

# The global carbon dioxide flux in soil respiration and its relationship to vegetation and climate

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## ABSTRACT

We review measured rates of soil respiration from terrestrial and wetland ecosystems to define the annual global CO<sub>2</sub> flux from soils, to identify uncertainties in the global flux estimate, and to investigate the influences of temperature, precipitation, and vegetation on soil respiration rates. The annual global CO<sub>2</sub> flux from soils is estimated to average ( $\pm$ S.D.)  $68 \pm 4$  PgC/yr, based on extrapolations from biome land areas. Relatively few measurements of soil respiration exist from arid, semi-arid, and tropical regions; these regions should be priorities for additional research. On a global scale, soil respiration rates are positively correlated with mean annual air temperatures and mean annual precipitation. There is a close correlation between mean annual net primary productivity (NPP) of different vegetation biomes and their mean annual soil respiration rates, with soil respiration averaging 24% higher than mean annual NPP. This difference represents a minimum estimate of the contribution of root respiration to the total soil CO<sub>2</sub> efflux. Estimates of soil C turnover rates range from 500 years in tundra and peaty wetlands to 10 years in tropical savannas. We also evaluate the potential impacts of human activities on soil respiration rates, with particular focus on land use changes, soil fertilization, irrigation and drainage, and climate changes. The impacts of human activities on soil respiration rates are poorly documented, and vary among sites. Of particular importance are potential changes in temperatures and precipitation. Based on a review of *in situ* measurements, the Q<sub>10</sub> value for total soil respiration has a median value of 2.4. Increased soil respiration with global warming is likely to provide a positive feedback to the greenhouse effect.

## 1. Introduction

Carbon dioxide is produced in soils by roots and soil organisms and, to a small extent, by chemical oxidation of carbon-containing materials (Lundegårdh, 1927). CO<sub>2</sub> is released from soils in the process variably referred to as soil respiration, soil-CO<sub>2</sub> evolution, or soil-CO<sub>2</sub> efflux. The rate at which CO<sub>2</sub> moves from the soil to the atmosphere is controlled by the rate of CO<sub>2</sub> production in the soil (the true soil respiration rate), the strength of the CO<sub>2</sub> concentration gradient between the soil and the atmosphere, and properties such as soil pore size, air temperature, and wind speed that influence the movement of CO<sub>2</sub> through and out of the soil.

On a global scale, soil respiration in terrestrial ecosystems is estimated to total 50–75 Pg C/yr

(Houghton and Woodwell, 1989; Schlesinger, 1977). By comparison, fossil fuel burning adds about 5 Pg C/yr to the atmosphere (ca. 1980–1982, Marland and Rotty 1984); even a small change in the soil respiration flux may rival the annual fossil-fuel loading of atmospheric CO<sub>2</sub>. Soil respiration is a major flux in the global carbon cycle, second in magnitude to gross primary productivity, which ranges from 100–120 Pg C/yr (Box, 1978; Bolin, 1983; Houghton and Woodwell, 1989), and equal to or greater than the estimated global terrestrial net primary productivity of 50–60 Pg C/yr (Box, 1978; Ajtay et al., 1979; Bolin, 1983; Olson et al., 1983; Houghton and Woodwell, 1989). The C-flux in soil respiration defines the rate of C-cycling through soils, thereby constraining estimates of above- and belowground detritus production and root respiration rates and enabling the estimation

of soil-C turnover rates. Despite its importance in the global carbon cycle, the global magnitude and distribution of soil respiration is poorly quantified.

Rates of soil respiration have been measured in a variety of ecosystems to examine rates of microbial activity, nutrient turnover, carbon cycling, root dynamics, and a variety of other soil processes. The understanding of soil respiration rates and factors that influence them therefore has a solid empirical base. Our objective is to summarize published estimates of soil respiration in terrestrial ecosystems, to investigate their relationship to mean climate data, and finally to provide a best estimate of the global CO<sub>2</sub> flux in soil respiration. We will also highlight those areas most in need of further research, discuss the major uncertainties in global extrapolation of the existing data, and review the effects of human activities on soil respiration rates. We will not discuss extensively the ways in which environmental variables influence soil respiration rates in specific study sites (see Schlesinger, 1977, Singh and Gupta, 1977). Our discussion will emphasize global patterns.

## 2. Soil respiration as an ecosystem process

Soil respiration is herein defined as the total CO<sub>2</sub> production in intact soils resulting from the respiration of soil organisms, roots, and mycorrhizae. This activity is sustained by organic matter inputs to the soil from aboveground and from roots. Three principal components of soil respiration may be defined: root respiration, surface-litter respiration, and the respiration of soil organic matter (including root detritus). The specific importance of each of these components varies widely among sites and has always been difficult to ascertain, because most methods disrupt the soil profile. Thus, soil respiration measurements are most useful for documenting total metabolic activity in the soil, for defining rates of carbon fluxes through soils, and for investigating soil-atmosphere interactions.

Soil respiration is often determined by measuring the flux of CO<sub>2</sub> from the soil surface. This soil-CO<sub>2</sub> efflux or evolution rate is approximately equal to the soil respiration rate on an annual basis unless significant losses of inorganic C occur through leaching or deposition, both of which

are generally negligible (Schlesinger and Melack, 1981; Schlesinger, 1985). However, soil respiration and CO<sub>2</sub> efflux rates may not be similar over shorter time steps. We will refer to annual CO<sub>2</sub> efflux rates as being equivalent to soil respiration, but emphasize that soil-CO<sub>2</sub> efflux rates, not actual soil respiration rates, are measured.

## 3. Global patterns of soil respiration

### 3.1. Selection of data

A wide variety of techniques has been applied to the measurement of CO<sub>2</sub> efflux from soils, and much of the variability observed among sites may be attributed to methodological differences among investigators. This has created difficulties in comparing data (Schlesinger, 1977; Singh and Gupta, 1977; Raich and Nadelhoffer, 1989). In summarizing published estimates of soil CO<sub>2</sub> efflux, we have included only those data based on most or all of one full year of measurements so that the annual soil respiration could be estimated. We do not include measurements made on soil cores because these exclude or modify root respiration. We also exclude data obtained with alkali absorption techniques if the surface area of the absorbant was less than 5% of the surface area of the covered ground; this leads to low estimates of soil respiration (Kirita, 1971a; Raich and Nadelhoffer, 1989).

With these constraints, we have tabulated all published estimates of annual CO<sub>2</sub> efflux from soils that we could find (Appendix), and included the mean annual temperature and precipitation for the different study sites. If climate data were not reported we used the data from a global climate data base with a 0.5° latitude by 0.5° longitude resolution (Legates and Willmott, 1988). Each study site was classified by vegetation type based on vegetation descriptions in the cited papers (Appendix).

