

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-to-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 (Schlesinger, 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-CO₂ 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 CO₂ fluxes from soils. To evaluate the sensitivity of soil-CO₂ 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-CO₂ 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 CO₂ 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-CO₂ 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 CO₂ 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-CO₂ 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 CO₂ 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-CO₂ 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:

$$R_S = F \times e^{(Q \cdot T_a)} \times [P / (K + P)] \quad (1)$$

In this equation R_S refers to the mean monthly soil-CO₂ efflux in g C m^{–2} d^{–1}, T_a 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:

$$R_S = 1.250 \times e^{(0.05452 \cdot T_a)} \times [P / (4.259 + P)] \quad (2)$$

($n = 335$, $r^2 = 0.62$). 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_a) for each of 67 420 grid cells (0.5° latitude × 0.5° longitude) covering a total 146.6 × 10⁶ km² of land, excluding Antarctica. Monthly air temperatures (T_a) 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)

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

$\geq 33.5^{\circ}\text{C}$., 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- CO_2 emissions. We tested our model by comparing predicted soil- 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- 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- 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

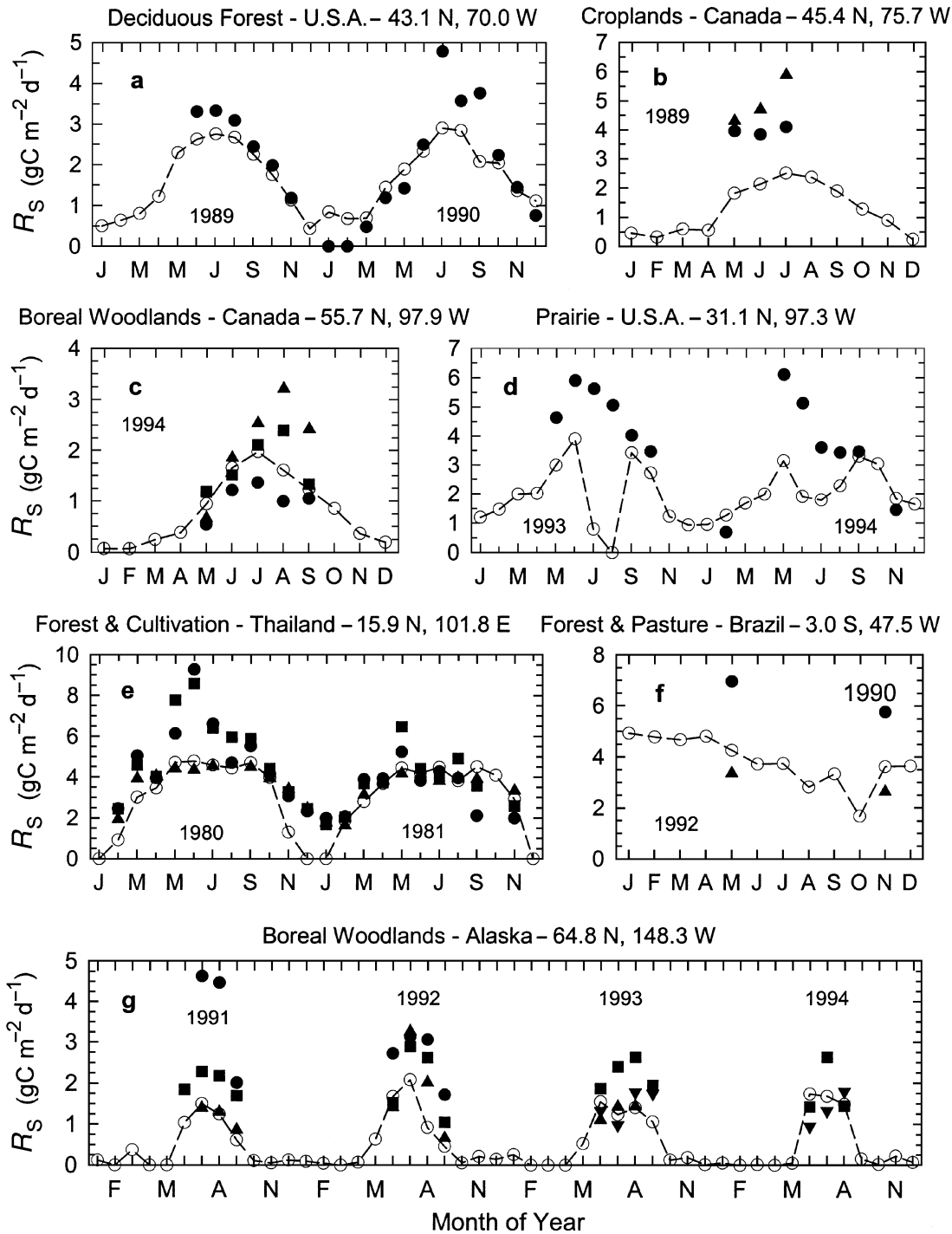


