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Spatial and temporal controls of soil respiration rate in a high-elevation, subalpine forest

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Abstract

We examined soil respiration to determine what measurable environmental variables can be used to predict variation in soil respiration rates, spatially and temporally, at a high-elevation, mixed conifer, subalpine forest site at the Niwot Ridge Ameriflux Site in Colorado. For three summers, soil respiration rates were measured using soil collars and a portable gas-exchange system. Transects of the collars were established to ensure spatial characterization of the litter-repleted areas beneath tree crowns and the litter-depleted open spaces between tree crowns. Soil temperature and soil moisture were both identified as important drivers of soil respiration rate, but were found to confound each other and to function as primary controls at different scales. Soil temperature represents a primary control seasonally, and soil moisture represents a primary control interannually. Spatially, organic layer thickness, ammonium concentration, water content, and the microbial and soil soluble carbon pools were found to predict variation from point to point. Soil microbial biomass strongly correlated to soil respiration rate, whereas root biomass was identified as a weak predictor of respiration rate and only when controlling for other variables. Spatial variation in soil respiration rate is highly determined by the depth of the soil organic horizon, which in this ecosystem varies predictably according to distance from trees. The conclusions that can be drawn from the study provide the foundation for the development of future models of soil respiration driven by fundamental variables of the climate and soil microenvironment.

Keywords: Carbon cycling; Microbial biomass; Root biomass; Temperature; Moisture; Organic matter; Model; Ameriflux; Colorado

1. Introduction

Globally, soil respiration is estimated to account for 20–38% of the total annual biogenic CO_2 emissions to the atmosphere (Raich and Schlesinger, 1992; Raich and Potter, 1995). Soil respiration has also been shown to be the primary control over latitudinal variation in net ecosystem CO_2 exchange (NEE) among European forest ecosystems (Valentini et al., 2000). In the face of future global warming, it is increases in soil respiration that are likely to mediate progressively lower rates of carbon sequestration (Raich and Schlesinger, 1992; Trumbore et al., 1996; Woodwell et al., 1998; Davidson et al., 2000). Despite its obvious importance to carbon cycle processes, soil respiration has proven to be extremely difficult to quantify in an accurate manner. Like many other soil processes, respiration exhibits high levels of spatial heterogeneity, especially across small spatial scales, and can be highly variable on diurnal, seasonal and interannual time scales (e.g. Zogg et al., 1996; Law et al., 1999; Stoyan et al., 2000; Buchmann, 2000; Casals et al., 2000; Savage and Davidson, 2001; Xu and Qi, 2001).

Estimates of soil respiration at the ecosystem scale are conventionally made in two ways. Point measurements are often 'scaled up' through a process of simple multiplication, whereby measurements per unit area are multiplied by representative areas of the entire ecosystem (e.g. Crill, 1991; Norman et al., 1992; Ryan et al., 1997; Lavigne et al., 1997). Alternatively, landscape-integrated measurements can be obtained directly using nighttime eddy covariance observations on a tower (e.g. Goulden et al., 1996; Grace et al., 1995). When compared, these methods often fail to agree (Goulden et al., 1996; Lavigne et al., 1997). It is well established that nighttime eddy covariance measurements can significantly underestimate the true ecosystem respiration rate (Goulden et al., 1996; Baldocchi et al., 2000; Lee, 1998), and scaling from point measurements can propagate

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multiple errors, especially when the soil is treated as spatially homogeneous (Lavigne et al., 1997).

The current study was undertaken as part of a project to quantify NEE in a high elevation coniferous forest in Colorado, USA. Previously, we reported that seasonal dynamics in ecosystem respiration are a primary determinant of annual NEE in this forest, with most of the respiratory influence occurring from soil processes (Monson et al., 2002). From these studies, ecosystem respiration has been estimated to be between 169 and 444 g m^{-2} (Monson et al., 2002). In the current study, we have focused on understanding the determinants of spatial and seasonal variance in soil respiration rate, with the goal of identifying useful respiration rate proxies for eventual scaling-up models and to provide insight into mechanisms controlling this variation. We measured soil respiration and associated covariates over three consecutive growing seasons and across several small-scale spatial transects. Overall, the studies provide the foundation for a statistical model capable of explaining much of the spatial and temporal variation in growing season soil respiration rate in this ecosystem.

2. Materials and methods

2.1. Field site

The Niwot Ridge Ameriflux site is located approximately 50 miles west of Boulder, CO (40°1′58″N: 105°32′47″W) at 3050 m elevation above sea level. The surrounding forest is dominated by mixed subalpine conifers, with the principal species being *Abies lasiocarpa* (subalpine fir), *Picea engelmannii* (Engelmann spruce) and *Pinus contorta* (lodgepole pine). The canopy is relatively open with an average gap fraction of 17%. The average canopy height is 11.4 m and the average mid-summer leaf-area index is 4.2 m^2 m^{-2} (Monson et al., 2002; Turnipseed et al., 2002). The site has a sparse, heterogeneous ground cover, mostly *Vaccinium* sp., lichens and occasionally moss. The site is on a granitic moraine and the soils are sandy with a distinct, thin (< 10 cm) organic horizon in most locations. The two major water inputs are from melting snow in the late-spring and convective rain storms in the summer.

