JOURNAL OF GEOPHYSICAL RESEARCH, VOL. 99, NO. D1, PAGES 1303–1315, JANUARY 20, 1994

Aspects of spatial and temporal aggregation in estimating regional carbon dioxide fluxes from temperate forest soils

David W. Kicklighter, Jerry M. Melillo, William T. Peterjohn,
Edward B. Rastetter, A. David McGuire, and Paul A. Steudler
The Ecosystems Center, Marine Biological Laboratory, Woods Hole, Massachusetts

John D. Aber
Institute for the Study of Earth, Oceans, and Space, University of New Hampshire, Durham

Abstract. We examine the influence of aggregation errors on developing estimates of regional soil-CO_2 flux from temperate forests. We find daily soil-CO_2 fluxes to be more sensitive to changes in soil temperatures (Q_{10} = 3.08) than air temperatures (Q_{10} = 1.99). The direct use of mean monthly air temperatures with a daily flux model underestimates regional fluxes by approximately 4%. Temporal aggregation error varies with spatial resolution. Overall, our calibrated modeling approach reduces spatial aggregation error by 9.3% and temporal aggregation error by 15.5%. After minimizing spatial and temporal aggregation errors, mature temperate forest soils are estimated to contribute 12.9 Pg C yr^{-1} to the atmosphere as carbon dioxide. Georeferenced model estimates agree well with annual soil-CO_2 fluxes measured during chamber studies in mature temperate forest stands around the globe.

1. Introduction

The evolution of carbon dioxide from soils is a major source of carbon to the atmosphere. On a global scale, soils are estimated to contribute 50–75 Pg C as carbon dioxide to the atmosphere each year [*Schlesinger*, 1977; *Houghton and Woodwell*, 1989; *Raich and Schlesinger*, 1992]. This contribution represents 20–38% of all the carbon dioxide entering the atmosphere [cf. *Post et al.*, 1990] from both natural and anthropogenic sources, including fossil fuel emissions. As the world continues to change, soil-CO_2 fluxes to the atmosphere may be altered over large regions, leading to changes in the global carbon budget. To quantify such changes, field measurements of soil-CO_2 flux must be aggregated over space and time to develop regional estimates of soil-CO_2 flux. The approach used to develop regional estimates from site-specific flux measurements may lead to large aggregation error if spatial and temporal variabilities in soil-CO_2 fluxes over a region are not taken into account. Large aggregation error impairs our ability to detect changes in regional soil-CO_2 fluxes. Because even small changes in regional fluxes may have significant effects on the global carbon budget [cf. *Jarvis et al.*, 1989], it is desirable to minimize aggregation error when developing regional estimates of soil-CO_2 flux.

Most regional estimates of soil-CO_2 flux have been developed from mean annual rates of litterfall [*Schlesinger*, 1977], net primary productivity [*Fung et al.*, 1987], or soil-CO_2 flux measured in field studies [*Raich and Schlesinger*, 1992]. To calculate regional estimates, mean annual rates of litterfall, net primary productivity (NPP) or soil-CO_2 fluxes are determined from a literature survey of field studies and then multiplied by the area covered by the region. Often, the mean annual fluxes are stratified by major vegetation types (or biomes) so that some spatial variations in soil-CO_2 fluxes are taken into account. Temporal variations in soil-CO_2 fluxes are generally ignored. Consequently, these approaches are limited for refining regional flux estimates or for assessing the effect of global change on soil-CO_2 fluxes.

Recently, *Jenkinson et al.* [1991] have estimated regional fluxes using a different approach. Relationships between environmental factors and decomposition rates are first defined in a model (the Rothamsted model [*Jenkinson*, 1990]). This model is then used with climatic data that has been aggregated temporally to monthly means and spatially over Holdridge's life zones [*Holdridge*, 1964] to estimate annual soil-CO_2 fluxes, associated with microbial respiration, from the world's biomes. Although this approach does consider seasonal variability, soil-CO_2 fluxes are constant spatially throughout the life zones so that the resulting regional estimates still contain significant spatial and temporal aggregation error.

Here, we describe an approach that attempts to minimize the spatial and temporal aggregation errors associated with developing regional soil-CO_2 flux estimates for temperate forests. Like *Jenkinson et al.* [1991], we define the important relationships observed between environmental factors and soil-CO_2 fluxes in a model, but we also recognize that these relationships may change at different temporal resolutions [cf. *Rastetter et al.*, 1992]. We attempt to minimize temporal aggregation error by accounting for such scale-dependent changes as we aggregate the relationships in a daily flux model to a monthly resolution. After developing the monthly flux model, we spatially extrapolate the model over the area covered by temperate forests using georeferenced databases. By partitioning the area covered by temperate forests into relatively fine areal units (0.5° longitude × 0.5° latitude), we also attempt to reduce the spatial aggregation error associated with our regional estimates [cf. *Burke et al.*, 1990;

Paper number 93JD02964.
0148-0227/94/93JD-02964$05.00

Rastetter et al., 1992]. After estimating regional soil-CO_2 fluxes for temperate forests using this approach, we quantify the spatial and temporal aggregation errors associated with developing regional estimates that ignore spatial and temporal variations in soil-CO_2 fluxes to examine the benefit of our approach.

2. Background

Soil-CO_2 fluxes are dependent upon the production of carbon dioxide in soils and the movement of soil-CO_2 to the atmosphere. Carbon dioxide is produced in soils from several processes [*Singh and Gupta*, 1977; *Schlesinger*, 1977], with aerobic respiration of microbes associated with decomposition, and root respiration as the dominant sources. Litter and root exudates provide the source of carbon for decomposition processes, but the rate of decomposition is also dependent upon a variety of factors, including soil temperature, soil aeration, soil moisture, substrate quality, and pH [*Singh and Gupta*, 1977; *Schlesinger*, 1977]. The quantities of soil organic matter and root biomass also influence production of carbon dioxide in soil [*Bridge et al.*, 1983; *Weber*, 1985; *Buyanovsky et al.*, 1987; *Ewel et al.*, 1987*a*]. Root respiration has been estimated to represent 33 to 72% of total soil respiration [*Edwards and Harris*, 1977; *Nakane et al.*, 1983; *Ewel et al.*, 1987*b*; *Edwards et al.*, 1989; *Behera et al.*, 1990; *Bowden et al.*, 1993]. Soil-CO_2 moves to the atmosphere from soils primarily by diffusion [*Simunek and Suarez*, 1993], but convection [*Witkamp*, 1969] and wind-induced exchange of air between the atmosphere and the soil [*Kimball and Lemon*, 1971] can also transfer soil-CO_2. The rate of diffusion is dependent upon soil temperature, soil moisture, and soil characteristics such as porosity [*Reiners*, 1973].

Although many environmental factors influence the biological and physical processes controlling soil-CO_2 fluxes, field studies have shown that temperature and moisture are the most important factors regulating soil-CO_2 fluxes in both disturbed and "undisturbed" sites [*Schlesinger*, 1977; *Edwards and Ross-Todd*, 1983; *Ewel et al.*, 1987*a*; *Gordon et al.*, 1987]. Surprisingly, the influence of climate and its variability over space and time have not been considered in developing regional estimates of carbon dioxide evolution from soils.

The spatial distribution of climatic factors can be described by georeferenced databases. If the observed relationship between soil-CO_2 fluxes and temperature and/or moisture can be defined in a model, the data in georeferenced databases can be used as input into the model to provide geographically specific estimates of soil-CO_2 fluxes [see also *Burke et al.*, 1991]. Regional estimates of soil-CO_2 fluxes are then obtained by summing the georeferenced fluxes over the area of interest. Unlike the approach based on mean fluxes for biomes, the extrapolation of a model with georeferenced databases allows better consideration of the variability in soil-CO_2 fluxes due to the spatial variability of climate. Using annual soil-CO_2 flux estimates from field studies at many sites across the globe, *Raich and Schlesinger* [1992] have already developed several equations relating annual soil-CO_2 fluxes to mean annual air temperature and/or annual precipitation. Although regional estimates determined by these equations account for more spatial variability in soil-CO_2 fluxes than those estimates based on mean biome fluxes, they still do not consider temporal variability in soil-CO_2 fluxes.

The georeferenced temperature and precipitation databases that are readily available have a monthly resolution [*Legates and Willmott*, 1990*a*, *b*; *Leemans and Cramer*, 1991], whereas field measurements of soil-CO_2 flux have a temporal resolution of hours to days. Therefore soil-CO_2 flux measurements must be aggregated over time before a flux model can be extrapolated over a region using these georeferenced databases. As soil-CO_2 fluxes are always varying, the inability of an aggregation approach to account for temporal variations in fluxes will lead to temporal aggregation error.

To determine monthly or annual soil-CO_2 fluxes, investigators have used a variety of approaches to aggregate the hourly or daily fluxes measured in field studies. Some investigators simply determine a mean daily flux and multiply this mean flux by the number of days in the period of interest [e.g., *Garrett and Cox*, 1973] so that temporal variation in soil-CO_2 fluxes is simply ignored. Other investigators attempt to account for temporal variation by interpolating fluxes between successive field measurements [e.g., *Anderson*, 1973; *Phillipson et al.*, 1975]. If frequent field measurements are taken, interpolation can account for much temporal variation in soil-CO_2 fluxes at a particular site. This approach implicitly assumes, however, that the temporal variability of climatic factors is constant over the region of interest when used to estimate regional fluxes. In a third approach, models based on observed relationships of daily soil-CO_2 flux with daily temperature and/or soil moisture have been developed and then used with either mean daily data [e.g., *Peterjohn et al.*, 1994] or mean biweekly data [*Tsutsumi et al.*, 1985] to estimate annual fluxes. Unlike the interpolation approach, this modeling approach allows better consideration of the variability in soil-CO_2 fluxes caused by both the spatial and the temporal variability of climate when estimating regional fluxes. Unfortunately, the direct use of monthly data with a daily model can introduce aggregation error [*Rastetter et al.*, 1992] into the flux estimate if the relationship between environmental factors and soil-CO_2 flux is nonlinear. To minimize the error associated with aggregating fine-scale relationships (e.g., a daily soil-CO_2 flux model) to a coarser (e.g., monthly) resolution, *Rastetter et al.* [1992] have suggested several transformation approaches.

