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Soil Respiration at Dominant Patch Types within a Managed Northern Wisconsin Landscape

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Abstract

Soil respiration (SR), a substantial component of the forest carbon budget, has been studied extensively at the ecosystem, regional, continental, and global scales, but little progress has been made toward understanding SR over managed forest landscapes. Soil respiration is often influenced by soil temperature (T_s), soil moisture (M_s), and type of vegetation, and these factors vary widely among the patch types within a landscape. We measured SR, T_s, M_s, and litter depth (LD) during the 1999 and 2000 growing seasons within six dominant patch types (mature northern hardwoods, young northern hardwoods, clearcuts, open-canopy Jack pine barrens, mature Jack pine, and mature red pine) on a managed forest landscape in northern Wisconsin, USA. We compared SR among and within the patch types and derived empirically based models that relate SR to T_s, M_s, and LD. Increased levels of soil moisture and higher temperatures in June–September 1999 may have accounted for the up to 37% overall higher SR than in this same period in 2000. In 2000, SR and T_s values were lower, and the sites may have been experiencing slight water limitations, but in general T_s was a much more accurate predictor of SR during this year. Empirical predictions of SR within each patch type derived from continuous T_s measurements were in close agreement with measured values of SR during 2000, but eight of 22 of the simulated values were significantly different (α = 0.05) from the rates measured in 1999. The young hardwoods consistently had the highest SR, whereas the pine barrens had the lowest. Results from our field studies and empirical models can help land managers assess landscape responses to potential disturbances and climatic changes.

Key words: soil respiration; managed landscape; dominant patch types; northern Wisconsin; empirical models; soil temperature; soil moisture; litter depth.

Introduction

The carbon flux between the soil and atmosphere takes place mainly in the form of carbon dioxide (CO_2) originating from microbial (heterotrophic) and root (autotrophic) respiration. This process, soil respiration (SR), is one of the main pathways of flux in the global carbon cycle, with mature northern temperate soils contributing roughly 12.4 Pg C per year to the atmosphere (Kicklighter and others 1994), about 50%–55% of gross primary production (GPP) (Janssens and others 2001). A number of investigators have suggested that SR acts as the primary factor in determining the carbon balance of an ecosystem at both the local and global scales (Valentini and others 2000; Janssens and others 2001; Luo and others 2002).

Although numerous studies have examined SR at the ecosystem scale (square meters) (Reiners 1968; Thierron and Laudelout 1996; Toland and Zak

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1994; Londo and others 1999; Widén and Majdi 2001), the regional scale (square kilometers), (Simmons and others 1996), the continental scale (Janssens and others 2001), and the global scales (Raich and Schlesinger 1992), little work has been devoted to studying SR across managed-landscape mosaics in which multiple patch types (specific ecosystems) cumulatively determine the SR of the landscape. Landscape-level studies of CO_2 exchange within northern temperate forested landscapes are especially critical because recent evidence suggests that the "missing carbon sink" may be accounted for in the soil of terrestrial ecosystems in the northern temperate latitudes (Ciais and others 1995; Pacala and others 2001; Myneni and others 2001). Furthermore, information about the differences in SR among the various patch types that comprise a managed landscape can help land managers understand how biological processes are altered by human-induced disturbances, such as controlled burning or timber harvest. SR has been hypothesized to act as an indicator of differences in productivity and past site disturbances at the ecosystem or regional scale (Janssens and others 2001; Striegl and Wickland 2001).

Previous studies have indicated that SR is strongly affected by soil temperature (T_s) and soil moisture (M_s) (Howard and Howard 1993; Lloyd and Taylor 1994; Raich and Potter 1995; Savage and Davidson 2001). This response of SR to fluctuations in T_s and M_s is often modeled using exponential or parabolic functions and the incorporation of a $T_s \times M_s$ interaction term (for example, see Wildung and others 1975; Alexander 1977; Raich and Schlesinger 1992; Londo and others 1999). Meanwhile, T_s and M_s can vary widely among and within the patch types in a landscape (Saunders 1998; Saunders and others 1999; Chen and others 1999); thus, the analysis of SR at the landscape level needs to take into account the dominant patch types in the landscape.

Scientific investigation of the carbon cycle within terrestrial ecosystems must consider land use, because this may have an equal or more severe impact on carbon flux than factors such as climate change or atmospheric composition (Tian and others 1999; Schimel and others 2000). This factor is even more critical for landscapes such as national forests that are intensively managed for multiple purposes. Adaptive management practices within the Chequamegon National Forest, a forested landscape in northern Wisconsin, aim to preserve an array of patch types that can act as different habitats with varying degrees of productivity, thereby maximizing biological diversity (Crow and others 1994)

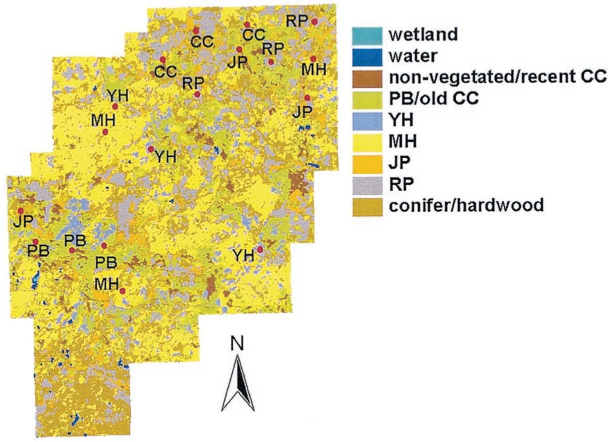

Figure 1. Study area within the landscape of the Chequamegon National Forest, Wisconsin, indicating the location of the sampled patch types. CC, clear-cuts; JP, Jack pine; MH, mature hardwoods; PB, pine barrens; RP, red pine; YH, young hardwoods.

(Figure 1). To date, management regimes within the Chequamegon National Forest have resulted in a landscape that is comprised of generally homogenous soils (Table 1) but numerous patch types. The resulting configuration is thus ideal for examining differences in SR within and among replicates of the patch types across the landscape without introducing confounding influences from heterogeneous soils. That is, patch types with significantly different SR rates within this landscape are likely to have basic differences in carbon cycling that are attributable to management practices and disturbance regimes. We therefore designed our study to answer the following questions:

1. How do SR, T_s, and M_s vary seasonally and interanually *within* the six dominant patch types (clear-cut, open-canopy pine barrens, mature Jack pine, mature red pine, mature northern hardwoods, and young northern hardwoods) in this northern Wisconsin landscape?
2. How well can the influence of biophysical controls, such as T_s and M_s, on SR be quantified within each of these patch types?
3. How does SR differ *among* the six dominant patch types?
4. How do T_s, M_s, and litter depth (LD) influence SR in each of these patch types?

