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This review places into context the role that forest ecosystems play in the global carbon cycle, and their potential interactions with climate change. We first examine the natural, preindustrial carbon cycle. Every year forest gross photosynthesis cycles approximately one-twelfth of the atmospheric stock of carbon dioxide, accounting for 50% of terrestrial photosynthesis. This cycling has remained almost constant since the end of the last ice age, but since the Industrial Revolution it has undergone substantial disruption as a result of the injection of 480 PgC into the atmosphere through fossil-fuel combustion and land-use change, including forest clearance. In the second part of this paper we review this 'carbon disruption', and its impact on the oceans, atmosphere and biosphere. Tropical deforestation is resulting in a release of $1.7 \, \text{PgC yr}^{-1}$ into the atmosphere. However, there is also strong evidence for a 'sink' for carbon in natural vegetation (carbon absorption), which can be explained partly by the regrowth of forests on abandoned lands, and partly by a global change factor, the most likely cause being 'fertilization' resulting from the increase in atmospheric CO_2. In the 1990s this biosphere sink was estimated to be sequestering $3.2 \, \text{PgC yr}^{-1}$ and is likely to have substantial effects on the dynamics, structure and biodiversity of all forests. Finally, we examine the potential for forest protection and afforestation to mitigate climate change. An extensive global carbon sequestration programme has the potential to make a particularly significant contribution to controlling the rise in CO_2 emissions in the next few decades. In the course of the whole century, however, even the maximum amount of carbon that could be sequestered will be dwarfed by the magnitude of (projected) fossil-fuel emissions. Forest carbon sequestration should only be viewed as a component of a mitigation strategy, not as a substitute for the changes in energy supply, use and technology that will be required if atmospheric CO_2 concentrations are to be stabilized.

Keywords: carbon sink; deforestation; climate change;
Kyoto Protocol; tropical forest

1. Introduction

In recent centuries, human activities have fundamentally altered many of the Earth's biogeochemical cycles. Among the first recognized and most prominent of these

changes has been the modification of the global carbon cycle. The dramatic release of carbon trapped by both prehistoric ecosystems (i.e. fossil fuels) and modern-day vegetation has led to a 31% increase in concentrations of atmospheric carbon dioxide (CO_2) from a preindustrial concentration of *ca.* 280 ppm to 368 ppm in 2000. This concentration has certainly not been exceeded during the past 420 000 years, and probably not during the past 20 million years. Moreover, *the rate of increase* in CO_2 concentration during the past century is at least an order of magnitude greater than the world has seen for the last 20 kyr (Prentice *et al.* 2001). CO_2 is the most important of the greenhouse gases that are increasingly trapping solar heat and warming the global climate. In addition to climatic warming, this extra carbon dioxide may have a number of effects on terrestrial ecosystems, from increasing plant growth rates and biomass to modifying ecosystem composition by altering the competitive balance between species.

The focus of this paper, and this theme issue, will be on the role of forests and forest management in this global carbon cycle. In their pre-agricultural state, forests are estimated to have covered *ca.* 57 million km^2 (Goldewijk 2001), and contained *ca.* 500 PgC ($1 PgC = 1 GtC = 10^{15}$ g of carbon) in living biomass and a further 700 PgC in soil organic matter (figure 3), in total holding more than twice the total amount of carbon in the preindustrial atmosphere and circulating 10% of atmospheric CO_2 back and forth into the biosphere every year through gross photosynthesis. A reduction of global forest cover has accompanied human history since the dawn of the agricultural revolution 8000 years ago, but by 1700 only *ca.* 7% of global forest area had been lost (Ramankutty & Foley 1999; Goldewijk 2001). The intensity and scale of human alteration of the biosphere has accelerated since the industrial revolution, and by 1990 *ca.* 20–30% of original forest area had been lost. This loss of forest cover has contributed 45% of the increase in atmospheric CO_2 observed since 1850. In recent decades, carbon emissions from fossil fuels have surpassed those from deforestation, but land-use change still contributes *ca.* 25% of current human-induced carbon emissions. However, just as the loss of forests has significantly contributed to the atmospheric 'carbon disruption', so good forest management, the prevention of deforestation, and the regrowth of forests have a significant potential to lessen the carbon disruption.

In this review we place into context the role of forests in the global carbon cycle and climate change. In § 2 we examine the preindustrial 'natural' carbon cycle, both in recent millennia and during the ice ages. In §§ 3 and 4 we review the anthropogenic 'carbon disruption', examining the influences of both land-use change and fossil-fuel combustion on the global carbon cycle, and the causes, magnitudes and uncertainties of the natural 'carbon sinks' in both oceans and terrestrial ecosystems. Finally, in § 5, we peer into the future and examine the influence that forest management and protection can play on the climate of the 21st century.

2. The natural global carbon cycle

(a) *The global carbon cycle before the industrial carbon disruption*

As our planet emerged from the last glacial maximum 11 000 years ago, the climate first warmed and became wetter, but subsequently underwent a slight cooling and aridification 8000 years before present (BP). Human populations and activities increased substantially during this epoch, the Holocene, but, until the Industrial
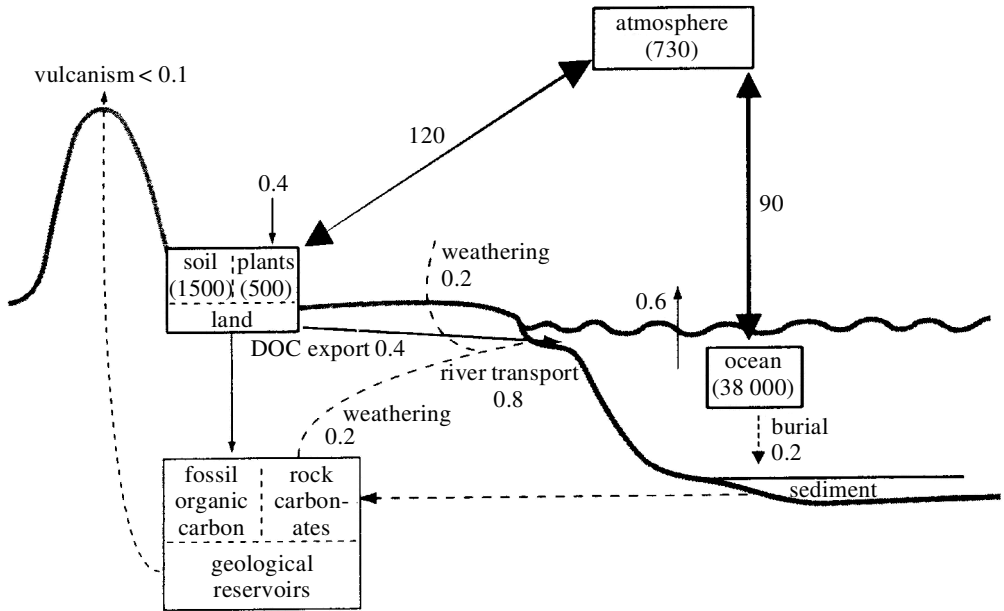
Figure 1. Main components of the carbon cycle. The thick arrows represent gross primary production and respiration by the biosphere and physical sea–air exchange. The thin arrows denote natural fluxes which are important over longer time-scales. Dashed lines represent fluxes of carbon as calcium carbonate. The units for all fluxes are PgC yr^{-1}; the units for all compartments are PgC.

