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Modeling soil CO_2 emissions from ecosystems

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Abstract. We present a new soil respiration model, describe a formal model testing procedure, and compare our model with five alternative models using an extensive data set of observed soil respiration. Gas flux data from rangeland soils that included a large number of measurements at low temperatures were used to model soil CO_2 emissions as a function of soil temperature and water content. Our arctangent temperature function predicts that Q_{10} values vary inversely with temperature and that CO_2 fluxes are significant below 0 °C. Independent data representing a broad range of ecosystems and temperature values were used for model testing. The effects of plant phenology, differences in substrate availability among sites, and water limitation were accounted for so that the temperature equations could be fairly evaluated. Four of the six tested models did equally well at simulating the observed soil CO_2 respiration rates. However, the arctangent variable Q_{10} model agreed closely with observed Q_{10} values over a wide range of temperatures ($r^2 = 0.94$) and was superior to published variable Q_{10} equations using the Akaike information criterion (AIC). The arctangent temperature equation explained 16–85% of the observed intra-site variability in CO_2 flux rates. Including a water stress factor yielded a stronger correlation than temperature alone only in the dryland soils. The observed change in Q_{10} with increasing temperature was the same for data sets that included only heterotrophic respiration and data sets that included both heterotrophic and autotrophic respiration.

Introduction

Exchanges of carbon (C) among the atmosphere, biota, soil, and water influence essential physical and biological processes from organismal to global scales. Respiration of soil organic carbon (SOC) by microbes and other soil organisms releases 50–75 pg of CO_2-C to the atmosphere annually, ~10 times the annual emissions from burning fossil fuels (Schimel et al. 1996). Accurate models of soil respiration are needed to calculate net ecosystem exchange (NEE) rates for different natural and managed systems. NEE is the net flux of C in or out of a system after accounting for CO_2 fixation (photosynthesis), respiration, depositional inputs of organic C, and erosional losses of organic C. NEE calculations help assess the degrees to which natural and managed systems are sources or sinks of C. Understanding

the primary controls of soil respiration is important because SOC represents a large C sink that is subject to losses in response to natural and anthropogenic disturbances. We will show how well different models simulate soil CO_2 fluxes from sites where heterotrophic respiration dominates and sites where both heterotrophic and autotrophic respiration are included. An objective of this paper is to quantify the temperature and water controls on soil respiration. Reliable models of soil CO_2 fluxes can be used to project how changes in land use and climate will affect SOC levels and atmospheric CO_2 concentrations.

We describe a new heterotrophic respiration sub-model used in the DAYCENT and CENTURY ecosystem models. DAYCENT (Parton et al. 1998; Kelley et al. 2000; Del Grosso et al. 2001) and CENTURY (Metherell et al. 1993; Parton et al. 1994) simulate plant growth, soil C and nitrogen (N) flows, and other ecosystem parameters. Heterotrophic respiration in soils is primarily a function of substrate quality and quantity (Janssens et al. 2001), soil temperature (Katterer et al. 1998), soil water content (Davidson et al. 1998; Leiros et al. 1999), microbial community (Holland et al. 2000), and acidity (Walse et al. 1998). Most SOC decomposition models account for differences in substrate quality and quantity by simulating different SOC pools with varying maximum decay rates (e.g. Parton et al. 1994; Coleman and Jenkinson 1999). In these types of models, maximum decay rates for each pool are usually attenuated using functions involving air or soil temperature, precipitation, or soil water potential (Burke et al. 2003). Walse et al. (1998) modeled decomposition of labile C as the growth rate of bacteria and decomposition of recalcitrant material as the growth rate of fungi using air temperature, soil moisture, and soil acidity as driving variables. Alternatively, Pastor and Post (1986) linked decomposition to NPP via N availability and assumed that decomposition is controlled by actual evapotranspiration (AET) and litter lignin and N concentrations.

Our primary goal was to improve the original temperature equation for decomposition used in the CENTURY ecosystem model (Parton et al. 1987). Terrestrial biogeochemical models that are designed for regional to global simulations require simple, general equations that relate processes, such as decomposition, to readily available environmental drivers. Previous decomposition models have been limited by a paucity of observations of CO_2 flux at freezing and sub-freezing temperatures (Katterer et al. 1998) and by assumptions that microbial activity in frozen or snow covered soils is negligible (Fahnestock et al. 1999). However, recently collected field data show that significant CO_2 flux rates can occur at zero and sub-zero temperatures (Brooks et al. 1996; Sommerfeld et al. 1996; Fahnestock et al. 1999). Many models (e.g. Raich and Potter 1995) use a constant Q_{10} temperature equation but Q_{10} values often vary depending on temperature range (Lomandeer et al. 1998; Holland et al. 2000; Xu and Qi 2001). Kirschbaum (1995) compared how well simulated Q_{10} values agreed with

Q_{10} values from observed CO_2 flux data. The best fitting models showed low (1–3) Q_{10} values at temperatures greater than 20 °C and high (8–10) Q_{10} values at 0 °C. Predicted Q_{10} values at low temperatures were limited by a lack of data for sub-0 °C temperatures and large variability in data from 0 to 5 °C. Field data collected over the past 5–10 years that included a large number of observations of CO_2 flux at sub-freezing temperatures yielded similar Q_{10} values at high temperatures but suggest that previous models overestimated Q_{10} values by a factor of $\sim$1.5–2 at temperatures near 0 °C. Our model developed with this new data is likely to be more general than other models because it includes a large number of observations at low temperatures.

