

Global patterns of carbon dioxide emissions from soils

James W. Raich

Department of Botany, Iowa State University, Ames

Christopher S. Potter

NASA Ames Research Center, Moffett Field, California

Abstract. We use semi-mechanistic, empirically based statistical models to predict the spatial and temporal patterns of global carbon dioxide emissions from terrestrial soils. Emissions include the respiration of both soil organisms and plant roots. At the global scale, rates of soil CO₂ efflux correlate significantly with temperature and precipitation; they do not correlate well with soil carbon pools, soil nitrogen pools, or soil C:N. Wetlands cover about 3% of the land area but diminish predicted CO₂ emissions by only about 1%. The estimated annual flux of CO₂ from soils to the atmosphere is estimated to be 76.5 Pg C yr⁻¹, 1–9 Pg greater than previous global estimates, and 30–60% greater than terrestrial net primary productivity. Historic land cover changes are estimated to have reduced current annual soil CO₂ emissions by 0.2–2.0 Pg C yr⁻¹ in comparison with an undisturbed vegetation cover. Soil CO₂ fluxes have a pronounced seasonal pattern in most locations, with maximum emissions coinciding with periods of active plant growth. Our models suggest that soils produce CO₂ throughout the year and thereby contribute to the observed wintertime increases in atmospheric CO₂ concentrations. Our derivation of statistically based estimates of soil CO₂ emissions at a 0.5° latitude by longitude spatial and monthly temporal resolution represents the best-resolved estimate to date of global CO₂ fluxes from soils and should facilitate investigations of net carbon exchanges between the atmosphere and terrestrial biosphere.

Introduction

Human-induced increases in the atmospheric concentrations of a variety of greenhouse gases have been underway over the past century and are expected to drive climate change in the coming decades. Carbon dioxide was responsible for an estimated 55% of the anthropogenically driven radiative forcing of the atmosphere in the 1980s and is predicted to have an even greater relative importance over the next century [Houghton *et al.*, 1990]. A highly resolved understanding of the sources and sinks of atmospheric CO₂, and how they are affected by climate and land use, is essential in the analysis of the global carbon cycle and how it may be impacted by human activities. Resolution of the spatial and temporal patterns of soil CO₂ fluxes provides opportunities both to better resolve the terrestrial carbon cycle and to identify and investigate controls over carbon exchanges between terrestrial ecosystems and the atmosphere.

Soils are of particular importance in the atmospheric CO₂ budget for a number of reasons. Soil organic matter contains a large reservoir of carbon, recently estimated at ~1600 Pg [Eswaran *et al.*, 1993], more than twice the atmospheric CO₂-C pool. Changes in the size of the soil C pool therefore can significantly affect atmospheric CO₂ concentrations. In fact,

concern has been raised about the potential for global warming to increase rates of CO₂ production by soils, thereby exacerbating the CO₂ loading of the atmosphere and providing a positive feedback to climate warming [e.g., Billings *et al.*, 1982; Schleser, 1982; Jenkinson *et al.*, 1991; Townsend *et al.*, 1992; Raich and Schlesinger, 1992; Körner and Arnone, 1992].

Soils are also major sources of CO₂, emitting 68–75 Pg yr⁻¹ of CO₂-C [Schlesinger, 1977; Raich and Schlesinger, 1992]. For comparison, the atmospheric pool of CO₂-C is about 760 Pg [Watson *et al.*, 1990]. Hence approximately 10% of the atmosphere's CO₂ passes through terrestrial soils each year. Temporal resolution of soil CO₂ efflux models is important because seasonal variation in rates of CO₂ fluxes from soils is a typical feature of many sites [e.g., Singh and Gupta, 1977; Schlesinger, 1977]. However, few global analyses of either the seasonal or spatial patterns of soil CO₂ fluxes have been published. Fung *et al.* [1987] estimated global decomposition-derived CO₂ fluxes based on seasonal temperature changes, but they did not consider the impacts of moisture.

Our objective is to describe, evaluate, and compare two empirically based, semi-mechanistic models of soil CO₂ emissions that are designed for global carbon analyses at a monthly temporal and 0.5° latitude by longitude spatial resolution. We then utilize these models to address several pertinent questions: How much CO₂ is released by terrestrial soils annually? How important are wetlands in modifying the global soil CO₂ efflux? What effects do land cover changes have on soil CO₂ emissions? To what extent do soil CO₂ emissions and atmospheric CO₂ concentrations covary

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temporally and spatially? Finally, we provide a state-of-the-knowledge global database of monthly CO₂ fluxes from terrestrial soils for eventual integration with similarly resolved estimates of global carbon flux rates.

Methods

Database Development

Published and unpublished (J.W.Raich) measurements of daily and/or mean monthly rates of carbon dioxide flux rates from intact soils were collated from the literature (see the appendix) to derive a data set for statistical analysis. Many of the data were estimated from published figures. Each datum, representing a single (or multiple) measurement(s) from a single site, was associated with the specific location of the study site, the month in which the measurement was collected, and the vegetation of that site. Data from sites containing vegetation that was substantially disturbed by humans (e.g., anthropogenic grasslands, croplands, young secondary forests, etc.) were noted.

As a general rule, averaging was avoided within vegetation types. However, if measurements were made during the same

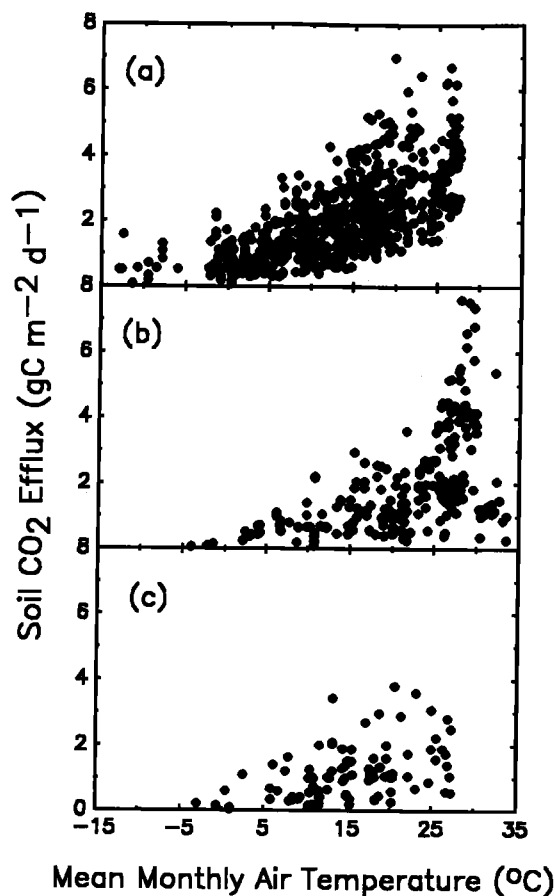


Figure 1. Data Used to Develop the Soil CO₂ Emission Models. Data sources are listed in the appendix. (a) All data from moist biomes with no dramatic dry season. (b) All data from sites having a distinct dry season. (c) All data from wetland sites. All points represent field-measured rates of total in situ soil CO₂ emissions.