We hypothesized that the interannual and seasonal variability in SR rates would be attributable to variations in the temperature and moisture regimes and that either T_s or LD would act as the dominant control over SR within and among all the patch types. Further, we hypothesized that the most re-

Table 1. Summary of Soil Characteristics for the Patch Types

Variable	CC	JP	MH	RP	PB	YH
Soil texture[a]						
A	89, 8, 2	88, 11, 1	79, 20, 1	89, 10, 1	88, 11, 1	83, 15, 2
E	90, 9, 1	90, 10, —	79, 19, 1	90, 10, —	89, 11, —	83, 16, 1
B	92, 7, 1	88, 11, 1	78, 19, 3	89, 9, 2	91, 8, 1	80, 17, 3
Soil pH						
A	3.34 (ab)	3.17 (ab)	3.21 (ab)	3.03 (b)	3.61 (a)	3.47 (a)
E	2.11	3.39	2.32	3.02	1.94	3.03
B	2.94	4.14	2.79	4.00	3.25	3.68
Soil total N (%)						
A	0.13 (b)	0.18 (ab)	0.25 (ab)	0.11 (b)	0.18 (b)	0.38 (a)
E	0.02	0.04	0.03	0.05	0.02	0.04
B	0.02	0.03	0.03	0.03	0.03	0.04
Soil total C (%)						
A	3.29 (ab)	4.73 (ab)	5.55 (ab)	3.05 (b)	3.52 (b)	7.99 (a)
E	0.52	0.90	0.65	1.08	0.31	0.71
B	0.49	0.62	0.55	0.65	0.58	0.86
Soil organic matter (%)						
A	6.17 (b)	9.98 (ab)	10.14 (ab)	6.26 (b)	9.18 (ab)	15.26 (a)
E	1.45	2.38	1.73	2.43	0.96	1.87
B	1.64	2.38	1.99	2.35	2.20	2.77

Different lower-case letters denote significant differences ($P < 0.0024$) among the patch types. Generally, significant differences were not seen in the E and B horizons. Lowland and seasonally waterlogged areas were not included in the analysis.
Data pertaining to soil pH, soil total nitrogen, soil total carbon, and soil organic matter are reprinted from Brosofske and others (2001) with permission from Elsevier Science.
CC, clear-cuts; JP, Jack pine; MH, mature hardwoods; RP, red pine; PB, pine barrens; YH, young hardwoods
[a]Soil texture data are given as percent sand, percent silt, and percent clay.

cently disturbed patch types (pine barrens and clear-cuts) would have the lowest soil respiration rates, whereas the intermediate-aged patch type (young hardwoods) would have higher SR relative to the mature patch types (Jack pine, red pine, and mature hardwoods).

METHODS

Study Site

Our study was conducted within the Washburn Ranger District of the Chequamegon National Forest, Wisconsin, USA (46°30–46°45' N, 91°02–91°22' W). The landscape is characterized by late Wisconsin-age glaciated landscapes and Precambrian shield bedrock. Topography is flat to rolling, and elevations range from 232 to 459 m. Between 66 to 70 cm of rain and 106–150 cm of snow falls as precipitation each year, and the growing season spans 120 to 140 days. The bedrock geology is characterized by Precambrian and Cambrian bedrock covered with 34–200 m of glacial drift. The soils are deep, loamy sands with little organic matter and are classified as Psamments and Orthods (Albert 1995) (Table 1).

We conducted our study within three replicates of six dominant patch types in this landscape: (a) mature Jack pine (*Pinus banksiana*), (b) mature red pine (*Pinus resinosa*), (c) open-canopy Jack pine barrens (PB) (burned less than 7 years previously), (d) clear-cut (5–8 years old, previously red and/or Jack pine sites), (e) mature northern hardwoods, and (f) young northern hardwoods (10–12 years old) (Figure 1). Data pertaining to the groundcover vegetation, topography (slope, aspect, and so forth), structural elements (for example, canopy cover), and precise method of site selection of these patch types are detailed by Brosofske and others (2001).

Measurements of SR and Driving Variables

SR measurements were taken on a weekly to bi-weekly basis over two sampling periods (June–September 1999 and April–October 2000) using a cylindrical chamber of known volume connected to an infrared gas analysis system (PP Systems, Haverhill, MA, USA). To create a tight seal with the soil respiration chamber, 10 collars measuring 10 cm in diameter and constructed from polyvinylchloride (PVC) tubing were installed at each site in the spring prior to taking measurements. All measure-

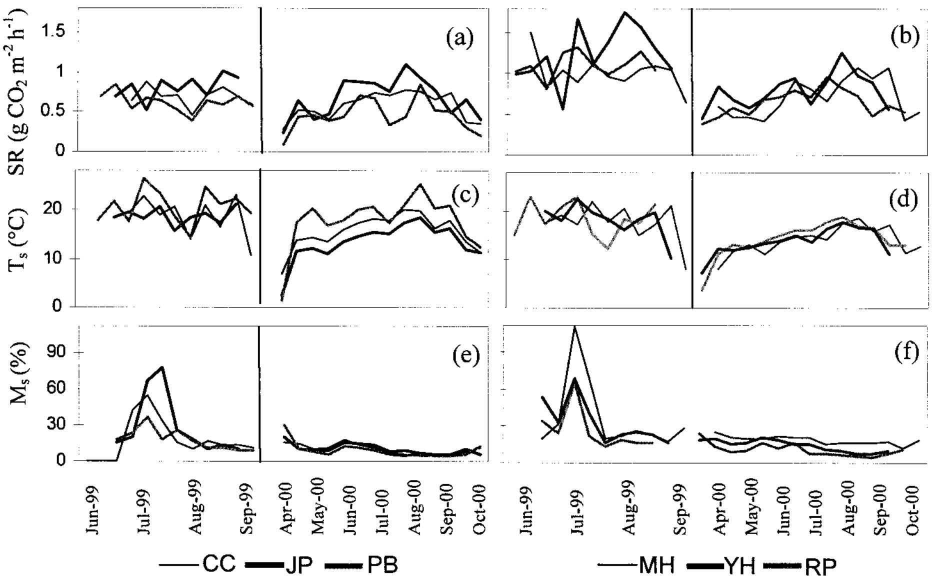

Figure 2. (**a, b**) Comparison of soil respiration (SR), (**c, d**) soil temperature (T_s) (5-cm depth), and (**e, f**) soil moisture (M_s) during the sampling periods of 1999 and 2000. The bold vertical line in each graph indicates a break in monitoring. CC, clear-cuts; JP, Jack pine; MH, mature hardwoods; PB, pine barrens; RP, red pine; YH, young hardwoods.

ments were taken at least 50 m from any roadside or edge. At the time of each SR measurement, soil temperature T_s (5-cm depth) was measured adjacent to each PVC collar using a digital thermometer. Additionally, T_s measurements (5-cm depth) were recorded continuously at hourly to half-hourly intervals at each site using HOBO four-channel external data loggers (Onset Corp., Pocasset, MA, USA). Soil samples were taken adjacent to the collars (at a 10-cm depth in the A horizon) with a soil probe at the time of SR measurement and oven-dried for 48 h at 105°C to determine gravimetric moisture contents (M_s) (% dry weight). Two reference weather stations, one at a pine barrens site and one in a clear-cut site, were installed during summer 1999. The stations measured standard climatic data once per minute and output 30-min averages (for example, air temperature, relative humidity, precipitation, photosynthetically active radiation [PAR], soil heat flux). Litter depth (LD) (cm) was measured in August 1999 and August 2000 at each of the 10 collars at each site.

Statistical Analysis

Data from each of the three replicates of the six patch types were pooled after determining that the measurements were statistically similar for all of the replicates using an analysis of variance ($P < 0.001$). Mean values of SR, T_s, and M_s were computed by patch type, and the Bonferroni method was applied to determine significant differences between the patch types and between the years 1999 and 2000 (Rice 1995). Linear and nonlinear regression analyses were performed to build statistical models designed to investigate the relationship among SR, T_s, M_s, and LD. Average daily values of T_s were computed based on the continuously collected temperature data and were used in our statistical models to simulate SR rates for the entire sampling session. Monthly average simulated SR rates were compared with the field-measured average monthly values. Additionally, the possible effect of T_s on SR was examined over a diurnal cycle within each patch type using the simulated soil respiration rates. All analyses were performed using the statistical software package SAS (SAS v. 8.0; SAS Institute, Cary, NC, USA) with a significance level of $\alpha = 0.05$.