### 3.2. Soil respiration in major vegetation biomes

Mean rates of soil respiration vary widely within and among major vegetation biomes (Table 1). The lowest rates of soil respiration occur in the coldest (tundra and northern bogs) and driest (deserts) biomes, and the highest rates occur in tropical moist forests where both temperature and

Table 1. Mean rates of soil respiration in different types of vegetation, based on the data in the Appendix

Vegetation type	Soil respiration rate (gC/m <sup>2</sup> /yr) (mean ± S.E.)	<i>n</i>	
Tundra	60 ± 6	11	e
Boreal forests and woodlands	322 ± 31	16	cde
Temperate grasslands	442 ± 78	9	bcd
Temperate coniferous forests	681 ± 95	23	b
Temperate deciduous forests*	647 ± 51	29	b
Mediterranean woodlands and heath	713 ± 88	13	b
Croplands, fields, etc.	544 ± 80	26	bc
Desert scrub	224 ± 38	3	de
Tropical savannas and grasslands	629 ± 53	9	bc
Tropical dry forests	673 ± 134	4	b
Tropical moist forests	1260 ± 57	10	a
Northern bogs and mires	94 ± 16	12	e
Marshes	413 ± 76	6	bcd

Letters in the final column refer to the results of a Duncan's multiple range test (SAS Institute 1985); vegetation types followed by the same letter do not have significantly different respiration rates.

\* Including mixed broad-leaved and needle-leaved forests.

moisture availability are high year-round. In most biomes the standard error of the soil respiration data exceeds 10% of the mean value. This exemplifies the inherent variability in nature, the coarse relationship between soil respiration and vegetation type, and the need for further work.

There are very few measurements of the CO<sub>2</sub> efflux from arid lands, including natural savannas, woodlands, drought-deciduous forests, and deserts. Arid and semi-arid lands cover about one-third of the terrestrial land surface (Dregne, 1976), so the lack of measurements in these areas represents a major deficiency in estimating global soil respiration. Two-thirds of the study sites listed in the Appendix are located between 30° and 60° latitude, so temperate regions are very well represented. The tropics cover about one-third of the global land area, contain a great diversity of biomes, and include regions with very high rates of soil respiration. However, few measurements of annual soil respiration have been made in the tropics. Therefore, despite an abundance of soil respiration data, global coverage is poor. Arid and tropical regions should be priorities for continued research.

Annual soil respiration rates correlate positively with aboveground net primary productivity

within northern peatlands (Moore, 1986) and with aboveground litter production in forest ecosystems (Schlesinger, 1977; Raich and Nadelhoffer, 1989). On a global scale, mean rates of soil respiration are positively correlated with mean productivity rates in different vegetation biomes (Fig. 1). These studies indicate a tight linkage between plant productivity and soil respiration, which is expected because primary production provides the organic fuel that drives soil metabolic activity. Further analyses of the relationship between soil respiration and plant productivity within specific vegetation types can provide much-needed insight into belowground carbon cycling processes (e.g., Raich and Nadelhoffer, 1989).

### 3.3. Climatic controls over soil respiration

On a global scale, soil respiration rates correlate significantly with mean annual air temperatures (Fig. 2), with mean annual precipitation (Fig. 3), and with the interaction of these two variables (Table 2). Temperature is the single best predictor of the annual soil respiration rate of a specific location, but inclusion of precipitation in the regression does increase the predictive power of the model (Table 2). Differences observed among vegetation types (Table 1) can be explained largely

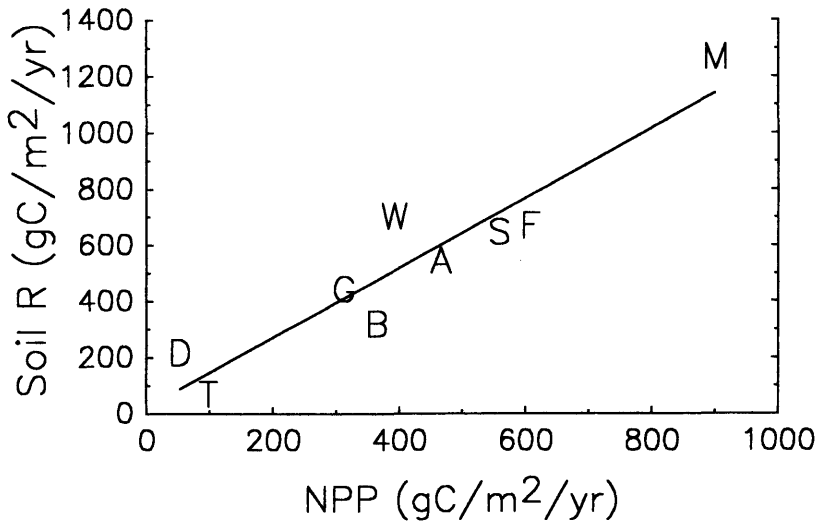


Fig. 1. The relationship between mean annual net primary productivity (NPP) and mean annual soil respiration for nine terrestrial vegetation biomes. Mean annual NPP was estimated for each biome from Whittaker and Likens (1975), Ajtay et al. (1979), and Olson et al. (1983). Mean annual soil respiration for each biome is from Table 1. A = agricultural lands, B = boreal forest and woodland, D = desert scrub, F = temperate forest, G = temperate grassland, M = moist tropical forest, S = tropical savanna and dry forest, T = tundra, and W = mediterranean woodland and heath. The least squares linear regression between soil respiration (SR) and NPP is:

$$SR = 1.24(NPP) + 24.5 \quad (r^2 = 0.87),$$

all units being gC/m<sup>2</sup>/yr.

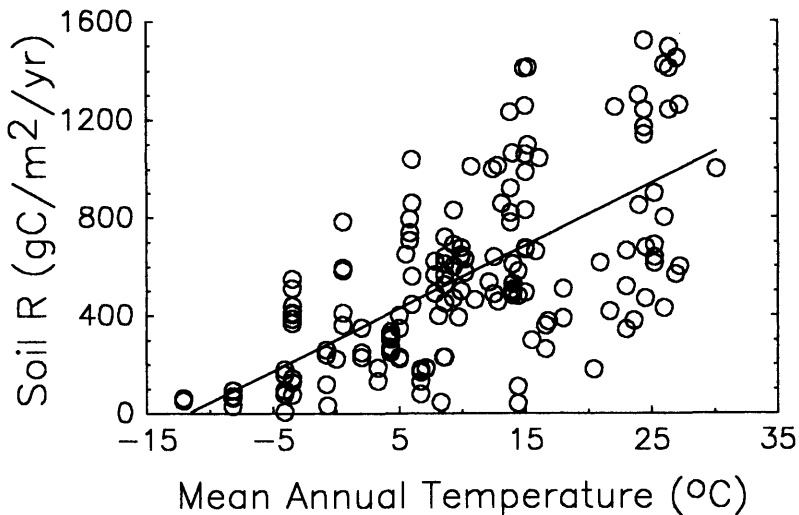


Fig. 2. Soil respiration and mean annual air temperature for sites listed in the Appendix. The line shows the least squares relationship between the two variables (Table 2).