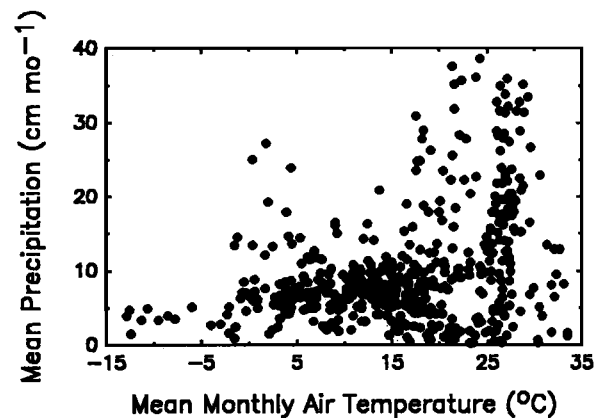


Figure 2. Range of mean monthly climatic conditions included in the data represented in Figure 1. Seven points associated with monthly rainfalls of >40 cm are not shown.

month in more than one year in a single site, or more than one time in a single site and month, then these data were averaged to obtain a mean monthly flux rate. We included all measurements that we could find with the following caveat: Data collected with static chambers were excluded if the area of absorption was <6% of the chamber area or if the chambers were inserted >5 cm into the soil. These techniques tend to underestimate actual fluxes [Raich and Nadelhoffer, 1989].

Each of these spatially referenced data was then aggregated with the appropriate climate, vegetation and soil data derived from geographically referenced data sets. These data sets included: mean monthly air temperature and mean monthly precipitation [Legates and Willmott, 1990a, b], soil organic carbon and nitrogen contents [Post *et al.*, 1982, 1985], soil type [Zobler, 1986], natural vegetation type [Matthews, 1983; Dorman and Sellers, 1989], and fractional wetland coverage [Matthews and Fung, 1987]. The final data set used in this work (Figure 1) contained 977 individual records from 72 grid cells (0.5° latitude by longitude) ranging from 71°18'N to 37°50'S, including data from every continent except Antarctica. Eighteen of Matthews' [1983] 30 natural vegetation classes were represented, as were 20 of 25 possible soil types. The climatic range of the included data was also very broad (Figure 2). About 10% of the data were from wetland habitats: this subset of data (Figure 1c) was analyzed separately.

Model Development

Carbon dioxide fluxes from terrestrial soils. Initial model development considered nonwetland sites only. Stepwise linear multiple regression was performed to identify the independent variables that were significantly related to monthly soil CO₂ efflux rates and which therefore could be used in predictive models. These initial analyses considered the continuous variables only (i.e., temperature, moisture status, soil carbon, soil nitrogen, and soil C:N). After identifying the independent variables that best correlated with soil CO₂ emissions, a variety of mechanistically based linear and nonlinear models were compared to determine the specific form of the relationships. Comparisons among different models were based on their r^2 values and evaluation of their residuals.

The variance observed in the collated data on soil CO₂ emissions increases with temperature (e.g., Figure 1a). Therefore all regression, correlation, and nonlinear modeling procedures were performed on both the raw and log-transformed data:

$$\log SR = \log(SR + 1.0) \quad (1)$$

where SR (g C m⁻² d⁻¹) is the soil CO₂ efflux rate. This transformation generated uniform variances with respect to temperature.

Carbon dioxide is produced in soils primarily by soil organisms and plant roots; our models were intended to predict the total CO₂ flux emanating from all heterotrophic activity in soils and from root respiration at the global scale. Relationships between environmental factors and soil biological activity have been widely investigated and provide a solid foundation of both data and theory upon which we based our models. Hence the models we developed are conceptually similar to a variety of previously developed empirical and mechanistic models of the effects of temperatures and moisture on decomposition or CO₂ production by soils [e.g., Bunnell *et al.*, 1977a; Howard and Howard, 1979; Nakane, 1980a; Schlentner and Van Cleve, 1985; Parton *et al.*, 1987; Carlyle and Than, 1988; O'Connell, 1990].

Temperature was the single most important variable for predicting the soil CO₂ flux. Both exponential (Q_{10}) and Arrhenius functions are commonly used to express the relationship between soil biological activity and temperature [Howard and Howard, 1979; Lloyd and Taylor, 1994]. We found that a Q_{10} relationship was superior to either linear, quadratic, or Arrhenius functions for prediction of global soil CO₂ fluxes.

Published rates of soil CO₂ efflux also correlated significantly with precipitation ($P < 0.001$, stepwise linear regression). Other measures of moisture availability were found to be poorer predictors of the influences of moisture in our models. These included P/PET and $P-PET$, where P is mean monthly precipitation and PET is monthly potential evapotranspiration as determined following Thornthwaite and Mather [1957].

The effect of precipitation on soil CO₂ emissions can be seen in Figure 1, where the relationship between temperature and CO₂ emissions is shown for both moist habitats (i.e., no significant dry season, Figure 1a) and dry habitats (sites with a dry season, Figure 1b). In dry habitats, soils are sometimes moist (e.g., during rainy seasons) and respire as actively as do soils in moist habitats. However, rates of soil CO₂ emissions are below their (temperature-defined) potential during dry months. We found that the relationship between precipitation and observed soil CO₂ efflux could be approximated using a hyperbolic function, with increasing rates of precipitation having sequentially lesser impacts on fluxes.

After temperature and moisture, the variables most frequently considered to be important in controlling rates of heterotrophic activity are the quantity and quality of substrate [e.g., Bunnell *et al.*, 1977b; Swift *et al.*, 1979; Heal and Ineson, 1984; O'Connell, 1990]. We evaluated directly the significance of including soil carbon pools, soil nitrogen pools, and soil C:N into our predictive models using stepwise linear

regression. None of these variables was found to be significantly related to soil CO₂ efflux at the global scale, after inclusion of temperature and precipitation.

Rates of soil respiration do vary among major plant biome types [Schlesinger, 1977; Singh and Gupta, 1977], but such variations may be explained by climatic differences among biomes. Despite the large number of locations in which soil CO₂ fluxes have been measured, coverage is very unequal with respect to vegetation and soil types. Whereas there exists much information from specific biomes that enables the development of vegetation-specific models [e.g., Kicklighter *et al.*, 1994], there are insufficient data to allow for either vegetation- or soil-specific model parameterizations that could be applied to provide global coverage.

On the basis of these considerations we developed two models for the prediction of terrestrial soil CO₂ emissions from global, monthly climate data. Model A is based on the log-transformed data, and model B is based on the untransformed data:

$$\text{Model A} \quad \log SR = F + (Q \times T \times (P/(K+P)))$$

$$SR = e^{\log SR} - 1.0$$

$$\text{Model B} \quad SR = F \times e^{Q \times T} \times (P/(K+P))$$

The log SR is as defined in Equation (1), SR (g C m⁻² d⁻¹) is the soil CO₂ efflux, F (g C m⁻² d⁻¹) defines the flux rate when the temperature is zero and moisture is not limiting, Q (°C⁻¹) represents the temperature coefficient, T (°C) is the mean monthly air temperature, P (cm) is the mean monthly precipitation, and K (cm month⁻¹) defines the half-saturation coefficient of the precipitation function. To prevent extrapolation of our models beyond the range of the input data (Figure 2), soil CO₂ fluxes were presumed to be zero at average monthly air temperatures of <-13.3°C and equal to the rate predicted at 33.5°C for all warmer temperatures.

Nonlinear modeling techniques [Wilkinson, 1990] were used to identify the values of the parameters F , K , and Q that best predicted monthly soil CO₂ fluxes for all nonwetland sites (Table 1). Least squares estimates of parameter values using both Quasi-Newton and Simplex methods [Wilkinson, 1990] gave identical results in all cases. Normal probability plots of residuals were linear, and residuals did not correlate significantly with any of the independent variables tested. Similar techniques were applied to evaluate other discreet subsets of the data such as moisture status (i.e., sites relatively free from water stress versus sites with a dry season), soil type, and vegetation type (biome), but the results did not improve our models and will not be considered further.

