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Belowground Carbon Allocation in Forest Ecosystems: Global Trends

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BELOWGROUND CARBON ALLOCATION IN FOREST ECOSYSTEMS: GLOBAL TRENDS[1]

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Abstract. Carbon allocation to roots in forest ecosystems is estimated from published data on soil respiration and litterfall. On a global scale, rates of in situ soil respiration and aboveground litter production are highly and positively correlated, suggesting that above- and belowground production are controlled by the same factors. This relationship also allows us to predict rates of total soil respiration and total carbon allocation to roots in forest ecosystems from litterfall measurements. Over a gradient of litterfall carbon ranging from 70 to 500 $g \cdot m^{-2} \cdot yr^{-1}$, total belowground carbon allocation increases from 260 to 1100 $g \cdot m^{-2} \cdot yr^{-1}$. The ratio of belowground carbon allocation to litterfall decreases from 3.8 to 2.5 as litterfall carbon increases from 70 to 200 $g \cdot m^{-2} \cdot yr^{-1}$, but changes little (2.5 to 2.2) as litterfall carbon increases from 200 to 500 $g \cdot m^{-2} \cdot yr^{-1}$. Use of this relationship permits the construction of simple carbon budgets that can be used to place upper limits on estimates of fine root production in forest ecosystems. Determining live-root respiration rates in forest ecosystems will further constrain the range of possible root production rates.

Key words: allocation; carbon; forests; litterfall; root production; soil respiration.

INTRODUCTION

How much of the carbon that is assimilated annually by forest ecosystems is allocated belowground? There is general agreement that much carbon is utilized in the production and maintenance of fine roots, the non-woody organs that absorb water and take up nutrients. However, relatively few measurements of either total belowground carbon allocation or fine root production have been made, and there is no general consensus about the relationship between above- and belowground production in forests.

Some investigators have suggested that within regions or specific forest types the ratio between belowground and aboveground net primary production may decrease with increasing soil moisture and nutrient availability (Nihlgård and Lindgren 1977, Ågren et al. 1980, Axelson 1981, Persson 1981, 1983, Linder 1987). Some have even suggested that low rates of aboveground production on relatively poor sites are largely offset by greater belowground production, resulting in similar rates of total net primary production on rich and poor sites (Keyes and Grier 1981). A third proposition is that fine root production increases in direct proportion to increases in aboveground production (Nadelhoffer et al. 1985).

The general lack of insight into the relationship between above- and belowground production in forest ecosystems results from the relatively few studies of belowground production. Also, measurements of belowground production are of uncertain accuracy. It has often been assumed that root:shoot production is sim-

ilar to root:shoot biomass (Bray 1963, Newbould 1968, Whittaker and Marks 1975). However, no general relationship between above- and belowground production has been definitively established. Additional techniques to test existing methods, to constrain estimates, and to identify relationships between above- and belowground production are needed. The use of soil carbon budgets is one such technique. In this paper we construct soil carbon budgets from published data, utilize these budgets to estimate belowground carbon allocation in forest ecosystems, and discuss the relationship between above- and belowground carbon allocation in forests of the world.

METHODS

The use of soil carbon budgets to estimate belowground carbon allocation in forests is based upon the concept of conservation of mass: all carbon that enters the soil must either leave the soil or increase soil carbon stocks. We couple this fact with the assumption that annual changes in total soil carbon storage in closed-canopy forests are small in comparison with annual fluxes of carbon into and out of the soil. In other words, we assume that forest–soil carbon stocks are in approximate steady state over the short term (1 yr). Under this assumption, the amount of carbon entering the soil yearly is approximately equal to the annual carbon loss. Our analysis considers soils to include soil organic matter and fine litter on the soil surface, excluding coarse woody debris on and above the soil.