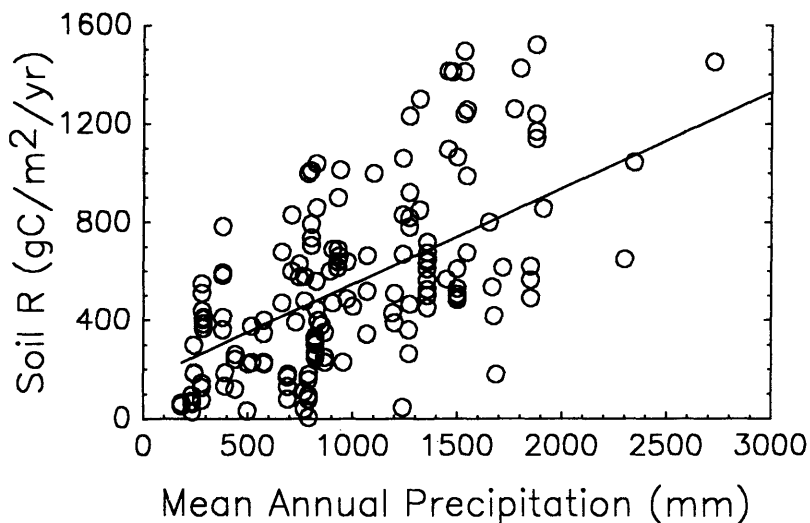


Fig. 3. Soil respiration and mean annual precipitation for sites listed in the Appendix. The line shows the least squares relationship between the two variables (Table 2). Two sites had  $>3000$  mm precipitation and are not shown here.

by differences in temperature and moisture availability among vegetation biomes.

Fung et al. (1987) provided linear regressions for predicting monthly soil respiration from air temperature in grasslands, temperate/boreal needle-leaved vegetation, temperate/boreal broad-leaved vegetation, and tropical/subtropical woody vegetation. Correlations ( $r^2$ ) ranged from 0.45 to 0.64. We investigated annual temperature-respiration relationships in each of the major vegetation biomes and found significant linear trends in

Table 2. Least-squares linear and multiple regression models describing the relationship between annual soil respiration rate (SR,  $\text{gC}/\text{m}^2/\text{yr}$ ) and the climate variables mean annual temperature ( $T$ ,  $^{\circ}\text{C}$ ) and mean annual precipitation ( $P$ , mm)

Model	$r^2$	F
$\text{SR} = 25.6T + 300$	0.42	121
$\text{SR} = 0.391P + 155$	0.34	83
$\text{SR} = 0.0178TP + 311$	0.48	151
$\text{SR} = (18.6T) + (0.192P) + 175$	0.47	73
$\text{SR} = (9.26T) + (0.0127TP) + 289$	0.50	80
$\text{SR} = (9.88T) + (0.0344P) + (0.0112TP) + 268$	0.50	53

All models are based on all data in the Appendix for which climate data were available. All models are significant at  $P = 0.0001$ .

boreal forests and woodlands ( $r^2 = 0.28$ ), temperate coniferous forests ( $r^2 = 0.49$ ), temperate deciduous forests ( $r^2 = 0.31$ ), and croplands ( $r^2 = 0.23$ ). Trends were not significant in other biomes, and the correlations within biomes were generally no better than the global correlation, i.e., little additional information was obtained by limiting the analysis to a single vegetation type. Further analysis of monthly data is warranted, however, to define temperate-soil respiration relationships on a finer time scale than our annual analysis provides. This is essential for investigating how global temperature changes might influence soil respiration rates, as predicted temperature changes vary seasonally (Houghton et al., 1990).

Brook et al. (1983) used regression techniques to analyze global relationships between growing-season  $\text{CO}_2$  concentrations in soils ( $p\text{CO}_2$ ) and climate and found that actual evapotranspiration rate (AET) was the best climatic predictor of  $p\text{CO}_2$ . Annual AET is also correlated with litter production and decomposition (Meentemeyer, 1978; Meentemeyer et al., 1982). Rates of evapotranspiration are influenced by soil temperatures and soil moisture, both of which have significant influences on soil respiration rates. Evapotranspiration rates may therefore be closely correlated to rates of soil respiration, but such a relationship has not yet been defined.

### 3.4. Global soil respiration

The annual global CO<sub>2</sub> flux in soil respiration was estimated by multiplying the land areas of major vegetation biomes by their mean annual soil respiration. This extrapolation is highly dependent upon the land areas used. Use of the biome areas published by Whittaker and Likens (1975), Ajtay et al. (1979), Olson et al. (1983), and Matthews (1983) leads to estimated total global soil respiration rates of 70, 63, 68, and 72 Pg C/yr. In each case a slightly different grouping of the soil respiration data was necessary. It was also necessary to combine several of the vegetation types defined by Ajtay et al., Olson et al., and Matthews due to incomplete data coverage. The mean estimate ( $\pm$  S.D.) for global soil respiration is  $68 \pm 4$  Pg/yr. Using a different extrapolation technique, Schlesinger (1977) predicted a global flux of 75 Pg/yr.

## 4. Soil carbon turnover

Soil respiration rates can be used to calculate the mean residence or turnover time of the soil carbon pool, provided an assumption is made regarding the contribution that live root respiration makes to total soil respiration. The remaining respiration

Table 3. *Estimated turnover time of soil carbon based on mean carbon pools (Schlesinger, 1984) and mean soil respiration rates (this paper)*

Vegetation type	Soil C (kg/m <sup>2</sup> )	Soil R (gC/m <sup>2</sup> /yr)	Turnover (yr)
Tundra	20.4	60	490
Boreal forests	20.6	322	91
Temperate grasslands	18.9	442	61
Temperate forests	13.4	662	29
Woodlands	6.9	713	14
Cultivated lands	7.9	544	21
Desert scrub	5.8	224	37
Tropical grasslands	4.2	629	10
Tropical lowland forests	28.7	1092	38
Swamps and marshes	72.3	200	520
Global total:			
1515 PgC in soil, CO <sub>2</sub> efflux of 68 PgC/yr			32

Turnover time is estimated based on the assumption that 30% of soil respiration is derived from root respiration.

is presumably derived from the decomposition of soil organic matter, representing the true turnover of this pool. Most studies indicate that live root respiration contributes 30 to 70% of the total soil respiration (Schlesinger, 1977). Table 3 shows the mean residence time of soil organic matter with the assumption that live roots contribute 30% of the total soil respiration. These values range from about 500 years in the peatlands of tundra, swamp and marsh sediments to 10 years in tropical grasslands. The global pool of soil organic matter has a mean residence time of about 32 years (Table 3).

In most soils the pool of organic carbon consists of a small pool near the surface with rapid turnover and a larger pool of refractory humic compounds that are dispersed throughout the lower profile. Radiocarbon (<sup>14</sup>C) dating of the organic matter in a soil sample shows the weighted average age of the organic carbon in a given horizon. Radiocarbon age of organic matter in a Canadian grassland was 250 years (Martel and Paul, 1974). Ages tend to increase with depth, reflecting relative turnover and abundance of the different forms of detritus. O'Brien and Stout (1978) showed that most of the soil organic matter in a New Zealand pasture was <100 years old, but the lower profile contained 16% which was at least 5700 years old.