Fig. 1 Comparisons between estimated (\ominus) and measured (solid symbols) soil- CO_2 emissions in various locations. (a) Data from a mixed deciduous forest in New Hampshire, based on Table 2 of Crill (1991). (b) Data from barley (\bullet) and fallow (\blacktriangle) fields in Ottawa, Canada, based on Table 2 of Rochette *et al.* (1992a). (c) Data from spruce (\bullet), aspen (\blacktriangle), and pine (\blacksquare) 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 Mielenick & Dugas (2000). (e) Data from upland cultivation (\bullet), seasonal forest (\blacktriangle), and shifting cultivation (\blacksquare) sites in Thailand, as estimated from Fig. 1 in Tulaphitak *et al.* (1985). (f) Data from forest (\bullet) and pasture (\blacktriangle) 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 Gullledge & Schimel (2000): floodplain alder (\bullet); floodplain white spruce (\blacktriangle); upland birch and aspen (\blacksquare); and upland white spruce (\blacktriangledown).

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 y⁻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 y⁻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 y⁻¹. Using the same approach, Raich & Potter (1995) estimated the long-term average global soil respiration to be 77.1 Pg C y⁻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 y⁻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)

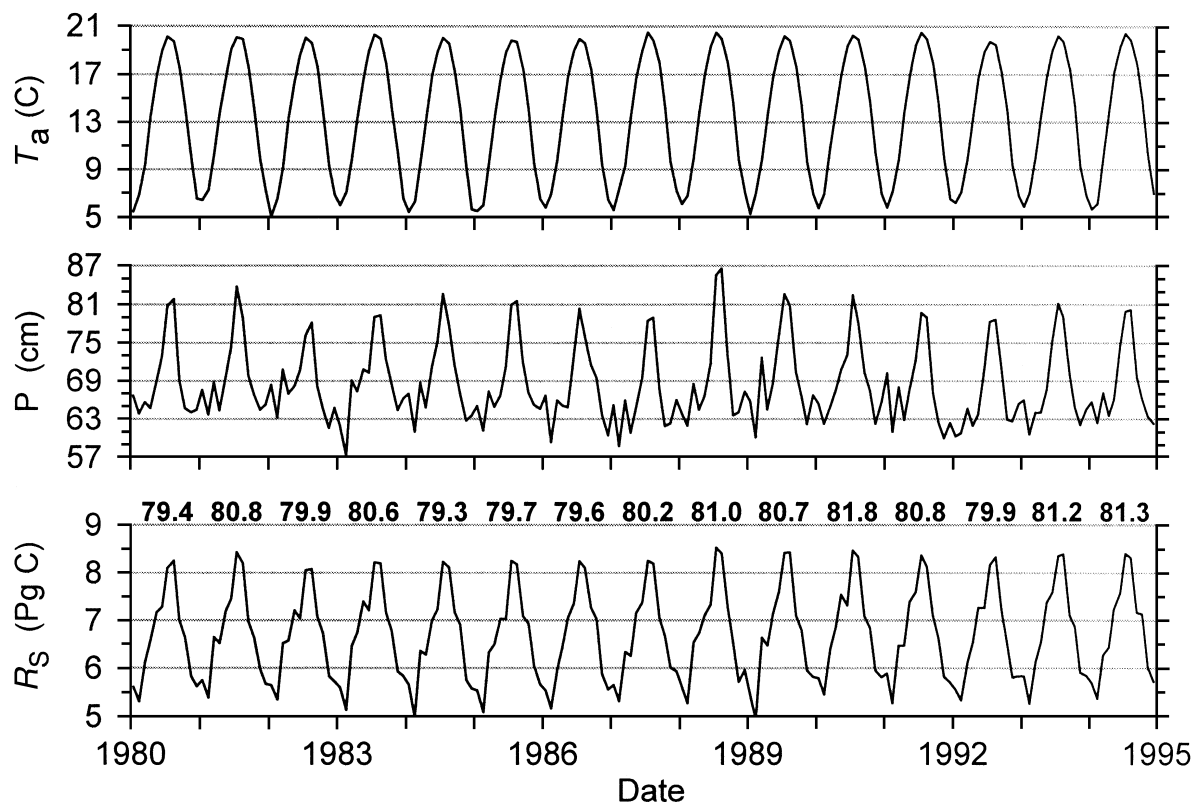


Fig. 2 Mean monthly temperatures, precipitation, and estimated soil respiration rates for the global land surface, 1980–94. Monthly temperature and precipitation data are from New *et al.* (2000); soil respiration rates were estimated using eq. (2) for each 0.5° latitude \times 0.5° longitude land grid cell, excluding Antarctica. The estimated annual R_s for each year is shown at the top of the lower figure.