The soil carbon budget

Soil organic matter is derived from two principal sources: detritus inputs from aboveground and fine-root inputs belowground. These inputs are balanced

by the decomposition of soil organic matter to CO_2; soil-CO_2 evolution is the major pathway of carbon loss from most forest soils. Although they remain poorly quantified, other fluxes of carbon into and out of the soil (precipitation, dry deposition, leaching, runoff, erosion) are minor in comparison with the major fluxes, and so have relatively little influence on the total soil carbon budget (Edwards and Harris 1977, Schlesinger 1977, 1984, Raich 1983). Therefore, in soils that are near steady state with respect to total organic carbon storage, annual inputs of detritus from above- and belowground sources are approximately equal to the annual respiration of decomposers in the soil, or:

$$R_h \approx P_a + P_b \qquad (1)$$

where R_h = heterotrophic respiration (organic matter decomposition), P_a = aboveground detritus production, and P_b = belowground detritus production, all expressed in units of carbon. In theory, then, it is possible to determine P_b by measuring both P_a and R_h. In fact, however, it is difficult to measure R_h in intact forest soils because CO_2 produced by soil organisms is intimately mixed with CO_2 produced by living roots. The sum of heterotrophic and autotrophic (live-root) respiration processes in the soil is referred to as soil respiration, i.e.:

$$R_s = R_h + R_r \qquad (2)$$

where R_s = soil respiration and R_r = root respiration. Combining Eqs. 1 and 2 gives:

$$R_s - P_a \approx P_b + R_r. \qquad (3)$$

Using this equation, total annual carbon allocation to roots ($P_b + R_r$) can be estimated from measurements of annual rates of soil respiration (R_s) and aboveground detritus production (P_a), both of which have been measured in forests throughout the world.

We utilize Eq. 3 and data available from published studies to estimate how much carbon is allocated to roots in forest ecosystems. We use measurements of litterfall to estimate aboveground detritus production, and therefore disregard, initially, carbon inputs to the soil from coarse woody detritus. The implications of this are further considered in the Discussion. We consider total carbon allocation to roots to be equal to the sum of carbon allocated to root detritus production plus root respiration ($P_b + R_r$). Root detritus production includes all carbon transferred from roots and their associated mycorrhizae to the soil, whether it be from exudation, sloughing of surface tissues, herbivory, or mortality; this is equivalent to what most investigators refer to as fine root production.

Soil respiration and litterfall in forests of the world

Soil respiration and litterfall have been measured in a variety of forests around the world (Appendix). Because both litterfall and soil respiration rates vary seasonally, only sites for which annual estimates of both fluxes were available were included in our analysis. We estimated annual rates of soil respiration in some tropical rain forest sites from short-term measurements because few data from the wet tropics are available. Litterfall rates shown in the Appendix refer to fine litterfall, as is typically measured with litter traps. Litterfall and soil respiration were not always measured in the same forest stands or during the same years, but we have attempted to include only those sites for which relatively accurate estimates of litterfall were available (see footnotes following the Appendix).

The comparison of measured rates of soil respiration is problematic due to the wide variety of techniques used by different investigators (Schlesinger 1977, Singh and Gupta 1977, Yoneda and Kirita 1978). Included in the Appendix are estimates derived from the static absorption of CO_2 with alkali solutions or soda lime in inverted chambers, infrared gas analysis of changes in CO_2 concentration of air passed through inverted chambers, measured changes in CO_2 concentration in the atmosphere inside inverted (static) chambers, and whole-forest gas-exchange techniques. The litterfall measurements, in contrast, were all made using similar collection techniques.

