Interannual variability in global soil respiration, 1980–94

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Abstract
We used a climate-driven regression model to develop spatially resolved estimates of soil-CO₂ emissions from the terrestrial land surface for each month from January 1980 to December 1994, to evaluate the effects of interannual variations in climate on global soil-atmosphere CO₂ fluxes. The mean annual global soil-CO₂ flux over this 15-y period was estimated to be 80.4 (range 79.3–81.8) Pg C. Monthly variations in global soil-CO₂ emissions followed closely the mean temperature cycle of the Northern Hemisphere. Globally, soil-CO₂ emissions reached their minima in February and peaked in July and August. Tropical and subtropical evergreen broad-leaved forests contributed more soil-derived CO₂ to the atmosphere than did any other vegetation type (∼30% of the total) and exhibited a biannual cycle in their emissions. Soil-CO₂ emissions in other biomes exhibited a single annual cycle that paralleled the seasonal temperature cycle. Interannual variability in estimated global soil-CO₂ production is substantially less than is variability in net carbon uptake by plants (i.e., net primary productivity). Thus, soils appear to buffer atmospheric CO₂ concentrations against far more dramatic seasonal and interannual differences in plant growth. Within seasonally dry biomes (savannas, bushlands and deserts), interannual variability in soil-CO₂ emissions correlated significantly with interannual differences in precipitation. At the global scale, however, annual soil-CO₂ fluxes correlated with mean annual temperature, with a slope of 3.3 Pg C y⁻¹ per °C. Although the distribution of precipitation influences seasonal and spatial patterns of soil-CO₂ emissions, global warming is likely to stimulate CO₂ emissions from soils.

Keywords: climate change, global carbon cycle, global warming, model, soil carbon dioxide emissions

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Introduction
Increasing atmospheric CO₂ concentrations have enhanced our need to understand better the global sources and sinks of carbon, and their responses to environmental changes. The dominant terrestrial source of CO₂ is soils. Carbon dioxide is produced in soils primarily by heterotrophic organisms and by respiration of living roots, and most CO₂ produced in soils is released to the atmosphere. This process, commonly called soil respiration, produces 75–80 Pg of CO₂-C annually (Schlesinger, 1977; Raich & Potter, 1995). This is more than 11 times the current rate of fossil fuel combustion (Marland et al., 2000) and indicates that ∼10% of the atmosphere’s CO₂ cycles through soils each year. Environmental changes that alter rates of soil respiration thus have a strong potential to influence atmospheric CO₂ levels.

Temperature has a strong impact on soil respiration rates, and the potential for increased rates of CO₂ production by soils in response to global warming suggests that a positive feedback between global warming and atmospheric CO₂ concentrations could arise (Schleser, 1982; Jenkinson et al., 1991; Raich & Schlesinger, 1992; Trumbore et al., 1996; Kirschbaum, 2000; Schlesinger & Andrews, 2000). Soil respiration is also controlled by moisture availability, with dry soils producing less CO₂ than wet soils (Parker et al., 1984; Davidson et al., 2000; Mielnick & Dugas, 2000). Hence, changes in moisture

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availability, driven by changing precipitation patterns, have the potential to offset or exacerbate temperature-driven changes in soil-CO$_2$ emissions (e.g., Saleska et al., 1999). Both global temperatures and precipitation patterns are expected to change in the future (e.g., Houghton, 1997), potentially altering CO$_2$ fluxes from soils. To evaluate the sensitivity of soil-CO$_2$ emissions to climatic variability, we developed spatially resolved estimates of global soil respiration using a monthly time-step from 1980 to 1994. This period included both wet and dry years, and six of the warmest years recorded to that time (Jones et al., 2000).

Materials and methods

We estimated the seasonal and spatial distribution of global soil-CO$_2$ emissions following the regression-based modeling approach of Raich & Potter (1995). This approach differs fundamentally from that of process-based ecosystem models, which simulate changes in state variables and elemental fluxes through time, but which also contain the many parameters needed to do so. Our model contains only three parameters, each of which is defined statistically using least-squares approaches, and is driven solely by weather data. Our model also predicts directly a single, widely measured flux—soil respiration—in contrast to ecosystem models that separately predict CO$_2$ production by heterotrophic soil organisms and by living roots, neither of which is measured directly in any intact ecosystem. One benefit of our approach is that the model predictions provide a truly independent, spatially and temporally resolved global dataset of soil-CO$_2$ emissions that can be used to corroborate the predictions of more complex ecosystem models.