Results

Temporal Variation in SR within the Patch Types

We found seasonal trends in SR rates within these patch types during the sampling period. Higher values of SR were observed between late June and late August; seasonal increases occurred during the late spring, and seasonal decreases began in early autumn (Figure 2a–c). These seasonal increases corresponded to soil warming and the growth of groundcover vegetation in the spring (E. Euskirchen personal observation), whereas the decreases were linked to soil cooling and the senescence of groundcover vegetation in the autumn.

Increased levels of soil moisture and higher temperatures may have accounted for the up to 37% overall higher rates of SR in June–September 1999 than in this same period in 2000. Significant differ-

Table 2. Comparisons between Means (SDs) of Soil Respiration (SR), Soil Temperature (T_s), and Soil Moisture (M_s) as Measured in June–September 1999 and 2000 at the Six Dominant Patch Types in the Landscape

	SR ($g\ CO_2\ m^{-2}\ h^{-1}$)		T_s (°C)		M_s (%)	
Ecosystem	1999	2000	1999	2000	1999	2000
CC	0.7 (0.12)	0.6 (0.14)	17.9 (4.4)	16.7 (2.3)	23.4 (16.0)	8.8 (4.2)[a]
MH	1.0 (0.22)	0.8 (0.25)[a]	17.5 (3.9)	14.7 (2.4)[a]	36.8 (30.0)	17.8 (2.9)[a]
JP	0.8 (0.15)	0.7 (0.22)	18.7 (1.7)	14.6 (2.3)[a]	28.3 (25.2)	9.5 (3.4)[a]
PB	0.6 (0.12)	0.5 (0.17)	20.6 (3.5)	19.5 (2.8)	17.7 (8.7)	7.0 (2.7)[a]
RP	1.1 (0.15)	0.7 (0.14)[a]	18.4 (3.6)	15.4 (2.1)[a]	26.0 (16.8)	9.2 (4.1)[a]
YH	1.2 (0.35)	0.8 (0.21)[a]	17.6 (3.6)	14.4 (2.2)[a]	33.1 (17.9)	13.4 (4.4)[a]

CC, clear-cuts; MH, mature hardwoods; JP, Jack pine; PB, pine barrens; RP, red pine; YH, young hardwoods.
[a]Means between the two years significantly different (α = 0.05) by t-test

ences between the mean rates of SR in June–September 1999 and 2000 were also found for mature hardwoods (1.0 g CO_2 $m^{-2}h^{-1}$ in 1999 versus 0.8 g CO_2 m^{-2} h^{-1} in 2000), red pines (1.1 g CO_2 m^{-2} h^{-1} in 1999 versus 0.7 g CO_2 m^{-2} h^{-1} in 2000), and young hardwoods (1.2 g CO_2 m^{-2} h^{-1} in 1999 versus 0.8 g CO_2 m^{-2} h^{-1} in 2000), (Table 2). Soil temperatures between the two years were significantly different for Jack pine (18.7°C in 1999 versus 14.6°C in 2000), young hardwoods (17.6°C in 1999 versus 14.4°C in 2000), mature hardwoods (17.5°C in 1999 versus 14.7°C in 2000), and red pine (18.4°C in 1999 versus 15.4°C in 2000) (Table 2). Additionally, soil moisture was significantly higher during 1999 within all the patch types (Table 2), mostly due to severe thunderstorms in early July.

SR, T_s, and M_s Interactions

Soil respiration rates within the patch types were primarily controlled by T_s. An exponential model using a Gauss-Newton estimation method yielded a statistically significant ($\alpha = 0.05$, $P < 0.001$) fit to the SR–T_s relationship, with T_s explaining between 45% and 73% of the variability in SR rates (Figure 3). The intercept ranged from 0.1466 (± 0.0365) for the pine barrens model to 0.3235 (± 0.0798) for the Jack pine model (Figure 3b and d). At any given soil temperature, predicted SR rates were highest in the young hardwoods, followed by the mature hardwoods and red pine, with the pine barrens and clear-cuts having the lowest rates (Figure 3). For the range of temperatures between 5°C and 25°C, this corresponded to Q_{10} values between 1.6 in the Jack pine and 2.0 in the young hardwoods. The range in rates of SR between the patch types increased as T_s increased; the lower range occurred at around 5°C (from 0.20 to 0.46 g CO_2 m^{-2} h^{-1}), and the higher range occurred at around 25°C (from 0.75 to 1.91 g CO_2 m^{-2} h^{-1}) (Figure 3).

The inclusion of an M_s term and a $T_s \times M_s$ interaction term into our temperature model substantially increased the R^2 values for three of the patch types (clear-cuts, pine barrens, and red pine) (Figure 4). These complete models explained between 46% and 74% of the variability in the SR data. The intercepts of the models with the M_s terms were lower than those with just T_s, ranging from 0.0398 (± 0.0256) in the pine barrens to 0.1408 (± 0.360) in the clear-cuts (Figures 3, 4).

Predicted Rates of SR

Over the course of the measurement period, the simulated soil respiration rates (Figure 5) generally reached a peak between late June (for example, in the red pines and clear-cut in 1999 and the mature hardwoods and young hardwoods in 2000) and late July (for example, the Jack pine and young hardwoods in 1999), a pattern that corresponded with measured SR rates (Figure 2). During the winter months, simulated values of SR were negligible (that is, less than 0.4 g CO_2 m^{-2} h^{-1}) when soil temperatures remained near 0°C (Figure 5). The average monthly values of simulated SR were in close agreement with the field-measured values during 2000 (Figure 6a–f), but in 1999 the simulated values tended to underpredict SR rates in the pine barrens, red pine, and young hardwoods (Figure 6d–f).

The diurnal variation in T_s was minimal during the summer months in all the patch types except the pine barrens. During the spring and fall, soil temperatures typically varied more markedly over a 24-h period, with warmest temperatures occurring in the mid- to late afternoon (Figure 7). These

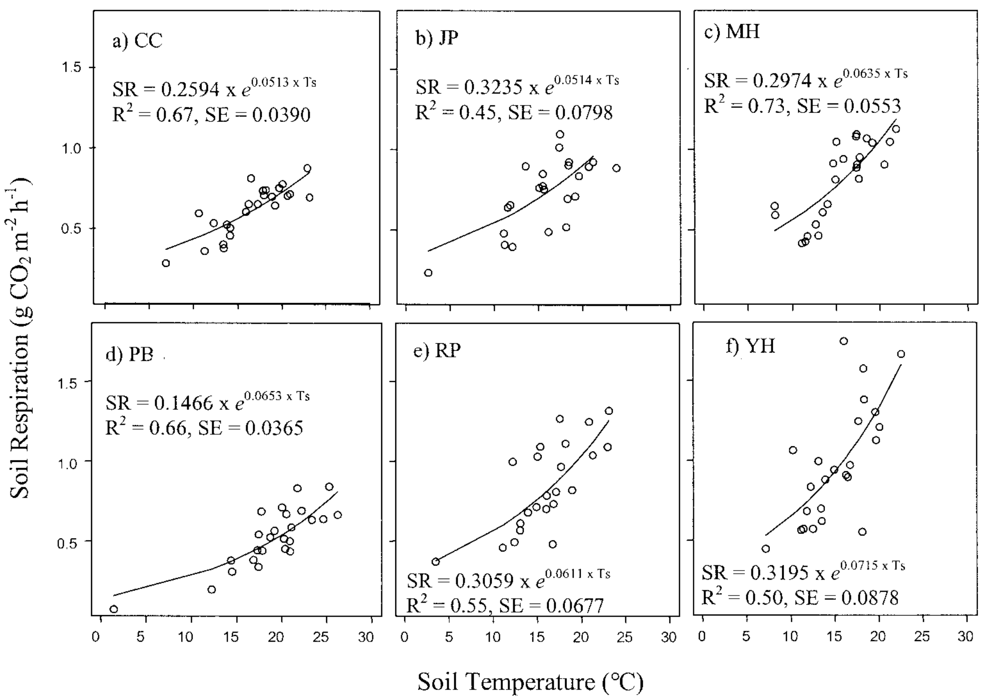

Figure 3. Relationship between soil respiration (SR) and soil temperature (T_s) for the six patch types. For all models, $P > F$ is < 0.0001 and SE is the standard error of the intercept term. Each point represents means among the three replicates of each patch type for each sampling session, or 30 individual measurements. CC, clear-cuts; JP, Jack pine; MH, mature hardwoods; PB, pine barrens; RP, red pine; YH, young hardwoods.