Many models have been developed to describe the relationship between daily soil-CO_2 fluxes and temperature and/or moisture at specific sites [*Reiners*, 1968; *Kirita*, 1971; *Froment*, 1972; *Anderson*, 1973; *Edwards*, 1975; *Coleman et al.*, 1976; *Reinke et al.*, 1981; *Nakane et al.*, 1984; *Tsutsumi et al.*, 1985; *Schlentner and Van Cleve*, 1985; *Rajvanshi and Gupta*, 1986; *Gordon et al.*, 1987; *Carlyle and Than*, 1988; *Norman et al.*, 1992]. Although any of these models may be used to develop regional estimates, less aggregation error may be introduced if more "generic" relationships between soil-CO_2 fluxes and climatic factors are used to develop estimates of regional fluxes. Recently, *Peterjohn et al.* [1994] have developed such a generic daily soil-CO_2 flux model for temperate deciduous forests by combining temporal data collected at several sites across the globe. As the temporal data came from forested sites that had not been disturbed for at least four decades, we consider the estimates determined by this model to represent potential soil-CO_2 fluxes from mature forests. Several studies [*Covington*, 1981; *Edwards and Ross-Todd*, 1983] have suggested that after clear-cutting there is a period of one to two decades of rapid soil carbon loss and accumulation. After this period the changes in the soil carbon pool are thought to be small, although they may continue to be slightly positive [*Wofsy et al.*, 1993].

To estimate regional soil-CO_2 fluxes from mature temperate forests, we use three steps: (1) modify the *Peterjohn et al.* [1994] model to estimate daily soil-CO_2 fluxes based on daily air temperatures rather than daily soil temperatures; (2) aggregate the daily relationship to a monthly resolution by calibrating [*Rastetter et al.*, 1992] a monthly model; and (3) extrapolate the resulting monthly model over the potential range of temperate forests across the globe. We restrict our analyses to temperate forests because ample data exist within this biome for model development and validation. We consider the general aggregation approach, however, to have applicability to all biomes and to be appropriate for the study of other gas fluxes.

3. Development of Daily Model

The model (equation (1a)) developed by *Peterjohn et al.* [1994] describes an exponential relationship between mean daily soil temperature and daily soil-CO_2 flux (Figure 1):

$$DCO_2 \text{ flux} = 0.4870 \times \exp^{0.1126(DT\text{soil})} \quad \text{(1a)}$$

$$DCO_2 \text{ flux} = 1.502 \times 3.083^{(DT\text{soil}-10)/10} \quad \text{(1b)}$$

where DCO_2 flux is the daily evolution of carbon dioxide from soils (g C m^{-2} d^{-1}), and DTsoil is the mean daily soil temperature (°C). This model may also be expressed as the Q_{10} function (equation (1b)), which has been used in other models [e.g., *Schlentner and Van Cleve*, 1985; *Gordon et al.*, 1987; *Carlyle and Than*, 1988; *Norman et al.*, 1992] to describe the influence of temperature on soil-CO_2 fluxes. Our Q_{10} coefficient (Q_{10} = 3.083) is similar to that found by *Peterjohn et al.* [1993]. To estimate monthly or annual fluxes from a site using this relationship, we require daily soil temperature measurements from that site. Most study sites do not routinely measure daily soil temperatures and we do not expect a georeferenced database of daily soil temperatures to be available in the near future. Therefore a model based solely on daily soil temperature is not very useful. Daily air temperature data, on the other hand, are more readily available and georeferenced global databases containing mean monthly air temperatures already exist [*Legates and Willmott*, 1990*a*; *Leemans and Cramer*, 1991]. Comparing the mean daily soil temperatures measured at a depth of 4 cm to mean daily air temperature measured at the NOAA weather station located at Harvard Forest, *Peterjohn et al.* [1994] found a linear relationship exists:

$$DT\text{soil} = 0.61(DT\text{air}) + 5.1 \quad \text{(2)}$$

where DTsoil is the mean daily soil temperature (°C) at 4-cm depth and DTair is the mean daily air temperature (°C). This linear regression of air temperature and soil temperature explains 90% of the variability in the data [*Peterjohn et al.*, 1994] and is consistent with results from other studies conducted in temperate forests [*Ino and Monsi*, 1969; *Kirita*, 1971; *Nakane et al.*, 1984]. Substituting (2) for the soil temperature variable into the daily soil-CO_2 flux model (equation (1a)), we can estimate daily soil-CO_2 flux as a function of mean daily air temperature:

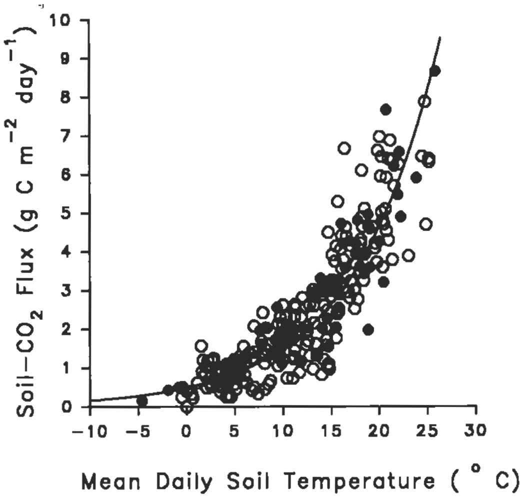

Figure 1. Relationship between mean daily soil-CO_2 flux and mean daily soil temperature (equation (1a)) for hardwood forests around the world. A linear regression of soil temperature to the natural logarithm of CO_2 flux explains 78% of the variability in the data ($p < 0.0001$; $n = 270$). Solid circles are data from nitrogen fertilization studies and soil-warming studies conducted at the Harvard Forest [*Peterjohn et al.*, 1994]. Data for other hardwood forests include Massachusetts [*Peterjohn et al.*, 1993], Minnesota [*Reiners*, 1968], Tennessee [*Edwards*, 1975], Missouri [*Garrett and Cox*, 1973], United Kingdom [*Anderson*, 1973], Italy [*De Santo et al.*, 1976], and Japan [*Nakane*, 1980].

$$DCO_2 \text{ flux} = 0.8647 \times \exp^{0.06869\,(DT\text{air})} \quad \text{(3a)}$$

$$DCO_2 \text{ flux} = 1.719 \times 1.988^{(DT\text{air}-10)/10} \quad \text{(3b)}$$

Although the relationship between mean daily soil temperature and mean daily air temperature is linear, we find that the Q_{10} coefficient (Q_{10} = 1.988) decreases with the substitution of mean daily air temperature for mean daily soil temperature (equation (3b)). This result is due to the damping of temperature fluctuations by the soil. Thus soil-CO_2 fluxes appear less sensitive to changes in mean daily air temperatures than to changes in mean daily soil temperatures. Soil-CO_2 fluxes predicted by this daily air temperature model agree well with fluxes measured at the Harvard Forest (Figure 2).

4. Aggregation of Daily Model to Monthly Resolution

To aggregate our daily model to a monthly resolution, we used the hierarchical approach described by *Parton et al.* [1992], which is also a variation of the calibration approach described by *Rastetter et al.* [1992]. Daily air temperature data, collected at the Harvard Forest NOAA weather station from January 1, 1988, to December 31, 1991, were used to estimate daily soil-CO_2 fluxes. We summed the daily fluxes for each month to obtain monthly soil-CO_2 fluxes. These monthly fluxes were then compared to mean monthly air temperatures for the same time period. We found that an

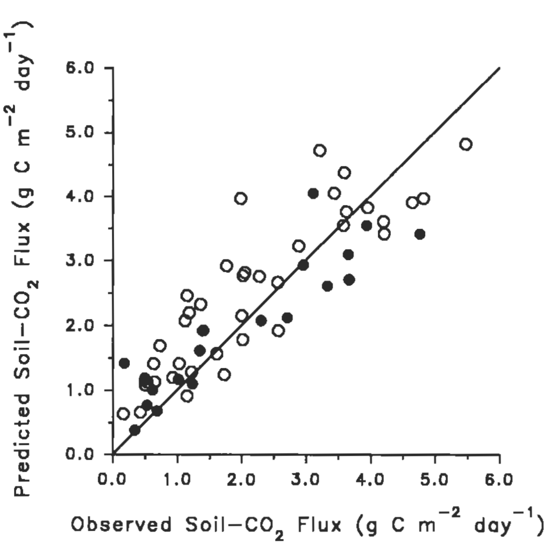

Figure 2. Observed versus predicted daily soil-CO$_2$ fluxes at the Harvard Forest ($r = 0.87$; $p < 0.001$; $n = 60$). Solid circles represent data that were not used in the development of the daily soil-CO$_2$ flux model.

exponential relationship exists between monthly soil-CO$_2$ fluxes and mean monthly air temperature (Figure 3):

$$M\mathrm{CO_2}\ \text{flux} = 27.46 \times \exp^{0.06844(MT\mathrm{air})} \tag{4a}$$

$$M\mathrm{CO_2}\ \text{flux} = 54.44 \times 1.983^{(MT\mathrm{air}-10)/10} \tag{4b}$$

where $M\mathrm{CO_2}$ flux is the monthly evolution of carbon dioxide from soils (g C m^{-2} month^{-1}), and MTair is the mean monthly air temperature (°C). By fitting monthly soil-CO$_2$ fluxes to mean monthly air temperatures collected at Harvard Forest, we were able to "calibrate" the monthly soil-CO$_2$ flux model (equation (4a)) using the daily model (equation (3a)). With our monthly model we were then able to use a georeferenced database of mean monthly air temperatures to develop georeferenced estimates of monthly soil-CO$_2$ fluxes for temperate forests around the globe.