2.2. Respiration measurements

Soil respiration rates were measured over the summers of 1999, 2000, 2001 using a vented, closed, soil chamber system (Li-6400-09, Li-Cor, Inc., Lincoln, Nebraska). Tree-to-tree transects of polyvinylchloride collars (80 cm^2) were inserted 1–2 cm into the soil immediately after snowmelt, and left in place throughout the summer. Fluxes of CO_2 were measured approximately every two weeks by sealing the chamber over the collars with a foam gasket, thus minimizing disturbance to the soil. A chamber 'drawdown'

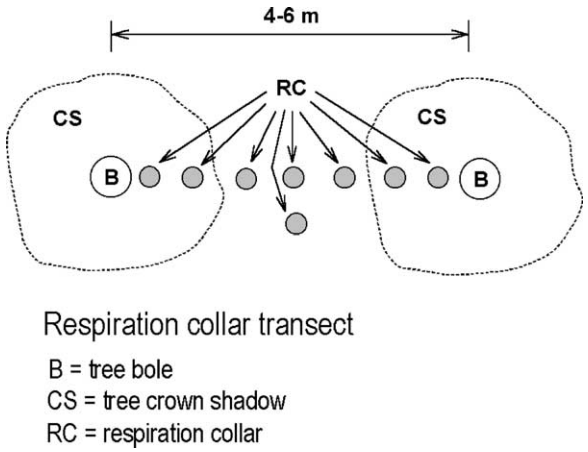

Fig. 1. Representation of the transects of soil collars used in the studies. The collars were placed across the space between two neighboring tree boles, traversing the crown space of the trees. The transects provided a good opportunity to observe respiratory dynamics within the context of broad spatial variation in soil litter content.

of 10 ppm CO_2 below ambient was used as the starting point for all respiration measurements. The chamber system is used to monitor the rate of increase in CO_2 concentration in the sealed collar and to automatically calculate the associated soil respiration rate. The collars were arranged into T-shaped transects between the boles of two trees, with a branch into the open gap between the trees (Fig. 1). During 1999, three such transects were established, and during 2000 and 2001, five transects were established, all within the area 100 m^2 west of the primary Ameriflux tower. Each transect was located within a 10 m^2 plot in which we additionally placed a series of ten collars at random locations. The latter collars were used for respiration measurements for a three week period, followed by destructive harvesting as described in Section 2.3. Along with each flux measurement, we took simultaneous soil moisture and temperature measurements. Soil moisture within the top 8 cm was measured with a cable tester (1502C Metallic TDR Cable Tester, Tektronix, Inc., Beaverton, OR) and dedicated time–domain reflectometry (TDR) steel probes (8 cm long) inserted vertically from the soil surface. Temperature was measured at a 5 cm depth with a copper-constantan thermocouple mounted in an aluminum probe.

2.3. Soil cores

The collars on the temporary, random arrays were excavated after three weekly measurements of soil respiration rate, as described above. Each collar had two 5.7 mm diameter cores removed from its center to a depth of approximately 18 cm, or until obstructed by rocks. Cores were split into organic and mineral layers based on visual soil inspection. The depth from the surface to the top of the mineral horizon was recorded, as well as distance to the nearest tree. One core was sealed in a plastic bag and stored in a freezer (− 25 °C) until used for root biomass estimates.

The other core was kept in a refrigerator and processed within 8 h for microbial biomass and soil chemical analyses.

2.4. Microbial and root biomass

Soils were sieved and homogenized with a 4.75 mm sieve. Approximately 5 g of each core was then extracted with a 0.5 M K_2SO_4 solution. Another 5 g was injected with 2 cm^3 of chloroform in a 50 cm^3 capped container, allowed to fumigate for 48 h, and subsequently extracted with 0.5 M K_2SO_4 solution. A colorimetric assay of reactive total C was used to determine C concentration in glucose equivalents. The difference between the fumigated C content and the non-fumigated C content was determined to be microbial C content, and is subsequently referred to as microbial biomass. The non-fumigated C content was taken as a measure of soluble C in the soil.

Samples were gently rinsed through a series of three successively smaller sieves (8.0, 4.75, and 2.0 mm) over a root tub to free roots from clumps of dirt and organic material. Roots were removed from the sieves and placed in a tray for hand sorting. All roots smaller than 5 mm in length were collected and sorted by diameter (<1, 1–2, and >2 mm), and assigned to dead or alive categories. Dead roots were distinguished from live roots on the basis of color, tensile strength and texture. All through-washed root fragments (<5 mm length) were collected on a 425 μm sieve and a subsample ($\sim 10\%$) was removed. The roots and root fragments were dried at 70 °C for three days and then weighed.

2.5. Other measurements

The unfrozen core was also used to determine gravimetric water content and organic matter content after subtracting the ash component following combustion in a 500 °C oven. The non-fumigated 0.5 K_2SO_4 soil extract was used for a colorimetric assay of ammonium concentration.

2.6. Statistical procedures

In order to evaluate seasonal trends at the site, the same collars were measured over the season. Because repeated-measures on the same collars are not independent trials, a repeated-measures analysis is necessary, and beneficial, as the spatial and temporal variations are explicitly defined and therefore, not confounded. A standard repeated-measure ANOVA could not be used without bias or data elimination because, on a given sampling date, not every collar could always be measured due to constraints of time and interruptions by inclement weather. A repeated-measures ANOVA also makes the assumption that the time intervals between each series of measurements are equivalent, which was not always the case in our study. Instead, we treated Julian date as a continuous variable in a hierarchical mixed-model design that included econometric measures of time-series autocorrelation. Our data suggested that each year experienced an inverse parabolic trend with a summer maximum, so we also looked at the quadratic effects of date over the season. The model was set up with respiration rate at a collar as the dependent variable with Julian date and Julian date-squared as fixed effects, soil temperature and soil moisture for the collar as covariates, the collar number as a random effect, and the nested position within plot as another random effect. Two autocorrelation terms, a moving average (ARMA) term and a lag-one autoregressive (ar(1)) term, were generated, then included in the model. If either failed to improve the log-likelihood of the model, it was deemed insignificant (Pinheiro and Bates, 2000).