Careful perusal of the techniques used to measure soil respiration in situ indicates that specific techniques result in unreliable or systematically biased estimates of soil respiration rates:

1) Low estimates of soil-CO_2 efflux are consistently obtained with the chemical absorption of CO_2 in static measurement systems when alkali absorbant is placed inside a vial that has an opening that covers <6% of the area covered by the chamber (see Fig. 1 in Walter 1952 or Fig. 1 in Lieth and Ouellette 1962). This technique apparently hinders the absorption of CO_2 by the alkali solution. Investigators using similar techniques with larger surface areas of absorbant directly exposed to the atmosphere inside the chambers consistently observe higher rates of CO_2 efflux (e.g., Kirita 1971, Nakane 1975, Ogawa 1978, Raich 1983, Nakane et al. 1984, Rajvanshi and Gupta 1986).

2) The insertion of chambers too far into the soil (e.g., ≥7 cm) consistently results in low estimates of soil respiration (e.g., Hilger 1963, Cowling and MacLean 1981, Anderson et al. 1983). Inserting chambers into the soil severs and isolates surface roots and prevents horizontal root growth into the chambers. Because fine roots release both CO_2 and decomposable organic matter into the soil, severing and isolating surface fine roots alters rates of CO_2 production in the soil. Wildung et al. (1975) clearly demonstrated that measured rates of soil respiration decreased with increasing depth of chamber placement. Estimates of soil respiration made with the techniques criticized above sometimes result in estimates of soil respiration that are lower than rates of litterfall in the same forests (open circles, Fig. 1),
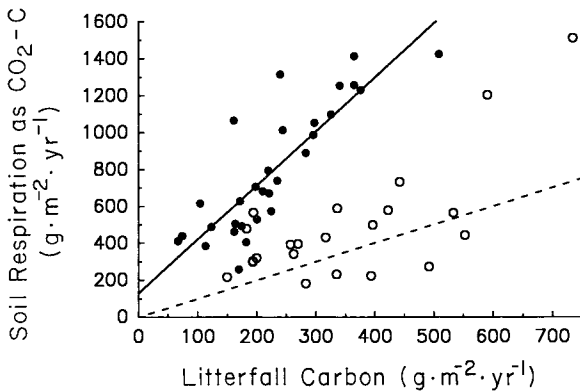
FIG. 1.   The relationship between soil respiration (measured as CO_2 carbon) and litterfall in forest ecosystems of the world. Data are from the Appendix. Soil respiration rates that were obtained with unreliable techniques are shown as open circles (O); all other values are shown as solid circles (●). The upper line (——) shows the linear regression between soil respiration and litterfall. The lower line (– – –) shows where soil respiration equals litterfall.

even though no significant annual accumulation of detritus is reported. We believe these techniques yield inaccurate or biased estimates of total soil respiration. We have therefore excluded from our analysis all data obtained with measurement systems where alkali absorbant is placed inside a vial which has an opening that is <6% of the surface area of soil within closed chambers, and where chambers were placed ≥7 cm deep in the soil. These are shown as open circles in Fig. 1, and are given superscripts 6 and 9, respectively, in the Appendix.

RESULTS

Soil respiration is directly related to aboveground litterfall in the reviewed reports by the least-squares regression:

$$R_s = (2.92 \, P_a) + 130$$
$$(r^2 = 0.71, \, P < .00001, \, n = 30)$$

where R_s is soil respiration and P_a is aboveground litterfall, both expressed as grams of carbon per square metre per year (assuming that litterfall is 48% carbon). The value of the intercept of this equation is not significantly different from zero ($.10 < P < .15$). This relationship is derived using data from forests in boreal, temperate, and tropical regions; from needle-leaved and broad-leaved forests; from forests on five continents; and from forests ranging from 27 to 170 yr of age (Appendix). On a global scale, soil respiration increases systematically with aboveground litterfall in forest ecosystems (Fig. 1).

This relationship allows us to construct simple soil carbon budgets for these forests. Carbon dioxide is produced in the soil by the decomposition of litter- and root-derived organic matter ($P_a + P_b$), and through

root respiration (R_r) (Eqs. 1 and 2). Along a gradient of aboveground litter carbon production ranging from 70–500 g·m^{-2}·yr^{-1}, fluxes of CO_2 carbon from soil surfaces increase from ≈330 to 1600 g·m^{-2}·yr^{-1}. Along this same gradient, the proportion of total soil respiration that is attributable to the decomposition of organic matter derived from litterfall (P_a) increases from 20 to 30% and the proportion derived from roots ($R_r + P_b$) decreases from 80 to 70%.

