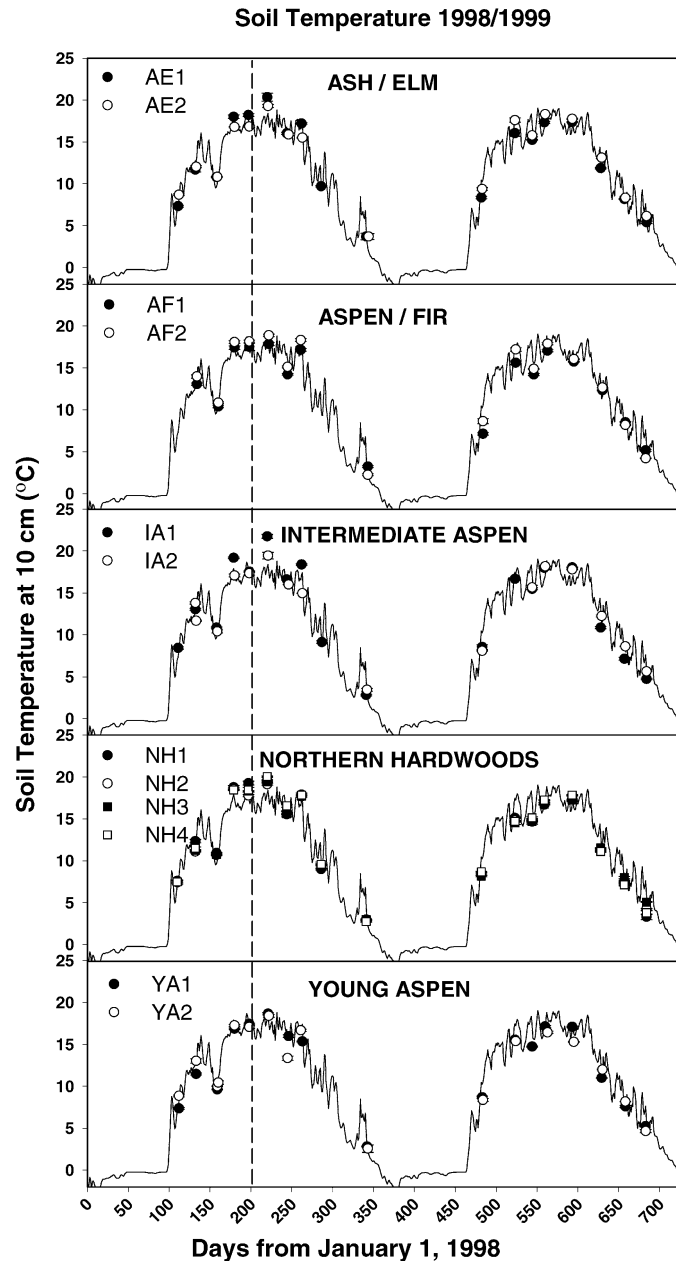


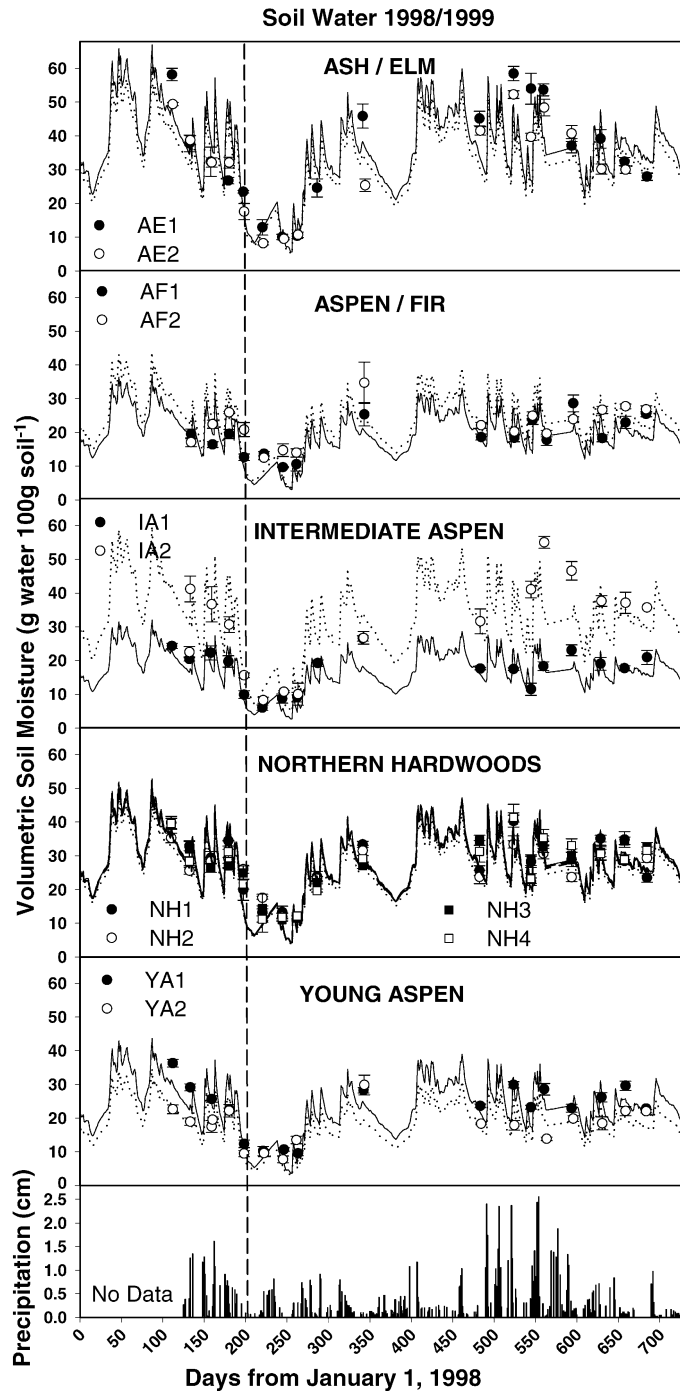
Figure 1. Shown are the point measurements and continuous soil temperature (10 cm) records for each plot. Symbols represent mean and standard error of point measurements at each site ($n = 8$) measured during midday. Lines indicate continuous daily means for each site. Solid lines are for plots '1'; dotted lines are for plots '2'. Vertical dashed line indicates the beginning of a summer drought, 1998.

2-year period of 1998–1999 displayed little seasonality in soil moisture except during the summer of 1998 (Figure 2). From mid-July to late-September of 1998 there was a sustained drop in soil moisture. Soil moisture was below the 2-year average for 81 continuous days. This period includes 78 continuous days when soil moisture was more than 25% below the 2-year average. In 1999, the longest continuous period when soil moisture was below average was 35 days. Mean annual soil moisture was significantly less in 1998 (9.23%, repeated measures analysis, $n = 730$, $p < 0.001$). There was a negative linear relationship between soil temperature (> 0 °C) and soil moisture during the drought year (1998) as indicated by Figures 1 and 2 ($n = 262$, $p < 0.001$). No such significant trend existed in the non-drought year (1999, $n = 258$, $p = 0.08$). In addition to the noticeable differences in soil moisture between the 2 years, differences among the sites were equally apparent (Figure 2).

