The carbon balance of tropical, temperate and boreal forests

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ABSTRACT

Forest biomes are major reserves for terrestrial carbon, and major components of global primary productivity. The carbon balance of forests is determined by a number of component processes of carbon acquisition and carbon loss, and a small shift in the magnitude of these processes would have a large impact on the global carbon cycle. In this paper, we discuss the climatic influences on the carbon dynamics of boreal, temperate and tropical forests by presenting a new synthesis of micrometeorological, ecophysiological and forestry data, concentrating on three case-study sites. Historical changes in the carbon balance of each biome are also reviewed, and the evidence for a carbon sink in each forest biome and its likely behaviour under future global change are discussed. We conclude that there have been significant advances in determining the carbon balance of forests, but there are still critical uncertainties remaining, particularly in the behaviour of soil carbon stocks.

INTRODUCTION

The increasing concentration of carbon dioxide in the atmosphere since the industrial revolution is among the most significant of human influences on the global environment. The source of this carbon dioxide has been convincingly ascribed to the use of fossil fuels, cement manufacture and deforestation, but considerable mystery remains because only a fraction of the estimated emissions of CO_2 remains in the atmosphere.

Between 1980 & 1989, it is estimated (Schimel 1995) that $5 \cdot 5 \pm 0 \cdot 5$ Gt C year^{-1} were released through fossil fuel combustion and cement production, and $1 \cdot 6 \pm 1 \cdot 0$ Gt C year^{-1} through tropical deforestation, resulting in total anthropogenic emissions of $7 \cdot 1 \pm 1 \cdot 1$ Gt C year^{-1}. Of this total, only $3 \cdot 3 \pm 0 \cdot 2$ Gt C year^{-1} (46%) remained in the atmosphere, and a combination of modelling and measurements of carbon isotopes and atmospheric O_2/N_2 ratios suggest that $2 \cdot 0 \pm 0 \cdot 8$ Gt C year^{-1} were transferred into the oceans. This leaves $1 \cdot 8 \pm 1 \cdot 6$ Gt C year^{-1} that are ascribed to a terrestrial 'missing sink', a term that encompasses land-use change processes such as forest regrowth resulting from abandonment of agricultural land in mid-latitudes, as well as ecophysiological processes such as enhanced forest growth attributable to CO_2 fertilization, nitrogen deposition and response to climatic anomalies. It should be emphasized that the above figures for the global carbon cycle, although frequently quoted, are the mean for the 1980s, and global emissions have already moved significantly above this level. Recent (1996) global emissions resulting from the use of fossil fuels and cement production are estimated to be $6 \cdot 5$ Gt C year^{-1} (World Energy Council, *Nature* **390,** p. 215) and increasing at a rate of about $0 \cdot 1$ Gt year^{-1}.

There is evidently considerable uncertainty about the magnitude of the terrestrial missing sink, and even larger uncertainty about its location. With a few significant exceptions, such as tropical grasslands (Scurlock & Hall 1998), the sink is thought to be largely in the world's forests, which are large reservoirs of both biomass and soil carbon (Table 1), and, on a total biome basis, the largest contributors to global primary productivity.

The net carbon budget of a forest is a fine balance between processes of carbon acquisition (photosynthesis, tree growth, forest ageing, carbon accumulation in soils), and processes of carbon release (respiration of living biomass, tree mortality, microbial decomposition of litter, oxidation of soil carbon, degradation and disturbance). These processes operate on a variety of time scales from diurnal to seasonal, interannual, interdecadal and beyond, and are influenced by a number of climatic and environmental variables, such as temperature, moisture availability and frequency of disturbance. Moreover, there are large differences between different forest types such as the humid tropical forests of Amazonia and the cold boreal forests of Siberia, so the major forest biomes need to be treated separately. In this article we first review the historical natural and anthropogenic processes that have affected the areal extent and total carbon balance of forest biomes. We then examine the evidence for a present-day carbon sink in the major biomes from forestry, micrometeorological and atmospheric studies. Utilizing three sites for which detailed data are available, we also present a comparison of carbon cycling in the tropical, temperate and boreal forest biomes (using a combination of micrometeorological, ecophysiological and forest mensuration measurements), and a discussion of the differing response of each forest type to environmental

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Forest biome	Area (Mha)	C Density: vegetation (t ha^{-1})	C Density: soils (t ha^{-1})	C Pool: vegetation (Gt)	C Pool: soils (Gt)
Boreal	1372	64	343	88	471
Temperate	1038	57	96	59	100
Tropical	1755	121	123	212	216
Total	4165	Mean 86	Mean 189	359	787

Table 1. The estimated current area extent and carbon stocks of the major forest biomes (from Dixon *et al.* 1994)

variables. Finally, we discuss the future behaviour of this sink under possible climatic change.

THE HISTORICAL AND CURRENT STATE OF FORESTS

The most extensive forest biomes are the boreal, temperate and tropical forests. The boreal forest (or taiga) occupies a circumpolar belt in high northern latitudes, between circumpolar tundra and temperate forests and grasslands (Larsen 1980). It is characterized by a limited number of conifer genera, particularly spruce (*Picea*), pine (*Pinus*), larch (*Larix*) and fir (*Abies*), and a few deciduous genera such as birch (*Betula*) and poplar (*Populus*). Temperate forests historically occupied many of the adjacent zones at lower latitudes (between 25° and 50° in both hemispheres), and range from deciduous forests in areas with moist, warm summers and frosty winters (Röhrig & Ulrich 1991), to broadleaf evergreen forests in moist regions with mild, nearly frost-free winters (Ovington 1983) and sclerophyllous forests in drier regions. Until this century, this was the forest biome which had been most affected by human activity. Principal genera include pines (*Pinus*), oaks (*Quercus*), beeches (*Fagus*), maples (*Acer*) and eucalypts (*Eucalyptus*). Tropical forests occupy a broad band across the Earth's warm, moist equatorial regions (Lieth & Werger 1989). They are dominated by evergreen or semi-deciduous broadleaf species, and range between montane forests, flooded forests and mangroves, with the most common type being dry ground (*terra firme*) lowland rain forest. These are characterized by tall stature (usually exceeding 30 m), a tightly closed canopy, and very high diversity (200–300 tree species per hectare).

The total carbon pool in forest ecosystems was recently estimated to be about 1150 Gt (Dixon *et al.* 1994), of which 49% is in the boreal forests, 14% in temperate forests and 37% in tropical forests. A further 1000 Gt are estimated to reside in non-forest ecosystems, such as savannas, grasslands, tundra, peatlands and wetlands (Adams *et al.* 1990). According to the figures of Dixon *et al.* 69% of the carbon is stored as soil organic matter, and 31% as living biomass. However, there is a marked contrast between high latitude and tropical forests: in the boreal zone, 84% of the carbon is in soil organic matter, and only 16% in the active living biomass, whereas in the tropics the carbon is partitioned more or less equally between vegetation and soil. The primary cause for this difference is temperature, which at high latitudes limits the growing season, and restricts decomposition and nutrient recycling, but at low latitudes encourages rapid decomposition of soil organic matter and rapid recycling of nutrients into vegetation growth. This contrast between these biomes may result in very different responses to global climate change.

Carbon sequestration since the last glacial maximum

The climate in all regions of the earth was very different at the last glacial maximum (LGM; 18 000 years before present), and all forest biomes have undergone major changes in distribution in recent prehistory. Low temperatures were associated with the presence of permanent ice sheets over much of northern North America and Eurasia, and air bubbles in ice cores reveal atmospheric CO_2 concentrations of approximately 200 μmol mol^{-1} (Barnola *et al.* 1987). The land area lost to permanent ice sheets was largely balanced by the exposure of new land on continental shelves as a result of lower sea levels. The climate was also more arid than today because of lower evaporation rates and atmospheric water vapour concentrations, and the lower CO_2 concentrations than at present may have reduced plant water-use efficiency and provided a competitive advantage for C_4-dominated grasslands over C_3-dominated forests (Cerling *et al.* 1997). As a result, drier, C_4-dominated vegetation types such as savannas, grasslands, and deserts were more extensive, and forest biomes smaller in area than today. Paleogeographical evidence (Adams *et al.* 1990; Crowley 1995) suggests that boreal and temperate forests were squeezed between the advancing ice sheets and steppe-tundra from the north, and the expanding semi-desert and dry steppe to the south. In the tropics the palynological evidence has generally implied a significant retreat of tropical rain forest into small pockets at the expense of expanding savanna, although some recent evidence (Colinvaux *et al.* 1996) has cast doubt on the extent of this retreat. In Indonesia this effect was compensated for by the exposure of large areas of continental shelf.

The change in carbon storage since the LGM is a matter of controversy. Using paleogeographical surveys and carbon density estimates for each biome, Adams *et al.* (1990) calculated that the total carbon in the terrestrial biosphere has increased from 970 Gt at the LGM to 2040 Gt at the present time, an increase of 1350 Gt. Most of this increase has come from the expansion of forests, particularly of boreal and temperate forests into areas of former ice-sheets, tundra and semi-desert, although the stocks of carbon in the extensive

present-day wetlands and peatlands are also a significant component (280 Gt). More recent estimates argue that the constriction of forest area at the LGM was not so severe, and suggest a smaller increase in terrestrial carbon storage of 500 ± 200 Gt (Prentice *et al*. 1994), 610 ± 110 Gt (Friedlingstein *et al*. 1995) or 900 ± 150 Gt (Crowley 1995).

An alternative insight into carbon storage changes since the LGM comes from the observation that glacial oceanic sediments were isotopically lighter than today. Broecker & Peng (1993) estimate a shift in $\delta^{13}C$ of 0·35‰; if this shift is due to a transfer of carbon from the ocean ($\delta^{13}C \sim 0\text{‰}$) to the terrestrial biosphere ($\delta^{13}C \sim -25\text{‰}$) it implies an increase of terrestrial carbon storage of 500 ± 230 Gt (Bird, Lloyd & Farquhar 1994). This value is consistent with the lower estimates of carbon uptake, but there are still a number of uncertainties in both methodologies, including possible sinks for marine carbon on continental shelves, and possible changes in the density of carbon storage in each terrestrial biome (Crowley 1995).

Whatever the exact figures, it is likely that all forest biomes have sequestered significant amounts of carbon since the LGM, and have acted as an indirect negative feed-back on the rise in CO_2 concentration since deglaciation. If this sequestered carbon were resident in the atmosphere, atmospheric CO_2 concentrations would be 130–640 μmol mol^{-1} higher than at present (1 Gt C ~ 0·47 μmol mol^{-1} CO_2), although in practice the oceans would have buffered much of this fluctuation in the long term. Much of this sequestration probably occurred rapidly at the time of deglaciation (Crowley 1995), but it is possible that the forest biomes have still not equilibrated after this sudden transition. A recent analysis of an Antarctic ice core (Indermühle *et al*. 1999) found that atmospheric CO_2 concentrations declined from a post-glacial maximum of 268 p.p.m., reached a minimum of 260 p.p.m. in the early Holocene (8200 years B.P.), and subsequently increased linearly to 285 p.p.m. at the start of this millenium. Together with $\delta^{13}C$ data, this implies that carbon storage in terrestrial biomes reached a maximum in the warm, moist, early Holocene, and has subsequently declined by 195 Gt C, probably due to a gradual cooling and aridification of Holocene climate.

Historical anthropogenic change

Since the discovery of fire management, all human societies have relied on modifications of forest landscapes with consequent changes in the carbon storage densities of forests (Perlin 1989). In particular, most of the European and Chinese temperate forests have been progressively cleared with the spread of pasture and cropland since 7000 BP (Williams 1990; Chang 1986) and only a small fraction of the original forest area survived into the industrial era. Clearance of tropical forests was much less, with notable localized exceptions in densely populated areas such as the central Mayan lowlands (Whitmore *et al*. 1990). Williams (1990) estimated that, world-wide, between 12 and 28% of the cleared land in 1978 had been cleared before 1750. However, it is probably only since the surge of human population and economic activity following the industrial revolution that the rate of clearance has exerted a significant influence on the global carbon cycle. The major types of land-use change that affect carbon storage are degradation and fragmentation of forests, clearance of forests for pastures and arable crops (both permanent and shifting cultivation), logging with subsequent forest regeneration or replanting, and abandonment of agriculture and replacement by regrowth or planting of secondary forest (i.e. deforestation, afforestation and reforestation). Many of these processes (shifting cultivation, logging, clearing for pasture and abandonment) involve dynamics between forest destruction and subsequent recovery, although the net effect has been a loss of carbon from forests (Table 2). A comprehensive review of these processes is provided by Houghton (1995, 1996a).

Expansion of agriculture since 1850

Over the period 1850–1990, Houghton (1996a) calculated the global area of land under cultivation to have increased from 289 Mha to 2517 Mha (1 ha = 10^4 m^2 = 10^{-2} km^2). However, the larger part of this has come from former temperate grasslands (1633 Mha), with forest clearance contributing only 27% (603 Mha). Most forest clearance in this recent period has been in the tropics (508 Mha; 84%), and temperate forests (91 Mha; 15%) with boreal forest clearance having a minor role (4 Mha; 0·6%). Rates of net temperate forest clearance were fairly constant at about 1 Mha year^{-1} between 1850 and 1970, and have subsequently declined to about zero. In the tropics, clearance rates hovered between 1 and 3 Mha year^{-1} between 1850 and 1930, but have since accelerated rapidly to about 12 Mha year^{-1} in 1990, so that tropical forest clearance constitutes almost all net forest clearance in the current decade.