We also performed a quantitative evaluation of the existing published variable Q_{10} temperature models (Parton et al. 1987; Jenkinson 1990; Lloyd and Taylor 1994; Kirschbaum 1995) using our extensive soil respiration data set (data not used to develop any of the models). The criteria for goodness of fit include an evaluation of how well the models fit the observed soil respiration fluxes and the observed changes in Q_{10} as a function of soil temperature. The comparison with the observed changes in the Q_{10} as a function of soil temperature is important because this reflects the ability of the models to simulate change in soil respiration as a function of change in soil temperature at different points along the soil temperature curve. This is quite important from an environmental change point of view because these soil temperature models are currently being used in biogeochemistry models to predict changes in carbon budgets as a function of changes in the soil temperature (Kirschbaum 1995). We believe this is the first formal comparison of existing soil temperature models using an independent data set.

To increase confidence in model testing, we used data from one site to parameterize the model and reserved a more extensive data set for model testing. Gas flux, soil temperature, and soil water content measurements from native short grass steppe soils were used to parameterize our new arctangent equation. Similar measurements from various native and disturbed systems were used for model testing. The temperature effect on measured soil CO_2 emissions can be confounded by site factors such as litter quality (Wang et al. 2000) and seasonal NPP patterns (Hogberg et al. 2001), so site and seasonal factors were accounted for in building and testing the model. We assumed that moisture stress can limit decomposition rates in dryland systems. The arctangent temperature equation was compared with alternative models using the conventional r^2 parameter and the Akaike information criterion (AIC). AIC combines elements of inferential statistics and information theory and is useful for model comparisons because it quantifies the amount of information that is lost when a model is used to approximate an observed phenomenon. We show that our model is superior to alternative models using statistical criteria because it better represents changes in Q_{10} values as a function of soil temperature.

Methods

Gas flux and ancillary measurements

The new data reported in this paper were collected from native, fertilized, and plowed shortgrass steppe soils and winter wheat/fallow fields in northeastern Colorado, and a sub-alpine meadow in Wyoming. The shortgrass steppe measurements were taken from 1992 to 1996 in plots representing different soil texture classes and fertility levels at the central plains experimental range (CPER) and the winter wheat/fallow measurements were taken on private land ~20 km southeast of the CPER during the same time period. The CPER (40 °8′23″N, 104°45′15″W) is located ~60 km northeast of Fort Collins, CO and average annual precipitation and temperature are ~32 cm and ~9.5 °C, respectively (Mosier et al. 1991, 1996, 1997). The sub-alpine meadow (Mosier et al. 1993) has mean annual precipitation and temperature of ~100 cm and ~−0.5 °C, respectively, and was sampled in 1991 and 1992. The plots were established at the USDA/Forest Service glacier lake ecosystem experiments site (GLEES) in the Snowy Range of the Medicine Bow Mountains (41°20′N, 106°20′W, elevation ~3182 m) in southeastern Wyoming ~65 km west of Laramie. At the Colorado and Wyoming sites PVC pipes (inside diameter = 20.3 cm, 4–6 per plot) were driven 8 cm into the soil within the plots to establish permanent gas flux measuring anchors. On sampling days, usually once per week, a 7.5 cm high-vented chamber was fitted onto the anchors and gas samples were extracted with a syringe at 0, 15, and 30 min after the chambers were attached (Mosier et al. 1991, 1993, 1997). Concentrations of CO_2 were measured by gas chromatography within 6 h of sampling and gas flux was calculated based on changes in CO_2 concentration as a function of time. Adjacent to the permanent anchors, soil temperature (T_{soil}) was measured at 5 cm depth with a handheld digital thermometer and six soil cores (inside diameter = 2.5 cm, depth = 15 cm) were combined, weighed, and oven dried so that bulk density and volumetric soil water content could be calculated.

Data sets used for model development and testing

Winter season data from the native shortgrass steppe soils were used to parameterize the temperature equation while year-round data from these soils normalized by season were used to parameterize the water equation. Two data sets were compiled for model validation. One, designated the temperate data set, included data from the managed fields in Colorado (plowed/fertilized pastures and winter wheat/fallow) previously described. This data set also included observations from winter wheat/fallow fields in western Nebraska (Kessavalou et al. 1998), alpine meadow and forest in Wyoming (Mosier et al. 1993), tall grass prairie soils in Kansas (Bremer et al. 1998), agricultural fields in Michigan (Robertson et al. 2000), mixed deciduous forests in Massachusetts

(Savage and Davidson 2001), and a beech forest in Germany (Brume 1995). A sub-set of this data set, designated the heterotrophic data set, was extracted to compile measured CO_2 flux rates that were due almost entirely to SOC decomposition because plots were kept vegetation free. Herbicides were applied to the winter wheat/fallow fields during the fallow season, some short-grass steppe plots were maintained vegetation free by plowing, and 15 m diameter gaps were cut out of the beech forest and kept vegetation free.

The data used for model building and testing were normalized by site and season so that the average flux was 1 unit at 12.5 °C for the growing and non-growing seasons. We normalized by site to account for differences in CO_2 flux rates that are driven by factors such as labile C availability and by season to account for the effect of plant phenology on measured flux rates. This was done for each site by dividing each data point from the growing season by the average growing season flux in the interval from 10 to 15 °C and dividing each data point from the non-growing season by the average non-growing season flux in the interval from 10 to 15 °C. Lloyd and Taylor (1994) used a similar approach to normalize soil CO_2 respiration data acquired from different studies. For the grassland, deciduous, and annually cropped systems the growing season was defined as May–October and the non-growing season as November–April. For the winter wheat/fallow rotations the growing season was the months from wheat planting to harvest and fallow months were designated non-growing season. All the observations from the beech forest used in this analysis were taken during the summer months. Measurements taken within the beech forest stand were assumed to be growing season and measurements taken in vegetation free gaps within the stand were classified non-growing season.