Revolution, atmospheric CO_2 concentration varied only a little, increasing overall from a post-glacial minimum of 260–285 ppm in the late 19th century (figure 2).

The relative constancy in CO_2 concentrations during the previous few millennia implies a rough constancy in the global carbon cycle. Figure 1 identifies the main global stocks of carbon and the principal fluxes among them for the natural or 'pre-carbon disruption' era. There are four main carbon stores, which are, in decreasing order of size, the geological, the oceanic, the terrestrial and the atmospheric reservoirs. Although the smallest component, it is changes in the atmospheric carbon store that ultimately provide the direct link between changes in the global carbon cycle and changes in climate.

The thick arrows in figure 1 denote the most important fluxes from the point of view of the contemporary CO_2 balance of the atmosphere: they represent gross primary production (i.e. absorption of carbon from the atmosphere through photosynthesis) and respiration (release of carbon to the atmosphere) by the land surface, and physical sea–air exchange. Under 'natural' conditions these two main carbon transfer pathways between the atmosphere and the land or the oceans are in approximate balance over an annual cycle, and represent a total exchange of 210 PgC yr^{-1}, of which the larger share (120 PgC yr^{-1}) is taken by the land (Prentice *et al.* 2001). This annual exchange is more than 25 times the total amount of carbon annually released into the atmosphere through human activities. Forests are responsible for about half of total terrestrial photosynthesis, and hence for *ca.* 60 PgC yr^{-1}. The processes governing this exchange are biological and physical, and hence are respon-

sive to climate. Consequently, a fractional net change in them resulting from small changes in climate (e.g. temperature) could match the magnitude of the human-linked emissions causing them.

A number of additional fluxes also occur as part of the natural carbon cycle (figure 1). The transfer by plants of $0.4 \, \text{PgC} \, \text{yr}^{-1}$ of inert carbon from the atmosphere to the soil is balanced by the outflow of dissolved organic carbon (DOC) through rivers to the sea (Schlesinger 1990). This outflow is joined by a flux of $0.4 \, \text{PgC} \, \text{yr}^{-1}$ of dissolved inorganic carbon (DIC) derived from the weathering of rock carbonates, which combine with atmospheric CO_2 to form DIC. In total, $0.8 \, \text{PgC} \, \text{yr}^{-1}$ flow through rivers to the sea, where all of the DOC and half of the DIC are ultimately respired to the atmosphere. This leaves $0.2 \, \text{PgC} \, \text{yr}^{-1}$ to be deposited in deep-sea sediments as fixed carbonates, the remains of dead marine organisms. These deposits are the precursors of carbonate rocks. Over still longer time-scales, organic matter is buried as fossil organic matter (including fossil fuels), and CO_2 is released into the atmosphere as a result of tectonic activity, such as vulcanism (Williams *et al.* 1992; Bickle 1994). These longer time-scale processes exert an important influence on atmospheric CO_2 concentrations on geological time-scales (millions of years), but have had little influence at the time-scale corresponding to human expansion (100 000 years).

(i) *Changes in atmospheric* CO_2 *over long and short time-scales*

The description of the carbon cycle in figure 1 is most relevant to the relatively constant climate of the Late Holocene, but atmospheric CO_2 concentrations have not always been so stable (figure 2). Very high concentrations of over 3000 ppm probably existed during at least two very early periods, 400 and 200 Myr BP (Berner 1997). As photosynthetic machinery evolved and became globally dominant, CO_2 was drawn out of the atmosphere and there is geochemical evidence pointing to concentrations of less than 300 ppm by *ca.* 20 million years BP (Pagani *et al.* 1999; Pearson & Palmer 1999, 2000). It is likely, therefore, that atmospheric CO_2 concentrations in the current century are significantly higher than at any time during the last 20 million years.

On more recent time-scales measurements of the constituents of deep-ice bubbles in the Antarctic have provided information on glacial–interglacial transitions. The high-quality measurements of the CO_2 record from the Vostock ice core give us clear-sighted vision of the past four glacial cycles, over a period of 420 kyr (Petit *et al.* 1999: Fischer *et al.* 1999). The results show atmospheric CO_2 concentrations varied between 180 and 300 ppm, with lower values during glacial epochs (figure 2a). It is likely that more C is stored on land during interglacials, and the observed higher atmospheric CO_2 during these periods must be accounted for by oceanic processes of C release. Overall, planetary orbital variations are clearly the pacemaker of such multi-millennial changes in climate, but coincidental changes in CO_2 concentration have played a key role in locking-in these 100 kyr cycles by amplifying their effects, rather than by initiating them (Lorius & Oeschger 1994; Shackleton 2000).

(b) *The terrestrial carbon cycle*

The storage of carbon on land is partitioned between soil and vegetation. Globally, soils contain more than 75% of all terrestrial carbon stocks, although their contribution to the total varies with latitude and land use (figure 3a). Forests and
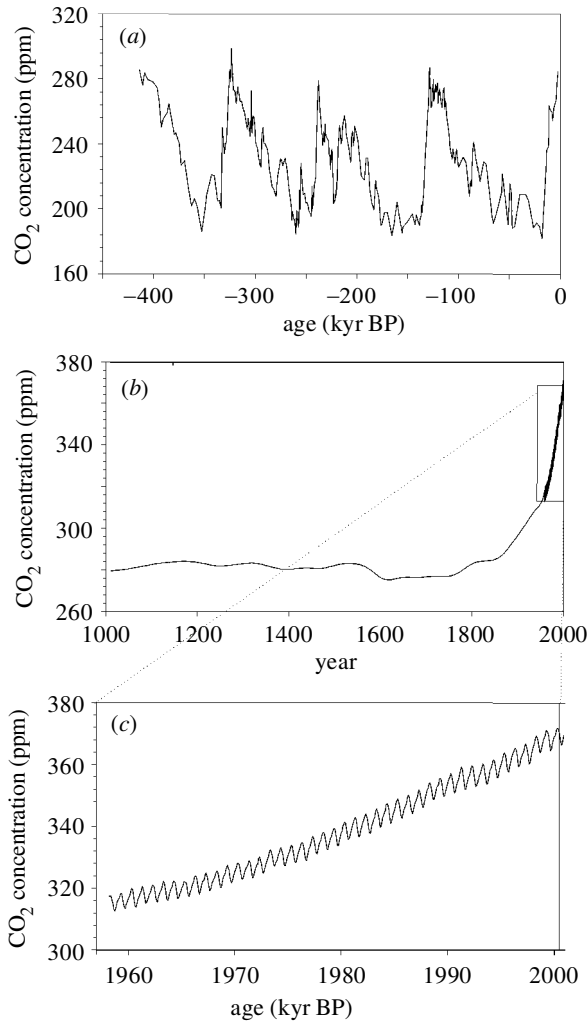
Figure 2. Variation in atmospheric CO_2 concentration on different time-scales. (*a*) CO_2 concentrations during glacial–interglacial transitions, obtained from measurements of CO_2 in deep-ice bubbles, from the Vostok Antarctic ice core (Petit *et al.* 1999; Fischer *et al.* 1999). (*b*) CO_2 concentrations during the last millennium, obtained from ice-cores at the Law Dome, Antarctica (Etheridge *et al.* 1996). (*c*) Direct measurements of CO_2 concentration in the Northern and Southern Hemispheres (Keeling & Whorf 2000).

wooded grasslands/savannahs are by far the biggest carbon storehouses, respectively accounting for *ca.* 47% and 25% of the global total. Other ecosystems tend to maintain comparatively little aboveground carbon, with the stock in soil varying between 100 and 225 PgC (figure 3*b*).