The models of Raich & Potter (1995) were based on regressions of measured soil respiration rates against mean monthly air temperature and rainfall data. However, many of the soil respiration measurements used to determine the model parameters were obtained with static-chamber methods that may underestimate true soil respiration rates (e.g., Ewel et al., 1987; Rochette et al., 1992b; Norman et al., 1997). We therefore recalculated the model parameters based on a new and largely independent data set of soil respiration measurements made almost entirely with dynamic, IRGA-based systems. To do so, we compiled published measurements of soil respiration made with dynamic chambers coupled to IRGA-based CO$_2$ measurement devices (Table 1). Each measurement was referenced to the month in which it was made and the site location. When more than one measurement was made within a particular site and month, those data were averaged to estimate the mean monthly soil-CO$_2$ flux for that month and site. When publications included data from more than one site at the same location (i.e., sites on different soils or with different vegetation covers), each site was incorporated into our database. For each location and month for which we found published soil respiration data, we appended mean monthly air temperature and precipitation data for the 1980–94 period based on New et al. (2000). Due to the paucity of dynamic-chamber data from arid regions, we included static-chamber measurements from deserts (Caldwell et al., 1977; Parker et al., 1983). We also included measurements of CO$_2$ emissions from snow-covered soils derived with a variety of techniques (Sommerfeld et al., 1993; Zimov et al., 1993; Winston et al., 1997). We did not distinguish disturbed sites from those containing natural vegetation, nor did we include any data from wetlands.

Our final data set encompassed mean monthly air temperatures ranging from −33.4 to 27.6°C, mean monthly precipitation levels of 0.8–47.3 cm, and measured soil-CO$_2$ emissions ranging from 0.03 to 9.84 g C m$^{-2}$ d$^{-1}$.

The model $B$ of Raich & Potter (1995) contains three parameters: $F$ (g C m$^{-2}$ d$^{-1}$) represents the soil respiration rate when the mean monthly air temperature is 0°C; $Q$ (°C$^{-1}$) defines the rate of change of the soil respiration rate with respect to temperature; and $K$ (mm mo$^{-1}$) is the half-saturation constant for a hyperbolic relationship between soil respiration and rainfall:

$$R_S = F \times e^{(Q-T_s)} \times \left[ P/(K+P) \right]$$  

(1)

In this equation $R_s$ refers to the mean monthly soil-CO$_2$ efflux in g C m$^{-2}$ d$^{-1}$, $T_s$ refers to the mean monthly air temperature (°C), and $P$ is the mean monthly precipitation (cm) for the period 1980–94. We used this equation and our new, IRGA-derived soil respiration data set to determine new model parameters, using the non-linear regression option of SYSTAT (Wilkinson 1990). The resulting model was:

$$R_s = 1.250 \times e^{(0.05452-T_s)} \times \left[ P/(4.259 + P) \right]$$  

(2)

($n=335$, $r^2=0.62$). In comparison with the model of Raich & Potter (1995) our new parameters suggest a slightly lower basal respiration rate ($F=1.250$ vs. 1.334), a greater temperature sensitivity ($Q=0.05452$ vs. 0.03992), and a much greater importance of precipitation ($K=4.259$ vs. 1.634). Thus, our newly parameterized model should be more sensitive to climatic fluctuations than was that of Raich & Potter (1995).

We used eq. (2) to predict mean monthly soil respiration rates ($R_s$) from climate ($P$ and $T_s$) for each of 67,420 grid cells (0.5° latitude × 0.5° longitude) covering a total 146.6 × 10$^6$ km$^2$ of land, excluding Antarctica. Monthly air temperatures ($T_s$) and precipitation ($P$) data for January 1980–December 1994 were obtained from New et al. (2000). We assumed that $R_s$ was equal to 0 at temperatures <−13.3°C, and was maximum at temperatures
Table 1  Site descriptions, locations, and sources of in situ soil respiration measurements used to develop our regression model (eq. 2)