Inter-annual differences of measured soil respiration

Soil respiration measured on three dates during the growing seasons of the drought and non-drought years is shown in Figure 3. Measurements ($n = 8$) for each site were made within 48 h of each other for a given sampling date. For measurement campaigns in June, July, and August, there was considerable variation between sites in both soil respiration and soil moisture while soil temperature was fairly constant between sites. Data measured on year days 159–161, 180–81, and 221–223 in 1998 were compared to the data measured on year days 158–159, 180–182, and 229–230 in 1999. The hypothesized effect of reduced soil respiration during the drought was masked on the measurement dates due to differences in soil temperature between 1998 and 1999. During the measurement period in June of 1998, soil temperatures were roughly 10 °C while in 1999, during approximately the same period (year days 158–159), the soil temperatures were 5 °C warmer (Figure 3). The opposite was true for July and August where higher temperatures in 1998 led to higher soil respiration measurements when compared to measurements taken during cooler periods in 1999. The temperature difference between 1998 and 1999, seen in Figure 3, confounded differences in soil moisture and therefore confounded the impact of soil moisture differences on soil respiration. At first examination of the data, it might erroneously be concluded that, since measured soil respiration was actually higher at all of the sites during the drought, the annual sum of CO₂ production could be higher as well. These misleading results in Figure 3 are

Figure 2. Shown are the point measurements and continuous soil moisture (15 cm) records for each plot. Symbols represent mean and standard error of point measurements at each site ($n = 4$) measured midday. Lines indicate continuous daily means for each site. Solid lines are for plots '1'; dotted lines are for plots '2'. NH1 (solid line), NH2 (long dash), NH3 (short dash), NH4 (dotted line). Vertical dashed line indicates the beginning of a summer drought, 1998.



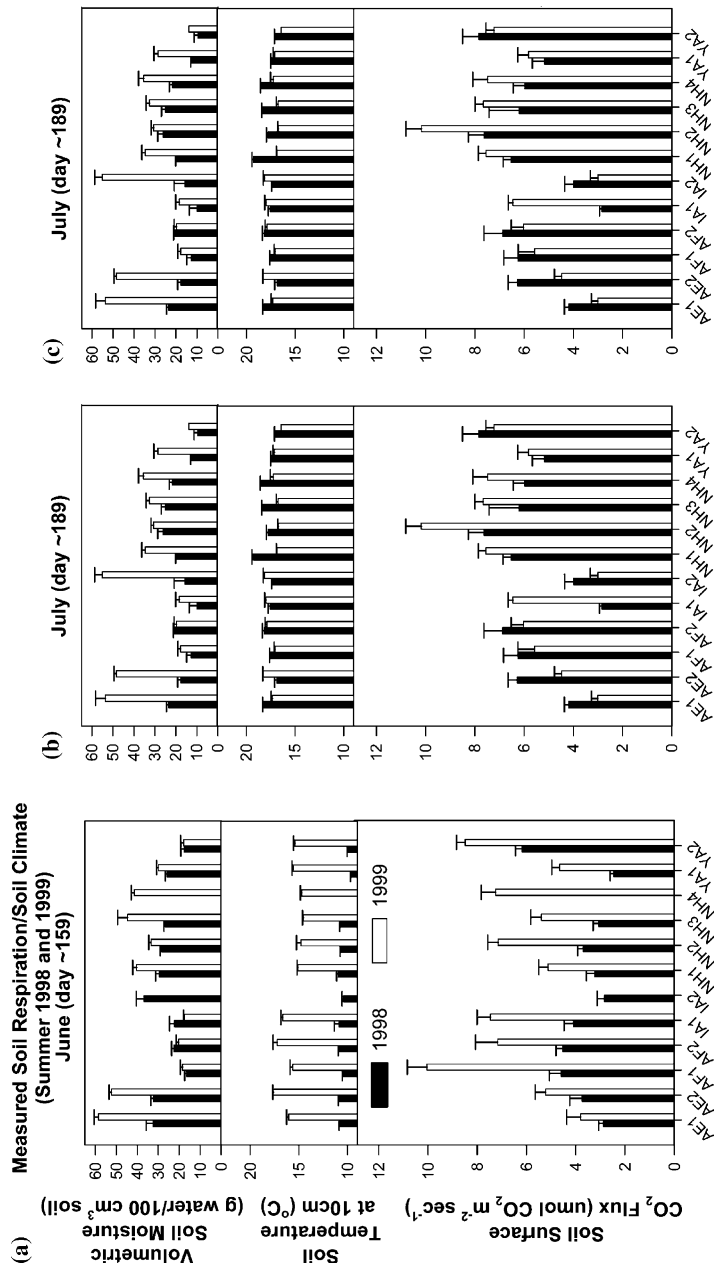


Figure 3. The measured soil climate and soil respiration for the same periods during each year. (a) for June (b) July (c) August. Error bars are standard errors of the 8 measurements per site per measurement date.

due only to the difference in soil conditions when the measurements were taken and do not indicate true, scaleable trends in soil respiration. These results do illustrate the need for continuous methods of measuring and modeling soil respiration so that seasonal and annual trends can more accurately be observed.

Developing and fitting models

Figure 4 shows site-specific fits of Eqs. (1) and (2). Much of the variation in soil respiration is explained by the simple linear function of Eq. (1) (R^2 ranging from 0.42 to 0.79) with coefficients similar to those estimated in an earlier analysis of a subset of these sites using data from the non-drought year (Bolstad et al. 2004). Eq. (2) resulted in similar fits; yet, a Corrected Akaike Information Criterion (AICc, Burnham and Anderson 2002) indicated that the fit of Eq. (2) did not reduce the AICc values sufficiently to support this model form. Actually, for 11 of the 12 sites the AICc technique moderately supported the use of the simpler linear fit of Eq. (1) (evidence ratios of 1.33–7.58). While both of the models explained most of the variation, the linear and exponential fits resulted in heteroscedastic residuals, violating the uniform variance assumptions necessary for an analysis of variance. The natural logarithm transformation included in Eq. (3) removed this non-constant variance.

We fit the transformed soil respiration data using a quadratic function, with soil temperature and *site code* as predictors; all terms including *site code* were significant (with all $p < 0.001$, see Table 5). The residuals from the transformed polynomial model (Eq. (3)), plotted as a function of soil moisture, showed the curvilinear influence of soil moisture on the temperature/soil respiration relationships (Figure 5). Adding quadratic terms for soil moisture improves the overall fit of the models, as did including a linear term for the interaction between soil temperature and soil respiration (Table 5). Figure 6 shows the proposed model with relationships between soil temperature, soil moisture, and soil respiration for AF2 and AE1, the sites with the highest and lowest rates of soil respiration modeled using Eq. (3) with *site code*.

Site and soil biological, chemical and physical characteristics (substituted for *site code*) were added to the model using a stepwise forward and backward procedure. Because many of these variables are correlated and they share significance in the model, we chose not to include many of the site and soil characteristics when a simpler yet still significant metric could be used. For example, including all the site and soil characteristics from Tables 1–4 yielded a quadratic temperature and moisture model with five significant linear terms: (1) *total soil tissue C:N*, (2) *coarse root mass* from 0 to 30 cm depth, (3) *carbon concentration of the forest floor*, (4) *basal area* of standing trees, (5) *LAI*. While this model had below-ground chemical and biomass components, as well as above-ground biomass components and explained much of the data variation ($R^2 = 0.90$, $MSE = 0.046$), simpler models performed comparably. A summary