DISCUSSION

There is, on a global scale, a highly significant, positive correlation between measured rates of soil respiration and aboveground litter production in forest ecosystems (Fig. 1). We use this relationship to estimate root contributions to soil respiration, which are assumed equal to total carbon allocation to roots, in forests (Fig. 2). Some of the variability in the data that is not explained by our linear regression is attributable to differences in methodologies used to measure litterfall and soil respiration, to annual variability in these rates, and, perhaps, to intersite variability in the soil respiration–litterfall relationship. Nevertheless, within the confidence limits of our regression there is a very clear trend for total root allocation to increase with litterfall.

Total carbon allocation to roots, as estimated by the difference between soil respiration and litterfall, increases from ≈260 to 1100 g·m^{-2}·yr^{-1} as production of aboveground litter carbon increases from 70 to 500 g·m^{-2}·yr^{-1} (Fig. 2). In fact, our estimates of root contributions to soil respiration are probably high because we ignored aboveground detritus inputs to the soil from herbs and from coarse woody debris. We also ignored
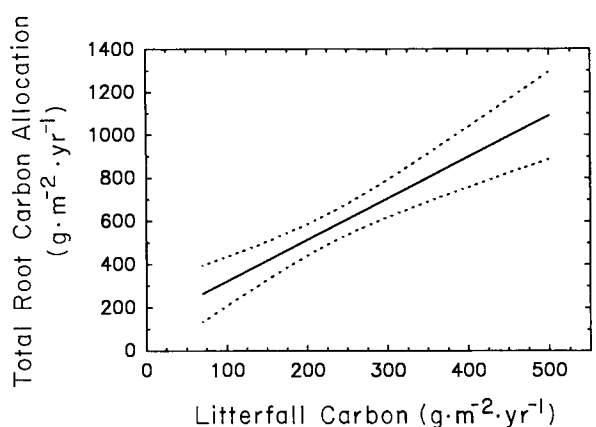

FIG. 2.   Predicted rates of total belowground carbon allocation (——) in forest ecosystems, as related to aboveground litterfall. Belowground carbon allocation is calculated as the difference between soil respiration and litterfall for individual forests, based on Eq. 3. The least-squares regression (solid line) is: root allocation = 1.92 (Litterfall) + 130 ($r^2 = 0.52$, $P < .001$, $n = 30$). The dotted lines (·····) show the 95% confidence limits of the relationship.

TABLE 1.   Production of litterfall, herb detritus, and coarse woody detritus (CWD) in some forest sites used in our analysis of soil carbon budgets. All litterfall values are from the Appendix. The references below give citations for herb and wood production data.

Location	Forest type	Litter-fall	Herbs	CWD	Reference
		Detritus (OM) production ($g \cdot m^{-2} \cdot yr^{-1}$)			
Costa Rica	Lowland wet	783	–*	375†	D. Lieberman, personal communication
Japan	Quercus-mixed	678	–	150‡	Nakane 1975
Japan	Pinus (age 40)	616	–	106‡	Nakane et al. 1984
Japan	Pinus (age 80)	709	–	130‡	Nakane et al. 1984
Malaysia	Dipterocarp	1060	–	930	Yoneda et al. 1977
Malaysia	Dipterocarp	1060	–	650†	Kato et al. 1978
Minnesota, USA	Quercus-mixed	457	10	–	Reiners and Reiners 1970
Minnesota, USA	Thuja-Betula	488	11	–	Reiners and Reiners 1970
Minnesota, USA	Fraxinus-mixed	412	30	–	Reiners and Reiners 1970
Missouri, USA	Quercus-Carya	507	16	166†	Rochow 1974
New Hampshire, USA	Mixed deciduous	460	2	102	Gosz et al. 1972
New York, USA	Quercus-Pinus	337	2	–	Whittaker and Woodwell 1969
Tennessee, USA	Liriodendron	335	–	104§	Harris et al. 1975
Tennessee, USA	Liriodendron	335	19§	–	Reichle et al. 1973
Tennessee, USA	Quercus-Carya	417	–	118	Harris et al. (1973), cited by Harmon et al. 1986
Washington, USA	Abies	218	5	–	Grier et al. 1981
Washington, USA	Pseudotsuga	257	63‖	–	Turner and Long 1975