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 $80.4 \pm 0.4 \text{ Pg C}$ 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-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.* $4 \text{ (Francey et al., 1995; Keeling et al., 1995)}$ to $<1 \text{ Pg C y}^{-1}$ (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 suggests 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. Kindermann *et al.* (1996) found that NPP from 1980 to 1993 varied (maximum–minimum) by 4.7 Pg C y^{-1} ,

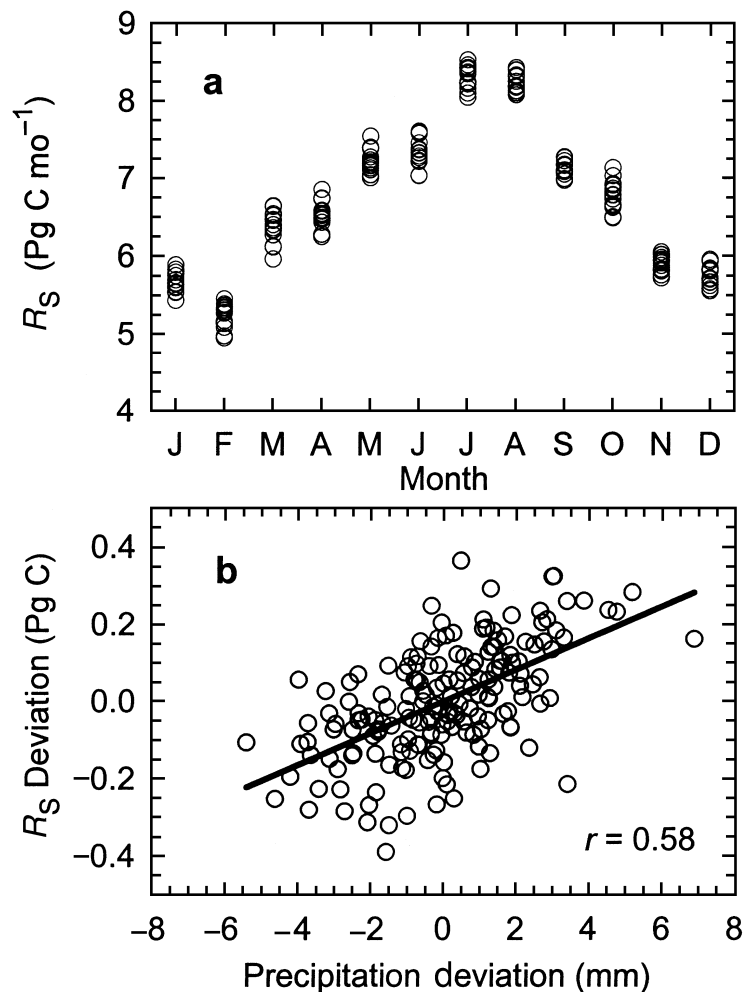


Fig. 3 (a) Estimated global soil-CO₂ emissions for each month January 1980–December 1994. (b) Deviations in monthly global soil respiration shown in relation to deviations in monthly global precipitation. Each plot contains 180 points; deviations refer to the monthly value minus the mean value for that month over the 15-month period.

whereas heterotrophic respiration (which they termed soil respiration) varied by 1.0 Pg C y^{-1} . In all these cases, the estimated interannual variability in net plant CO₂ uptake (NPP) is more than twice what we predicted for soil-CO₂ emissions, which is itself less than variability in the atmospheric CO₂ pool. We conclude from this that soils buffer fluctuations in atmospheric CO₂ concentrations by providing relatively consistent, year-round supplies of CO₂ 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_H fluxes dampened net CO₂ 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-CO₂ 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-CO₂ 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-CO₂ 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 CO₂ emissions by an average of 3.3 Pg C y^{-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-CO₂ 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