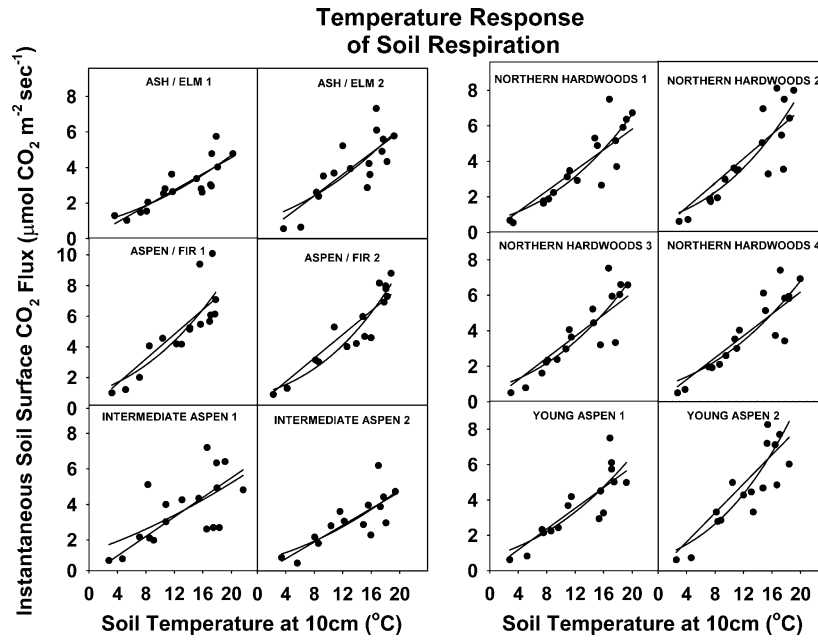


Figure 4. Models of soil respiration based on soil temperature at 10 cm. Shown are the fit simple linear models and the fit Lloyd and Taylor function.

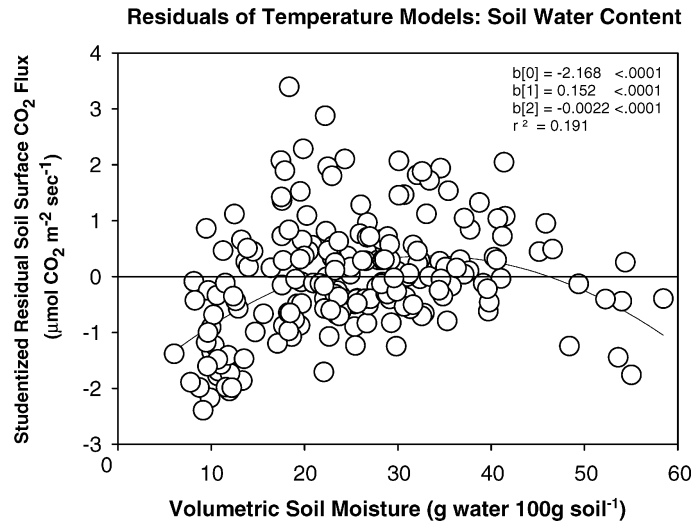


Figure 5. Studentized residuals from Eq. (3), fit without the moisture terms, are plotted against soil moisture content measured concurrently with each soil respiration measurement. Coefficients are from: $studentized\ residual = b_0 + b_1 * soil\ water\ content + b_2 * soil\ water\ content^2$.

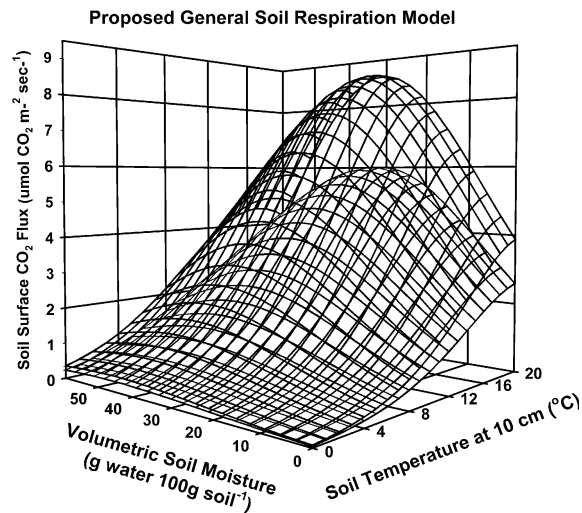


Figure 6. The general fit of Eq. (3) using 'site code'. The high and low curves are for AF2 and AE1, respectively. The z-axis in the figure (soil respiration), has been transformed to the units of measured soil respiration to provided clarity and uniformity.

of the estimated soil respiration model parameters from the fit of Eq. (3) is given in Table 5. We chose to report the results from a (1) *soil temperature* only model with *site code* as a factor, (2) a model with *soil temperature*, *soil water content (SWC)* and *site code*, (3) *soil biomass*, (4) *soil C:N*, (5) *above-ground net primary production (ANPP)*, or (6) *2 year annual mean of soil water content*. All models shown were significant ($p < 0.001$, R^2 ranged from 0.84 to 0.90, Table 5). Including all four of the general site/soil characteristics did not result in a valid model; only *soil C:N* remained as a significant variable.

Including the *soil C:N* provided the best results (lowest MSE, 0.053), and, of all the site/soil characteristics models, we feel this model would be the easiest to expand to other sites. Quantifying the C:N of the soil biomass, the mass of the soil biomass, or the ANPP at a site would all involve lengthy and expensive studies, but measuring the C:N of the bulk soil would be relatively easy in comparison and potentially the most universal. Mean annual soil moisture may also prove useful when expanding this soil respiration model to other areas. Soil moisture could be an approximate surrogate for landscape position because these sites are all within a similar landscape. However, for all subsequent scaling we will use Eq. (3) with *soil C:N* as a variable to differentiate site variance for the reasons listed above.

Model performance

Scatter diagrams of the model predictions vs. the observed measurements show relatively strong model performance (Figure 7, closed symbols). The original

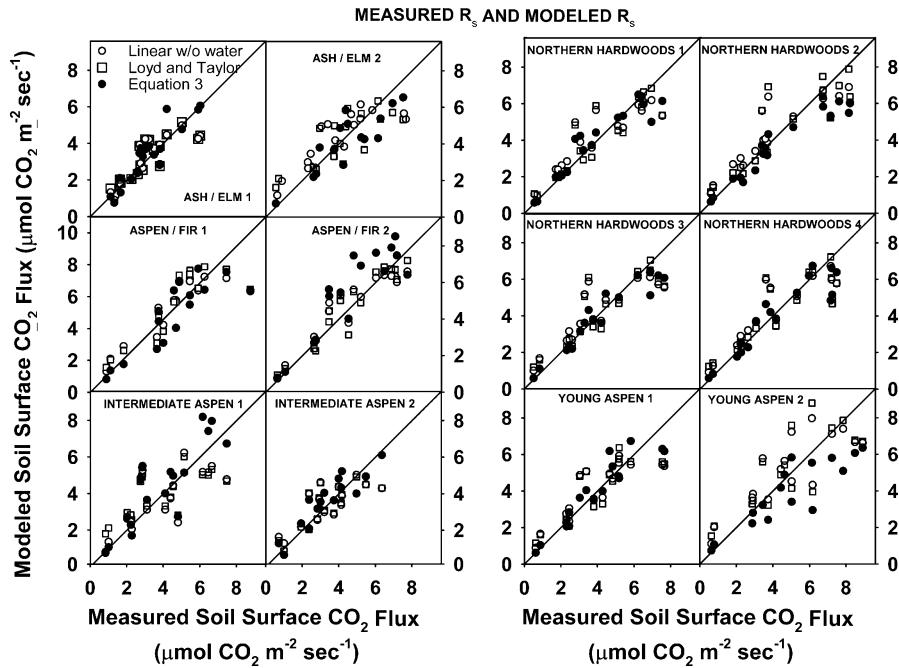


Figure 7. Predicted vs. observed soil respiration for linear, Lloyd and Taylor, and Eq. (3) models. The solid symbols are for the site-specific models. The open symbols are for the pooled model. r^2 , β_1 , and SE of β_1 are given for the linear fits of predicted vs. observed values when the site specific models and the pooled models are used to predict soil respiration.

linear model, Eq. (1), and the Lloyd and Taylor model, Eq. (2), are shown as well (Figure 7, open symbols). Both Eqs. (1) and (2) performed relatively well for the individual sites although there was more variability than when using Eq. (3) with *soil C:N* as a variable to differentiate sites. Although Eq. (3) was chosen for annual estimations of respired carbon, discrepancies between measured and model rates of soil respiration do exist. Modeled soil respiration from sites NH2 and YA2 appear to be underestimated by Eq. (3) while soil respiration from AF2 appears to be overestimated (Figure 7). Although the linear (Eq. (1)) and exponential models (Eq. (2)) appear to fit well (Figure 4), we chose the statistically valid Eq. (3) for the remaining analyses and comparisons.

