

## Estimating Root Plus Rhizosphere Contributions to Soil Respiration in Annual Croplands

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### ABSTRACT

Although soil respiration represents an important C transfer from terrestrial ecosystems to the atmosphere, the effects of environmental and biological factors on soil respiration rates are not adequately understood. This is due primarily to the variety of processes that produce CO<sub>2</sub> within the soil. Thus, separating the main CO<sub>2</sub>-producing processes is needed to improve our understanding of soil C cycling and dynamics. Here, we describe and test a model that estimates soil CO<sub>2</sub> emissions derived from anabolic and catabolic processes, representing organic matter decomposition and root + rhizosphere respiration, respectively. Our model is based on the exponential response of organic matter decomposition with respect to temperature, and it requires only measurements of total soil CO<sub>2</sub> emissions and soil temperature as inputs. To test the model, we relied on published measurements of soil respiration rates and soil temperatures in a maize (*Zea mays* L.) field in Ottawa, Canada, and on independent estimations of soil and root contributions for this field made on the basis of stable-C isotope measurements of soil-derived CO<sub>2</sub>. Model-based and isotope estimations correlated significantly ( $r^2 = 0.91$ ,  $P < 10^{-9}$ ) on a daily basis. Model-based estimations for root + rhizosphere respiration rates for the entire growing season totaled 145 g C m<sup>-2</sup> or 27% of CO<sub>2</sub> emissions, and those based on C isotopes totaled 158 g C m<sup>-2</sup> or 30% of the total emissions. The excellent correspondence between model-based and isotope-based estimations suggests that this relatively simple model can be used to distinguish root from soil contributions to soil CO<sub>2</sub> emissions in temperate-zone, annual croplands free of significant water stress.

THE RELEASE OF carbon dioxide from soils to the atmosphere is the single largest pathway by which C is lost from soils in most annual cropping systems (Buyanovsky et al., 1987; Paustian et al., 1990; Paul et al., 1999). Measurements of soil CO<sub>2</sub> emissions therefore provide useful insights into soil C cycling, and provide a basis for evaluating soil C dynamics and potential C sequestration under different crop management systems (e.g., Lundegårdh, 1927; Monteith et al., 1964; Alvarez et al., 1995; Franzluebbers et al., 1995; Duiker and Lal, 2000). The use of soil respiration measurements to evaluate soil C balances is confounded, however, by the whole-soil nature of the flux. Carbon dioxide is produced in soils by a variety of processes, including both root respiration and heterotrophic oxidation of soil organic matter (SOM). The specific effects of environmental variables on root and microbial processes in soils may differ (e.g., Kirschbaum, 1995; Boone et al., 1998),

but measurements of total soil-CO<sub>2</sub> emissions represent only their sum. Thus, distinguishing among different soil CO<sub>2</sub>-producing processes is required if soil respiration measurements are to be used to investigate controls over those individual processes. It would be particularly useful to distinguish the CO<sub>2</sub> produced during SOM decomposition from the CO<sub>2</sub> produced by root and rhizosphere respiration (Fig. 1) because this distinction would enable soil-CO<sub>2</sub> efflux measurements to be used to evaluate in situ SOM decay and turnover rates or, alternatively, in situ rates of root and rhizosphere respiration.

Figure 1 illustrates the flux of C through the crop-soil system. For simplification, erosional losses of SOM and organic matter inputs from outside the system, such as manure applications, have been excluded; in locations where those processes are important they would need to be incorporated into the mass balance. Crop harvests are not included in Fig. 1 because they reflect removals of biomass before its incorporation into the soil. Figure 1 indicates that only the quantity of C that actually passes through the soil food web (flows 1 → 2 + 4 → 6 in Fig. 1) is useful for quantification of soil C loss rates, or determination of SOM turnover rates. Flow-path 1 → 3 → 5 represents photosynthetic products that are consumed directly by roots, mycorrhizae, and rhizosphere-associated organisms in their respiratory pathways (i.e., catabolic processes), without ever being diverted to secondary metabolic pathways (i.e., anabolic processes) that lead to the formation of proteins, structural materials, and secondary compounds that are enzymatically decomposed within soils. Observed temporal variations in soil respiration rates (Flow 7 in Fig. 1) may reflect changes in either SOM decomposition (Flow 6) or in root and rhizosphere respiration (Flow 5). Thus, observed correlations between environmental variables and soil respiration rates cannot be assumed to reflect the independent effects of those environmental variables on the individual processes generating CO<sub>2</sub> within the soil.