When vegetation dominated by C<sub>3</sub> plants is replaced by C<sub>4</sub> plants, or vice-versa, changes in the <sup>13</sup>C/<sup>12</sup>C ratio of soil organic matter can also be used to calculate the residence times of different organic matter fractions in the soil profile. The turnover times indicated by such studies are also consistent with the values in Table 3. For instance, Skjemstad et al. (1990) found that the turnover in an Australian pasture ranged from 60 to 276 years, tending to increase with depth. In a tropical savanna of the Ivory Coast, Martin et al. (1990) found that the 52 to 70% of the carbon turned over in 16 years, when C<sub>4</sub> vegetation was replaced by C<sub>3</sub> vegetation after fire. This gives a mean residence time of 17.5 years for soil organic matter in the profile, assuming an exponential pattern of decay.

## 5. Human impacts on soil respiration rates

Humans modify the landscape and environment in many ways, yet the effects of these modifications

on major biogeochemical processes are poorly known. Changes in the structure or species composition of plant communities, soil chemical and physical properties, soil microclimate, precipitation chemistry, and global climate may all affect rates of soil respiration. To what extent are these changes of potential importance in modifying the global flux of CO<sub>2</sub> from soils to the atmosphere? Could changes in soil respiration augment or compensate for the CO<sub>2</sub> released by burning fossil fuels?

### 5.1. Land use changes

Relatively few direct comparisons have been made of soil respiration rates in natural and disturbed vegetation. The CO<sub>2</sub> efflux from wheat was greater than that from native grassland vegetation in Missouri (Buyanovsky et al., 1987) and in Saskatchewan (De Jong et al., 1974). Grass-covered soil released more CO<sub>2</sub> than did forest vegetation in Germany (Dörr and Münnich, 1987). Similarly, newly cropped plots generated by slash-and-burn released more CO<sub>2</sub> than an uncut forest plot in Thailand (Tulaphitak et al., 1983). It appears that conversion of native vegetation increases soil respiration, but additional comparisons are needed.

Forest cutting has been reported to increase (Gordon et al., 1987; Hendrickson et al., 1989), decrease (Nakane et al., 1986), and have no effect (Edwards and Ross-Todd, 1983; O'Connell, 1987) on soil-CO<sub>2</sub> evolution rates (Table 4). In a *Pinus*

*elliottii* plantation in Florida, soil respiration rates were very high in the first year following clear-cutting, apparently due to the higher soil temperatures and the decomposition of logging debris that was incorporated into the soil during site preparation. A nine-year-old plantation, however, had lower rates than did a 29-year-old plantation (Ewel et al., 1987a, b). Edwards and Ross-Todd (1983) examined the potential impacts of forest felling on soil-CO<sub>2</sub> efflux and concluded that any changes occurring due to increased forest harvest in the USA were small in comparison with annual CO<sub>2</sub> releases due to fossil-fuel burning.

### 5.2. Fertilization

Lundegårdh (1927) stated that fertilization of agricultural crops generally increases soil respiration rates, but few direct comparisons of annual CO<sub>2</sub> efflux from fertilized and unfertilized crops have been made. Fertilized and unfertilized barley in Sweden had similar soil respiration rates (Paustian et al., 1990). Kowalenko et al. (1978) reported that N-fertilization depressed soil-CO<sub>2</sub> efflux from fallow vegetation and reduced microbial activity in laboratory incubations. However, *in situ* differences between fertilized and control plots were small and not significant. Fertilization depressed soil respiration rates in native grassland of Saskatchewan (De Jong et al., 1974).

In forests, too, the impacts of fertilization on soil respiration rates are ambiguous. Fertilization with a broad array of mineral nutrients increased

Table 4. Direct comparisons of soil respiration rates in uncut and recently clearcut forests

Forest type, location	Soil respiration (g/m <sup>2</sup> /yr)		Year <sup>a</sup>
	control	cut stand	
<i>Picea glauca</i> , Alaska, USA	440	530 <sup>b</sup>	2-4
<i>Populus tremuloides</i> , Ottawa, Canada	320	303 <sup>b</sup>	1st
same	355	299 <sup>b</sup>	2nd
same	328	320 <sup>b</sup>	3rd
<i>Pinus densiflora</i> , Japan	1255	676	1st
<i>Pinus elliottii</i> , Florida, USA	1300	2600	1st
<i>Quercus-Carya</i> , Tennessee, USA	529	488	1st
<i>Eucalyptus</i> , Victoria, Australia	830	1060	2nd

Sources of all data are shown in the Appendix.

<sup>a</sup> Refers to the year following cutting during which measurements were made.

<sup>b</sup> Mean of two sites.

soil respiration rates in pine forests studied by Repnevskaya (1967). Irrigation with wastewater high in inorganic N increased rates of soil respiration in a young *Pinus rigida* stand in Massachusetts, but this increase could be attributed to the water additions alone (J. W. Raich, unpublished data). Responses of drained peat-bog forests to a variety of fertilizers were variable, with no change, stimulations, and decreases in soil respiration rates being reported from different sites (Silvola et al., 1985).

Although potentially increasing organic matter decomposition and plant productivity, fertilization may also decrease relative C allocation to roots (Waring and Schlesinger, 1985). The net result of these different effects may vary among sites, soils, and vegetation types, and no clear patterns are apparent in the available data. Short- and long-term effects of fertilization may also differ as vegetation adapts to the new nutrient regime (Chapin et al., 1986). Therefore, the potential impacts of fertilization on soil respiration rates are poorly documented, but appear to be small.

### 5.3. Irrigation and drainage

Irrigation acts to overcome the limitations imposed by drought, especially in arid lands, and should therefore stimulate soil respiration

rates. In a 27-year-old *Pinus rigidus* forest in Massachusetts, irrigation with wastewater effluent stimulated soil respiration rates from a mean of 500 gC/m<sup>2</sup>/yr in the control plots to 680 gC/m<sup>2</sup>/yr in the irrigated plots (Fig. 4). The effluent had very high N-concentrations, but there was no apparent fertilization effect during the first two years of irrigation (J. W. Raich, unpublished data). Similar results were found in Saskatchewan grassland, where irrigation with or without fertilization stimulated soil respiration equally (de Jong et al., 1974).

Wetland drainage increases soil aeration, and should therefore increase soil respiration rates by removing the oxygen limitation to soil organisms. Soil respiration rates in northern peatlands were shown to be positively correlated with depth to the water table by Moore and Knowles (1989) and Luken and Billings (1985). Increased rates of soil respiration were observed after peatland drainage in Finland (Silvola et al., 1985), but this response was most notable in poorly decomposed peats. Virgin mires accumulate soil C, but become CO<sub>2</sub> sources to the atmosphere after drainage (Silvola, 1986). Higher rates of soil respiration from drained peatlands account for the observed loss of organic carbon from many wetland soils of the world (Hutchinson, 1980; Armentano and Menges, 1986).