In forested ecosystems, carbon accumulates through the absorption of atmospheric CO_2 and its assimilation into biomass. Carbon is stored in various pools in a forest ecosystem: above- and below-ground living biomass, including standing timber, branches, foliage and roots; and necromass, including litter, woody debris, soil organic matter and forest products. Approximately 50% of the dry biomass of trees is
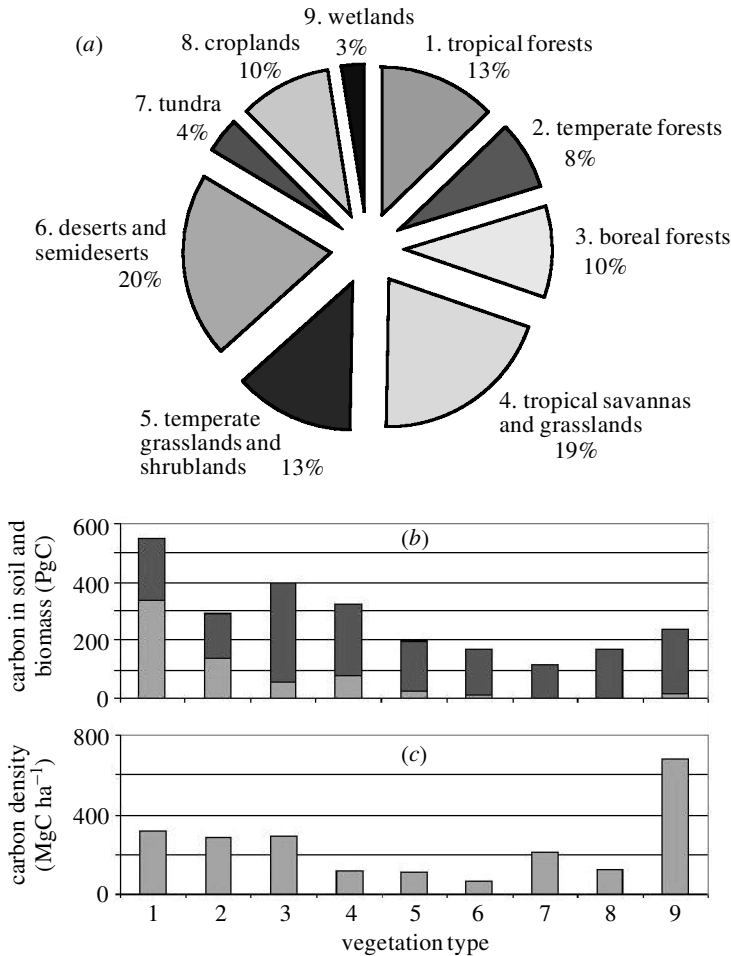
Figure 3. Global area and carbon content of different vegetation types. (a) The area of each vegetation type as a percentage of the global total (13.73×10^9 ha). The legend in panel (a) is used in (b) and (c): (b) total carbon (PgC) in soil (dark shading) and vegetation (light shading); (c) total carbon density (MgC ha^{-1}). Data from Roy et al. (2001) and Dixon et al. (1994).

carbon. Any activity that affects the amount of biomass in vegetation and soil has the potential to sequester carbon from, or release carbon into, the atmosphere. In total, boreal forests account for more carbon than any other terrestrial ecosystem (26%), while tropical and temperate forests account for 20% and 7%, respectively (Dixon et al. 1994; Prentice et al. 2001). There are, however, considerable variations among forest types in where carbon accumulates. Up to 90% of the carbon in boreal ecosystems is stored in soil, while in tropical forests the total is split fairly evenly above and below ground. The primary reason for this difference is temperature, which at high latitudes restricts soil-organic-matter decomposition and nutrient recycling, but at low latitudes encourages rapid decomposition and subsequent recycling of nutrients. In wetlands carbon in plant biomass is also a small proportion of the total carbon present: slow decomposition rates in water-laden soils (e.g. peaty soils) has led to a high carbon density in these environments (figure 3b).
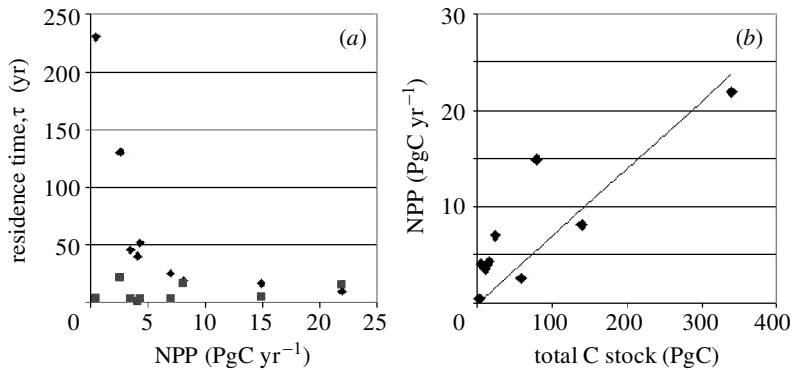
Figure 4. The relationships between (*a*) net primary productivity (NPP, PgC yr^{-1}) and the residence time for carbon in soil (diamonds) and biomass (squares), and (*b*) between NPP and total (soil plus biomass) carbon stock. The vegetation types are those used in figure 3. Data from Roy *et al.* (2001) and Dixon *et al.* (1994); the relationship in the right-hand panel is significant (NPP = 0.07 C stock, $r^2 = 0.6$, $P < 0.05$).

Between 30 and 50% of the total amount of carbon absorbed by vegetation (gross primary production (GPP)) is used to support plant metabolic processes and is released back to the atmosphere as a by-product of respiration (Amthor & Baldocchi 2001). The remaining carbon is fixed as organic matter above or below the ground and is termed net primary production (NPP). Vegetation types vary in their NPP according to climate, soil type and species composition. Although broadleaf temperate forests are highly productive for part of the year, seasonality constrains their NPP, and this is effect is felt more strongly at higher latitudes.

Clearly, carbon is processed at different rates through different vegetation types. This value, expressed as the average residence time for assimilated carbon (τ, in years), can be estimated by dividing the total stock by the NPP. The result is different for soil and vegetation (figure 4*a*). With plant biomass, there is no strong relationship between NPP and τ, with τ ranging in non-crops between 3 and 22 years. However, there is a strong relationship between NPP and τ for soil: in tropical forests, where NPP is high, carbon residence time in soil is relatively short (*ca.* 10 years), while in colder environments, where NPP can be an order of magnitude lower, residence times are much longer (*ca.* 2–300 years). If we focus on plant biomass alone, the sink capacity of different types of vegetation is proportional to the product of their NPP and residence time, which turns out to be proportional to the existing biomass carbon stock. Figure 4*b* shows there is also a linear relationship between NPP and the carbon stock in plant biomass, a consequence of residence times in biomass being approximately constant across woody ecosystems.