Seasonal patterns and inter-annual differences of modeled soil respiration

Seasonal patterns of modeled and measured soil respiration (Figure 8) closely followed seasonal patterns of temperature (Figure 1), which were relatively similar between years. Because of the 1998 drought (days 200–250), soil

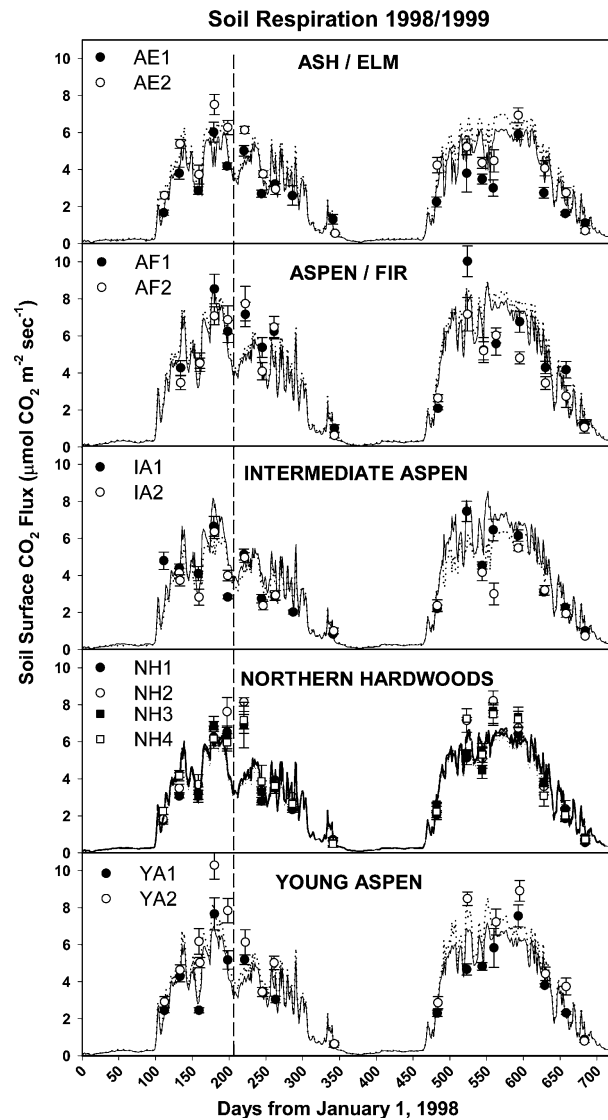


Figure 8. Shown are the point measurements and the continuous predicted values of soil respiration for each site. Symbols represent mean and standard error of point measurements at each site ($n = 8$) measured during midday. Lines indicate continuous daily means for each site. Solid lines are for plots '1'; dotted lines are for plots '2'. NH1 (solid line), NH2 (long dash), NH3 (short dash), NH4 (dotted line). Vertical dashed line indicates the beginning of a summer drought, 1998.

moisture differed greatly between the 2 years and the effects on soil respiration were evident (Figure 8). In 1998, peak rates of modeled soil respiration (the peak of the daily means) ranged from 5.35 to 8.25 $\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$

Table 3. Below-ground (0–30 cm) plot biological, chemical and physical characteristics.

Site code	Forest floor mass (g m ⁻²)	% C forest floor	% N forest floor	Fine root mass (g m ⁻²)	Coarse root mass (g m ⁻²)	% C roots	% N roots	Soil biomass (g m ⁻²)	Rock volume (l m ⁻³)	% C loose soil	% N loose soil	C:N loose soil	C:N organic matter
AE1	681.12 (125.84)	42.52 (1.06)	1.43 (0.04)	471.34 (49.33)	614.32 (138.66)	44.18 (0.88)	1.33 (0.07)	1766.79	12.35 (2.65)	1.92 (0.26)	0.16 (0.02)	12.24	29.70
AE2	752.73 (123.13)	37.74 (1.3)	1.32 (0.06)	502.94 (58.19)	405.98 (107.25)	40.86 (0.81)	1.32 (0.06)	1661.66	2.84 (0.34)	1.37 (0.1)	0.09 (0.01)	14.50	28.62
AF1	1128.03 (132.69)	33.72 (2.06)	1.11 (0.06)	460.89 (30.3)	341.32 (72.67)	40.01 (0.8)	1.05 (0.05)	1930.25	14.05 (3.41)	1.98 (0.08)	0.10 (0.01)	19.66	30.49
AF2	1674.71 (280.39)	38.98 (1.35)	0.78 (0.04)	411.99 (40.3)	298.81 (52.94)	43.74 (2.66)	0.84 (0.85)	2385.51	15.13 (3.96)	1.64 (0.17)	0.08 (0.01)	19.59	50.10
IA1 ^a	888.98 (317.07)	42.79 (3.63)	1.24 (0.06)	180.82 (103.45)	27.75 (27.75)	42.91 (1.64)	1.45 (0.01)	1097.56	23.02 (20.95)	1.64 (0.17)	0.08 (0.01)	19.59	34.58
IA2	1045.06 (176.46)	39.24 (1.79)	1.12 (0.05)	156.67 (19.15)	91.67 (45.74)	43.01 (0.74)	1.34 (0.07)	1293.4	3.12 (0.92)	2.50 (0.08)	0.20 (0.01)	12.73	35.09
NH1	550.76 (97.37)	33.59 (1.38)	0.96 (0.04)	879.60 (62.36)	781.21 (102.92)	37.22 (1.26)	0.75 (0.04)	2211.57	9.83 (1.6)	1.96 (0.07)	0.15 (0.01)	13.24	35.07
NH2	922.95 (184.55)	35.48 (1.35)	1.14 (0.08)	204.83 (25.24)	143.11 (59.7)	43.43 (0.96)	1.05 (0.05)	1270.88	8.61 (1.27)	1.78 (0.05)	0.14 (0.01)	12.69	31.13
NH3	811.80 (192.77)	38.71 (1.92)	1.51 (0.16)	315.99 (57.25)	258.91 (80.95)	40.42 (2.73)	1.01 (0.63)	1386.70	19.79 (4.44)	2.31 (0.08)	0.18 (0.01)	12.94	25.58
NH4	1184.19 (283.81)	36.24 (1.81)	0.92 (0.04)	578.51 (38.05)	248.17 (36.83)	43.47 (0.97)	0.81 (0.03)	2010.87	25.64 (5.83)	2.30 (0.06)	0.17 (0.01)	13.88	39.60
YA1	885.74 (183.1)	32.61 (2.19)	1.11 (0.06)	446.95 (58.93)	434.94 (161.59)	41.02 (2.58)	1.18 (0.7)	1767.63	8.83 (1.31)	2.10 (0.05)	0.14 (0.01)	14.95	29.45
YA2	1657.46 (227.31)	43.28 (1.59)	1.09 (0.05)	454.28 (98.09)	310.46 (78.89)	42.19 (1.33)	1.10 (0.05)	2422.20	5.58 (1.84)	1.95 (0.13)	0.10 (0.01)	19.21	39.57

^aOnly two soil cores were taken because of the large amount of rocks at this site that were greater in size than the auger diameter. Summary data is followed by standard error when applicable (SE).