We investigated spatial variation at the site using the summer 2000 respiration measures that accompanied the soil cores. Initial data exploration was done by correlation matrices, one-way regressions, and residual analysis. Inspection of model residuals, normal probability plots (Q–Q plots) and a Cook's distance analysis revealed that one of the individual collars had undue influence on the model and was creating model instability. The collar had an extremely high respiration rate and, though no data recording error could be identified, we designated it an outlier and dropped it from subsequent analysis. Nine parameters were identified as suitable for inclusion in a multiple regression model predicting soil respiration rate: soil temperature, distance to nearest tree, organic layer thickness, ammonium concentration, gravimetric water content, organic (ash) content, soluble carbon concentration, microbial biomass, and total root biomass. We used a stepwise regression to determine which of these parameters could be significantly included in a multiple regression. Several parameters were correlated, so the resulting model was investigated for multi-collinearity, and found to be robust to random data removal. We also used factor analysis with varying numbers of factors, and principal component analysis (PCA) to explore whether data reduction would improve the model. The resulting component matrices were used to generate factor/component scores for each collar, and regressed against respiration rates or put into multiple regressions. Soil organic matter content, soluble carbon concentration, and microbial biomass were consistently observed to cluster together into a single factor/component. This is predictable behavior as soluble carbon and microbial biomass are both subsets of organic matter content.

3. Results

3.1. Controls by temperature and moisture over soil respiration

The three summers of observation (1999, 2000 and 2001) presented varying climatic combinations (Fig. 2). The summer of 1999 was cooler and wetter than the other two

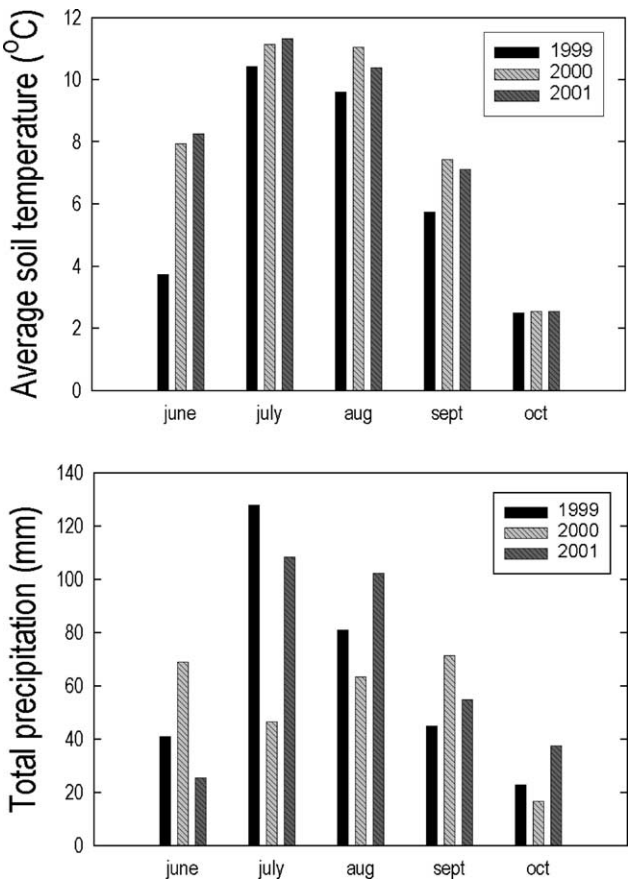

Fig. 2. Patterns in mean air temperature and precipitation during the three growing seasons used for observations in the study.

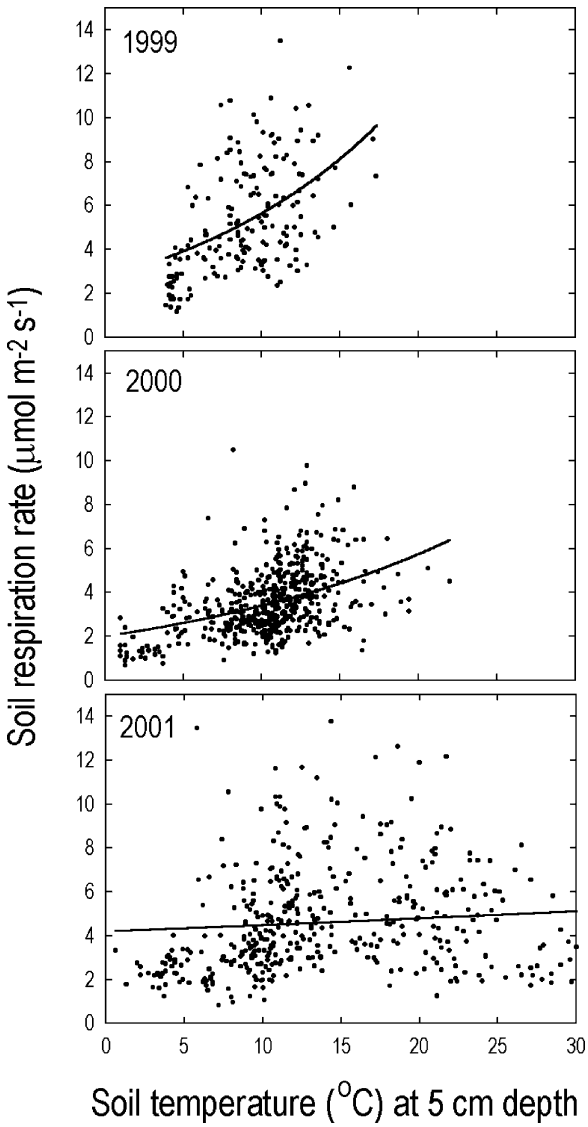

Fig. 3. The relationship between soil respiration rate and soil temperature using all data measured during each of three growing seasons. The best exponential (1999 and 2000) or linear (2001) fits are presented by the solid lines.