To evaluate the potential impacts of human-induced land cover changes on global soil CO₂ fluxes, we also parameterized our global models independently for two broad classes of land use: natural vegetation and disturbed vegetation (Table 1). For this classification, natural vegetation was considered to be any relatively mature vegetation similar in structure to the native vegetation of a specific region. Disturbed vegetation included all other sites.

Carbon dioxide fluxes from wetlands. Observed rates of CO₂ emissions from wetland soils are generally lower than

Table 1. Parameter Values for Log-Transformed (model A) and Untransformed (model B) Non-Linear Models for the Prediction of Monthly CO₂ Emissions From Terrestrial Soils

	Parameter				
	F , g C m ⁻² d ⁻¹	Q_{10} , °C ⁻¹	K , cm month ⁻¹	r^2	Global Flux Pg C yr ⁻¹
<i>Log-Transformed Model (A)</i>					
All data	0.611	0.0379	2.57	0.45	77.6
Natural vegetation	0.579	0.0396	2.19	0.50	-
Disturbed vegetation	0.695	0.0339	3.77	0.34	-
<i>Untransformed Model (B)</i>					
All data	1.33	0.0399	1.63	0.41	77.1
Natural vegetation	1.17	0.0459	1.39	0.47	79.1
Disturbed vegetation	1.63	0.0306	1.94	0.30	-

The global flux estimate is not corrected for wetlands. A dash indicated that that extrapolation was not done.

those observed from nonwetland sites (Figure 1) and do not correlate significantly with precipitation. Soil CO₂ fluxes from wetlands are linearly correlated with temperature:

$$\text{Model C} \quad \log \text{SR} = 0.282 + (0.0271 \times T) \quad r^2 = 0.27$$

$$\text{SR} = e^{\log \text{SR}} - 1.0$$

$$\text{Model D} \quad \text{SR} = 0.286 + (0.0568 \times T) \quad r^2 = 0.23$$

These models correspond with models A and B, respectively, where T (°C) represents the mean monthly air temperature. In both models the intercepts are not significantly different from zero, but the slopes are ($P < 0.001$). The relatively low r^2 values are reflective of the variability that occurs within and among wetlands; even on a site-specific basis the relationship between temperature and soil CO₂ efflux is weak yet significant [e.g., Pulliam, 1993].

Evaluation of the Models

The range of climatic conditions present within our input data is very broad (Figure 2), but it does not include all conditions present across the terrestrial landscape. Our model predictions are therefore based primarily on the interpolation of statistically defined relationships, but some extrapolation to unstudied climates was necessary for global coverage. We evaluated our predictions in two ways. First, we compared our predictions with published estimates of annual soil respiration rates in specific locations, as tabulated by Raich and Schlesinger [1992]. Second, we compared our predictions with predictions derived from application of a previously published annual model [Raich and Schlesinger, 1992]:

$$\text{Sr}_a = (9.26 \times T_a) + (0.0127 \times T_a \times P_a) + 289 \quad (2)$$

where Sr_a (g C m⁻² yr⁻¹) refers to the annual soil respiration rate, T_a (°C) is the mean annual air temperature, and P_a (mm) is the mean annual precipitation. The same global temperature and precipitation data used to run our models were used to run

this annual model, but mean annual climate data were used in the annual model.

Many of the studies used to develop the annual model are identical to those used to develop our monthly model, although only annual flux rates were used in the first case. The annual model therefore does not provide a validation check of our monthly models. Nevertheless, the annual model best approximates our current abilities to statistically predict soil CO₂ flux rates at global scales. Direct comparison of our model results with predictions from the annual model, and with measured rates of annual soil respiration, furnish useful yardsticks against which the monthly models can be compared. They also provide a direct measure of the effects of predicting global CO₂ flux rates at annual versus at monthly time steps. Comparisons among these various data were based on linear regressions of predicted versus observed soil CO₂ emissions.

Results

Environmental Controls Over Soil Carbon Dioxide Fluxes

Our statistical analyses of published data indicate that seasonal and spatial variations in soil CO₂ fluxes from terrestrial biomes are principally dependent upon temperature and moisture status, the latter as predicted by precipitation (Figure 3). These are the same variables that control rates of soil respiration in situ [e.g., Singh and Gupta, 1977]. The lack of any statistical correlations with other variables is likely due in part to the scale of our efforts: Our data set includes all of the variability in soil CO₂ efflux encountered globally. Hence all variation due to measurement techniques as well as differences attributed to vegetation or soils are included. At the global scale, soil CO₂ fluxes are best predicted by climatic factors alone.

Estimated Q_{10} values of our models (Table 1) range from 1.4 to 1.6. The Q_{10} value is frequently observed to change with temperature [Howard and Howard, 1979; Lloyd and Taylor, 1994], but at the global scale we found too much variation in the data (e.g., Figure 1) to argue that this effect is important. We did test the temperature-dependent Arrhenius function described by Lloyd and Taylor [1994, equation 11], but it provided less satisfactory residuals than did the Q_{10} model (model B) with our global data set.

It is often assumed that there is an optimum temperature beyond which increasing temperatures depress soil metabolism, and this effect is often included in decomposition or soil respiration models [e.g., Schlenker and Van Cleve, 1985; Parton et al., 1987; O'Connell, 1990]. The observed or estimated optimum temperature for decomposition varies greatly among substrates and models (e.g., 33–34°C [O'Connell, 1990], ~36°C [Parton et al., 1987], 55°C [Davidson, 1979], and >60°C [Wiant, 1967]). The range of our data extended to only 33.5°C, and there was no justification for developing a more complex model to include a high-temperature optimum for soil CO₂ efflux.

Our results suggest that precipitation rates of <2 cm month⁻¹ reduce soil CO₂ fluxes to less than 50% of their potential in non-wetland sites (Figure 3b). Even so, the influence of precipitation was secondary to that of temperature when viewed at the global scale.

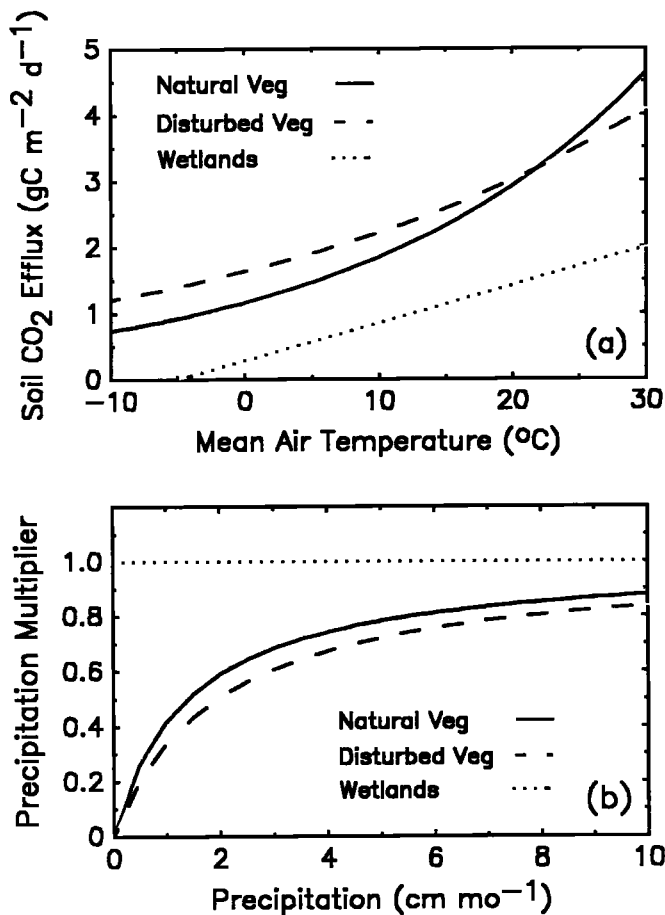


Figure 3. Modeled relationships between soil CO₂ emissions and mean monthly (a) air temperatures and (b) precipitation. Shown are the relationships defined for model B based on parameterization of the model with data from natural vegetation and from sites dominated by disturbed vegetation (including croplands). Soil CO₂ fluxes from wetlands are predicted from temperature alone, based on model D. Parameter values are listed in Table 1. The all-data parameterization used in our global extrapolation (Plate 1) has relationships between the two shown here.