<table>
<thead>
<tr>
<th>Vegetation or Land Cover</th>
<th>Latitude</th>
<th>Longitude</th>
<th>Reference</th>
</tr>
</thead>
<tbody>
<tr>
<td>snow</td>
<td>69</td>
<td>-162</td>
<td>Zimov et al. (1993)</td>
</tr>
<tr>
<td>old black spruce</td>
<td>55.7</td>
<td>-97.9</td>
<td>Winston et al. (1997)</td>
</tr>
<tr>
<td>two jack pine stands</td>
<td>55.7</td>
<td>-97.9</td>
<td>Winston et al. (1997)</td>
</tr>
<tr>
<td>clearcut jack pine</td>
<td>53.9</td>
<td>-104.7</td>
<td>Striegl &amp; Wickland (1998)</td>
</tr>
<tr>
<td>jack pine woodland</td>
<td>53.9</td>
<td>-104.7</td>
<td>Striegl &amp; Wickland (1998)</td>
</tr>
<tr>
<td>mixed forest</td>
<td>45.4</td>
<td>-75.7</td>
<td>Lessard et al. (1994)</td>
</tr>
<tr>
<td>maize</td>
<td>45.4</td>
<td>-75.7</td>
<td>Lessard et al. (1994)</td>
</tr>
<tr>
<td>maize</td>
<td>45.4</td>
<td>-75.7</td>
<td>Rochette et al. (1999)</td>
</tr>
<tr>
<td>broadleaf forest</td>
<td>45.2</td>
<td>-93.0</td>
<td>Reiners (1968)</td>
</tr>
<tr>
<td>broadleaf forest, well drained</td>
<td>42.5</td>
<td>-72.2</td>
<td>Davidson et al. (1998)</td>
</tr>
<tr>
<td>broadleaf forest, poorly drained</td>
<td>42.5</td>
<td>-72.2</td>
<td>Davidson et al. (1998)</td>
</tr>
<tr>
<td>two desert shrub sites</td>
<td>41.9</td>
<td>-113.1</td>
<td>Caldwell et al. (1977)</td>
</tr>
<tr>
<td>alpine meadow under snow</td>
<td>41.3</td>
<td>-106.3</td>
<td>Sommerfeld et al. (1993)</td>
</tr>
<tr>
<td>Quercus ilex woodland, 2 sites</td>
<td>41.2</td>
<td>0.9</td>
<td>Piñol et al. (1995)</td>
</tr>
<tr>
<td>five aspen stands</td>
<td>41</td>
<td>-106</td>
<td>Smith &amp; Resh (1999)</td>
</tr>
<tr>
<td>three grassland sites</td>
<td>39.1</td>
<td>-16.6</td>
<td>Bremer et al. (1998)</td>
</tr>
<tr>
<td>four oak forest sites</td>
<td>36.0</td>
<td>-84.3</td>
<td>Hansen et al. (1993)</td>
</tr>
<tr>
<td>Liriodendron forest</td>
<td>35.6</td>
<td>-84.2</td>
<td>Edwards &amp; Harris (1977)</td>
</tr>
<tr>
<td>two Cryptomeria plantations</td>
<td>32.8</td>
<td>130.7</td>
<td>Ohashi et al. (1999)</td>
</tr>
<tr>
<td>desert</td>
<td>32.5</td>
<td>-106.8</td>
<td>Parker et al. (1983)</td>
</tr>
<tr>
<td>two pine plantations</td>
<td>29.7</td>
<td>-82.2</td>
<td>Ewel et al. (1987)</td>
</tr>
<tr>
<td>tropical seasonal forest</td>
<td>9.2</td>
<td>-79.9</td>
<td>Kursar (1989)</td>
</tr>
<tr>
<td>tropical seasonal forest</td>
<td>-3.0</td>
<td>-47.5</td>
<td>Davidson et al. (2000)</td>
</tr>
<tr>
<td>secondary forest</td>
<td>-3.0</td>
<td>-47.5</td>
<td>Davidson et al. (2000)</td>
</tr>
<tr>
<td>two pasture sites</td>
<td>-3.0</td>
<td>-47.5</td>
<td>Davidson et al. (2000)</td>
</tr>
</tbody>
</table>

\( \geq 33.5^\circ C \), as did Raich & Potter (1995). Land cover was derived from DeFries et al. (1998) by resampling their 8-km grid data to dominant land cover in half-degree cells. Polar land cells without vegetation (polar ice and rock land, total area = \( 3.4 \times 10^6 \text{ km}^2 \)) were assumed to have no soil respiration; this included most of Greenland. We did not modify our estimates for wetland coverage, but Raich & Potter (1995) found that wetlands had minor impacts on total global soil-\( \text{CO}_2 \) emissions. We tested our model by comparing predicted soil-\( \text{CO}_2 \) emissions with published measurements gathered from studies that were not used to define the parameters of our regression model.