Model goals and assumptions

Our intention was to develop a simple soil respiration sub-model that could be used by general ecosystem models. Models designed for regional and global applications require simple equations based on readily available abiotic drivers (e.g. precipitation, temperature) to simulate ecosystem processes. These models do not include many of the factors (e.g. microbial community) that control processes such as decomposition, so regressions between simulated and observed soil respiration rates often show r^2 values less than 0.5. In contrast to investigating the controls on decomposition rates that are not considered by many global biogeochemical models, our goal was to develop and test a general temperature equation that would apply to a large range of conditions.

We assumed that the amount of substrate controls the maximum decomposition rate and that this can be reduced by unfavorable soil temperatures and moisture stress. Our sub-model quantifying the effects of soil temperature and water content on respiration assumes that labile C availability is known from measurements or is simulated by a model. We assumed that measured

respiration rates during the non-growing season were due primarily to SOC decomposition while both decomposition and root respiration made significant contributions to measured flux rates during the growing season. The majority of measured heterotrophic CO_2 emissions are from decomposition of the more labile C pools (Trumbore et al. 1990; Schimel et al. 1994). Consequently, we would not necessarily expect our temperature equation to apply to decomposition of the more recalcitrant fractions of SOC, which may have a less sensitive temperature response (Liski et al. 1999).

Model development

Winter season CO_2 flux data from the native shortgrass steppe soils were used to quantify the effect of temperature on SOC decomposition while winter and summer data normalized by season were used to parameterize the water equation. These factors are simply multiplied in our heterotrophic respiration (R_H) sub-model:

$$R_H = F(T_{soil}) * F(\mathrm{RWC}), \tag{1}$$

where R_H is the combined effect of water and temperature on decomposition. $F(T_{soil})$ is the temperature effect normalized to 1 at 30 °C:

$$F(T_{soil}) = 0.56 + (1.46 * \arctan(\pi * 0.0309 * (T_{soil} - 15.7)))/\pi \tag{2}$$

and $F(\mathrm{RWC})$ is the water effect normalized to 1 at RWC = 100%:

$$F(\mathrm{RWC}) = 5 * (0.287 + (\arctan(\pi * 0.009 * (\mathrm{RWC} - 17.47)))/\pi), \tag{3}$$

where RWC is the measured soil relative water content. The arctangent function was used because it allows for varying sensitivity of the response variable (respiration) to the independent variable (temperature or water). Parameters in Eqs. (2) and (3) were obtained using observed values and optimization.

Figure 1a shows the response of winter season CO_2 emissions to soil temperature (T_{soil}) when water was not strongly limiting, and $F(T_{soil})$, our variable Q_{10} arctangent function. Figure 1b shows the response of normalized CO_2 emissions to RWC when temperature was not strongly limiting. The overall model explained a reasonable amount of the variability in normalized CO_2 emissions for the data set used for model building, although high observed values tended to be strongly underestimated (Figure 1c). Using the entire model building data set, the primary effect of temperature was significant ($r^2 = 0.27$), the primary effect of water was insignificant ($r^2 = 0.01$), and the interaction between water and temperature was significant ($r^2 = 0.47$). The primary effect of water was significant when data points subject to temperature limitation ($T_{soil} < 15$ °C) were eliminated (Figure 1b), providing further evidence that temperature and water interact to control decomposition rates in these soils.

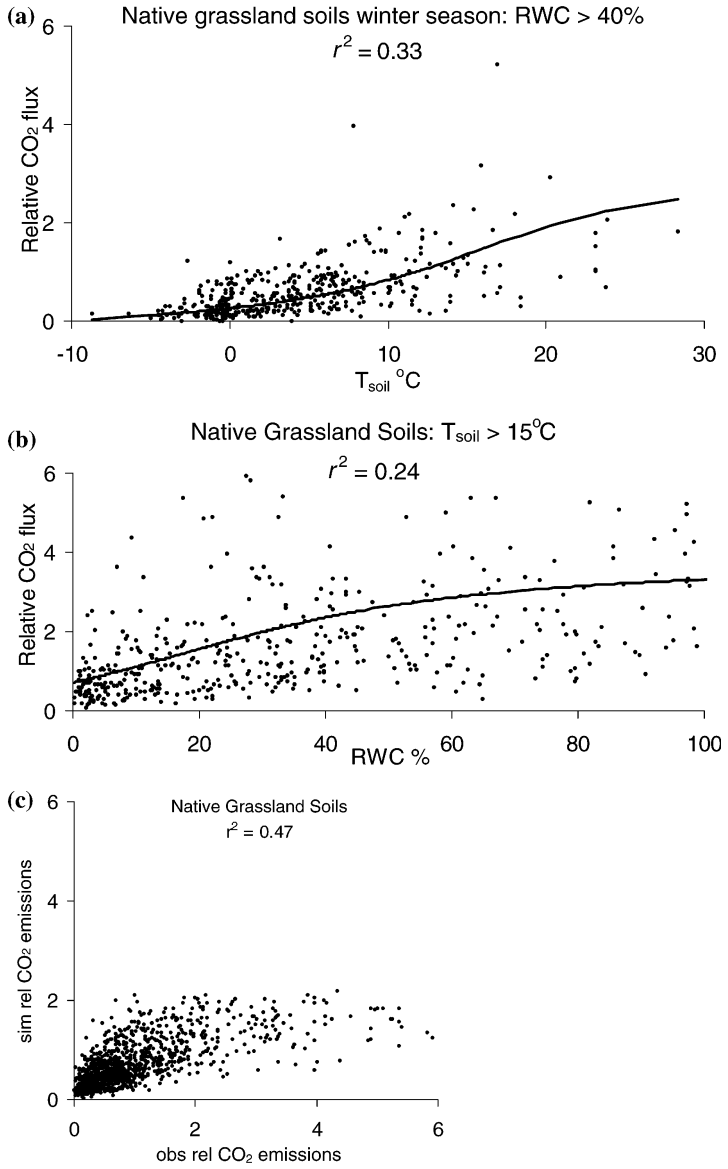

Figure 1. (a) Non-growing season CO_2 emissions as a function of soil temperature for native shortgrass steppe soils used for model building, (b) relative CO_2 emissions for year round data from the shortgrass steppe used to parameterize the relative water content (RWC) equation, and (c) simulated relative CO_2 emissions as a function of soil temperature and RWC versus observed relative CO_2 emissions.