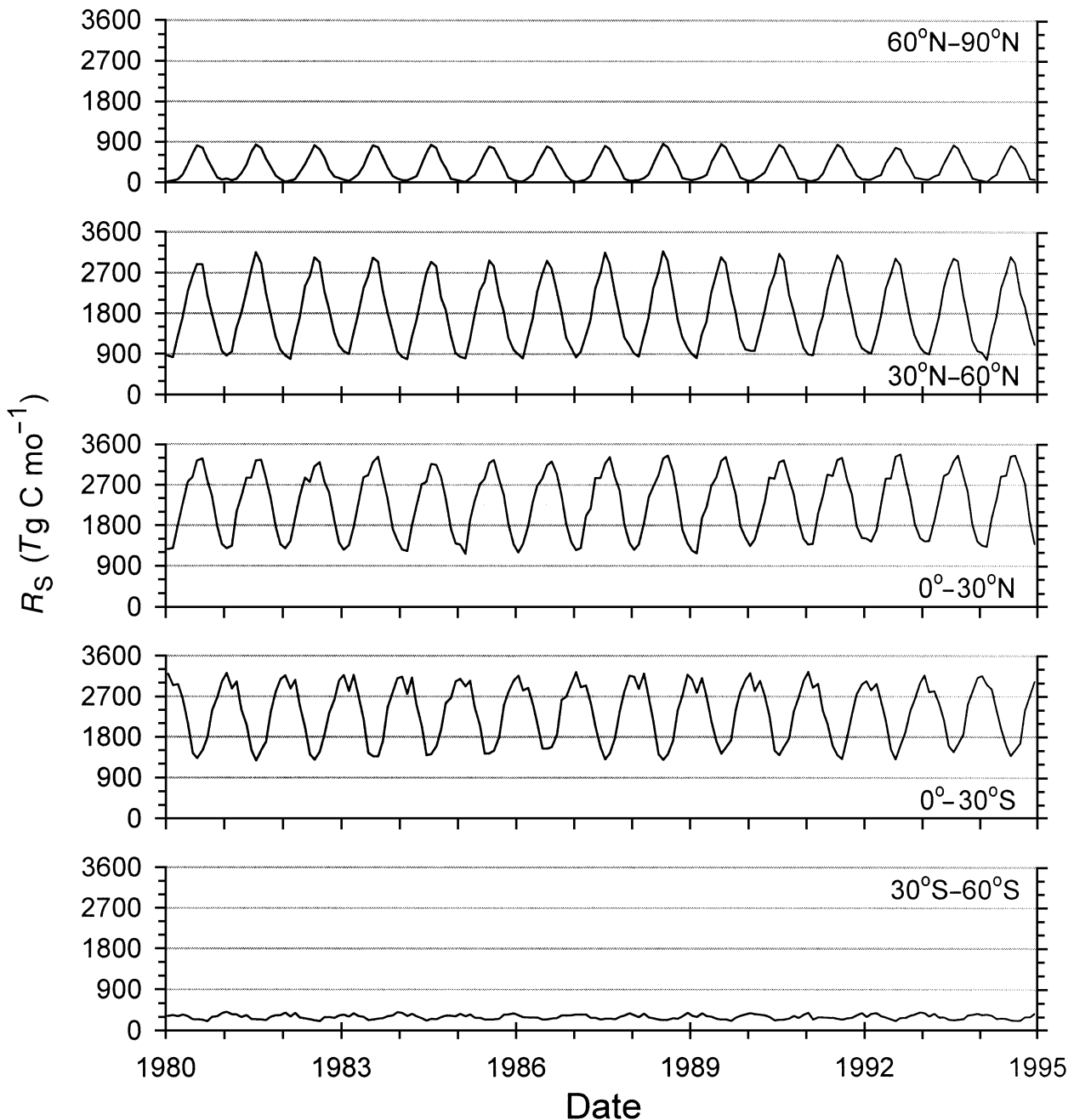


Fig. 4 Estimated monthly soil respiration for each 30° latitudinal belt from the North Pole to 60°S latitude. No predictions were made for Antarctica.

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 (Schlesinger, 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 PgC (Jenkinson *et al.*, 1991; Schimel *et al.*,