Results

Testing the model

Comparing measured soil-\( \text{CO}_2 \) emissions with model predictions (Fig. 1) requires an awareness that the observed and predicted fluxes are fundamentally different. Model predictions refer to mean fluxes over entire half-degree grid cells containing many vegetation types, soils, etc., whereas measurements are made on specific plots within those grid cells (e.g., Savage et al. 1997). For instance, the data from New Hampshire (Fig. 1a) were collected within a forest preserve, whereas much of the local landscape is disturbed. Further, most investigators measure soil respiration for no more than a few days per month, whereas our model predicts mean monthly fluxes. There are also obvious discrepancies between the global climate data used to drive the model and observed weather. In both Texas (Fig. 1d) and Thailand (Fig. 1e) the climate database showed no precipitation during some months, generating predictions of zero soil respiration. Each of these problems will diminish as more soil respiration measurements are made and global databases improve.

Given these caveats, model predictions captured reasonably well both the seasonal patterns in soil-\( \text{CO}_2 \) emissions, and the magnitudes of fluxes observed in a variety of sites at different locations (Fig. 1). Mean square errors of these predictions (Fig. 1), calculated as the average of all (observed–predicted)\(^2 \) values for each month over which measurements were made, ranged from 0.1 in Fig. 1(c) to 6.2 in Fig. 1(d). In calculating the MSE we averaged measurements from multiple sites within grid cells, when necessary, to determine the unweighted mean.
Fig. 1  Comparisons between estimated (--) and measured (solid symbols) soil-CO₂ emissions in various locations. (a) Data from a mixed deciduous forest in New Hampshire, based on Table 2 of Crill (1991). (b) Data from barley (●) and fallow (▲) fields in Ottawa, Canada, based on Table 2 of Rochette et al. (1992a). (c) Data from spruce (●), aspen (▲), and pine (■) woodlands in Manitoba, as estimated from Fig. 3 of Savage et al. (1997). (d) Data from a tallgrass prairie in Texas, as estimated from Fig. 3 in Mielnick & Dugas (2000). (e) Data from upland cultivation (●), seasonal forest (▲), and shifting cultivation (■) sites in Thailand, as estimated from Fig. 1 in Tulaphitak et al. (1985). (f) Data from forest (●) and pasture (▲) sites in Para, Brazil, based on Table 2 of Davidson & Trumbore (1995). (g) Data from taiga forest stands in interior Alaska, as estimated from Fig. 1 in Gulledge & Schimel (2000): floodplain alder (●); floodplain white spruce (▲); upland birch and aspen (■); and upland white spruce (▼).
observed value. The regression-based nature of our model predisposes it for use across the entire range of monthly climates encompassed by the underlying data.

Seasonality of soil-CO₂ emissions

Over 1980–94 predicted global-scale soil-CO₂ emissions followed closely the seasonal temperature cycle (Fig. 2). Nevertheless, the influence of precipitation on CO₂ emissions was evident, as seen in the ragged nature of the predicted soil respiration cycle (Fig. 2). Across all 15 years, global soil-CO₂ emissions were minimal during February and maximal during July and August (Fig. 3a). Variability in predicted emissions was greatest in March and minimal in September (Fig. 3a). Deviations in soil respiration, defined for each month as the predicted global soil-CO₂ efflux minus the monthly mean efflux (based on $n = 15$ for each month) correlated directly with deviations in precipitation (Fig. 3b; $r = 0.58$, $P < 0.02$ assuming 14 d.f.), but not with temperature deviations ($r = 0.29$). This indicates that the global-scale variability seen within months among years was due primarily to variations in precipitation.

Tropical and north-temperate regions had substantially larger soil respiration fluxes than did other latitudinal belts (Fig. 4). Soil-CO₂ emissions from the 0–30°S latitude belt were maximal during the Northern Hemisphere’s winter (Fig. 4), when global emissions were minimal (Fig. 2). Thus, the Northern Hemisphere dominated the global soil-CO₂ flux, due largely to its disproportionate share of land area.