Our water function uses RWC as a metric for soil water availability because it accounts for differences in water stress on biological activity at a given water content driven by soil physical properties. Volumetric water content was converted to relative RWC using the following:

$$\mathrm{RWC} = (W - \mathrm{WP})/(\mathrm{FC} - \mathrm{WP}) \quad (4)$$

where W is the measured volumetric soil water content, WP the wilting point, and FC the field capacity. FC and WP were estimated for each soil using soil texture data and time series data of soil water content. Both WP and FC tend to increase as clay content increases (Saxton et al. 1986) and more water must be removed from sandy than clayey soils to inhibit canopy conductance (Landsberg and Waring 1997; Bernier et al. 2002).

Model comparisons

Competing models and model comparison criteria

We compared our arctangent model with the original CENTURY equation (Parton et al. 1987), an exponential model, a linear model (Walse et al. 1998), the variable Q_{10} Kirschbaum model (Kirschbaum 1995) and the variable Q_{10} Lloyd and Taylor empirical model (Lloyd and Taylor 1994). To fairly compare the alternative temperature equations, we accounted for the effects of site specific factors, (e.g., substrate availability), coarse plant phenology, and water limitation on measured soil respiration rates. Simulated and observed Q_{10} values as well as CO_2 flux rates were used in model comparisons. We defined Q_{10} as the ratio of the rate of a process at 5 °C above a particular temperature to the rate of the process at 5 °C below that temperature. For an exponential function, $y = a * e^{(bx)}$, the Q_{10} does not vary with temperature and can be calculated as $Q_{10} = e^{(10b)}$. Q_{10} values were calculated for the two validation data sets by sorting the data by temperature and deriving the best fitting exponential function for normalized CO_2 respiration as a function of temperature for overlapping 10 °C ranges centered at integer temperature values in the range from 5 to 25 °C. For the variable Q_{10} models (Kirschbaum, Lloyd and Taylor, arctangent, original CENTURY, linear), Q_{10} values were calculated by dividing the functional output at 5 °C above the temperature range midpoint by the functional output at 5 °C below the temperature range midpoint for the same integer temperature midpoints for which observed Q_{10} values were calculated.

In addition to the correlation coefficient (r^2) we also used Akaike's information criterion (AIC) and Akaike weights (w_r) to compare models. AIC combines the Kullback–Leibler (K–L) discrepancy, the dominant paradigm in information theory, with maximum likelihood estimation, the dominant paradigm in statistics (Burnham and Anderson 1998). Traditional statistical inference is concerned with the probability that a data set would be observed

given that a model (hypothesis) is correct. Conversely, inference based on likelihood is concerned with the likelihood of a model being superior to competing models when compared using a set of observations. The K–L distance is appropriate for model comparisons because it quantifies the information that is lost when a set of model outputs, q, is used to approximate a true distribution, p (Sakamoto 1986). The absolute K–L distance cannot usually be calculated for a particular model because truth (e.g. the true relationship between soil temperature and decomposition) is unknown. However, Akaike (1973) showed that likelihood can be used to estimate the relative K–L distance for alternative models and to determine which competing model is closest to truth as manifested by a particular data set. AIC estimates the expected relative K–L distance and the model with the lowest AIC value is considered the best model. This criterion accounts for goodness of fit as well as over-fitting the data because AIC includes a penalty proportional to the number of free parameters in the model. AIC is calculated as:

$$\mathrm{AIC} = -2\log(L(\theta_r) + 2K, \tag{5}$$

where $L(\theta_r)$ is the maximized likelihood estimate for a model and its parameters, θ_r, compared to a data set, and K is the number of parameters in the model that were allowed to vary when fitting the model to a particular data set. $L(\theta_r)$ is calculated as

$$L(\theta_r = -0.5\log\frac{\sum_{n=1}^{N}(\log(\mathrm{obs}) - \log(\mathrm{sim}))^2}{N}, \tag{6}$$

where N is the number of data points with observed and simulated values. To compare models Akaike weights (w_r) were calculated

$$w_r = \frac{e^{\left[\frac{-\Delta_r}{2}\right]}}{\sum_{i=1}^{R} e^{\frac{-\Delta_r}{2}}} \tag{7}$$

Δ_r is the difference in AIC values between model r and the model with the minimum AIC value and R is the number of models being compared. The Akaike weight of model $r(w_r)$ may be interpreted as the probability that model r is the best model (i.e. has the minimum K–L distance) given the data set used for model testing and the designated set of competing models (Burnham and Anderson 1998).

Model comparisons

Model comparisons for the six models were performed using the heterotrophic and temperate data sets described previously. The heterotrophic data set was used because the measured CO_2 flux rates were the result of primarily

heterotrophic respiration, so the ability of the models to simulate SOC decomposition could be isolated. The temperate data set was also used even though it contains measurements that are driven to a significant extent by root respiration because this allowed for model testing using a large number of data points collected from different sites.