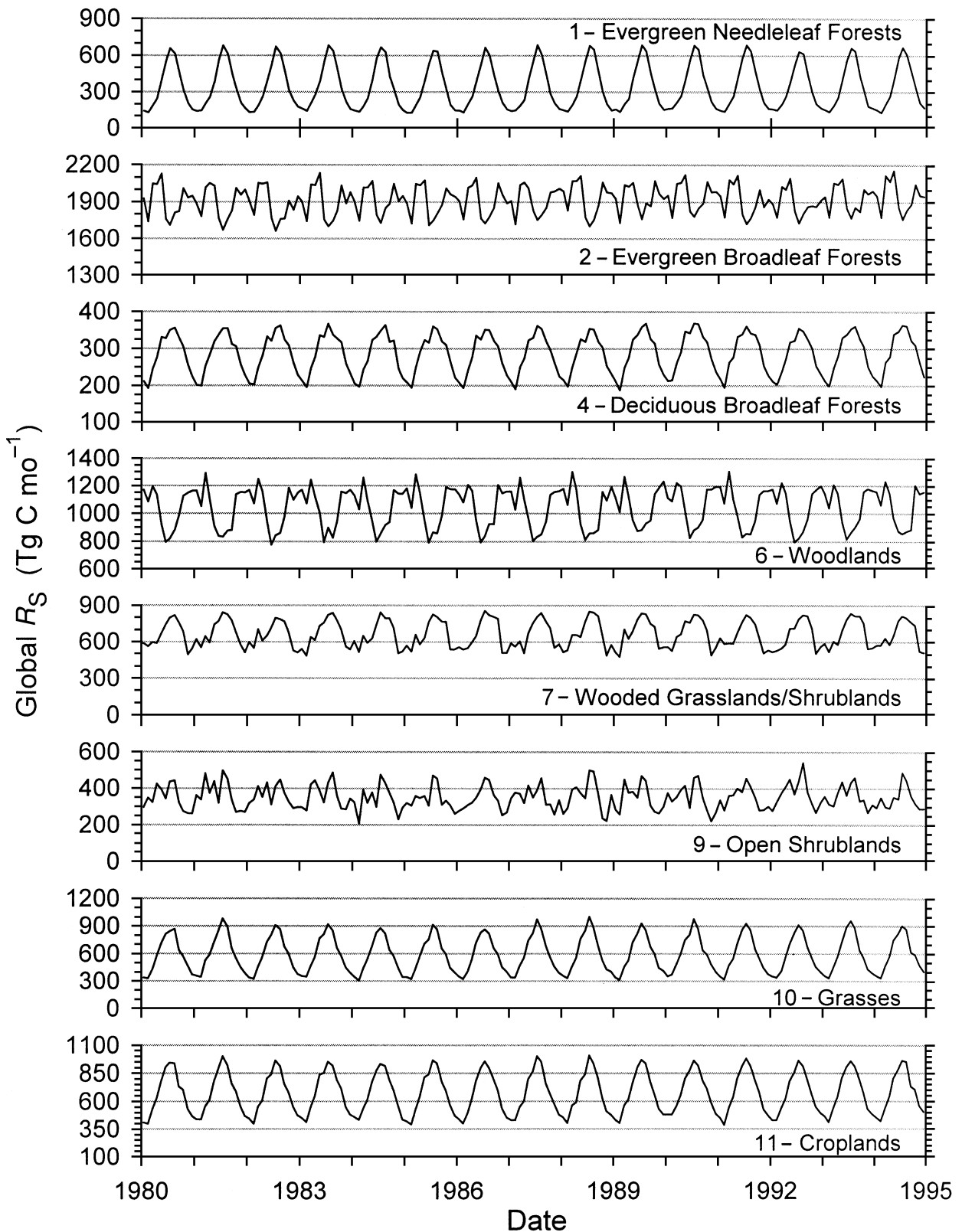


Fig. 5 Estimated monthly soil respiration in each of eight major land-cover types. Land-cover classes are named and numbered according to DeFries *et al.* (1998). Note that the y-axis scales differ among plots.

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 × 0.5° longitude. All soil respiration, temperature, and precipitation data refer to means over the period January 1980–December 1994

Land-cover type*	Number of grid cells	Area (km ²)	Soil Respiration (Pg C y ⁻¹)		MAT† (°C)		MAP‡ (mm y ⁻¹)	
			Mean	CV (%)	Mean	CV (%)	Mean	CV (%)
1 – Evergreen needleleaf forests	5778	10705600	4.12	2.0	3.1	3.3	816	0.7
2 – Evergreen broadleaf forests	5770	17394748	22.94	1.1	24.6	0.2	2214	0.7
3 – Deciduous needleleaf forests	1728	2624313	0.59	3.8	-6.9	3.3	425	1.3
4 – Deciduous broadleaf forests	1987	4669196	3.43	1.4	13.9	0.5	1141	0.4
5 – Mixed forests	2793	5612332	2.51	2.4	5.2	2.0	842	1.0
6 – Woodlands	7524	17642765	12.53	0.8	15.4	0.3	1031	0.7
7 – Wooded grasslands/shrublands	3813	10927601	7.95	1.2	23.5	0.2	846	0.9
8 – Closed bushlands or shrublands	1968	5525457	2.75	3.5	21.5	0.2	429	1.4
9 – Open shrublands	4903	13017205	4.22	3.0	18.1	0.3	264	0.9
10 – Grasses	7748	17333777	7.11	1.9	8.9	0.9	588	0.5
11 – Croplands	5514	12985531	8.08	1.1	13.7	0.5	925	0.5
12 – Bare	5562	15385568	2.76	7.6	16.0	0.5	123	2.0
13 – Mosses and lichens	7881	9329759	1.43	2.8	-10.5	1.3	351	0.7
14 – Polar ice and rockland	4451	3406453	0§	-	-	-	-	-
Global land total¶	67420	146560303	80.41	1.0	13.3	0.4	823	0.4

*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.

