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ORIGINAL PAPER

Changes in seasonal soil respiration with pasture conversion to forest in Atlantic Canada

L. Kellman · H. Beltrami · D. Risk

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Abstract This study compares approximately weekly soil respiration across two forest–pasture pairs with similar soil, topography and climate to document how conversion of pasture to forest alters net soil CO_2 respiration. Over the 2.5 year period of the study, we found that soil respiration was reduced by an average of 41% with conversion of pasture to forest on an annual basis. Both pastured sites showed similar annual soil respiration rates. Comparisons of the paired forests, one coniferous and the other broadleaf, only showed a significant difference over one annual cycle. Enhanced soil respiration in pastures may be the result of either enhanced root respiration and/or microbial respiration. Differences in pasture–forest soil respiration were primarily observed during the July through September summer period at all sites, suggesting that this is the critical period for observing and documenting differences. Evaluation of the soil microclimatic controls on soil respiration suggest that soil temperature exerts a major control on this process, and that examining these relationships on a seasonal rather than weekly basis provides the strongest relationships in poorly drained soils. Consistently greater pastured site Q_{10}s (2.52;2.42) than forested site Q_{10}s (2.27; 2.17) were observed, with paired-site differences of 0.25.

Keywords Carbon cycle · Soil respiration · Soil carbon dioxide · Afforestation

Introduction

Exchanges of carbon (C) between terrestrial soils and the atmosphere comprise an important component of the global carbon budget. Soils are the largest source of non-anthropogenic CO_2 and hold approximately twice the mass of carbon held in the atmosphere and three to five times the mass of carbon in aboveground vegetation (IPCC 2001). As a result, small changes in the magnitude of C-exchanges between soils and the atmosphere can have important consequences for global atmospheric CO_2 levels and thus global climate.

Short-term changes in soil-atmosphere C-exchange rates are largely related to external environmental perturbations arising from alterations in landuse patterns. Associated changes in vegetation alter soil microclimates by shifting temperature and moisture patterns, sources and magnitudes of organic matter inputs to soils, and soil physical properties that control gas exchange processes (Kirschbaum 2000; Raich

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L. Kellman (✉) · H. Beltrami · D. Risk
Environmental Sciences Research Centre, St. Francis Xavier University, Antigonish, Nova Scotia, Canada B2G 2W5
e-mail: lkellman@stfx.ca

and Tufekcioglu 2000; Raich and Schlesinger 1992). While both root and microbial respiration contribute to total soil respiration, studies estimate that on an annual basis, root and microbial respiration each comprise approximately 50% of total soil respiration (Hogberg et al. 2001; Hanson et al. 2000). Within this annual period, however, the proportions of contributions from these sources at different sites vary due to seasonal peaks in root respiration, complex biochemical controls on root respiration, seasonal availability of fresh organic matter, and long term differences in soil chemistry resulting from different vegetation (Atkin et al. 2005; Fahey et al. 2005; Lavigne et al. 2003; Kirschbaum 2000; Ollinger et al. 2002). To better evaluate the impact of landuse alterations on soil CO_2 respiration it is important to quantify changes in soil CO_2 emissions associated with shifts in vegetation cover and to identify the major controls on these processes. Ultimately, long-term soil-atmosphere CO_2 projections rely upon field studies and ecosystem-level variations in these exchange processes and need to be documented.

A number of studies have attempted to evaluate differences in vegetation-related controls on soil respiration (Raich and Tufekcioglu 2000; Smith and Johnson 2004; Kaye and Hart 1998). Raich and Tufekcioglu (2000) presented data from studies across a broad range of vegetation types and observed significant differences between paired forest–grassland sites and paired coniferous-broadleaf forest sites. They found that soil respiration from grasslands was consistently greater than forests (approximately 20% on average), while coniferous forest soil respiration was approximately 10% lower than paired broadleaf forests. They point to a need for more comparative studies between forest-grassland and forest-forest pairs to verify these findings and better understand controlling processes. In a comparison between a juniper woodland-grassland pair in Kansas (USA), Smith and Johnson (2004) documented 38% higher soil respiration from the grassland versus woodland soils. Temperature exerted a dominant control in this study with the grassland site Q_{10} 0.2 greater than the woodland site.