* No data.
† Based on growth increment of trees.
‡ Includes branches and boles between 1 and 10 cm diameter only. Larger diameter branches were not measured.
§ Assuming that herbs are 48% carbon.
‖ Includes understory litterfall not measured with litter baskets.

carbon fluxes in throughfall, stem flow, leaching, runoff, and erosion, but these are probably minor in most closed-canopy forests (e.g., Edwards and Harris 1977, Schlesinger 1977, 1984, Raich 1983).

Herbaceous litterfall averages 5% (range <0.1–25%) of fine litterfall in nine of the temperate forests listed in the Appendix (Table 1). If this value is typical of forests at large, ignoring detritus inputs from herbs has caused us to overestimate total belowground allocation by ≈3%.

Coarse woody detritus production ranges from 20 to 90% of fine litterfall in 10 sites included in our analysis (Table 1), but can exceed fine litterfall inputs in other forests (Harmon et al. 1986, Vogt et al. 1986). However, only part of the carbon in woody litterfall is added to soils; much is released as CO_2 rather than being incorporated into the soil. We emphasize this because fine litterfall measurements and soil respiration measurements have similar biases: litterfall measurements do not include inputs of coarse woody debris, and soil respiration measurements do not include CO_2 released from coarse woody detritus on the soil surface. For example, losses of carbon as CO_2 from the decomposition of coarse woody detritus in Pasoh Forest, Malaysia, were higher than measured rates of woody litterfall and totalled half those from soil respiration (Yoneda et al. 1977).

Coarse woody debris is an important component of aboveground detritus production. Some carbon from woody debris is incorporated into soils and we have

therefore underestimated aboveground detritus inputs to the soil. We assume that the magnitude of the woody detritus-to-soil carbon flux is insufficient to alter the general pattern that we have observed, but we recognize that our estimates of total belowground production are high by an undefined amount. If most carbon in woody detritus is released to the atmosphere without first entering the soil, as we assume, then the error due to ignoring carbon fluxes from woody detritus is small. More information on this subject is needed.

Despite these limitations our analysis indicates that total carbon allocation to roots increases with increasing litterfall (Fig. 2). This finding is consistent with Schlesinger's (1977) observation that forest soil respiration and litterfall increased in direct proportion to one another along a latitudinal gradient. These results suggest that aboveground litter production and belowground carbon allocation are strongly interrelated in forests: either one process controls the other, or both are controlled by the same factors.