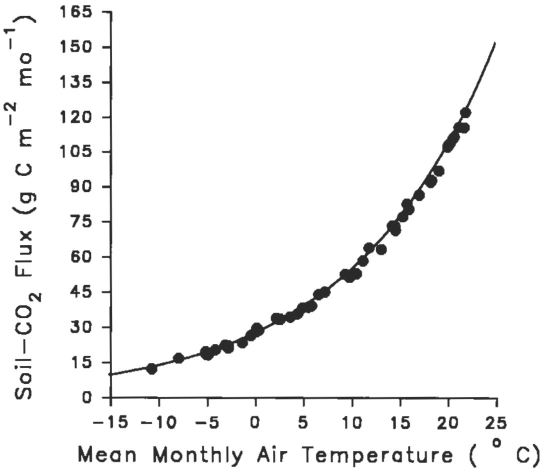

Figure 3. Relationship between mean monthly air temperature and monthly soil-CO$_2$ fluxes (equation (4a)) at the Harvard Forest. A linear regression of soil temperature to the natural logarithm of CO$_2$ flux explains 99.7% of the variability in the data ($p < 0.0001$; $n = 48$). Monthly soil-CO$_2$ fluxes, represented by the circles, are determined by summing the estimates of the daily soil-CO$_2$ flux model.

5. Application of Model to Global Temperate Forests

Our monthly soil-CO$_2$ flux model uses data only from temperate deciduous forest stands. Several studies [*Witkamp*, 1966; *Reiners*, 1968; *Jorgensen and Wells*, 1973], however, have shown that sites experiencing similar climatic conditions and productivity rates have similar soil respiration rates regardless of forest type. To evaluate these observations, we use mean monthly air temperature data from the potential range of temperate coniferous forests, temperate mixed forests, and temperate broadleaf evergreen forests, in addition to temperate deciduous forests (Figure 4), to spatially extrapolate our monthly soil-CO$_2$ flux model. The global coverage and locations of these biomes are delineated using a georeferenced database of potential vegetation [*Melillo et al.*, 1993] developed from extant maps. The database is gridded at a resolution of 0.5° longitude × 0.5° latitude and each grid cell is assumed to be occupied by a single vegetation type. Of the 6150 grid cells representing nonwetland temperate forests, 37% of the grid cells are identified as temperate mixed forests; 26% as temperate deciduous forests; 20% as temperate broad-leaved evergreen forests; and 17% as temperate coniferous forests.

A corresponding data set of mean monthly air temperatures [*Legates and Willmott*, 1990*a*], based on long-term-averaged air temperatures (1920–1980), is associated with the vegetation data set using the longitude and latitude of each grid cell. The monthly air temperatures of each grid cell are entered into the monthly model to produce a georeferenced database of monthly soil-CO$_2$ fluxes. The monthly fluxes are summed over the year for each grid cell to estimate annual fluxes. Regional estimates are then determined by summing the annual soil-CO$_2$ fluxes of all grid cells within a biome.

6. Comparison of Georeferenced Model Estimates to Site-Specific Data

To examine how well our monthly model predicted soil-CO$_2$ fluxes at specific sites, we compare annual estimates from our model to the annual soil-CO$_2$ fluxes from field observations (Table 1) described by *Raich and Schlesinger* [1992]. We restrict our analyses to those sites that measured soil-CO$_2$ fluxes throughout the year. Because our estimates represent rates from mature forests, we also restrict our analyses to sites that have not been disturbed for at least 29 years prior to field measurements. Of the 21 temperate forest stands used in the comparison (Table 1), six stands are also used in the development of our monthly model. Several forest stands are located within the same grid cell so that our model predictions are based on air temperature data from only 13 unique grid cells.

Comparing the georeferenced annual flux estimates from our model to site-specific data (Figure 5*a*), we find, in general, that the model provides good estimates of soil-CO$_2$ fluxes for different sites across the globe regardless of forest type. Of the discrepancies between predicted and observed soil-CO$_2$ fluxes, many appear to be caused by the relatively

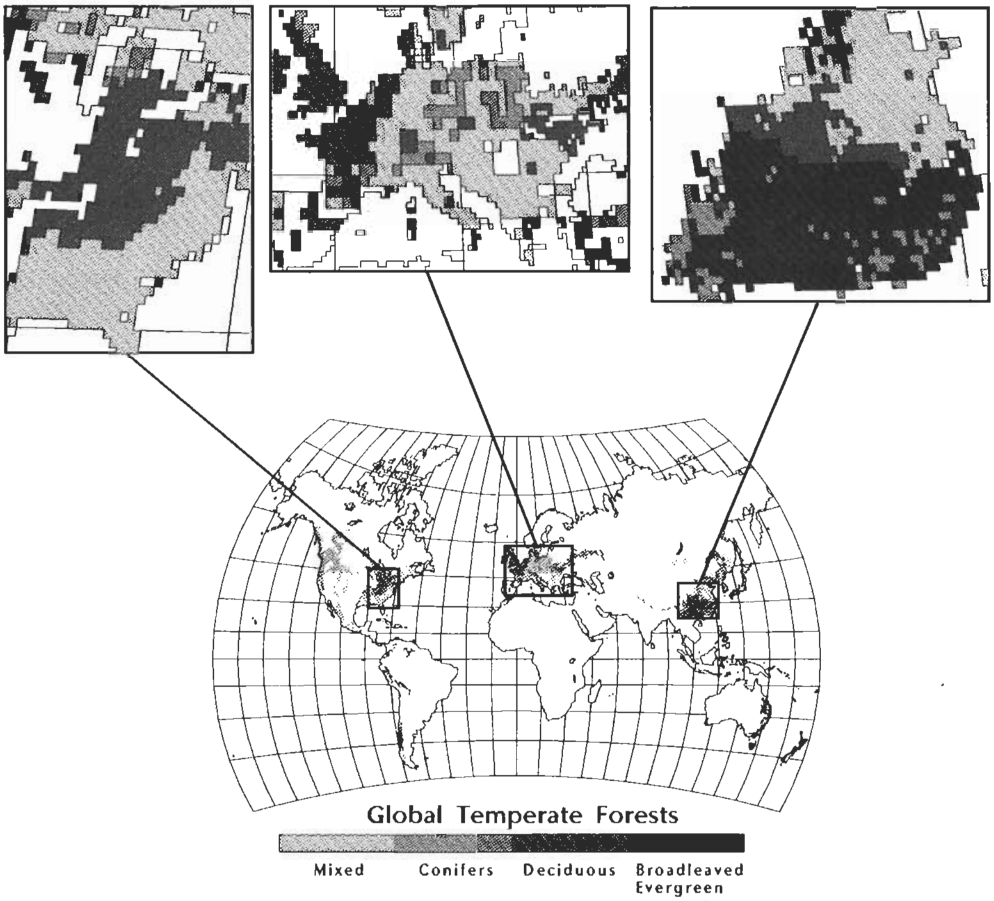

Figure 4. Global distribution of temperate forests.

Table 1. Sites Used to Evaluate Soil-CO$_2$ Flux Models

Location	Dominant	Annual Soil-CO$_2$ Flux, g m^{-2} yr^{-1}	Reference
		Deciduous Forest Stands	
Massachusetts	mixed deciduous	650[a]	data for year 1988 in Table 3
Tennessee	*Liriodendron tulipifera L.*	1065[a]	*Edwards and Harris* [1977]
	Quercus-Carya	529	*Edwards and Ross-Todd* [1983]
	Quercus prinus	610	*Edwards et al.* [1989]
Minnesota	*Quercus*-mixed	794[a]	*Reiners* [1968]
	Fraxinus-mixed	707	*Reiners* [1968]
North Carolina	*Quercus*-mixed	857	Wade [*Edwards et al.*, 1989]
Washington	*Alnus rubra*	565	*Vogt et al.* [1980]
United Kingdom	*Castanea sativa*	630[a]	*Anderson* [1973]
	Fagus sylvatica	575[a]	*Anderson* [1973]
Japan	*Quercus*-mixed	1272, 1556, 1098[a]	*Nakane* [1975]; *Kirita* [1971]
	Quercus-mixed	1045	*Kirita* [1971]; *Yoneda and Kirita* [1978]
		Coniferous Forest Stands	
Massachusetts	*Pinus resinosa*	565	Bowden [*Raich and Schlesinger*, 1992]
Florida	*Pinus elliottii*	1300	*Ewel et al.* [1987*a*, *b*]
Washington	*Abies amabilis*	620	*Vogt et al.* [1980]
	Pseudotsuga menziesii	490	*Vogt et al.* [1980]
	Tsuga heterophylla	650	*Vogt et al.* [1980]
Japan	*Chamaecyparis obtusa*	536	*Tsutsumi et al.* [1985]
		Mixed Forest Stands	
Massachusetts	*Quercus-Pinus*	648	Raich [*Raich and Schlesinger*, 1992]
Japan	*Fagus-Abies*	494	*Nakane* [1980]
Germany	*Fagus-Picea*	470	*Dörr and Münnich* [1987]

[a] Data from these study sites are used to develop daily soil-CO$_2$ flux model [*Peterjohn et al.*, 1994].

