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Determinants of growing season soil CO_2 flux in a Minnesota grassland

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Abstract. Soil CO_2 flux was measured across 947 plots at 7 experimental grassland sites at the Cedar Creek Natural History Area in order to determine the relationships between soil CO_2 flux and environmental factors, living plant biomass, and soil C and N. Soil CO_2 flux increased as the day progressed, and was positively related to aboveground biomass, belowground biomass, and soil % C. However, most of the variation in soil CO_2 flux explained by a multiple regression model ($r^2 = 0.55$) was attributed to the different experimental sites (61%). Soil CO_2 flux increased with increasing aboveground plant biomass (explaining 16% of the model variation), belowground plant biomass (12%), and soil C and C:N ratio (6%). The length of time between aboveground biomass in a plot was clipped and soil CO_2 flux varied among plots. Soil CO_2 flux declined with increased time since clipping, supporting the idea that recently fixed carbon is a significant component of soil CO_2 flux. Soil CO_2 flux did not follow standard Q_{10} relationships. Over a 20 °C temperature range, soil CO_2 flux tended to be lower in warmer plots. More work is necessary to understand what factors explain the large differences that were seen among experimental sites in soil CO_2 flux that could not be explained by biomass or soil properties.

Introduction

Soil CO_2 flux to the atmosphere is a significant component of the global C cycle, equivalent to approximately 10% of the atmospheric CO_2 pool (Jenkinson et al. 1991), and represents the second largest flux between terrestrial ecosystems and the atmosphere (Raich and Tufekcioglu 2000). Soil CO_2 flux integrates root and microbial activity (Raich and Nadelhoffer 1989; Schlesinger and Andrews 2000) and represents total belowground C metabolism. Although the large variation among ecosystem types in annual soil CO_2 flux has been correlated with factors such as annual precipitation and temperature (Raich and Schlesinger 1992), there has been little work to determine if variation in soil CO_2 flux among and within ecosystems is best explained by variation in environmental factors, living plant biomass, or soil C and N.

Temperature has been the abiotic factor most associated with patterns of soil CO_2 flux (Lloyd and Taylor 1994; Raich and Potter 1995; Boone et al. 1998) and models of ecosystem carbon exchange (e.g. Ryan (1991); Raich and Tufekcioglu (2000); Keith et al. (1997)). However, some studies show weak relationships between temperature and soil CO_2 flux or root respiration (Ham et al. 1995; Lambers et al. 1996; Craine et al. 1998), and better relationships with factors that affect sources of fixed C, such as light supply and interception (Craine et al. 1998; Fitter et al. 1999). Although soil temperature and soil CO_2 flux generally may be well-correlated within a site at annual time scales, or among sites that have broadly different climates, this relationship may not adequately predict soil CO_2 flux within or across sites at shorter time scales, especially since respiration can acclimate to changes in temperature (Ryan 1991; Amthor et al. 1994; Bryla et al. 1997).

To predict patterns of ecosystem C cycling, future models of soil CO_2 flux will need to be based on mechanistic data that go beyond within-site differences in soil temperature and soil moisture or differences among broad ecosystem types (e.g. biomes). We measured soil CO_2 flux once in each of 947 experimental grassland plots at the Cedar Creek Natural History Area. We then determined the power of biomass, soil C and N, soil temperature, and other temporal factors to explain variation in soil CO_2 flux as well as the relationship between these factors and soil CO_2 flux.

Material and methods

Sites

Soil CO_2 flux was measured in five grassland experiments that have plots in seven experimental sites at the Cedar Creek Natural History Area, MN (Tilman 1988). Soils in all experimental sites are sandy (greater than 90% sand) with C content 0–20 cm no greater than 2% Experiment 001 (E001) is the long-term fertilization experiment for which plots in four fields of different successional age have been subjected to different amounts of fertilization (0–80 g N m^{-2} yr^{-1}) since 1982 (Tilman and El Haddi 1992). One field (Field D) is burned 2 out of every three years. Plots are primarily composed of mixtures of C_3 and C_4 perennial grasses with the dominance of C_3 grasses increasing with increasing fertilization, but also include annual grasses, annual forbs, and perennial forbs. Experiments 120 and 123 (E120 and E123) were seeded in 1994, and have plots that vary in the diversity and composition of C_3 grasses, C_4 grasses, perennial forbs, and legumes (Tilman et al. 1996, 1997). At the time of measurement of soil CO_2 flux, E123 had not been burned since its inception, while E120 had been burned annually. In Experiment 141 (E141), atmospheric CO_2, N supply (ambient and +4 g N m^{-2} yr^{-1}), and plant diversity and composition of C_3 grasses, C_4 grasses, forbs, and legumes are manipulated in a (Reich et al. 2002; Craine et al. 2002b). Data on soil CO_2 flux from elevated CO_2 plots in E141 were not included in this analysis. E111 is a long-term monoculture experiment in which 33 species of native and naturalized Cedar Creek