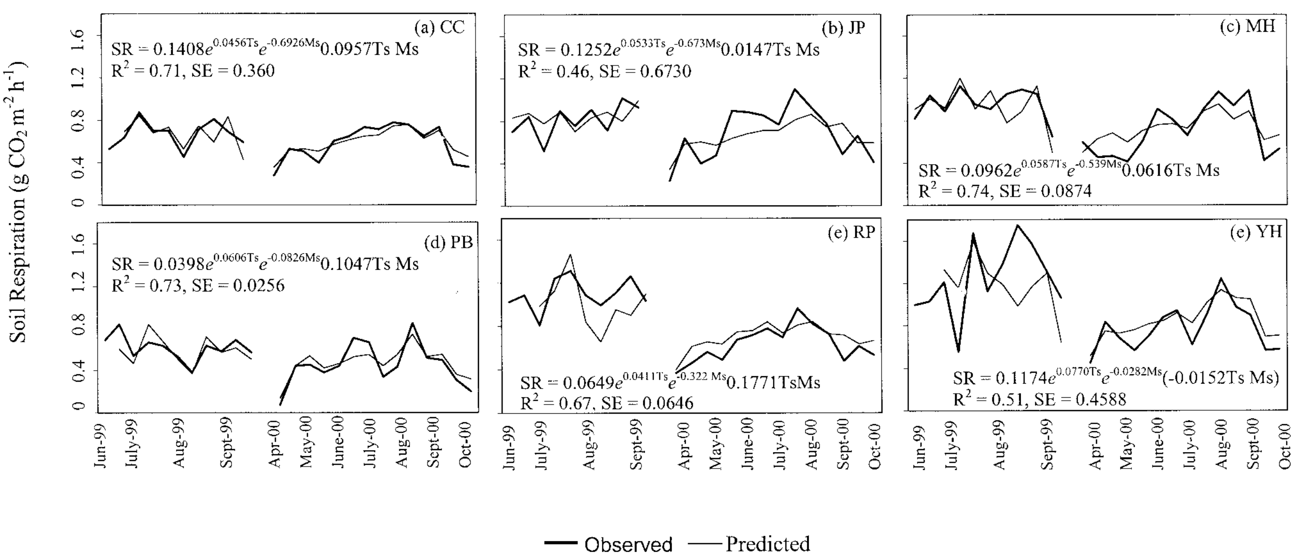

Figure 4. Predicted rates of soil respiration (SR) using models based on soil temperature (T_s) and soil moisture (M_s) compared to observed SR. For all models, $P > F$ is < 0.0001 and SE is the standard error of the intercept term. Each point represents means among the three replicates of each patch type for each sampling session, or 30 individual measurements. CC, clear-cuts; JP, Jack pine; MH, mature hardwoods; PB, pine barrens; RP, red pine; YH, young hardwoods.

increases in soil temperature also caused a slight peak in the simulated SR rates during these mid-to late afternoon hours (Figure 7).

Controls on SR among Patch Types

There were significant differences in SR between some of the patch types within the landscape based on data averaged over the 1999 and 2000 sampling periods (Figure 8a). The rates of SR (mean ± SD) in the pine barrens (0.51 ± 0.23 g CO_2 m^{-2} h^{-1}), clear-cuts (0.61 ± 0.24 g CO_2 m^{-2} h^{-1}), and Jack pine (0.73 ± 0.36 g CO_2 m^{-2} h^{-1}) were significantly lower than the rates in the young hardwoods (0.96 ± 0.48 g CO_2 m^{-2} h^{-1}). However, rates of SR in the red pine plantations (0.79 ± 0.39 g CO_2 m^{-2} h^{-1}) and mature hardwoods (0.81 ± 0.43 g CO_2

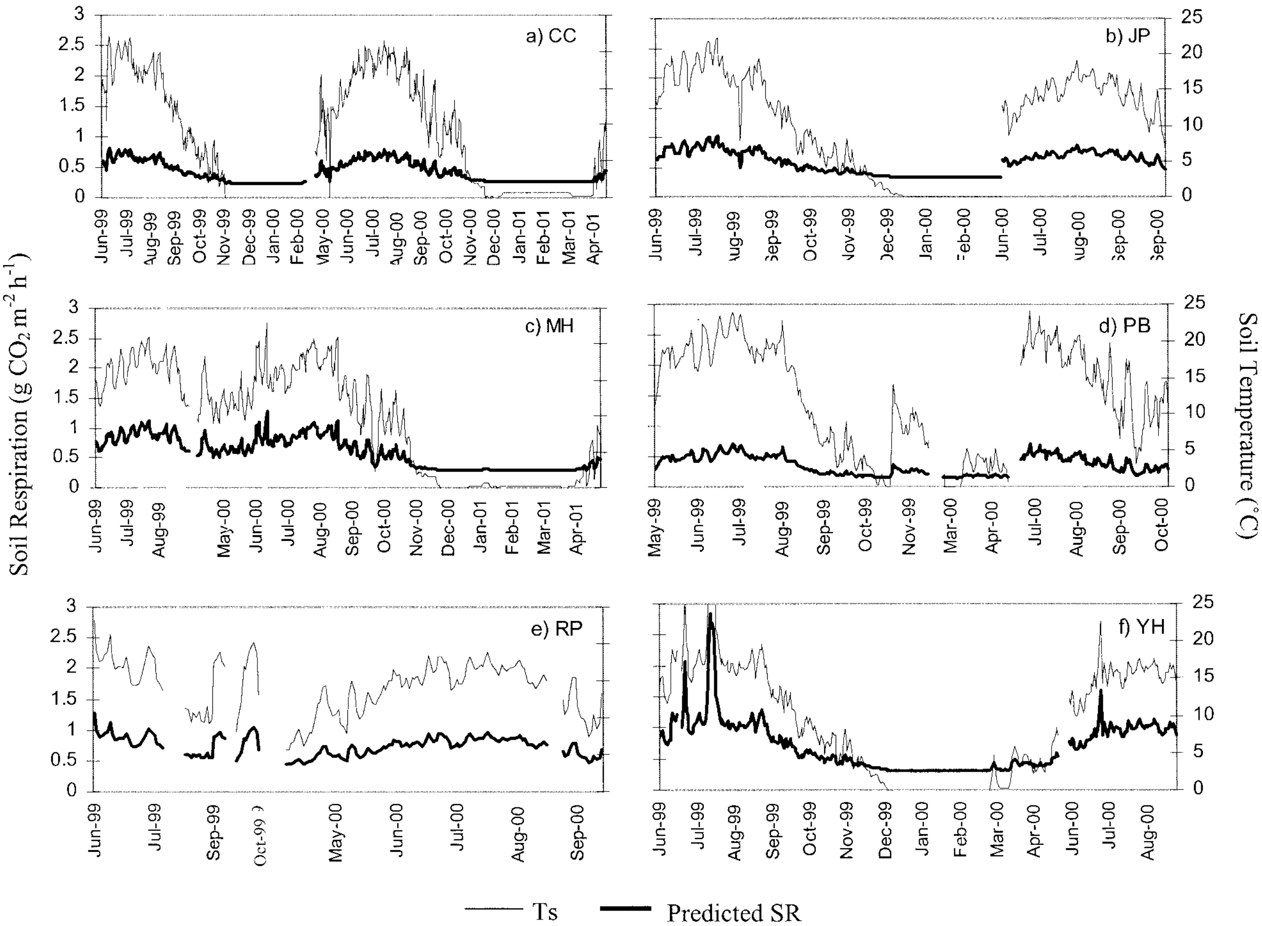

Figure 5. Predicted soil respiration (SR) based on the models presented in Figure 3 and soil temperature (T_s) data collected every 30 min and averaged over a 24-h period. CC, clear-cuts; JP, Jack pine; MH, mature hardwoods; PB, pine barrens; RP, red pine; YH, young hardwoods.

m^{-2} h^{-1}) were not significantly different from the young hardwoods. Furthermore, SR rates were significantly lower at the clear-cuts and pine barrens than the mature hardwoods, and the red pine plantations had significantly lower SR rates than the pine barrens.