Surface flux methods are typically used to obtain information about soil-atmosphere CO_2 exchange rates. Although subsurface methods (Risk et al. 2002a) allow elucidation of the processes controlling these exchanges, they are very labor-intensive and surface flux methods are more widely utilized for quantifying exchange rates over long periods. Subsurface methods have suggested, however, that surface fluxes may reflect changes in subsurface CO_2 transport and storage rather than instantaneous CO_2 production, particularly in poorly drained soils (Risk et al. 2002a, b). In such instances, this could reduce the likelihood of observing clear relationships between driving processes such as soil temperature changes and surface flux emissions. It can be expected that in relatively well drained soils with high rates of gas diffusivity that relationships might be more clearly established than in soils where diffusivity is relatively poor (i.e., due to fine-textured poorly drained soils). In such cases it would be instructive to establish whether it is more appropriate to group data on a seasonal basis to establish and quantitatively describe these relationships.

In this study we investigate how reforestation of previously pastured soils in a temperate-boreal transition area of Atlantic Canada has altered the rates of CO_2 exchange over a two and a half year period. We use adjacent paired pasture–forest sites with similar soils, topography and climate, ensuring that measured differences are a result of differences in vegetation cover and associated effects of soil microclimate and properties. Soils at these sites are poorly drained and previous studies (Risk et al. 2002a, b) have suggested that short term effects of soil CO_2 storage and transport might obscure relationships between soil CO_2 efflux and controlling physical variables such as temperature. We therefore grouped approximately weekly data at these sites to produce 3-month seasonal averages of CO_2-exchanges and soil physical characteristics. These data allow us to: (a) quantify how reforestation of previously pastured soils alters soil respiration, (b) determine whether microclimatic controls on these processes are best evaluated using seasonally grouped data in poorly drained soils, and (c) identify critical seasonal periods for evaluating changes in soil respiration associated with changes in landuse patterns in Atlantic Canada.

Study site and methods

The study was conducted from August 2001 to December 2003 at two paired pasture–forest sites in Northeastern Nova Scotia, Canada. The paired sites are located less than 30 km distance apart; at each site the pasture–forest pair is separated by only several hundred meters, with each encompassing a minimum area of 1 ha. The dominant surrounding landuse at these sites is forest of varying ages. The sites are less than 10 m above sea level, have an average mean annual temperature of 5.5°C and a mean annual precipitation of approximately 1,290 mm. The region is described as humid to perhumid with potential evapotranspiration often exceeding precipitation from May through August (Cann and Hilchey 1954). The soils at the sites are classified as podzols (Table 1) and are characterized by light brown clay loam over reddish brown clay loam showing distinct gray and yellow medium mottles (Cann and Hilchey 1954).

The Crystal Cliffs site includes a pasture (Pasture-CC) and deciduous forest (Forest-CC) pair. The Pasture-CC vegetation cover is composed of mainly grasses and sedge species. The Forest-CC is approximately 60 years old and composed of 90% trembling aspen with some Oak and Red Spruce. The Pomquet site includes a pasture (Pasture-P) and coniferous forest (Forest-P) pair. The Pasture-P is composed of mainly grasses and sedge species. The Forest-P is approximately 50 years old and is composed of approximately 86% Red Spruce with some Trembling Aspen, Sugar Maple, Paper Birch and Balsam Fir.

Table 1 Selected characteristics of soils at the study sites [from Cann and Hilchey 1954]

Soil type	Depth (cm)	pH	% Gravel	% Sand	% Silt	% Clay
Queens	0–5	4.7	–	–	–	–
	5–20	4.6	21.0	20.0	38.8	41.2
	20–36	4.7	18.0	19.2	31.6	49.2
	36–51	6.3	8.5	15.2	29.2	55.6

Both paired sites are situated in a part of the Acadian Forest Region of Atlantic Canada that was deforested and converted to farmland over the past several centuries. Early European settlement, a need for resources, and agricultural activities resulted in the depletion of the Acadian forest of Nova Scotia. By the turn of the 1900s, agricultural land use area peaked. Current agricultural land area is now estimated to be only one third of the peak, with the largest decline observed since 1958 (Johnson 1986). Much of this agricultural area has undergone reconversion to forest. Standing forest inventory of the province is thought to be higher now than at any other time since 1800 when forest inventories were first initiated. The study sites are typical of this regional trend. Both the Crystal Cliffs and Pomquet sites were cleared for pasture in the early period of European settlement until the recent reforestation (Johnson 1986). As such they represent examples of forest–pasture–forest conversion typical of this and many other regions.