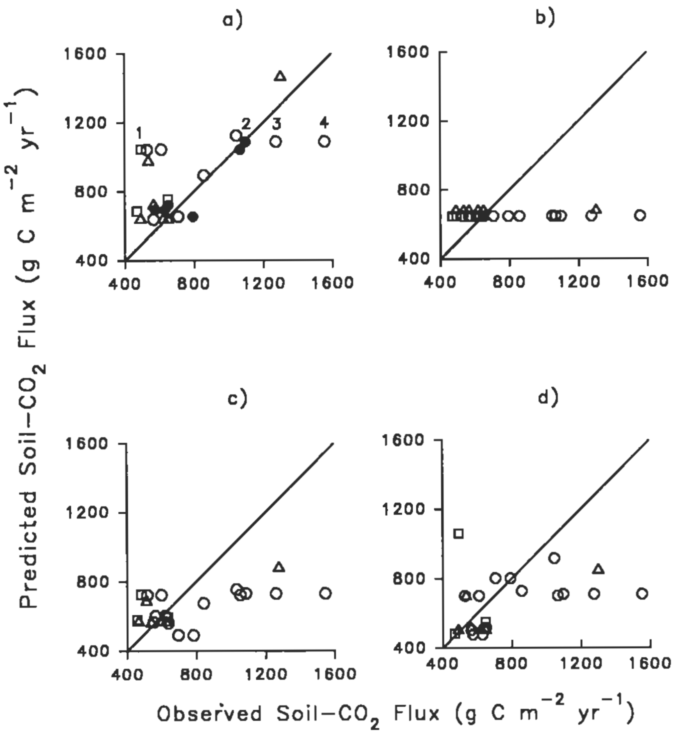

Figure 5. Observed versus predicted annual soil-CO_2 fluxes for 21 mature forest stands across the globe. Predicted soil-CO_2 fluxes are based on (a) the calibrated monthly soil-CO_2 flux model ($r = 0.66$; $p < 0.001$; $n = 23$); (b) mean biome fluxes ($r = -0.15$; n.s.; $n = 23$); (c) an annual soil-CO_2 flux model based on mean annual air temperature ($r = 0.59$; $p < 0.01$; $n = 23$); and (d) an annual soil-CO_2 flux model based on mean annual air temperature and annual precipitation ($r = 0.39$; n.s.; $n = 23$), as described by *Raich and Schlesinger* [1992]. Triangles represent coniferous forests. Circles represent deciduous forests. Squares represent mixed forests. Solid symbols represent data used to develop daily soil-CO_2 flux model. Stands designated as "1," "2," "3," and "4" are described in text. All observed data were used in the development of the mean biome flux estimates and the annual soil-CO_2 flux models [see *Raich and Schlesinger*, 1992].

coarse spatial scale of our georeferenced databases and our use of long-term average temperature data. For example, the model overestimates the soil-CO_2 flux of a beech/fir forest stand ("1" in Figure 5*a*) located at high elevation in Japan [*Nakane*, 1980]. In this case, the variation in temperature associated with elevational changes on a mountain occurs at too fine of a scale to be detected by our georeferenced database, which has a 0.5° longitude × 0.5° latitude spatial resolution. In another example, model estimates are compared to 3 years of soil-CO_2 fluxes ("2", "3", and "4" in Figure 5*a*) from the same evergreen oak forest stand [*Kirita*, 1971; *Nakane*, 1975]. The model underestimates fluxes for two of the years but provides a reasonable estimate for one of the years. Because our georeferenced data set of mean monthly air temperature is based on long-term averages of air temperatures, year-to-year variation in temperatures may have caused additional discrepancies between our estimates and observed soil-CO_2 fluxes. Issues of scale do not explain all the outliers. Some discrepancies may be caused by the influence of other environmental factors not considered in our model, such as moisture or substrate quality.

Despite these discrepancies our monthly modeling approach (Figure 5*a*) estimates the observed soil-CO_2 fluxes better than other approaches (Figures 5*b*–5*d*). Because the mean biome flux approach (Figure 5*b*) assigns a constant soil-CO_2 flux to every grid cell, this approach will always either overestimate or underestimate fluxes measured at specific sites. In contrast, the estimates developed by extrapolating models with georeferenced databases (Figures 5*a*, 5*c*, 5*d*) are able to track the spatial variation in the observed fluxes although models differ in their ability to track this variation. Our model is better at predicting soil-CO_2 fluxes, in part, because our modeling approach attempts to account for temporal variation in fluxes in addition to spatial variation. In section 7 we will compare the aggregation error associated with several approaches used to aggregate field measurements of soil-CO_2 flux temporally to estimate an annual flux at specific sites.

7. Significance of Temporal Aggregation Error Associated With Estimating Site-Specific Soil-CO_2 Fluxes

To evaluate the importance of temporal aggregation error in estimating fluxes, we determine annual soil-CO_2 fluxes from daily fluxes measured at the Harvard Forest during 4 years (Table 2) using five aggregation approaches. First, we use the daily air temperature data from the Harvard Forest NOAA station as input into our daily flux model (equation (3a)) to estimate daily soil-CO_2 fluxes. The daily flux estimates are then summed for each year. Because this approach accounts for the most variation in soil-CO_2 fluxes of all the approaches, we use these annual estimates as a baseline (Table 2) to be compared with the estimates from the other aggregation approaches.

For a second aggregation approach, daily soil-CO_2 fluxes measured during nitrogen fertilization studies at the Harvard Forest are averaged each year to determine a mean daily flux for that year. The mean daily flux is then multiplied by the number of days per year. By ignoring all temporal variations in soil-CO_2 fluxes, this "mean measured flux" approach (equation (5)) underestimates the baseline fluxes at Harvard Forest by approximately 13.5% (Table 2). Because the mean measured fluxes are based on data collected for only 1.6 to 3.3% of the annual time periods, this approach misses much of the variation in soil-CO_2 fluxes due to seasonal and day-to-day variations in temperature. As the number of sampling days increase, we find better agreement of this approach with the baseline data indicating that data must be collected with an adequate sampling frequency to determine a reasonable annual flux using this approach.

Our third aggregation approach uses the daily flux model (equation (3a)) with mean monthly temperatures to estimate an "average" daily soil-CO_2 flux that was then multiplied by the number of days per month. Although this approach accounts for the seasonal variation in soil-CO_2 fluxes over the year, fluxes are considered to be constant throughout any particular month. This "monthly constant model" (equation (6)) estimates annual soil-CO_2 fluxes that are still 3.5% lower than the baseline fluxes at the Harvard Forest (Table 2). The small discrepancy between these estimates

Table 2. Comparison of Annual Estimates of Soil-CO_2 Flux Among Various Temporal Aggregation Approaches

			Year			
	Model	Equation	1988	1989	1990	1991
Number of sampling days per year			12	11	6	7
Mean soil-CO_2 flux ($DAVGCO_2$) (g C m^{-2} d^{-1})			1.776	1.776	1.560	1.440
Baseline soil-CO_2 flux (based on daily model)	$DCO_2{}^a = 0.8647 \times e^{0.06869(DT\text{air})}$	(3*a*)	673	676	715	712
	Aggregation Approach					
Mean measured flux	$YRCO_2{}^b = DAVGCO_2 \times YRNDAYS$	(5)	650	648	569	526
Monthly constant model	$MCO_2{}^c = (0.8647 \times e^{0.06869(MT\text{air})}) \times MONNDAYS$	(6)	651	654	690	683
Adjusted monthly constant model	$MCO_2{}^c = (0.8647 \times e^{0.06869(MT\text{air})}) \times MONNDAYS \times 1.04^d$	(7)	677	680	718	710
Calibrated monthly model	$MCO_2{}^c = 27.46 \times e^{0.06844(MT\text{air})}$	(4*a*)	673	677	715	708

Soil-CO_2 flux data are from the control plots of the nitrogen fertilization studies conducted at the Harvard Forest. Units are g C m^{-2} yr^{-1} unless specified otherwise.

[a] DCO_2, daily soil-CO_2 flux (g C m^{-2} d^{-1}); *DT*air, mean daily air temperature (degrees Celsius); annual CO_2 flux determined by summing estimated daily fluxes.

[b] $YRCO_2$ annual soil-CO_2 flux (g C m^{-2} yr^{-1}); *YRN*DAYS, number of days in a year.

[c] MCO_2, monthly soil-CO_2 flux (g C m^{-2} $month^{-1}$); *MT*air, mean monthly air temperature (degrees Celsius); *MONN*DAYS, number of days per month; annual CO_2 flux determined by summing estimated monthly fluxes.

[d] The correction factor (1.04) is determined by using the statistical expectation operator (see text).

indicates that the day-to-day variation in soil-CO_2 fluxes is a small source of error in estimating monthly fluxes.

In addition to the hierarchical or "calibration" approach described in section 4, *Rastetter et al.* [1992] suggest that aggregation error may be reduced by a "partial transformation" of the fine-scale relationships using the statistical expectation operator. In this approach, monthly soil-CO_2 fluxes are determined using the daily flux model (equation (3a)) with mean monthly temperatures as described for the monthly constant model, but these estimates are adjusted by a correction factor determined by the aggregation procedure described in the Appendix. We calculate this correction factor to be a constant, 1.04 (see Appendix for details), indicating that the use of the monthly constant model (equation (6)) will underestimate the "true" monthly soil-CO_2 fluxes by only 4%. This "adjusted monthly constant model" (equation (7)) estimates annual soil-CO_2 fluxes that are, on average, 100.3% of the baseline fluxes at Harvard Forest.

Our final temporal aggregation approach is the calibrated modeling approach (equation (4a)) described above. Of all the aggregation approaches the annual soil-CO_2 fluxes predicted by our "calibrated monthly model" (equation (4a)) are the closest (99.9%) to the baseline fluxes at Harvard Forest. With the exception of 1991 the annual estimates from the calibrated monthly model are within 2 g C m^{-2} yr^{-1} (about 0.3%) of the baseline fluxes. The 4 g C m^{-2} yr^{-1} discrepancy in 1991 (Table 2) results from some unusually warm days in December that our calibrated monthly model, using mean monthly air temperature, is unable to detect.

8. Regional Soil-CO_2 Flux Estimates

After extrapolating our calibrated monthly model (equation (4a)) with the georeferenced databases, we estimate that potential nonwetland temperate forest soils contribute 12.9 Pg C yr^{-1} as carbon dioxide to the atmosphere. This estimate is 39% higher than a regional estimate based on extrapolating mean biome soil-CO_2 fluxes described by *Raich and Schlesinger* [1992] for temperate forests (Table 3) and 50 to 58% higher than the regional estimates based on extrapolating the annual soil-CO_2 flux models (Table 3) of *Raich and Schlesinger* [1992]. In general, soil-CO_2 fluxes estimated from our model follow the latitudinal temperature gradient (Figure 6) so that lower-latitude temperate forests have higher soil-CO_2 fluxes than higher-latitude forests. In addition, soil-CO_2 flux estimates decrease in mountainous regions reflecting the reduced air temperatures in these areas.