All land-cover types showed seasonality in their soil-CO₂ emissions (Fig. 5), in most cases following the annual temperature cycle of the Northern Hemisphere. Evergreen broad-leaved forests, however, exhibited two annual maxima (Fig. 5) that apparently reflect temporally offset contributions from the northern and southern tropics; minima occurred in February and July, 1–2 months after the winter and summer solstices.

Annual soil-CO₂ emissions

From 1980 to 1994 global soil respiration was predicted to average 80.4 Pg C yr⁻¹ (Table 2). Among land-cover types, evergreen broad-leaved forests had the highest rates of soil-CO₂ production throughout this 15-y period (Fig. 5) and contributed far more soil-respired CO₂ than did any other vegetation type (Table 2). Although interannual variability in global soil-CO₂ emissions was relatively low (CV = 1%, Table 2), it was relatively high within barren lands, deciduous needleleaf forests, and closed bushlands and shrublands (Table 2). In the latter case, estimated annual emissions correlated directly with annual precipitation ($r = 0.81$, $P < 0.01$), suggesting that interannual variations in precipitation were responsible for the interannual variability in predicted soil-CO₂ fluxes in that biome. This was true also in evergreen broadleaf forests, in wooded grasslands and shrublands (i.e., savannas), in open shrublands, and in barren lands ($r = 0.53$, 0.51, 0.87 and 0.96, respectively). In contrast, annual soil-CO₂ emissions correlated most closely with mean annual temperatures in croplands ($r = 0.67$, $P < 0.01$). Permanent croplands could be buffered from the effects of interannual precipitation variability if they are more widespread in regions with dependable precipitation. However, since many croplands are irrigated, our results for that biome may be biased by our use of precipitation inputs alone as a measure of water availability.

Despite correlations between precipitation variability and predicted soil-CO₂ emissions within specific biomes, there was no correlation between estimated annual global soil-CO₂ emissions and global precipitation. Precipitation controls over global soil-CO₂ emissions seem to be restricted to regional scales, with spatial differences canceling one another out at the global scale. Among years, estimated total global soil respiration correlated significantly with air temperature over land ($r = 0.87$, Fig. 6), but not with precipitation ($r = 0.18$). Nor did the residuals of the temperature relationship correlate with precipitation ($r = −0.20$). This was true despite that our model was very sensitive to low amounts of precipitation (e.g., Fig. 1d,e) and ignored soil moisture storage, which may buffer ecosystem processes against precipitation deficits (e.g., Raich et al., 1991). On average, soil-CO₂ emissions increased 3.3 Pg C yr⁻¹ for each 1°C increase in the mean temperature over land.

Discussion

From 1980 to 1994, mean global soil respiration was estimated to average 80.4 Pg C yr⁻¹. Using the same approach, Raich & Potter (1995) estimated the long-term average global soil respiration to be 77.1 Pg C yr⁻¹. However, this is not evidence that soil-CO₂ emissions have increased in recent years. There are three main differences between our current predictions and those of Raich & Potter (1995). We used more recent land cover and climate data, we recalculated the model parameters using more recent soil respiration data, and we used monthly weather data instead of mean monthly weather data. We used the model parameters of Raich & Potter (1995) to estimate soil respiration for the 1980–94 period, using our current climate database, and found that global soil-CO₂ emissions averaged 82.4 ± 0.5 Pg C yr⁻¹. This higher estimate resulted primarily from the higher basal respiration rate ($F = 1.334 g C m⁻² d⁻¹$) in the 1995 parameter set. We also predicted global emissions using our new model parameters, but driven by mean (1980–94)
monthly climate data. In that case, global soil respiration was estimated to be 83.8 Pg C y\(^{-1}\), 3.4 Pg larger than the mean of the individual-year estimates. This overestimate is a result of our hyperbolic precipitation function (eq. 2); drier-than-average months diminish predicted soil-CO\(_2\) emissions more than wetter-than-average months stimulate them. Our current estimate of a mean annual global soil-CO\(_2\) efflux of 80.4 ± 0.4 Pg C is therefore an improvement in many respects, but applies to 1980–94 only, and we cannot estimate the mean pre-1980 flux from our data.