Soil CO₂ emissions from wetlands are predicted to average about 2 g C m⁻² d⁻¹ lower than emissions from nonwetland sites at similar temperatures (Figure 3a). Hence the data we cumulated indicate that there is a substantial impact of soil saturation on soil CO₂ fluxes.

At the global scale we had few data sets that could be used to describe the quantity and quality of organic matter that could be respired by soils. We found no significant impact of soil carbon pools, soil nitrogen pools, or soil C:N on observed soil CO₂ efflux. We had insufficient data to rigorously investigate the effects of soil type, as defined by *Zobler* [1986], on soil CO₂ fluxes.

Global Carbon Dioxide Fluxes From Soils

Application of models A (log-transformed) and B (untransformed) to the entire global terrestrial landscape results

in global soil CO₂ efflux estimates of 77.6 and 77.1 Pg C yr⁻¹, respectively. Highest CO₂ emissions occur in the tropical moist forest biome; lowest rates occur in cold (tundra) and dry (desert) regions. Previous data summaries have led to the same conclusions [e.g., *Schlesinger*, 1977; *Raich and Schlesinger*, 1992].

Inclusion of wetland areas diminishes the global totals for models A and B to 76.4 and 76.5 Pg C yr⁻¹, respectively (Plate 1), based on a wetland area of 4.5 × 10⁶ km². Therefore, although wetlands cover about 3% of the terrestrial area, their inclusion in the global analyses diminishes predicted soil CO₂ emissions by only about 1%.

Effects of land cover changes. We found no substantial differences among parameter values identified separately for natural vegetation, disturbed vegetation, or for all sites combined (Table 1). The effect of using different parameters on model predictions was not great (Figure 3), but they were consistent with the variable nature of disturbance. There was a general trend for model parameterizations from disturbed site data to be less sensitive to the independent variables (temperature and precipitation) than were model parameterizations based on natural vegetation only (Figure 3). That is, disturbance in general decreased our ability to predict soil CO₂ fluxes from climate data alone.

The estimated impacts of past land cover changes on soil CO₂ emissions were evaluated with model B by comparing estimates derived by parameterization of the model with natural vegetation only with estimates derived using parameters based on disturbed sites only (Table 1). For this analysis all vegetation in cultivation (*Dorman and Sellers*' [1989] class 12) was considered disturbed, and all other vegetation was considered natural and without wetlands. Predicted global soil CO₂ emissions under this scenario were 78.9 Pg C yr⁻¹, 1.8 Pg greater than the estimate derived from including all data in the model parameterization. The estimated global CO₂ flux of an entirely undisturbed world, again based on model B, was 79.1 Pg C yr⁻¹, which is 0.2–2.0 Pg C yr⁻¹ greater than our estimates for current land cover conditions.

Seasonal variations. Soil CO₂ emissions vary seasonally as well as spatially. Overall, CO₂ emission rates match periods of active plant growth, with maximal fluxes coinciding with summer in both temperate zones and remaining high throughout the year in the near-equatorial regions (Figure 4). This is to be expected, as those factors favoring soil metabolic activity also generally favor plant growth. As a result, soils produce more CO₂ when plants are most able to utilize it. However, both of our models predict significant CO₂ emissions from soils even during dormant seasons (Figure 4).

Evaluation of the Models

Predicted soil CO₂ fluxes from all three models correlated significantly ($P < 0.001$) and linearly with published estimates of annual CO₂ fluxes, the latter as tabulated by *Raich and Schlesinger* [1992]. We did not include wetlands in these comparisons. Correlation coefficients (r^2) of 0.48 and 0.49 for models A and B, respectively ($n = 163$), were essentially identical to that of the annual model ($r^2 = 0.49$). Constant terms were not significantly different from zero (for the annual model, $0.10 > P > 0.05$), and slopes were not significantly different from 1.0. The three models did not differ significantly