summers. In particular, wet weather in mid-June and late-July 1999, caused the co-occurrence of warm, wet soil conditions. The summer of 2000 exhibited considerably warmer soil temperatures than in 1999, but concomitantly with extremely dry soils. Although rains were normal in June 2000, July exhibited an extreme drought. The summer of 2001 was drier and hotter than normal in early-July (due to a lack of significant June rain), but exhibited nearly normal temperatures and rainfall by late-July.

When data from all soil respiration measurements within a single growing season were pooled and regressed against temperature, significant linear relationships were identified, although they had poor predictive value (1999 $r^2 = 0.271$, $p < 0.001$, $b = 0.442$; 2000 $r^2 = 0.196$, $p < 0.001$, $b = 0.199$; 2001 $r^2 = 0.031$, $p < 0.031$, $b = 0.042$). Exponential curve fitting, though theoretically justified, resulted in a worse fit (Fig. 3; 1999 $r^2 = 0.247$, $b = 0.0729$; 2000 $r^2 = 0.181$, $b = 0.0526$; 2001 $r^2 = 0.0117$, $b = 0.0658$). When data for all plots measured within a single day, or clustered group of days, was averaged, and regressed against temperature, a clearer relationship emerged (Fig. 4). While it is recognized that the regressions relating mean soil respiration rate to mean temperature violate one assumption of regression analysis, i.e. the independent variable be error-free, this violation should not affect the fundamental conclusion that the variables are correlated and tend to scale together with predictable relationships.

Compared to temperature, soil moisture was a poor predictor of soil respiration rate. When data for all three years were pooled and regressed against respiration, the relationship exhibited a high degree of scatter (Fig. 5). An upper surface below which 90 or 95% of the data fell was imposed on the combined data set to provide a reference at any given soil moisture level. When data for each year were separately analyzed in relation to this surface, some trends were evident. For example, the highest respiration rates did not occur at the wettest sites, or during the wettest periods, but rather in slightly drier soils, and the highest rates disappeared as the soil reached its driest extremes. Additionally, it is clear that in 2000, which had the driest summer of the three year study period, respiration rates were

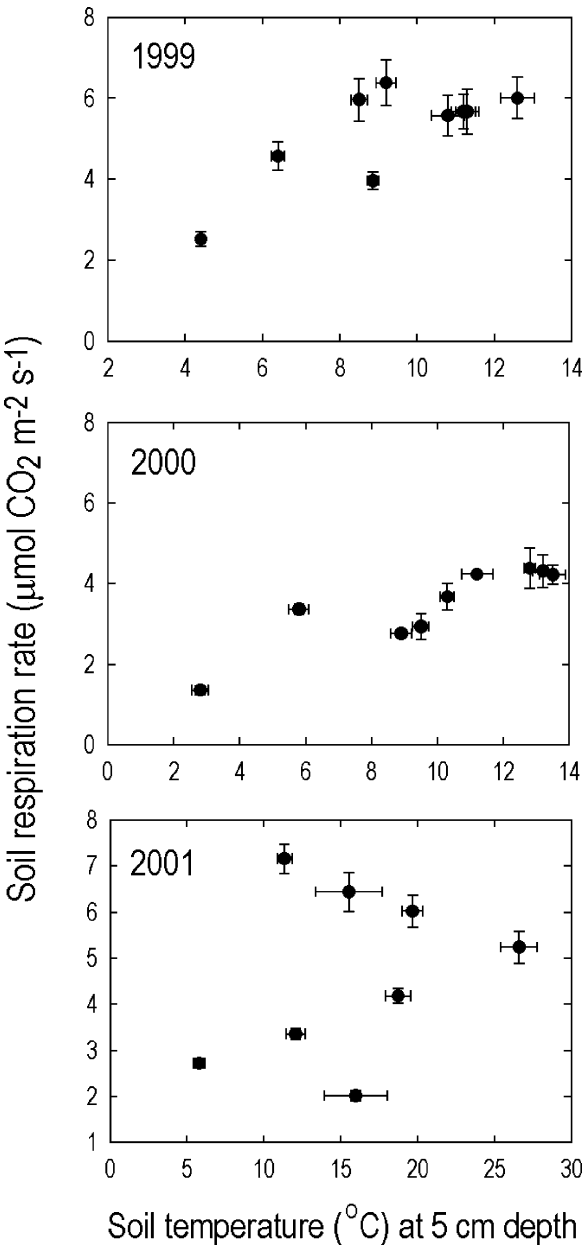

Fig. 4. The relationship between the mean soil respiration rate (mean of different soil collars measured on the same date) and mean soil temperature. Note the difference in the temperature range in 2001, compared to 1999 and 2000. Bars represent standard errors.