For example, a highly significant, positive correlation between soil temperature and soil-CO<sub>2</sub> emissions is frequently observed in field studies (e.g., Rochette et al., 1991; Alvarez et al., 1995; Luo et al., 2001; Tufekcioglu et al., 2001). Such data suggest that higher temperatures may stimulate the heterotrophic oxidation of SOM and deplete soil C pools (e.g., Schleser, 1982; Jenkinson et al., 1991; Raich and Schlesinger, 1992; Amundson, 2001). Soil-warming experiments generally support the hypothesis that increased temperatures stimulate soil respiration rates (Rustad et al., 2001), but higher rates of soil respiration do not necessarily indicate faster rates of SOM decomposition (Flow 6 in Fig. 1); they may

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Published in Soil Sci. Soc. Am. J. 69:634–639 (2005).  
doi:10.2136/sssaj2004.0257

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**Abbreviations:** DOY, day of year; SOM, soil organic matter.

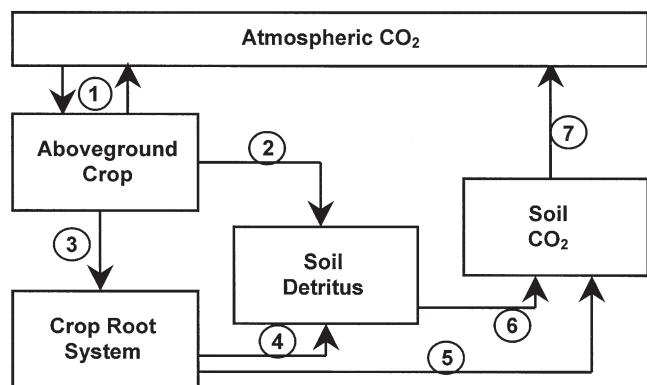


Fig. 1. Carbon fluxes through the crop-soil system. 1 = net crop production, generating organic matter from atmospheric CO<sub>2</sub>. 2 = aboveground crop residues returned to the soil surface. 3 = below-ground C allocation, that is, fluxes of C from shoots to root systems. 4 = root mortality and other inputs of organic matter from root systems to the soil. 5 = root, mycorrhizal, and rhizosphere respiration. 6 = CO<sub>2</sub> produced by the heterotrophic oxidation of detritus in the soil. 7 = surface soil CO<sub>2</sub> efflux, or soil respiration.

represent increased rates of root and rhizosphere respiration (Flow 5 in Fig. 1) (Andrews et al., 1999; Kirschbaum, 2000; Andrews and Schlesinger, 2001).

Indeed, several studies provide evidence that seasonal changes in soil respiration rates correlate with plant growth processes rather than with temperature per se (Yoneda and Okata, 1987; Rochette et al., 1992; Craine et al., 1999; Högberg et al., 2001; Kuzyakov and Cheng, 2001; Franzluebbers et al., 2002). These results imply that recent canopy photosynthesis drives soil respiration rates by influencing shoot-to-root C transport, and that the commonly observed correlation between temperature and soil respiration rate is due, at least in part, to increased plant growth at higher temperatures. In annual croplands there is a variety of soil CO<sub>2</sub>-producing processes that occur only during the growing season; the initiation and termination of these belowground processes may generate seasonal patterns in soil-CO<sub>2</sub> emissions that correlate with temperature, even if temperature has no effect on SOM decay rates (e.g., Fig. 2). Distinguishing the sources of CO<sub>2</sub> released from soils is a necessary prerequisite to understanding the mechanisms causing changes in soil-to-atmosphere CO<sub>2</sub> fluxes in response to land-use, cropping system, soil management, or environmental changes (Bowden et al., 1993; Cheng, 1996; Kelting et al., 1998). Our ability to do so currently is limited to sites where distinct C-isotope signatures exist between soils and plant roots (e.g., Robinson and Scrimgeour, 1995; Rochette et al., 1999; Ehleringer et al., 2000), but such conditions are unusual and reflect recent, dramatic changes in plant cover. A robust method for quantifying the sources of soil-derived CO<sub>2</sub> in a broader range of conditions is needed.