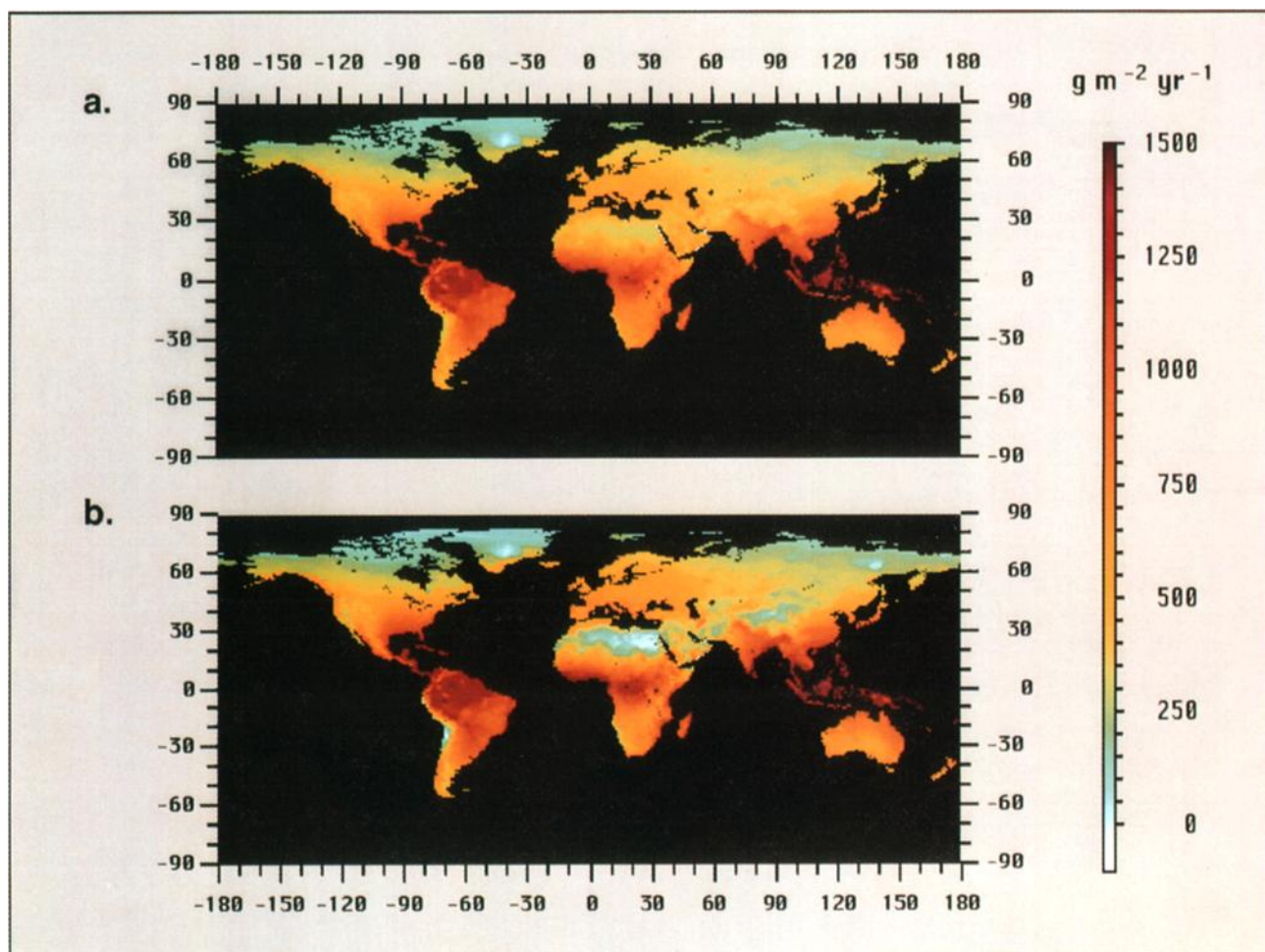


Plate 1. Global annual soil CO₂ emissions as predicted by the (a) log-transformed model A and (b) the untransformed model B, including corrections for wetlands (models C and D, respectively).

in their slopes. These analyses indicate that both of our global models provide quantitatively meaningful estimates of annual soil CO₂ emissions and that the reliability of our annual predictions is not diminished in any way by the monthly timescale of our model.

Discussion

Global Fluxes of Carbon Dioxide From Soils

On the basis of model B and its wetland counterpart model D we estimate the annual CO₂ flux from soils (i.e., soil respiration), including wetland soils, to be 76.5 Pg C yr⁻¹ over a terrestrial area of 149×10^6 km². This is just slightly higher than *Schlesinger's* [1977] estimate of 75 Pg C yr⁻¹. *Schlesinger* based his estimate on *Reiners'* [1973] analysis of terrestrial detritus production coupled with an estimate of the ratio of soil respiration to detritus production. *Raich and Schlesinger* [1992] estimated the global flux to be 68 Pg C yr⁻¹, based on extrapolation of biome-specific mean soil respiration rates to biome land areas as defined by different investigators. Our estimate is derived from available information on the spatial and temporal patterns of climatic conditions that influence soil CO₂ emissions and nonlinear modeling techniques

Neither of our models explained more than half of the variability present in measured soil CO₂ emissions (Table 1). This is in part due to the spatial and temporal scale of our model. The majority of the data used to parameterize our models was based on daily measurements of fluxes at square meter scales in specific months, but we applied this data to monthly models at 10^3 -km² scales under average climate conditions. One effect of scaling up from small to larger scales is a general loss of sensitivity of the model predictions to variable environmental attributes [e.g., *O'Neill*, 1979; *Rastetter et al.*, 1992]. Methodological differences among soil respiration studies [*Singh and Gupta*, 1977] and discrepancies between global data sets and on-site conditions also increase the unexplained variance in our models. Nevertheless, we explained 30-50% of the variability encountered in the global data with relatively simple models containing only three parameters.

There remain uncertainties in the spatial estimation of soil CO₂ emissions, principally due to the lack of information available from very dry biomes and during very cold months. Our models A and B provided similar estimates of the global magnitude of soil CO₂ fluxes but differed in their predictions of the spatial distribution of emissions. Particularly notable are

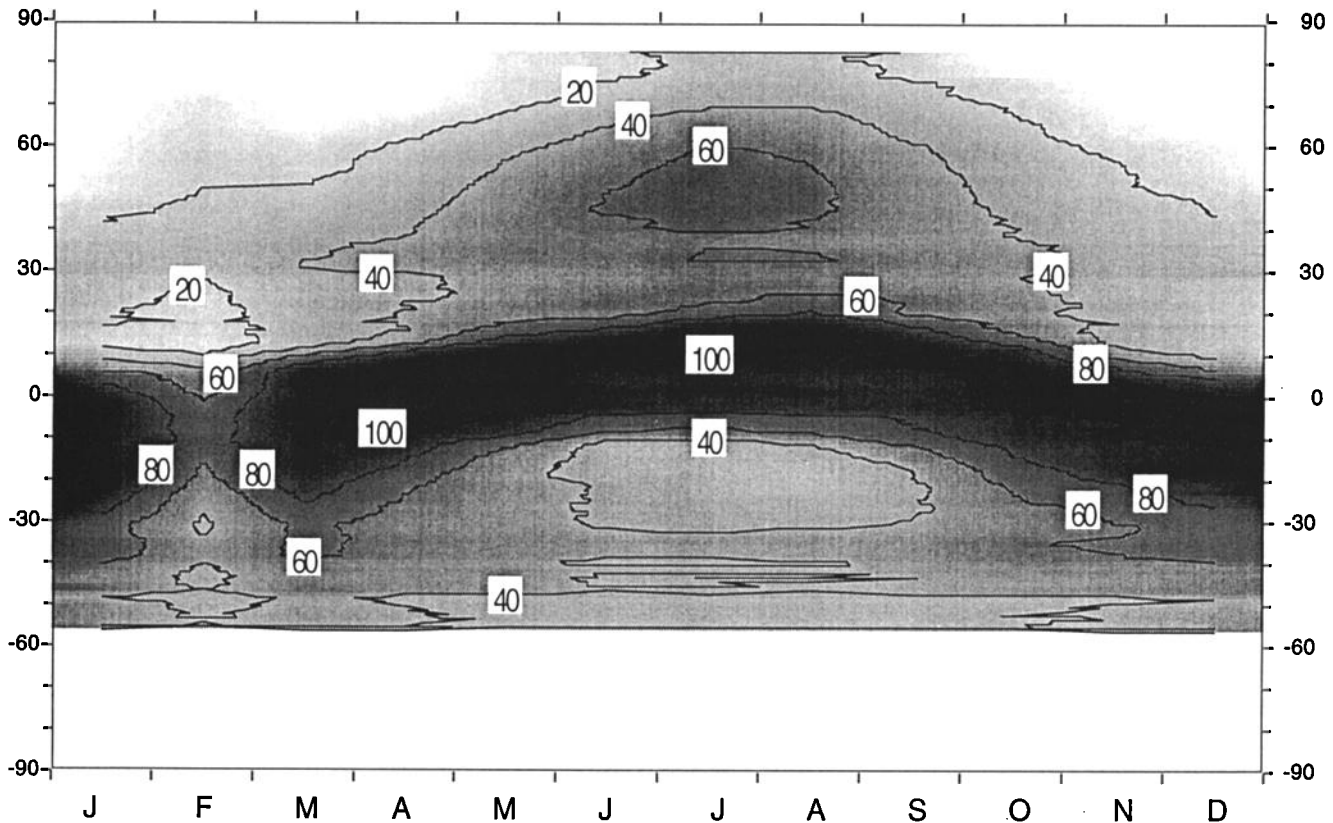


Figure 4. Predicted seasonal and spatial dynamics of soil CO₂ emissions based on models B and D. The oceans are neutral (no fluxes) in this analysis. Units are g C m⁻² month⁻¹.

differences in predicted CO₂ fluxes from the deserts of North Africa, the Arabian Peninsula, and continental Asia, where model B predictions are clearly lower than those of model A (Plate 1).