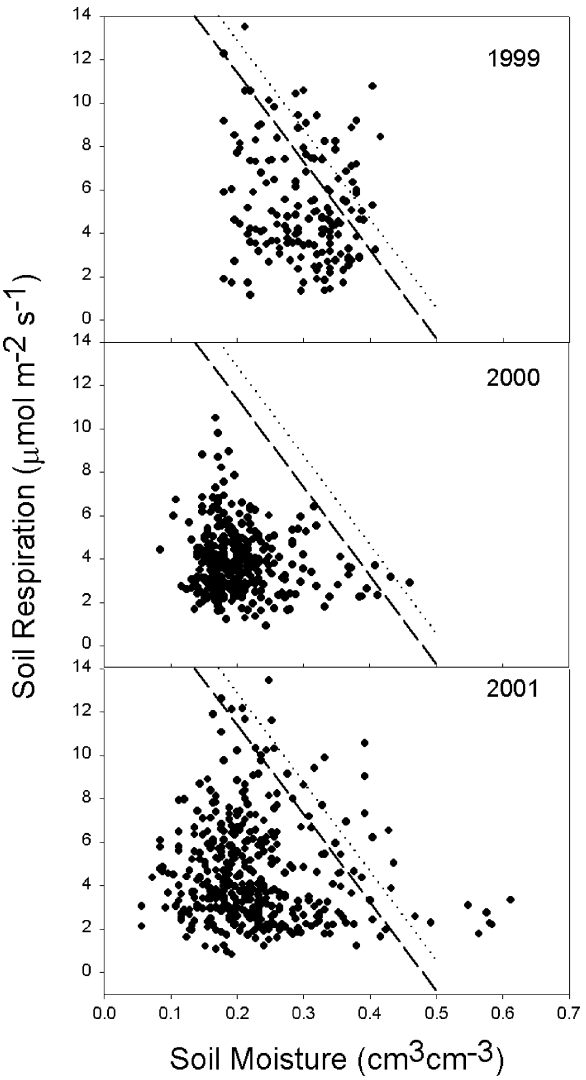

Fig. 5. The relationship between soil respiration rate and soil moisture content. The dotted and solid lines represent the boundaries, below which 95 and 90% of the total data points (pooled for all three years) fall, respectively. The same lines are presented in all three panels for comparison.

depressed further below the reference surface at any given soil moisture level, compared to the other years. Because the mid-summer temperature of 2000 was similar to that for 2001, but mid-summer precipitation was considerably less, the lower respiration rates in 2000 presumably reflect the cumulative, long-term effects of a dry year.

The effects of soil temperature were confounded by soil moisture: the wettest sites, and wettest times of the summer, also tended to be the coolest sites and times of the summer. Evidence of this confounding effect is seen in the fact that in both 2000 and 2001, which had drier summers than 1999, we observed a maximum concentration of respiration rates near soil moisture levels of 0.25 $cm^3\ cm^{-3}$, considerably below the maximum concentration in 1999; but in 2001, we also observed higher respiration rates at soil moisture levels above 0.3 $cm^3\ cm^{-3}$, compared to 2000. We interpret these results to reflect the fact that although snow melt began at approximately the same time in both 2000 and 2001 (in late-April), it was slower in 2001, providing higher levels of soil moisture later into the spring and early-summer. Thus, the lower soil respiration rates at high soil moisture in 2000, compared to 2001, was due to lower springtime soil temperatures at the highest soil moisture values.

In a converse way, soil moisture affected the respiration × temperature response; e.g. low soil moisture prevented the stimulation of respiration by high temperature. This was particularly evident in the temperature–respiration relation in 2001 (Fig. 3). This relationship is

particularly poor, and a visual inspection of the scatter plot reveals a large number of high respiration rates at medium temperatures and lower respiration rates at higher temperatures. At the very high temperatures of 2001, respiration was relatively depressed. These high temperature extremes were observed during late-June and early-July 2001, when several consecutive hot days occurred. Typically, this is the period when this ecosystem will receive the hottest weather, and in 2001 it occurred as predicted by long-term patterns, with seven consecutive days exhibiting maximum air temperatures (at 21.5 m above the ground surface) above 20 °C (the average temperature for this period was 18.9 ± 0.5 °C for 2001 and 16.9 ± 0.8 °C for 2000). In 2000, for comparison, the mid-summer warm weather did not occur as predicted by long-term patterns, with only one day above 20 °C. In 2001, this period of predicted warm weather was preceded by lower-than-normal rainfall in June (Fig. 2), meaning that not only was the mid-summer weather warm, it was also dry. In 2001, it appeared as though the soil respiration rate did not respond to the exceptionally high temperatures during the mid-summer stretch of warm weather, probably due to concomitant soil drying. (Note that because the summer of 2000 did not exhibit the predicted high temperature extremes in mid-summer, as were exhibited in 2001, we did not observe a suppressed region of the respiration × temperature interaction in the high-temperature range in Fig. 3).