LD was a better predictor of mean SR rates between the patch types than T_s or M_s values averaged over both of the 1999 and 2000 sampling periods (Figure 8b–d). LD was positively correlated with SR; the lowest average LD and SR occurred in the pine barrens (average, 0.49 cm) and the highest occurred in the young hardwood (average, 2.85). The range of average T_s between patch types was narrow, between roughly 15°C and 19°C (Figure 8c); the lowest temperatures and highest SR rates occurred in the young hardwoods, and the warmest temperatures and lowest SR rates were measured in the pine barrens. Consequently, the SR–T_s relationship fit a negative exponential curve (Figure 8c).

Average M_s varied from about 12% to 27% dry weight. This SR–M_s relationship fit a parabolic curve. This finding reflected a decrease in SR in the extremely dry soils of the pine barrens and the more saturated soils of the mature hardwoods, with respiration rates peaking at around 21% dry weight in the young hardwoods (Figure 8d). Overall, the young hardwoods had the highest SR rates, deepest LD, and coolest soil temperatures, whereas the pine barrens had the lowest SR rates, least LD, warmest soil temperatures, and driest soil (Figure 8).

Discussion

Moisture and SR within Patch Types

Northern temperate forests in the Great Lakes region receive frequent precipitation throughout the growing season and in general experience only temporary water shortages. However, precipitation during some summers may deviate significantly from the average, and the relationship between SR

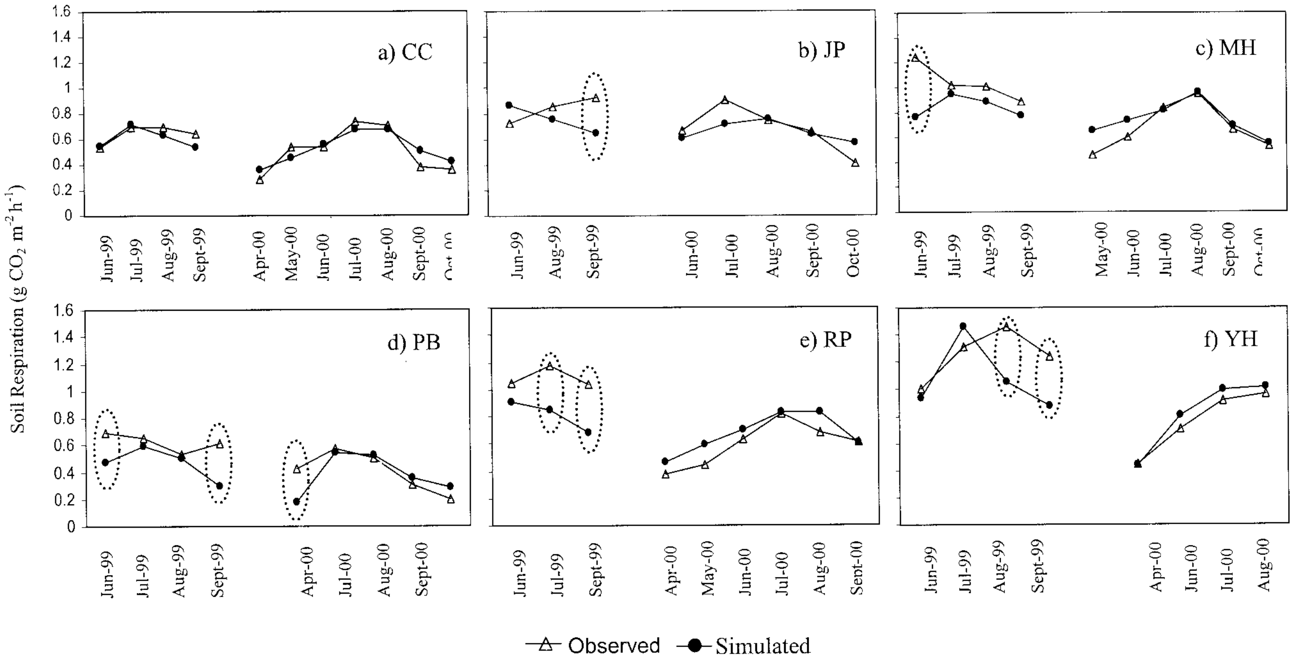

Figure 6. Measured versus simulated average monthly soil respiration (SR). The simulated SR rates are calculated using the continuously monitored soil temperature (T_s) data (5-cm depth) and the models presented in Figure 5. Circled pairs of points represent those that are significantly different ($\alpha = 0.05$) by *t*-test. CC, clear-cuts; JP, Jack pine; MH, mature hardwoods; PB, pine barrens; RP, red pine; YH, young hardwoods.

and T_s is likely to become confounded by soil moisture during these years. For example, SR was more accurately predicted by T_s in 2000 than in 1999 for four of the patch types (Figure 6d and e). Data collected at our weather station showed that the months from June to September 1999 had an above-average 93 cm of rain, whereas for this same period in 2000 total rain amounted to a slightly below-average 56 cm. In 2000, the drier year, the sandy soils drained rapidly, so there was considerably less measured variation in near-surface soil moisture than in 1999, when the soils remained more moist. Increased levels of soil moisture and higher temperatures may have accounted for the overall higher SR during June–September 1999 (Figure 2 and Table 2). These results indicate that interannual variability in SR within these patch types is best predicted with models that incorporate both a temperature and moisture component (see also Parker and others 1983; Savage and Davidson 2001; Xu and Qi, 2001; Chen and others 2002). Furthermore, this interannual variation has implications for the overall carbon balance of the landscape. For example, warmer, wetter years could potentially cause the landscape to act as a net source of carbon rather than a net carbon sink (see also Valentini and others 2000; Savage and Davidson 2001).

On a weekly basis, M_s did not have a distinct effect on SR within the Jack pine, mature hardwood, or young hardwoods sites. The inclusion of a soil moisture term did not account for a greater percent of the variance based on the R^2 values derived from on the data collected during the 1999 and 2000 sampling periods, when adequate precipitation fell at these patch types. It is possible that we would find a significant increase in the predictive capabilities of the weekly SR models within these patch types if we were to formulate soil respiration prediction models from data collected during times of severe water limitations (e.g., if June–September precipitation had been much less than the 56 cm that fell in 2000). Moreover, on a longer-term basis, it is apparent that the moisture regime at these sites had some cumulative effect on SR; the optimally moist soils at the young hardwoods site did seem to contribute to its overall higher average rates of SR, and the more saturated soils at the mature hardwoods site were probably a factor that lowered the average SR values at this patch type (e.g., see Figure 8c).