C_3 grasses, C_4 grasses, forbs, legumes, and woody species were grown for five years as monoculture before measuring soil CO_2 flux (Craine et al. 2002a).

Measurements

Measurements of soil CO_2 flux were performed with the LI-COR 6200 gas exchange system (LI-COR, Lincoln, NE, U.S.A.) fitted with the LI-COR 6400-09 soil respiration chamber. Measurements occurred at one or two locations within the plot. At each location, aboveground vegetation had recently been clipped to the soil level in a 1 m × 0.1 m strip for determination of aboveground biomass (see below). In the recently clipped area, a plastic collar, 10 cm across and 5 cm high was inserted approximately 2.5 cm into the soil. Soil CO_2 flux was measured on these collars. Each measurement consisted of 6 5-second integrations of soil CO_2 flux that spanned a 60-second period. At the beginning of each measurement, CO_2 in the chamber was scrubbed down to below ambient CO_2 concentration with soda lime and allowed to rise as CO_2 diffused in to the chamber. Soil CO_2 flux was then calculated at the ambient CO_2 concentration using linear regression (see Craine et al. (1998) for more details on measuring soil CO_2 flux). On average, plots were measured within 100 minutes of clipping. These soil CO_2 flux data have not been previously published, except for E111 (Craine et al. 2002a) and E141 (Craine et al. 2002b).

Total soil C and N were determined from up to four 2.5 cm diameter cores taken at multiple location within a plot to a depth of 20 cm (soil % C for E001, 0–15 cm; E111, 0–10 cm). Soil cores were obtained either the year of soil CO_2 flux measurement (E111, E120) or within the four previous years (4 yrs for E001, 3 for E141, and 1 for E120). Soil % C can be assumed to be relatively stable over this period (long-term measured rates of soil C accumulation are estimated at 2% per year (Knops and Tilman 2000). Soils were passed through a 1 mm sieve, dried to constant mass at 55 °C, and C and N concentrations were determined with a Carlo-Erba NA 1500 elemental analyzer (CE Elantech Incorporated, Lakewood, New Jersey). Of the 947 observations, data for only 5 measurements of soil C were missing. There were replaced by the mean soil % C for that particular experiment and field.

For belowground plant biomass (roots, rhizomes, crowns, etc.), one to three 5.08 cm diameter, 20 cm deep cores were taken in each area where aboveground biomass was clipped, except for E120 (0–30 cm) and E001 (0–15) cm. Most of the belowground plant biomass at Cedar Creek is located within the upper 15 cm of soil and variation in relationships due to the variation in sampling depth for these two experiments should be minimal. Belowground biomass was measured in the same year as soil CO_2 flux, except for E001, in which it was measured two years previously. For all experiments, belowground biomass was generally measured within 50 cm of the soil CO_2 flux collar. For aboveground biomass, 1–4 1 m × 10 cm clip strips were sampled in each plot during the year soil CO_2 flux was measured. Aboveground biomass included both green biomass and litter that was produced during that growing season.

Data analysis

Soil CO_2 flux was modeled as a function of the day of the year (linear and quadratic terms included), time of day (coded to range from 0.0 to 1.0), soil temperature at 10 cm, time since the aboveground vegetation was clipped, soil % C, soil C:N, belowground biomass, aboveground biomass, and a categorical classification of the experimental site in which soil CO_2 flux was measured (e.g. Field A or Field E111). Including the identity of the experimental site in the model partitions the variance in soil CO_2 flux that is due to average differences among experimental sites from the variance that is associated with parameters such as aboveground biomass, which may have differed on average among sites. Soil % C and soil %N were highly correlated ($r = 0.97$) and therefore only soil % C was included in the analysis. In addition to the main effect, all pairwise interactions for all terms were included, except those involving day of year and experimental site identity. Interactions with these two effects were often confounded since different experimental sites were measured on different days and there could be large differences in average properties among experimental sites. Additionally, it was not our goal to examine relationships between parameters and soil CO_2 flux within sites, as much as overall relationships that included both within and between site variation.