Published measurements of soil respiration rates in deserts range from 184 to 300 g C m⁻² yr⁻¹ ($n=3$ [Raich and Schlesinger, 1992]), whereas rates predicted by model A average 406 g C m⁻² yr⁻¹ (Table 2). Few field measurements of in situ soil CO₂ emissions from deserts have been published, but generally low rates of plant productivity in deserts suggest that soil CO₂ production rates should also be low. In model A the constant term (F) defines a lower limit to the soil CO₂ flux at temperatures $>0^{\circ}\text{C}$, regardless of precipitation. Hence it appears that the log-transformed model (model A) overestimates soil CO₂ fluxes under extremely dry conditions. In contrast, predicted soil CO₂ fluxes are equal to zero in model B whenever monthly precipitation equals zero.

Both models predict soil CO₂ efflux rates in tundra to average >200 g C m⁻² yr⁻¹ (Table 2), whereas measured rates average 60 g C m⁻² yr⁻¹ [Raich and Schlesinger, 1992]. It therefore appears that both models may overestimate soil CO₂ fluxes under very cold conditions. Part of this may be attributed to the lack of near-zero measurements in the published literature. Investigators tend not to measure soil CO₂ fluxes during very cold periods when rates are presumably very low (see Sommerfeld *et al.* [1993] and Zimov *et al.* [1993]). Our empirical approach includes only published data, not the many presumed zero values that occur during wintertimes. Our

statistically defined relationships are therefore biased toward positive values based on published data from more temperate latitudes.

Tundra may also have unique attributes that are not accounted for in our simple models. For instance, the presence of permafrost may alter the relationship between soil and air temperatures upon which our model depends. Also, peat accumulation in tundra soils [e.g., Chapin *et al.*, 1980] may diminish CO₂ emission rates below those that would be predicted in soils that are not storing appreciable amounts of their annual production. It is also possible that the field-based estimates of CO₂ flux from tundra soils, which are based on summertime emissions alone, are somewhat low.

Despite these limitations both models A and B provide very good estimates of the global magnitude and distribution of soil CO₂ emissions. Total CO₂ fluxes from tundra and deserts combined are $\sim 10\%$ of the global fluxes predicted from both models. In all other biomes, which include $\sim 90\%$ of the global CO₂ emissions, model predictions generally are similar to measured flux rates. Both models A and B were as reliable as was the annual model for predicting the spatial distribution of annual soil CO₂ efflux rates. However, their capacity to predict the seasonal pattern of flux rates greatly enhances their utility in analyses of global carbon cycling.

Environmental Controls Over Soil Carbon Dioxide Fluxes

Effects of temperature. We found the Q_{10} of soil CO₂ efflux to be 1.5 when all non-wetland data were included in the

Table 2. Mean Rates of Soil CO₂ Efflux and Net Primary Productivity (NPP) in Different Biomes

Vegetation Type ^a	Mean Soil CO ₂ Efflux			
	NPP	Model A	Model B	Eq. (2)
Broadleaf evergreen trees	1027	1050	1098	1185
Broadleaf deciduous trees	315	506	566	463
Broadleaf and needleleaf trees	316	450	505	421
Needleleaf evergreen trees	226	332	364	314
Needleleaf deciduous trees	153	233	245	161
Broadleaf trees, groundcover	559	776	788	795
Perennial grasslands	180	611	584	603
Broadleaf shrubs with grass	469	750	776	717
Broadleaf shrubs with soil	115	514	490	513
Tundra	80	204	217	179
Bare soil and desert	28	406	282	476
Cultivation	288	559	585	428

^aBased on the work by *Dorman and Sellers* [1989].

NPP is derived from Table 7 of *Potter et al.* [1993]. Soil CO₂ fluxes are predicted by model A, model B, and equation (2). Wetland fluxes predicted from Models C and D are included in the soil flux estimates. All units are g C m⁻² yr⁻¹.

model. Published estimates of the Q_{10} of soil respiration from individual sites varies substantially, but the median of reported values is about 2.4 [*Raich and Schlesinger*, 1992]. The apparent discrepancy between our low Q_{10} estimates and those reported in the literature is explained in part by our use of air versus soil temperature as an independent variable. Air temperature typically fluctuates more in vegetated sites than does soil temperature. As a result, Q_{10} values calculated from air temperature are lower than those based on soil temperature [e.g., *Kicklighter et al.*, 1994]. This is shown in Figure 5, where the Q_{10} for soil CO₂ efflux is 2.0 ($r^2 = 0.84$) based on soil temperature and is 1.7 ($r^2 = 0.88$) based on air temperature. Microbes are more metabolically responsive to soil than to air temperatures.

Effects of moisture. In our models, precipitation is used as a surrogate for soil moisture status. Soil moisture content is dependent upon a number of variables including water inputs, of which precipitation is one dominant flux. However, water demand and soil properties also influence the availabilities of water and oxygen to decomposers and roots, so consideration of precipitation alone is an admitted weakness in our models. Nevertheless, at the global scale inclusion of precipitation in our models did improve their predictive capacity. Precipitation is widely measured, precipitation data are available at the global scale, and the seasonal and spatial distribution of precipitation is predicted by global climate models. From an empirical, predictive standpoint, use of precipitation as an independent variable in our models allows for direct estimation of global soil CO₂ flux rates, obviates the requirement for a detailed soil moisture model and the requisite input data to run such a model, and provides a means of statistically investigating the possible effects of precipitation changes on soil CO₂ flux rates.

The effects of moisture availability on soil metabolic activity have received much study. In general, three phases of moisture effects on soil biota can be identified [e.g., *Ino and Monsi*,

1969; *Hunt*, 1977; *Skopp et al.*, 1990]. When soils are relatively dry, metabolic activity increases with increasing moisture availability. There follows generally a broad region over which moisture has little effect; soil biological activity is at or near its potential. In general, this occurs when soils are 50-80% saturated [*Clark*, 1967; *Alexander*, 1977; *Linn and Doran*, 1984]. When soils are too wet, oxygen deficiencies inhibit aerobic respiration [*Skopp et al.*, 1990]. Most models of decomposition or soil respiration [e.g., *Parton et al.*, 1987; *Schlenker and Van Cleve*, 1985; *Raich et al.*, 1991] include each of these phases. Our model includes only the first two of these three phases, but wetlands were modeled independently. Hence the impacts of soil saturation on soil CO₂ fluxes are included as a spatial component in our global estimates.

Inclusion of wetlands into our global extrapolation diminished our estimate of global soil CO₂ emissions by 0.6-1.2 Pg C yr⁻¹. Nevertheless, rates of soil CO₂ efflux from wetlands are, on the average, substantially lower than are those from better drained sites when corrected for temperature (Figure 3a). This finding is consistent with the concepts just discussed.