3. The 'carbon disruption' and the Anthropocene

In the previous section we described the quasi-equilibrium state of the global carbon cycle that prevailed throughout the Holocene, and for most of human history. In recent centuries, however, human economic activity and population have accelerated enormously. Although these activities had profound local environmental effects, such as large-scale urban and industrial pollution, until recently the Earth as a whole

appeared to be a vast resource of raw materials and sink for waste products. This perspective began to change in the late 20th century. One of the most important agents contributing to this change of perspective was the appearance of a measurement that served as a quantifiable index that humans were altering the Earth's fundamental biogeochemical cycles at a global scale. This index was the concentration of carbon dioxide in the atmosphere as measured at Mauna Loa in Hawaii since 1958, and is illustrated in figure 2*c*.

The data show that atmospheric CO_2 concentrations have risen inexorably, with some seasonal and interannual variations. They indicate that the quasi-equilibrium Holocene state of the global carbon cycle, one of the most fundamental of the great global cycles, is being disrupted. This 'carbon disruption' was one of the first signals that biogeochemical cycles were being disrupted at a global scale, and subsequently evidence has emerged of similar disruption to other biogeochemical cycles. For example, the release of SO_2 to the atmosphere by coal and oil burning, globally *ca.* 160 Tg yr^{-1}, is at least twice as large as the sum of all natural emissions; more nitrogen is now fixed synthetically and applied as fertilizers in agriculture than is fixed naturally in all terrestrial ecosystems (Vitousek *et al.* 1997); and mechanized fishing removes more than 25% of the primary production of the oceans in the upwelling regions and 35% in the temperate continental-shelf regions (Pauly & Christensen 1995).

Such large-scale disruption has led to the suggestion that the modern era could be thought of as a new geological era, the Anthropocene (Crutzen 2002), with a proposed starting date in the late 18th century, coinciding with James Watt's invention of the steam engine in 1784. This represents a fundamental change of viewpoint, and a recognition that human activities and the functioning of the Earth system are now intimately entwined.

In this section we review the history and nature of the 'carbon disruption' that has been a herald of the Anthropocene. Although the rise in CO_2 may have a direct effect on terrestrial ecosystems, the most well-known effect is its potential to be the major gas driving greenhouse warming. Before examining these effects we will review the history and magnitude of emissions.

(*a*) *Fossil-fuel combustion*

Figure 5 shows the annual rate of CO_2 emissions through fossil-fuel combustion and cement production since 1750, divided between regions (Marland *et al.* 2001). By 1998, a total of 270 Pg of carbon had been emitted by these processes. Europe (including Russia) was responsible for 41% of this total, and North America for a further 31%, figures that point clearly to where the greatest burden of responsibility lies for initiating a solution to this problem. More recently, emissions from the East Asian industrial region have increased rapidly, and currently Europe, North America and East Asia each account for 25% of global fossil-fuel emissions. In terms of process, coal combustion has accounted for 51.2% of global emissions, oil for 34.4%, gas for 11.3% and cement production 1.9% of total emissions. Recently, oil and gas have risen in prominence, and the current (1998) partition of emissions is coal 35.7%, oil 42.0%, gas 18.5% and cement production 3.1%.

Fossil-fuel combustion represents the return to the atmosphere of carbon that was originally trapped by the biosphere and then transferred to geological reservoirs,
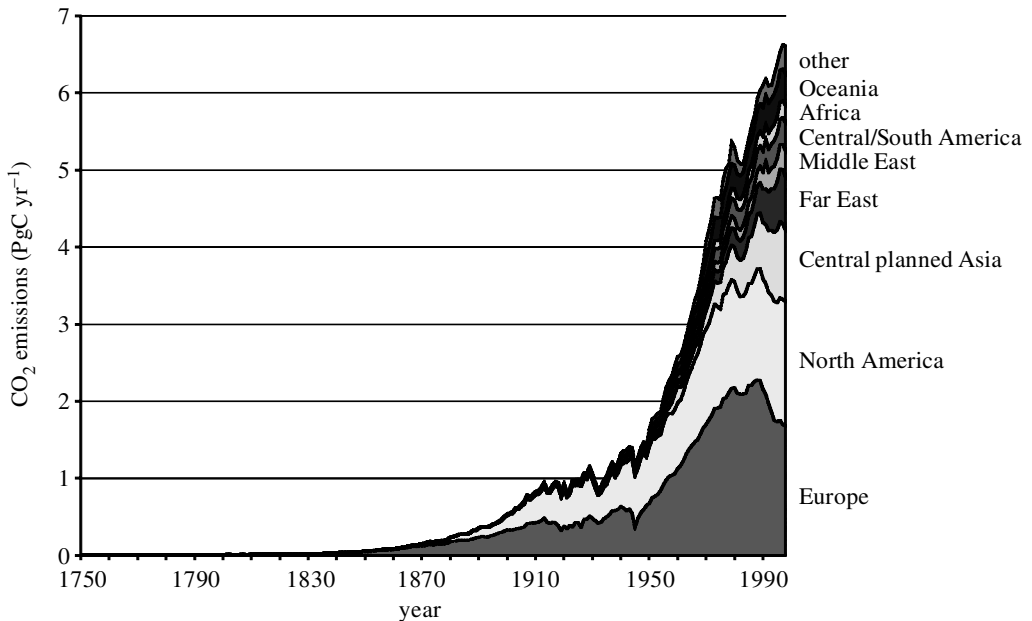
Figure 5. Total carbon emissions from fossil-fuel combustion and cement production since 1750, divided by region. Data from Marland (2001).

effectively being removed from the fast carbon cycle. The other principal source of carbon in the modern carbon disruption has been the direct transfer of carbon from the biosphere to the atmosphere, principally through the conversion of forests into croplands and pasture. This is a process older than human civilization, but the rate of change has accelerated rapidly in recent centuries.

(i) *Land-use change*

Since the discovery of fire management, most human societies have relied on modifications of natural landscapes with consequent changes in the carbon storage densities of forests, savannahs and grasslands (Perlin 1989). In particular, most temperate forests of Europe and China, and the monsoon and dry forests of India, have been progressively cleared with the spread of pasture and cropland since 7000 yr BP (Williams 1990) and only a fraction of the original forest area survived into the industrial era. Long-term clearance of tropical rain forests was much less, with notable localized exceptions such as the areas occupied by Mayan civilization in the Americas (Whitmore *et al*. 1990) and the Khmer civilization in Cambodia.

Goldewijk (2001) built a spatially explicit historical database of potential vegetation cover and historical land use to estimate the areas of natural vegetation cover lost to cropland and pasture (see table 1). By 1700, forest cover had declined by *ca.* 7%, with similar losses in steppes and shrublands. Since the industrial revolution and the era of European global colonization these processes have accelerated sharply, and by 1990 forest area had declined by 30%, steppes/savannahs/grasslands by 50%, and shrublands by 75%.

These figures only cover total conversion to pasture and cropland, and do not include the degradation of apparently intact natural ecosystems, which has also led

Table 1. *Areal extent of natural and anthropogenic ecosystems at various periods of history,*
with percentage declines relative to pre-agricultural areal extent

(All areas shown $\times 10^6$ km^2.)