One of the primary aims of the current study was to construct a reliable, predictive model of soil respiration rate as a function of time during the growing season. It was assumed a priori that the primary covariates that determine the modeled response to time would be temperature and soil moisture. Within the general set of data for the entire three year period, there were spatial and temporal sources of variation that made it difficult to identify clear relationships between soil respiration rate and the covariates of interest. Given our focus on predicting seasonal variation, we did not deal explicitly with space-dependent variation in the data. Instead, spatial variation was treated as a random effect in a hierarchal mixed model, with individual collars nested within plots. We examined both the linear and quadratic effects of Julian date on respiration rate, treating Julian date as a continuous variable, and looking at autocorrelation terms (Table 1). The autocorrelation procedures create parameters that describe the correlation structure in the error residual term. An ANOVA can then be used to determine whether the added parameters significantly improve the predictive accuracy of the model. For data collected in the summer of 2000, autocorrelation terms did not improve model accuracy, and were therefore left out ($L = 0.76$, $p = 0.78$). For the other two years, the inclusion of autocorrelation terms did reduce error in the models (1999 $L = 22.47$, $p < 0.0001$; 2001 $L = 6.67$, $p = 0.0098$). During the growing seasons of 1999 and 2000, the model predicted significant relationships between respiration rate and Julian date (either linear or quadratic) and the basis for this relationship appeared to be variance in soil temperature. During the growing season of 2001, a significant relationship was once again predicted for Julian date, but this time the basis for the relationship appeared to be soil moisture, rather than soil temperature.

3.2. Controls over spatial variation in soil respiration rate

To better understand the causes of variance in soil respiration rate among collars, we conducted a combination of single parameter regressions and multiple regressions, using principle component analyses and factor analyses as

Table 1
Summary statistics of a repeated-measures, mixed hierarchical model describing the relationship of soil respiration to covariates soil temperature and soil moisture. The model treats collars nested within plots and treats time (Julian date) as a continuous variable

	Coefficient	Standard error	df	*F*	*p*
1999					
Intercept	−20.93	5.0534	1	17.1584	<0.0001
Julian date	0.2275	0.0504	1	20.3771	<0.0001
Julian date, quadratic effect	−0.0005	0.0001	1	19.2670	<0.0001
Soil temperature	0.0911	0.0294	1	5.8345	0.0164
Soil moisture	2.1022	1.8146	1	1.3422	0.2478
2000					
Intercept	−46.7395	9.0822	1	168.2377	<0.0001
Julian date	0.4547	0.0843	1	68.5382	<0.0001
Julian date, quadratic effect	−0.0010	0.0002	1	50.3980	<0.0001
Soil temperature	0.2978	0.0956	1	9.2266	0.0029
Soil moisture	−3.5581	3.9449	1	0.8135	0.3688
2001					
Intercept	−17.7193	4.4314	1	15.9884	0.0001
Julian date	4.1847	0.0458	1	16.2943	0.0001
Julian date, quadratic effect	−0.0004	0.0002	1	9.1518	0.0027
Soil temperature	0.0055	0.0085	1	0.4145	0.5202
Soil moisture	2.3004	0.8457	1	7.3995	0.0069

Table 2
Summary of measured parameters relevant to soil respiration at the Niwot Ridge Ameriflux site

Parameter	Mean	Std Deviation	*n*
Number of live trees within 100 cm[a]	2	1.8	50
Number of dead trees within 30 cm	0.3	0.6	50
Organic layer thickness (cm)	6	2.7	50
Mineral layer depth to first impediment (cm)	2.8	3.6	50
Litter thickness (cm)	1.6	0.7	39
Organic layer (%C)	58.8	21.5	46
Mineral layer (%C)	10.7	5.3	16
Organic layer total roots (g cm^{-3})	0.0145	0.0095	49
Organic layer live roots (g cm^{-3})	0.013	0.0089	49
Organic layer dead roots (g cm^{-3})	0.0015	0.0013	50
Mineral layer total roots (g cm^{-3})	0.0024	0.0141	27
Mineral layer live roots (g cm^{-3})	0.0217	0.0125	28
Mineral layer dead roots (g cm^{-3})	0.0021	0.0021	27
Organic layer bulk density (g cm^{-3})	0.46		
Mineral layer bulk density (g cm^{-3})	1.023		

[a] Trees >1 cm diameter at breast height (dbh).

exploratory data reduction. The independent variables for these analyses were measures of the soil environment determined coincidently with each respiration measurement (Table 2). One potential criticism of this approach is that we confounded time and plot by sampling a different plot, among the five plots, during each sampling interval. This was required because of the destructive nature of the sampling. We assessed the potential for systematic errors due to this approach by comparing the variance in respiration rate among collars within a plot to the variance in mean respiration rate among plots (obtained from the permanent collar transects in each plot). Our mixed model from 2000 determined that variation within plots was greater than variation between plots (data not shown).

Simple one-way regressions revealed the surprising result that root biomass could not predict soil surface respiration rates (Table 3). This result held for all measured diameter classes of biomass (<2, 2–5, >5 mm), as well as dead root biomass. Other components of the soil carbon pools were successful predictors of respiration rate, with organic layer thickness and microbial biomass being the best. Several mineral layer components could also successfully predict soil respiration.

A stepwise regression was used to construct the most parsimonious model of soil respiration rate (Table 4). Nine parameters were selected to be included based on criteria of data completeness and scientific interest, although we ended up with six significant parameters. Nearly all the chosen parameters concerned the organic (uppermost) horizon of the soil including soil temperature at 5 cm, distance to the nearest tree, thickness of the organic layer, organic layer ammonium concentration, organic layer gravimetric water content, total organic matter content (ash content), soluble carbon concentration, microbial biomass, and root biomass. The parameters that were eventually excluded were temperature, distance to nearest tree, and organic matter content. Interestingly, root biomass provided a significant reduction in error when included in the multiple regression model. Clearly, it is only a useful predictor when other parameters are controlled.