Using the stepwise regression protocol of JMP 4.0 (SAS, Cary NC), all the above-mentioned parameters were included in a linear regression model and then parameters with $p > 0.05$ were serially deleted. Main effects that were not significant but were part of significant interactions were retained in the final model. The relative amount of the total explainable variance that was accounted for by an individual parameter was calculated as the ratio of the sum of squares for a given parameters in the model sum of squares. Variable inflation factors (VIFs) for all parameter in the model were relatively low (< 6) indicating a low degree of colinearity among parameters. Analysis of leverage plots for each parameter revealed no apparent heteroscedasticity in relationships, nor outliers that would be determining relationships.

Results

Twelve parameters or interactions were significant predictors of soil CO_2 flux (Table 2), together explaining 55% of the total variation. The identity of the experimental site accounted for 61% of the explained variation in soil CO_2 flux, belowground biomass and aboveground biomass (including interactions) about 12% and 16% each respectively, and soil % C and soil C:N (with associated interactions) 6%. Soil temperature, time of day, time since clipping, and the interaction between time of day and time since clipping accounted the other 4% of the explained variation.

Across all plots, soil CO_2 flux increased with increased belowground biomass and aboveground (Table 2). The relationship between belowground biomass and

Table 1. Mean and standard deviation of selected parameters for each field. Included are the day and year that measurements in the field were begun, the soil temperature at 10 cm (TSoil10), soil % C, soil C:N, belowground plant biomass (BGB), aboveground plant biomass (AGB), and soil CO_2 flux (SCF)

Field	Experiment	n	Day of year	Year	TSoil10 (°C)	Soil % C	Soil C:N	BGB (g m^{-2}	AGB (g m^{-2}	SCF (μmol m^{-2} s^{-1})
E001-A	E001	54	187	1997	18.60 ± 2.19	0.87 ± 0.16	11.72 ± 0.92	617 ± 174	99 ± 44	3.16 ± 0.59
E001-B	E001	51	208	1997	26.14 ± 1.32	0.69 ± 0.20	12.97 ± 1.01	777 ± 401	198 ± 93	7.11 ± 2.17
E001-C	E001	54	222	1997	22.62 ± 2.18	1.05 ± 0.15	12.05 ± 0.67	525 ± 420	172 ± 101	4.20 ± 0.85
E001-D	E001	43	208	1997	18.26 ± 1.71	1.06 ± 0.33	12.65 ± 1.00	606 ± 360	177 ± 93	7.58 ± 1.67
E111	E111	126	231	1997	20.51 ± 2.77	0.42 ± 0.09	10.36 ± 0.73	569 ± 307	218 ± 130	3.80 ± 1.01
E120/123	E120	293	216	1997	29.21 ± 3.44	0.48 ± 0.16	11.45 ± 1.02	989 ± 421	331 ± 157	3.86 ± 1.53
E120/123	E123	146	200	1998	25.26 ± 2.27	0.47 ± 0.08	11.11 ± 0.81	716 ± 320	505 ± 220	3.58 ± 1.50
E141	E141	182	224	1999	21.05 ± 2.49	0.63 ± 0.13	11.12 ± 0.64	199 ± 215	141 ± 178	5.27 ± 1.25

Table 2. Results of the model of soil CO_2 flux. Parameters included field identity (Field), time of day (Daytime; 0–1 d), soil temperature at 10 cm (TSoil10; °C), time since aboveground biomass was clipped (TSinceClip; 0–1 d), Soil % C, Soil C:N, root biomass (BGB; g m^{-2}), aboveground biomass (AGB; g m^{-2}), and day of year (removed from model). For continuous variables, the estimate mean (± s.e.) represents the predicted relationship between the parameter and soil CO_2 flux. For example, for each additional 1 g of belowground biomass, soil CO_2 flux increases 0.0012 μmol m^{-2} s^{-1}. For experimental site identity, we include least squares means for each field, which represents the average soil CO_2 flux compared at equivalent values for all other parameters