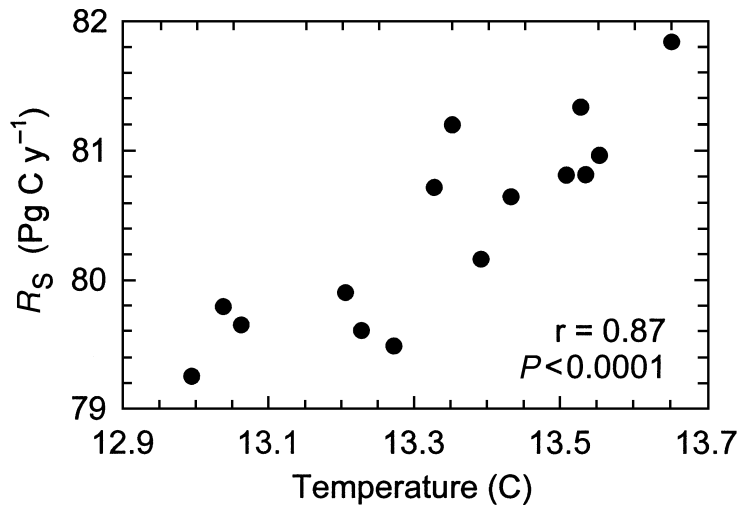


Fig. 6 Estimated annual global soil respiration shown in relationship to the mean annual air temperature over land. The equation of the least-squares linear regression between temperature (*T*) and *R_S* is: $R_S = 36.2 + 3.32 \times T$ ($n = 15$, $r^2 = 0.75$, $P < 0.0001$).

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-CO₂ 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 forests, 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 inter-site 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, Potter & Klooster (1998) estimated that NPP from 1983 to 1988 averaged 57.6 Pg C y⁻¹, and that R_H 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_H and R_S , 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 heterotrophic respiration of rhizosphere organisms (Hanson *et al.*, 2000), whereas our 30% estimate is for 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-CO₂ 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

- Andrews JA, Harrison KG, Matamala R, Schlesinger WH (1999) Separation of root respiration from total soil respiration using carbon-13 labeling during free-air carbon dioxide enrichment (FACE). *Soil Science Society of America Journal*, **63**, 1429–1435.
- Andrews JA, Schlesinger WH (2001) Soil CO₂ dynamics, acidification, and chemical weathering in a temperate forest with experimental CO₂ enrichment. *Global Biogeochemical Cycles*, **15**, 149–162.
- Boone RD, Nadelhoffer KJ, Canary JD, Kaye JP (1998) Roots exert a strong influence on the temperature sensitivity of soil respiration. *Nature*, **396**, 570–572.
- Bremer DJ, Ham JM, Owensby CE, Knapp AK (1998) Responses of soil respiration to clipping and grazing in a tallgrass prairie. *Journal of Environmental Quality*, **27**, 1539–1548.
- Caldwell MM, White RS, Moore RT, Camp LB (1977) Carbon balance, productivity, and water use of cold-winter desert shrub communities dominated by C₃ and C₄ species. *Oecologia*, **29**, 275–300.
- Conway TJ, Tans PP, Waterman LS, Thoning KW (1994) Evidence for interannual variability of the carbon cycle from the National Oceanic and Atmospheric Administration/Climate Monitoring and Diagnostics Laboratory Global Air Sampling Network. *Journal of Geophysical Research*, **99**, 22831–22855.
- Cramer W, Bondeau A, Woodward FI *et al.* (2001) Global response of terrestrial ecosystem structure and function to CO₂ and climate change: results from six dynamic global vegetation models. *Global Change Biology*, **7**, 357–373.