Several modes of data reduction were attempted. PCA and factor analysis can both be viewed as ways to reduce a large number of parameters to a few if the parameters reflect the same underlying process. Using factors derived from these analyses, instead of isolated parameters, can remove multi-collinearity (model instability due to parameters with low tolerances or high levels of correlation). Since many of the variables in this analysis were correlated, this line of investigation was warranted. Using PCA, we found six independent components that explained 74% of the total variance in the data (Table 5). Component 1 is a combination of soil carbon terms, including microbial biomass C, percentage of soil organic C, and soil concentration of soluble C. Component 2 is related to the collar's distance to the nearest tree and tree density within a 1 m radius of the collar. This component explains a significant amount of the variance in respiration rate, with a negative correlation. This should be interpreted to mean that the closer a collar is to a tree, the higher the respiration rate. Component 3 is a combination of organic layer thickness and moisture content, which are well correlated (data not shown). Component 3 does not explain a significant

Table 3
Correlation table for one-way regressions divided between mineral and organic horizons. Numbers are Pearson correlation coefficients

		Respiration	Mineral horizon				Organic horizon		
			%Organic	Soluble C	Root biomass	Microbial biomass	Root biomass	Microbial biomass	Thickness
Organic horizon	Thickness	0.318***	0.320	−0.018	0.391**	−0.083	0.105	−0.042	
	Microbial biomass	0.345***	0.007	0.360	0.245	0.398*	−0.163		
	Root biomass	0.111	0.176	0.041	−0.090	−0.256			
Mineral horizon	Microbial biomass	0.109	−0.039	0.518**	0.138				
	Root biomass	0.017	0.214	0.253					
	Soluble C	0.195*	0.356*						
	%Organic	0.211*							

*$p < 0.1$, **$p < 0.05$, ***$p < 0.001$.

Table 4
Parameter descriptions of multiple regression model of collar-to-collar variation in soil respiration rate: $r^2 = 0.4963$; $F = 5.747$; df = 6 and 35; $p = 0.0003$

Parameter	Coefficient	Error	F	p
Organic layer thickness	0.1153	0.0459	6.2971	0.0169
Ammonium concentration	0.0273	0.0131	4.3218	0.0450
Gravimetric water content	0.0211	0.0078	7.3149	0.0105
Soluble C content	−0.0020	0.0009	5.3532	0.0267
Microbial biomass	0.0013	0.0004	11.7019	0.0016
Root biomass	26.9910	12.1049	4.9720	0.0323
Residual intercept	0.7251	0.5000	2.9960	0.1562

amount of the variance in respiration rate, whereas organic layer thickness alone does. Component 4 consists of soil temperature, which within the PCA is a significant predictor of soil respiration rate, though it is not when regressed on its own against soil respiration rate. Component 5 is a combination of total live root biomass and dead tree/log density within a 30 cm radius of the collar. Component 6 is a combination of soil ammonium concentration and dead root biomass. Neither component 5 nor 6 significantly predicted soil respiration rate, and neither explained much of the total variance in the data set. Factor scores for each collar generated for component 1 did not improve the predictability of the multiple regression model above the stepwise regression model. Forcing the inclusion of the total organic C content, a non-significant parameter seemed instead to slightly weaken the model. We were able, through random data deletion, to decide that multi-collinearity was not a significant problem with our final model.

4. Discussion

Soil respiration rate in this subalpine forest ecosystem displayed a high level of spatial and temporal variability.

Table 5
Variance in total seasonal and spatial measurements of soil respiration rate explained by various components of the PCA

Component	Total variance	% of variance	Cumulative%
1	2.395	18.42	18.42
2	1.884	14.49	32.91
3	1.358	10.45	43.36
4	1.342	10.32	53.68
5	1.322	10.17	63.85
6	1.308	10.07	73.92

Component 1 is a combination of soil carbon terms: microbial biomass, percentage of soil organic C, and soil concentration of soluble C. Component 2 is distance to nearest tree and tree density. Component 3 is organic layer thickness and moisture content. Component 4 is soil temperature. Component 5 is live root biomass and dead tree/log density within 30 cm of the collar. Component 6 is soil ammonium concentration and dead root biomass.

The causes of this variation were not consistent, and often, were not obvious. Soil moisture content, for example, which has been found to be correlated with soil respiration rate in past studies (e.g. Buchmann, 2000), helped to explain collar-to-collar variance in respiration rate but not without including several covariates in a multiple regression model, and not when included in the overall seasonal model.

In our study, the most obvious effect of soil moisture appeared to be as a constraint on the maximum rate of respiration for the site, a pattern that was observable across years with varying amounts of summer precipitation (Fig. 5). Other interannual soil respiration studies have also found soil respiration to be depressed under drought conditions (Savage and Davidson, 2001).

Two causes can be proposed for this constraint: (1) the direct effects of moisture on soil microbial biomass, and (2) the indirect effects of moisture on the amount of photosynthate available as substrate for belowground root and rhizosphere respiration. Since the effect of soil moisture on spatial variance in respiration rate was small, the second cause may be the primary one. The latter hypothesis is supported by our past ecosystem scale measurements; we have shown that NEE was reduced in the summer of 2000, a year with significant spring and summer drought (Monson et al., 2002). The measured NEE rate was high during the early-summer of 1999, just after complete melting of the snow, when we also observed a peak in both soil moisture and soil respiration rate. Recent studies have demonstrated that photosynthetically assimilated carbon is released into the atmosphere via soil respiration within a week at a coniferous boreal forest (Högberg et al., 2001).