Table 4. Below-ground (30–60 and 60–100 cm) plot biological, chemical and physical characteristics.

Site code	Rock volume (l m ⁻³)	Fine root mass (g m ⁻²)	Coarse root mass (g m ⁻²)	% C roots	% N roots	% C loose soil	% N loose soil
<i>30–60 cm</i>							
AE1	24.95 (17.12)	180.4 (72.64)	276.28 (252.88)	45.64 (1.15)	1.1 (0.14)	1.27 (0.01)	0.08 (0)
AE2	6.48 (0.45)	250.63 (37.29)	295.21 (190.32)	37.47 (3.04)	0.87 (0.08)	0.79 (0.17)	0.04 (0.01)
AF1	44.31 (22.63)	318.33 (50.96)	273.34 (83.2)	39.49 (1.71)	0.69 (0.03)	0.73 (0.01)	0.02 (0.01)
AF2	18.38 (15.65)	283.85 (38.29)	563.08 (278.39)	38.81 (1.81)	0.56 (0.08)	0.69 (0.04)	0.02 (0.01)
IA1 ^a	33.17 (11.34)	167.09 (54.47)	59.99 (11.04)	40.86 (3.39)	0.86 (0.09)	–	–
IA2	6.31 (7.43)	232.55 (30.03)	122.37 (61.35)	29.92 (3.71)	0.89 (0.05)	0.61 (0.03)	0.05 (0.01)
NH1	42.13 (43.03)	165.26 (23.55)	89.15 (60.47)	39.71 (3.69)	0.78 (0.03)	1.03 (0.02)	0.07 (0.01)
NH2	32.73 (9.62)	246.43 (84.9)	425.57 (197.82)	37.6 (3.05)	0.64 (0.04)	0.94 (0.08)	0.06 (0.01)
NH3	40.77 (18.88)	84.95 (11.38)	180.4 (48.36)	45.52 (1.47)	0.74 (0.03)	1.32 (0.19)	0.08 (0.01)
NH4	35.60 (24.49)	234.65 (30.28)	425.15 (86.21)	46.15 (0.99)	0.52 (0.06)	1.17 (0.03)	0.08 (0.01)
YA1 ^b	7.56	158.12	80.74	33.44	0.71	0.70 (0.01)	0.04 (0.01)
YA2	11.54 (11.19)	332.49 (117.41)	263.53 (206.72)	44.69 (1.23)	0.79 (0.12)	0.92 (0.16)	0.04 (0.01)
<i>60–100 cm</i>							
AE1	14.23	33.64	38.69	45.71	1.00	0.33 (0.06)	0.01 (0.01)
AE2	2.48 (0.79)	22.71 (5.88)	14.30	43.28 (2.25)	1.10 (0.2)	0.22 (0.05)	0.01 (0.01)
AF1	58.72 (34.34)	50.46 (18.50)	32.80	45.6 (1.99)	0.72 (0.03)	0.51	0.01
AF2	37.89 (19.73)	158.12 (37.01)	503.76 (412.95)	38.93 (3.01)	0.74 (0.01)	0.48 (0.03)	0.01 (0.01)
IA1 ^a	–	–	–	40.46	1.17	0.3 (0.03)	0.02 (0.01)
IA2	12.63 (12.34)	47.94 (37.85)	5.88	46.28 (0.46)	0.95 (0.18)	0.39 (0.14)	0.02 (0.01)
NH1	47.13 (48.54)	47.10 (8.41)	22.71	47.31 (1.38)	0.84 (0.01)	0.37 (0)	0.02 (0.01)
NH2	94.33 (65.83)	44.58 (15.98)	–	45.42 (1.66)	0.69 (0.08)	0.71 (0.25)	0.04 (0.02)
NH3	59.61 (0.45)	193.44	721.62	40.78 (6.6)	0.45 (0.21)	0.65 (0.04)	0.04 (0.01)
NH4	76.38 (39.81)	157.28 (64.76)	1015.14 (991.59)	42.64 (0.3)	0.95 (0.07)	0.19 (0.05)	0.01 (0.01)
YA1 ^b	10.48	26.07 (10.93)	4.21	–	–	–	–
YA2	29.21 (13.80)	121.95 (24.39)	89.15	44.69 (1.23)	0.79 (0.12)	0.41 (0.01)	0.01 (0.01)

^aOnly two soil cores were taken because of the large amount of rocks at this site that were greater in size than the auger diameter.

^bOnly one contained roots and rocks from 30 to 60 cm.

‘–’ denotes missing samples. Summary data is followed by standard error (SE) when applicable, e.g. $n > 1$.

Table 5. Model coefficients for estimating soil respiration from soil temperature, soil moisture, and site characteristics.

Model type	df ²	Model coefficients ^{a,b}						MSE	R ²	Model p-value	
		b ₀	b ₁	b ₂	b ₃	b ₄	b ₅				b ₆
Eq. (1) + site code	12	-	0.3285	NA	NA	NA	NA	NA	1.422	0.936	<0.001
p-Values			<0.001								<0.001
Eq. (3) + site code	13	-1.2789	0.3247	-0.0087	NA	NA	NA	NA	0.074	0.844	<0.001
p-Values		<0.001	<0.001	<0.001							<0.001
Eq. (3) + site code	16	-2.9619	0.3639	-0.0080	0.0870	-0.0010	-0.0014	*	0.046	0.900	<0.001
p-Values		<0.001	<0.001	<0.001	<0.001	<0.001	0.0005	<0.001			<0.001
Eq. (3) + soil biomass	5	-2.2876	0.3206	-0.0081	0.0534	-0.0009	-	-	0.065	0.859	<0.001
p-Values		<0.001	<0.001	<0.001	<0.001	<0.001	-	0.0016			<0.001
Eq. (3) + C:N soil	6	-3.5450	0.3623	-0.0083	0.0818	-0.0010	-0.0011	0.0468	0.053	0.885	<0.001
p-Values		<0.001	<0.001	<0.001	<0.001	<0.001	0.0073	<0.001			<0.001
Eq. (3) + ANPP	5	-1.8440	0.3221	-0.0081	0.0522	-0.0008	-	-0.00036	0.067	0.855	<0.001
p-values		<0.001	<0.001	<0.001	<0.001	<0.001	-	0.0345			<0.001
Eq. (3) + mean SWC	6	-2.1187	0.3654	-0.0084	0.0759	-0.0008	-0.0011	-0.0258	0.054	0.886	<0.001
p-Values		<0.001	<0.001	<0.001	<0.001	<0.001	0.0061	<0.001			<0.001

^aParameters for use with Eq. (1):

$$R_s = b_0 + b_1(\text{soilT})$$

^bParameters for use with Eq. (3):

$$\ln(R_s) = b_0 + b_1(\text{soilT}) + b_2(\text{soilT}^2) + b_3(\text{SWC}) + b_4(\text{SWC}^2) + b_5(\text{soilT} * \text{SWC}) + b_6(\text{site/soil characteristics})$$

* denotes 'site code' as a factor, each site had one of the 12 site specific coefficients.

-, denotes a coefficient that is not significant.