Of the forest types, our model predicts the largest source of carbon dioxide (Table 3) to be mixed forests (34% of the estimate for all temperate forests) followed by broad-leaved evergreen forests (28%), deciduous (22%), and coniferous forests (16%). The relative contribution of carbon dioxide from broad-leaved evergreen forest soils is greater than its relative areal extent (Table 3) because this vegetation type has a larger coverage in warmer climates than the other types (Figure 4). In contrast, the relative contribution of carbon dioxide from forest soils estimated by the mean biome soil-CO_2 flux approach is determined by the relative area of the different forest types.

By reducing spatial and temporal aggregation errors, our calibrated monthly model estimates higher regional soil-CO_2 fluxes than the other approaches. *Raich and Schlesinger* [1992], however, use data from disturbed sites to develop their mean biome flux estimates and annual soil-CO_2 flux models so that the differences between these estimates and those of our calibrated monthly model may also reflect the effects of disturbance on soil-CO_2 fluxes. To better understand the influence of spatial and temporal aggregation errors

Table 3. Comparison of Regional Estimates of Soil-CO_2 Flux From Temperate Forest Soils Between This Study and *Raich and Schlesinger* [1992]

	Coniferous	Deciduous	Mixed	Broad-leaved Evergreen	Total
Number of grid cells	1081	1614	2250	1205	6150
Total land area ($km^2 \times 10^6$)	2.40	3.55	5.09	3.18	14.22
Soil-CO_2 Flux Approach					
This study					
calibrated monthly model, Pg C yr^{-1}	2.01	2.79	4.39	3.67	12.9
Raich and Schlesinger [1992]					
mean biome soil-CO_2 flux,[a] Pg C yr^{-1}	1.63	2.30	3.29	2.06	9.28
annual soil-CO_2 flux model (*T*air),[b] Pg C yr^{-1}	1.38	1.94	2.96	2.31	8.59
annual soil-CO_2 flux model (*T*air and Prec),[c] Pg C yr^{-1}	1.31	1.78	2.78	2.31	8.18

[a] Soil-CO_2 flux = 681 g C m^{-2} yr^{-1} for coniferous forests; Soil-CO_2 Flux = 647 g C m^{-2} yr^{-1} for all other temperate forests.

[b] CO_2 flux = 25.6 (*T*air) + 300; CO_2 flux is annual soil-CO_2 flux (g C m^{-2} yr^{-1}); *T*air is mean annual air temperature (degrees Celsius).

[c] CO_2 flux = 9.26 (*T*air) + 0.0127 (*T*air) (Prec) + 289; CO_2 flux is annual soil-CO_2 flux (g C m^{-2} yr^{-1}); *T*air is mean annual air temperature (°C); Prec is annual precipitation (millimeters).

on regional estimates of soil-CO_2 flux, we quantify the errors associated with ignoring spatial and temporal variations in soil-CO_2 fluxes in sections 9 and 10.

9. Significance of Spatial Aggregation Error Associated With Estimating Regional Soil-CO_2 Fluxes

To evaluate the importance of spatial aggregation error, we develop regional estimates of soil-CO_2 flux using our calibrated monthly model with air temperatures aggregated at four spatial resolutions [cf. *Burke et al.*, 1990]: global, hemispheric, biome, and grid cell (Table 4). Because the grid cell resolution accounts for the most spatial variability in soil-CO_2 fluxes of all the spatial resolutions, we use this resolution as a baseline for examining spatial aggregation error (Table 4).

To aggregate temperatures for an element at a particular spatial resolution, we average each monthly temperature over all the grid cells comprising the area of that element. For example, to obtain monthly air temperatures for an element representing all temperate forests in the northern hemisphere, we average monthly air temperatures over the 5650 grid cells comprising temperate forests in the northern hemisphere. We enter these averaged monthly temperatures into our calibrated monthly model to determine monthly soil-CO_2 fluxes. After summing the monthly fluxes over the year, we multiply the annual fluxes by the corresponding areas of the elements. Then, we add the fluxes of each element together to obtain a regional flux estimate for all temperate forests at that spatial resolution. For the global and hemispheric resolutions, we proportion the fluxes from the various forest types based on their relative area for later comparison to fluxes estimated at a biome resolution (Table 4).

By ignoring all spatial variations in soil-CO_2 fluxes, the regional flux estimated at a global resolution is 9.3% less than our baseline estimate (Table 4). By considering the forests in each hemisphere separately, we obtain a regional estimate that is 7.0% less than our baseline estimate. By accounting for differences in soil-CO_2 fluxes from the different forest types, we obtain a regional estimate that is 5.4% less than our baseline estimate, indicating that soil-CO_2 fluxes are still highly variable within biomes.

In general, soil-CO_2 fluxes estimated from each of the different forest types also increase as more spatial variability is considered. At the biome resolution, however, fluxes from mixed, coniferous, and deciduous forests are less than the respective fluxes estimated at the global and hemispheric resolutions. Because monthly air temperatures aggregated over all broad-leaved evergreen forests are always higher than the aggregated temperatures of the other forest types (Figure 7), the relative contribution of carbon dioxide from this forest type is underestimated at the global or hemispheric resolutions (Table 4).

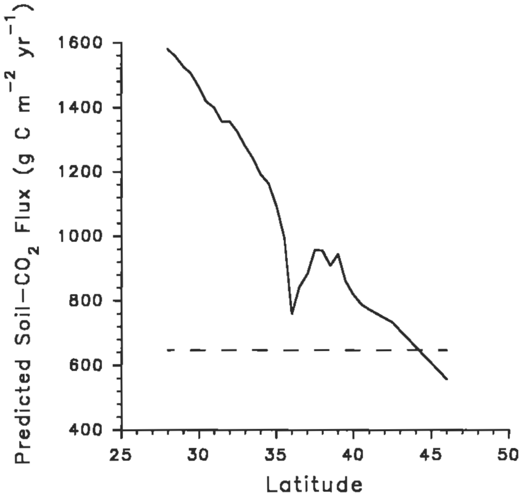

Figure 6. Annual soil-CO_2 fluxes from temperate forests as estimated by our calibrated monthly soil-CO_2 flux model (solid curve) and by the mean biome flux approach (dashed line) along a north-south transect in eastern North America (82.0°W). The "dip" in soil-CO_2 fluxes estimated by our model is where the transect crosses the Appalachian Mountains.

Table 4. Comparison of Regional Soil-CO$_2$ Fluxes From Temperate Forest Soils As Determined by the Calibrated Monthly Model at Different Spatial Resolutions

	Soil-CO$_2$ Flux, Pg C yr^{-1}				
Spatial Resolution	Coniferous	Deciduous	Mixed	Broad-Leaved Evergreen	Total
Global resolution ($N^a = 1$)[b]	1.98	2.92	4.20	2.62	11.7
Hemispheric resolution ($N = 2$)[c]	1.99	2.97	4.24	2.78	12.0
Biome resolution ($N = 8$)[d]	1.82	2.67	4.14	3.53	12.2
Grid cell resolution ($N = 6150$)[e]	2.01	2.79	4.39	3.67	12.9

[a] N represents the number of elements at that spatial resolution.

[b] One element represents all temperate forests.

[c] One element represents all the temperate forests in the northern hemisphere. The other element represents all the temperate forests in the southern hemisphere.

[d] Each element represents one of the four forest types (i.e., coniferous, deciduous, mixed, and broad-leaved evergreen) within one of the hemispheres.

[e] The elements are simply the 0.5° longitude × 0.5° latitude grid cells used to estimate the regional soil-CO$_2$ flux described in section 8.

A comparison of the seasonal distribution of the aggregated air temperatures for broad-leaved evergreen forests to the other forest types in the northern hemisphere (Figure 7) also shows that air temperatures are less variable for broad-leaved evergreen forests (range: 7.9° to 25.9°C) than for the other forest types (range: −3.3° to 22.3°C). By accounting for some of the spatial differences in the seasonal variation of fluxes, both spatial and temporal aggregation errors are reduced when estimating regional soil-CO$_2$ flux at the biome resolution. Similarly, the temporal aggregation error associated with the 6-month offset in seasons between the two hemispheres is reduced when air temperatures are spatially aggregated by hemisphere. Thus temporal aggregation error is not independent of spatial aggregation error.

10. Significance of Temporal Aggregation Error Associated With Estimating Regional Soil-CO$_2$ Fluxes

To evaluate the importance of temporal aggregation error, we need to compare the regional fluxes estimated by our calibrated monthly model to a regional estimate that does not consider temporal variability in soil-CO$_2$ fluxes. By using mean annual air temperature with the daily flux model (equation (3a)), we can develop an annual flux estimate, in which fluxes are assumed to be constant throughout the year:

$$YR\mathrm{CO_2\ flux} = 0.8647 \times \exp^{0.06869(YRT\mathrm{air})} \times YRN\mathrm{DAYS} \qquad (8)$$

where YRCO$_2$ flux is the annual evolution of carbon dioxide from soils (g C m^{-2} yr^{-1}), YRTair is the mean annual air temperature (degrees Celsius) and YRNDAYS is the number of days per year. After extrapolating this "annual constant" model with a georeferenced database, we obtain a regional estimate associated with the greatest amount of temporal aggregation error (Table 5). This aggregation error results from two sources: (1) the inability of the model to account for all temporal variations in fluxes (see section 7) within an element (i.e., model-specific temporal aggregation error); and (2) spatial differences in the temporal variations among the elements (see section 9) used to estimate regional fluxes (i.e., spatially dependent temporal aggregation error). To examine the influence of these sources of error on regional estimates, we extrapolate the annual constant model (equation (8)), the monthly constant model (equation (6)), the adjusted monthly constant model (equation (7)), and our calibrated monthly model (equation (4a)) with air temperatures aggregated at the four spatial resolutions described in section 9.