Predictions of SR

The simulations of SR based on the continuously collected T_s data should be viewed with some caution, particularly for the predicted values calculated

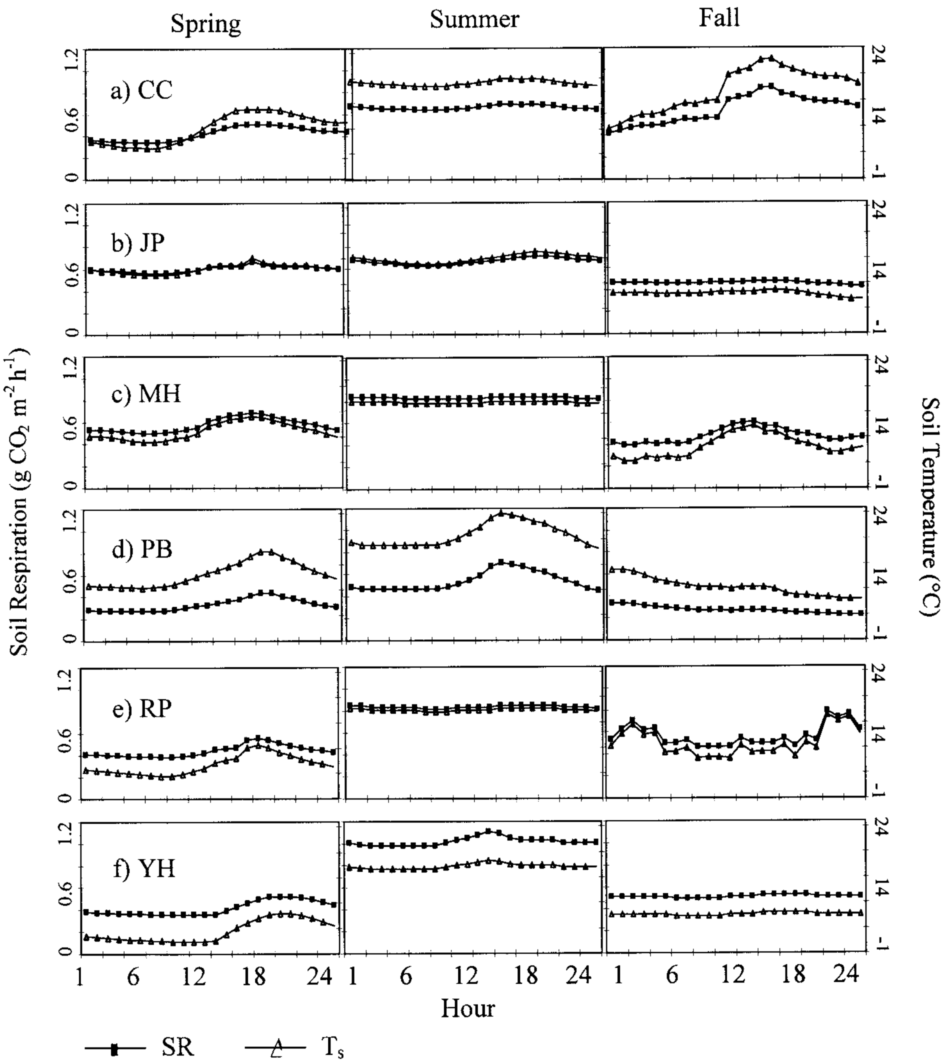

Figure 7. Measured diurnal variations in soil temperature (T_s) and simulated diurnal variations in soil respiration (SR) during spring, summer, and fall. The simulated values of SR are calculated using the models presented in Figure 4. The diurnal variations in T_s represent individual days but are representative of that particular season. During the winter months, T_s remains near freezing. CC, clear-cuts; JP, Jack pine; MH, mature hardwoods; PB, pine barrens; RP, red pine; YH, young hardwoods.

within the winter months. During the winter months, T_s frequently fell below the values measured in the field that is, below the values on which the exponential models in Figure 3 are based); consequently, the values presented here are extrapolated. At a smaller time-step, diurnal variations in T_s could cause a subsequent change in the respiration activities of the autotrophs and heterotrophs, although it is possible that there is a time lag that is not captured in our models (S. Ma and others unpublished) (Figure 7). The diurnal variation in SR caused by changes in T_s would generally remain larger in the spring and autumn months, when there are greater fluctuations in the diurnal soil temperatures, than in the summer and winter. However, the diurnal variation at a site may also be attributable to lower wind speeds at night, which causes less CO_2 transport by advection than occurs during the daytime, when wind speeds are generally higher (Widén and Majdi 2001).

SR among and within Patch Types

Given that average LD, an indicator of aboveground productivity, was a better predictor of SR *among* the patch types within this landscape than average T_s (Figure 8), it is possible that over the longer term (for example, years) aboveground controls have a greater influence on both autotrophic and heterotrophic SR than T_s. Still, to examine this relationship in more concrete terms, litter fall may act as a more reliable predictor of aboveground productivity than LD because litter fall is a flux, whereas LD is a pool. Although no litter fall fata were available for this study, they are critical to future investigations.

As for autotrophic respiration, the T_s effect on

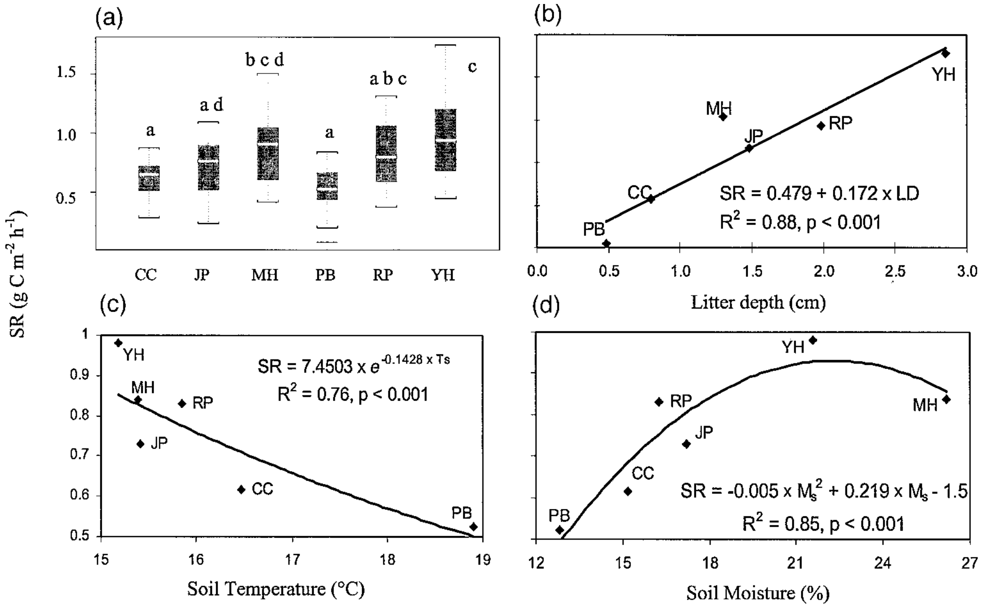

Figure 8. Comparisons of soil respiration (SR) between patch types using averaged data from the 1999 and 2000 sampling periods. **a** Mean, maximum, minimum, and outlying values of SR; letters above boxes indicate significant differences. **b** Relationship between average litter depth (LD) (LD) within the six patch types and average SR. The line depicts the least-squares relationship between the two variables, **c** the relationship between average soil temperature (T_s) and average SR, and **d** the relationship between average soil moisture (M_s) and average SR. CC, clear-cuts; JP, Jack pine; MH, mature hardwoods; PB, pine barrens; RP, red pine; YH, young hardwoods.

roots generally remains constrained by GPP. Roots can only respire that which they are allocated and are therefore linked to aboveground controls on carbohydrate availability (Raich and Nadelhoffer 1989). Heterotrophic respiration may also be better predicted by productivity than T_s. Heterotrophs commonly favor the less resilient soil organic matter fractions, often utilizing the new litter inputs near the surface, the amount of which is related to the productivity of a given patch type (Alexander 1977). That is, vegetation activity and the labile carbohydrate provided to the autotrophs and heterotrophs by recent photosynthesis generally drive much of the variation in SR (for example, see Russell and Voroney 1998).