The objective of this paper is to describe and test a new model-based approach for estimating the two main sources of soil-derived CO<sub>2</sub>, root + rhizosphere respiration and SOM decomposition, with particular reference to annual crop fields in moist temperate regions. This new approach does not depend on recent changes in crop cover, does not require analysis of C isotopes, and

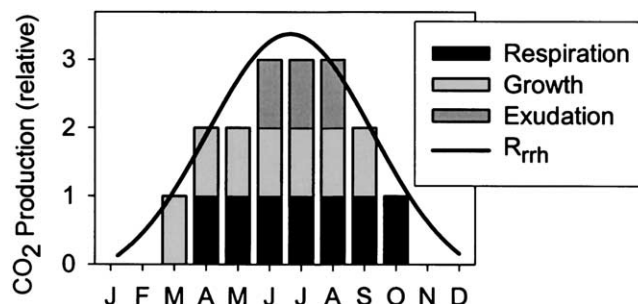


Fig. 2. Hypothetical representation of seasonally variable CO<sub>2</sub> sources from different root processes contributing to total soil respiration. Root processes that generate CO<sub>2</sub> directly (root growth and root respiration) or indirectly (microbial respiration of root exudates) are shown to be seasonal, turning on and off depending on crop growth and phenology. A strongly seasonal pattern of total CO<sub>2</sub> production by roots (*R<sub>rrh</sub>*) is generated, even though none of the individual process rates correlate with temperature.

should be widely applicable to studies of in situ SOM dynamics in annual cropping systems of moist temperate regions.

## MATERIALS AND METHODS

### Model Conceptualization

Our objective requires that the CO<sub>2</sub> that is produced during the aerobic respiration of simple carbohydrates by living roots, mycorrhizae, and rhizosphere organisms (Flow 5, Fig. 1) be distinguished from the CO<sub>2</sub> that is produced during the decomposition of SOM and plant residues (Flow 6, Fig. 1). We refer to these two processes as root + rhizosphere respiration (*R<sub>rrh</sub>*) and SOM decomposition (*R<sub>som</sub>*), respectively. Over any given time step, the total amount of CO<sub>2</sub> that is emitted from the surface of the soil to the atmosphere (Flow 7, Fig. 1), that is, soil respiration (*R<sub>soil</sub>*), reflects the sum of these two sources:

$$R_{\text{soil}} = R_{\text{som}} + R_{\text{rrh}} \quad [1]$$

Temperate-zone annual croplands provide a situation where the two main sources of CO<sub>2</sub> in soils (Fluxes 5 and 6 in Fig. 1) may be more easily distinguished because root + rhizosphere respiration is limited to the cropping phase, when living plants are present. During the rest of the year only soil heterotrophic activity produces CO<sub>2</sub>. Thus, the two main sources of CO<sub>2</sub> in soils are segregated in time, to some extent, and it is necessary only to distinguish these two sources during the growing season. In the following model description, we emphasize that *R<sub>soil</sub>* and *T<sub>soil</sub>* (i.e., soil temperature in °C) are measured values, whereas *R<sub>som</sub>* and *R<sub>rrh</sub>*, when shown in italics, are values estimated by the model.

Seasonal patterns of soil respiration in moist temperate-zone systems can be modeled as a function of temperature using

$$R_{\text{soil}} = R_{\text{soil0}} \times \exp(Q \times T_{\text{soil}}) \quad [2]$$

where *R<sub>soil</sub>* is the measured, in situ soil respiration rate (e.g., g C m<sup>-2</sup> d<sup>-1</sup>), the parameter *R<sub>soil0</sub>* is the soil respiration rate when *T<sub>soil</sub>* = 0°C, and *Q* is the temperature coefficient (units = °C<sup>-1</sup>). This model has been widely applied to evaluation of soil respiration data (e.g., Nakane, 1980; Silvola et al., 1985; Kieth et al., 1997; Law et al., 1999; Mielenick and Dugas, 2000; Luo et al., 2001) and is generally applicable to data from sites without significant water stress. The *Q<sub>10</sub>* of this relationship is equal to  $\exp(Q \times 10)$ . Reported *Q<sub>10</sub>* values of in situ soil

respiration vary widely, but are usually  $>2$ , and are often much higher (Raich and Schlesinger, 1992).