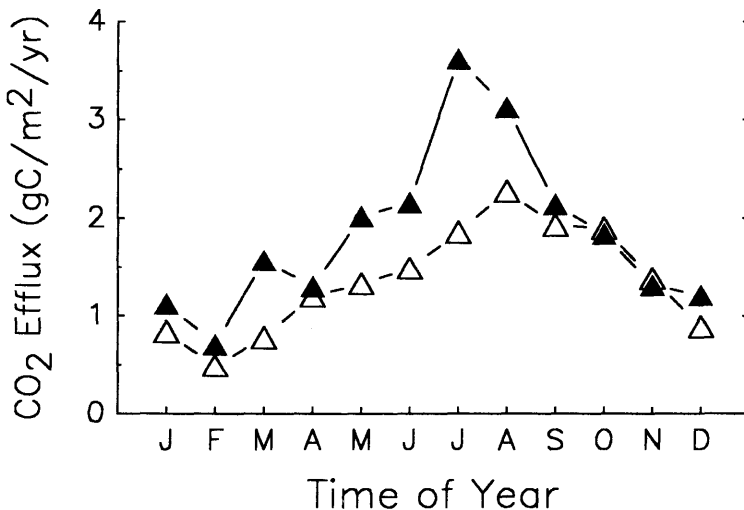


Fig. 4. Mean monthly soil-CO<sub>2</sub> efflux in a 27-year-old *Pinus rigida* forest growing on sandy soil in Falmouth, Massachusetts, USA, based on two years of monthly measurements (open symbols), and for the same forest that was irrigated throughout the growing season with wastewater effluent (solid symbols).



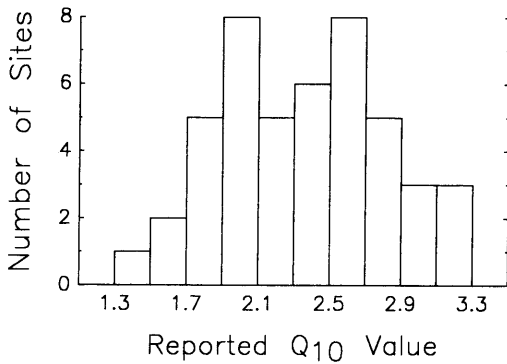


Fig. 5. Frequency histogram of reported  $Q_{10}$  values for total *in situ* soil respiration rates as reported in the literature. Each site represents a specific study site or a full year of measurement within a specific study site. Data in this figure were obtained from Monteith (1968), Kirita (1971b), Kucera and Kirkham (1971), Anderson (1973), Nakane (1975, 1980), Yoneda and Kirita (1978), Chapman (1979), Bridge et al. (1983), Nakane et al. (1984, 1986), Tsutsumi et al. (1985), Buyanovsky et al. (1986), Dörr and Münnich (1987), Yoneda and Okata (1987), and J. W. Raich (unpublished data).

#### 5.4. Temperature changes

Global climate models predict temperature increases due to potential greenhouse warming in the near future (Houghton et al., 1990), and the significant correlation between soil respiration rates and temperature suggests greater rates of soil respiration that might further enhance the accumulation of greenhouse gases. The specific relationship found between temperature and soil respiration varies among sites, but a logarithmic relationship is often reported (Singh and Gupta, 1977). Numerous authors have reported  $Q_{10}$  values for *in situ* soil respiration rates, and although reported  $Q_{10}$  values vary, the median value is about 2.4 (Fig. 5). These data are based on seasonal changes in soil temperatures and soil respiration rates, so the seasonal pattern of temperature change is important. Schleser (1982) argued that the  $Q_{10}$  value of soil respiration was higher at low than at high temperatures, indicating that temperature increases in northern latitudes would have greater impacts on soil respiration rates than would similar changes in warmer climates. If temperature changes do occur, and if they are translated into higher soil temperatures, then we can expect increases in soil respiration rates due to the increased temperatures, all other

factors being equal. However, because precipitation patterns are also expected to change, the specific effects of predicted temperature changes on soil respiration rates will require more detailed analysis.

## 6. Summary and Conclusions

Our compilation suggests that the annual release of  $\text{CO}_2$  from soils is about 68 Pg of carbon. This value sets an upper limit on the net primary production (NPP) of the terrestrial biosphere, about which there is much uncertainty (Schlesinger, 1991). Our value suggests that NPP is not likely to exceed 68 Pg, plus the amount of aboveground vegetation that is consumed by fires [2 to 5 Pg, Crutzen and Andreae (1990)] and respired by herbivores [3 Pg, Whittaker and Likens (1973)]. The NPP value of 60 Pg, which is widely accepted in models of the global carbon cycle (Solomon et al., 1985; Houghton et al., 1990), may be somewhat too high, because it allows only 8 Pg for the respiration of live roots. The regression for Fig. 1 suggests that terrestrial NPP is about 55 PgC/yr, if total soil respiration is 68 PgC/yr.

Based on compilations of data from the literature, Schlesinger (1977) and Raich and Nadelhoffer (1989) suggest that the loss of carbon from soil respiration ranges from 2.5 to 2.9 times the input of carbon to the soil in aboveground litterfall in forests. If this factor is similar in other ecosystems, then the global soil respiration of 68 Pg yields a global litterfall of about 25 Pg for terrestrial ecosystems. Belowground production of root detritus is often as large as the aboveground deposition of litter (Vogt et al., 1986; Nadelhoffer and Raich, *in press*). Thus, total detritus production on land, roughly equivalent to total NPP, is about 50 Pg/yr. This value is close to Whittaker and Likens (1973) estimate of terrestrial productivity (48 Pg/yr) and Meentemeyer et al.'s (1982) estimate for detritus production on land (55 Pg/yr). The remaining portion of soil respiration, 18 Pg/yr or 26%, is derived from the respiration of live roots and mycorrhizae. Global root respiration may exceed this estimate because some detritus decomposes aboveground in plant canopies and in standing or fallen, dead timber.

Soil respiration is responsive to temperature

(Fig. 2), and increases when soil temperatures are raised experimentally (Billings et al., 1982; Van Cleve et al., 1990). If soil respiration is 68 Pg/yr and the  $Q_{10}$  relationship for the metabolic activity in soils is 2.4, then the increased respiration from soils with a uniform global warming of 0.3° at the end of the next decade could raise soil respiration by almost 2 Pg/yr, adding significantly to atmospheric CO<sub>2</sub>. A similar calculation using the regression of Fig. 2 suggests a 1.2% increase amounting to nearly 1 PgC/yr. At that time, the change in soil respiration would amount to about 20 to 40% of the estimated annual fossil fuel emissions. A recent similar analysis by Jenkinson et al. (1991) suggests during the next 60 years there will be a net loss of 61 PgC from terrestrial soils, or 19% of the fossil fuel input over the same interval. It is possible that the change may be lower if the pool of labile soil organic matter is depleted significantly. However, since  $Q_{10}$  values tend to be somewhat higher at low temperatures (Schleser,

1982), where the greatest increases in global temperature are expected, these are conservative estimates of the effect of global warming on soil respiration. Increased soil respiration with global warming is likely to provide a positive feedback to the greenhouse effect.