**Interannual variability in the global carbon cycle**

Over the 15-\(\text{y}\) period considered, the difference between the estimated maximum and minimum annual global soil-CO\(_2\) emissions was 2.6 Pg C. By comparing this with other global C flux estimates, we can evaluate the relative impact that interannual differences in soil-CO\(_2\) fluxes may have on atmospheric CO\(_2\) anomalies. Annual increases in the atmospheric CO\(_2\) pool between 1981 and 1992 varied (maximum–minimum) by 3.95 Pg C (Conway et al., 1994). Estimates of the interannual variability (maximum–minimum) in net annual CO\(_2\) uptake by the oceans range from c. 4 (Francey et al., 1995; Keeling et al., 1995) to < 1 Pg C y\(^{-1}\) (Lee et al., 1998) during 1982–95. If the estimates of Lee et al. (1998) are correct, then interannual differences in the amplitude of the atmospheric CO\(_2\) signal are driven primarily by interannual differences in terrestrial C fluxes.

Keeling et al. (1995) estimated that terrestrial biosphere between 1980 and 1994 varied from a CO\(_2\) sink of 2.5 Pg C y\(^{-1}\) to a CO\(_2\) source of 2.6 Pg C y\(^{-1}\), which suggest a variability that is twice as great as that we predicted for soil respiration. From 1983 to 1988 global terrestrial net primary productivity (NPP) was estimated to range from 53.9 to 59.4 Pg C y\(^{-1}\), and heterotrophic respiration from 55.9 to 58.5 Pg C y\(^{-1}\) (Potter & Klooster, 1998). This latter estimate has the same variability as do our estimates of soil respiration, which includes CO\(_2\) derived from live root respiration. Terrestrial NPP is even more variable according to Maisongrande et al. (1995), who predicted that annual NPP varied (maximum–minimum) by 10.8 Pg C from 1986 to 1991. Kiemer et al. (1996) found that NPP from 1980 to 1993 varied (maximum–minimum) by 4.7 Pg C y\(^{-1}\),
whereas heterotrophic respiration (which they termed soil respiration) varied by 1.0 Pg C yr\(^{-1}\). In all these cases, the estimated interannual variability in net plant CO\(_2\) uptake (NPP) is more than twice what we predicted for soil-CO\(_2\) emissions, which is itself less than variability in the atmospheric CO\(_2\) pool. We conclude from this that soils buffer fluctuations in atmospheric CO\(_2\) concentrations by providing relatively consistent, year-round supplies of CO\(_2\) that dampen the effects of more extreme intra- and interannual variations in plant C uptake. This conclusion is consistent with Potter & Klooster (1998), who suggested that \(R_{HI}\) fluxes dampened net CO\(_2\) fluxes from the terrestrial biosphere to the atmosphere, with about a two-year lag period relative to NPP.

**Soil respiration and global warming**

Despite relatively low interannual variability in global soil-CO\(_2\) emissions (Table 2), climatic variability did affect our emission estimates. Within seasonally dry biomes (i.e., savannas, closed bushlands and shrublands, open shrublands, and barren lands), annual precipitation correlated directly with estimated annual soil-CO\(_2\) emissions. At the monthly scale, deviations in estimated global soil respiration correlated positively with deviations in precipitation (Fig. 3b). Thus, seasonal and annual variations in precipitation influence the spatial and seasonal dynamics of estimated soil-CO\(_2\) emissions. However, these dynamics are largely lost at the global annual scale: interannual differences in estimated global soil respiration correlated significantly with temperature (Fig. 6), but not with precipitation. Higher mean temperatures stimulated global soil CO\(_2\) emissions by an average of 3.3 Pg C yr\(^{-1}\) per °C over the mean global temperature range 13.0–13.7 °C.

These results do not contradict directly the proposition that soil C turnover rates are independent of temperature (Giardina & Ryan, 2000). Higher soil-CO\(_2\) fluxes in response to higher temperatures can result either from increased loss rates of detrital C, or from emissions resulting from increased C inputs to the soil. For instance, if root respiration rates increase in response to higher
temperatures (e.g., Boone et al., 1998), soil respiration rates may increase even if there are no changes in soil C stocks. An analogous example is provided from the Duke Forest free-air CO₂ enrichment (FACE) study, where increased CO₂ enhanced soil respiration rates primarily by stimulating C fluxes through roots (Andrews et al., 1999; Andrews & Schlesinger, 2001) without apparently altering soil organic matter storage.