Studies demonstrate that soil respiration rates in vegetation-free plots increase with temperature (e.g., Monteith et al., 1964; Alvarez et al., 1995; Rochette et al., 1999; Duiker and Lal, 2000), demonstrating that  $R_{\text{som}}$  is a function of temperature. Modifying Eq. [2] we get:

$$R_{\text{som}} = R_{\text{som0}} \times \exp(Q_{\text{som}} \times T_{\text{soil}}) \quad [3]$$

where  $R_{\text{som0}}$  refers to the rate of  $\text{CO}_2$  production by heterotrophic oxidation of SOM when  $T_{\text{soil}}$  equals  $0^\circ\text{C}$ . From Eq. [1]  $R_{\text{rrh}}$  can be estimated by difference:

$$R_{\text{rrh}} = R_{\text{soil}} - R_{\text{som}} \quad [4]$$

with the following two caveats. First, because least-squares linear regression provides a best estimate of parameter values but rarely explains 100% of the variance in a relationship, estimated  $R_{\text{som}}$  (Eq. [3]) will occasionally be greater than measured  $R_{\text{soil}}$ , resulting in negative estimates of  $R_{\text{rrh}}$  (Eq. [4]) as statistical artifacts. Therefore:

$$\text{IF } R_{\text{som}} > R_{\text{soil}} \text{ THEN } R_{\text{som}} = R_{\text{soil}} \quad [5]$$

Second, for purposes of temperate-zone annual cropping systems, we assume that there is no root + rhizosphere respiration during the crop-free period, that is, when soil temperatures are at or below freezing:

$$\text{IF } T_{\text{soil}} \leq 0 \text{ THEN } R_{\text{som}} = R_{\text{soil}} \quad [6]$$

where  $T_{\text{soil}}$  is measured in  $^\circ\text{C}$ . In Eq. [6] any basal temperature may be used in place of  $0^\circ\text{C}$ , to limit predictions to the cropping period, when living roots are present (e.g., Jones et al., 1991).

### Defining Model Parameter Values

To apply this model to estimate the individual contributions of  $R_{\text{som}}$  and  $R_{\text{rrh}}$  to the total soil respiration flux, measurements of total soil- $\text{CO}_2$  emissions ( $R_{\text{soil}}$ ) and soil temperatures ( $T_{\text{soil}}$ ) throughout the growing season or year are needed. Given these data, the model requires that the values of only two parameters,  $R_{\text{som0}}$  and  $Q_{\text{som}}$  (Eq. [3]), be defined.

In annual croplands of temperate zones with no winter crop, there is no root + rhizosphere contribution to the total soil respiration flux during the crop-free period. Therefore, in such systems, the value of  $R_{\text{soil0}}$  (Eq. [2]) provides a direct, statistically defined estimate of  $R_{\text{som0}}$  (Eq. [3]). The value of  $R_{\text{soil0}}$  ( $= R_{\text{som0}}$ ) can be defined from field measurements of  $R_{\text{soil}}$  and  $T_{\text{soil}}$ , via linear regression of the linearized form of Eq. [2]:

$$\ln(R_{\text{soil}}) = \text{intercept} + Q \times T_{\text{soil}} \quad [7]$$

with  $R_{\text{soil0}}$  being equal to  $\exp(\text{intercept})$ . To complete the model, we assume that the value of the parameter  $Q_{\text{som}}$  (Eq. [3]) equals  $\ln(2)/10$ , that is, that the  $Q_{10}$  of SOM decomposition = 2. A literature review of laboratory-based studies found that a  $Q_{10} = 2$  adequately described the temperature effect on SOM decomposition across a temperature range of approximately 5 to  $35^\circ\text{C}$  (Kätterer et al., 1998). Also, based on field studies in three cropping systems in Japan, the  $Q_{10}$  of SOM decay was found to average 2 (range 1.9–2.2) (Koizumi et al., 1993).

To summarize the model, measurements of soil respiration and soil temperature gathered throughout the growing season or year are used to statistically define the value of  $R_{\text{soil0}}$  (Eq. [2]) via linear regression (Eq. [7]), and this value is assumed equal to  $R_{\text{som0}}$  (Eq. [3]). Then,  $R_{\text{som}}$  is predicted from soil temperature data under the assumption that the  $Q_{10}$  of SOM decay = 2:

$$R_{\text{som}} = R_{\text{soil0}} \times \exp\{[\ln(2)/10] \times T_{\text{soil}}\} \quad [8]$$

At each measurement period,  $R_{\text{rrh}}$  is estimated from Eq. [4], as corrected by Eq. [5] and [6].