NA, denotes a variable that was not used in the model.

for AE1 and AF2, respectively. In 1999, the peak rates for all sites were higher and ranged from 5.56 to 8.60 $\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$ again for AE1 and AF2, respectively. Our predicted peak rates of modeled soil respiration were similar to those in the literature that were derived using similar measurement methods: $\sim 3.8 \mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$ in mixed ash fen (Reiners 1968), $9.3 \mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$ in boreal aspen (Russel and Voroney 1998), $\sim 5.6 \mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$ in mixed hardwoods (Davidson et al. 1998), $4.0\text{--}6.0 \mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$ in Norway spruce (Buchmann 2000), $4.5 \mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$ in boreal spruce/pine (Moren and Lindroth 2000).

The daily time step fluctuations of soil respiration (seen in Figure 8) mask the seasonal, annual and inter-site differences. To illustrate this, the daily-predicted values of soil respiration were averaged and plotted by month (Figure 8). By collapsing the data into monthly means, the intra and inter-annual and the inter-site differences in soil respiration are more apparent. The general shape of the peak for each year is similar, but the maximum of the monthly means is visually less for the drought year of 1998. This pattern in the monthly means indicates an overall annual reduction in the total carbon respired by the soil during a year with a substantial period of low soil moisture. Figure 8 also shows that the effect is not equal among all sites. Large variation within any given month is evident from the intra-month ranges.

Discussion

Annual estimates of modeled soil carbon release

Annual soil carbon, released as carbon dioxide, for 1998 and 1999 was predicted from Eq. (3) using *soil C:N* (Table 5). The annual soil carbon fluxes ranged from 8.6 to 13.6 $\text{Mg C ha}^{-1} \text{ yr}^{-1}$ for the 2-year period (Table 6), and were highest for the aspen–fir sites (AF1,2), young aspen site (YA2), and the drier intermediate aspen site (IA1). Cumulative soil carbon releases were lowest for the ash–elm and northern hardwoods sites (AE1, NH1-4, Figure 8 and Table 6). Cumulative annual soil respiration was lower in ash–elm sites possibly due to higher soil moisture during spring and early summer. Soil moisture during these periods was in the region of the soil respiration response function (Figure 6) where high moisture can reduce soil respiration. Moisture at these levels may inhibit aerobic microbial activity, reduce gas diffusion, or in some other way inhibit soil CO_2 flux. The higher respiration rates at the aspen/fir sites (AF1,2) could be due to the relative maturity of these sites (Table 1) and the potential for large amounts of forest floor mass and soil organic matter (Olson 1963; Covington 1981; Yanai et al. 2003), although our soil biomass data did not indicate such a trend (Table 3). *Soil biomass* (roots + forest floor) was a significant term in our model and positively related to soil respiration (Table 5), which provides some evidence to this hypothesis.

Table 6. Annual carbon release and average soil climate for 1998/1999.

Site code	1998				1999				Annual difference	
	Temperature °C	Soil moisture g water/100 cm ³ soil	C released Mg ha ⁻¹ yr ⁻¹	Temperature °C	Soil moisture g water/100 cm ³ soil	C released Mg ha ⁻¹ yr ⁻¹	Temperature °C	Soil moisture g water/100 cm ³ soil	C released Mg ha ⁻¹ yr ⁻¹	Carbon released Mg ha ⁻¹ yr ⁻¹
AE1	8.15	34.09	8.93	8.14	37.56	10.04	8.14	37.56	1.10	11.00
AE2	8.15	30.80	9.88	8.14	33.94	11.37	8.14	33.94	1.49	13.07
AF1	8.15	18.83	10.65	8.14	20.74	12.65	8.14	20.74	2.00	15.78
AF2	8.15	22.28	11.43	8.14	24.55	13.57	8.14	24.55	2.13	15.73
IA1	8.15	16.28	9.92	8.14	17.94	11.73	8.14	17.94	1.81	15.42
IA2	8.15	30.42	9.08	8.14	33.52	10.47	8.14	33.52	1.39	13.27
NH1	8.15	26.88	9.06	8.14	29.62	10.63	8.14	29.62	1.57	14.75
NH2	8.15	24.38	8.57	8.14	26.86	10.13	8.14	26.86	1.56	15.41
NH3	8.15	26.60	8.91	8.14	29.31	10.47	8.14	29.31	1.55	14.84
NH4	8.15	26.10	9.26	8.14	28.75	10.90	8.14	28.75	1.63	14.99
YA1	8.15	22.19	9.18	8.14	24.45	10.90	8.14	24.45	1.72	15.74
YA2	8.15	17.62	10.11	8.14	19.41	11.99	8.14	19.41	1.88	15.66

Gårdenäs (2000) noted that in a Norway spruce stand, litter moisture explained much of the variation of soil respiration, but neither mineral–soil water content, nor air or litter temperature was significant. These conclusions must be interpreted in context of their short, 3-week measurement periods, because soil temperature at rooting depths would vary little during this short period, and soil temperatures from shallower depths were apparently not correlated to their relatively flat rates of soil respiration. Measurements on a subset of our sites, not reported here, indicate litter contributions are much lower and less variable in our stands. In addition, frequent rains, cool temperatures, and a humid environment maintain high litter moistures for much of the growing season, thereby reducing litter contributions to overall soil flux variability.

Similar to our peak rates reported in the previous section, annual estimates of respired carbon calculated in this study ($8.6\text{--}13.6 \text{ Mg C ha}^{-1} \text{ yr}^{-1}$) also compare to those previously published for northern forests: $7.1 \text{ Mg C ha}^{-1} \text{ yr}^{-2}$ in mixed ash fen (Reiners 1968), $8.1 \text{ Mg C ha}^{-1} \text{ yr}^{-1}$ in boreal aspen (Russel and Voroney 1998), $7.1\text{--}8.5 \text{ Mg C ha}^{-1} \text{ yr}^{-1}$ in mixed hardwoods (Davidson et al. 1998), $7.1 \text{ Mg C ha}^{-1} \text{ yr}^{-1}$ in Norway spruce (Buchmann 2000), $12.3 \text{ Mg C ha}^{-1} \text{ yr}^{-1}$ in boreal spruce/pine (Moren and Lindroth 2000). The published estimates listed above were calculated using measurement methods similar to ours. Estimates of annual carbon release using uncorrected alkali absorption methods (see Grogan 1998) tend to be lower than those measured with IRGA based systems: $3.7 \text{ Mg C ha}^{-1} \text{ yr}^{-1}$ in eastern mixed hardwoods (Bowden et al. 1993), $4.8 \text{ Mg C ha}^{-1} \text{ yr}^{-1}$ in Lake States mixed hardwoods (Toland and Zak 1994).

Modeled cumulative annual soil respiration was reduced by the late summer drought of 1998 (Table 6). Annual mean soil moisture ranged from 16.28 to $34.09 \text{ g water}/100 \text{ cm}^3$ soil during 1998 (IA1 and AE1, respectively), and from 17.94 to $37.56 \text{ g water}/100 \text{ cm}^3$ soil for the same sites in 1999. Soil C respired during 1998 ranged from 8.6 to $11.4 \text{ Mg C ha}^{-1} \text{ yr}^{-2}$ (respectively for NH2 and AF2). In 1999, these sites released 10.5 and $13.6 \text{ Mg C ha}^{-1} \text{ yr}^{-2}$, differences of 11.55 and 14.38%. The drought-induced decline in soil respiration seen between 1998 and 1999 is similar to that seen in other studies (Davidson et al. 1998; Kaye and Hart 1998).