Logging since 1850

In contrast to forest clearance, most logging over the past century has been in the temperate and boreal zones. Rates of logging of boreal forests have steadily increased from about

Table 2. The change in area of forest in the boreal, temperate and tropical regions since 1850 (from Houghton 1995)

Biome	Area 1850 (Mha)	Area 1980 (Mha)	Area change (%)	Net C release (Gt C)
Boreal	1172	1167	0·5	4
Temperate	1583	1492	6	27
Tropical	2675	2167	19	52
Total Forest	5430	4827	11	83

1 Mha year^{-1} in 1850 to 3·5 Mha year^{-1} in 1980, and in temperate forests from 3 Mha year^{-1} in 1850 to 6 Mha year^{-1} in 1980 (Houghton 1996a). In contrast, logging of tropical forests was below 0·5 Mha year^{-1} in 1850, was still less than 2 Mha year^{-1} in 1950, but has since accelerated to 8 Mha year^{-1} in 1980, overtaking temperate forest logging only in the mid-1970s. Overall, 1069 Mha of forest were logged between 1850 and 1990, an area that was 77% larger than the area of forest converted to agriculture. Once logged, however, forests are frequently left to recover and sequester carbon; hence the overall impact of logging on CO_2 emissions is less than that of land clearance.

Forest degradation and fragmentation

Fragmentation of remaining areas of forest is a common side-effect of logging and clearance (Skole & Tucker 1993). In areas of forest that are close to cleared areas, there is frequently low level use of forest wood, and even in protected areas there appears to be a loss of biomass subsequent to fragmentation, perhaps driven by changes in microclimate (Laurance *et al.* 1997, 1998). These processes are hard to assess and quantify, and so are rarely included in estimates of carbon release by forest clearance.

The amount of carbon released through forest conversion can be estimated by use of a land-use model which combines historical data of clearance and abandonment with subsequent response curves of carbon stocks in live vegetation, soils, slash and wood products. Using such an approach, Houghton (1996a) estimated that, between 1850 and 1980, a net 83 Gt C were released by forest clearance and logging, and a further 14 Gt C by clearance of desert scrub and temperate grasslands. The annual net release increased from 0·3 Gt C year^{-1} in 1850 to 1·6 Gt C year^{-1} in 1980–90.

According to Houghton's estimates, the expansion of croplands has been responsible for the largest net carbon release (63 Gt C), followed by logging and regrowth of forests (23 Gt C) and conversion of forests to pasture (10 Gt C). These are net values, and thus take into account regrowth after logging and abandonment of agriculture.

Current anthropogenic change

Over the period 1980–90, Hall & Uhlig (1991) estimated the net effect of changes in land use to be a release of 1·1 ± 0·5 Gt C year^{-1}, whereas Houghton (1996a) calculated a net release of 1·6 ± 0·5 Gt C year^{-1}. The difference between these two estimates is primarily the result of different assumptions about the mean biomass of cleared tropical forest. The current net release is almost entirely the result of land-use changes in the tropics, with changes in temperate and boreal forests having almost no net effect. Most of the net release results from clearance of tropical forests for croplands (55%) or cattle pasture (20%), with the expansion of logging and shifting cultivation each contributing about 12%. Houghton's estimates for individual regions are 0·6 ± 0·3, 0·7 ± 0·3 and 0·3 ± 0·2 Gt C year^{-1} for Latin America, tropical Asia and tropical Africa, respectively. None of these calculations include the effects of degradation and fragmentation of superficially intact primary forest, or take into account the impact of illegal and unmonitored logging.

THE CARBON CYCLE OF INTACT FORESTS

As summarized above, forest clearance and degradation continue to be a major source of atmospheric CO_2. Less clear, however, is the extent to which intact or low disturbance forests are currently sinks for carbon dioxide. In recent years considerable progress has been made in understanding the processes which determine forest carbon balance, through a combination of physiological, micrometeorological and mensurational studies. In this section we discuss the carbon dynamics of various intact forest biomes, and the interaction between climate and the carbon cycle. All forest biomes contain a significant amount of spatial heterogeneity, but at the same time have fundamental properties (related to climate and plant phenotype) that are characteristic of that biome. Rather than attempt to describe each biome in all its complexity, we shall here illustrate and contrast the properties of different biomes by concentrating on three intensively studied sites: a Canadian boreal forest (Jarvis *et al.* 1997;

Table 3. Location and properties of the three forest sites

	Boreal	Temperate	Tropical
Coordinates	53°59' N, 105°7' W	35°57' N, 84°17' W	2°35' S, 50°06' W
Nearest town	Prince Albert, Canada	Oak Ridge, USA	Manaus, Brazil
Forest type	Evergreen coniferous	Winter deciduous broadleaved	Evergreen broadleaf terra firme
Main species	*Picea mariana* Black spruce	*Quercus alba, Quercus pinus, Carya ovata* Oak–hickory mix	> 200 species/hectare
Canopy closure	Inter crown spaces	Closed	Closed
Max. leaf area index	3·3	4·9	5–6
Average canopy height (m)	9	26	30
Age (years)	115	55	Old growth
Basal area (m^2 ha^{-1})	31·5	20·1	29
Above ground dry biomass (Mg ha^{-1})	50–60	155–170	330–370

Rayment 1998; Massheder 1998; Rayment & Jarvis 1999a), a North American deciduous temperate forest (Baldocchi & Harley 1995; Harley & Baldocchi 1995; Greco & Baldocchi 1996; Baldocchi 1997) and an Amazonian tropical rain forest (Higuchi *et al*. 1997; Malhi *et al*. 1998; Grace *et al*. 1999; Malhi *et al*. unpublished data). Some details of these sites are given in Table 3. These three forests have strongly contrasting climatological and biophysical properties (described in the next section) and represent the three major categories of forest types. Measurements of net ecosystem exchange (NEE) using eddy covariance techniques have been made at the tropical and temperate sites since 1995 and were made at the boreal forest site in 1994 and throughout 1996. During these periods, additional intensive measurements have been made of the main component processes, particularly canopy photosynthesis, soil CO_2 efflux, and tree and litter dynamics.

Characteristics of each site

Climate at these three sites differs markedly, particularly with respect to the degree of seasonality and length of growing season. The main features of the prevailing climates are given in Table 4. Extreme seasonality occurs at the boreal forest site with wide seasonal and daily ranges in temperature, radiation input and day length. These variations are much less evident at the temperate forest site and minimal at the tropical forest site.

The boreal forest site exhibits extreme seasonality in day length and air temperature. Winter conditions are severe, and soils remain frozen until late spring. The frost-free season lasts between 50 and 100 d, the growing season about 100 d and the photosynthetic season about 170 d. Annual precipitation is low, but in spite of this the site is not in general short of water, because of low evaporation rates and impeded drainage (Jarvis *et al*. 1997). The site is situated in the southern, mixed forest zone of the Canadian boreal forest, in a flat landscape composed of a patchwork of pure and mixed stands of black and white spruce, jack pine, aspen, fen and post-glacial lakes. The study site was dominated ($\approx 90\%$) by evergreen black spruce (*Picea mariana*), which can take advantage of mild days in spring and autumn when broadleaf species would not be in full leaf. About 10% of the stand is composed of deciduous tamarack (*Larix laricina*), with occasional jack pine (*Pinus banksiana*) and balsam poplar (*Populus balsamifera*). The stand was fairly uniform in age (≈ 115 years), probably because it developed after fire, which

plays an important role in the natural dynamics of the boreal forest landscape (Payette 1992). The forest floor had a hummock-hollow microtopography dominated by peat moss (*Sphagnum* spp.), with some mixed feather mosses in drier areas. The living moss overlay a 2–10 cm thick layer of dead moss, which in turn overlay dense acidic peat. Away from hummocks the soil was generally anaerobic and waterlogged. There was no permafrost at this site. As is the case for many boreal forests (Schulze *et al*. 1999), nutrient availability is restricted by slow decomposition rates in the cold, waterlogged soils. The black spruce-peat moss community (muskeg) is the dominant community of the North American boreal region, and is particularly well-adapted to cold, nutrient-poor, waterlogged soils (Larsen 1980).

At the other extreme, the forest in central Amazonia experiences year-round warm temperatures, and comparatively small ranges of diurnal and seasonal temperature and day length. Annual precipitation is high, but shows significant interannual variability and, despite popular impression, distinct seasonality. The dry season usually lasts from mid-June to late October (Shuttleworth 1988), and is associated with the northward migration of the Inter-Tropical Convergence Zone (McGregor & Nieuwolt 1998). The old clay oxisols predominant in the region have high porosity (between 56 and 64%), but much of the porosity is concentrated in large pores, which drain rapidly, or very fine pores containing water that is inaccessible to plants (Correa 1984). Hence the available water capacity is low, and the forest can experience significant water stress in the dry season (Malhi *et al*. 1998; Williams *et al*. 1998). The soils are heavily leached and nutrient-poor (Sanchez 1989), and there is very rapid and tight nutrient cycling between the living vegetation, litter and soil pools. The dense forest consists of evergreen or semi-deciduous broadleaf species with very high diversity (200–300 species per hectare). Thus, it may be argued that the bulk ecophysiological properties of tropical forest are much more representative of the mean plant phenotype appropriate to given physical conditions, rather than the adaptations of a particular species. Analysis of soil phytoliths and macroscopic charcoal from a similar nearby site showed no evidence of fire or anthropogenic disturbance in the past 500 years (Piperno & Becker 1996).

The climate of the temperate region spans a wide range of intermediate conditions that influence productivity, including both low winter temperatures and low summer water availability. At the site in Tennessee the climate is mild and annual precipitation is high. Rainfall is fairly evenly dis-

Table 4. Climate at the three forest sites

	Boreal	Temperate	Tropical
Average summer temperature (°C)	17	23	27 (dry season)
Average winter temperature (°C)	–20	5	24 (wet season)
Precipitation (mm)	400	1400	2200
'Growing' season (d)	100	180	365
CO_2 influx period	mid-April – early October	mid-April – mid-November	All year
Dry period	–	mid-June – late August	mid-June – late October

tributed through the year, but water stress is a frequent occurrence in July and August (Greco & Baldocchi 1996). The growing season is 150–200 d and summer day length is moderately long. The canopy is typically in full leaf by day 140 (Baldocchi 1997). The stand is dominated by deciduous broadleaf species, particularly oak (*Quercus alba, Quercus prinus*) and hickory (*Carya ovata*), with occasional maple (*Acer rubrum*), tulip poplar (*Liriodendron tulipifera*) and loblolly pine (*Pinus taeda*). The soil is an infertile cherty silt-loam. A feature distinguishing this site from the boreal and tropical sites is that it is essentially an 'old field succession' resulting from abandonment of agricultural land when the area around the Oak Ridge National Laboratory was fenced off in 1941. The stand is still in a phase of active growth on previously non-forested land, and in that sense its dynamics are not strictly comparable with the mature boreal and tropical forest stands. However, it is representative of many temperate forests in North America and Europe, that are regrowing following abandonment of agricultural lands (Moffat 1998).

The total stocks of carbon at each site are given in Table 5. For the tropical site the values are taken from a number of studies in the 1990s that were summarized by Higuchi *et al.* (1997); the temperate site values come from a 1983 inventory described by Edwards *et al.* (1989); and the boreal site values from above-ground and below-ground studies described by Gower *et al.* (1997) and Steele *et al.* (1997), respectively. Where inventory values were given in dry biomass, carbon was assumed to constitute 48% of dry biomass (from Carvalho *et al.* 1998). At the tropical site no soil carbon inventory was undertaken, and we use the mean tropical forest value of 162 t C ha^{-1} estimated by Post *et al.* (1982). The value for foliage biomass at the boreal site includes shrub and moss biomass, estimated at 1·1 t C ha^{-1}. The below-ground woody detritus pool includes both branch and leaf litter, but also tree stumps and fallen trunks.

The total stocks of carbon at the boreal and tropical sites are remarkably similar in amount (Table 5), but the balance amongst the components is very different. Similar to the global pattern (Table 1), there is much more C in the soil at the boreal site than at the tropical forest site, but only a quarter as much in the vegetation above ground. The temperate forest site contains only modest amounts of both below-ground and above-ground carbon, which probably reflects the young age of the stand. In addition, the temperate forest inventory was taken in 1983, when the stand was only 42 years old, 14 years prior to the flux studies described in the next section. Approximately 60% of total carbon is stored on or below ground at the tropical and temperate sites, whereas 90% of carbon is below ground at the boreal site, predominantly in the form of organic detritus.