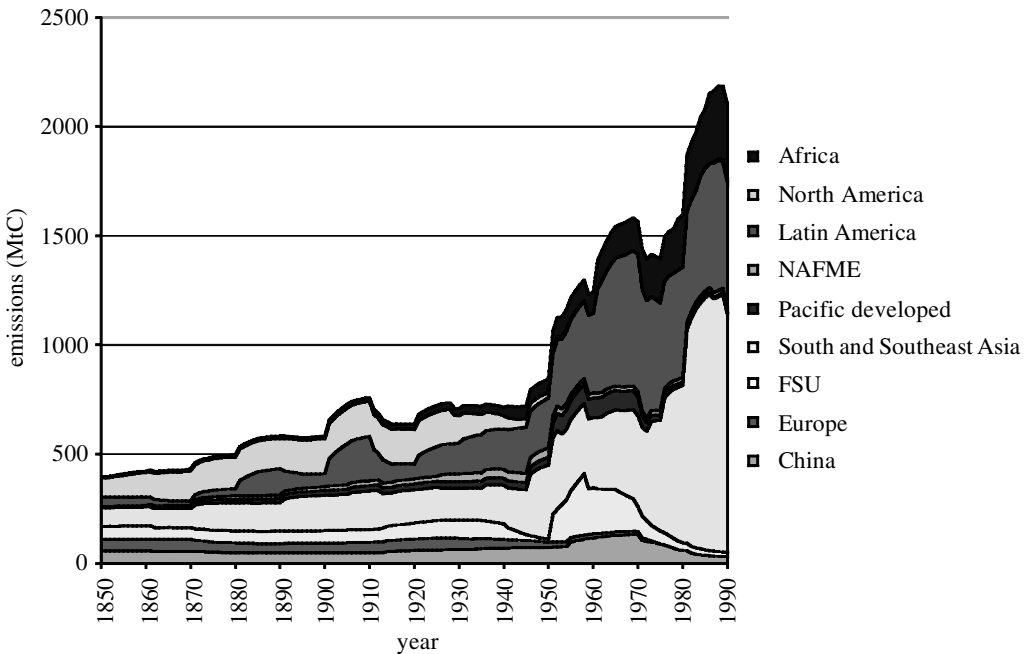|	undisturbed area	1700		1850		1990	
		area	% change	area	% change	area	% change
forest/woodland	58.6	54.4	−7.17	50.00	−14.68	41.50	−29.18
steppe/savanna/ grassland	34.3	32.1	−6.41	28.70	−16.33	17.50	−48.98
shrubland	9.8	8.7	−11.22	6.80	−30.61	2.50	−74.49
tundra/desert	31.4	31.1	−0.96	30.40	−3.18	26.90	−14.33
cropland	0	2.7		5.40		14.70	
pasture	0	5.2		12.80		31.00	

Figure 6. Estimated net carbon emissions from land-use change, divided by region. Data from Houghton (1999) and R. A. Houghton (2002, personal communication). The key follows the vertical distribution of shading in the figure.

to a substantial release of carbon. DeFries (1999) compared current and potential vegetation maps with land-use-change data from Houghton (1999) to estimate that agricultural expansion prior to 1850 resulted in the loss of 48–57 PgC, compared with 124 PgC from land-use change since 1850 (see below).

Figure 6 shows the net carbon emissions since 1850 caused by land-use change, as estimated by Houghton (1999; R. A. Houghton 2002, personal communication). Because deforestation, logging and regrowth are more difficult to monitor than indus-
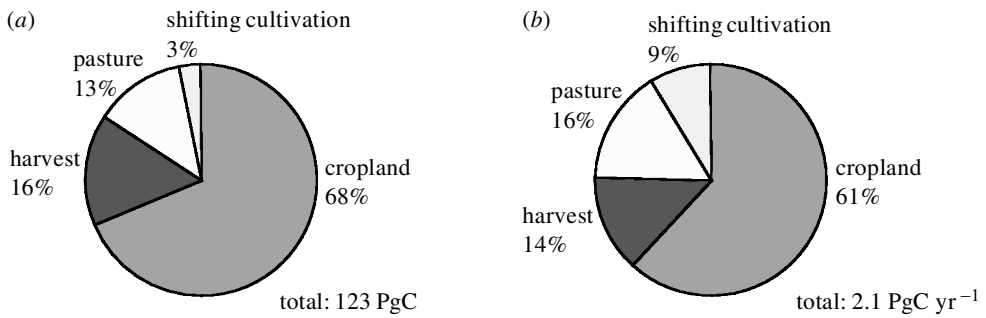
Figure 7. (*a*) Estimated total net carbon emissions from land-use change 1850–1990; (*b*) estimated annual emissions from land-use change in the year 1990. Data from Houghton (1999) and R. A. Houghton (2002, personal communication).

trial activity, and the net carbon emissions from deforestation more difficult to quantify, there is greater uncertainty in this figure than in figure 5. Houghton estimates that a total of 124 GtC was emitted between 1850 and 1990. There are remarkable variations over time. In particular, temperate deforestation rates have slowed greatly and there has even been a recent net expansion of forest cover in North America and Europe, whereas deforestation in the tropics has surged since the 1950s, which accounts for almost all current emissions. Different regions have surged at different times in response to political priorities: for example, sub-tropical Latin America in the 1900s, the Soviet Union in the 1950s and 1960s, the tropical Americas in the 1960s and 1980s, and tropical Asia in the 1980s.

The division of land-use change between various processes is illustrated in figure 7. The major types of land-use change that affect carbon storage are

  (i) the permanent clearance of forest for pastures and arable crops;

 (ii) shifting cultivation that may vary in extent and intensity as populations increase or decline;

(iii) logging with subsequent forest regeneration or replanting; and

(iv) 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. A review of these processes is provided by Houghton (1996).

Of the various processes, the expansion of croplands at the expense of natural ecosystems has dominated and continues to dominate the net efflux of carbon from the terrestrial biosphere, with the regions of highest activity being the tropical forests of Southeast Asia (0.76 PgC yr^{-1} in 1990) and Africa (0.34 PgC yr^{-1} in 1990). The conversion of forest into cattle pasture has gradually increased in importance and is concentrated almost entirely in Latin America (0.34 PgC yr^{-1} in 1990 compared with 0.16 PgC yr^{-1} from cropland expansion in the same region). Net emissions from wood harvesting are dominated by logging in Southeast Asia (0.19 PgC yr^{-1} in 1990; 66% of total emissions from harvesting), and China (0.07 PgC yr^{-1} in 1990; 23% of
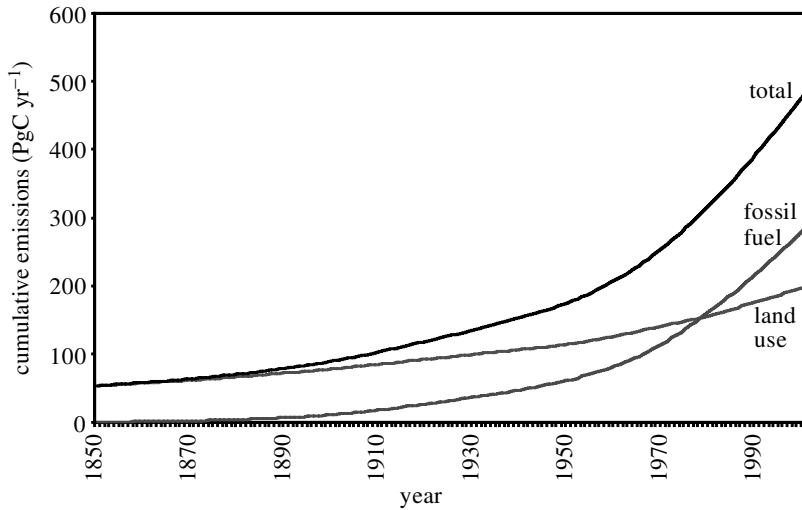
Figure 8. Total accumulated carbon emissions from land-use change and fossil-fuel combustion, 1850–2000. Data sources as in figures 5 and 6, with land-use-change values for 1991–2000 assumed to be constant at 1990 values.

total emissions). In the 19th century, shifting cultivation was in decline because of the abandonment of agricultural lands (often under tragic conditions) by indigenous peoples in the Americas and Southeast Asia. Since the mid-20th century, however, increasing population pressures have led to an increase in cultivation area and a decrease in rotation times, and shifting cultivation has become an increasing source of carbon. In North America and Europe, there has been a gradual abandonment of agricultural lands and regrowth of forests that have resulted in a carbon sink.