Two methods were used to avoid confounding the effect of temperature on respiration with the effects of seasonal and site specific factors. One way is to include a site/seasonal multiplier in the respiration equation and the other is to normalize CO_2 flux rates for each site to a common value at a given temperature (similar to Lloyd and Taylor (1994). Using the former method, we fit a multiplier (M) for the growing and non-growing seasons for each site in the following respiration equation:

$$R_{\text{soil}} = F(T_{\text{soil}}) * F(\text{RWC}) * M, \tag{8}$$

where M(kg CO_2-C ha^{-1} d^{-1}) was optimized by minimizing the AIC for simulated versus observed CO_2 flux rates. No parameters in the arctangent function, $F(T_{\text{soil}})$, or the original CENTURY, Lloyd and Taylor and Kirschbaum functions were allowed to vary ($K = 0$ in the AIC equation). Simulated respiration rates were calculated in a similar manner for the exponential and linear models except that in addition to M, the curve shape or slope parameter was also allowed to vary ($K = 1$) when optimizing the exponential or linear functions.

Results

Table 1 summarizes the results of model comparisons with the two data sets. The arctangent, original CENTURY, Llloyd and Taylor and Kirchbaum all performed equally well using both the r^2 and the AIC criterion for the heterotrophic CO_2 flux data sets. The Akaike weights (w_r) imply that the exponential, linear, original CENTURY, arctangent, Lloyd and Taylor and Kirschbaum models have 3, 8, 22, 22, 22, and 23% probabilities, respectively, of being the best model when compared using this data set. The r^2 and w_r values were also similar for the arctangent, original CENTURY, Lloyd and Taylor and Kirschbaum models when compared using the temperate data sets (Table 1). However, when observed versus simulated Q_{10} values were compared the w_r values indicate that the arctangent function has a 41% probability of being the best model and the Lloyd and Taylor is second best (Table 1). The r^2 parameter could not be calculated for the exponential using observed and simulated Q_{10} values because Q_{10} does not vary with the exponential.

Figure 2 provides further evidence that the arctangent function is superior for estimating the effect of temperature on decomposition. There is a strong pattern of decreasing Q_{10} with increasing temperature for both the heterotrophic and temperate data sets (Figure 2). The original CENTURY and Kirschbaum equations have the proper trend but tend to over-estimate Q_{10} values,

Table 1. Comparisons of best fitting linear and exponential functions, the original CENTURY decomposition equation, and our new arctangent equation using Akaike weights (w_r) and correlation coefficients (r^2) for simulated versus observed CO_2 flux rates for two data sets and simulated versus observed Q_{10} values from both of the data sets

Function	Heterotrophic data (CO_2 flux)		Temperate data (CO_2 flux)		Combined data (Q_{10} values)	
	w_r	r^2	w_r	r^2	w_r	r^2
Linear	0.08	0.41	0.08	0.31	0.04	0.40
Exponential	0.03	0.41	0.08	0.31	0.10	
Original CENTURY	0.22	0.49	0.22	0.31	0.11	0.89
Kirchbaum	0.22	0.46	0.22	0.30	0.11	0.82
Lloyd and Taylor	0.23	0.48	0.17	0.31	0.22	0.94
Arctangent	0.22	0.48	0.23	0.32	0.42	0.94

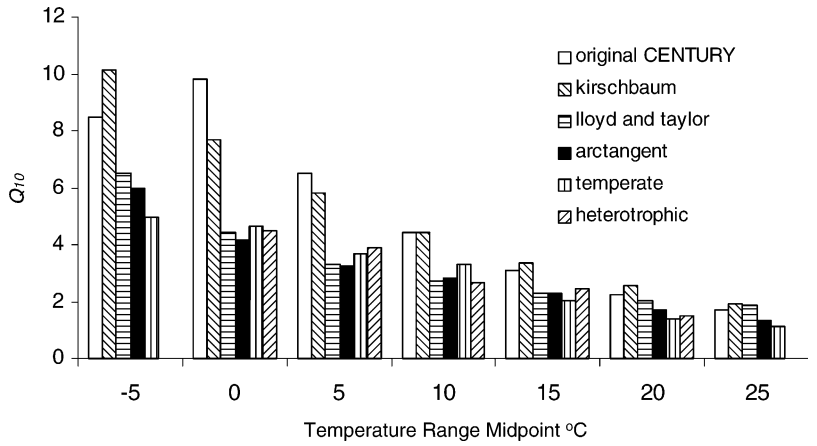

Figure 2. Q_{10} values for different temperature ranges predicted by the original CENTURY temperature equation, our new arctangent equation, and calculated for observations from two data sets used for model testing. There were not sufficient data points to calculate Q_{10} values for all temperature ranges for the heterotrophic data set.

particularly at low temperatures. Kirschbaum (1995) also showed that the Jenkinson et al. (1991) model greatly overestimated Q_{10} values for soil temperature less than 1 °C. The Lloyd and Taylor and arctangent equations were quite similar when temperature were less than 20 °C, while the Lloyd and Taylor equation tended to overestimate Q_{10} for higher temperatures.

Seasonal, biome and land management effects on soil respiration

We compared the M values that were optimized for growing and non-growing season at each site as previously described. The data showed strong evidence

that plant phenology is a major driver of within site CO_2 flux rates and that differences in average flux rates among sites are often related to NPP and SOC levels (Figure 3, Table 2). Excluding the alpine forest soil, the ratio of M values for summer compared to winter ranged from 1.6 to 2.6, suggesting that roots are responsible for a significant proportion of observed CO_2 flux rates during the growing season. Growing season M values tended to vary directly with NPP and non-growing season with SOC levels. The linear regression between non-growing season M value and SOC for the 7 sites with available SOC data yielded an r^2 value of 0.84.