Stand dynamics

The carbon balance of a forest ecosystem as a whole is the resultant of the dynamics of the component processes that comprise the system. The NEE, or carbon balance, between a forest and the atmosphere can be measured using micrometeorological techniques such as eddy covariance (see section entitled Eddy covariance below). The NEE can be considered in terms of its two principal components, acting in opposite directions: the influx of CO_2 in canopy photosynthesis, and the combined effluxes of CO_2 resulting from autotrophic and heterotrophic respiration. These components can be quantified using two different strategies: a 'bottom-up' strategy of integrating small-scale measurements of photosynthesis, litterfall, etc. (Rayment & Jarvis 1999c), and a 'top-down' approach of decomposing the NEE into bulk photosynthetic and respiratory fluxes (as in Baldocchi 1997; Malhi *et al.* 1998). These bulk fluxes, and their relation to environmental variables, act as a constraint with which to verify the completeness or accuracy of the scaling

	Tropical	Temperate	Boreal
Above ground			
(1) tree foliage	4·6	1·6	6·2
(2) tree branches	58	15·1	6·7
(3) tree stems	117	57·1	36·3
(4) Total above ground	217	79	49·2
Below ground			
(5) leaf and wood detritus	41·4	11·7	6·2
(6) fine roots	38	N/K	2·8
(7) coarse roots	26	19·1	8·0
(8) root detritus	N/K	8·7	1·2
(9) soil organic matter	162	55·7	390·4
(10) Total below ground	230	62	409
Ecosystem total	447	169	458
(Below-ground/Ecosystem total)	60%	56%	89%
Biomass carbon (4) + (6) +(7)	243·6	93·0	60·0
(Biomass/Ecosystem Total)	55%	55%	13%

Table 5. Estimated stocks of C (Mg ha^{-1}) at the three forest sites. See text for data sources

N/K, not known.

|	Tropical	Temperate	Boreal
Component fluxes:			
Above ground vegetation:			
(1) Gross photosynthesis of tree foliage (G_p)	3040[1]	1725	963
(2) Respiration of tree foliage	410[2]	191	216[7]
(3) Respiration of tree wood	390[2]	196	87[8]
(4) Leaf and wood detritus	700[3]	360[4]	51[5]
(5) Net biomass increment	170[3]	150[4]	110[5]
(6) Transport to roots (1) – (2) – (3) – (4) – (5)	1370	828	499
Below ground vegetation:			
(7) Respiration of roots	680[1]	395	143[6]
(8) Net root biomass increment	60[1]	39	30[6]
(9) Root detritus production	630[1]	395	326
(10) Total ground respiration	1650[2]	753	592
(11) Heterotrophic Respiration (10) – (2) – (3)	970	359	449
(12) Autotrophic Respiration (15) – (11)	1480	782	446
Soil:			
(13) Change in SOM (4) + (9) – (11)	+360	+396	–72
(14) Total C influx (1)	3040	1725	963
(15) Total C efflux (14) – (16)	2450	1140	895
(16) Net ecosystem exchange (NEE)	590	585	68
(17) N_p (1) – (2) – (3) – (7)	1560	944	517
or (4) + (5) + (8) + (9)			
(18) N_p/G_p (17)/(1)	51%	55%	54%
Mean carbon residence times (years):			
(19) Biomass	16	10	12
(20) Soil and litter	15	10	106
(21) Total ecosystem	29	18	89

[1] from Malhi *et al*. 1998, Malhi *et al*. unpublished data; [2] from Meir *et al*. 1996, for another site in Rondonia; [3] from Higuchi *et al*. (1997); [4] from Edwards *et al*. 1989; [5] from Gower *et al*. 1997; [6] from Steele *et al*. 1997; [7] from Rayment 1998; [8] from Lavigne & Ryan 1997

up of measurements made at smaller scales. Continuous long-term measurements enable the main components of the carbon balance to be integrated on an annual basis, and the interannual variation in the carbon budget to be investigated.

The dynamics of these fluxes can be better understood by breaking them down into their subcomponents and making a carbon balance above and below ground. Table 6 shows values for the major components of the carbon cycle at each site. Above ground, if total canopy photosynthesis G_p, determined from eddy covariance or chamber measurements [item (1) in Table 6], above-ground autotrophic respiration of foliage (2) and wood (3), and above-ground net primary production, $N_{p,AG}$ are known, the amount of carbon translocated below ground *via* the stems (6) can be fairly accurately calculated by difference. $N_{p,AG}$ includes both leaf and wood production; if not directly measured, it can be estimated as approximately equal to the sum of detritus production (leaf litter and tree mortality; (4)) and the net increment in above-ground biomass (5). Below ground, this translocated carbon (6) is allocated among the less well-known processes of net root biomass increment (8), root respiration (7), and detritus production (9), the last including processes such as fine root turnover, rhizodecomposition (sloughing of the root cap), root exudation, and carbon transfer to mycorrhizae, all of which are only measurable with low degrees of accuracy.

Accounting for net root biomass increment (8) leaves a combined estimate of root respiration (7) and combined detritus production (9). The input of detritus from roots (9) and from above-ground (4) comprises the flux of carbon from autotrophs to soil organic carbon (SOC). If the SOC is neither increasing nor decreasing in amount on interannual timescales, this influx would equal the efflux of heterotrophically respired CO_2 from the soil (11). Since the soil CO_2 efflux can be independently measured (or obtained by difference between the net ecosystem flux and the net influx of CO_2 in canopy photosynthesis plus the above-ground autotrophic respiration), it is therefore possible to determine whether the SOC may be increasing or decreasing in amount (13), something very difficult to determine by stock taking. This approach is dependent only on quantification of the changes in root biomass (8), and not on accurate partitioning of below-ground carbon fluxes between autotrophic (12) and heterotrophic (11) respiration. If the changes in root biomass have not been accurately estimated, the approach can still provide estimates of changes in total below-ground carbon (i.e. roots plus SOC).

Simplified annual carbon balance diagrams (see Table 6) are shown in Fig. 1. The approach we have taken in Table 6 is to use the eddy covariance-measured NEE (16) as a constraint that modifies the calculated rates of soil respiration
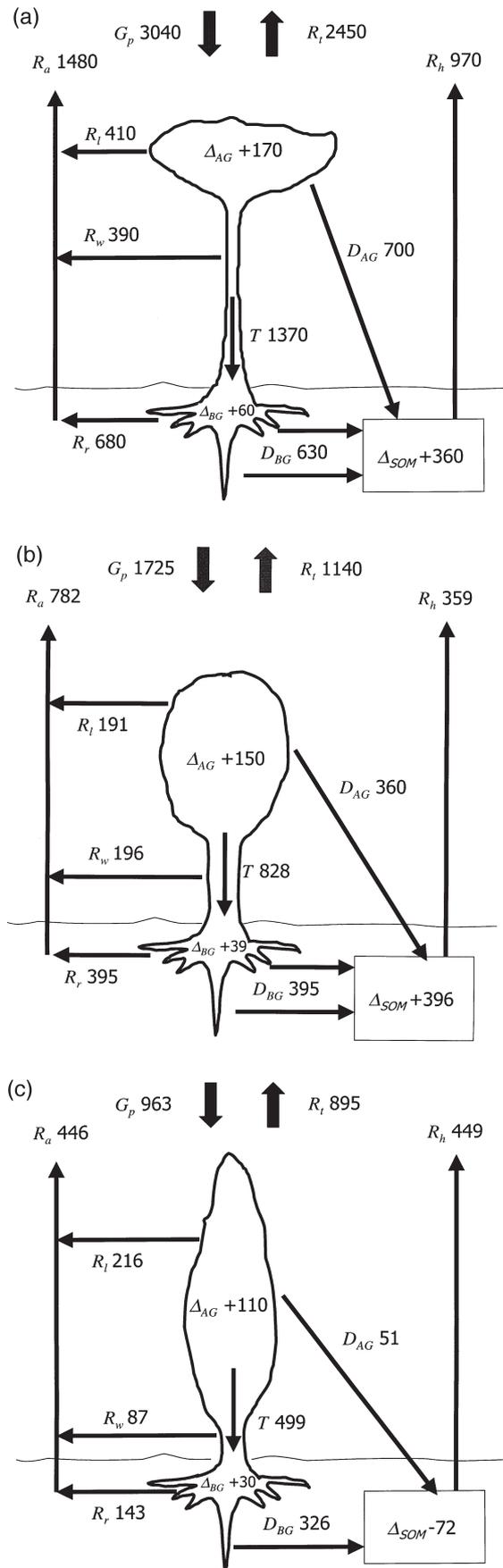
and change in SOC. G_p (1), was calculated for the boreal site from branch bag measurements (Rayment & Jarvis 1999c), for the temperate site by application of the CANOAK photosynthesis model to the data (similar to Baldocchi & Harley 1995), and for the tropical site by subtraction of estimated daytime respiration (Malhi *et al.* 1998). Moss photosynthesis may also account for a significant fraction of G_p at the boreal forest (Williams & Flanagan 1998), but was not included here. The total system respiration (15) was then calculated by subtracting the NEE from G_p. Above-ground, leaf (2) and wood (3) respiration were estimated or modelled from chamber measurements (Meir 1996; Baldocchi & Harley 1995; Rayment 1998; Lavigne & Ryan 1997), and detritus production measured from litter traps and studies of tree mortality rates (Higuchi *et al.* 1997, Edwards *et al.* 1989; Gower *et al.* 1997). Below-ground, the only detailed measurements of root growth and turnover were provided for the boreal site by Steele *et al.* (1997). For the other sites, we assumed that the net root biomass increment (8) was proportional to the above-ground biomass increment, and to the ratio of root biomass to above-ground biomass. The next step was to allocate the remaining below-ground carbon flux between root respiration (7) and detritus production (9). For the tropical site this was guessed to be approximately equally divided between these two components after estimates for large root production and mortality were excluded (see Grace *et al.* 1999), and for the temperate site the flux was guessed to be exactly equally divided between the two components. For the boreal site root respiration rates were estimated by Steele *et al.* (1997), and we allocated the residual carbon flux to root detritus production (9). The change of carbon in soil organic matter was then constrained as the difference between the detritus input terms ((4) + (9)) and the heterotrophic respiration (11) estimated above. In addition, the net primary production, N_p (17), can then be calculated as the sum of above-ground and below-ground biomass increases and detritus production.

The main difference between the three C budgets is that G_p, and hence N_p and the general magnitude of the carbon cycle, show a decreasing trend from the tropical site via the temperate site to the boreal site. Consequently, there is a much larger translocation of C to below the ground at the tropical site, and much higher rates of root and heterotrophic respiration. The calculation suggests large rates of increase in soil carbon at the tropical and temperate sites, and a small

Figure 1. Estimated annual total carbon flows for each study site. All units are g C m^{-2} year^{-1}. The data sources are described in Table 6. (a) Tropical rain forest near Manaus, Amazonas, Brazil; (b) temperate deciduous oak-hickory forest, Tennessee, USA; (c) boreal evergreen black spruce forest, Saskatchewan, Canada. G_p, gross primary production; R_t, total respiration; R_a, autotrophic respiration; R_h, heterotrophic respiration; R_l, leaf respiration; R_w, above-ground wood respiration; R_r, root respiration; D_{AG}, above-ground detritus (litterfall and mortality); D_{BG}, below-ground detritus (root mortality, fine root turnover and exudation); T, below-ground carbon translocation; Δ_{AG}, above ground net biomass carbon increment; Δ_{BG}, below-ground net biomass carbon increment; Δ_{SOM}, net increment in soil organic carbon.

loss of soil carbon at the boreal site. However, this analysis uses data from a number of sources and some degree of guesswork, particularly for below-ground carbon dynamics at the tropical and temperate sites. It should therefore be regarded as illustrative of general principles rather than a precise quantification. The values for the temperate site should be treated with particular caution: as this is a regrowth forest and the inventory data were collected 14 years prior to the flux measurements, it is likely that the above-ground carbon allocation is underestimated, and hence the residual increment in below-ground carbon is overestimated.

The mean residence times for carbon for each component of the ecosystem can be estimated by dividing the total carbon stocks (Table 5) by the rates of carbon input. For the biomass this rate of input is equal to N_p (17), and for soil carbon the input is the rate of detritus production ((4) + (9)). Mean carbon residence times for living biomass, an average of short leaf, twig and root residence times and large trunk residence times, are in the range 10–20 years for all three forests and longest for the high biomass tropical forest. The soil carbon residence time for the tropical site is similar, but the residence time for the boreal soil is on the order of a century. In terms of carbon that is actively turning over, this boreal soil residence time may be an overestimate, as a substantial proportion of the deep soil carbon may be totally inactive, neither receiving carbon through detritus production nor losing carbon through microbial decomposition. Once again, the residence times for the temperate site are likely to be underestimated, as the biomass and soil carbon stocks are likely to be substantially less than those for an equivalent old-growth forest. The apparent difference between the calculated total ecosystem residence time (21) and the sum of the soil (20) and biomass (19) residence times is due to the discrepancy between N_p and the rates of detritus production.

As argued above, the measurements of NEE on an annual basis should provide a major constraint that closes the forest carbon balance. However, there are likely to be significant differences between estimates of annual NEE derived from eddy flux measurements and estimates derived from integration of the measurements of component processes. This is because there are uncertainties with both measurement methodologies: first, measurements of each of the component processes have large error terms associated with them (Rayment 1998), and second there are still some uncertainties attached to the post-collection analysis procedures of the eddy covariance data (discussed in 4·1).

Influence of climate on carbon dynamics

Many of the properties and much of the temporal variation of carbon dynamics at each site can be related to three predominant climatic variables: light availability, temperature and soil moisture availability.

Light

Incident light (or photosynthetic photon flux density, PPFD) is the most immediate environmental control on photosynthesis.