The results presented above are derived by Houghton (1999) from estimates of land-cover change derived from the Food and Agriculture Organization (FAO). Recent studies in a number of countries have suggested that the FAO may be over-estimating land-cover change (e.g. Steininger *et al.* (2001) for Bolivia, Houghton *et al.* (2000) for Brazil). Conversely, there are a number of processes that may be contributing to carbon emissions but that are not included in these calculations. These include forest degradation without loss of forest cover; illegal, unmonitored logging; and hidden ground fires (Nepstad *et al.* 1999) and may add *ca.* 0.4 GtC yr^{-1} to the estimate of net carbon emissions (Fearnside 2000).

The cumulative CO_2 emissions since 1850 (including fossil-fuel change and land-use change) are shown in figure 8. In total, *ca.* 480 GtC had been emitted to the atmosphere as a result of human activity by the end of 2000 (91% of this since 1850, 50% of this since only 1968). The overall contribution from fossil-fuel combustion only surpassed that from land-use change in the 1970s, but fossil-fuel combustion now accounts for 75% of current emissions.

4. Impacts of the 'carbon disruption'

(a) The atmosphere

High-precision measurements of the concentration of atmospheric CO_2, pioneered at Mauna Loa in Hawaii (Keeling & Whorf 2000), and now made at a number

Table 2. *Direct global warming potentials of greenhouse gases affected by human activities*

(The time horizon used to estimate the CO_2-equivalent warming potential for each gas is 100 years (the atmospheric residence time for CO_2 varies from 5–200 years). Warming potential is an index used to express relative global warming contribution due to atmospheric emission of a kg of a particular greenhouse gas compared with the emission of a kilogram of CO_2. Concentration units are expressed by volume: ppm denotes parts per million; ppb, parts per billion; ppt, parts per trillion. CO_2 denotes carbon dioxide, CH_4, methane, N_2O, nitrous oxide and HFC-23, hydrofluorocarbon-23.)

gas	lifetime (yr)	warming potential (CO_2 equivalent)	concentration in 1998	rate of change of concentration	preindustrial concentration
CO_2		1	365 ppm	1.5 ppm yr^{-1}	280
CH_4	12	23	1745 ppb	7.0 ppb yr^{-1}	700
N_2O	114	296	314 ppb	0.8 ppb yr^{-1}	270
HFC-23	260	12 000	14 ppt	0.55 ppt yr^{-1}	*ca.* 0

of stations around the world, show an unequivocal increase in concentration over nearly half a century (figure 2c). CO_2 concentrations are fairly uniform across the globe because the mixing time-scale for the lower global atmosphere is approximately one year, while the lifetime for CO_2 in the atmosphere is much longer, varying from 5 to 200 years. However, slightly higher concentrations are found in the Northern Hemisphere than in the Southern, a planetary-scale 'smoking gun' reminding us of the high rates of fossil-fuel combustion in northern mid-latitudes. The rate of increase in atmospheric CO_2 is dramatic: it has averaged *ca.* 0.4% per year since 1980, although net emissions to the atmosphere vary annually between *ca.* 2 and 6 PgC yr^{-1}, mainly as a result of changes in oceanic and terrestrial uptake that overlie the continuous human-related outflow of CO_2. The effects of El Niño events, for example, can temporarily result in high rates of CO_2-release to the atmosphere because of reduced terrestrial uptake in tropical ecosystems experiencing increased temperatures, droughts, fires and cloudiness (Prentice *et al.* 2001). At a finer, sub-annual, time-step, the repeated sinusoidal pattern in CO_2 concentration (figure 2c) shows us that hemisphere-scale behaviour in gross ecosystem metabolism can also be detected as natural systems respond to seasonality in climate.

Although the increase in atmospheric CO_2 concentration may affect the biosphere directly, the main cause for concern about rising CO_2 is its role as a greenhouse gas (GHG). GHGs allow short-wave solar radiation to pass into the Earth's atmosphere, but they absorb some of the long-wave thermal radiation that is emitted back out towards space. This has a warming effect on our atmosphere, and is termed 'positive radiative forcing'. CO_2 is not the most effective GHG, but it exists at relatively high concentrations, and consequently contributes the largest proportion of the total radiative forcing from GHGs. Other GHGs such as methane and nitrous oxide are more efficient at trapping radiant energy. They can be compared with CO_2 by calculating 'CO_2 equivalents': the warming potential of each gas compared with CO_2 over a specified time horizon, often 100 years. Methane (CH_4) and nitrous oxide (N_2O) have 23 and 296 times the warming potential of CO_2, respectively, but their atmospheric concentrations are much lower. Other GHGs, such as hydrofluorocarbons, have warming potentials that are an order of magnitude higher still (table 2).
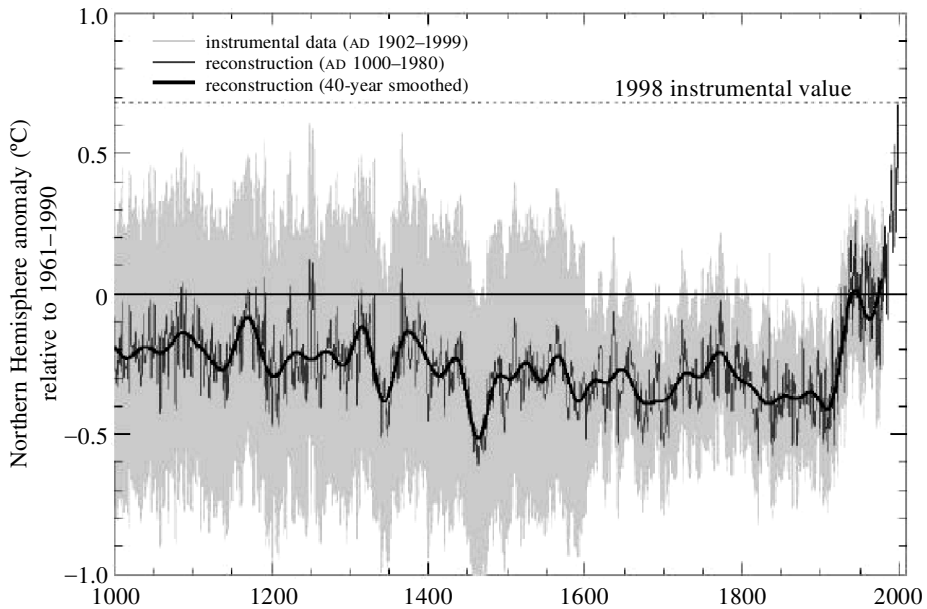
Figure 9. Temperature for the Northern Hemisphere for the last millennium. Direct measurements are shown as a thin grey line. Other data are reconstructed from proxy measurements: tree rings, corals, ice cores and historical records. The thick black line is a 40-year smoothed average; the shaded grey is the uncertainty in the temperature (two standard errors).