The alpine meadow is in a depositional zone, has high NPP, high SOC levels and also had the highest growing and non-growing season M values, while the SOC depleted agricultural soils had low M values. Similarly, the native tallgrass prairie has higher SOC and NPP than the native shortgrass steppe and also has higher M values. The winter wheat/fallow fields in NE had higher M values than the winter wheat fallow fields in CO. The CO fields had been in production for more than twice as long as the NE fields and are depleted in SOC to a greater extent than the NE fields. The plowed pasture had a higher M value than the native pasture during the winter even though SOC levels were similar, probably a result of increased decomposition rates resulting from disturbance of soil aggregates.

The results in Table 2 show that our model generally did better (higher r^2) simulating fluxes due primarily to heterotrophic respiration (non-growing season) than fluxes that included a large proportion of root respiration (growing season). This is expected because the model was parameterized to simulate respiration from SOC decomposition. A meaningful r^2 parameter could not be calculated with temperature as the independent variable for the alpine meadow and forest during the non-growing season because under the

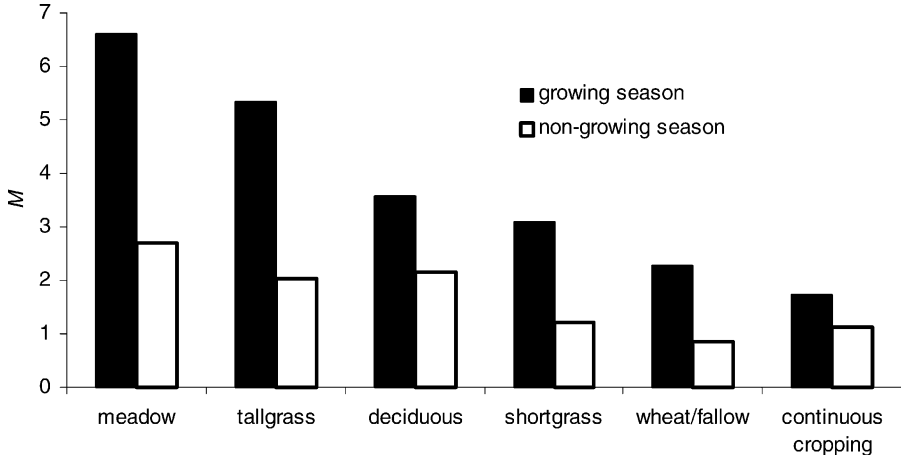

Figure 3. Growing season and non-growing season optimized multipliers (M) for the shortgrass steppe soils used for model building and some of the soils used for model testing.

Table 2. Correlation coefficients (r^2) for the linear regression between our soil respiration model and measured soil respiration rates and optimized site/season specific soil respiration rates (M in kg CO_2-C ha^{-1} d^{-1}) at 30 °C and no water stress

Vegetation type	$r^2_{\text{non-growing}}$	$r^2_{\text{growing-season}}$	$M_{\text{non-growing}}$	$M_{\text{growing-season}}$
Native shortgrass CO	0.28	0.46	0.057	0.151
Plowed pasture CO	0.69		0.064*	
Fertilized shortgrass CO	0.52	0.31	0.070	0.151
Wheat/fallow CO	0.46	0.24	0.042*	0.112
Wheat/fallow NE	0.49	0.20	0.052*	0.152
Tallgrass KS	0.85	0.77	0.099	0.262
Continuous cropping MI	0.16	0.13	0.055	0.086
Mixed deciduous MA	0.48	0.38	0.106	0.176
Beech Germany	0.51	0.72	0.063*	0.116
Alpine meadow WY		0.54	0.133	0.325
Alpine forest WY		0.32	0.35	0.280

*Indicates plots kept free of vegetation by plowing, herbicide, or tree removal.

snow pack the range of observed temperatures was confined to -3 to -1 °C (Sommerfeld et al. 1996). Such a narrow range of values for the independent variable is not sufficient to allow for the possibility of a significant regression.

Discussion

We described a variable Q_{10} temperature model used to simulated SOC decomposition and showed that all of the variable Q_{10} models performed equally well when compared to the observed CO_2 flux data while the arctangent and Lloyd and Taylor functions were best at simulating the observed changes in Q_{10} as a function of temperature. Many researchers have found evidence that Q_{10} values vary with temperature range (e.g. Lomander et al. 1998; Holland et al. 2000; Xu and Qi 2001). Kirschbaum (1995) compared simulated Q_{10} values from different models and from incubations as a function of temperature and showed that Q_{10} values decrease as temperature increases. Our model and the data we compiled for model testing provide further evidence that Q_{10} varies inversely with temperature but our data suggests that Q_{10} values are lower than those reported by Kirschbaum (1995) for low temperatures (< 10 °C). There are several reasons for this discrepancy. The lack of CO_2 flux data at sub-freezing temperatures led to unreliable Q_{10} estimates at low temperatures. Q_{10} values reported in Kirschbaum (1995) were calculated from individual studies whereas the Q_{10} values in this paper were calculated from an aggregated set of normalized data from various sites. Also, the Q_{10} values in Kirschbaum et al. (1995) were calculated from CO_2 flux from incubations in which other factors (e.g. substrate availability, moisture) were less likely to be limiting than in the field soils that we analyzed.

The effects of site factors and plant phenology were accounted for when comparing models by including a site/seasonal multiplier in the model or by

normalizing the data by site/season. Models were compared using a large data set that included measurements driven by heterotrophic and autotrophic respiration (temperate data set) and a data set for which measured CO_2 flux rates were due almost entirely to decomposition because the plots were maintained vegetation free. Comparisons with the heterotrophic and temperate data sets show that most of the models compare well with observed soil CO_2 respiration data. The preponderance of the evidence (Table 1, Figure 2) supports the conclusion that the arctangent and Lloyd and Taylor models are the best models because they also correctly predicted the observed Q_{10} changes with increasing temperature.