The regional fluxes estimated by the annual constant model are 1.5 to 2.0 Pg C yr^{-1} (12.8 to 15.5%) less than the fluxes estimated by our calibrated monthly model at corresponding spatial resolutions (Table 5). The difference between the model estimates increases with finer spatial resolutions. Because the annual constant model uses annual rather than monthly data, this model does not consider spatial differences in the seasonal variability of air temperatures. As a result, the differences between the regional estimates of the models are due to both model-specific and spatially dependent temporal aggregation error. By using georeferenced databases with finer spatial resolutions, spatially dependent temporal aggregation error is reduced when estimating regional fluxes.

In contrast, the regional fluxes estimated by the monthly constant model are consistently 0.4 to 0.5 Pg C yr^{-1} (3.4 to 4.2%) less than the fluxes estimated by our calibrated monthly model at all corresponding spatial resolutions (Table 5). As the georeferenced database defines seasonal variations of air temperatures for both of these models, the differences between the regional estimates are due only to model-specific temporal aggregation error. This error is insensitive to changes in spatial resolution because these models use input data with the same temporal resolution.

In extrapolating our calibrated monthly model (equation (4a)) spatially, we assume implicitly that the variation of the mean daily air temperatures from the mean monthly air temperature for all temperate forests is similar to that found at the Harvard Forest. This variation, however, may be spatially dependent like the seasonal variation of air temperatures. We do not consider this component of aggregation

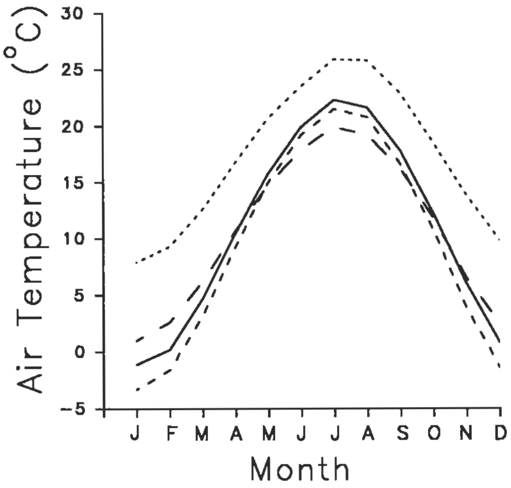

Figure 7. Seasonal distribution of mean monthly air temperatures aggregated by temperate forest types in the northern hemisphere: mixed forests (solid curve); coniferous forests (long-dashed curve); deciduous forests (medium-dashed curve); and broad-leaved evergreen forests (short-dashed curve).

error because we do not have any georeferenced information about the variation of the mean daily air temperatures from the mean monthly air temperature (e.g., standard deviation). If such information becomes available, the adjusted monthly constant model (equation (7)), which explicitly considers this variability, may provide a better approach to estimate regional soil-CO$_2$ fluxes than our calibrated monthly model. Based on currently available information, our calibrated model estimates regional fluxes similar to the adjusted monthly constant model (Table 5).

11. Other Issues

Our calibrated monthly model enables us to account for much more of the natural variability in soil-CO$_2$ fluxes due to the spatial and temporal variations in climate than other available approaches. The discrepancies between model estimates and field observations, however, indicate that the estimates can still be improved. Although our simple model can be refined to account for the influence of other environmental factors on soil-CO$_2$ fluxes from temperate forests, the spatial extrapolation of process models similar to CENTURY [*Parton et al.*, 1987], MBL-GEM [*Rastetter et al.*, 1991], or FOREST-BGC [*Running and Coughlan*, 1988] may be required to account for all of the factors influencing soil-CO$_2$ fluxes from temperate forests, especially if the forests have been disturbed. As georeferenced databases at a daily resolution are not available, soil-CO$_2$ fluxes measured in field studies must be aggregated to a monthly or annual resolution to calibrate or validate process models. If the temporal variations of soil-CO$_2$ fluxes are ignored in developing such calibration data, the resulting regional estimates may be associated with considerable aggregation error. Finally, as the estimates of any model are limited by the resolution of the input data, more "realistic" model estimates of soil-CO$_2$ flux may be achieved by using georeferenced databases with finer spatial and temporal resolutions to further reduce aggregation errors.

Temperate forests, excluding wetlands, represent only 11% of the land area of the globe so regional fluxes from other biomes also need to be estimated before a global soil-CO$_2$ flux can be determined. Unlike temperate forests, fluxes in other biomes may be regulated by soil moisture or by a combination of soil moisture and soil temperature [*Wildung et al.*, 1975; *Tesarova and Gloser*, 1976; *Gupta and Singh*, 1981; *Fouseki and Margaris*, 1981; *Schlentner and Van Cleve*, 1985; *Rajvanshi and Gupta*, 1986; *Rout and Gupta*, 1989]. Complex relationships between soil-CO$_2$ fluxes and soil moistures and/or soil temperatures can exist in some of these biomes [*Schlentner and Van Cleve*, 1985; *Gordon et al.*, 1987; *Carlyle and Than*, 1988]. Such complex relationships may be difficult to aggregate using a statistical expectation operator. The hierarchical approach, which uses estimates from a daily model to calibrate a monthly model, provides an easier method for coarse-scale relationships to

Table 5. Comparison of Regional Soil-CO$_2$ Fluxes (Pg C yr^{-1}) From Temperate Forest Soils As Determined From Various Temporal Aggregation Approaches at Different Spatial Resolutions

	Spatial Resolution			
Temporal Aggregation Approach	Global	Hemispheric	Biome	Grid Cell
Annual constant model	10.2	10.2[b]	10.4	10.9
Monthly constant model	11.3	11.5[c]	11.7	12.4
Adjusted[a] monthly constant model	11.8	12.0	12.2	12.9
Calibrated monthly model	11.7	12.0[d]	12.2	12.9

[a] Soil-CO$_2$ flux estimates of the monthly constant model are multiplied by 1.04 to correct for aggregation error (see text).

[b] Annual soil-CO$_2$ flux of 695 g C m^{-2} yr^{-1} assigned to all temperate forests in northern hemisphere and annual soil-CO$_2$ flux of 903 g C m^{-2} yr^{-1} assigned to all temperate forests in southern hemisphere.

[c] Annual soil-CO$_2$ flux of 801 g C m^{-2} yr^{-1} assigned to all temperate forests in northern hemisphere and annual soil-CO$_2$ flux of 920 g C m^{-2} yr^{-1} assigned to all temperate forests in southern hemisphere.

[d] Annual soil-CO$_2$ flux of 830 g C m^{-2} yr^{-1} assigned to all temperate forests in northern hemisphere and annual soil-CO$_2$ flux of 958 g C m^{-2} yr^{-1} assigned to all temperate forests in southern hemisphere.

emerge from fine-scale relationships of soil-CO_2 fluxes with temperature or moisture. Although the exponential relationship of air temperatures with soil-CO_2 fluxes is reflected in both the monthly and the daily resolutions for temperate forests, the emergent monthly relationship of soil-CO_2 fluxes with temperature and moisture does not necessarily have the same form as the daily relationship. Indeed, a simple relationship between monthly soil-CO_2 fluxes and mean monthly temperature and moisture may be calibrated from the estimates derived from a complex daily relationship. Like soil temperature, daily soil moistures also are not measured on a routine basis so that a proxy is required to extrapolate soil-CO_2 fluxes that depend upon moisture. A proxy for soil moisture can be a simple function of LAI [*Norman et al.*, 1992] or a complex function of precipitation, temperature, vegetative cover, and soil properties [*Vorosmarty et al.*, 1989].

Our regional estimates do not incorporate the influence of land use on soil-CO_2 fluxes so that they do not quantify contemporary fluxes from temperate forests but rather serve as a baseline for future comparisons to estimates of soil-CO_2 fluxes from disturbed temperate forests. Land use alters the relationship between soil-CO_2 flux, ecosystem processes, and environmental factors so that soil-CO_2 fluxes may increase, decrease, or even remain the same after disturbance [cf. *Raich and Schlesinger*, 1992]. Several studies [*Bolin*, 1977; *Woodwell et al.*, 1978; *Schlesinger*, 1984] have estimated that disturbance causes an additional release of 0.1 to 2.0 Pg C yr^{-1} to the atmosphere from global soils based on mean changes in soil organic matter. As the spatial and temporal aggregation errors associated with developing regional soil-CO_2 flux estimates from temperate forests can be the same magnitude as this change (0.8 to 15.5% of our regional estimate for temperate forests), the reduction of these aggregation errors is highly desirable.

Appendix

The use of a fine-scale relationship (e.g., daily soil-CO_2 flux model (equation (3a)) with coarse-scale data (e.g., mean monthly air temperature) can add aggregation error to the resulting estimates if the fine-scale relationship is nonlinear. The statistical expectation operator [*Rastetter et al.*, 1992] can be used to transform or "transmutate" [*O'Neill*, 1979] the "fine-scale" relationship in the daily model (equation (3a)) to a "coarse-scale," monthly relationship. For our study the statistical expectation operator can be expressed as

$$\frac{f_M(MTair)}{NDAYS} = E[f_D(DTair)]$$

$$= \int_{-\infty}^{\infty} f_D(DTair)\,p(DTair)\; dDTair \qquad (A1)$$

where *MT*air is the mean monthly air temperature (degrees Celsius), $f_M(MTair)$ is the monthly evolution of carbon dioxide from soils as a function of mean monthly air temperature (g C m^{-2} $month^{-1}$), *N*DAYS is the number of days in a month, *DT*air is mean daily air temperature (°C), $E[f_D(DTair)]$ is the expected daily evolution of carbon dioxide from soils as a function of mean daily air temperature (g C m^{-2} d^{-1}), $f_D(DTair)$ is the daily soil-CO_2 flux model (equation (3a)), and $p(DTair)$ is the probability density function for mean daily air temperature within a month. Mean daily air temperatures are, typically, normally distributed about the mean monthly temperature (Figure A1). The probability of a particular mean daily air temperature is