The relative constancy in atmospheric CO_2 concentration during the millennium leading up to the end of the 19th century (figure 2*b*) is also reflected in the temperature trace. Figure 9 shows Northern Hemisphere temperatures obtained from thermometers and proxy measurements from 1000 up to 1998. A small but continuous cooling from 1000 is abruptly broken around 1900, and temperatures rise from then until the present. Overall, the global mean temperature has gone up by 0.6 °C ± 0.2 °C, 95% confidence) since 1861. 1998 is considered to have been the warmest year on record, and crucially, temperatures are now sufficiently high to exceed the bounds of uncertainty associated with the proxy measurements made for historical times (figure 9). During the same period the atmospheric CO_2 concentration has also risen steeply (figure 2*b*). The 31% increase in atmospheric CO_2 since 1750 is now thought to be responsible for 60% of all GHG-induced warming.

It is not surprising, therefore, that the modelling of climate scenarios for the next 100 years is strongly dependent on the amount of CO_2 that is predicted to be released into the atmosphere. Since fossil-fuel combustion currently contributes three-quarters of all CO_2 emissions (figure 10) the socio-economic model underpinning fuel-consumption estimates strongly influences future climate scenarios. Using the full range of potential economic scenarios, the IPCC (2001) projected future temperature increases over the next 100 years to range from 1.5 to 5.8 °C, and the atmospheric CO_2 concentration to rise from the current value of 368 to between 500 and 1000 ppm. Very approximately, these model outputs suggest that *every* 3 Pg *of C emissions will result in an extra* 1 ppm *atmospheric* CO_2 *concentration by 2100, and that each extra* ppm *will increase global mean temperatures in 2100 by a little less than* 0.01 °C. These conversion factors vary according to assumptions about the
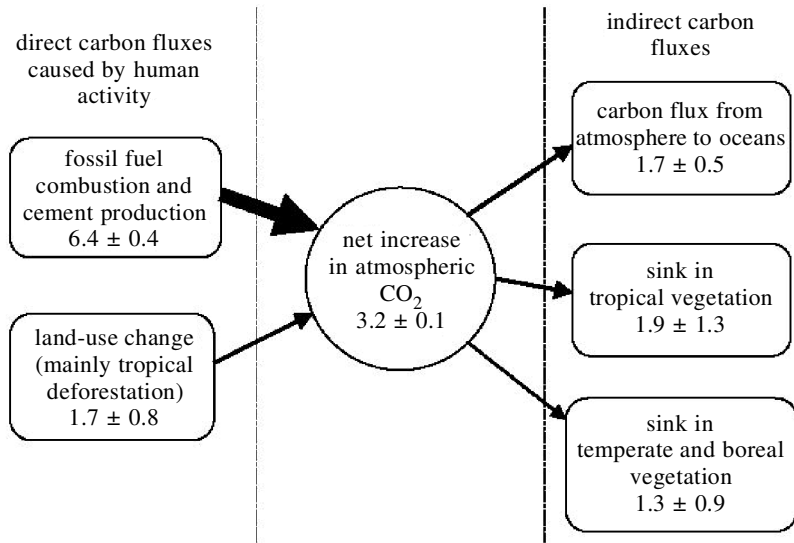
Figure 10. An estimate of the human-induced carbon cycle in the 1990s (units are PgC yr^{-1}). The carbon flows from fossil-fuel emissions to the atmosphere and the net carbon flows to the ocean and land are known with relatively high confidence. The partitioning of the net land sink between human activity and 'natural' carbon sinks is less certain, as is the partition between tropical and temperate regions.

temporal trend in emissions and the future behaviour of ocean and terrestrial carbon cycles, but provide a crude tool for estimating the climatic impacts of various carbon mitigation scenarios.

Although the warming experienced since the 19th century is marked, it does not directly reflect the total amount of CO_2 released as a result of human activities. Only a fraction of this total is ultimately added to the atmospheric CO_2 stock because of re-absorption by the oceans and the land surface. An estimate of the contemporary (1990s) fast carbon cycle is illustrated in figure 10 (The Royal Society 2001). In this figure, the carbon flows from fossil-fuel emissions to the atmosphere, and the net carbon flows to ocean and land are known with relatively high confidence (see below). A simple balance equation requires that, despite ongoing tropical deforestation, there is a net terrestrial carbon sink of 1.5 PgC yr^{-1}. The partitioning of the net terrestrial sink between human activities (primarily a source) and 'natural' carbon sinks is less certain, as is the partition between tropical and temperate regions. The partition between tropical and temperate regions is derived from studies of the atmospheric distribution of CO_2 (Prentice *et al.* 2001). The biggest uncertainty in this budget comes from quantification of land-use-change emissions: if these are overestimated, the terrestrial carbon sink is overestimated.

Currently, *ca.* 8.1 PgC yr^{-1} are emitted as CO_2, from industrial activity and tropical deforestation, but only 40% (3.2 PgC yr^{-1}) of this makes a net contribution to the atmospheric build-up (figure 10). It is this 40% that contributes to the radiative forcing of the Earth's atmosphere, but to understand the future of this radiative forcing it is also essential to understand the fate and permanence of the remaining 60%. The focus of this theme issue is the management of the land surface for car-

bon sequestration but, before describing land surface processes in some detail, we summarize the role played by the oceans in absorbing CO_2 from the atmosphere.

(b) The oceans

About 50 times more carbon resides in the oceans than in the atmosphere. Large-scale exchange between the two occurs over time-scales of hundreds of years, but CO_2 is readily exchanged across the sea–air interface on much shorter time-scales because of its high solubility and chemical reactivity in water. On an annual basis, the oceans absorb $1.7(\pm 0.5)$ PgC yr^{-1} from the atmosphere (Prentice *et al.* 2001). In spite of uncertainty in a number of processes, the precision in this estimate is relatively high, reflecting consistency between model outputs, values derived from measurements of atmospheric O_2 and $\delta^{13}C$, and scaled-up *in situ* measurements (Sabine *et al.* 1999; Orr *et al.* 2001; Prentice *et al.* 2001).

The transfer of CO_2 into or out of the oceans occurs naturally, mediated by both physical and biological processes. Molecular diffusion across the sea–air interface can occur in either direction, the net flux depending on the difference in the partial pressure of CO_2 in each medium ($pCO_{2\,air}$ and $pCO_{2\,sea}$). The rate of this transfer into water is modelled as a function of wind speed, but depends on sea temperature, salinity and pH.

Once in solution, 99% of the CO_2 reacts chemically with water to produce bicarbonate and carbonate ions, leaving 1% in the original dissolved, non-ionic form of CO_2. The carbon may then be the subject of further chemical reactions or be absorbed into biomass by phytoplankton. Photosynthesis in the oceans produces particulate organic carbon that sinks to significant depth. Most of this exported carbon ultimately returns to the surface by way of the underlying oceanic circulation, outgassed as CO_2, usually a large distance from its source. The effect of this 'biological pump' mechanism is large: the atmospheric concentration of CO_2 would be 200 ppm higher in its absence (Maier-Reimer *et al.* 1996). A second biological process occurs at the same time, whereby marine organisms, supplied with carbon by phytoplankton, fix carbonate ions by synthesizing calcium carbonate shells, which then sink, thus removing carbonate from the surface waters and reducing their alkalinity. This process tends to increase $pCO_{2\,sea}$ and acts in opposition to the main biological pump effect. The ratio between these two processes determines the overall effect of biological activity on surface ocean $pCO_{2\,sea}$ and hence the natural air-sea exchange rate of CO_2.