Fixed Campbell Scientific Towers are located at each of the four measurement sites, measuring an array of aboveground and belowground climatic data, including air temperature and soil temperature and moisture at several depths within the upper 1 m of the soil profile (Beltrami 2001; Beltrami and Kellman 2003; Risk et al. 2002a, b). Data are stored on Campbell Scientific dataloggers and downloaded regularly. Representative soil samples were collected from instrumented soil pits for characterization of the percent carbon content through the mineral soil profile. Sampling depth increments were similar between pasture–forest pairs, but differed between the two sets of paired sites. Soils were dried, milled and analyzed for percent carbon content on a Eurovector Elemental Analyzer.

Ten measurements of carbon dioxide surface flux were taken at approximately weekly intervals at each site using manually vented surface flux chambers (Risk et al. 2002b). Chambers had an internal volume of 0.00109 m^3 and a surface area of 0.00754 m^2. On each sampling occasion, chambers were placed randomly on the soil surface, within 10 m of the meteorological station. Samples were collected from paired pasture–forest sites within less than an hour of each other and generally at the same time of day on each sampling day, alternating between mid-morning and mid-afternoon at each set of paired sites. Gas samples were collected using 6 ml Labco Exetainers and analyzed within 24 h in the laboratory using a Licor LI-7000 IR Analyzer. Sample collection, transferal, handling and analytical errors were less than 10%. Cross-calibration with a Licor LI-8100 automated surface flux system was made and a correction applied for observed underestimations in surface flux measurements using the manual chambers.

Annual soil respiration rates are estimated from weekly surface flux data at each site. These estimates are made for the entire 2.5 year measurement period and for complete individual years (2002; 2003). Paired *t*-tests are used to determine whether site differences are significant at the $P = 0.05$ level. The strength of the soil respiration–temperature relationships are examined using the weekly data for annual and seasonal periods. To evaluate the advantage of using seasonally averaged versus weekly data surface flux and climatological data were grouped into 3-month periods (Summer: July–September; Fall: October–December; Winter: January–March; Spring: April–June) for analysis. To produce single 3-month seasonal flux values the surface flux data were used to obtain monthly averages that were then averaged in order to ensure that months with larger numbers of soil respiration measurements were not weighted more heavily than months with fewer. Seasonal soil respiration between pasture–forest pairs was compared in order to identify the seasonal periods that controlled soil respiration differences at paired sites.

Results

Soil carbon data from the mineral soil show similar percent carbon distributions between sites (Fig. 1), with close to 4% carbon at the top of the mineral soil, dropping to close to 0.1% below 60 cm depth. Soil respiration trends for each site over the two and a half year measurement period are illustrated in Fig. 2. Surface fluxes show a distinct pattern, particularly at the pasture sites, peaking during the growing season and remaining close to zero during the coldest periods. Surface fluxes are highly variable on individual measurement days at each site, as indicated by the large standard deviations.

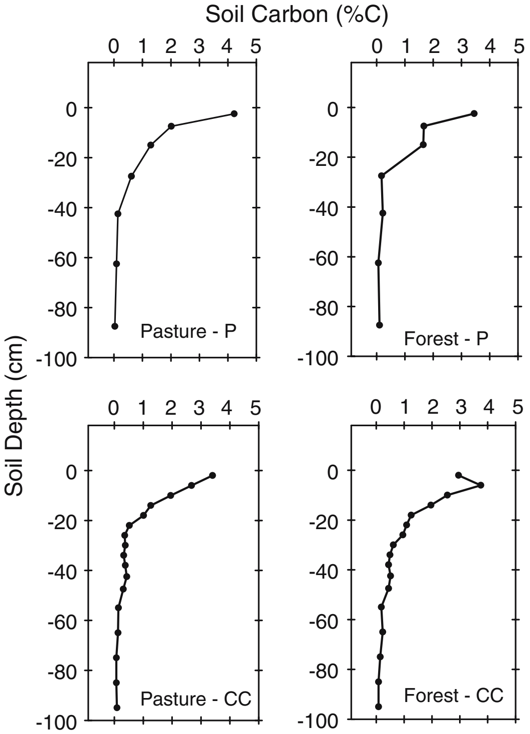

Fig. 1 Soil organic carbon measurements from bulked samples from a single pit in close proximity to the meteorological data at each of the (**a**) Pasture-CC, (**b**) Forest-CC, (**c**) Pasture-P and (**d**) Forest-P sites. Zero soil depth represents the organic soil–mineral soil interface. The coefficient of variation of repeat soil samples is less than 3.5%