## 7. Acknowledgments

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## Appendix. Annual soil respiration rates ( $\text{gC} \cdot \text{m}^{-2} \cdot \text{yr}^{-1}$ ) in the world's major terrestrial biomes

Soil R	Location	Vegetation, locality, references
<i>Tundra</i>		
53	71°18' N 156°40' W	Wet sedge tundra, Barrow, Alaska (Billings et al., 1978)
62	71°18' N 156°40' W	Same site (Chapin et al., 1980)
64 <sup>h</sup>	68°47' N 148°51' W	Tussock tundra, Alaska (Giblin et al., 1991)
95 <sup>h</sup>	68°47' N 148°51' W	Hilltop heath (Giblin et al., 1991)
94 <sup>h</sup>	68°47' N 148°51' W	Hillslope shrub/lupine tundra (Giblin et al., 1991)
64 <sup>h</sup>	68°47' N 148°51' W	Footslope <i>Equisetum</i> (Giblin et al., 1991)
29 <sup>h</sup>	68°47' N 148°51' W	Wet sedge tundra (Giblin et al., 1991)
70 <sup>h</sup>	68°47' N 148°51' W	Riverside willow (Giblin et al., 1991)
56 <sup>f</sup>	68° N 149° W	Tussock tundra, various locations in Alaska (Poole and Miller, 1982)
34 <sup>f</sup>	68° N 149° W	Shrub tundra, various locations in Alaska (Poole and Miller, 1982)
42 <sup>f</sup>	68° N 149° W	Lichen heath, various locations in Alaska (Poole and Miller, 1982)
<i>Boreal Forest and Woodland</i>		
120°	67°30' N 33° E	Lichen-pine stand, USSR (Repnevskaya, 1967)
260°	67°30' N 33° E	Red bilberry bush-pine stand (Repnevskaya, 1967)
240°	67°30' N 33° E	Immature whortleberry bush-pine stand (Repnevskaya, 1967)
260	67°30' N 33° E	Moist whortleberry bush-pine stand (Repnevskaya, 1967)
224	66°22' N 29°20' E	<i>Picea abies</i> woodland, Finland (Havas and Mäenpää, 1972)
144	64°52' N 148° W	Forested bog, Alaska (Luken and Billings, 1985)
440	64°45' N 148°15' W	<i>Picea glauca</i> , Alaska (Gordon et al., 1987)

## Appendix (cont'd)

Soil R	Location	Vegetation, locality, references
550	64°45' N 148°15' W	Same, clear-cut 3 years earlier (Gordon et al., 1987)
510	64°45' N 148°15' W	Same, clear-cut 2 years earlier (Gordon et al., 1987)
411	64° N 148° W	<i>Picea glauca</i> , Alaska (Schlentner and Van Cleve, 1985)
386	64° N 148° W	<i>Populus tremuloides</i> , Alaska (Schlentner and Van Cleve, 1985)
405	64° N 148° W	<i>Betula papyrifera</i> , Alaska (Schlentner and Van Cleve, 1985)
369	64° N 148° W	<i>Picea mariana</i> , Alaska (Schlentner and Van Cleve, 1985)
350	62°51' N 30°53' E	Drained <i>Pinus sylvestris</i> peatland (Silvola et al., 1985)
230	62°51' N 30°53' E	Drained <i>Pinus-Betula</i> peatland (Silvola et al., 1985)
250	62°51' N 30°53' E	Drained <i>Picea abies</i> swamp (Silvola et al., 1985)
<i>Temperate Grassland</i>		
187	50°36' N 107°45' W	Matador grassland, Saskatchewan (de Jong et al., 1974)
132	50°36' N 107°45' W	Same site (Warembourg and Paul, 1977)
830 <sup>a</sup>	48°40' N 16°55' E	<i>Alopecurus</i> meadow, Czechoslovakia (Tesarova and Gloser, 1976)
600 <sup>a</sup>	48°40' N 16°55' E	<i>Festuca</i> meadow, Czechoslovakia (Tesarova and Gloser, 1976)
230	40°49' N 104°46' W	Short-grass prairie, Colorado (Coleman et al., 1976)
488	38°50' N 92°02' W	Tallgrass prairie, Missouri (Buyanovsky et al., 1987)
457	38°50' N 92°02' W	Same site (Kucera and Kirkham, 1971)
662	36°57' N 96°33' W	Tallgrass prairie, Oklahoma (Risser et al., 1981)
390	33°30' N 81°40' W	Successional grassland, S. Carolina (Coleman, 1973)
<i>Temperate Coniferous Forest</i>		
490 <sup>a</sup>	47°23' N 121°57' W	<i>Pseudotsuga menziesii</i> , Washington (Vogt et al., 1980)
650 <sup>a</sup>	47°23' N 121°57' W	<i>Tsuga heterophylla</i> , Washington (Vogt et al., 1980)
620 <sup>a</sup>	47°19' N 121°35' W	<i>Abies amabilis</i> , Washington (Vogt et al., 1980)
260 <sup>c</sup>	46°00' N 77°25' W	Unburned 63-yr-old <i>Pinus banksiana</i> , Quebec (Weber, 1985)
250 <sup>c</sup>	46°00' N 77°25' W	63-yr-old <i>Pinus banksiana</i> , burned 1962 (Weber, 1985)
270 <sup>c</sup>	46°00' N 77°25' W	63-yr-old <i>Pinus banksiana</i> , burned 1963 (Weber, 1985)
250 <sup>e</sup>	46°00' N 77°25' W	19-yr-old <i>Pinus banksiana</i> , Quebec (Weber, 1985)
250 <sup>e</sup>	46°00' N 77°25' W	Treeless shrub stand, Quebec (Weber, 1985)
565	42°30' N 72°15' W	<i>Pinus resinosa</i> plantation, Massachusetts (R. D. Bowden, personal communication)
525	42°30' N 72°15' W	Same site, low N fertilization (R. D. Bowden, personal communication)
450	42°30' N 72°15' W	Same site, high N fertilization (R. D. Bowden, personal communication)
500 <sup>i</sup>	41°40' N 70°35' W	Young <i>Pinus rigida</i> , Massachusetts (J. W. Raich, unpublished data)
677 <sup>i</sup>	41°40' N 70°35' W	Same, irrigated with wastewater (J. W. Raich, unpublished data)
1000 <sup>b</sup>	38°00' S 143°30' E	<i>Pinus radiata</i> , Victoria, Australia (Carlyle and Than, 1988)
536	35°05' N 135°50' E	<i>Chamaecyparis obtusa</i> , Japan (Tsutsumi et al., 1985)
987	34°24' N 132°31' E	<i>Pinus densiflora</i> , Japan (Nakane et al., 1984)
1255	34°24' N 132°31' E	older <i>P. densiflora</i> , Japan (Nakane et al., 1984, 1986)
676	34°24' N 132°31' E	Same site, recently clearcut (Nakane et al., 1986)
509	33°30' N 81°40' W	20-year-old <i>Pinus palustris</i> , S. Carolina (Reinke et al., 1981)