Whilst the light response curve of an individual leaf can be approximated by a non-rectangular hyperbola (Prioul & Chartier 1977), most forest canopies exhibit a quasi-linear relationship between photosynthesis and PPFD at low and medium PPFD ($< 1000\ \mu$mol m^{-2} s^{-1}), when photon availability is the limiting variable, but a diminished response at higher PPFD, when carboxylation rate becomes limiting (Ruimy *et al*. 1995). The degree of linearity of the whole-canopy light response curve is a function of leaf area, photosynthetic capacity and the vertical distribution profile of nitrogen within the canopy. Leaf area influences canopy carbon uptake by increasing absorption of PPFD, by increasing the population of photosynthetic reaction centres and by shading the soil, thereby reducing its heating and respiration. Calculations generated by a coupled canopy photosynthesis/micrometeorology model (Baldocchi *et al*. unpublished data) show that the canopy photosynthesis–light response curve of vegetation with high photosynthetic capacity (V_{cmax} equals 100 μmol m^{-2} s^{-1}) is hyperbolic when a canopy is sparse (Leaf Area Index, LAI = 1), but is linear when the canopy is closed (LAI = 5). The linearity is reduced if leaf nitrogen concentrations are higher in the light-rich upper canopy than in the understory (Sellers *et al*. 1992).

Availability of light is strongly affected by cloudiness and low sun-angle conditions, but the effect of this on canopy photosynthesis is partially counteracted by the increased proportion of diffuse solar radiation, which is more effective at penetrating deeper layers of the forest canopy and illuminating usually shaded leaves (Wang & Jarvis 1990).

At mid- and high latitudes, the availability of light controls potential photosynthesis by determining the maximum length of the growing season in spring and autumn. Away from the tropics, variation in day length and noon solar zenith angle are the predominant constraints that define potential photosynthesis of a forest. Cloudiness can affect light availability on daily or weekly timescales, but in mid-latitude climates there is rarely a strong seasonal cycle in cloudiness (Peixoto & Oort 1996). In the tropics, variations in day length and noon solar zenith angle have only small effects on light availability, whereas variations in cloudiness have a relatively larger influence on both diurnal and seasonal timescales. Most tropical regions do exhibit a distinct seasonality in cloudiness and rainfall, associated with the north–south movement of the Inter-Tropical Convergence Zone (McGregor & Nieuwolt 1998). For example, in central Amazonia there are only five rain days/month in September, but 25 rain days/month in March, and the monthly mean solar radiation varies between 20 MJ day^{-1} in the dry season and 14 MJ day^{-1} in the wet season (Malhi *et al*. 1998).

On the other hand, the dry season in many tropical regions is associated with biomass burning, and clear-sky solar radiation can locally be severely reduced. During the El Niño-associated fires of late 1997 (Brown 1998), the sun was not visible for over a month in the 'clear sky' dry season in central Borneo (M. Clearwater, personal communication), and was much reduced in Amazonia. In the boreal forest, fires occur naturally in most summers as a result of lightning strikes, and forests burn with an average return time at any

one site of between 100 and 150 years (Payette 1992). High-level smoke travels long distances in the deep convective boundary layers that develop over the boreal forests and also intermittently reduces photosynthesis substantially.

Temperature

At the extremely low temperatures that occur in winter in the boreal region, chloroplast organization breaks down and Photosystem 2 becomes inactivated (Strand & Öquist 1985; Öquist & Strand 1986) and may take eight or more weeks during the spring to recover fully (Strand & Lundmark 1995, Bergh & Linder 1999). Through the growing season, leaf temperature also has an effect on maximum rates of photosynthesis by affecting Rubisco specificity for CO_2 and O_2 (Long & Drake 1991), and in particular by enhancing photorespiration at high temperatures (Long 1991; Lloyd *et al.* 1995) with the result that photosynthesis in trees (almost all C_3 plants) has a well-defined, broad optimal temperature (Neilson, Ludlow & Jarvis 1972). An indirect, but probably more important, influence of temperature is that high leaf temperatures also result in large atmospheric water vapour saturation deficits and evaporation rates, so that carbon uptake is limited by stomatal closure (Sandford & Jarvis 1986). However, the major influence of temperature on net carbon balance is through its effects on rates of both autotrophic and heterotrophic respiration. Arrhenius-type models (Lloyd & Taylor 1994) provide an appropriate description of this relationship, although in practice a simpler exponential relationship, with a global mean Q_{10} temperature coefficient of approximately 2·4, will usually suffice (Raich & Schlesinger 1992). Thus the respiration rate more than doubles for a 10° C rise in temperature.

In middle and high latitudes, an additional effect of temperature on photosynthesis is its potential to inflict frost damage on buds and leaves. As the annual cycle of air temperature lags some weeks behind that of insolation, the main effect is to constrict the length of the photosynthetic season in the spring, when frosts can curtail daytime photosynthesis below expectation (Beadle *et al.* 1985). Photo-inhibition of photosynthesis occurs when temperature is low (< 5 °C) and irradiance high (Strand & Öquist 1985).

Temperature is thus a major determinant on seasonal processes which regulate both carbon gain and carbon loss in temperate and boreal forests. In the tropics, seasonality in temperature is generally minimal; for the central Amazonian forest, for example, the annual range in monthly mean temperature is 2 to 4 °C (Malhi *et al.* 1998). On interannual timescales, however, temperature may influence the carbon balance of all biomes.

Soil moisture

In high latitudes the start of the photosynthetically active season is determined by the availability of soil moisture. Frozen soil prevents water uptake by roots so that leaf turgor and stomatal opening are dependent on the limited supply of stored water within the trees (Whitehead & Jarvis

1981). As air temperature rises and the snow cover begins to thaw, melt water at close to 0 °C percolates down through the soil, replacing the ice and enabling water uptake. In high and mid-latitudes, soil moisture reserves are largely replenished by autumn and winter precipitation (Waring & Running 1978), so lack of soil moisture has little impact on spring growth, but may restrict photosynthesis and growth in the late summer. During the growing season soil moisture availability is a function of precipitation, runoff and evapotranspiration rates, and the moisture retention properties of the soil. Soil moisture therefore shows more small-scale spatial variability within a forest ecosystem than PPFD or temperature. Lack of soil moisture primarily reduces carbon uptake by inducing stomatal closure, but may also affect carbon (and nutrient) release by restricting microbial decomposition. In the tropics, soil-moisture stress may become significant in the dry season, because of high evapotranspiration rates and the low available water capacity in many old, highly eroded tropical clay soils (Hodnett *et al.* 1995). Together with PPFD, the availability of soil moisture is probably the most significant environmental variable in the tropics.

Seasonal cycles of carbon uptake and loss

The seasonal dynamics of each of the forest sites in are illustrated in Fig. 2. The tropical data shown were collected in 1995/1996, the temperate data in 1997, and boreal data in 1996. Figure 2(a) illustrates the annual cycle of daytime uptake of carbon (daytime photosynthesis plus respiration
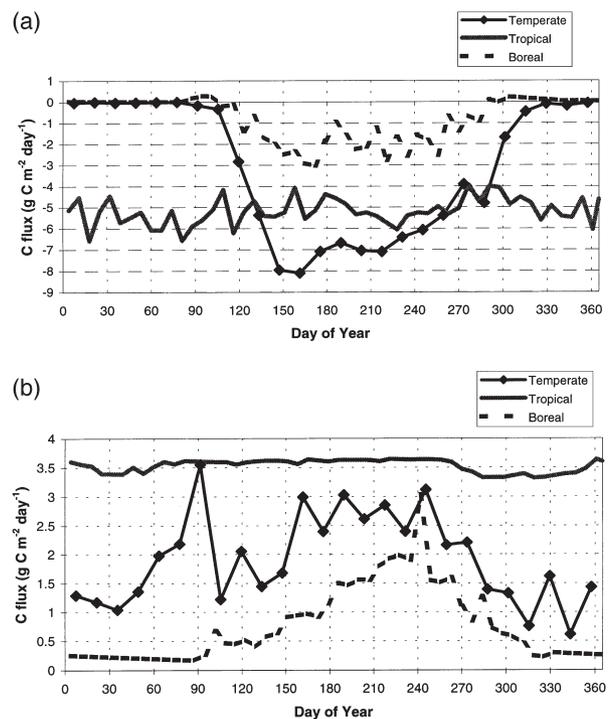
Figure 2. Annual cycle of (a) daytime uptake, and (b) night-time release of carbon at the boreal (short dashed line), temperate (solid line with diamonds) and tropical (solid line) sites.

loss) and Fig. 2(b) shows the night-time release of carbon at each site. It should be emphasized that the three data sets have not been analysed in an identical manner, primarily because of uncertainties in the best method of interpreting night-time eddy covariance measurements. These uncertainties are discussed later in the section entitled Eddy covariance, but for completeness we describe the correction procedures applied to each data set here. In the boreal site, a correction factor for night-time respiration is included on low wind-speed nights, as described by Jarvis *et al.* (1997). Measurements were not made throughout the entire winter, and the low winter efflux has been estimated by linear interpolation between measurements made at the start and end of winter, when temperatures were –15 °C to –30 °C. At the temperate site, the night-time flux has been adjusted by using an advection correction of the type proposed by Lee (1998). At the tropical site, no night-time correction has been applied, but large gaps in the data have been interpolated using a semi-empirical light, temperature and water vapour pressure deficit (VPD) response model (Malhi *et al.* 1998). In addition, the tropical data set actually runs from September 1995 to August 1996, but here has been presented as a continuous annual cycle from January to December for the purposes of comparison.

Daytime uptake

The tropical forest site showed the least seasonality in both daytime uptake (mean value 5·2 g C m^{-2} d^{-1}) and night-time release (mean value 3·5 g C m^{-2} d^{-1}), although there was significant seasonality in canopy photosynthetic capacity: Malhi *et al.* (1998) showed that peak photosynthetic rates decline markedly in the dry season, and a modelling analysis by Williams *et al.* (1998) concluded that this was most likely because of shortage of soil moisture causing large reductions in soil hydraulic conductivity. However, this reduction in capacity is partially compensated for by increased sunshine-hours in the dry season. Overall, water availability slightly outweighs cloudiness as a controlling variable, and the tropical daytime uptake rates shown in Fig. 2 are higher in the wet season (mean 6 g C m^{-2} d^{-1}) than in the dry season (mean 4 g C m^{-2} d^{-1}). On the other hand, the balance between these two variables may be different in other tropical regions, such as western Amazonia, where the dry season is less pronounced and overcast days more frequent. On any individual day, carbon uptake at the tropical site can vary between 1 g C m^{-2} d^{-1} on very overcast days to 9 g C m^{-2} d^{-1} on sunny days in the wet season. In the dry season most days are sunny and the day-to-day variation is much reduced. Cold periods of low temperature and PPFD, associated with fronts of cold air originating in high southern latitudes (Marengo, Nobre & Culf 1997), suppress both net CO$_2$ efflux at night and net influx during the daytime (Grace *et al.* 1996).

Seasonality in both carbon uptake and release is much more evident in boreal and temperate forests (Fig. 2). The predominant latitudinal constraint on daily carbon uptake is day length, but the start of the growing season is also constrained by air and soil temperatures. In the temperate deciduous forest, the 'growing season' is determined by the emergence of leaves in the spring and the subsequent development of the foliar canopy. In 1997, leaf growth started at the beginning of April (day 90) and rapidly reached a ceiling value around day 140 (Greco & Baldocchi 1996). During winter there is a small but significant loss of carbon, but, as the canopy develops, photosynthesis surges rapidly, peaking in mid-June at about 12 g C m^{-2} d^{-1} (approximately 1·5 times the rate of the tropical rain forest), after which the rates remain fairly constant until mid-September, before declining as the days shorten. The leaves begin to senesce after approximately 180 d.

In the boreal evergreen, black spruce forest, the length of the active season is strongly influenced by the length of the frost-free period. The growing season begins and ends with abrupt temperature transitions. As the thaw begins in the spring and snow starts to melt, the temperature rises rapidly towards zero and as it passes through about –1·5 °C (in mid-April in 1996), CO$_2$ exchange switches from carbon loss to carbon gain (Massheder 1998). When the thaw occurs late, substantial amounts of solar radiation are effectively wasted and the annual carbon gain is correspondingly small. Carbon uptake rises to a peak of 3 g C m^{-2} d^{-1} in late June, and then fluctuates at around 2 g C m^{-2} d^{-1} until mid-September. Both uptake and loss rates are much smaller at all times in the boreal black spruce forest.

Night-time CO$_2$ efflux

For these forests, soil respiration rates are primarily determined by temperature, and to a lesser extent by soil water content and the quantity and quality of the soil organic matter. In tropical forests, more than 70% of respiratory CO$_2$ originates from autotrophic and heterotrophic processes within the soil biomass (Meir *et al.* 1996). At the Amazonian site, soil temperature is the main cause of diurnal variability of soil respiration, both through its mean diurnal cycle (23·0–24·5 °C at 5 cm depth; Malhi *et al.* 1998) and sudden drops in temperature (typically 2 °C) associated with rainfall. Seasonally, soil temperature is higher in the dry season (daily mean 26 °C) than in the wet season (24 °C), but soil moisture is much reduced. There was little evidence of measurable seasonality in respiration rates in the eddy covariance data shown here, but the late dry season was not directly studied. Soil chamber measurements by Sotta (1998) at the same site in 1997 suggest that respiration rates decline as the soil dries down. Litter fall rates are highest in the dry season, but much of the litter accumulates until the start of the rainy season (November/December), when a flush of decomposition would be expected. Thus, as with photosynthesis, a balance of opposing factors (litter pool size and soil temperature on one side, soil moisture on the other) acts to lessen the seasonal variability in tropical soil respiration.