### Testing the Model

We applied this model to previously published measurements of total soil respiration and soil temperatures (Rochette et al., 1999) in a maize field in Ottawa, Canada ( $45^\circ 22' \text{ N lat.}$ ,  $75^\circ 43' \text{ W long.}$ ). Maize was planted on day of year (DOY) 145 in 1996, into a formerly cropped field that had not previously supported  $\text{C}_4$  vegetation, and which therefore had a distinct  $\text{C}_3$  signature in its SOM. Glycophosphate was applied on DOY 124, the soil was moldboard plowed on DOY 134, was disked on DOY 137 and 138, and was fertilized on DOY 137. Soil temperatures were monitored at 20-cm depth with copper-constantan thermocouples. Soil respiration was measured 18 times from DOY 148 to DOY 303 using a dynamic closed-chamber system described by Rochette and Flanagan (1997).

We tested the accuracy of the model's predictions of root + rhizosphere respiration using stable C-isotope analyses of soil-emitted  $\text{CO}_2$ . The details and results of that study are described fully by Rochette et al. (1999). In brief, the  $\delta^{13}\text{C}$  of  $\text{CO}_2$  emitted from the soil surface represented a mixture of root + rhizosphere respiration, derived from the maize ( $-13.65\text{‰}$ ), and SOM decomposition, derived from the previous  $\text{C}_3$  vegetation ( $-24\text{‰}$ ). A two-pool mixing model was applied to  $\delta^{13}\text{C}$  measurements of soil-emitted  $\text{CO}_2$  to determine the proportional contributions of the two isotopically distinct soil- $\text{CO}_2$  sources, as the maize grew and senesced (Rochette et al., 1999).

### RESULTS

Total soil- $\text{CO}_2$  emissions ( $R_{\text{soil}}$ ,  $\text{g C m}^{-2} \text{ d}^{-1}$ ) from the maize field correlated significantly with soil temperature ( $T_{\text{soil}}$ ,  $^\circ\text{C}$ ):

$$\ln(R_{\text{soil}}) = -0.236(\pm 0.336) + \exp[0.08156(\pm 0.01823) \times T_{\text{soil}}] \quad [9]$$

( $n = 18$ , adjusted  $r^2 = 0.53$ ,  $P < 0.001$ ,  $F_{1,16} = 20.0$ ). Standard errors of the parameter estimates are shown in parentheses. The value of  $R_{\text{soil0}} = \exp(-0.236) = 0.79 \text{ g C m}^{-2} \text{ d}^{-1}$ . This value was incorporated into Eq. [8] to predict  $R_{\text{som}}$  for each date for which independent, isotopically based determinations of  $R_{\text{rrh}}$  were made. Then,  $R_{\text{rrh}}$  was estimated as the difference between measured total soil respiration and model-estimated  $R_{\text{som}}$  (Eq. [4]–[6]). Based on the model,  $R_{\text{rrh}}$  ranged from zero on DOY 155, 162, 176, 282, and 303, to a maximum rate of  $3.0 \text{ g C m}^{-2} \text{ d}^{-1}$  on DOY 247. Over the entire measurement period (DOY 155–303),  $R_{\text{rrh}}$  totaled  $145 \text{ g C m}^{-2}$ , or 27% of  $R_{\text{soil}}$ , whereas  $R_{\text{som}}$  totaled  $388 \text{ g C m}^{-2}$ .

Based on C-isotope measurements of soil-emitted  $\text{CO}_2$ ,  $R_{\text{rrh}}$  in the maize field was determined to be  $158 \text{ g C m}^{-2}$ , or 30% of measured  $R_{\text{soil}}$  and 17% of total net crop C assimilation (Rochette et al., 1999). Model-based estimates of daily  $R_{\text{rrh}}$  and  $R_{\text{som}}$  were also very similar to the independently derived, isotopically based determinations made by Rochette et al. (1999) (Fig. 3). Model-estimated rates of  $R_{\text{rrh}}$  ( $\text{g C m}^{-2} \text{ d}^{-1}$ ) correlated significantly with isotopically determined rates according to:

$$R_{\text{rrh}}(\text{model}) = 0.975 \times R_{\text{rrh}}(\text{isotopes}) - 0.0346 \quad [10]$$