Although both litter production and total belowground allocation increase together, there is considerable uncertainty about whether the ratio of aboveground to belowground carbon allocation changes along the litterfall gradient. The null hypothesis that there is no change in the root allocation–litterfall ratio with increasing litterfall cannot be ruled out. According to our best estimate, however, relative carbon allocation to roots decreases from 3.8 to 2.5 as litterfall carbon increases from 70 to 200 $g \cdot m^{-2} \cdot yr^{-1}$, but changes little
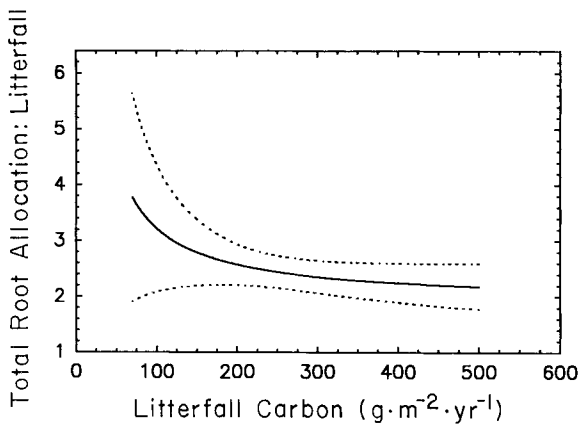
FIG. 3. Predicted ratio between total belowground carbon allocation and aboveground litterfall along a gradient of increasing rates of aboveground litter production in forest ecosystems (———). This figure is derived from Fig. 2. The dotted lines (· · · ·) are direct transformations of the confidence limits around the relationship shown in Fig. 2.

as litterfall carbon increases from 200 to 500 $g \cdot m^{-2} \cdot yr^{-1}$ (solid line, Fig. 3). Uncertainty about the ratio of above- to belowground carbon allocation is greatest at the low end of the litterfall gradient (dotted lines, Fig. 3). We emphasize that the global scale of our data set may mask important intraregional variability.

In conclusion, the use of soil carbon budgets provides much needed insight into patterns of carbon allocation in forests, and may serve as a useful check on independent estimates of fine root production. Although we cannot distinguish the CO_2 produced by living roots from that produced by the decomposition of root detritus, we can estimate the sum of these two processes and thereby place an upper limit on total carbon allocation to roots in forest ecosystems. Root respiration and its contribution to total soil respiration have been estimated in three of the sites used in our analysis. In a 50-yr-old *Liriodendron* forest in Tennessee, and 80-yr-old *Pinus densiflora* forest of Japan, and a Florida *Pinus elliottii* plantation, the proportion of total soil respiration attributed to live-root respiration was 35 (Edwards and Harris 1977), 50 (Nakane et al. 1983), and 62% (Ewel et al. 1987b), respectively. These studies show that live-root respiration can be a major contributor to total soil respiration, accounting for between one-third and two-thirds of the annual carbon release from forest soils. Additional measurements of root respiration rates in forest ecosystems may enable us to constrain further the upper limit to root detritus production.

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APPENDIX

Annual rates of soil respiration and fine litterfall in forest ecosystems.