- Crill PM (1991) Seasonal patterns of methane uptake and carbon dioxide release by a temperate woodland soil. *Global Biogeochemical Cycles*, **5**, 319–334.
- Davidson EA, Belk E, Boone RD (1998) Soil water content and temperature as independent or confounded factors controlling soil respiration in a temperate mixed hardwood forest. *Global Change Biology*, **4**, 217–227.
- Davidson EA, Trumbore SE (1995) Gas diffusivity and production of CO₂ in deep soils of the eastern Amazon. *Tellus*, **47B**, 550–564.
- Davidson EA, Verchot LV, Cattânio JH, Ackerman IL, Carvalho JEM (2000) Effects of soil water content on soil respiration in forests and cattle pastures of eastern Amazonia. *Biogeochemistry*, **48**, 53–69.
- DeFries RS, Hansen M, Townshend JRG, Sohlberg R (1998) Global land cover classifications at 8 km spatial resolution: the use of training data derived from landsat imagery in decision tree classifiers. *International Journal of Remote Sensing*, **19**, 3141–3168.
- Edwards NT, Harris WF (1977) Carbon cycling in a mixed deciduous forest floor. *Ecology*, **58**, 431–437.
- Ewel KC, Cropper WP Jr, Gholz HL (1987) Soil CO₂ evolution in Florida slash pine plantations. I. Changes through time. *Canadian Journal of Forest Research*, **17**, 325–329.
- Francey RJ, Tans PP, Allison CE, Enting IG, White JWC, Troller M (1995) Changes in oceanic and terrestrial carbon uptake since 1982. *Nature*, **373**, 326–330.
- Giardina CP, Ryan MG (2000) Evidence that decomposition rates of organic carbon in mineral soil do not vary with temperature. *Nature*, **404**, 858–861.
- Gulledge J, Schimel JP (2000) Controls on soil carbon dioxide and methane fluxes in a variety of taiga forest stands in interior Alaska. *Ecosystems*, **3**, 269–282.
- Hanson PJ, Edwards NT, Garten CT, Andrews JA (2000) Separating root and soil microbial contributions to soil respiration: a review of methods and observations. *Biogeochemistry*, **48**, 115–146.
- Hanson PJ, Wullschlegler SD, Bohlman SA, Todd DE (1993) Seasonal and topographic patterns of forest floor CO₂ efflux from an upland oak forest. *Tree Physiology*, **13**, 1–15.
- Houghton J (1997) *Global Warming: the Complete Briefing*, 2nd edn. Cambridge University Press, Cambridge.
- Janssens IA, Lankreijer H, Matteucci G *et al.* (2001) Productivity overshadows temperature in determining soil and ecosystem respiration across European forests. *Global Change Biology*, **7**, 269–278.
- Jenkinson DS, Adams DE, Wild A (1991) Model estimates of CO₂ emissions from soil in response to global warming. *Nature*, **351**, 304–306.
- Jones PD, Parker DE, Osborn TJ, Briffa KR (2000) Global and hemispheric temperature anomalies – land and marine instrumental records. In: *Trends: A Compendium of Data on Global Change*. Carbon Dioxide Information Analysis Center, Oak Ridge National Laboratory, US Department of Energy, Oak Ridge, Tennessee.
- Keeling CD, Whorf TP, Wahlen M, van der Plicht J (1995) Interannual extremes in the rate of rise of atmospheric carbon dioxide since 1980. *Nature*, **375**, 669–670.
- Kindermann J, Würth G, Kohlmaier GH (1996) Interannual variation of carbon exchange fluxes in terrestrial ecosystems. *Global Biogeochemical Cycles*, **10**, 737–755.
- Kirschbaum MUF (2000) Will changes in soil organic carbon act as a positive or negative feedback on global warming? *Biogeochemistry*, **48**, 21–51.
- Kursar TA (1989) Evaluation of soil respiration and soil CO₂ concentration in a lowland moist forest in Panama. *Plant and Soil*, **113**, 21–29.
- Lee K, Wanninkhof R, Tkahashi T, Doney SC, Feely RA (1998) Low interannual variability in recent oceanic uptake of atmospheric carbon dioxide. *Nature*, **396**, 155–159.
- Lessard R, Rochette P, Topp E, Pattey E, Desjardins RL, Beaumont G (1994) Methane and carbon dioxide fluxes from poorly drained adjacent cultivated and forest sites. *Canadian Journal of Soil Science*, **74**, 139–146.
- Lieth H (1973) Primary production: Terrestrial ecosystems. *Human Ecology*, **1**, 303–332.
- Maisongrande P, Ruimy A, Dedieu G, Saugier B (1995) Monitoring seasonal and interannual variations of gross primary productivity, net primary productivity and net ecosystem productivity using a diagnostic model and remotely-sensed data. *Tellus*, **47B**, 178–190.
- Marland G, Boden TA, Andres RJ (2000) Global, regional, and national CO₂ emissions. In: *Trends: A Compendium of Data on Global Change*. Carbon Dioxide Information Analysis Center, Oak Ridge National Laboratory, US Department of Energy, Oak Ridge, Tennessee.
- Mielnick PC, Dugas WA (2000) Soil CO₂ flux in a tallgrass prairie. *Soil Biology and Biochemistry*, **32**, 221–228.
- New M, Hulme M, Jones P (2000) Representing twentieth century space-time climate variability. II. Development of 1901–1996 monthly grids of terrestrial surface climate. *Journal of Climate*, **13**, 2217–2238.
- Norman JM, Kucharik CJ, Gower ST, Baldocchi DD, Crill PM, Rayment M, Savage K, Striegl RG (1997) A comparison of six methods for measuring soil-surface carbon dioxide fluxes. *Journal of Geophysical Research*, **102**, 28771–28777.
- Ohashi M, Gyokusen K, Saito A (1999) Measurement of carbon dioxide evolution from a Japanese cedar (*Cryptomeria japonica* D. Don) forest floor using an open-flow chamber method. *Forest Ecology and Management*, **123**, 105–114.
- Parker LW, Freckman DW, Steinberger Y, Driggers L, Whitford WG (1984) Effects of simulated rainfall and litter quantities on desert soil biota: Soil respiration, microflora, and protozoa. *Pedobiologia*, **27**, 185–195.
- Parker LW, Miller J, Steinberger Y, Whitford WG (1983) Soil respiration in a Chihuahuan desert rangeland. *Soil Biology and Biochemistry*, **15**, 303–309.
- Piñol J, Alcañiz JM, Rodà F (1995) Carbon dioxide efflux and pCO₂ in soils of three *Quercus ilex* montane forests. *Biogeochemistry*, **30**, 191–215.
- Potter CS, Klooster SA (1998) Interannual variability in soil trace gas (CO₂, N₂O, NO) fluxes and analysis of controllers on regional to global scales. *Global Biogeochemical Cycles*, **12**, 621–635.
- Raich JW, Nadelhoffer KJ (1989) Belowground carbon allocation in forest ecosystems: Global trends. *Ecology*, **70**, 1346–1354.