The SR–T_s relationship (and the resulting Q_{10}) may seem stronger than it really is because leaf area and photosynthesis tend to increase in the spring and decrease in the fall, coincident with changes in T_s. Nevertheless, even though the SR–T_s relationship may be confounded by this correlation between temperature and vegetation activity, on a weekly basis T_s was a reliable predictor of SR *within* the patch types. The predictive value is linked to the wide range of temperatures measured within the patch types from late spring to autumn; moreover, the daily activity level of autotrophs and heterotrophs are highly temperature dependent (Alexander 1977). For example, T_s within the pine barrens varied by nearly 28°C (from 0.3°C to 28°C) on a weekly basis; and within red pine patch types, T_s varied by 20°C (from 3°C to 23°C) (Figure 3). In contrast, the average T_s between the patch types varied by only 4°C (Figure 8c).

Furthermore, because the patch types with higher temperatures were to some extent constrained by moisture, predictions of SR between patch types using T_s alone fit a negative exponential function (Figure 8b and c), whereas predictions of SR using T_s alone within the patch types fit a positive exponential function. Moreover, the inverse correlation of temperature and SR at the landscape scale may also be related to increased groundcover, leaf area index, and shading of the soil by the more active vegetation types (for example, the young hardwoods). Examination of only the negative exponential temperature response curves could be misleading; at the landscape–scale the response of SR was negatively correlated to increases in soil temperature, whereas within the patch types the response was positively correlated.

Although we did not find a significant difference in SR between mature coniferous forests and mature broad-leaved forests, SR was slightly lower for red pine and Jack pine than for mature hardwoods (Figure 8a). The average LD and T_s at these sites were nearly equal (Figure 8b and c), but the soil was more moist within the mature hardwoods than at the coniferous sites (Figure 8d). SR within the red pine and Jack pine patch types was apparently limited by insufficient moisture, whereas in the mature hardwoods it may have been hindered by an overabundence of moisture (Figure 8d). In a meta-analysis of six studies at five temperature sites where soil characteristics were the same among the stands, Raich and Tufekcioglu (2000) found that coniferous forests had SR rates that were on average 10% lower than broad-leaved forests. Other researchers have compared SR rates at broad-leaved and coniferous forest types, but the soil characteristics varied between the stands, thereby, confounding the analysis (for example, see Reiners 1968; Schlenter and Van Cleve 1985; Widén and Majdi 2001). None of these studies has provided a definitive explanation for the differences between the coniferous and broad-leaved forest types, although it has been suggested that these are due to factors such as dissimilarities in litter quality, litter production, or root respiration rates (Raich and Tufekcioglu 2000).

Management and Landscape-level Modeling

The variation in the intercepts of the temperature response curves between the patch types within this landscape sites (Figure 3) and the corresponding wide range in Q_{10} values (from 1.61 for the Jack pine to 2.03 for the young hardwoods, using the range of temperatures from 5°C to 25°C) shows that the temperature response can fluctuate as widely within a landscape as it can on a regional or global scale (Simmons and others 1996; Raich and Schlesinger 1992). Furthermore, the average M_s and LD over the sampling periods were also variable between sites. Therefore, it would not be advisable to infer landscape-level rates of SR using the results from a single site.

Differences in the rates of SR within this landscape should be of particular interest to land managers because they provide an indication of how varying disturbance regimes can affect a biological process. For example, similarities in SR between the clear-cut and pine barrens sites indicate that timber harvest mimicked the effect of the fires in the pine barrens on this component of carbon cycling. The low SR rates observed in the pine barrens and clear-cuts may be attributable to lower rates of root respiration at these sites. Root respiration may account for more than half of total SR (Hanson and others 2000), but the burning and harvesting regimes in the pine barrens and clear-cuts may have decreased the overall root biomass, leading to a subsequent decline in total SR (see also Behera and others 1990; Ewel and others 1987). Similarly, the young hardwoods are likely to be experiencing higher rates of root respiration as the stands regenerate and fine-root biomass increases, thereby causing them to have higher rates of total SR.

At the young hardwood sites, high rates of microbial respiration could also be occurring as populations profit from increased substrate availability. However, at the mature hardwood, Jack pine, and red pine sites, it is possible that the pool of labile carbon in the soil has been utilized by the microbes, leading to an overall decline in SR. In the clear-cuts and pine barrens, there may have also been an increase in soil microbial respiration following the tree harvest, but this increase was not large enough to offset the decline in root respiration (see also Toland and Zak 1994). Historically, the separation of the relative contributions of the autotrophs and heterotrophs to total SR has remained problematic, and this is an area that warrants further exploration.

Similarly, from the SR standpoint, planting to a stand of conifers rather than a stand of hardwoods seems to have the same effect on average soil respiration rates across the mature hardwood sites and the Jack pine and red pine sites. It is also clear that clear-cutting a stand of pine did not significantly alter the total rate of SR at this site, since the mature coniferous sites did not have significantly different rates of SR than the clear-cut. However, it is likely that timber harvest did vary the relative contributions of autotrophic and heterotrophic respiration—a modification that, in the longer term, may modify the storage of organic matter in these soils. Furthermore, there was no significant difference in SR between young and mature hardwoods.

Finally, since LD acted as an important variable in predicting SR, it is likely that the amount of slash and other woody debris left behind from logging practices may also serve as a key predictive variable in SR models. Decomposition of slash is a major input of carbon into the soil organic matter pool; in the years following timber harvest, it would enhance soil carbon availability and lead to an increase in soil respiration (Raich and Nadelhoffer 1989; Jurik and others 1991; Striegl and Wickland 2001). It is also possible that other disturbances, such as fire, act to remove litter and woody debris, thereby producing effects at different scales for carbon flux and stock (Euskirchen and others 2002; Schulze and others 2000). A previous study within this landscape (Saunders and others 2002) found that decomposition rates varied significantly between some of the patch types and concluded that these differences may be attributable to such factors as variations in canopy cover and litter composition and litter quality.

Future Directions and Concluding Remarks

We chose a landscape scale for this study because it enables an assessment of multiple patch types under varying management regimes. The landscape-level approach is useful in determining the effect of forest and land-use management practices on soil respiration. Furthermore, this study has provided a foundation upon which we can base numerous other research projects within this landscape. Future studies within this landscape will measure SR at other patch types (for example, young pines, mixed conifer–hardwood) within the area of edge influence (which can be extensive and significantly different from the ecosystem interior in fragmented landscapes) and on a diurnal basis. In addition, the empirical models presented in this study will be used to estimate historical values of SR within this landscape based on remotely sensed data for the years 1987–98. Finally, the relative importance of SR within the carbon budget of this landscape will be determined using micrometeorological techniques.

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REFERENCES

Albert DA. 1995. Regional landscape ecosystems of Michigan, Minnesota, and Wisconsin: a working map and classification. USDA–Forest Service General Technical Report NC-178. St. Paul (MN): North Central Forest Experiment Station

Alexander M. 1977. Introduction to soil microbiology. New York: Wiley, p 467.

Behera N, Joshi SK, Pati DP. 1990. Root contribution to total soil metabolism in a tropical forest from Orissa, India. For Ecol Manage 36:125–34.

Brosofske KD, Chen J, Crow TR. 2001. Understory vegetation and site factors: implications for a managed Wisconsin landscape. For Ecol Manage 146:75–87.