Our finding that higher temperatures will promote higher rates of soil respiration is consistent with the hypothesis that warmer temperatures will promote net losses of soil organic C (Schleser, 1982; Townsend et al., 1992; Trumbore et al., 1996; Schlesinger & Andrews, 2000). Previous analyses suggest that a 1 °C increase in the mean temperature would lead to global soil C losses ranging from 11 to 33 Pg C (Jenkinson et al., 1991; Schimel et al.,...
Fig. 5  Estimated monthly soil respiration in each of eight major land-cover types. Land-cover classes are named and numbered according to DeFries et al. (1998). Note that the y-axis scales differ among plots.
Table 2  Areal extent and estimated mean annual global soil respiration, mean annual temperature, and mean annual precipitation for each of 14 land-cover types defined in our database. All grid cells were 0.5° latitude x 0.5° longitude. All soil respiration, temperature, and precipitation data refer to means over the period January 1980–December 1994.

<table>
<thead>
<tr>
<th>Land-cover type</th>
<th>Number of grid cells</th>
<th>Area (km²)</th>
<th>Soil Respiration (Pg C y⁻¹)</th>
<th>MAT (°C)</th>
<th>MAP (mm y⁻¹)</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td></td>
<td>Mean</td>
<td>CV (%)</td>
<td>Mean</td>
</tr>
<tr>
<td>1 – Evergreen needleleaf forests</td>
<td>5778</td>
<td>10,705,600</td>
<td>4.12</td>
<td>2.0</td>
<td>3.1</td>
</tr>
<tr>
<td>2 – Evergreen broadleaf forests</td>
<td>5770</td>
<td>17,394,748</td>
<td>22.94</td>
<td>1.1</td>
<td>24.6</td>
</tr>
<tr>
<td>3 – Deciduous needleleaf forests</td>
<td>1728</td>
<td>2,624,313</td>
<td>0.59</td>
<td>3.8</td>
<td>–6.9</td>
</tr>
<tr>
<td>4 – Deciduous broadleaf forests</td>
<td>1987</td>
<td>4,669,196</td>
<td>3.43</td>
<td>1.4</td>
<td>13.9</td>
</tr>
<tr>
<td>5 – Mixed forests</td>
<td>2793</td>
<td>5,612,332</td>
<td>2.51</td>
<td>2.4</td>
<td>5.2</td>
</tr>
<tr>
<td>6 – Woodlands</td>
<td>7524</td>
<td>17,642,765</td>
<td>12.53</td>
<td>0.8</td>
<td>15.4</td>
</tr>
<tr>
<td>7 – Wooded grasslands/shrublands</td>
<td>3813</td>
<td>10,927,601</td>
<td>7.95</td>
<td>1.2</td>
<td>23.5</td>
</tr>
<tr>
<td>8 – Closed bushlands or shrublands</td>
<td>1968</td>
<td>5,525,457</td>
<td>2.75</td>
<td>3.5</td>
<td>21.5</td>
</tr>
<tr>
<td>9 – Open shrublands</td>
<td>4903</td>
<td>13,017,205</td>
<td>4.22</td>
<td>3.0</td>
<td>18.1</td>
</tr>
<tr>
<td>10 – Grasses</td>
<td>7748</td>
<td>17,333,777</td>
<td>7.11</td>
<td>1.9</td>
<td>8.9</td>
</tr>
<tr>
<td>11 – Croplands</td>
<td>5514</td>
<td>12,985,531</td>
<td>8.08</td>
<td>1.1</td>
<td>13.7</td>
</tr>
<tr>
<td>12 – Bare</td>
<td>5562</td>
<td>15,385,568</td>
<td>2.76</td>
<td>7.6</td>
<td>16.0</td>
</tr>
<tr>
<td>13 – Mosses and lichens</td>
<td>7881</td>
<td>9,329,759</td>
<td>1.43</td>
<td>2.8</td>
<td>–10.5</td>
</tr>
<tr>
<td>14 – Polar ice and rockland</td>
<td>4451</td>
<td>3,406,453</td>
<td>0§</td>
<td>–</td>
<td>–</td>
</tr>
<tr>
<td>Global land total</td>
<td>67,420</td>
<td>146,560,303</td>
<td>80.41</td>
<td>1.0</td>
<td>13.3</td>
</tr>
</tbody>
</table>

*Following DeFries et al. (1998). Polar ice and rockland was defined as Type 12 located north of 60°N latitude. †Area-weighted mean annual temperature over land. ‡Area-weighted mean annual precipitation on land. §We assumed that there was no soil respiration from polar ice and rockland. *Antarctica is excluded from all columns.