Site soil respiration comparisons

The pastured sites showed annual total soil respiration (± 1SE) of 425 (± 45)and 455 (± 51) gC/m^2/year for Pasture-CC and Pasture-P, respectively (Table 2). Both sites showed a higher total soil respiration for the year 2002 than for 2003, but with ranking unchanged. The forested sites had much lower soil respiration: 281 (± 33) and 236 (± 25) gC/m^2 for Forest-CC and Forest-P respectively. Soil respiration at Forest-CC was greater in 2002 than 2003, with Forest-P showing the opposite trend. The pastured sites had statis-

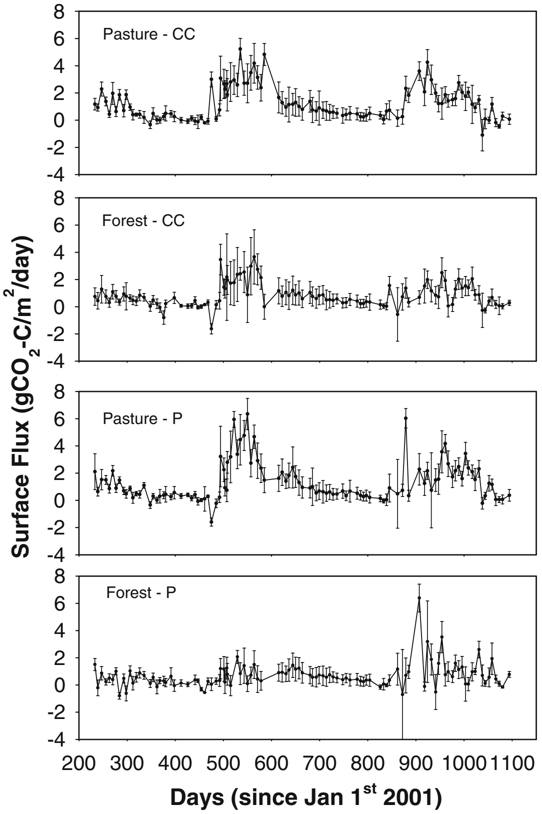

Fig. 2 Temporal series in soil respiration measurements for each site for the entire measurement period at the (**a**) Pasture-CC, (**b**) Forest-CC, (**c**) Pasture-P and (**d**) Forest-P sites. Each soil respiration point represents an average of 10 chamber measurements for a total of more than 4,000 surface flux measurements from all sites combined. Errors are one standard deviation

tically significant ($P < 0.05$) and consistently higher soil respiration than adjacent forested sites with Pasture-P 48% higher than Forest-P and Pasture-CC 34% higher than Forest-CC (Table 3). On average, pastured sites showed a 41% greater soil respiration than paired forest sites. The Pomquet sites showed greater differences between 2002 (approximately 59%) and 2003 (approximately 31%), while the Crystal Cliffs sites showed virtually no difference between these 2 years. Differences between the two pastured and the two forested sites were not significant ($P > 0.05$) for the 2.5 year measurement period and the individual 2002 and 2003 annual series with the exception of a significant difference observed between the Forest-CC and Forest-P in 2002 (Table 3).

Weekly temperature and soil respiration relationships

Relationships between averaged site surface flux and soil temperature at 5 cm depth for the entire data series at each site (Fig. 3) show weak relationships (R^2 of 0.17–0.48) with pastured sites showing the strongest relationships. Correlations between soil respiration and soil temperature during seasonal periods (Table 4) are also poor, with spring showing the strongest relationships (all are significant) and winter the weakest (none are significant). With the exception of Pasture-P, none of the summer relationships are significant.

Seasonally averaged temperature, moisture and soil respiration relationships

To investigate whether seasonally averaged soil respiration data provided better relationships with microclimatic controls, monthly mean data from each 3-month seasonal period was averaged to obtain a single seasonal soil respiration and soil microclimate value. Over the period of this study this yielded 10 soil respiration–microclimate values at each site that were used to determine soil respiration–soil microclimate relationships.