Models A and B treat moisture effects on soil CO₂ emissions differently. The hyperbolic function in model B (Figure 3b) includes only the first two phases of moisture impact; no allowance is made for soil saturation effects. Our assumption is that nonwetland, terrestrial soils drain on a monthly basis, regardless of precipitation. Although the same hyperbolic

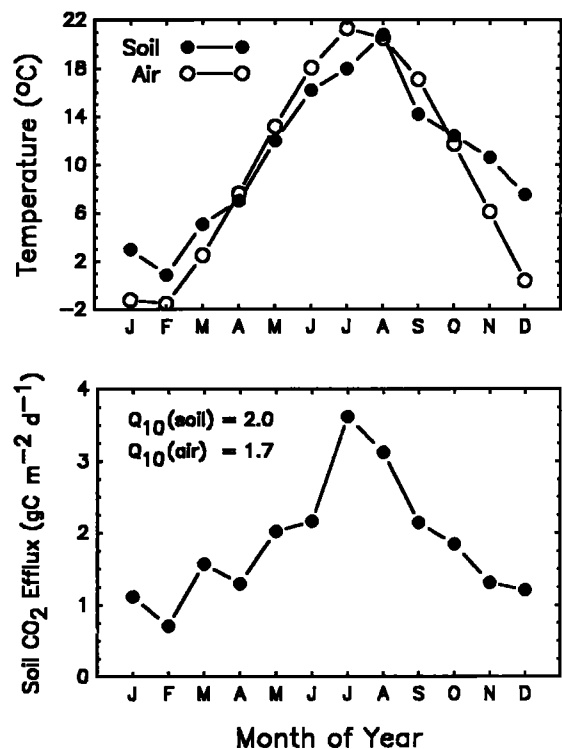


Figure 5. (top) Mean monthly air and soil temperatures and (bottom) soil CO₂ emissions from a young, irrigated pine stand in Massachusetts (J. W. Raich unpublished data, 1988). The Q_{10} values are based on regression analysis of the equations $SR = F \times e^{Q_{10} \times T}$, where T (°C) is the mean monthly temperature and SR (g C m⁻² d⁻¹) is the soil CO₂ efflux.

function is used in model A, it appears as an exponent in the model. *Carlyle and Than* [1988] found that the ability to predict soil respiration rates in their study site was greatly improved by including a moisture-dependent Q_{10} coefficient. This is the case in Model A: the precipitation function is a direct multiplier on the Q_{10} coefficient. Low rates of precipitation dampen the temperature effect, and zero precipitation generates a CO₂ efflux estimate equal to the parameter F (Table 1).

Effects of substrate quantity and quality. We were unable to discern any significant relationships between carbon pools or available estimates of organic matter quality and soil CO₂ flux at the global scale. Nevertheless, identifying a relationship between substrate quality and soil CO₂ emissions is of importance if one exists, as increases in atmospheric CO₂ concentrations are predicted to increase the C:N in litter production [*Norby et al.*, 1986; *Colteaux et al.*, 1991]. To further investigate the possible importance of shifts in litter C:N on soil CO₂ fluxes, we can compare directly rates of CO₂ emissions from moist temperate forest dominated by broadleaved deciduous trees with those from coniferous forests. These two forest types differ substantially in their nutrient-cycling characteristics, with coniferous forests producing litter with lower mineral nutrient concentrations [e.g., *Cole and Rapp*, 1981]. Despite their dissimilarities, there is no apparent difference between these forest types with respect to their observed soil CO₂ emissions (Figure 6).

Effects of land use. Despite a lack of real differences among the various model parameterizations (Table 1), the statistical method we applied provides the best available means of identifying trends in the published data and for using these data to generate testable hypotheses concerning the potential effects of human activities on global soil CO₂ fluxes. We found that disturbance in general diminished our ability to predict soil CO₂ fluxes from climate data alone. Disturbance takes many forms, and our model parameterizations for disturbed sites represent the net effects of the many types of disturbance present on the landscape.

Assuming that 100% of the area within cultivation cells (i.e., *Dorman and Sellers'* [1989] class 12) was disturbed and all

other cells were 100% natural vegetation, global CO₂ emissions were estimated to be 1.8 Pg C yr⁻¹ greater than those predicted from the all-data parameterization. Predicted global CO₂ emissions from an all-natural world are 79.1 Pg C yr⁻¹, excluding wetlands. This value is 2.0 Pg C yr⁻¹ greater than predicted by the all-data model parameterization and 0.2 Pg C yr⁻¹ greater than the disturbance scenario just discussed. Taken at face value, these comparisons suggest that past human modifications of the terrestrial land cover have had the net effect of diminishing current global soil CO₂ emissions by 0.2-2.0 Pg C yr⁻¹ on average.

Soil Carbon Dioxide Fluxes and Net Primary Productivity

Soil CO₂ emissions are derived from both the decomposition of organic matter and live root respiration. Because they include a plant respiratory component, predicted soil CO₂ emissions should exceed net primary productivity (NPP) under most conditions. Our global estimate of soil CO₂ efflux (i.e., 76.5 Pg C yr⁻¹) is about 60% higher than current levels of NPP as estimated by *Potter et al.* [1993], and about 30% higher than current NPP as estimated by *Ruimy and Saugier* [1994]. Our estimated flux from an all-natural world (i.e., 79.1 Pg C yr⁻¹) is about 40% higher than the predicted NPP of an all-natural world [*Melillo et al.*, 1993]. These estimates are consistent with previous work that suggests that soil respiration exceeds NPP by 25-50% [*Raich and Schlesinger*, 1992].

The specific relationship between predicted soil CO₂ efflux and NPP varies among vegetation types (Table 2). However, predictions from both of our models indicate that NPP and soil CO₂ emissions are positively correlated and that soil CO₂:NPP declines as NPP increases (linear regression of data in Table 2, $P < 0.001$). Very high differences between our estimated soil CO₂ fluxes and *Potter et al.*'s [1993] NPP estimates occur in deserts, tundra, dry shrublands, and perennial grasslands (Table 2). These are all biomes that include either dry or very cold seasons and in which relatively few studies of seasonal variations in soil CO₂ emissions have been conducted. Additional measurements of soil CO₂ fluxes throughout the year are needed in these environments.

Soil Fluxes and Atmospheric CO₂

Atmospheric CO₂ concentration data are available for a number of locations around the world. These data, when combined with estimates of C fluxes through vegetation and soils, can provide a constraint upon both the magnitude and spatial distribution of the CO₂ emissions predicted by our models. We compared predicted soil CO₂ emissions with mean monthly atmospheric CO₂ concentrations for each of three latitudinal bands: 60-90°N, 30-60°N, and 0-30°N (Figure 7). Atmospheric CO₂ data were derived from *Conway et al.* [1988] and *Keeling et al.* [1989]; means for the period 1981-1984 were calculated for this comparison.

This comparison (Figure 7) highlights two important points. First, atmospheric CO₂ concentrations decline during the summer (approximately May-September) in the northern hemisphere due to net C uptake by vegetation [*Tucker et al.* 1986; *Conway et al.*, 1988]. These same months are when maximum CO₂ emissions from soils occur; soils produce CO₂ when vegetation is most able to assimilate it. Second, soil CO₂

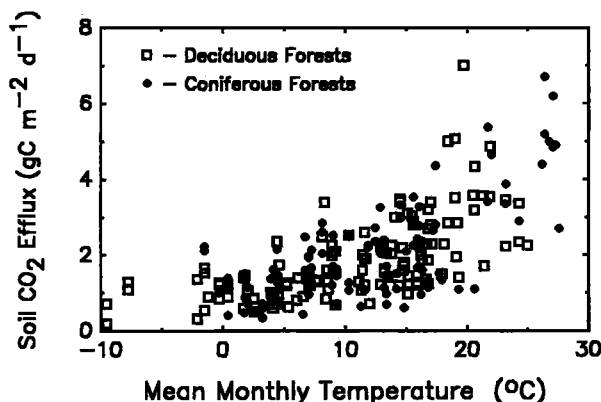


Figure 6. Soil CO₂ emissions from temperate deciduous and coniferous forests shown in relation to mean monthly air temperature. Only data from moist biomes (Figure 1a) are included.