Location	Latitude	Age[1] (yr)	Forest type	CO_2 efflux ($g \cdot m^{-2} \cdot yr^{-1}$)	Litterfall ($g \cdot m^{-2} \cdot yr^{-1}$)	Reference
			Coniferous forests			
Alaska, USA	64°45'	133	*Picea glauca*	1610[2]		Gordon et al. 1987
Alaska, USA	64°45'	134[3]	*P. glauca*		155[3]	Van Cleve et al. 1983
Alaska, USA	64°45'	75	*P. glauca*	1508[2]		Schlentner and Van Cleve 1985
Alaska, USA	64°45'	75	same site		139	K. Van Cleve, *personal communication*
Washington, USA	47°23'	45	*Pseudotsuga*	1790[4]		Vogt et al. 1980
Washington, USA	47°23'	42	same site		257	Turner and Long 1975
Washington, USA	47°19'	170	*Abies*	2260[4]		Vogt et al. 1980
Washington, USA	47°19'	180	same site		218	Grier et al. 1981
Quebec, Canada	46°00'	64	*Pinus banksiana*	950[2,5]	353[5]	Weber 1985, 1987
Japan	35°	?	*Chamaecyparis*	796[6]	312[7]	Chiba 1977
Japan	35°	?	*P. densiflora*	1440[6]	535[7]	Chiba 1977
Japan	35°	?	*P. densiflora*	1170[6]	415[7]	Chiba 1977
Japan	34°24'	40	*P. densiflora*	3620	616	Nakane et al. 1984
Japan	34°24'	80	*P. densiflora*	4600	709	Nakane et al. 1984
Japan	33°30'	?	*Abies firma*	1580[6]	660[7]	Chiba 1977
Japan	33°30'	?	*Tsuga*	1250[6]	546[7]	Chiba 1977
Florida, USA	30°	29	*P. elliottii*	4820		Ewel et al. 1987*a*
Florida, USA	30°	29	same site		499	Gholz et al. 1985
			Mixed conifer and broad-leaved temperate forests			
Minnesota, USA	45°20'	?	*Thuja-Betula*	2710		Reiners 1968
Minnesota, USA	45°20'	?	same site		488	Reiners and Reiners 1970
New York, USA	40°50'	43	*Quercus-Pinus*	1700[8]		Woodwell and Botkin 1970
New York, USA	40°50'	43	same site		337	Whittaker and Woodwell 1969
Japan	34°	?	*Fagus-Abies*	1810	364	Nakane 1980
			Temperate broad-leaved forests			
Alaska, USA	64°50'	70	*Populus tremuloides*	1414[2]		Schlentner and Van Cleve 1985
Alaska, USA	64°50'	70	*P. tremuloides*		237	K. Van Cleve, *personal communication*
Alaska, USA	64°50'	70	*Betula papyrifera*	1484[2]		Schlentner and Van Cleve 1985
Alaska, USA	64°50'	70	*B. papyrifera*		380	K. Van Cleve, *personal communication*
England	51°20'	~45	*Castanea sativa*	2306		Anderson 1973*a*
England	51°20'	~45	same site		357	Anderson 1973*b*
England	51°20'	~50	*Fagus sylvatica*	2107		Anderson 1973*a*
England	51°20'	~50	*F. sylvatica*		467	Anderson 1973*b*
Belgium	50°04'	80	*Quercus*-mixed	669[4,6]		Froment 1972
Belgium	50°04'	80	same site		590	Duvigneaud and Denaeyer-De Smet 1970
Minnesota, USA	45°20'	?	*Quercus*-mixed	2912		Reiners 1968
Minnesota, USA	45°20'	?	same site		457	Reiners and Reiners 1970
Minnesota, USA	45°20'	?	*Fraxinus*-mixed	2592		Reiners 1968
Minnesota, USA	45°20'	?	same site		412	Reiners and Reiners 1970
New Hampshire	43°56'	55	Mixed deciduous	2460[2]		Goreau 1981
New Hampshire	43°56'	55	same site		460	Gosz et al. 1972
France	43°30'	150	*Quercus ilex*	1757[9]	380	Billès et al. 1971
France	43°30'	M	*Q. ilex*	2156[9]	700	Lossaint 1973
Missouri, USA	39°	50	*Quercus-Carya*	3715	507	Garrett and Cox 1973
Tennessee, USA	35°58'	36	*Liriodendron*	1850[4]	341	Edwards and Ross-Todd 1979
Tennessee, USA	35°58'	>37	*Quercus-Carya*	1940[4]		Edwards and Ross-Todd 1983
Tennessee, USA	35°58'	>37	same site		417	Johnson et al. 1982
Tennessee, USA	35°58'	50	*Liriodendron*	3905	335[7]	Edwards and Harris 1977
Nara, Japan	35°	M	*Quercus*-mixed	5180	760	Kirita 1971
Nara, Japan	35°	M	*Quercus*-mixed	4025[5]	678[5]	Nakane 1975
Japan	33°30'	?	*Carpinus*	1100[6]	402[7]	Chiba 1977
Japan	33°30'	?	*Fagus crenata*	1110[6]	402[7]	Chiba 1977
Japan	33°20'	?	*Castanopsis*	2075[6]	404[7]	Chiba 1977
Japan	33°20'	?	*Machilus*	2070[6]	1110[7]	Chiba 1977
Minimata, Japan	32°	M	*Quercus*-mixed	3860[5]	620	Kirita 1971
			Tropical and subtropical forests			
NSW, Australia	29°	M	Mixed rain	3260	590	Richards 1981
India	29°58'	M	Monsoon	2500[4]	438	Rajvanshi and Gupta 1986

APPENDIX. Continued.