The seasonal soil respiration versus 5 cm soil temperature relationships for each of the 4 sites show strong exponential relationships, with R^2 values ranging from 0.58 for the Forest-P to 0.87 for the Pasture-P (Fig. 4). Estimates of Q_{10} yield

Table 2 Site soil respiration (R_s) estimates

Site	R_s 2001–2003 (± SE) (gC/m^2/year)	R_s 2002 (± SE) (gC/m^2/year)	R_s 2003 (± SE) (gC/m^2/year)
Pasture-CC	425 (±45)	517 (±80)	366 (±66)
Forest-CC	281 (±33)	342 (±64)	245 (±44)
Pasture-P	455 (±51)	533 (±95)	440 (±74)
Forest-P	236 (±25)	219 (±32)	305 (±50)

Table 3 Differences in annual site respiration

Sites Compared	2001–2003 (% difference)	2002 (% difference)	2003 (% difference)
Pasture-P versus Forest-P	48.1*	58.9*	30.7*
Pasture-CC versus Forest-CC	33.9*	33.8 *	33.0*
Forest-CC versus Forest-P	15.9	36.1*	–24.4
Pasture-P versus Pasture-CC	6.6	2.9	16.8

* Indicates significant relationships, $P < 0.05$

highs of 2.52 and 2.42 for the Pasture-CC and Pasture-P sites, respectively, with lows of 2.27 and 2.17 for the Forest-CC and Forest-P sites, respectively. However, all relationships between seasonally averaged soil respiration and soil moisture were weak (R^2 0.26–0.36; data not plotted).

The seasonal average daily soil respiration data for the entire measurement period for each forest-pasture pair (means ± 95 percent CI) only point to significant differences in the July to September summer period amongst paired pasture-forest sites (Fig. 5).

Discussion

Our study suggests that reforestation of pastured soils reduces soil respiration. This is consistent with other studies in finding soil respiration is greater in pastured/grassland soils than forest soils. Differences are comparable (this study 41% difference on average for paired pasture–forest sites) compared to findings of 38% by Smith and Johnson (2004) and 20% by Raich and Tufekcioglu (2000). Although the magnitude of the difference varied from year to year, the differences were large and demonstrated a consistent pattern. Pastured sites showed similar rates of annual soil respiration with some variability between annual measurement periods. There was no clear pattern related to the forest type (coniferous vs broadleaf) with significant differences only observed in the 2002 annual period where broadleaf soil respiration exceeded coniferous respiration by 36%.

Soil organic carbon contents of the mineral soils at these sites show similar profile concentration patterns at each site. Although percent C contents are similar amongst sites, there may be differences in the structure of the SOC pools (i.e., chemical composition and susceptibilty to decomposition) that might provide contrasting temperature responses in the microbial component of soil respiration between sites that are not evident in analysis of the bulk carbon data alone. Recent studies (e.g., Russell et al. 2004; Gleason and Ewel 2002; Six et al. 2000) suggest that changes in the labile or rapidly cycling pool are typically more easily detected than changes in the total carbon pool and may therefore provide a more reliable indicator of SOC change.

Although thus study does not investigate soil organic carbon (SOC) turnover rates, other studies suggest higher net soil respiration for grassland vs forest soils translates to a net reduction in SOC turnover over time (Smith and Johnson 2004) and hence a net storage of SOC associated with conversion from pasture to forest. These data do point to a reduction in total soil respiration of 182 gC/m^2 on an annual basis for this region approximately 50 years following pasture conversion to forest. Further study that considers differences in root respiration and SOC decomposition rates would be required to determine whether this translates into a net soil carbon store at these sites.

Most studies examining soil respiration–vegetation–microclimate relationships utilize instantaneous CO_2 surface flux—soil microclimate data to estimate controlling variables. Data collected for this study were collected from fine textured and poorly drained soils in which instantaneous soil respiration—soil microclimate relationships might be obscured by poor soil CO_2 transport. A previous study at these study sites (Risk et al. 2002a, b) suggested that correlations between surface flux and of the main microclimatic driver of soil respiration, soil temperature, were obscured by CO_2 storage and transport problems.