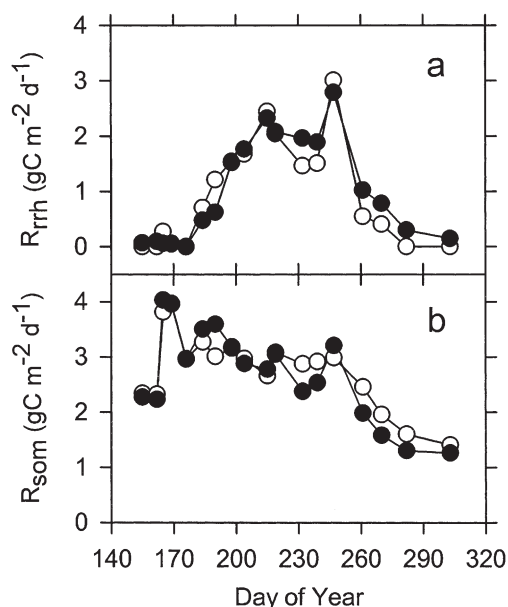


Fig. 3. Observed (solid symbols) and model-estimated (open symbols) rates of soil-CO<sub>2</sub> production resulting from (a) root + rhizosphere respiration ( $R_{rh}$ ) and (b) the decomposition of soil organic matter ( $R_{som}$ ) in a maize (*Zea mays* L.) field at Ottawa, Canada. Observed data are from Rochette et al. (1999).

( $n = 18$ ,  $r^2 = 0.91$ ,  $F_{1,16} = 170.1$ ,  $P < 10^{-9}$ ). The slope of this equation was not different from 1.0, and the intercept was not significantly different from zero. The sum of  $R_{rh}$  and  $R_{som}$  equals the measured soil respiration rate (Eq. [1]), so the absolute errors of the model-based estimates of  $R_{rh}$  (Fig. 3a) are equal to those for SOM decomposition ( $R_{som}$ , Fig. 3b).

## DISCUSSION

Despite widespread use of soil respiration measurements to understand better the cycling of C through soils, the inability to distinguish among the dominant processes producing CO<sub>2</sub> within soils greatly limits the interpretability of soil respiration data. Carbon dioxide is produced by the oxidation of simple carbohydrates by roots, mycorrhizae, and closely associated rhizosphere organisms (i.e., root + rhizosphere respiration,  $R_{rh}$ ), and via microbial decomposition of SOM and plant residues (i.e., SOM decay,  $R_{som}$ ). Root + rhizosphere respiration represents C that has not entered the detrital pathway, and therefore has relatively little direct influence on SOM dynamics. Estimates of the turnover times of soil detritus require that CO<sub>2</sub> production resulting from the oxidation of structural compounds produced by living organisms (i.e.,  $R_{som}$ ) be quantified separately from the CO<sub>2</sub> that is produced by  $R_{rh}$ . At the same time, CO<sub>2</sub>-producing processes such as root and mycorrhizal growth, root and mycorrhizal respiration, and the heterotrophic respiration of simple carbohydrates exuded by roots to the rhizosphere, all of which contribute to  $R_{rh}$ , are all expected to vary seasonally yet are difficult to quantify based on measurements of  $R_{soil}$ . Our ability to investigate important processes governing C cycling within intact soils, and to define their individual interac-

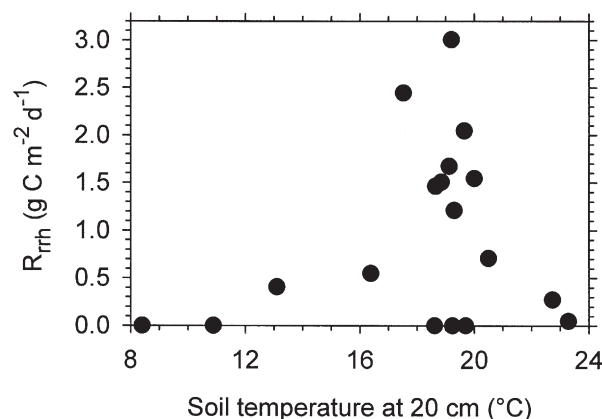


Fig. 4. Model-predicted root + rhizosphere respiration ( $R_{rh}$ ) in a maize field in Ontario, shown in relation to soil temperature. Each point represents a single days data. The two variables are not correlated (linear regression,  $n = 18$ ,  $r^2 = 0.05$ ,  $P = 0.36$ ). The relationship between predicted and isotopically determined  $R_{rh}$  is shown in Fig. 3.

tions with environmental variables, are limited by our inability to isolate these different processes without disrupting them.