Night-time carbon efflux rates in the temperate oak-hickory and boreal spruce forest sites follow the seasonal changes in soil temperature. At the oak-hickory site in 1997, rates rose from a constant 1 g C m^{-2} d^{-1} to a steady

4 g C m^{-2} d^{-1} in the June–August period (slightly higher than the tropical rain forest), as the average daily soil temperature rose to approximately 22 °C, before falling away again in September. In a study of soil respiration in this region, Hanson *et al.* (1993) found that, although soil temperature explained most of the seasonal pattern, soil moisture availability and root metabolic activity (linked to gross productivity) were also significant factors.

At the boreal site in winter-time there is a small but persistent efflux of about 0·2 g C m^{-2} d^{-1}, when insulation by permanent snow cover maintains surface soil temperature at close to zero, whereas air temperatures are –15 to –35 °C (Rayment & Jarvis 1999b). During the spring thaw, CO_2 exchange rates rise rapidly from this winter-time value; respiration initially picks up more rapidly than photosynthesis, resulting in a brief peak of carbon loss from the system. Respiration rates increase steadily as the summer progresses, reaching 2 g C m^{-2} d^{-1} by August, before dropping away again through September and October to the winter basal rate as the soil becomes frozen again. The high water table close to the soil surface and low soil temperatures restrict soil CO_2 efflux from April through to August, when the water table lowers and temperatures rise (Rayment & Jarvis 1999b). Point-to-point variation in soil CO_2 efflux is large. Chamber measurements (Rayment & Jarvis 1997) have shown that this local heterogeneity is related to the depth of accumulated soil organic matter (Rayment & Jarvis 1999b) which may reach 0.5 m or more in boreal forests.

To conclude, the broad photosynthetic responses of temperate and tropical broadleaf forests to light and temperature are very similar. The differences between tropical and temperate deciduous forests in the annual course of CO_2 fluxes are driven by the seasonality of day length, timing of bud burst and senescence, variation in cloud cover, and soil moisture availability. The light sensitivity of the boreal spruce forest seems less pronounced than that of the broadleaf forests (but is consistent with that measured at other coniferous forests, e.g. Ruimy *et al.* 1995). The total canopy leaf nitrogen is probably the major factor limiting boreal canopy photosynthetic activity: boreal forests are generally chronically N-deficient (Linder 1995; Schulze *et al.* 1999), as much of the organic nitrogen is held in the cool and often waterlogged soil, and therefore only slowly released by decomposition processes.
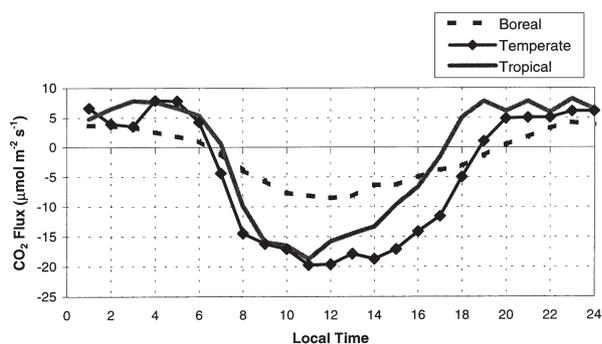
Diurnal cycles

Figure 3 illustrates the mean diurnal CO_2 cycle at each site during a high productivity part of the year (June for the boreal and temperate sites, November/December for the tropical site). The similarity of both photosynthetic and respiration rates per unit ground area of the tropical and temperate forest sites is remarkable: both sites have similar LAI (Table 3) and show peak uptake rates of 18 to 20 μmol m^{-2} s^{-1} just before noon, and mean night-time respiration rates of 5 to 7 μmol m^{-2} s^{-1}. However, the longer day length in the temperate zone (15 h against 12 h) results in higher overall daily uptake rates in the oak-hickory forest. In the boreal forest, where LAI is much smaller, both uptake and respiration rates are less than half those of the two other forests, and the daily totals are much less, despite a day length of 20 h.

Interannual variability

The data shown in Fig. 2 were all collected in 1996 or 1997 and thus present a snapshot of the bulk physiology of three forests. In recent years, however, long-term eddy covariance studies have shown that there can be considerable interannual variability in carbon dynamics (Goulden *et al.* 1996a). This variability is primarily driven by variations in the controlling climatic variables outlined above, but is also modulated by the response and recovery times of each forest biome.

As discussed above, the primary meteorological determinants of the carbon balance of intact stands are: (1) the length of the growing season determined by the radiation inputs and modified by soil and air temperatures in spring and autumn; (2) the length of the period of snow cover; (3) the amount of cloud cover in the growing season; and (4) the occurrence of drought in the late summer or dry season. Cloudiness and drought can directly limit photosynthetic uptake in the growing season, whereas the cold period controls the overall length of the growing season through its impact on phenology. Snow cover can be important in insulating the soil surface from extremely low temperatures, thus permitting a moderate amount of soil respiration throughout the winter (Goulden *et al.* 1996a; Rayment & Jarvis 1999b). At the temperate deciduous Harvard Forest, in Massachusetts, Goulden *et al.* (1996a) found NEE to vary between –2·8 and –1·4 t C ha^{-1} year^{-1} over the five years 1990–95, and concluded that interannual climate variations may modify terrestrial CO_2 exchange in the northern hemisphere by about 1 Gt C year^{-1}. Measurements and calculations indicate that an advance of 2 weeks in the start of the growing season at the temperate forest site would lead to a change in NEE of 1 t C ha^{-1} year^{-1} (Baldocchi, unpublished). In a sensitivity analysis of NEE of an old-growth

Figure 3. Average diurnal cycle of net CO_2 fluxes (eddy covariance flux plus within-canopy accumulation) at the three sites at a time of high productivity: June for boreal (short-dashed line) and temperate sites (solid line with diamonds), November/December for the tropical site (solid line).

Scots pine/Norway spruce forest in central Sweden, Lindroth *et al.* (1998) suggested that annual respiration would increase by 10% (74 g C m^{-2}) for a 1 °C rise in temperature. Photosynthesis would need to increase by 12% to compensate for this increased respiration; and thus the net effect is for larger carbon loss in warm years. In contrast, model sensitivity calculations for a 35-year-old boreal Norway spruce forest in northern Sweden (Bergh 1998; Bergh, McMurtrie & Linder 1998) suggest that a 2 °C rise in temperature would increase the length of the photosynthetic season by 3 weeks, and lead to an increase in annual N_p of 17 to 18%. Using the model of Lloyd *et al.* (1995), Grace *et al.* (1995b) found respiration of the tropical forest to increase by 144 g C m^{-2} per degree rise in temperature.

One of the primary drivers of global interannual climate variability is the El Niño Southern Oscillation, the quasi-periodic redistribution of equatorial surface waters in the Pacific Ocean (Allan, Lindesey & Parker 1996). In the tropics, El Niño is strongly associated with enhanced dry seasons in both eastern Amazonia and Indonesia and enhanced rainfall in western South America (Ropelewski & Halpert 1987). The overall influence is probably one of increased carbon loss, either through water stress causing reduced photosynthesis and increased tree mortality, or more dramatically through drought-induced fires, as evidenced in Indonesia and Amazonia in the intense 1997–98 El Niño (Brown 1998; Barbosa 1998). The impact of reduced water availability should also be counteracted by enhanced numbers of hours of sunshine in these regions; for example Clark & Clark (1994) observed that tree growth was higher in sunny dry years at a tropical forest site in Costa Rica. In many regions this effect is likely to be confounded, however, by smoke emitted from forest fires, with an extreme example being the great smoke haze that enveloped south-east Asia in late 1997 (Nichol 1998).

In mid- and high latitudes in the Americas the correlation is weaker, but El Niño is associated with mild, wet winters, with a reduced period of snow cover (Brown & Goodison 1996; Cayan 1996). The overall effect is likely to be one of enhanced carbon uptake because the mild winter induces a lengthened growing season (Goulden *et al.* 1996a). Additionally, in drought-prone areas, the enhanced winter precipitation may fully recharge soil water reserves and reduce the likelihood of a late summer drought. The impact of El Niño on temperate and boreal Eurasia is less evident.

Braswell *et al.* (1997) examined the correlation between interannual variations in lower tropospheric mean temperature and satellite-derived vegetation indices (normalized difference vegetation index, NDVI) for a number of biomes. In high latitude forests, warm years were correlated with high NDVI in the same years, suggesting increased productivity, but with a reduction in NDVI 1 to 2 years later. In C$_3$-dominated tropical and arid areas the opposite pattern was observed, with reduced NDVI in warm years, probably associated with increased water stress, but increased NDVI 1 to 2 years later. C$_4$ savannas and grasslands showed a similar pattern to high latitude forests. Braswell *et al.* suggested that the observed 1–2 years lag in NDVI was associated with the

response time of soil microbial activity: warm (cool) years are associated with increased (reduced) biomass inputs to the soil at high (low) latitudes, which lead to increased (reduced) microbial competition for nutrients, and thereby to reduced (increased) plant growth in subsequent years. Globally they found that temperature anomalies were associated with lagged maxima in NDVI and lagged minima in the rate of increase of atmospheric CO$_2$ concentration, with a lag time of 1·5–2 years. The observed anticorrelation with rate of CO$_2$ increase suggests that, globally, the response of tropical productivity and/or high latitude soil respiration is more significant than the response of high latitude productivity or low latitude respiration. Possibly correlations between temperature and atmosphere–ocean CO$_2$ fluxes must also be considered, however.

While the description of climatic controls outlined above describes the impact of climatic variability on intact forest stands, catastrophic events (such as drought, flood, fire and wind-throw) may have a spatially variable impact, but a strong influence on the overall carbon balance of the biome at regional scale. For example, drought may reduce forest photosynthesis and increase tree mortality, shifting the carbon balance towards a net source, but a more significant factor may be associated fires that turn patches of the forest into strong, albeit temporary, carbon sources. Wind-throw may create similar patches. Since such events are not infrequent, the interannual variability of the spatially integrated net biome production (NBP; Schulze *et al.* 1999) is likely to be different to the variability of NEE of a particular stand. The influence of spatial heterogeneity on the relationship between NEE and NBP is discussed further below.

MEASURING THE CURRENT CARBON BALANCE OF FORESTS

In recent years there has been an accumulating body of evidence for a net sink of carbon in the terrestrial biosphere. In this section, we discuss the evidence for such a sink in the major forest biomes. The three principal approaches to estimating the carbon balance of forest biomes are micrometeorological measurements of surface fluxes, biomass inventories and the inversion of atmospheric gas concentrations. All three approaches still have methodological problems, but are pointing towards a combined net terrestrial carbon sink (excluding deforestation) of 1 to 3 Gt C year^{-1}. However, the exact partitioning of carbon sequestration amongst the tropical, temperate and boreal forest biomes remains unclear.

Eddy covariance

This micrometeorological technique relies on directly measuring the turbulent transport of CO$_2$ above a forest canopy (Moncrieff, Jarvis & Valentini 1999). In principle, the net carbon balance of a site can be directly measured by integrating eddy covariance measurements of CO$_2$ fluxes over the diurnal, seasonal and annual cycles. The technological combination of sonic anemometers and fast response CO$_2$ analysers matured in the late 1980s, and field measurements

have subsequently been made in a range of biomes, including temperate, boreal and tropical forests. There has been an evolution from initial short-term, localized field studies, to long-term multiple site campaigns, such as, BOREAS in the Canadian boreal forest (Sellers *et al.* 1997), investigating larger spatial and temporal scales, to long-term monitoring networks spanning whole continents (e.g. Euroflux in Europe (Aubinet *et al.* 1999), Ameriflux in North America). The range of measurements required at long-term monitoring sites is described by Baldocchi *et al.* (1996).

Although eddy covariance has already been demonstrated to provide reliable estimates of the bulk photosynthesis and respiration of a forest site (Baldocchi 1997; Jarvis *et al.* 1997; Malhi *et al.* 1998), there is still lingering uncertainty as to whether it can yet provide accurate measurements of the net carbon balance. The net balance is the relatively small net sum of opposite daytime and night-time fluxes, and a small error in measurements in one of these periods could lead to miscalculation of the net carbon balance, even though the bulk photosynthesis and respiration may look plausible (Moncrieff, Malhi & Leuning 1996).

Much of the uncertainty has focused on the night-time fluxes, an area that was ignored in much of traditional micrometeorology because of its irrelevance to energy and water budgets. On calm nights, respired CO_2 tends to accumulate within the forest canopy, and is transferred to the atmosphere through intermittent events. Several studies (Goulden *et al.* 1996b; Jarvis *et al.* 1997) have demonstrated that respiration rates estimated as the sum of the eddy flux and the accumulation of CO_2 within the forest canopy on calm nights are not consistent with the estimates from eddy covariance in windy conditions. This discrepancy has led to the suggestion that eddy covariance is 'missing' some of the nocturnal CO_2 flux (Goulden *et al.* 1996b). The phenomenon appears less pronounced, but still apparent, in tropical forests (Grace *et al.* 1996; Malhi *et al.* 1998). Possible physical mechanisms suggested to account for this missing flux focus on lateral advection of the respired CO_2 within the forest canopy, either down hillslopes or away from 'cool spots' of subsiding air (Goulden *et al.* 1996b). However, if this were the case the phenomenon would be apparent only at sites at local topographic peaks, whereas in fact it appears at the majority of sites independent of local topography (A. Grelle, personal communication) Alternatively, the problem may be methodological, if the detrending and coordinate rotation schemes currently used in the analysis of eddy covariance data are not appropriate for the intermittent turbulence that is a characteristic feature of stable atmospheric conditions at night. Conversely, there are still arguments that there is no problem with the eddy covariance measurements, but that the problem lies with the respired CO_2 residing very close to, or remaining within, the soil surface and thus not being adequately captured by within-canopy measurements of CO_2 accumulation (Malhi *et al.* 1998). Yet another possibility is that there is a genuine reduction in soil CO_2 efflux in non-turbulent conditions because of reduced pressure pumping of air out of soil pore spaces (T.A. Black, personal communication). A very promising recent contribution to the debate has

been made by Lee (1998), who argues that net vertical advection of CO_2 because of horizontal flow convergence and divergence has previously been neglected. Inclusion of this term (most significant at night) makes a significant impact on the calculated net carbon balance and reduces the dependence of measured nocturnal respiration on wind speed (Baldocchi *et al.* 1999). However, some theoretical disagreements with Lee's treatment have been voiced (Finnigan 1999) and it remains to be seen whether this problem is solved.