Chen J, Falk M, Euskirchen ES, Paw UK, Suchanek K, Ustin S, Bond BJ, Brosofske KD, Phillips N, BI R. 2002. Biophysical controls of carbon flows in three successional Douglas-fir stands based upon eddy-covariance measurements. Tree Physiol 22:171–80.

Chen J, Saunders SC, Crow TR, Naiman RJ, Brosofske KD, Mroz GD, Brookshire BL, Franklin JF. 1999. Microclimate in forest patch types and landscape ecology. BioScience 49:288–97.

Ciais P, Tans PP, Trolier M, White JWC, Francey RJ. 1995. A large northern hemisphere terrestrial CO_2 sink indicated by the 13C/12C ratio of atmospheric CO_2. Science 269:1098–202.

Crow TR, Haney A, Waller DM. 1994. Report on the scientific roundtable on biological diversity convened by the Chequamegon and Nicolet National Forests. USDA Forest Service General Technical Report NC-166. St. Paul (MN): North Central Forest Experimental Station

Euskirchen ES, Chen J, Li H, Gustafson EJ, Crow TR. 2002. Modeling landscape net ecosystem productivity (LandNEP) under alternative management regimes. Ecol Model 154:75–91.

Ewel KC, Cropper WP, Gholz HL. 1987. Soil CO_2 evolution in Florida slash pine plantations. II. Importance of root respiration. Can J For Res 17:330–3.

Hanson PJ, Edwards NT, Garten CT, Andrews JA. 2000. Separating root and soil microbial contributions to soil respiration: a review of methods and observations. Biogeochemistry 48: 115–46.

Howard DM, Howard PJA. 1993. Relationships between CO_2 evolution, moisture content and temperature for a range of soil types. Soil Biol Biochem 25:1537–46.

Janssens IA, Lankreijer H, Matteucci G, Kowalski AS, Buchmann N, Epron D, Pilegaard K, Kutsch W, Longdoz B, Grünwald T, and others. 2001. Productivity overshadows temperature in determining soil and ecosystem respiration across European forest. Global Change Biol **7:**269–78

Jurik TW, Briggs GM, Gates DM. 1991. Soil respiration of five aspen stands in northern lower Michigan. Am Midl Nat 126: 68–75.

Kicklighter DW, Melillo JM, Peterjohn WT, Rastetter EB, McGuire AD, Steudler PA, Aber JD. 1994. Aspects of spatial and temporal aggregation in estimating regional carbon dioxide fluxes from temperate and forest soils. J Geophys Res 99:1303–5.

Lloyd J, Taylor A. 1994. On the temperature dependence of soil respiration. Funct Ecol 8:315–23.

Londo AJ, Messina MG, Schoenholtz SH. 1999. Forest harvesting effects on soil temperature, moisture, and respiration in a bottomland hardwood forest. Soil Sci Soc Am J 63:637–44.

Luo Y, Wan S, Hui D, Wallace L. 2001. Acclimatization of soil respiration to warming in a tall grass prairie. Nature 413: 622–5.

Myneni RB, Dong J, Tucker CJ, Kaufmann RK, Kauppi PE, Liski J, Zhou L, Alexeyev V, Hughes MK. 2001. A large carbon sink in the woody biomass of northern forests. Proc Natl Acad Sci USA 98:14784–9.

Pacala SW, Hurtt GC, Baker D, Peylin P, Houghton RA, Birdsey RA, Heath L, Sundquist ET, Stallard RF, Ciais P, and others. 2001. Consistent land- and atmosphere-based 2001. Consistent land- and atmosphere-based U.S. carbon sink estimates. Science **292:**2316–20

Parker LW, Miller J, Steenberg Y, Whitford WG. 1983. Soil respiration in a Chihuahuan Desert rangeland. Soil Biol Biochem 15:303–9.

Raich JW, Nadelhoffer KJ. 1989. Belowground carbon allocation in forest ecosystems: global trends. Ecology 70:1346–54.

Raich JW, Potter CS. 1995. Global patterns of carbon dioxide emissions from soils. Global Biogeochem Cycles 9:23–36.

Raich JW, Schlesinger WH. 1992. The global carbon dioxide flux in soil respiration and its relationship to vegetation and climate. Tellus 44B:81–99.

Raich JW, Tufekcioglu A. 2000. Vegetation and soil respiration: correlations and controls. Biogeochemistry 48:71–90.

Reiners WA. 1968. Carbon dioxide evolution from the floor of three Minnesota forests. Ecology 49:471–83.

Rice JA. 1995. Mathematical statistics and data analysis. 2nd ed Belmont (CA): Wadsworth, pp 602.

Russell CA, Voroney RP. 1998. Carbon dioxide efflux from the floor of a boreal aspen forest. I. Relationship to environmental variables and estimates of C respired. Can J Soil Sci 78:301–10.

Saunders SC. 1998. Multiscale relationships between pattern and process in a managed forest landscape [dissertation]. Michigan Technological University, Houghton, MI, USA

Saunders SC, Chen J, Drummer TD, Crow TR. 1999. Modeling temperature gradients across edges over time in a managed landscape. For Ecol Manage 117:17–31.

Saunders SC, Chen J, Drummer TD, Crow TR, Brosofske KD, Gustafson EJ. 2002. The patch mosaic and ecological decomposition across spatial scales in a managed landscape of northern Wisconsin, USA. Basic Appl Ecol 3:49–64.

Savage KE, Davidson EA. 2001. Interannual variation of soil respiration in two New England forests. Global Biogeochem Cycles 15:337–50.

Schimel D, Melillo J, Tian H, McGuire AD, Kicklighter D, Kittel T, Rosenbloom N, Running S, Thornton P, Ojima D, and others. 2000. Contribution of increasing CO_2 and climate to carbon storage by ecosystems in the United States. Science **287:**2004–6

Schlenter RE, Van Cleve K. 1985. Relationships between CO_2 evolution from soil, substrate temperature, and substrate moisture in four mature forest types in interior Alaska. Can J For Res 15:97–106.

Schulze E-D, Wirth C, Heimann M. 2000. Managing forests after Kyoto. Science 289:2058–9.

Simmons JA, Fernandez IJ, Briggs RD, Delaney MT. 1996. Forest floor carbon pools and fluxes along a regional climate gradient in Maine, USA. For Ecol Manage 84:81–95.

Striegl RG, Wickland KP. 2001. Soil respiration and photosynthetic uptake of carbon dioxide by ground-cover plants in four ages of Jack pine forest. Can J For Res 31:1540–50.

Thierron V, Laudelout H. 1996. Contribution of root respiration to total CO_2 efflux from the soil of a deciduous forest. Can J For Res 26:1142–8.

Tian H, Melillo JM, Kicklighter DW, McGuire AD, Helfrich J. 1999. The sensitivity of terrestrial carbon storage to historical climate variability and atmospheric CO_2 in the United States. Tellus 51B:414–52.

Toland DE, Zak DR. 1994. Seasonal patterns of soil respiration in intact and clear-cut northern hardwood forests. Can J For Res 24:1711–6.

Valentini R, Matteucci G, Dolman AJ, Schulze E-D, Rebmann C, Moors EJ, Granier A, Gross P, Jensen NO, Pilegaard K, and others. 2000. Respiration as the main determinant of carbon balance in European forests. Nature **404:**861–5

Widén B, Majdi H. 2001. Soil CO_2 efflux and root respiration at three sites in a mixed pine and spruce forest: seasonal and diurnal variation. Can J For Res 31:786–96.

Wildung RE, Garland TR, Buschborn RL. 1975. The interdependent effects of soil temperature and water content on soil respiration rate and plant root decomposition in arid grassland soil. Soil Biol Biochem 7:373–8.

Xu M, Qi Y. 2001. Soil Global Change Biol 6:667–77.