- Raich JW, Potter CS (1995) Global patterns of carbon dioxide emissions from soils. *Global Biogeochemical Cycles*, **9**, 23–36.
- Raich JW, Rastetter EB, Melillo JM, Kicklighter DW, Steudler PA, Peterson BJ, Grace AL, Moore B III, Vorosmarty CJ (1991) Potential net primary productivity in South America: Application of a global model. *Ecological Applications*, **1**, 399–429.
- Raich JW, Schlesinger WH (1992) The global carbon dioxide flux in soil respiration and its relationship to vegetation and climate. *Tellus*, **44B**, 81–99.
- Raich JW, Tufekcioglu A (2000) Vegetation and soil respiration: Correlations and controls. *Biogeochemistry*, **48**, 71–90.
- Reiners WA (1968) Carbon dioxide evolution from the floor of three Minnesota forests. *Ecology*, **49**, 471–483.
- Rochette P, Desjardins RL, Gregorich EG, Pattey E, Lessard R (1992a) Soil respiration in barley (*Hordeum vulgare* L.) and fallow fields. *Canadian Journal of Soil Science*, **72**, 591–603.
- Rochette P, Flanagan LB, Gregorich EG (1999) Separating soil respiration into plant and soil components using analyses of the natural abundance of carbon-13. *Soil Science Society of America Journal*, **63**, 1207–1213.
- Rochette P, Gregorich EG, Desjardins RL (1992b) Comparison of static and dynamic closed chambers for measurement of soil respiration under field conditions. *Canadian Journal of Soil Science*, **72**, 605–609.
- Saleska SR, Harte J, Torn MS (1999) The effect of experimental ecosystem warming on CO₂ fluxes in a montane meadow. *Global Change Biology*, **5**, 125–141.
- Savage K, Moore TR, Crill PM (1997) Methane and carbon dioxide exchanges between the atmosphere and northern boreal forest soils. *Journal of Geophysical Research*, **102**, 29279–29288.
- Schimel DS, Braswell BH, Holland EA, McKeown R, Ojima DS, Painter TH, Parton WJ, Townsend AR (1994) Climatic, edaphic, and biotic controls over storage and turnover of carbon in soils. *Global Biogeochemical Cycles*, **8**, 279–293.
- Schleser GH (1982) The response of CO₂ evolution from soils to global temperature changes. *Zeitschrift für Naturforschung*, **37**, 287–291.
- Schlesinger WH (1977) Carbon balance in terrestrial detritus. *Annual Review of Ecology and Systematics*, **8**, 51–81.
- Schlesinger WH, Andrews JA (2000) Soil respiration and the global carbon cycle. *Biogeochemistry*, **48**, 7–20.
- Smith FW, Resh SC (1999) Age-related changes in production and below-ground carbon allocation in *Pinus contorta* forests. *Forest Science*, **45**, 333–341.
- Sommerfeld RA, Mosier AR, Musselman RC (1993) CO₂, CH₄, and N₂O flux through a Wyoming snowpack and implications for global budgets. *Nature*, **361**, 140–142.
- Striegl RG, Wickland KP (1998) Effects of a clear-cut harvest on soil respiration in a jack pine – lichen woodland. *Canadian Journal of Forest Research*, **28**, 534–539.
- Townsend AR, Vitousek PM, Trumbore SE (1992) Tropical soils could dominate the short-term carbon cycle feedbacks to increased global temperatures. *Climatic Change*, **22**, 293–303.
- Trumbore SE, Chadwick OA, Amundson R (1996) Rapid exchange between soil carbon and atmospheric carbon dioxide driven by temperature change. *Science*, **272**, 393–396.
- Tulaphitak T, Pairintra C, Kyuma K (1985) Changes in soil fertility and tilth under shifting cultivation. III. Soil respiration and soil tilth. *Soil Science and Plant Nutrition*, **31**, 251–261.
- Valentini R, Matleucci G, Dolman AJ *et al.* (2000) Respiration as the main determinant of carbon balance in European forests. *Nature*, **404**, 861–865.
- Wilkinson L (1990) *SYSTAT: the System for Statistics, Version 5.0*. SYSTAT, Inc, Evanston, Illinois.
- Winston GC, Sundquist ET, Stephens BB, Trumbore SE (1997) Winter CO₂ fluxes in a boreal forest. *Journal of Geophysical Research*, **102**, 28,795–28,804.
- Zimov SA, Zimova GM, Daviodov SP, Daviodova AI, Voropaev YV, Voropaeva ZV, Prosiannikova SF, Semiletova IV, Semiletov IP (1993) Winter biotic activity and production of CO₂ in Siberian soils: a factor in the greenhouse effect. *Journal of Geophysical Research*, **98**, 5017–5023.