The annual cycle of net ecosystem exchange of each of the case-study sites is shown in Fig. 4. This is the algebraic sum of the directionally opposed daytime and night-time fluxes shown in Fig. 2. Figure 4 should be viewed with some caution because of the uncertainties outlined above. The boreal forest data have been empirically corrected for possible under-estimation of night-time efflux at low wind speeds (Jarvis *et al.* 1997) and this reduced the initially estimated annual NEE by 46% to the present value. Similar corrections have not been made to the temperate and tropical forest data because of lack of evidence that such a correction was necessary. Thus part of the difference between the value of NEE for the boreal black spruce site and the other two sites might be attributable to this correction.

The tropical forest appears to be a net sink of CO_2 throughout the year, whereas the higher latitude forests are sinks throughout most of the growing season and sources throughout the winter. All three forests, however, can be carbon sources on warm, cloudy days in the summer when photosynthetic rates are low and soil respiration rates are high. NEE at the tropical forest site peaks in the early wet season (December to March), and then declines steadily to minimum values in the late dry season (October to November). This seasonality is the resultant of two opposing factors: variation in soil moisture status and amount of cloud cover. The observed minimum in the dry season indicates that soil moisture availability is a more important constraint than available sunshine at this site.

NEE at the temperate site is positive throughout the winter, and rises to a maximum in early March when warming temperatures result in a peak of respiration of accumulated autumn and
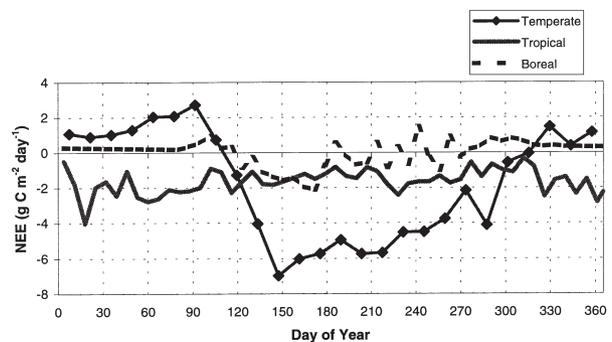
Figure 4. Annual cycle of net ecosystem exchange (NEE) of carbon (sum of daytime uptake and night-time release) in 1996 at the boreal (short dashed line), temperate (solid line with diamonds) and tropical (solid line) sites.

winter litter. It then rapidly becomes negative as leaf development and photosynthetic activity commences, peaking in late May when the canopy is in full foliage. At its peak, NEE at the temperate site is three to four times greater than at the tropical site, due to the longer day length (Fig. 3) and the lower respiration rates. Respiration rates are closer in magnitude to the mean N_p of a site, and therefore are lower at the temperate site than at the tropical site, despite the fact that monthly mean productivity is higher at the temperate site in the summer.

The boreal site shows a similar seasonal cycle in NEE, but with greatly reduced amplitude (Fig. 4). Its peak values of NEE in May are similar to those of the tropical forest. The site is an increasingly frequent carbon source on cloudy days in late summer, when soil temperatures are at a maximum, and there is a net loss of carbon on about one-quarter of the days during the growing season.

The overall eddy covariance estimates of annual NEE at the boreal, temperate and tropical sites for the year shown indicate sinks of 70, 585 and 590 g C m^{-2} years^{-1}, respectively. As a comparison with other measurements, in the boreal forest biome Lindroth *et al.* (1998) reported a net carbon *source* of 70 to 220 g C m^{-2} years^{-1} (depending on the correction scheme used) for an old-growth Norway spruce-dominated forest in central Sweden and Black *et al*. (1996) reported a net carbon sink of 130 g C m^{-2} years^{-1} in a broadleaf hazel nut/aspen forest in Saskatchewan. In the temperate forest biome, Goulden *et al*. (1996a) reported a net sink of between 140 and 280 g C m^{-2} years^{-1} (depending on year) in the mixed deciduous Harvard Forest, in Massachusetts. Valentini *et al*. (1996) reported a net sink of 450 g C m^{-2} years^{-1} for a managed beech forest in the Appenines in central Italy, and Hollinger *et al*. a net sink of 290 g C m^{-2} for a mixed deciduous forest in Maine. In the tropics, no other long-term record of CO$_2$ flux exists, although Grace *et al*. (1995b) inferred a net sink of 100 g C m^{-2} years^{-1} that was based on modelled extrapolation of 54 d of measurements in Rondonia, southern Amazonia.

All these values should currently be treated with some caution until the issue of correct measurement of night-time fluxes is resolved. With the notable exceptions of the boreal forest sites in Sweden (Lindroth *et al*. 1998) and Manitoba, Canada (Goulden *et al*. 1998), most sites show a net sink of carbon dioxide, and the reported net fluxes are much larger at the temperate and tropical forest sites than at the boreal forest sites. This probably arises because the bulk photosynthetic and respiratory fluxes are larger in temperate and tropical forests, and therefore a small proportional change in these bulk fluxes produces a larger net carbon differential than it would in the lower productivity boreal forests.

Biomass inventories

Another approach to estimating the carbon balance of ecosystems is through the use of conventional forest inventory methods. Measurements of the diameter at breast height of trees can be converted to estimates of living, above-ground biomass using empirical allometric relations determined for each tree species. By comparing successive inventories, rates of tree recruitment, biomass growth, tree mortality and net biomass increment can be determined. Carbon usually constitutes between 45 and 55% of dry tree biomass (Carvalho *et al*. 1998). The carbon stocks of detritus in deadwood and litter pools can also be directly measured (Vogt, Greer & Vogt 1986).

The advantage of biomass inventories over micrometeorological techniques is that they are direct, fairly unambiguous, technologically simple and relatively low cost, and can thus be used to monitor changes in tree carbon stocks over wide areas and long time periods. The main disadvantage of forest carbon inventories from the point of view of carbon sequestration is that they are almost invariably incomplete, particularly with respect to changes in below-ground carbon, in both roots and soil organic matter. In addition they are labour-intensive and provide only intermittent records of carbon stocks, which may not capture the effects of seasonal and interannual changes. As shown earlier, a combination of forest inventory and micrometeorological approaches can provide new insights into the above-ground and below-ground flows of carbon.

Temperate and boreal forests

The long history of commercial use of northern hemisphere mid-latitude forests (North America, Europe and Russia) has resulted in extensive records of forest inventories and changes in land use. Thus it is possible to estimate biomass changes not only in mature forests, but also across the patchwork of forested landscapes affected by (and recovering from) natural disturbance and human activity, and thereby arrive at a comprehensive estimate of biomass changes of the biome as a whole.

Syntheses of forest inventory data have been published for Canada (Apps & Kurz 1994), the United States (Turner *et al*. 1995), Europe (Kauppi, Mililainen & Kyysela 1992; Spiecker *et al*. 1996) and the former USSR (Kolchugina & Vinson 1993). By compiling and comparing such data, Dixon *et al*. (1994) estimated that the northern temperate and boreal forests were accumulating 0·7 ± 0·2 Gt C year^{-1}, and Houghton (1996b) estimated a net uptake of 0·8 Gt C year^{-1}. Houghton's figure includes net annual increments of living biomass (0·5 Gt C), wood products (0·14 Gt C), slash (0·08 Gt C), soil (0·08 Gt C) and peatlands (0·02 Gt C), although the figures for slash, soil and peat are based on measured initial stocks and estimated respiration rates, and not on direct measurements. This estimate of Houghton's is significantly different from the net source of 0·03 Gt C year^{-1} estimated by Houghton & Hackler (1995) on the basis of land-use change alone. This difference arises because the biomass inventory approach incorporates any measured increase of biomass in undisturbed forests, and higher than expected rates of regrowth in recovering forests.

Tropical forests

There have been few attempts to synthesize forest inventory data from tropical forests to arrive at a large-scale net carbon balance. Moreover, the high tree species diversity of tropical

forests (typically 200–300 species per hectare) and wide range of tree sizes complicates the use of empirical relationships between d.b.h. and above-ground biomass, expanding the need for detailed destructive sampling (Brown *et al.* 1995). Thus there have been few attempts to estimate biomass change across the patchwork of disturbed and regrowth forest areas.

Recently, Phillips *et al.* (1998) have compiled data from forest inventories across 68 sites in apparently undisturbed forests across the tropics. They concluded that there is large variability between plots, but that the South American plots demonstrate a mean rate of carbon accumulation of $0·68 \pm 0·33$ t C ha^{-1} years^{-1} in above-ground biomass, implying a net accumulation of $0·6 \pm 0·3$ Gt C year^{-1} in neotropical forests as a whole. In African and Asian forests, there was no apparent net increase in biomass, but too few plots were analysed to be confident in this conclusion. If the difference between tropical forests in Amazonia, Africa and Asia is genuine, it may reflect the larger population density and low level of human-induced disturbance in the pale-otropics, or be linked to the more maritime climate of the Asian forests. The primary source of uncertainty in this analysis is the limited number and spatial extent of the individual plots, together with limited understanding of natural disturbance dynamics in tropical forests. There may be a bias in selection of plots to forests recovering from disturbance, rather than to those currently losing biomass as a result of recent wind-throw, fire or flood (Nelson 1994). Alternatively, if the forest plots were biased towards mature stands that were more inclined to tree mortality, or degraded by human intervention, the spatial mean biomass increase may have been underestimated (Brown & Lugo 1992).

Overall forests

This compilation of forest inventory data suggests that overall there is a global net accumulation of $1·4$ Gt C year^{-1} in biomass in boreal, temperate and tropical forests. If the accumulation rates of secondary tropical forests and of wood products are also incorporated, together with better estimates for paleotropical forests, it is tempting to conclude that increase in forest biomass can account for the entire missing sink of $1·8 \pm 1·6$ Gt C year^{-1}. However, accumulation of carbon above ground in the trees is only a part of a full carbon inventory, and leaves major uncertainties about what is happening to carbon below ground in both root biomass and soil organic matter. These stocks may be increasing in response to increased growth and detritus production, or else decreasing because of enhanced fine-root turnover, autotrophic and heterotrophic respiration, resulting from climate warming, particularly at high latitudes. The fate of the stocks of soil carbon in this regard is crucial, but difficult to determine. To measure changes in stocks accurately through inventory over assessment periods as short as 5 or 10 years is impractical. Possibly the only sure way to determine if these stocks are changing is to measure the influxes and effluxes of carbon to and from the soil compartment, so that a full carbon inventory is likely to require a combination of both stocktaking and flux measurements (Steffen *et al.* 1998).

Net ecosystem exchange and net biome production

An issue that arises in any attempt to extrapolate from individual site measurements, whether micrometeorological or forestry-based, is the extent to which measurements of net carbon balance at individual sites are representative of the carbon balance of the whole forest biome, that is, the extent to which NEE represents NBP. A crucial factor is the extent to which intermittent, medium-scale disturbances determine forest stand dynamics. Many boreal and temperate forests are certainly affected by fire on a time-scale of a century (Payette 1992); the pattern of natural disturbance in tropical forests is less obvious or well understood, but may involve a combination of fire, drought, floods and storm blow-downs (Nelson 1994). If such disturbances are frequent or extensive, the forest may be composed of a patchwork of stands of various ages, each of them growing and accumulating carbon at a different rate until the next major disturbance. If forest patches are always recovering from the previous disturbance, and always disturbed again before they reach equilibrium, it is conceivable that the net biome production, NBP, is zero, even when measurements of NEE at all sites away from areas undergoing disturbance always indicate strong carbon uptake.

In principle, this should not present a problem as long as there are a sufficient number of measurement sites to capture the occasional disturbed patch and the full range of recovering patches, and there is no bias against obtaining data from disturbed sites. The extent to which such a bias exists remains unclear: in the extreme case there can be no tower-based eddy covariance measurements of CO_2 fluxes during forests fires, and we have to rely on other means, such as remote sensing of fires, to estimate carbon emissions. To estimate NBP on a regional scale we must take into account the regional mosaic of disturbance and recovery, and hence consider whether we are adequately sampling spatial heterogeneity (Schulze *et al.* 1999).

Micrometeorological and forestry measurements tackle spatial heterogeneity at different scales. Eddy covariance measures carbon balance over an area of tens to thousands of hectares (Malhi *et al.* 1998), and the measured carbon balance is not likely to be affected by random variability on this scale, such as canopy gap dynamics. However, eddy covariance sites have tended to be short-term and few in number, except during intensive campaigns such as BOREAS, and thus may not capture the range of natural disturbance and recovery at regional scale. Forestry plots frequently only cover a few hectares, and thus measurements at any particular site are more prone to being affected by small-scale forest dynamics. They are very low-cost, however, and can thus provide a dense and long-term network with which to capture regional scale carbon balance.