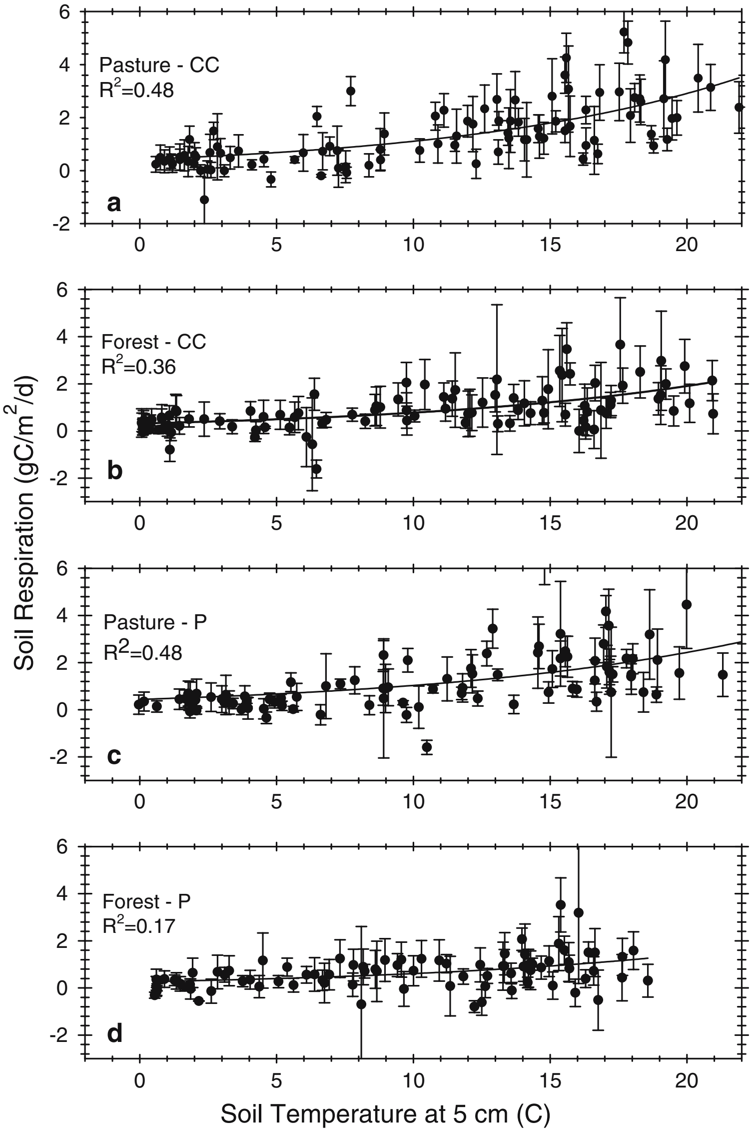

Fig. 3 Soil respiration versus soil temperature relationships at (**a**) Pasture-CC, (**b**) Forest-CC, (**c**) Pasture-P and (**d**) Forest-P for the 2.5 year 2001–2003 data series. Soil temperatures are measured at each site at 5 cm depth. Each soil respiration point represents an average of 10 chamber measurements. Error bars are one standard deviation. All relationships are significant ($P < 0.05$)

This dataset provided an ideal opportunity to explore the utility of using seasonally grouped data to quantify microclimatic controls on soil respiration.

Table 4 Seasonal relationships (R^2) between soil respiration and temperature

	Pasture-CC	Forest-CC	Pasture-P	Forest-P
Summer	0.11	0.08	0.20*	0.01
Fall	0.11*	0.21*	0.35*	0.01
Winter	0.00	0.00	0.00	0.02
Spring	0.62*	0.38*	0.41*	0.22*

* Indicates significant relationships, $P < 0.05$

Consistent with other surface flux studies of this nature, strong relationships between soil respiration and soil temperature were observed, while those with soil moisture were quite weak. Soil moisture is not limiting at these sites, which may explain the weak relationship between soil respiration and moisture. The soil respiration–temperature relationships were strongest at these sites when seasonally averaged values were used to describe these relationships rather than weekly data. Exponential functions best described the relationships at all sites, with marked differences in the temperature response of pastured versus