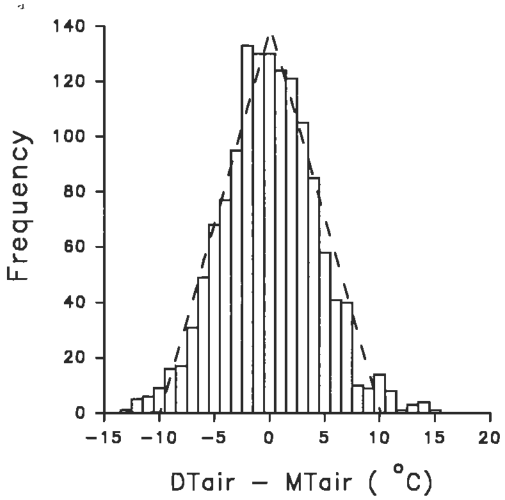

Figure A1. Distribution of the deviations of mean daily air temperatures (*DT*air) from mean monthly air temperatures (*MT*air) for Harvard Forest data collected between January 1, 1988, and December 31, 1991. The dashed triangle represents a linear approximation of the distribution of these deviations from mean monthly air temperatures.

$$p(DTair) = \frac{1}{s(2\pi)^{1/2}} \exp^{-[(DTair-MTair)^2]/2s^2} \qquad (A2)$$

where *s* is the standard deviation of *DT*air from *MT*air. Multiplying the daily soil-CO_2 flux model (equation (3a)) with (A2), we obtained an equation that we have not been able to integrate. As an alternative, we noted that the normal distribution of mean daily temperatures can be approximated with a triangular probability density function (Figure A1). After trial and error we developed the following probability distribution:

For $MTair - 10.0 < DTair \leq MTair$

$$p(DTair) = 0.01\ [DTair - (MTair - 10.0)] \qquad (A3a)$$

For $MTair < DTair \leq MTair + 10.0$

$$p(DTair) = 0.1 - 0.01\ (DTair - MTair) \qquad (A3b)$$

Elsewhere

$$p(DTair) = 0.0 \qquad (A3c)$$

Combining the daily soil-CO_2 flux model (equation (3a)) and this probability distribution (A3), we obtain the following expectation operator:

$$\frac{f_M(MTair)}{NDAYS} = E[f_D(DTair)]$$

$$= \int_{MTair-v}^{MTair} a\ \exp^{b(DTair)}\ [g(DTair - (MTair - v)]\ dDTair$$

$$+ \int_{MTair}^{MTair+v} a\ \exp^{b(DTair)}\ [c - g(DTair - MTair)]\ dDTair$$

$$(A4)$$

where a is the coefficient in the daily soil-CO_2 flux model (0.8647 in equation (3a)), b is the coefficient in the exponent of the daily soil-CO_2 flux model (0.06869 in (3a)), v is the deviation of triangle's lower vertices from MTair ($v = 10$), c is the height of triangle ($c = 0.1$), and g is the absolute value of the slope of the line connecting each of the triangle's lower vertices to the upper vertex ($g = c/v = 0.01$). Variables v and c were selected so that the area within the triangular probability density function equals 1. Integrating (A4) and combining terms, we obtain

$$\frac{f_M(M\text{Tair})}{N\text{DAYS}} = E[f_D(D\text{Tair})]$$

$$= a \exp^{b(M\text{Tair})} \frac{g}{b^2}(e^{bv} + e^{-bv} - 2) \qquad \text{(A5)}$$

However, (A5) is simply the daily model (equation (3a)) multiplied by $g(e^{bv} + e^{-bv} - 2)/b^2$, which is a constant (= 1.04). Thus our "corrected" monthly model, $f_M(M\text{Tair})$, equals the daily model (equation (3a)) multiplied by 1.04 to correct for temporal aggregation and then multiplied by NDAYS to convert from daily to monthly fluxes.

Acknowledgments. We thank E. A. Griffin, K. M. Newkirk, D. S. Schimel, I. C. Burke, and an anonymous reviewer for their comments of the manuscript. L. Thomson and D. Martin produced the map of global temperate forests. This work was supported jointly by funds from the Northeast Regional Center of DOE's National Institute for Global Environmental Change, NASA's EOS Program, and a cooperative agreement with the EPA Laboratory in Athens, Ga. We are especially indebted to NSF's Harvard Forest LTER project for providing the long-term climatic data that was essential to our research.

References

Anderson, J. M., Carbon dioxide evolution from two temperate, deciduous woodland soils, *J. Appl. Ecol.*, *10*, 361–378, 1973.

Behera, N., S. K. Joshi, and D. P. Pati, Root contribution to total soil metabolism in a tropical forest soil from Orissa, India, *For. Ecol. Manage.*, *36*, 125–134, 1990.

Bolin, B., Changes of land biota and their importance for the carbon cycle, *Science*, *196*, 613–615, 1977.

Bowden, R. D., K. J. Nadelhoffer, R. D. Boone, J. M. Melillo, and J. B. Garrison, Contributions of aboveground litter, belowground litter, and root respiration to total soil respiration in a temperate mixed hardwood forest, *Can. J. For. Res.*, *23*, 1402–1407, 1993.

Bridge, B. J., J. J. Mott, and R. J. Hartigan, The formation of degraded areas in the dry savanna woodlands of northern Australia, *Aust. J. Soil Res.*, *21*, 91–104, 1983.

Burke, I. C., D. S. Schimel, C. M. Yonker, W. J. Parton, L. A. Joyce, and W. K. Lauenroth, Regional modeling of grassland biogeochemistry using GIS, *Landscape Ecol.*, *4*, 45–54, 1990.

Burke, I. C., T. G. F. Kittel, W. K. Lauenroth, P. Snook, C. M. Yonker, and W. J. Parton, Regional analysis of the central Great Plains: Sensitivity to climate variability, *BioScience*, *41*, 685–692, 1991.

Buyanovsky, G. A., C. L. Kucera, and G. H. Wagner, Comparative analyses of carbon dynamics in native and cultivated ecosystems, *Ecology*, *68*, 2023–2031, 1987.

Carlyle, J. C., and U. B. Than, Abiotic controls of soil respiration beneath an eighteen-year-old *Pinus radiata* stand in south-eastern Australia, *J. Ecol.*, *76*, 654–662, 1988.

Coleman, D. C., R. Andrews, J. E. Ellis, and J. S. Singh, Energy flow and partitioning in selected man-managed and natural ecosystems, *Agro-Ecosystems*, *3*, 45–54, 1976.

Covington, W. W., Changes in forest floor organic matter and nutrient content following clear cutting in northern hardwoods, *Ecology*, *62*, 41–48, 1981.

De Santo, A. V., A. Alfani, and S. Sapio, Soil metabolism in beech forests of Monte Taburno (Campania Apennines), *Oikos*, *27*, 144–152, 1976.

Dörr, H., and K. O. Münnich, Annual variation in soil respiration in selected areas of the temperate zone, *Tellus*, *39*(B), 114–121, 1987.

Edwards, N. T., Effects of temperature and moisture on carbon dioxide evolution in a mixed deciduous forest floor, *Soil Sci. Soc. Am. Proc.*, *39*, 361–365, 1975.

Edwards, N. T., and W. F. Harris, Carbon cycling in a mixed deciduous forest floor, *Ecology*, *58*, 431–437, 1977.

Edwards, N. T., and B. M. Ross-Todd, Soil carbon dynamics in a mixed deciduous forest following clear-cutting with and without residual removal, *Soil Sci. Soc. Am. J.*, *47*, 1014–1021, 1983.

Edwards, N. T., D. W. Johnson, S. B. McLaughlin, and W. F. Harris, Carbon dynamics and productivity, in *Analysis of Biogeochemical Cycling Processes in Walker Branch Watershed*, edited by D. W. Johnson and R. I. Van Hook, pp. 197–232, Springer-Verlag, New York, 1989.

Ewel, K. C., W. P. Cropper, Jr., and H. L. Gholz, Soil CO_2 evolution in Florida slash pine plantations, I, Changes through time, *Can. J. For. Res.*, *17*, 325–329, 1987*a*.

Ewel, K. C., W. P. Cropper, Jr., and H. L. Gholz, Soil CO_2 evolution in Florida slash pine plantations, II, Importance of root respiration, *Can. J. For. Res.*, *17*, 330–333, 1987*b*.

Fouseki, E., and N. S. Margaris, Soil metabolism and decomposition in a phryganic (East Mediterranean) ecosystem, *Oecologia*, *50*, 417–421, 1981.

Froment, A., Soil respiration in a mixed oak forest, *Oikos*, *23*, 273–277, 1972.

Fung, I. Y., C. J. Tucker, and K. C. Prentice, Application of advanced very high resolution radiometer vegetation index to study atmosphere-biosphere exchange of CO_2, *J. Geophys. Res.*, *92*, 2999–3015, 1987.

Garrett, H. E., and G. S. Cox, Carbon dioxide evolution from the floor of an oak-hickory forest, *Soil Sci. Soc. Am. Proc.*, *37*, 641–644, 1973.

Gordon, A. M., R. E. Schlentner, and K. Van Cleve, Seasonal patterns of soil respiration and CO_2 evolution following harvesting in the white spruce forests of interior Alaska, *Can. J. For. Res.*, *17*, 304–310, 1987.

Gupta, S. R., and J. S. Singh, Soil respiration in a tropical grassland, *Soil Biol. Biochem.*, *13*, 261–268, 1981.

Holdridge, L. R., *Life Zone Ecology*, Tropical Science Center, San Jose, Costa Rica, 1964.

Houghton, R. A., and G. M. Woodwell, Global climatic change, *Sci. Am.*, *260*, 36–44, 1989.

Ino, Y., and M. Monsi, An experimental approach to the calculation of CO_2 amount evolved from several soils, *Jpn. J. Bot.*, *20*, 153–188, 1969.

Jarvis, P. G., Atmospheric carbon dioxide and forests, *Philos. Trans. R. Soc. London, Ser. B*, *324*, 369–392, 1989.

Jenkinson, D. S., The turnover of organic carbon and nitrogen in soil, *Philos. Trans. R. Soc. London, Ser. B*, *329*, 361–368, 1990.