An alternative strategy is to attempt to quantify the NBP, by directly measuring CO_2 fluxes at a regional scale that incorporates natural disturbance. This can be done at landscape scale by making budgets of the amounts and isotopic composition of CO_2 and other gases in the atmospheric boundary layer to estimate local fluxes (Denmead *et al.*

1996; Culf *et al*. 1999), or by measuring NEE with aircraft-borne eddy covariance systems (Crawford *et al*. 1996). A larger scale alternative is to use a global network of gas concentration measurements to estimate continental-scale fluxes, as discussed below.

Atmospheric CO_2, $^{13}CO_2$ and O_2/N_2 Studies

The net carbon balance of the terrestrial biosphere as a whole can be examined by analysis of the global atmospheric pattern of concentrations and isotopic composition of CO_2 and O_2, as measured at flask sampling stations around the globe (Ciais *et al*. 1995; Francey *et al*. 1995; Keeling *et al*. 1995). In principle, if the global distribution of CO_2 is known, and the global transport and dispersion rates estimated from meteorological models, the models can be inverted to provide a spatial surface map of sources and sinks of CO_2 (Fan *et al*. 1998; Bousquet *et al*. 1999, Rayner *et al*. 1999). Monitoring the ratio $^{13}C/^{12}C$ and O_2/N_2 provides a further handle on the partition of the fluxes between oceans and terrestrial biosphere (Keeling *et al*. 1995; Ciais *et al*. 1995).

The isotopic ratio $\delta^{13}C$ is particularly useful because C_3 photosynthesis (the primary mechanism in a forest carbon sink) has a strong discriminating effect on this ratio ($\delta^{13}C_{leaves}$ ~ –27 to –32‰; $\delta^{13}C_{atmosphere}$ ~ –7 to –8‰; Lloyd *et al*. 1996), whereas the dissolution of CO_2 in ocean water (the major alternative carbon sink mechanism) and C_4 photosynthesis ($\delta^{13}C_{leaves}$ ~ –11 to –15%) have less impact. Similarly, changes in O_2 concentration (measured relative to more stable N_2 concentrations) are related to CO_2 fluxes via biotic processes and combustion, but insensitive to the dissolution of CO_2 in ocean water (Keeling *et al*. 1996b).

This approach holds great promise as a future global biosphere monitoring strategy, but until now has tended to yield contradictory results. Some earlier studies (Keeling *et al*. 1989; Tans, Fung & Takahashi 1990; Enting & Mansbridge 1991; Ciais *et al*. 1995), indicated a very strong extra-tropical sink (range –0·7 to –4·3 Gt C year^{-1}) and generally a large net tropical source (range +0·3 to +1·7 Gt C year^{-1}). The studies covered different years, so some of the discrepancies may result from interannual variability. Many studies (Francey *et al*. 1995; Keeling *et al*. 1995; Rayner *et al*. 1998) have indicated strong interannual variability in terrestrial fluxes, although correlation of this variability to climatic factors such as El Niño events is unclear.

The earlier, latitudinally averaged studies had a number of methodological difficulties, however, and more recent studies have attempted to incorporate continental-scale resolution. A regional analysis by Fan *et al*. (1998) suggested that the terrestrial sink is almost entirely localized in North American temperate forests (1·7 ± 0·5 Gt C year^{-1}) with Eurasia being a weak sink (0·1 ± 0·6 Gt C year^{-1}) and the rest of the world a weak source (0·1 ± 0·6 Gt C year^{-1}). However, this somewhat controversial result is contradicted in a study by Rayner *et al*. (1999) which, using global CO_2 measurements over the period 1980–95 and a long-term record of $^{13}C/^{12}C$ and O_2/N_2, suggests net sinks of 0·3 and

0·2 Gt C year^{-1} in the North American temperate and boreal zones, respectively, 0·2 Gt C year^{-1} in Europe and zero in Siberia. For the terrestrial tropics they estimate a net sink of 0·2 Gt C year^{-1}, implying a tropical carbon sequestration rate of approximately 1·8 Gt C year^{-1} to compensate for the tropical deforestation rates estimated by Houghton (1996a). A recent analysis of CO_2 concentrations alone (Bousquet *et al*. 1999) also suggests modest sinks in North America (0·5 Gt C year^{-1}) and Europe (0·3 Gt C year^{-1}), similar to Rayner *et al*. (1999), but a very large sink in Siberia (1·5 Gt C year^{-1}) that is offset by a large net tropical source of 1·1 Gt C year^{-1}, particularly concentrated in tropical Asia (0·8 Gt C year^{-1}).

There is clearly no current consensus in these results from inverse modelling. Perhaps the study of Rayner *et al*. (1999) is the only one which approaches consistency with the current, albeit inconclusive, ground-based evidence. The lack of consistency amongst studies suggests that this approach still faces a number of problems. Amongst the principle difficulties are the following:

1 The inverse problem is very poorly constrained, and frequently an *a priori* guess of terrestrial sources and sinks is made to help constrain the solution (Enting, Trudinger & Francey 1995).

2 The current network of long-term flask sampling sites is rather sparse and strongly biased towards coastal sites that sample the marine boundary layer, and is thus not well suited to determining the terrestrial carbon budget. The network is particularly sparse over the southern oceans and tropical continents but this problem will diminish as the network continues to be extended. North America is the best-covered continent, and therefore the most constrained in any regional analysis (Fan *et al*. 1998).

3 A number of the long-term records appear to have methodological errors in the early years. For example, prior to 1988 the three longest ^{13}C records (as described by Keeling *et al*. 1995, Francey *et al*. 1995 and Nakazawa *et al*. 1997) show major differences from one another in interannual behaviour that appear to be too large to be of source/sink origin and imply systematic error.

4 The tropics in particular are almost totally unconstrained because the intensity of tropical convection results in vigorous mixing and dilution of any CO_2 signal vertically through the troposphere and horizontally to higher latitudes (Denning, Fung & Randall 1995). The carbon balance of the tropics is therefore more or less estimated as a residue of the results calculated for mid- and high latitudes. If the complex mixing between tropical and mid-latitudes is inaccurately modelled, it is possible that any carbon sink at tropical latitudes can 'leak out' and appear as a sink at mid- and high latitudes.

5 The atmospheric boundary layer is shallower in winter and at higher latitudes, and so changes in concentrations of gases are more sensitive to surface fluxes in such conditions. The covariance of this effect with seasonality of photosynthesis and respiration in the biosphere produces an interhemispheric CO_2 concentration gradi-

ent even if there were no net fluxes (Denning, Fung & Randall 1995). Accurate modelling of the seasonal and latitudinal variation of boundary layer height, and of the transport of CO_2 between the atmospheric boundary layer and the free atmosphere, is required to compensate for this effect.

FUTURE SCENARIOS

Global climate change

IPCC (1995) estimates as a 'best guess' that global mean temperature will increase by 2·4 °C by 2100, with a range of 0·8 °C to 4·5 °C according to climate model and CO_2 emission scenario. The warming is concentrated more on land (typically 3 to 4 °C) than over oceans (0 to 2 °C), predominantly because of the larger thermal inertia of the oceans. Almost all models predict a mean warming of 5 to 6 °C in the boreal region, predominantly in late autumn and winter because of the late formation of sea ice, but with only a 2 to 4 °C warming in summer, when the influence of ice is much reduced. In the temperate region the predicted warming is also mainly in winter, but generally smaller (typically 1 to 2 °C), because of the cooling effect of industrial aerosol emissions in North America, Europe and East Asia. A mean warming of 3 to 4 °C is predicted for the tropics, but less (1 to 3 °C) in the more maritime Asian tropics, with little evident seasonality.

Predictions of future precipitation and soil moisture are less reliable than those of temperature. Mean global precipitation is predicted to increase with global warming, because of higher atmospheric water vapour content and enhanced poleward transport and convergence of water vapour. Precipitation is expected to increase in winter by 0·0 to 0·5 mm d^{-1} in boreal and temperate latitudes, but much of this excess precipitation may be lost in run-off and have little impact on summer soil moisture, because the soil is close to saturation in winter. A reduction in summer soil moisture content is predicted for mid- and high latitudes, because of little change in precipitation but enhanced evapotranspiration resulting from higher surface temperatures. In the tropics mean precipitation is predicted to increase by 0·0 to 1·0 mm d^{-1} and the Asian monsoon will probably strengthen, but there is little agreement on the general spatial pattern of increase. Many models predict a change in the distribution of sea surface temperature similar to El Niño conditions, and this would imply an intensified and prolonged dry season in Indonesia and central and eastern South America, and intensified rain in western South America.

A primary difficulty in assessing the response of forests to climate change is that each climatic variable may have both positive and negative effects on forest carbon balance. For example, higher soil temperatures result in both enhanced soil respiration (Raich & Schlesinger 1992) and enhanced soil mineralization and nutrient availability to the trees (Melillo *et al.* 1993); enhanced precipitation is also associated with enhanced cloud cover; higher air temperatures may lead to longer growing seasons but also to enhanced moisture stress. The history of vegetation distribution since the LGM (already considered above) suggests that, without anthropogenic limitations, a change to a warmer, moister climate results in an overall expansion of forest biomes at the expense of tundra at high latitudes, at the expense of semiarid vegetation in mid-latitudes, and at the expense of savanna in the tropics. However, the upper temperature and moisture limits to these processes of replacement are not known. Moreover, the response of forest biomes to rapid change may involve a number of transient phenomena with different response times, such that a biome may switch from being a carbon source to a sink or vice versa as climate change proceeds.

For example, a temperature rise at high latitudes will lead to higher respiration rates, and oxidation of soil carbon, much of which has accumulated at high latitudes over the past 12 000 years since the retreat of the ice sheets. Increased evapotranspiration may also increase late summer moisture stress and thus decrease late summer photosynthesis. On the other hand, higher temperatures may also result in a lengthened growing season and enhanced decomposition and release of soil nutrients. The modelling study by Bergh (1998) of a young Norway spruce stand predicted a three-week extension of the growing season and a 17% increase in N_p for a 2 °C rise in temperature. For a 4 °C rise in temperature there was a seven-week extension of the growing season but no further increase in N_p, because of the compensating effects of enhanced tissue respiration. Overall, the field evidence suggests that these opposing effects are currently in approximate balance: NEE measurements at the nine BOREAS forest sites (Sellers *et al.* 1997) indicate only small net sinks in the Canadian boreal forest during the unusually warm years of the 1990s. In particular, the study by Goulden *et al.* (1998) of a black spruce site at the northern limit of the forest in Manitoba showed that the net sequestration of carbon into woody biomass was balanced by the release of ancient soil carbon as a direct result of the lowering of the permafrost layer. A number of recently initiated soil-warming experiments (Bergh & Linder 1999) may shed further light on this issue over the next 10 years.

Atmospheric and satellite data provide further insights: Keeling *et al.* (1996a) reported that the amplitude of the annual cycle of CO_2 concentration has increased since the 1960s by 20% at mid-latitudes and by 40% at high latitudes, and the increase was largest in warm years. These observations can be explained both by increased carbon uptake in photosynthesis, and by enhanced winter respiration. In addition, the timing of the drawdown in spring has advanced by seven days, implying a lengthening growing season. Myneni *et al.* (1997) found a similar pattern in remotely sensed vegetation indices at high latitudes (45°N to 70°N). There is therefore significant evidence for increasing vegetation activity resulting from warming temperatures at high latitudes – what remains unclear is the corresponding response of the soil carbon pools.

There is similar uncertainty with regard to the future of tropical forests: possible increase in productivity, resulting from CO_2 and N fertilization (see the following section),

may be compensated for by enhanced respiration of the soil carbon pool. One source of uncertainty is the role of enhanced soil mineralization rates at higher temperatures. A number of authors (Melillo *et al.* 1993) have argued that this will have an important impact in boosting nutrient availability in resource-poor tropical soils, whereas Houghton, Davidson & Woodwell (1998) have recently argued that most of the enhanced nutrient supply will be utilized by soil microbes with little extra being available for plant growth. Depending on its seasonal distribution, enhanced precipitation is likely to mitigate soil moisture limitation in the dry season and allow expansion of rain forest into savannas, but its uncertain spatial distribution may lead to gains in some areas balanced by losses in others. In addition, the associated increase in cloudiness is likely to reduce photosynthesis so that the overall effect may be little increase in forest productivity. Figure 3 demonstrates that for the Amazonian site these two factors (precipitation and cloudiness) balanced each other in 1996 so that there was almost no difference in NEE between the wet and dry seasons.

Increases in CO_2 concentration

The average atmospheric CO_2 concentration has increased from a pre-industrial concentration of about 280 μmol mol^{-1} to 364 μmol mol^{-1} in 1997, and is currently increasing at about 1·5 μmol mol year^{-1} (Keeling & Whorf 1998). This is likely to have a fertilizing impact on global C_3 photosynthesis and to increase water-use efficiency; the extent and evidence for this effect is comprehensively discussed elsewhere in this volume.