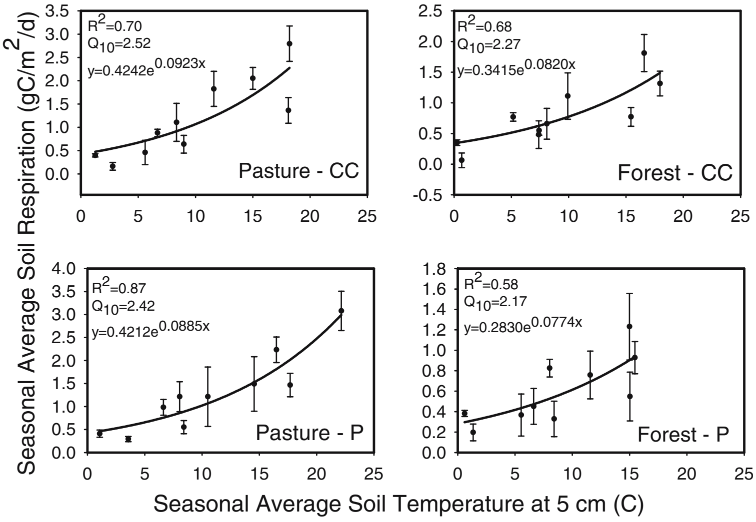

Fig. 4 Seasonally averaged soil respiration versus soil temperature exponential relationships for (**a**) Pasture-CC, (**b**) Forest-CC, (**c**) Pasture-P and (**d**) Forest-P for the 2.5 year 2001–2003 measurement period. Each data point represent a single seasonal soil respiration–soil temperature data point derived by averaging monthly means of approximately weekly surface fluxes measurements at each site. Summarized for each site are the R^2 values, Q_{10} values and the exponential soil respiration–soil temperature relationship. All relationships are significant ($P < 0.05$)

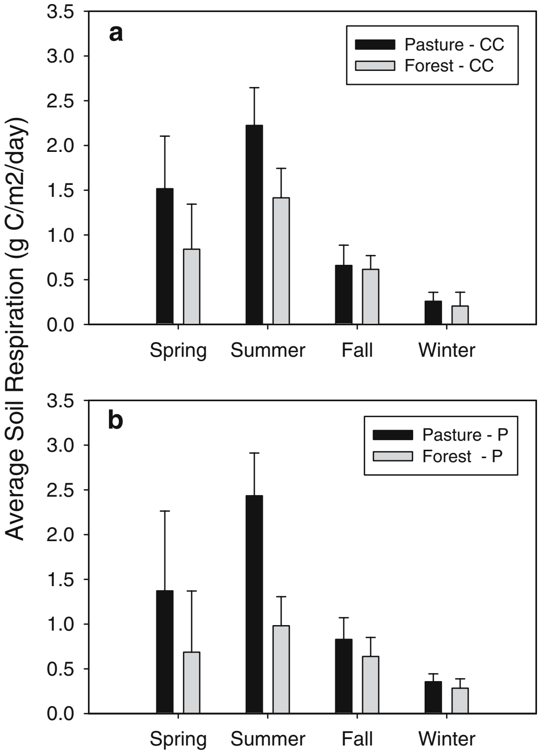

Fig. 5 Seasonally averaged soil respiration for the paired pasture–forest sites of (**a**) Crystal Cliffs and (**b**) Pomquet for the 2001–2003 measurement period. Error bars represent the 95% confidence intervals

forested soils. In fact, both paired sites had Q_{10} values in the pastures which were 0.25 greater than those in the paired forests. This suggests a consistent difference in the temperature sensitivity of soil respiration from each site. The extent to which this is driven by the temperature response of microbes or roots (Boone et al. 1998) cannot be resolved in this study. The Q_{10} values observed within a particular time period may be affected by variables such as seasonal peaks in root respiration, seasonal availability of fresh organic matter and long term differences in soil chemistry resulting from different vegetation. However, they are unlikely to confound overall temperature–respiration relationships because these individual factors do not mimic temperature patterns.

This study demonstrates that virtually all differences in soil respiration in paired pasture–forest sites are found during the growing season, in the summer period extending from July through September in Atlantic Canada. Differences are not significant during the remainder of the year. A more complete investigation of whether root and microbial contributions remain similar between these sites during these periods would provide more information about rates of turnover of SOC.

Conclusions

Ecosystem-level changes in carbon cycling can be expected to arise with conversion of pasture to forest. Consistent with other studies, we demonstrate that net soil respiration rates are reduced on an annual basis as a consequence of this conversion. Seasonal soil respiration differences were only significantly different during the summer period at these sites.

Temperature exerted a dominant control on soil respiration in this study. Grouping surface flux and soil temperature data on a seasonal basis in the poorly drained soils that characterized these sites demonstrated much stronger soil respiration–temperature relationships than using the weekly data. This is an approach that should be considered in other studies when quantifying temperature-soil respiration measurements in poorly drained soils.

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