Fig. 6  Estimated annual global soil respiration shown in relationship to the mean annual air temperature over land. The equation of the least-squares linear regression between temperature (T) and Rs is:

\[ R_s = 36.2 + 3.32 \times T \] (n = 15, \( r^2 = 0.75, P < 0.0001 \).

1994). Our work differs fundamentally from these previous studies in many ways. For example, we do not have soil organic matter in our model. Also, previous estimates refer to cumulative C losses through time, whereas ours refer to the short-term responses of soils to interannual climate variability. Therefore, our results do not provide evidence that previous studies have overestimated soil C losses in response to global warming.

Soil respiration and the global carbon cycle

Our approach is based on statistical analyses of in situ soil respiration measurements gathered within intact ecosystems in many locations under widely differing climatic conditions, land uses, and vegetation covers (Table 1). Should global warming occur, it will occur one year at a time, and it will be accompanied by changes in precipitation. Thus, our analysis of the effects of recent climatic
variability on soil-CO$_2$ fluxes is appropriate for evaluating the potential responses of soils to climatic changes.

Based on summary data from the EUROFLUX project, Janssens et al. (2001) reported that, whereas temperature was the dominant variable influencing seasonal patterns of soil respiration within non-water-stressed soils, mean annual temperature did not correlate with observed rates of soil respiration among forests. Rather, differences in soil respiration among sites correlated with ecosystem C fluxes (i.e., gross primary productivity) (Janssens et al., 2001), and differences among sites in net ecosystem productivity were controlled more by differences in ecosystem respiration than production (Valentini et al., 2000). The significant correlation between rates of plant production and soil respiration has long been recognized (Schlesinger, 1977; Raich & Nadelhoffer, 1989; Raich & Schlesinger, 1992; Raich & Tufekcioglu, 2000), but plant productivity is highly dependent upon both temperature and moisture availability (e.g., Lieth, 1973), as is soil respiration. Our regression-based model did not incorporate factors such as soil type, species composition, or other non-climatic variables that influence plant productivity in individual sites, but rather incorporated intersite variations in such factors within the model parameters. More complex models that incorporate additional factors that influence plant production may provide better-resolved estimates of soil respiration by explaining some of the inter-site variability not encompassed within our model. Clearly, future changes in soil and ecosystem carbon fluxes will depend upon factors other than just temperature and rainfall, and more complex models are needed to fully assess the responses of terrestrial ecosystems to multiple environmental changes (e.g., Cramer et al., 2001). Nevertheless, our model does provide global-scale estimates of mean fluxes, and how they vary among years based on variations in weather. Our model also provides an independently derived, statistically based, spatially and temporally resolved database against which the predictions of more complex, and more difficult-to-parameterize models, can be compared.

Using the CASA model, Poter & Klooster (1998) estimated that NPP from 1983 to 1988 averaged 57.6 Pg C y$^{-1}$, and that $R_{HI}$ averaged 57.1 Pg C y$^{-1}$. Over the same period, we estimated that soil respiration averaged 80.0 Pg C y$^{-1}$. The difference between $R_{HI}$ and $R_{SO}$, i.e., 23 Pg C y$^{-1}$, provides an estimate of global root respiration. Thus, globally, about 30% of soil respiration can be attributed to the respiration of live roots. This is lower than the overall mean of 50% found in forests (Hanson et al., 2000), which covered 28% of the land area in our global database. However, estimates of root respiration vary widely among studies, and include autotrophic respiration only. Additionally, root respiration contributions to total soil respiration vary among land-cover types, with estimates ranging from 12% to 38% in croplands to 50–93% in arctic tundra (Raich & Tufekcioglu, 2000). Our global mean masks such inter-site variations. Despite its importance, this flux often is missing from terrestrial C models.

In conclusion, our results suggest that soil-CO$_2$ emissions increase with increasing global temperature, and that variations in the timing and distribution of precipitation do not override this basic global pattern. This finding may suggest either that soils are losing organic C in response to global warming or that soil C cycles faster (i.e., more inputs and outputs) as temperatures increase. Either way, the warm global temperatures of the 1980s and 1990s appear to have already altered the terrestrial C cycle.

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References


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