The largest reduction of annual soil respiration attributed to a decline in soil moisture occurred in the young aspen site (YA1) where soil annual soil respiration was reduced by 14.95%. We feel that these large differences in annual soil respiration resulting from a relatively small difference in mean annual soil moisture are in part due to the timing of low soil moisture. The highest soil temperatures and the highest respiration rates typically occur in late summer. Given sufficient moisture during these periods, substantial soil C is respired during relatively short time periods. High soil moisture during early spring or winter, while leading to higher mean annual soil moisture, do not substantially increase soil respiration, because respiration during those periods is limited by low temperatures. Soil moisture near the surface is

typically in excess in spring, due to snowmelt, and may remain at or above optimal moisture levels well into summer. Mid- to late-summer drought, as occurred here, while short in duration, may have relatively large impacts on cumulative annual soil C flux.

It should be noted that our measurement methods do not capture rain-related respiration pulses such as those identified by Lee et al. (2004); they found that hardwood forest floors were very sensitive to moisture in the upper soil, especially to an irrigation that simulated a precipitation event. The spike of soil respiration lasted only as long as the irrigation was active, and the soil respiration rates returned to pre-irrigation levels within approximately 10 min after the irrigation had stopped. Their analyses do suggest soil carbon losses of up to 5–10% of the annual total due to rain events. Our comparisons among sites and the nature of the drought response are not likely to change because we avoided measurements during rainfall events. Total annual flux estimates could underestimate true annual fluxes if the observations made by Lee et al. (2004) compare to conditions at other sites and are not accounted for.

Site differences of annual estimates of soil carbon release

Landscape position and topography can alter the amount and the availability of soil water. Despite similar seasonal trends in soil moisture, differences in the relative magnitude of soil water among sites (chronically wet or dry) are evident in Figures 2 and 3. Differences in soil texture can influence soil moisture, as can variations in infiltration rates and subsurface flow which both affect soil water residence times and therefore the relative amount of soil moisture at a given location. Soil texture did not vary greatly among sites (Table 1) and a conversion of soil water content to matric potential through published equations was inconclusive and added variability to the analyses; however, small differences in micro-topography appear to be important in driving soil moisture. The ash/elm sites (AE1,2) and intermediate aspen 2 (IA2) were along creeks and small depressions, so inherently had higher soil moistures. Young aspen 2 (YA2), had relatively low soil moisture, as did the aspen/fir sites (AF1,2) which were located on localized mounds. These differences in soil moisture caused by site micro-topography could have potentially led to the modeled differences in soil respiration even though soil temperatures were similar among sites.

Landscape position and topography not only affected the amount of soil water at any given time but also the annual range of soil water conditions. The minimum annual soil moisture was roughly equal for all sites but the annual maximum was very different. This annual range of soil moisture, represented by annual soil moisture means for the study sites, appears to be negatively associated with the total carbon respired annually from the soils (Figure 10a). The typically wet sites (AE1,2 and IA2) generally released less carbon than the

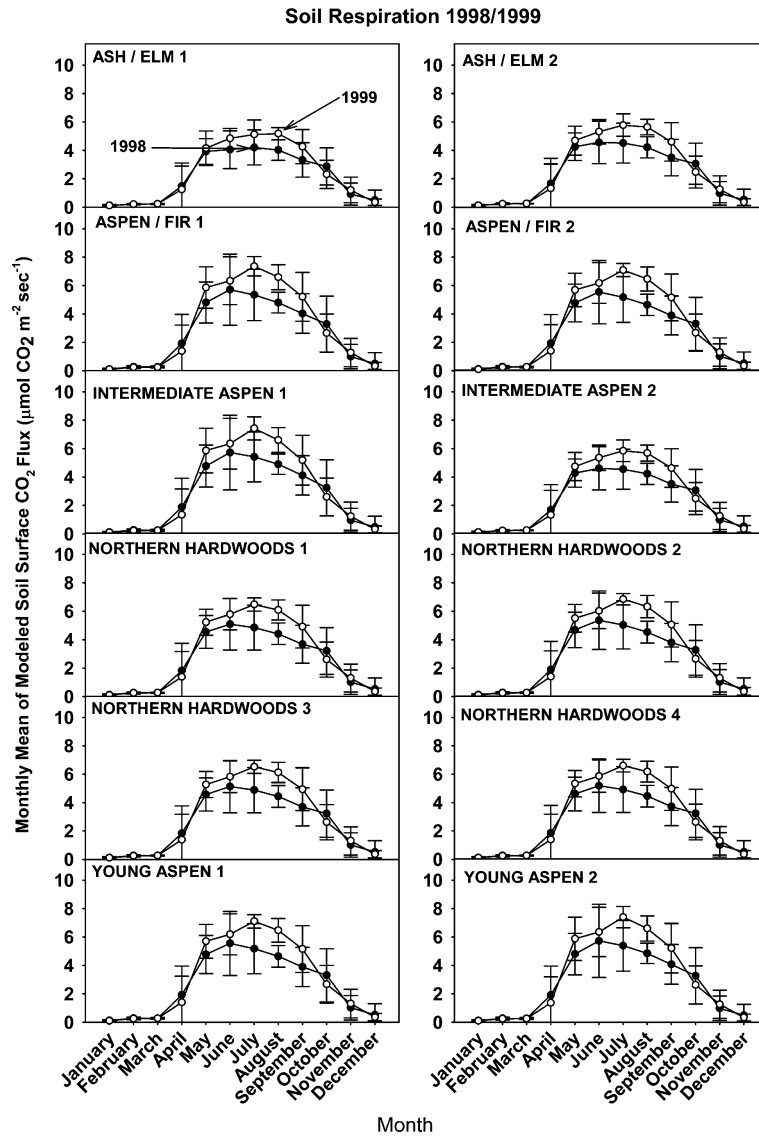


Figure 9. Shown are the mean monthly predicted rates of soil respiration for each site including the range for each month. Closed symbols are for 1998 and open symbols are for 1999.

drier sites in both the drought and non-drought years, possibly due to the intermittent anaerobic conditions and/or diffusion inhibition during saturation that can occur at wetter sites. Compared to the drought year, the non-drought year shows a steeper decline in annual soil respiration with increasing site soil moisture, although the slopes are not significantly different (Figure 10a; Wald test statistic, $p = 0.608$, $df = 20$).

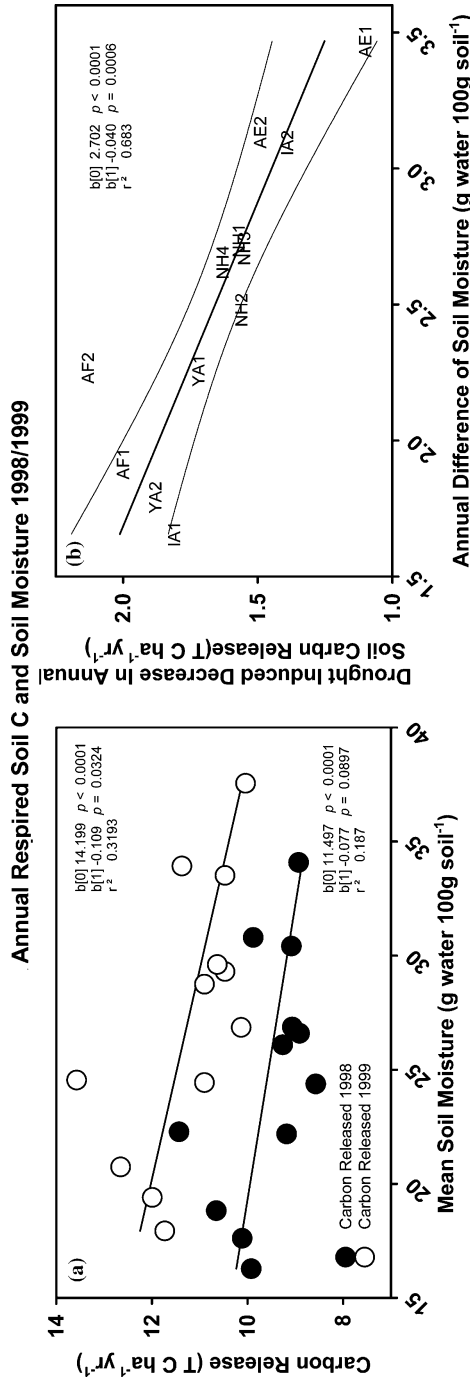


Figure 10. (a) The effects of the annual mean soil moisture on the total amount of respired soil carbon. (b) Regression of the difference of annual carbon release between the drought and non-drought year and the difference of soil moisture where: $drought-induced\ difference = a + b * soil\ moisture\ difference$ (g water 100 g soil⁻¹).