## Appendix (cont'd)

Soil R	Location			Vegetation, locality, references
519	33°	N	73° E	<i>Pinus roxburghii</i> forest, India (Rout and Gupta, 1989)
1300	30°	N	82° W	<i>Pinus elliottii</i> , Florida (Ewel et al., 1987a, b)
850	30°	N	82° W	Same, 9-yr-old site
2600	30°	N	82° W	Same, clear-cut site
<i>Temperate Broad-leaved and Mixed Forests</i>				
630	51°20' N	1°05' E		<i>Castanea sativa</i> , England (Anderson, 1973)
575	51°20' N	1°05' E		<i>Fagus sylvatica</i> , England (Anderson, 1973)
470 <sup>a</sup>	49°20' N	8°40' E		<i>Fagus-Picea</i> , Germany (Dörr and Münnich, 1987)
565 <sup>a</sup>	47°23' N	121°57' W		<i>Alnus rubra</i> , Washington (Vogt et al., 1980)
334 <sup>e</sup>	46°00' N	77°25' W		<i>Populus tremuloides</i> , Quebec (Weber, 1990)
317 <sup>e</sup>	46°00' N	77°25' W		Same, burned before leaf flush (Weber, 1990)
318 <sup>e</sup>	46°00' N	77°25' W		Burned after leaf flush (Weber, 1990)
304 <sup>e</sup>	46°00' N	77°25' W		Cut before leaf flush (Weber, 1990)
311 <sup>e</sup>	46°00' N	77°25' W		Cut after leaf flush (Weber, 1990)
794	45°30' N	93°10' W		<i>Quercus</i> -mixed, Minnesota (Reiners, 1968)
707	45°30' N	93°10' W		<i>Fraxinus</i> -mixed, Minnesota (Reiners, 1968)
739	45°30' N	93°10' W		<i>Thuja-Betula</i> swamp, Minnesota (Reiners, 1968)
610	42°30' N	72°15' W		Mixed-hardwood forest, Massachusetts (R. D. Bowden, personal communication)
720	42°30' N	72°15' W		Same site, low N fertilization (R. D. Bowden, personal communication)
640	42°30' N	72°15' W		Same site, high N fertilization (R. D. Bowden, personal communication)
648 <sup>i</sup>	41°40' N	70°35' W		<i>Quercus-Pinus</i> , Massachusetts (J. W. Raich, unpublished data)
464	40°50' N	72°50' W		<i>Quercus-Pinus</i> , New York (Woodwell and Botkin, 1970)
1013	38°48' N	92°12' W		<i>Quercus-Carya</i> , Missouri (Garrett and Cox, 1973)
505 <sup>a</sup>	35°58' N	84°17' W		young <i>Liriodendron</i> , Tennessee (Edwards and Ross-Todd, 1979)
1065	35°58' N	84°17' W		older <i>Liriodendron</i> , Tennessee (Edwards and Harris, 1977)
529 <sup>a</sup>	35°58' N	84°17' W		<i>Quercus-Carya</i> , Tennessee (Edwards and Ross-Todd, 1983)
483	35°58' N	84°17' W		Same, clearcut, residue left (Edwards and Ross-Todd, 1983)
492	35°58' N	84°17' W		Same, residue removed (Edwards and Ross-Todd, 1983)
610	35°58' N	84°17' W		<i>Quercus prinus</i> , Tennessee (Edwards et al., 1989)
857	35°03' N	83°25' W		<i>Quercus</i> -mixed, North Carolina (Wade, in Edwards et al., 1989)
1414	34°45' N	135°55' E		<i>Quercus</i> -mixed, Japan (Kirita, 1971)
1098	34°45' N	135°55' E		<i>Quercus</i> -mixed, Japan (Nakane, 1975)
494	34°05' N	136°05' E		<i>Fagus-Abies</i> , Japan (Nakane, 1980)
1045	32°	N	130°30' E	<i>Quercus</i> -mixed, Japan (Kirita, 1971; Yoneda and Kirita, 1978)
<i>Mediterranean woods, heathland</i>				
399	56°15' N	10°35' E		<i>Calluna</i> heath, Denmark (Brown and Macfadyen, 1969)
1010	50°40' N	1°55' W		<i>Calluna</i> heath, England (Chapman, 1979)
580	43°30' N			<i>Quercus ilex</i> forest, Madeleine, France (Billès et al., 1971)
480	43°30' N			150-yr-old <i>Quercus ilex</i> forest, Rouquet (Billès et al., 1971)

## Appendix (cont'd)

Soil R	Location	Vegetation, locality, references
110	43°30' N	30-yr-old <i>Quercus ilex</i> coppice, France (Billès et al., 1975)
378	38° N 24° E	Mediterranean ecosystem (Fouseki and Margaris, 1981)
1230 <sup>a</sup>	37°50' S 144°00' E	<i>Eucalyptus regnans</i> woodland, Victoria, Australia (Ellis, 1969)
780 <sup>a</sup>	37°50' S 144°00' E	<i>E. obliqua</i> woodland, Victoria, Australia (Ellis, 1969)
920 <sup>a</sup>	37°50' S 144°00' E	<i>E. sieberiana</i> woodland, Victoria, Australia (Ellis, 1969)
820 <sup>a</sup>	37°50' S 144°00' E	<i>E. radiata</i> woodland, Victoria, Australia (Ellis, 1969)
1060	34°30' S 116°10' E	2-yr-old <i>E. diversicolor</i> , Western Australia (O'Connell, 1987)
830	34°30' S 116°10' E	40-yr-old <i>E. diversicolor</i> forest, unburned (O'Connell, 1987)
670	34°30' S 116°10' E	40-yr-old <i>E. diversicolor</i> forest, burned (O'Connell, 1987)
<i>Crops, Settlement, Fields, and Fringeland</i>		
224	60°10' N 17°38' E	Unfertilized barley, Sweden (Paustian et al., 1990)
229	60°10' N 17°38' E	Fertilized barley, Sweden (Paustian et al., 1990)
348	60°10' N 17°38' E	Fertilized <i>Festuca</i> , Sweden (Paustian et al., 1990)
400	60°10' N 17°38' E	Unfertilized <i>Medicago</i> , Sweden (Paustian et al., 1990)
595	56°01' N 92°50' E	Wheat on ordinary chernozem, 1964 (Vugakov and Popova, 1968)
784	56°01' N 92°50' E	Wheat on leached chernozem, 1964 (Vugakov and Popova, 1968)
584	56°01' N 92°50' E	Wheat on podzolized chernozem, 1964 (Vugakov and Popova, 1968)
412	56°01' N 92°50' E	Wheat on leached chernozem, 1966 (Vugakov and Popova, 1968)
362	56°01' N 92°50' E	Wheat on dark-gray soil, 1966 (Vugakov and Popova, 1968)
230 <sup>a</sup>	53°10' N 8°45' E	Mean of 2 heavily disturbed sites, Germany (Mathes and Schriefer, 1985)
80	52°40' N 25°20' E	Vegetation-free peat, USSR (Belkovskiy and Reshetnik, 1981)
170	52°40' N 25°20' E	Perennial grasses on peat, USSR (Belkovskiy and Reshetnik, 1981)
180	52°40' N 25°20' E	Winter rye on peat, USSR (Belkovskiy and Reshetnik, 1981)
130	52°40' N 25°20' E	Potatoes on peat, USSR (Belkovskiy and Reshetnik, 1981)
393	51°50' N 0°20' W	Vegetation-free soil, England (Monteith et al., 1964)
690 <sup>a</sup>	49°20' N 8°40' E	Grass-covered soil, Germany (Dörr and Münnich, 1987)
1040 <sup>d</sup>	45°25' N 75°40' W	Fallow vegetation, clay loam soil, Ontario (Kowalenko et al., 1978)
860 <sup>d</sup>	45°25' N 75°40' W	Same, fertilized (Kowalenko et al., 1978)
560 <sup>d</sup>	45°25' N 75°40' W	Fallow vegetation, sand soil, Ontario (Kowalenko et al., 1978)
445 <sup>d</sup>	45°25' N 75°40' W	Same, fertilized (Kowalenko et al., 1978)
41	43°30' N	<i>Brachypodium</i> pasture, France (Billès et al., 1975)
640 <sup>h</sup>	38°50' N 92°20' W	Wheat, Missouri (Buyanovsky et al., 1986, 1987)
1410	34°50' N 135°25' E	<i>Solidago</i> field, Japan (Yoneda and Okata, 1987)
430	25°18' N 80°01' E	Crop rotation, India (Singh and Shekhar, 1986)
1495	15°55' N 101°45' E	Shifting cultivation plot, Thailand (Tulaphitak et al., 1983)
1410	15°55' N 101°45' E	Upland cultivation plot, Thailand (Tulaphitak et al., 1983)
<i>Desert scrub</i>		
187	41°52' N 113°05' W	<i>Atriplex</i> , Utah (Caldwell et al., 1977)
184	41°52' N 113°05' W	<i>Ceratoides</i> , Utah (Caldwell et al., 1977)
300	32°30' N 106°30' W	Chihuahuan desert, New Mexico (Parker et al., 1983)