Jenkinson, D. S., D. E. Adams, and A. Wild, Model estimates of CO_2 emissions from soil in response to global warming, *Nature*, *351*, 304–306, 1991.

Jorgensen, J. R., and C. G. Wells, The relationship of respiration in organic and mineral soil layers to soil chemical properties, *Plant Soil*, *39*, 373–387, 1973.

Kimball, B. A., and E. R. Lemon, Air turbulence effects upon soil gas exchange, *Soil Sci. Soc. Am. Proc.*, *35*, 16–21, 1971.

Kirita, H., Studies of soil respiration in warm-temperate evergreen broadleaf forests of southwestern Japan, *Jpn. J. Ecol.*, *21*, 230–244, 1971.

Leemans, R., and W. P. Cramer, The IIASA database for mean monthly values of temperature, precipitation and cloudiness of a global terrestrial grid, *Res. Rep. RR-91-18*, 61 pp., Int. Inst. of Appl. Syst. Anal., Laxenburg, Austria, 1991.

Legates, D. R., and C. J. Willmott, Mean seasonal and spatial variability in global surface air temperature, *Theor. Appl. Climatol.*, *41*, 11–21, 1990*a*.

Legates, D. R., and C. J. Willmott, Mean seasonal and spatial variability in gauge-corrected global precipitation, *Int. J. Climatol.*, *10*, 111–127, 1990*b*.

Melillo, J. M., A. D. McGuire, D. W. Kicklighter, B. Moore III,

C. J. Vorosmarty, and A. L. Schloss, Global climate change and terrestrial net primary production, *Nature*, *363*, 234–240, 1993.

Nakane, K., Dynamics of soil organic matter in different parts on a slope under evergreen oak forest, *Jpn. J. Ecol.*, *25*, 206–216, 1975.

Nakane, K., Comparative studies of cycling of soil organic carbon in three primeval moist forests, *Jpn. J. Ecol.*, *30*, 155–172, 1980.

Nakane, K., M. Yamamoto, and H. Tsubota, Estimation of root respiration rate in a mature forest ecosystem, *Jpn. J. Ecol.*, *33*, 397–408, 1983.

Nakane, K., H. Tsubota, and M. Yamamoto, Cycling of soil carbon in a Japanese red pine forest, I, Before a clear-felling, *Bot. Mag.*, *97*, 39–60, 1984.

Norman, J. M., R. Garcia, and S. B. Verma, Soil surface CO_2 fluxes and the carbon budget of a grassland, *J. Geophys. Res.*, *97*, 18,845–18,853, 1992.

O'Neill, R. V., Transmutations across hierarchical levels, in *Systems Analysis of Ecosystems*, edited by G. S. Innis and R. V. O'Neill, pp. 59–78, International Co-operative, Fairland, Md., 1979.

Parton, W. J., D. S. Schimel, C. V. Cole, and D. S. Ojima, Analysis of factors controlling soil organic matter levels in Great Plains grasslands, *Soil Sci. Soc. Am. Proc.*, *51*, 1173–1179, 1987.

Parton, W. J., D. S. Ojima, D. S. Schimel, and T. G. F. Kittel, Development of simplified ecosystem models for applications in earth system studies: The CENTURY experience, in *Modeling the Earth System*, edited by D. Ojima, pp. 281–302, UCAR/Office for Interdisplinary Earth Studies, Boulder, Colo., 1992.

Peterjohn, W. T., J. M. Melillo, F. P. Bowles, and P. A. Steudler, Soil warming and trace gas fluxes: Experimental design and preliminary flux results, *Oecologia*, *93*, 18–24, 1993.

Peterjohn, W. T., J. M. Melillo, P. A. Steudler, K. M. Newkirk, F. P. Bowles, and J. D. Aber, Responses of trace gas fluxes and N availability to experimentally elevated soil temperatures, *Ecol. Appl.*, in press, 1994.

Phillipson, J., R. J. Putman, J. Steel, and S. R. J. Woodell, Litter input, litter decomposition and evolution of carbon dioxide in a beech woodland-Wytham Woods, Oxford, *Oecologia*, *20*, 203–217, 1975.

Post, W. M., T.-H. Peng, W. R. Emanuel, A. W. King, V. H. Dale, and D. L. DeAngelis, The global carbon cycle, *Am. Sci.*, *78*, 310–326, 1990.

Raich, J. W., and W. H. Schlesinger, The global carbon dioxide flux in soil respiration and its relationship to vegetation and climate, *Tellus*, *44*(B), 81–99, 1992.

Rajvanshi, R., and S. R. Gupta, Soil respiration and carbon balance in a tropical *Dalbergia sisso* forest ecosystem, *Flora*, *178*, 251–260, 1986.

Rastetter, E. B., M. G. Ryan, G. R. Shaver, J. M. Melillo, K. J. Nadelhoffer, J. E. Hobbie, and J. D. Aber, A general biogeochemical model describing the responses of the C and N cycles in terrestrial ecosystems to changes in CO_2, climate, and N deposition, *Tree Physiol.*, *9*, 101–126, 1991.

Rastetter, E. B., A. W. King, B. J. Cosby, G. M. Hornberger, R. V. O'Neill, and J. E. Hobbie, Aggregating fine-scale ecological knowledge to model coarser-scale attributes of ecosystems, *Ecol. Appl.*, *2*, 55–70, 1992.

Reiners, W. A., Carbon dioxide evolution from the floor of three Minnesota forests, *Ecology*, *49*, 471–483, 1968.

Reiners, W. A., Terrestrial detritus and the carbon cycle, *Brookhaven Symp. Biol.*, *24*, 303–327, 1973.

Reinke, J. J., D. C. Adriano, and K. W. McLeod, Effects of litter alteration on carbon dioxide evolution from a South Carolina pine forest floor, *Soil Sci. Soc. Am. J.*, *45*, 620–623, 1981.

Rout, S. K., and S. R. Gupta, Soil respiration in relation to abiotic factors, forest floor litter, root biomass and litter quality in forest ecosystems of Siwaliks in northern India, *Acta Oecol. Oecol. Plant.*, *10*, 229–244, 1989.

Running, S. W., and J. C. Coughlan, A general model of forest ecosystem processes for regional applications, I, Hydrologic balance, canopy gas exchange and primary production processes, *Ecol. Modell.*, *42*, 125–154, 1988.

Schlentner, R. E., and K. Van Cleve, Relationships between CO_2 evolution from soil, substrate temperature, and substrate moisture in four mature forest types in interior Alaska, *Can. J. For. Res.*, *15*, 97–106, 1985.

Schlesinger, W. H., Carbon balance in terrestrial detritus, *Annu. Rev. Ecol. Syst.*, *8*, 51–81, 1977.

Schlesinger, W. H., Soil organic matter: A source of atmospheric CO_2, in *The Role of Terrestrial Vegetation in the Global Carbon Cycle: Measurement by Remote Sensing, SCOPE 23*, edited by G. M. Woodwell, pp. 111–127, John Wiley, New York, 1984.

Simunek, J., and D. L. Suarez, Modeling of carbon dioxide transport and production in soil, 1, Model development, *Water Resour. Res.*, *29*, 487–497, 1993.

Singh, J. S., and S. R. Gupta, Plant decomposition and soil respiration in terrestrial ecosystems, *Bot. Rev.*, *43*, 449–528, 1977.

Tesarova, M., and J. Gloser, Total CO_2 output from alluvial soils with two types of grassland communities, *Pedobiologia*, *16*, 364–372, 1976.

Tsutsumi, T., Y. Nishitani, and M. Sakai, On the effects of soil fertility on the rate of soil respiration in a forest, *Jpn. J. Ecol.*, *35*, 207–214, 1985.

Vogt, K. A., R. L. Edmonds, G. C. Antos, and D. J. Vogt, Relationships between CO_2 evolution, ATP concentrations and decomposition in four forest ecosystems in western Washington, *Oikos*, *35*, 72–79, 1980.

Vorosmarty, C. J., B. Moore III, A. L. Grace, M. P. Gildea, J. M. Melillo, B. J. Peterson, E. B. Rastetter, and P. A. Steudler, Continental scale models of water balance and fluvial transport: An application to South America, *Global Biogeochem. Cycles*, *3*, 241–265, 1989.

Weber, M. G., Forest soil respiration in eastern Ontario jack pine ecosystems, *Can. J. For. Res.*, *15*, 1069–1073, 1985.

Wildung, R. E., T. R. Garland, and R. L. Buschbom, The interdependent effects of soil temperature and water content on soil respiration rate and plant root decomposition in arid grassland soils, *Soil Biol. Biochem.*, *7*, 373–378, 1975.

Witkamp, M., Rates of carbon dioxide evolution from the forest floor, *Ecology*, *47*, 492–494, 1966.

Witkamp, M., Cycles of temperature and carbon dioxide evolution from litter and soil, *Ecology*, *50*, 922–924, 1969.

Wofsy, S. C., M. L. Goulden, J. W. Munger, S.-M. Fan, P. S. Bakwin, B. C. Daube, S. L. Bassow, and F. A. Bazzaz, Net exchange of CO_2 in a mid-latitude forest, *Science*, *260*, 1314–1317, 1993.

Woodwell, G. M., R. H. Whittaker, W. A. Reiners, G. E. Likens, C. C. Delwiche, and D. B. Botkin, The biota and the world carbon budget, *Science*, *199*, 141–146, 1978.

Yoneda, T., and H. Kirita, Soil respiration, in *Biological Production in a Warm-Temperate Evergreen Oak Forest of Japan*, edited by T. Kira, Y. Ono, and T. Hosokawa, pp. 239–249, University of Tokyo Press, 1978.

D. W. Kicklighter, A. D. McGuire, J. M. Melillo, W. T. Peterjohn, E. B. Rastetter, and P. A. Steudler, The Ecosystems Center, Marine Biological Laboratory, Woods Hole, MA 02543.

J. D. Aber, Institute for the Study of Earth, Oceans and Space, University of New Hampshire, Durham, NH 03824.

(Received March 19, 1993; revised October 4, 1993;
accepted October 9, 1993.)