Parameter	Estimate	df	Sum of squares	F ratio	Prob > F
Intercept	0.73 ± 0.70				0.30
Experimental site		6	661.76	73.63	<0.001
E001-A	3.28 ± 0.24				
E001-B	6.55 ± 0.23				
E001-C	3.29 ± 0.23				
E001-D	7.23 ± 0.30				
E111	4.64 ± 0.18				
E120/E123	3.90 ± 0.11				
E141	5.38 ± 0.11				
DayTime	1.53 ± 0.55	1	11.74	7.84	<0.01
TSoil10	0.02 ± 0.02	1	21.80	1.46	0.23
TSinceClip	−1.06 ± 1.32	1	0.88	0.59	0.44
DayTime*TSinceClip	−20.81 ± 6.88	1	11.97	7.99	< 0.01
Soil % C	0.89 ± 0.30	1	11.62	7.75	<0.01
TSinceClip*Soil % C	17.32 ± 4.12	1	18.03	12.03	<0.001
Soil C:N	0.10 ± 0.05	1	5.28	3.52	0.06
TSoil10*Soil C:N	0.03 ± 0.01	1	17.84	11.91	<0.001
TSinceClip*Soil C:N	−2.83 ± 0.89	1	16.53	11.03	<0.001
BGB	0.0012 ± 0.0001	1	119.64	79.87	<0.001
DayTime*BGB	0.0027 ± 0.0009	1	8.52	5.69	<0.05
AGB	0.0028 ± 0.0004	1	96.97	64.73	<0.001
TSoil10*AGB	0.00040 ± 0.00007	1	45.90	30.64	<0.001
TSinceClip*AGB	−0.03 ± 0.01	1	31.62	21.11	<0.001

soil CO_2 flux was only 42% as great as for aboveground biomass indicating that per unit biomass, aboveground biomass had a greater influence on soil CO_2 flux then belowground biomass (i.e. the C that is allocated belowground is respired by a larger biomass and/or over longer time periods). Soil CO_2 flux was greater in soils with higher carbon concentrations, but soil C:N did not significantly affect soil CO_2 flux.

Soil temperature was not a significant predictor of soil CO_2 flux, although the interactions between soil temperature and both aboveground biomass and soil C:N were positive and significant. Soil CO_2 flux showed no simple seasonal pattern as there was neither a linear nor quadratic relationship between day of year and soil CO_2 flux (data not shown). At daily time scales, soil CO_2 flux increased as the day progress from morning to late afternoon (Table 2) and there was a positive interaction between the time of day and belowground biomass, such that plots with higher biomass show greater increases in soil CO_2 flux as the day progresses.

By itself, the time since clipping was not a significant predictor of soil CO_2 flux, yet there were significant pairwise interactions between the time since clipping and time of day, aboveground biomass, soil C:N, and soil % C. Soil CO_2 flux declined more quickly after clipping later in the day, in plots with high aboveground biomass, and plots with high soil C:N. Soil CO_2 flux declined less quickly after clipping in plots with the highest soil % C.

Discussion

Most of the explainable variation in soil CO_2 flux was associated with the identity of the experimental site. Although measurements in each experimental unit were made at different times of the year, the lack of significance of the day of year term implies that differences in measurement times were not responsible for differences in soil CO_2 flux among experimental sites. Likewise, the importance of the experimental site identity term does not represent differences among experimental sites in average biomass or soil C and N concentrations. Consequently, there are still unmeasured factors that were consistently associated with differences in soil CO_2 flux in different experimental sites.

Soil moisture was not measured but is unlikely to have been a major factor. Three experiments were watered periodically during the growing season (E120, E123, and E111) and for only one unwatered experimental unit (E001, Field C) was precipitation less than 31 mm during the 7 days previous to measurement of soil CO_2 flux (6.4 mm).

Although decomposition and respiration are sensitive to soil moisture and soil temperature, a large part of soil CO_2 flux is derived from recently fixed carbon and soil CO_2 flux responds to changes in source potential associated with clipping aboveground biomass (Craine et al. (1998); this study), shading (Craine et al. 1998), and weekly variation in radiation (Fitter et al. 1999). Autotrophic respiration is thought to comprise 40–60% of total soil CO_2 flux (Raich and Schlesinger 1992), an assertion supported by physiological studies (Boume et al. 1996; Van der Werf 1996) and empirical studies (Ewel et al. 1987; Haynes and Gower 1995; Lamade et al. 1996; Landsberg and Waring 1997). The relationships between soil CO_2 flux and time of day and also time since clipping of aboveground biomass should then be due to the principle that C transfers belowground are greater as photosynthate accumulates during the day, and C reserves diminish after aboveground biomass has been removed.