Location	Latitude	Age[1] (yr)	Forest type	CO_2 efflux (g·m⁻²· yr⁻¹)	Litterfall (g·m⁻²· yr⁻¹)	Reference
Costa Rica	10°26′	M	Lowland wet	4500[10]		Raich 1983
Costa Rica	10°26′	M	same forest		783	Gessel et al. 1980
Venezuela	10°	M	Cloud forest	820[6]	820	Medina and Zelwer 1972
Venezuela	8°56′	M	Seasonally dry	1830[6]	825	Medina and Zelwer 1972
Venezuela	8°37′	M	Cloud forest	850[6,10]		Medina and Zelwer 1972
Venezuela	8°37′	M	Cloud forest		697	Fassbender and Grimm 1981
E. Malaysia	4°	M	Alluvial	1630[9]		Anderson et al. 1983
E. Malaysia	4°	M	same site		1150	Proctor et al. 1983
E. Malaysia	4°	M	Dipterocarp	2120[9]		Anderson et al. 1983
E. Malaysia	4°	M	same site		880	Proctor et al. 1983
E. Malaysia	4°	M	Heath	2690[9]		Anderson et al. 1983
E. Malaysia	4°	M	same site		920	Proctor et al. 1983
W. Malaysia	2°58′	M	Dipterocarp	5220	1060	Ogawa 1978
Brazil	2°50′	M	Terra firme	4610[11]		Keller et al. 1986, Wofsy et al. 1988
Brazil	2°50′	M	Terra firme		790	Franken et al. 1979
Brazil	2°50′	M	Terra firme		730	Klinge and Rodrigues 1968
Venezuela	1°54′	M	Caatinga	1450[6]		Medina et al. 1980
Venezuela	1°54′	M	same site		561	Cuevas and Medina 1986
Venezuela	1°54′	M	Terra firme	1000[6]		Medina et al. 1980
Venezuela	1°54′	M	same site		1025	Cuevas and Medina 1986
Zaire	1°	M	*Brachystegia*	4410[9,10]		Hilger 1963, Maldague and Hilger 1963
Zaire	1°	M	*Brachystegia*		1230	Laudelot and Meyer 1954
Zaire	1°	M	*Gilbertiodendron*	5540[9,10]		Hilger 1963, Maldague and Hilger 1963
Zaire	1°	M	*Gilbertiodendron*		1530	Laudelot and Meyer 1954, Hilger 1963

[1] M indicates a mature forest that has not apparently been heavily disturbed by humans. A question mark (?) indicates a forest or plantation of unstated age.

[2] Total for the snow-free season only: does not include soil respiration occurring beneath a snow cover. Length of the study season is: 153 d (Schlentner and Van Cleve 1985, Gordon et al. 1987), 8 mo (Goreau 1981), 7 mo (Weber 1987).

[3] Mean value from several different stands dominated by the same species.

[4] Estimated from figure in text.

[5] Mean value of several study plots in the same forest.

[6] Surface area of alkali absorbant <6% of surface area covered by closed chamber.

[7] Assuming litterfall is 48% carbon.

[8] Includes respiration of vegetation <1 m tall.

[9] Chambers installed ≥7 cm deep in soil.

[10] Annual rate estimated from short-term measurements reported by authors.

[11] Annual value derived from measurements made in similar forests in two locations during July (Wofsy et al. 1988), December, and March (Keller et al. 1986). Santos and Crisi (1981) measured soil respiration with a static chamber technique in a nearby forest and reported CO_2 flux rates similar to those of Keller et al. (1986).