The desiccation of the periodically wet sites should expose more organic matter to aerobic decay and increase soil respiration. If soil moisture were to continue to decrease at the wet sites, microbial activity and autotrophic respiration may then decline. Our data do not show a rise and decline of soil respiration during the drought indicating that this pattern occurred at the wet sites. We do, however, see smaller differences in the annual carbon released from the soil in the wetter sites between a drought and a non-drought year (Figure 10b). This trend of a decreasing drought effect on carbon release with increasing site annual soil moisture range might suggest that the periodically wet sites do not respond the same as dry sites where low soil moisture can quickly limit below-ground activity. A higher frequency, continuous sampling design could allow the resolution of these trends within and over multiple years (Irvine and Law 2002).

A relative measure of site soil moisture and the continuous effects of soil moisture on soil respiration could aid in quantifying these trends elsewhere. The argument to use mean site soil moisture in modeling efforts is supported by the correlation of mean site soil moisture to the *soil C:N* (-0.814) and the weak correlation to *ANPP* (0.522) indicated by our data. This implies that relationships of *soil C:N* and *ANPP* to soil respiration could potentially be accounted for by replacing either with mean site soil moisture (see Table 5 for equation coefficients). Unfortunately, mean site soil moisture can vary greatly across years, as shown by our data, and would complicate model runs spanning multiple years. Using a static measure of landscape position, such as elevation, would eliminate this problem. The differential drought effect among sites indicates that the relative moisture of a forest stand should be included when calculating annual carbon budgets for landscapes that include a diversity of forest communities.

We note the apparent lack of a strong effect of dominant vegetation type on site respiration response. As found by Bolstad et al. (2004), respiration rates from sites dominated by one species or vegetation type were no more similar than sites from another vegetation type. The influence of vegetation type on cumulative soil respiration is less than site or other stand characteristics across the relatively homogenous set of site conditions observed here. This may be due to the adaptability and dominance of aspen across a wide range of soil moisture conditions, and because all our study sites and most of the upland landscape in our region supports mesic deciduous vegetation types. This suggests information on vegetation type is of limited utility for broad-scale estimates of annual soil respiration, at least in landscapes similar to that represented here. A suite of co-varying factors related to mean soil moisture were more strongly related to among-site variations in soil respiration than vegetation type.

Our Eq. (3) model is not proposed as a general solution for estimating annual soil respiration across future years or a broader range of sites. However, these results may guide the development of a general relationship, and may aid in predicting soil and site respiration as well a net ecosystem

carbon exchange. Our analyses indicate that soil temperature varies little among closed-canopy stands at any one point in time, although it may vary significantly across years. Soil moisture can vary significantly across stands as well as within and among years; and, when combined with soil temperature, act as the primary drivers of inter-annual variation in soil respiration in closed-canopy deciduous forests of the Lake States. Soil moisture has a significant, curve-linear effect on soil respiration where respiration is inhibited by high or low soil moistures. Important differences in response vary in conjunction with a suite of related site factors, and these factors are generally associated with site soil moisture status. Further work should test the generality of the curve-linear relationships across a broader range of sites and years, and attempt to identify an easily measurable set of characteristics related to soil C, N, moisture, or productivity that represent among-site variation in respiration.

Conclusions

Our measurements show soil respiration responds to, not only temperature, but also moisture and a set of correlated site conditions across forest types in northern Wisconsin. We used a soil respiration model based on soil temperature and soil moisture to predict the impact low soil moisture would have on annual cumulative respired carbon. Our data indicate that, during drought conditions, soil moisture can limit below-ground activity and reduce the amount of respired carbon released to the atmosphere in these Lake States forests. The severity, the timing, and the duration of a drought, as well as landscape position will influence the magnitude of this change. Including short-term and long-term trends in soil moisture when developing soil respiration models, as well as other biological and chemical factors that vary across the landscape, could increase the utility of such models when dealing with diverse tracts of forests.

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Appendix AIncrement growth.^a

Term	df	Coefficient	SE	Prob > t	SS	adjR ²	Model p-value
Intercept		0.8088	0.039	<0.001		0.422	<0.001
dbh	1	0.0180	0.002	<0.001	7.768		
Site code	11				26.426		
AE1		0.2256	0.053	<0.001			
AE2		-0.1069	0.065	0.099			
AF1		0.3634	0.069	<0.001			
AF2		0.3285	0.070	<0.001			
IA1		-0.0546	0.062	0.378			
IA2		0.0499	0.073	0.497			
NH1		-0.3023	0.062	<0.001			
NH2		-0.2066	0.063	0.001			
NH3		-0.3992	0.071	<0.001			
NH4		-0.5427	0.067	<0.001			
YA1		0.2522	0.068	<0.001			
YA2							

^a $Y = b_0 + b_1 * X$ where X diameter at breast height (DBH, cm), and Y is the radial increment growth (mm).

Model coefficients for creating site specific soil climate records by correcting soil climate data from micro-meteorology station at AF1.

Soil temperature.^a

n	b_1	SE	Prob > t	b_2	SE	Prob > t	\sqrt{MSE}	adjR ²	Prob > F
193	1.3311	0.034	<0.001	-0.0198	0.002	<0.001	1.304	0.847	<0.001

^aCorrection equation: $Y = b_1 * X + b_2 * X^2$ where X uncorrected hourly soil temperature data (°C at 10 cm) from the micro-meteorology station at AF1, and Y is the site specific soil temperature means from the LiCor 6400 (steel-embedded, copper-Constantan thermocouple, type T).

Soil moisture.^a

Site code	Plot	n	b_1	SE	Prob > t	\sqrt{MSE}	adjR ²	Model p-value
AE	1	16	199.0569	14.707	<0.001	11.151	0.919	<0.001
	2	14	179.8610	11.820	<0.001	8.419	0.943	<0.001
AF	1	14	109.9375	6.705	<0.001	4.469	0.950	<0.001
	2	14	130.1210	7.748	<0.001	5.146	0.953	<0.001
IA	1	16	95.0732	4.641	<0.001	3.523	0.963	<0.001
	2	14	177.6483	12.821	<0.001	8.681	0.932	<0.001
NH	1	16	156.9590	3.766	<0.001	2.865	0.991	<0.001
	2	16	142.3668	4.121	<0.001	3.123	0.987	<0.001
	3	15	155.3396	7.045	<0.001	5.069	0.970	<0.001
	4	15	152.3934	4.938	<0.001	3.611	0.985	<0.001
YA	1	15	129.5592	4.438	<0.001	3.289	0.983	<0.001
	2	15	102.8557	4.973	<0.001	3.562	0.966	<0.001

^aCorrection equation: $Y = b_1 * X$ where X uncorrected soil moisture data (cm³ water/cm³ soil at 15 cm) from the micro-meteorology station near AF1, and Y is the site specific soil moisture (100 cm³ water/cm³ soil or % at 15 cm) from the point measurements made in conjunction with point soil respiration measurements.

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