Belowground and aboveground biomass, and soil C:N interacted with time of day and/or time since clipping. As the day progressed, plots with high belowground biomass would have more C allocated belowground than plots with low belowground biomass. In the plots with high belowground biomass, the rate of respiration of recently fixed C by belowground biomass and/or associated microbes would

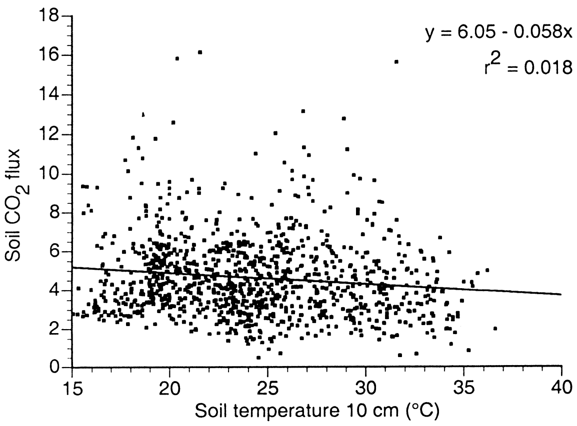

Figure 1. Relationship between soil temperature at 10 cm and soil CO_2 flux (μmol m^{-2} s^{-1}) for all plots.

have increased more than in the plots with low belowground biomass. Likewise, since plots with high aboveground biomass would have allocated more C belowground than plots with low aboveground biomass, clipping would have decreased C allocation belowground more than in plots with low aboveground biomass.

Soil temperature explained very little of the variation observed for soil CO_2 flux. In fact, there was a trend for a negative relationship between soil CO_2 flux and soil temperature over the 20 °C variation in soil temperature (10 cm depth) that was encountered (Figure 1). Most likely, the slightly negative relationship is due to plots with greater leaf area having greater C allocation belowground and more shading by the canopy. Plots with low leaf area are warm and have less C allocated belowground. Although soil temperature may be associated with a large amount of the variation in soil CO_2 flux for a given experimental site over the course of a year, this may be due to correlations with other factors. For example, diel patterns of soil CO_2 flux and temperature at a particular experimental site do not always follow Q_{10} relationships (Davidson et al. 2000), implying that seasonal relationships may not be caused by differences in soil temperature as much as differences in source potential of photosynthate. Soil temperature interacted with both aboveground biomass and soil C:N. These interactions may have been due to either direct effects of temperature on photosynthesis or to correlations between soil temperature and other factors, such as levels of photosynthetically active radiation.

Although there may be no simple mechanism to describe why there were interactions between soil C:N and both soil temperature and time since clipping, the dominance of perennial C_4 grasses has been shown to increase soil C:N ratios both at Cedar Creek (Wedin and Pastor 1993) and elsewhere (e.g. Johnson and Wedin (1997)). If C_4 grasses have greater relative allocation of C belowground, this would make plots high C:N ratios (due to the presence of C_4 grasses) more sensitive to factors that affect C fixation. In general, more research is necessary to understand the complex relationships among the various factors associated with the C economy of grassland ecosystems, especially the activity of the vegetation.

Conclusions

Soil CO_2 flux results from the decomposition of older C and the respiration of younger, labile C by roots and microbes. Models of soil CO_2 flux will most likely need to model respiration of each component separately. There is increasing evidence that models of soil CO_2 flux that incorporate only soil temperature and soil moisture will be inadequate to mechanistically understand soil CO_2 flux.

Although we saw good relationships between biomass and soil CO_2 flux, most of the variation in soil CO_2 flux was explained by the identity of the experimental site, which did not relate to differences in biomass, soil C and C:N ratio, or simple relationships with day of year. Moreover, soil C and C:N explained little of the variation in soil CO_2 flux and there was an overall negative relationship between soil temperature and soil CO_2 flux. Interactions with other factors, such as time since slipping of aboveground biomass and time of day, imply that soil CO_2 flux is greatly affected by plant physiological controls over photosynthate production and allocation belowground. More research is necessary to understand how much additional variance can be explained by environmental factors such as ambient soil moisture, radiation, or nutrient availability or biotic factors such as vegetation composition/structure or microbial biomass.

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