## Appendix (cont'd)

Soil R	Location	Vegetation, locality, references
<i>Tropical Savanna and Grassland</i>		
470	29°58' N 76°51' E	Mixed grassland, India (Gupta and Singh, 1981)
690	23°11' N 75°43' E	<i>Themeda</i> grassland, India (Upadhyaya et al., 1981)
640	23°11' N 75°43' E	<i>Iseilema</i> grassland, India (Upadhyaya and Singh, 1981)
900	23°11' N 75°43' E	<i>Sehima</i> grassland, India (Upadhyaya et al., 1981)
615	23°11' N 75°43' E	<i>Dichanthium</i> grassland, India (Upadhyaya et al., 1981)
568	20°30' N 84° E	Mixed grassland, India (Behera and Pati, 1986)
380	19°38' S 146°50' E	Semi-arid woodland, Australia (Holt et al., 1990)
600 <sup>j</sup>	14°36' S 132°12' E	<i>Eucalyptus</i> woodland, Australia (Bridge et al., 1983)
800	6°13' N 5°02' W	Lamto Savanna, Ivory Coast (Lamotte, 1975)
<i>Tropical and Subtropical Dry Forest</i>		
666	33° N 73° E	Mixed deciduous forest, India (Rout and Gupta, 1989)
345	33° N 73° E	Scrub forest, India (Rout and Gupta, 1989)
680 <sup>a</sup>	29°58' N 76°51' E	<i>Dalbergia</i> monsoonal forest, India (Rajvanshi and Gupta, 1986)
1000 <sup>b</sup>	25°42' N 83°22' E	<i>Shorea robusta</i> forest, India (Singh and Shukla, 1977)
<i>Tropical and Subtropical Moist Forest</i>		
890		Subtropical forest, New South Wales, Australia (Richards, 1981)
1250	18°20' N 65°49' W	El Verde (E. Cuevas, personal communication)
1240	15°55' N 101°45' E	Semi-deciduous forest, Thailand (Tulaphitak et al., 1983)
1450	9°09' N 79°51' W	Seasonally deciduous forest, Panama (Kursar, 1989)
1424	2°59' N 102°18' E	Dipterocarp forest, Malaysia (Ogawa, 1978)
1260	2°50' S 59°57' W	Terra firme forest, Brazil (Keller et al., 1986; Wofsy et al., 1988)
1520	0°48' N 24°24' E	<i>Gilbertiodendron</i> forest, Zaire (Maldague and Hilger, 1963)
1170	0°48' N 24°24' E	<i>Brachystegia</i> forest, Zaire (Maldague and Hilger, 1963)
1140	0°48' N 24°24' E	<i>Scorodophloeus</i> forest, Zaire (Maldague and Hilger, 1963)
1240	0°48' N 24°24' E	Island forest, Zaire (Maldague and Hilger, 1963)
<i>Northern Bogs and Mires</i>		
33	68°22' N 19°03' E	Ombrotrophic mire, Sweden (Svennson, 1980)
127	64°52' N 148° W	<i>Andromeda</i> bog, Alaska (Luken and Billings, 1985)
76	64°52' N 148° W	<i>Carex</i> lawn, Alaska (Luken and Billings, 1985)
80	55°43' N 66°42' W	Poor fen, Quebec (Site 1, Moore, 1986)
95	55°43' N 66°42' W	Transitional fen (Site 2, Moore, 1986)
160	55°43' N 66°42' W	Transitional fen (Site 3, Moore, 1986)
160	55°43' N 66°42' W	Rich fen (Site 4, Moore, 1986)
180	55°43' N 66°42' W	Very rich fen (Site 5, Moore, 1986)
79	54°48' N	String sites in fen, Quebec (Moore, 1989)
80	54°48' N	Flark sites in same fen (Moore, 1989)
7	54°48' N	Pool sites in same fen (Moore, 1989)
46	54°46' N 2°21' W	<i>Sphagnum</i> -dominated areas in blanket bog, England (Clymo and Reddaway, 1971)

## Appendix (cont'd)

Soil R	Location	Vegetation, locality, references
<i>Marshes</i>		
640	41°35'N 70°35'W	Short <i>Spartina alterniflora</i> , Massachusetts (Howes et al., 1985)
360	35°20'N 79°11'W	Short <i>Spartina alterniflora</i> , South Carolina (Morris, 1988)
264	35°20'N 79°11'W	Tall <i>Spartina alterniflora</i> , South Carolina (Morris, 1988)
616	29°45'N 90°35'W	Freshwater marsh, Louisiana (Smith et al., 1983)
180	29°35'N 90°20'W	Brackish marsh, Louisiana (Smith et al., 1983)
418	29°15'N 90°05'W	Saltwater marsh, Louisiana (Smith et al., 1983)

<sup>a</sup> Estimated from figure in text.

<sup>b</sup> Extrapolated to an annual rate from 262-day total.

<sup>c</sup> Estimated from figure and table in text, presuming a 183-day growing season.

<sup>d</sup> Total for a six-month growing season.

<sup>e</sup> Total for a seven-month growing season.

<sup>f</sup> Assuming a 90-day growing season.

<sup>g</sup> Total for the six-month wet season only.

<sup>h</sup> Assuming a 75-day growing season.

<sup>i</sup> Soil respiration was measured monthly for two years with the soda lime technique described by Raich et al. (1990).

<sup>j</sup> Total for wet season only.

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