When using AIC and w_r, model error is calculated as the difference between ln(observed) and ln(simulated) whereas r^2 uses non-transformed data. The effect of using the natural logarithm is that model errors at low observations are given weights proportional to errors when observations are high. The r^2 parameter tends to discount model errors when observations are low and to over-emphasize the importance of simulating high values correctly. For these and other reasons, the utility of r^2 as a tool for model comparisons has been questioned (MsQuarrie and Tsai 1998).

Analysis of data from various soils supports our assumptions that substrate availability is a primary inter-site control of soil CO_2 respiration and that seasonal NPP patterns, as well as temperature, are important intra-site controls. Optimized non-growing season multipliers (M in Table 2, Figure 3) varied by more than a factor of two among sites and are at least partially the result of differences in substrate availability. For example, non-growing season M was higher for the tallgrass prairie than the shortgrass steppe and the prairie has higher SOC ($\sim$5 kg C m^{-2} versus $\sim$3 kg C m^{-2}). Within sites, plant phenology and temperature both strongly influenced respiration rates in most of the soils we tested. Growing season M values were higher than non-growing season M values. This implies that at a given temperature more respiration occurs during the growing season because root respiration makes a greater contribution to total flux rates. It is important to account for seasonal differences in labile C availability because, as was pointed out by Gu et al. (2004), temperature sensitivity will be overestimated if changes in labile C and temperature are in phase and underestimated if changes in labile C and temperature are out of phase. Comparison of growing and non-growing season M values suggests that roots are responsible for a significant portion (35–65%) of total respiration during the growing season. This is consistent with isotope data showing that $\sim$35–50% of soil CO_2 emissions from shortgrass steppe soils during the growing season were due to decomposition (Pendall et al. 2003) and $\sim$55% of soil CO_2 emissions from temperate forests late in the growing season were due to rhizosphere respiration (Andrews et al. 1999). Similarly, radiocarbon data collected along an elevational gradient showed that SOM decomposition was responsible for $\sim$20–50% of CO_2 flux during the growing season and close to 100% during the non-growing season (Wang et al. 2000).

Although our new arctangent function represents an improvement in predicted Q_{10} values compared to previous models, our model still explained less than 50% of observed CO_2 fluxes at many sites. Correlation coefficients are relatively low for several reasons. Bulk soil water and temperature are used to drive the model but these do not account for the heterogeneity in environmental conditions in microsites populated by microbes. The ability to model soil CO_2 flux data is limited by the inherent variability of this type of data. Factors not included in the model, such as within season fluctuations in labile C availability, also contribute to model error.

Our model is also limited by the reliability of key model drivers. The equations were parameterized using measured values for soil water and temperature and we used simple site/seasonal multipliers to account for the effects of these factors on respiration rates. In practice, the presented soil respiration model will be incorporated into comprehensive ecosystem models that simulate soil water, temperature, labile C availability, plant phenology, etc. Some of these drivers of respiration are better simulated than others. Ecosystem models have been compared with observed soil water and temperature data from soils of different textures and found to perform reasonably well (Frolking et al. 1998; Parton et al. 1998; Del Grosso et al. 2001). In addition to simulating soil water content correctly, soil hydraulic properties (e.g. field capacity, wilting point) need to be reliably simulated. It is not soil water content alone that controls water stress but the interaction between water content and soil hydraulic properties that determine how tightly water is held in the soil matrix. For example, canopy stomatal conductance can remain uninhibited at water contents below 50% water filled pore space (WFPS) in sandy soils whereas canopy conductance can be restricted in clay soils at water contents $>80\%$ WFPS (Landsberg and Waring 1997; Bernier et al. 2002). In global ecosystem models, hydraulic properties that influence water stress are often calculated based on texture. This is another limitation to our decomposition sub-model because other factors besides soil texture (e.g. SOM content, degree of aggregation) that influence soil hydraulic properties are often ignored.

In contrast to soil water and temperature, we know of no comparisons of observed and simulated labile C availability, partly because this is difficult to measure directly. Another difficulty is that models simulate the autotrophic and heterotrophic components of soil respiration separately whereas most measurements of CO_2 flux contain both components. Consequently, we believe that the largest potentials to improve CO_2 respiration models are to increase the reliability of labile C estimates and to better represent autotrophic respiration. Plant phenology and NPP allocation patterns are major controls on root respiration and labile C availability. Below ground C allocation controls the autotrophic component of soil respiration while senescence patterns of above and below ground biomass control C inputs and influence the heterotrophic component. For most of the analyses in this paper we only considered phenology in a simple manner and assumed a discrete growing season versus non-growing season dichotomy (Figure 3). In reality, more continuous changes

in plant phenology control autotrophic respiration and C inputs to the soil. To explore this further, we used our existing temperature and water functions and optimized 12 monthly multipliers instead of just two growing season/non growing season multipliers for the data sets that had a sufficient number of year-round observations. Figure 4 shows results for the shortgrass steppe and mixed deciduous forest sites. Both sites show a strong seasonal pattern even though temperature and water have been accounted for which provides evidence that autotrophic respiration and labile C availability are primary controls on soil CO_2 fluxes.

The patterns of m values in Figure 4 during the growing season are likely driven by the autotrophic component of soil respiration, which appears to be correlated with NPP, at least for the systems examined for this analysis. Patterns of m values during the non-growing season are likely dominated by the heterotrophic component of soil respiration. At both sites, m values are higher in autumn than spring, presumably because of increased C inputs from plant senescence in autumn. Large inputs from leaf drop in the deciduous forest result in larger m values in autumn than in the shortgrass steppe where above ground litter inputs are less pulse driven. We suggest that more continuous changes in NPP drive autotrophic respiration whereas more discrete pulses of C from biomass senescence drive heterotrophic respiration. This implies that both the autotrophic and heterotrophic components of soil respiration can be tied to total NPP, C allocation patterns, and plant phenology. Although dependence of our SOM decomposition model on accurate representation of labile C availability and reliance on CO_2 flux data that contain an uncertain proportion of root respiration are potential limitations, these contingencies also provide an opportunity to improve respiration estimates because changes in autotrophic respiration and labile C availability are apparently highly correlated with plant NPP and phenology, which can be predicted.