Use of the described model allows for the estimation of rates of both SOM decomposition and root + rhizosphere respiration. Decomposition was assumed to be temperature dependent, based on numerous studies (e.g., Douglas and Tedrow, 1959; Clark and Gilmour, 1983; Rochette et al., 1999), and the value of  $R_{soil0}$  (Eq. [8]), which reflects the overall quantity and quality of SOM present within the entire biologically active soil profile, was assumed to be constant over the course of the year. Under these assumptions, there was no significant correlation between temperature and  $R_{rh}$  (Fig. 4), despite that root respiration rates are reported to increase with temperature (e.g., Szaniawski and Kielkiewicz, 1982; Burton et al., 2002). This indicates that factors other than temperature controlled rates of root + rhizosphere respiration in the maize field. Those factors are likely related to growth-related shifts in root growth, biomass, exudation rates, etc., as the maize crop grew, flowered, matured, and senesced. That is, crop processes, not environmental factors, likely drove seasonal changes in  $R_{rh}$  and, as a result, the seasonal pattern of total  $R_{soil}$ , as shown hypothetically in Fig. 2. Partitioning of total soil CO<sub>2</sub> emissions into  $R_{som}$  and  $R_{rh}$  provides a mechanism whereby phenological and plant-growth variables can be evaluated and incorporated into mechanistically based C-cycling models.

A variety of approaches have been applied previously to estimate root contributions to total soil respiration in annual cropping systems. Root respiration was estimated to total 12 to 15% of total soil respiration ( $R_{soil}$ ) in a winter wheat field, and from 35 to 40% of  $R_{soil}$  in a soybean field in Missouri (Buyanovsky et al., 1987; Buyanovsky and Wagner, 1995). In four Swedish agroecosystems root respiration ranged from 26 to 29% of  $R_{soil}$  (Paustian et al., 1990). In a crop-fallow-crop-fallow system in India, root respiration totaled 14% of  $R_{soil}$  over the entire year (Singh and Shekhar, 1986). At the Rothamsted Experimental Station, Monteith et al. (1964)

found that  $R_{\text{soil}}$  beneath crops averaged 50 to 75% higher than rates in fallow plots during the growing season, indicating that  $R_{\text{rrh}}$  averaged 33 to 43% of  $R_{\text{soil}}$  in the cropped fields. These studies suggest a relatively large amount of variability among croplands, but this is no doubt due in part to differing definitions of root respiration, and to the different approaches applied to estimate its magnitude (Hanson et al., 2000).

The model we describe focuses on metabolic pathways (Fig. 1) rather than organisms. Aerobic respiration is similar among roots, mycorrhizal fungi, and soil microbes, and may therefore be considered a single metabolic pathway ( $R_{\text{rrh}}$ ), regardless of the organisms involved. Similarly, a variety of soil organisms degrade and utilize organic materials within soils, thus contributing to SOM decomposition ( $R_{\text{som}}$ ). These correspond to catabolic and anabolic metabolism pathways, respectively. The model we describe does not attempt to distinguish among organisms contributing to  $R_{\text{rrh}}$ , nor among organisms that contribute to  $R_{\text{som}}$ ; it does distinguish between the two principle metabolic pathways that commonly are included in soil C-cycling models.

Application of the model described in this paper to measured soil respiration rates and soil temperatures in an Ottawa maize field indicated that  $R_{\text{rrh}}$  contributed 27% of the cumulative growing-season soil-respired  $\text{CO}_2$ , compared with the 30% contribution estimated from isotopic measurements of soil-derived  $\text{CO}_2$  (Rochette et al., 1999). Across the growing season, contributions of  $R_{\text{rrh}}$  (i.e., model-simulated  $R_{\text{rrh}}$ ) to  $R_{\text{soil}}$  varied from 0 to 50%, the latter on DOY 247 (Fig. 3). More than 30% of the total  $R_{\text{soil}}$  was estimated to derive from root activities from DOY 198 to DOY 247, coinciding with the period of maximum maize growth (Rochette et al., 1999). Thus, the model herein described captured both the magnitude and seasonal variability in  $R_{\text{rrh}}$  fluxes previously described based on C-isotope studies.