Our observations support the conclusion that soil temperature is one of the best statistical predictors of soil respiration, but like soil moisture, not consistently. Temperature was a good predictor of respiration rate seasonally, i.e. rates tended to increase from the beginning to the middle of the growing season along with seasonal temperatures. However, temperature was not a good predictor of variance at the collar-to-collar scale, meaning that diurnal temperature changes could not be used as a temperature correction for a spatial variation model. Temperature is a primary control of the rates of all metabolic reactions, and therefore one would predict temperature to cause a diurnal effect. Apparently, the effect of other factors, predominantly spatial factors associated with soil organic matter content, override the influence of diurnal changes in temperature in determining the collar-to-collar variance in measured respiration rate. The parameters of the seasonal respiration models varied interannually, a phenomenon also observed by Savage and Davidson (2001) at well-drained sites within the Harvard Forest. Like Savage and Davidson, we also interpret that the seasonal effect of temperature is confounded with moisture. In 2001, mid-summer drought caused by high atmospheric VPD and limited precipitation caused respiration rates at the highest temperatures to be

suppressed (Fig. 3). Warm late-spring temperatures during a slow snow melt in 2001 caused respiration rates at high soil moisture to be elevated, compared to 2000 (Fig. 5). It is clear that without complete statistical analysis, correlated effects such as these may confound interpretations of the primary drivers of seasonal respiration dynamics. Other researchers have found similar roles of soil moisture in controlling soil respiration at their sites. Davidson et al. (1998) found that the confounding effects of soil moisture and soil temperature at medium to high soil moistures obscured the temperature response of soil respiration.

Soil temperature explained only part of the variation in the respiration rates at the site and only by averaging across sampling days, relevant relationships could be generated (Fig. 4). These relationships did not appear to improve with an exponential fit. If the true fit is linear rather than exponential, then seasonal effects of soil temperature are not likely due to kinetic effects on enzyme function. Instead, the seasonal temperature dependence may represent shifts in the primary sources that account for the bulk of the respiratory CO_2 flux (e.g. heterotrophs, roots, or mycorrhizae). There are too few points with this sort of integrated treatment of the data to determine the true shape of the curve with confidence, but it presents the possibility of different temperature controls over soil respiration at different temporal scales.

The results of the stepwise regression analysis suggest that spatial variability in soil respiration rate at this subalpine forest site is best predicted by six primary soil variables: organic layer thickness, organic layer ammonium concentration, organic layer water content, soluble C concentration, and microbial and root biomass (Table 4). The dominant role of soil organic fractions in controlling spatial variance in soil respiration rate was supported in the PCA (Table 5). Ammonium concentration, the primary form of available nitrogen in this system, was correlated to root biomass (data not shown). Roots must obtain nitrogen through active, energy-driven transport, and in areas of high ammonium concentration, enhanced root metabolism may account for the high respiration rates. The multiple regression model takes into account the effects of both ammonium concentration and root biomass, controlling one or the other. With such control, ammonium concentration still explains a significant amount of the variance in respiration rate (Table 4), suggesting that high ammonium concentrations cause respiration hotspots not related to differences in root biomass, perhaps reflecting sites with high rates of decomposition and microbial nitrification. The soluble C fraction was difficult to define, as precise chemical analyses of this material were not conducted in this project. It most likely represents a combination of root exudates and carbon released through incomplete decomposition. The soluble C fraction was negatively correlated to respiration rate within a multiple regression, but uncorrelated with respiration rate in a one-way regression. Interestingly, mineral layer soluble carbon was positively correlated with respiration (Table 3), which probably reflects organic carbon that is leached from the organic layer and creates local hotspots of respiration in the otherwise less active mineral layer.

In the multiple regression analysis, microbial biomass explained a significant amount of the variance in respiration, whereas root biomass did not. Several past studies have noted the importance of microbial biomass as a primary determinant of soil respiration rate (Kelting et al., 1998; Buchmann, 2000; Priess and Folster, 2001; Priha and Smolander, 1997; Davidson et al., 1998; Ross et al., 1999; Zak et al., 1999; Giardina and Ryan, 2000). This stands in apparent contrast to the result that many researchers have observed that root respiration accounts for 50% of soil respiration (e.g. Nakane et al., 1996; Högberg et al., 2001, etc.; reviewed by Hanson et al. (2000)). An important caveat to this study is that the chloroform fumigation technique we used to measure microbial C content detects both free-living microbes and mycorrhizal fungi. The conifers at this site are heavily infected with ectomycorrhizal fungus. The fact that root biomass (measured on hand-sorted samples without the fungal layer) explained little of the variance in surface carbon flux suggests that much of the 'root respiration' at this site may be fungal in origin. Ectomycorrhizal fungal respiration should function as root respiration in manipulation studies, yet be measured as microbial biomass in this experimental design. A precise understanding of the relationship of mycorrhizal fungi to free-living microbes as components of the control of soil respiration rate by microbial biomass remains to be elucidated.

We have used a variety of statistical approaches to characterize the primary temporal and spatial controls over soil respiration rate in this high-elevation, subalpine forest ecosystem. Variation in temperature appears to be the primary temporal control seasonally, whereas variation in moisture appears to be the primary temporal control interannually. Variation in soil C pools, especially those represented by microbial biomass appear to be the primary spatial control over respiration rate. Further studies looking at spatial patterns in specific carbon pools, particularly fungal pools, and how they relate to soil respiration, are justified by these results. An integrative factor that appears to subsume the effects of soil C pools, and accurately predict spatial variance in soil respiration rate, is the organic layer thickness. Gradients in organic layer thickness can be detected across a landscape with a regular sampling grid. Further studies are focusing on organic layer thickness as a possible primary scaling factor, capable of supporting predictions of soil respiration rate across broader spatial scales.

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