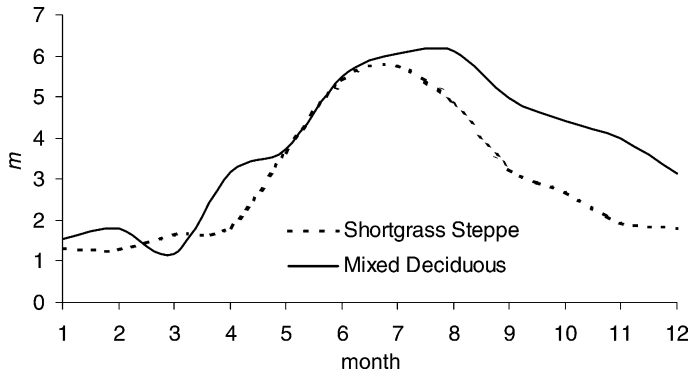

Figure 4. Monthly optimized multipliers (m) for the shortgrass steppe soils used for model building and the mixed deciduous forest used for model testing.

One reliable way to infer above ground NPP and plant phenology is with remote sensing. Constraining plant phenology in ecosystem models with satellite data would likely lead to better simulation of the seasonal patterns of autotrophic respiration and labile C availability and hence, better estimation of soil CO_2 emissions. Below ground C allocation patterns influence labile C availability but are more difficult to predict. Some plant species show changes in below ground allocation when fertilized or grown under elevated CO_2 conditions (e.g. Shaw et al. 2002; Butnor et al. 2003) and models such as DAYCENT (Parton et al. 1998; Del Grosso et al. 2001), assume that below ground C allocation is controlled by plant phenology and environmental/nutrient stress. An alternative, and perhaps complementary, approach could be used for species, such as sunflower, that appear to have a fixed NPP:GPP ratio (Chen et al. 2000). Models that predict both gross photosynthesis and above ground productivity could also predict below ground productivity assuming that NPP:GPP is constant. Constraining plant dynamics simulated by ecosystem models with remotely sensed data and developing more mechanistic models that better simulate the controls on labile C availability and the autotrophic component of soil respiration would improve simulated estimates of soil CO_2 flux.

For model testing purposes, we assumed that heterotrophic and root respiration have the same relative response to temperature, i.e. only scalar multipliers were used to distinguish growing season from non-growing season flux rates. However, there is evidence that root respiration is more sensitive to temperature changes in the 10–20 °C range than heterotrophic respiration in a deciduous forest (Boone et al. 1998). Nonetheless, aggregated data from different systems show that our equation designed to model SOC decomposition can successfully simulate temperature responses during the growing season in many soils (Table 2) and Q_{10} values were similar for the heterotrophic and temperate data sets (Figure 2). We also assumed that water stress response was the same for autotrophic and heterotrophic respiration. However, heterotrophic respiration is less sensitive to soil water content than autotrophic respiration and decreases substantially only when soils are close to air dryness or saturation (O'Connell 1990). One reason autotrophic respiration is more sensitive is that plants are subject to high water demand when the vapor pressure deficit is high and hence can show stress at moderate soil water contents.

Our water equation rarely explained more than 10% of the observed intra-site variability in respiration rates and the interaction between our water and temperature functions increased r^2 values by more than 5% compared to the temperature equation alone only for the dryland soils (shortgrass steppe and winter wheat/fallow) that were studied. We suspect that we did not detect a strong water effect in the non-dryland soils because these soils lacked a sufficient number of data points which exhibited water stress. Similarly, Boone et al. (1998) concluded that soil moisture was unrelated or weakly correlated with soil moisture content for deciduous forest soils. However, Savage and

Davidson (2001) used a multi-year data set and showed that differences in precipitation patterns can explain a significant proportion of the observed variability in inter-annual CO_2 emissions from deciduous forests. We suggest that the likelihood of finding a statistically strong water effect is dependent upon the universe of data that is analyzed and that failure to do so does not mean that water is not a primary control on soil respiration rates. Overall, our data are consistent with other research (e.g. Billings et al. 1998) showing that in non-saturated soils temperature is usually a more important control than water and that the interaction between water and temperature can be important (Davidson et al. 1998; Xu and Qi 2001).

Conclusions

This paper supports the findings of other researchers that different factors interact to control soil respiration rates. Substrate availability and NPP explain a large proportion of the inter-site variability in CO_2 emission rates while temperature and plant phenology often explain a majority of the observed within site variability (Janssens et al. 2001). Our model explained between 16 and 85% of the observed within season variability in CO_2 flux rates (Table 2). This suggests that water and temperature are primary within site controls for some, but not all systems. Similarly, we found a correlation between SOC and potential respiration rates but differences in SOC levels among sites are not always correlated with average CO_2 flux rates and other factors such as microbial community may be important (Holland et al. 2000). But for many soils, substrate availability, plant phenology, soil temperature, and soil water availability are primary controls on decomposition rates and can be modeled reasonably well. In addition to a need for more mechanistic models of plant phenology and C allocation patterns, another major limitation of the existing models is the uncertainty in estimates of Q_{10} values for soil temperature >20 °C. This uncertainty is primarily due to the lack of adequate data sets to characterize soil respiration fluxes for soil temperature >20 °C.

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