In recent years a number of studies have attempted to model the response of the terrestrial biosphere to rising CO_2 concentrations (Kohlmaier *et al.* 1987; Goudriaan 1992, Polglase & Wang 1992; Gifford 1994; Friedlingstein *et al.* 1995; Lloyd & Farquhar 1996). It now appears likely that enhanced atmospheric CO_2 concentrations will increase forest productivity, with a resulting terrestrial carbon sink of 1 to 2 Gt C year^{-1}. It must be emphasized that a sequestration rate of 2 Gt C year^{-1} does not require that global net primary productivity, N_p, be increased by this amount; the lag time between carbon acquisition through primary production and carbon loss through respiration is also important. The net carbon sequestration by an ecosystem is the balance between carbon uptake, equal to N_p, and carbon respiration, which is approximately equal to the value of N_p, τ years in the past, where τ is the mean residence time for carbon in the ecosystem. For a linear increase in N_p followed by a linear increase in respiration with lag time τ, the rate of carbon sequestration can therefore be estimated as $dM/dt = \tau\, dN_p/dt$ (Taylor & Lloyd 1992), where M is the total (plant and soil) carbon density, and τ can be calculated as $\tau = M/N_p$. We estimate τ to be 30, 20, and 90 years for the tropical, temperate and boreal case-study sites, respectively (Table 6). This calculation should be treated with some caution: as explained in the section entitled Stand dynamics, above, the calculated value of τ for the boreal forest may be an overestimate, and that for the temperate forest may be an

underestimate. If a terrestrial carbon sink of 2 Gt C year^{-1} were exclusively and evenly distributed over the current extent (4165 Mha) of tropical, temperate and boreal forests (Table 1), this is equivalent to a per unit area sequestration rate of 50 g C m^{-2} year^{-1}. Assuming that the values of N_p and τ calculated for each case-study site (Table 6) are representative of the appropriate biome, the rates of increase of N_p required to generate this sequestration rate are 1·7, 2·5 and 0·6 g C m^{-2} years^{-1}, or, relative to current values of N_p, 0·1, 0·2 and 0·1% year^{-1} for the tropical, temperate and boreal forests, respectively. This seems a very plausible possibility.

Many of the model studies (Polglase & Wang 1992; Gifford 1994; Wang & Polglase 1995; Lloyd & Farquhar 1996) suggest that the most productive biomes (i.e. tropical and warm temperate forests) should dominate the direct response to CO_2 fertilization. Even allowing for the likelihood of a warming-lengthened growing season at high latitudes (Myneni *et al.* 1997), it seems difficult to argue for a carbon sink focused solely at high latitudes, as suggested by some global CO_2 inversion studies (described in the section on CO_2 $^{13}CO_2$ and O_2/N_2 studies, above). In addition to boosting overall forest productivity, CO_2 fertilization may increase the competitive advantage of C_3 forests against C_4 grasslands and savannahs, and lead to the expansion of forests in transition areas. However, this factor may be counteracted by the higher light-use efficiency of C_4 plants at high temperatures.

Increasing rates of N deposition

Human activity has also had a major impact on the global nitrogen cycle: global nitrogen fixation is estimated to have increased from a natural biological rate of 0·09 to 0·13 Gt N year^{-1} to about 0·25 Gt N year^{-1}, with a current annual rate of increase of 0·6% year[1] (Galloway *et al.* 1995). This increase is the result of fertiliser production (about 0·08 Gt N year^{-1}), cultivation of legumes, pulses, groundnuts and rice (about 0·04 Gt N year^{-1}) and fossil fuel combustion (0·02 Gt N year^{-1}). Fossil fuel combustion directly releases NO_x into the atmosphere, but much of the N release associated with land use is also released to the atmosphere, in the form of ammonia (NH_3) from pastures and fertilized fields, as NO and N_2O from fertilized soils, and as HNO_3 from biomass burning. However, reactive N compounds have short atmospheric residence times of hours to days, so that N is rapidly deposited downwind of emission areas, particularly in East Asia, eastern North America and Europe, where deposition rates can be up to 100 kg N ha^{-1} year^{-1}. In boreal and tropical forest areas, deposition rates are generally much lower (5 to 10 kg N ha^{-1} year^{-1}) because of distance from major sources, except in areas adjacent to biomass burning (particularly in West Africa) where deposition may reach about 60 kg ha^{-1} year^{-1} (Galloway *et al.* 1995). However, because of the highly effective, turbulent exchange between forest canopies and the atmosphere, rough coniferous forest canopies, in particular, may scavenge 30 kg N ha^{-1} year^{-1} at sites where the nominal deposi-

tion rate is only 5 kg ha^{-1} year^{-1} (D. Fowler, personal communication).

Several recent studies have attempted to estimate the effect of increased N deposition on carbon sequestration (Townsend *et al*. 1996; Holland *et al*. 1997). They suggest a global N-induced carbon sequestration rate of the order of 1 Gt C year^{-1}, similar to that estimated to be induced by CO_2 fertilization, and concentrated particularly in high deposition areas such as eastern North America, central Europe and East Asia. Experimental studies on young trees show significant interactions between N and CO_2 fertilization effects (McGuire, Melillo & Joyce 1995; Jarvis 1998). The combination of elevated CO_2 concentration and N inputs may well be the reason why tree growth is on the increase (see section entitled Biomass inventories, above). On the other hand, a recent study of uptake of ^{15}N tracer at nine temperate forest sites found that only a small fraction (20%) of added N was fixed by vegetation, with most ending up in soils (Nadelhoffer *et al*. 1999). A key question is whether the global forests will become carbon-saturated in the foreseeable future, thus losing their carbon sequestration capacity as suggested by Cao & Woodward (1998). With the present, increasing scale of N inputs, this does not seem very likely, but the damaging effects of acute high rates of N deposition to forests near centres of population and industry (Schulze 1989) may also dampen carbon sequestration rates.

Another question is whether increases in plant productivity will be limited by availability of other nutrients, in particular phosphorus, which is relatively immobile but vital to productivity (Smeck 1985). Tropical forest soils, particularly, in Amazonia, contain very low amounts of available phosphorus (Vitousek & Sandford 1986) and the primary supply is mineralization of soil organic matter and inorganic compounds. It has therefore often been assumed that low phosphorus availability may limit the CO_2 fertilization of tropical forests (Friedlingstein *et al*. 1995; McKane *et al*. 1995). On the other hand, Lloyd (1999) argues that there is much recent evidence that high CO_2 concentrations improve plant carbohydrate availability, which in turn enhances phosphorus acquisition processes such as mycorrhizal colonization (Wang, Rey & Jarvis 1998; Staddon & Fitter 1998), production of phosphatase enzymes which break down soil organic P compounds (Duff, Sarath & Plaxton 1994), and exudation of organic acids which increases mineralization of inorganic P (Bolan *et al*. 1994). Thus the forest phosphorus cycle may simply speed up to meet the demands of enhanced plant growth.

Where is the forest carbon sink?

In conclusion, most modelling studies suggest that CO_2 and N fertilization are boosting global forest primary productivity, and this in turn results in a carbon sequestration rate of 1 to 3 Gt C year^{-1}, a result that is in accordance with requirements to balance the global carbon budget (see Introduction), and with field biomass studies (see section on biomass inventories, above). A case can be made for a significant carbon sink in each major forest biome: in tropical forests because of CO_2 fertilization of their intrinsic high

productivity, in temperate forests because of regrowth and high N deposition rates, and in boreal forests because of their lengthening growing season. Indeed, it is likely that the terrestrial carbon sink is not confined to or dominated by any one biome or region.

The direction of the effect of climate change is less certain, but for the moment its effects are particularly concentrated at boreal latitudes. There the evidence suggests that warming temperatures are leading to an enhanced growing season, but this effect may be negated or reversed by enhanced oxidation of soil carbon. This underlines the importance of understanding and monitoring the behaviour of soil carbon, which is as important to the carbon balance of the terrestrial biosphere as is the vegetation.

Some simple insight can be obtained by inverting the calculations in the section on increases in CO_2 concentration, above. If we assume that, for whatever reason, N_p has risen uniformly at 0.1% year^{-1} in all three forest biomes for several decades, we can examine where the carbon is likely to be sequestered. The sequestration rate for each biome is proportional to the area of the biome (from Table 1), the intrinsic N_p per unit area (from Table 6, assuming the case-study sites are representative), and the carbon residence times (from Table 6, calculating the soil carbon residence times using the same value of N_p as for biomass carbon residence times). The calculation predicts a global sequestration rate of 1.59 Gt C year^{-1}, of which 0.78 Gt C year^{-1} (49%) is in tropical forests, 0.18 Gt C year^{-1} (11%) is in temperate forests and 0.63 Gt C year^{-1} (40%) in boreal forests. Within the tropical forest, the calculation suggests that 54% of the sequestration is in biomass and 46% in soil organic matter, in the temperate forest 54% is in biomass, and in the boreal forest only 13% is in biomass. Overall, 38% of the sequestration is calculated to be in biomass, and 62% in soil. The results are simplistic but nonetheless instructive. There is likely to be a large carbon sink in intact tropical forests, because of their large area and high productivity, unless a factor such as phosphorus availability is strongly limiting N_p increase. Moreover, if there is already a carbon sink in tropical forest biomass, as suggested by Phillips *et al*. (1998), there is also likely to be a further sink of similar magnitude in tropical forest soils, unless rising temperatures are resulting in enhanced soil respiration. Although the temperate forest calculation should be treated with caution because of the unusual case-study site, the result does suggest that total sequestration in temperate forests is small because of their limited area coverage. However, as many of these forests are actively regrowing, their rates of increase of N_p may be higher than for other forests. It is much more difficult to sequester carbon in boreal forest biomass than in the other forests, because of the low productivity of boreal forest. Unless boreal forest N_p is increasing much more rapidly in boreal forests than in other forests, a boreal carbon sink is much more likely to be in the soil, because of its long carbon residence time. However, the size of the boreal forest active carbon pool may be much smaller than the value estimated here, or there may be enhanced carbon loss as a result of high latitude climate warming. Put another way, if boreal

forest soils are losing carbon, it seems unlikely that boreal forest biomass is sequestering sufficient carbon in compensation to result in a large boreal carbon sink. The behaviour of the soil carbon reserves is critical.

The future: management of terrestrial carbon resources

With the agreement of the Kyoto Protocol in December 1997, the terrestrial carbon cycle has attained a new political prominence. This protocol provides for reduction of carbon emissions not only by limiting fossil fuel production, but also by increasing net carbon sequestration in managed terrestrial vegetation, particularly forests. Individual industries are also increasingly keen to show themselves to be 'carbon neutral' by offsetting their carbon emissions against sequestration by forests, both outside or within the limited provisions of the Protocol (i.e. afforestation, reforestation and deforestation since 1990; Steffen *et al*. 1998). Thus the new challenge is the management of carbon resources, both to conserve existing stocks and to remove carbon from the atmosphere by adding to them.

However, there remains some uncertainty as to the magnitude and geographic location of the carbon sink in existing old-growth forests. As reviewed in this paper, research into terrestrial carbon sequestration has advanced rapidly in recent years, but all scientific approaches (whether global atmospheric, micrometeorological or forest inventory-based) still face a number of methodological difficulties. Until these problems are solved and there is greater consistency in results from various scientific approaches, appropriate caution needs to be applied when extrapolating wider conclusions about the terrestrial carbon sink. In the post-Kyoto world, the location of the terrestrial carbon sink will become an issue with enormous political and economic ramifications, and tentative scientific findings may be seized upon and over-interpreted by various political lobbies. However, this political interest arises precisely because the results have important implications, and, as long as the scientific caveats are made explicit, they have an important role in informed political debate.

Another major source of uncertainty is the behaviour of soil carbon stocks. Globally, the long-term carbon balance is determined as much by the replenishment and depletion of the large stock of carbon in the soil, as by changes in vegetation biomass. Carbon management programmes must incorporate this stock of carbon in the soil. Conventional forest management is mainly concerned with the volume and value of the stem wood product, and shows little regard for soil carbon stocks, which can be particularly vulnerable to management operations (Cannell, Dewar & Pyatt 1993).

Where the stock of carbon in soil and trees is large, as in old-growth stands, preservation becomes especially important. Superficially, it might seem advantageous for C sequestration to harvest an old-growth stand with NEE = 0, put much of the timber into long-lifetime timber products such as buildings, and replace the forest with a young, fast-growing stand with NEE = 5 t C ha $^{-1}$ years $^{-1}$. However,

with current practice, much of the biomass carbon is rapidly lost to the atmosphere via decomposition of waste products, fuel consumption and paper production. For example, Harmon, Ferrell & Franklin (1990) estimated for timber harvests in the north-west U.S. that only 42% of harvested timber ended up as long-lived products, and stocks of carbon in living biomass on the site would take 200 years to be replaced by regrowth. They concluded that the conversion of 1·5 Mha of old-growth forests to plantations in western Oregon and Canada has resulted in the release of 1·6 Gt C to the atmosphere.

To understand natural systems and meet management goals effectively, we shall need complete C inventories of forest stands, as attempted here, with good estimates or measurements of the influxes and effluxes of carbon, and sound knowledge of the variables and the processes that drive and constrain the fluxes. This knowledge needs to be integrated with an understanding of forest dynamics, disturbance and variability at landscape scale to arrive at carbon balance of whole biomes, In this review we have tried to show how well we are currently equipped with this knowledge. There is clearly far better knowledge of the carbon balance of forests today than when reviewed for temperate forests, for example, by Jarvis & Leverenz (1983), but it still lacks integration in a holistic framework comprising ecophysiology (the nutrient, water and energy balances), natural forest dynamics and spatial patterns of land use management and natural variability.

This paper has attempted to show some of the issues and uncertainties that will need to be addressed as we move into an era when the understanding and management of the carbon cycle of terrestrial vegetation will become of increasing importance.

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