Perhaps the largest uncertainty in applying our model is the determination of the temperature coefficient of soil respiration (i.e.,  $Q$  in Eq. [7]), and the corresponding temperature coefficient of SOM decay (i.e.,  $Q_{\text{som}}$  in Eq. [3]). It is important to recognize that the temperature coefficient is dependent on where temperature was measured (e.g., Morén and Lindroth, 2000; Rayment and Jarvis, 2000), because the amplitude of the soil temperature cycle typically decreases as the depth of measurement increases (Hillel, 1998). Rochette et al. (1999) measured soil temperature at three depths: 10, 20, and 40 cm. In the model description above we used data from the intermediate depth to best reflect the mean soil-profile temperature. Independent analyses of Rochette et al.'s  $R_{\text{soil}}$  data using soil temperatures measured at 10, 20, and 40 cm gave estimates of  $Q$  (Eq. [2] and [7]) = 0.0671, 0.0816, and 0.112, respectively, or  $Q_{10}$  values of 2.0, 2.3, and 3.1. The corresponding basal metabolism rates (i.e.,  $R_{\text{soil}0}$  in Eq. [2]) decreased from 0.99 to 0.49  $\text{g C m}^{-2} \text{d}^{-1}$  over this same temperature-depth range (i.e., 10–40 cm). Regardless of the depth at which temperature was monitored, model-predicted  $R_{\text{rrh}}$  was significantly related to isotope-determined  $R_{\text{rrh}}$  [Eq. 10], with  $r^2$  values of 0.88 to 0.94 (linear regression,  $P <$

$10^{-8}$ ), when it was assumed that  $Q_{\text{som}}/Q = 0.85$  [i.e.,  $[\ln(2)/10]/0.08156$ ]. That value was determined from our results based on soil temperatures at 20 cm (Eq. [9]). Because different investigators measure soil temperatures at different depths, we suggest that the value of  $Q_{\text{som}}$  (Eq. [8]) may be defined as equal to  $Q \times 0.85$ , rather than being assumed to be  $\ln(2)/10$ . This modification may allow the model to be more universally applicable to different situations and studies. With that modification, the model properly simulated the isotopically determined fluxes of  $\text{CO}_2$  from both  $R_{\text{rrh}}$  and  $R_{\text{som}}$ , at both seasonal and daily scales, regardless of the depth at which temperature was monitored.

Previous attempts to distinguish root from soil contributions to total soil respiration have largely depended on either (i) isolating and thereby modifying these integrated processes, or (ii) quantifying the isotopic compositions of  $\text{CO}_2\text{-C}$  produced by roots and soil heterotrophs, and their proportional contributions to total soil respiration. Only the latter approach seems to be uniformly applicable to intact cropping systems, but isotopic approaches require that there be a distinct isotopic difference between the crop and the residual SOM. That is only infrequently the case.

We suggest that the model we present here may be used to estimate daily, seasonal, and annual contributions of  $R_{\text{rrh}}$  and  $R_{\text{som}}$  to total soil respiration, and thereby provides a useful tool for investigating within-soil C-cycling processes, and their individual responses to crop management or environmental conditions. Requirements for application of the model are measurements of soil respiration rates and soil temperatures throughout the growing season or year. Isotopic analyses of soil-derived  $\text{CO}_2$  are not necessary. Independent testing of the model is needed, but partitioning of soil-derived  $\text{CO}_2$  fluxes into anabolic ( $R_{\text{som}}$ ) and catabolic ( $R_{\text{rrh}}$ ) sources would substantially improve our capacity to understand in situ soil C-cycling processes. Soil respiration determines to a large extent whether a particular ecosystem functions as a source or as a sink of C. The model presented here allows for a better evaluation of the environmental factors that affect root + rhizosphere respiration and allows for a better quantification of SOM loss and turnover rates, which are needed to estimate potential sequestration of C in cropland soils.

## ACKNOWLEDGMENTS

We thank Philippe Rochette for sharing his original data with us. The work was funded by the U.S. National Science Foundation (DEB-0343766) and the college of Liberal Arts and Sciences at Iowa State University.

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