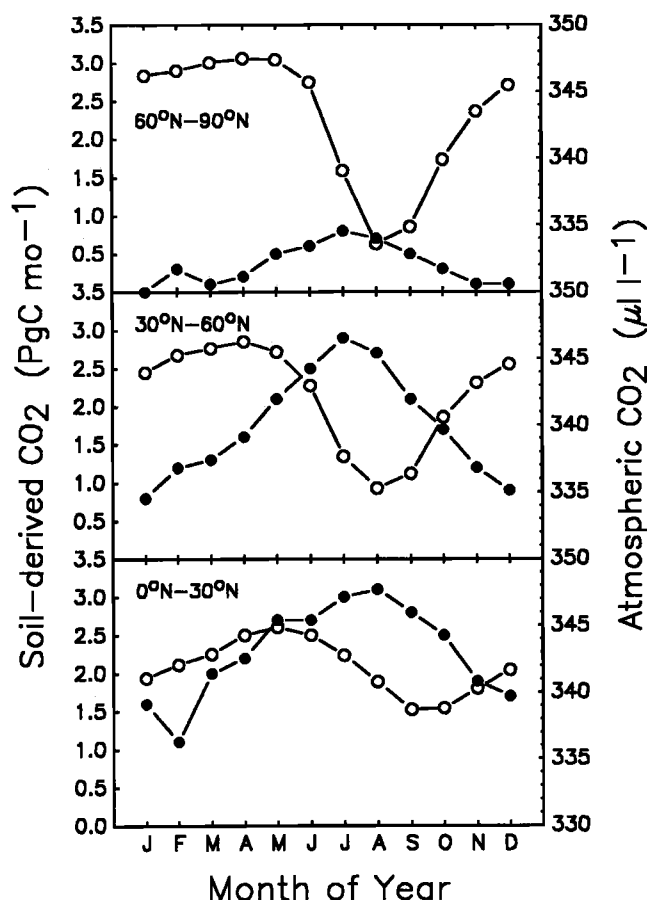


Figure 7. Predicted monthly rates of soil CO₂ emissions (solid symbols) for 30° latitudinal belts in the northern hemisphere, and the mean monthly atmospheric CO₂ concentrations (open symbols) for the same regions. Atmospheric CO₂ levels are based on the mean values for each month during 1981-1984. For the 60°-90° belt the atmospheric data are based on the means of sites BRW, MBC, and STM of *Conway et al.* [1988]. For the 30°-60° belt the atmospheric data are means of sites CBA, NWR, and AZR. The atmospheric data for 0°-30° are from Mauna Loa Observatory [Keeling *et al.*, 1989].

emissions are predicted to occur throughout the year and therefore contribute to the observed increases in atmospheric CO₂ that occur during winter months.

A complete evaluation of terrestrial-atmosphere C exchanges will require spatially and temporally resolved estimates of net C uptake (i.e., net ecosystem productivity) by terrestrial ecosystems. Spatially and temporally resolved estimates of terrestrial NPP already exist [Melillo *et al.*, 1993; Potter *et al.*, 1993; Ruimy and Saugier, 1994]. Our estimates of soil CO₂ emissions can be used independently to estimate total decomposition in terrestrial ecosystems, if reasonable assumptions are made concerning the amount of respiration-derived CO₂ in soil respiration. Such efforts should facilitate resolution of the global carbon cycle and enhance evaluations of the potential impacts of global changes on terrestrial carbon budgets.

Role of Statistical Models in Global Analyses

In the past decade a number of mechanistically based models have been developed for the evaluation of terrestrial carbon cycling processes at regional to global scales (e.g., CENTURY [Parton *et al.*, 1988]; FOREST-BGC [Running and Coughlan, 1988; Running and Gower, 1991]; TEM [Melillo *et al.*, 1993]; CASA [Potter *et al.*, 1993]; LINKAGES [Pastor and Post, 1986; Pastor, 1986]; IMAGE-2 [Vloedbeld and Leemans, 1993]). A rationale of these efforts is that modeling the underlying physical and biological processes that control ecosystem dynamics provides a firm theoretical basis for testing hypotheses at the process level and facilitates analyses of the effects of environmental changes. Statistical summaries such as our own provide an objective benchmark against which the output from more detailed, mechanistically based models can be evaluated. Furthermore, the statistical approach has at least two advantages when applied to global analyses. Our models contain only three parameters, the values of which are statistically defined, and the independent variables in our models are derived from weather station data. A statistical evaluation of the existing empirical information is a useful and necessary step in global analyses.

At the same time, the lack of a detailed mechanistic basis does limit the applicability of statistical models in the analyses of global change issues. The statistical approach we used is useful principally for documenting trends in the existing global data and for evaluating broadscale patterns that occur as a result of these trends. However, the importance of specific factors such as substrate quality or land cover in affecting rates of soil CO₂ emissions can be masked by the variability present in the data and the resulting simplicity of our models. The lack of a statistically significant trend in a global data set does not prove that any given variable is unimportant. Rather, it demonstrates that we were unable to identify its importance at the global scale and highlights the need for additional studies.

Our models, although simple, do have a mechanistic foundation. Air temperature is used as a surrogate for soil temperature, precipitation is used as a surrogate for soil moisture availability, and the relationships we defined are similar to those commonly used to model decomposition and soil respiration. At the global scale these relationships are rather poorly resolved as a result of the great spatial variability encountered within and among terrestrial grid cells. Improved global data sets of environmental parameters and an improved understanding of the impacts of within-grid cell heterogeneity on larger-scale processes will improve our abilities to investigate global carbon cycling processes. However, this latest global CO₂ flux estimate includes the greatest amount of available information, provides the best resolved spatial and temporal estimates of soil CO₂ flux rates, and represents our best current estimate of global soil CO₂ emissions.

Appendix

Soil CO₂ emission data used in this analysis was derived from the following sources: Anderson [1973], Behera and Pati [1986], Beyer [1991], Billès *et al.* [1971], Brumme and Beese [1992], Buyanovsky *et al.* [1986, 1987], Caldwell *et al.* [1977], Carlyle and Than [1988], Chapman [1979], Dörr and Münnich [1987], Edwards and Ross-Todd [1979, 1983], Ellis [1969,

1974], Ewel et al. [1987], Fouseki and Margaris [1981], Giblin et al. [1991], Gordon et al. [1987], Goreau [1981], Gupta and Singh [1981], Havas and Mäenpää [1972], Hülger [1963], Holt et al. [1990], Howes et al. [1985], Hunt [1977], Johnson and Todd [1984], Joshi et al. [1991], Kucera and Kirkham [1971], Kursar [1989], Luken and Billings [1985], May and Risser [1973], Monteith et al. [1964], Moore [1989], Morris and Whiting [1986], Nakane [1980a, b], Nakane et al. [1984, 1986], Ogawa [1978], Parker et al. [1983], Poole and Miller [1982], Pulliam [1993], Rai and Srivastava [1981], Raich [1983], Raich et al. [1985], J. W. Raich [unpublished data 1988, 1992], Rajvanshi and Gupta [1986], Reiners [1968], Repnevskaya [1967], Risser et al. [1981], Schlentner and Van Cleve [1985], Silvola et al. [1985], Singh [1984], Singh et al. [1988], Singh [1977], Steudler et al. [1991], Tesarova and Gloser [1976], Tulaphitak et al. [1983], Upadhyaya and Singh [1981], Villecourt [1973], Vogt et al. [1980], Weber [1985, 1990], Wofsy et al. [1988], Yoda and Nishioka [1982], Yoneda and Okata [1987].

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C.S. Potter, NASA Ames Research Center, Mail Stop 239-20, Moffett Field, CA 94305. (e-mail: chrisp@gaia.arc.nasa)

J.W. Raich, Iowa State University, Department of Botany, 353 Bessey Hall, Ames, IA 50011-1020. (e-mail: jraich@iastate.edu)

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