The absorption of anthropogenic CO_2 is a purely physical process and is considered to be superimposed upon the biological pump systems that are ultimately controlled by the supply of nutrients from deep water (Falkowski 1994). Uptake of CO_2 from the atmosphere occurs by enhancing natural exchange processes: a higher $pCO_{2\,air}$ leads to an increased mean atmosphere–ocean concentration gradient, and hence to increased oceanic sink activity and reduced source activity. The spatial pattern of oceanic circulation creates geographically separated upwellings of 'old' deep water, rich in organic carbon that may have been out of contact with the atmosphere for many years. The air–sea exchange of CO_2 reaches a physico-chemical equilibrium quickly relative to the slow tempo of oceanic circulation, and hence the long-term rate of net CO_2 absorption is ultimately limited by the rate at which oceanic circulation brings currents of deep water to the surface.

The future uptake potential of CO_2 by the oceans is likely to be controlled by a number of factors. The principal constraint is chemical: as atmospheric CO_2 concentration increases, the ratio of bicarbonate to carbonate ions also increases. This reduced availability of carbonate ions impairs the capacity for dissolved CO_2 to dissociate ionically, and hence reduces the capacity for CO_2 to dissolve from the air into the water in the first place. This effect is significant and places heavy constraints on absorption at higher atmospheric CO_2 concentrations. In addition, the velocity of oceanic circulation places an upper limit on the net rate of CO_2 absorption and the reduced solubility of CO_2 in water at higher temperatures will still further reduce transfer to the oceans. Overall, models indicate that the annual atmosphere–ocean flux of CO_2 will become larger over the 21st century, reaching 4.5–6.7 PgC yr^{-1} by the end of the century, but that the rate of increase will slow, particularly after the first 30–50 years.

(c) *The terrestrial biosphere*

As both the atmospheric stock and ocean sink of CO_2 are well determined (but the land-use-change source less so), a simple balance equation requires that there is a terrestrial carbon sink of *ca.* 3.2 PgC yr^{-1}, as illustrated in figure 10. Attempts to measure the terrestrial carbon sink directly are hampered by the spatial heterogeneity of carbon-transfer processes in the terrestrial biosphere. Given their spatial extent, biomass and productivity, forests are prime candidates for the location of the major portion of this carbon sink (Malhi *et al.* 1999; Malhi & Grace 2000). This seems to be confirmed by field observations. Extensive inventories of forest biomass in temperate and boreal regions suggest that there has been a substantial increase in the carbon stock in northern forest biomass, of the order of 0.6 Pg yr^{-1}. Such extensive inventories are not available in most tropical forest regions, but a compilation of results from forest plots in old-growth forests shows that these forests are increasing in biomass, resulting in a land carbon sink of 0.85 ± 0.25 PgC yr^{-1} (Phillips *et al.* 1998, 2002). The forest inventory estimates do not include changes in soil and litter carbon. When forest productivity and biomass are increasing, it is likely that soil and litter carbon reserves are also increasing, in total by an amount similar to the increase in reserves in living biomass if soil and biomass residence times are similar. This suggests a total sink of *ca.* 1.5 PgC yr^{-1} in tropical forests (Malhi *et al.* 1999), and 1.2 Pg yr^{-1} in temperate forests, implying that forests account for most of the terrestrial carbon sink (2.7 PgC yr^{-1} out of 3.2 PgC yr^{-1}), although it is possible that savannahs and grasslands also play a part.

What may be causing this terrestrial sink? A number of processes are likely to be responsible, each with their own regional pattern. Firstly, there is the *recovery of forests on abandoned agricultural lands*. This is a major factor in Europe and North America, and the change of age structure within forests appears to be a more important factor than the expansion of forest area. Another likely factor is CO_2 *fertilization*, where the rising atmospheric concentrations of CO_2 are stimulating plant photosynthesis, with consequences for the amount of carbon stored in plant biomass, litter and soil-organic carbon. Results from over 100 recent experiments in which young trees have been grown exposed to doubled atmospheric CO_2 concentrations have demonstrated an increase in tree growth of 10–70% (Norby *et al.* 1999; Idso 1999). A key uncertainty is the extent to which the fertilization effect is limited by
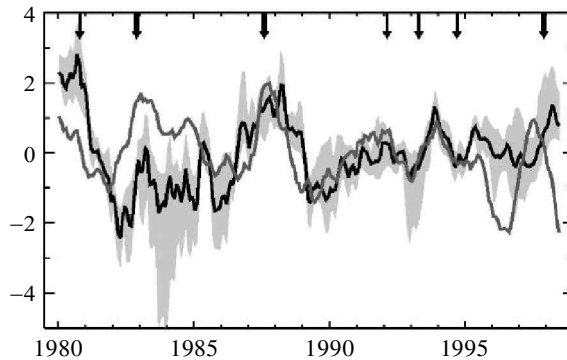
Figure 11. Solid black line, time-series of the carbon balance of tropical land regions ($20°$ N to $20°$ S), inferred from an inversion at global atmospheric CO_2 concentrations with an estimate of uncertainty (grey shading). The dark-grey line shows the carbon balance inferred from a biogeochemical model, which does not include deforestation. The tropics tend to be a major source of carbon in El Niño years, which are indicated by arrows. Most of the interannual variation in the terrestrial carbon balance is localized in the tropics (from Bousquet *et al.* 2000).

availability of other nutrients such as nitrogen and phosphorus. It has been suggested that plants may respond by investing a greater proportion of their extra carbon into the production of roots and root exudates to increase their nutrient supply (Lloyd *et al.* 2002). These high CO_2 effects may affect all forest ecosystems, but they may be particularly important in tropical regions where productivity is intrinsically high. Increased atmospheric CO_2 also results in an *enhanced water-use efficiency*, which may lengthen the growing season of plants in seasonally dry regions. Finally, human activities have resulted in an *enhanced global nitrogen cycle*, through the release of nitrogen oxides during fossil fuel and biomass combustion and the release of ammonia through fertilizer use, farming and industry (Galloway *et al.* 1995). There is evidence that nitrogen deposition is enhancing forest growth in temperate regions (Nadelhoffer *et al.* 1999; Oren *et al.* 2001); this effect is less important in boreal and tropical regions which are further from the nitrogen sources and, in the case of tropical regions, constrained by lack of phosphorus (Tanner *et al.* 1998).

Whatever the causes of the carbon accumulation in forest regions, there is also great interannual variability in the carbon balance. This is apparent both from ecophysiological models of forest processes, and from studies of the spatial distribution of atmospheric CO_2, which indicate that tropical regions are the primary driver for much of this interannual variability. Figure 11 shows a time-series of the net carbon balance of tropical land regions, as derived from an atmospheric study (which includes land-use-change effects), and from a biosphere model (which does not include land-use change). Tropical regions become a net carbon source during El Niño years because dry conditions in much of Amazonia and tropical Asia result in greater fire incidence (both anthropogenic and natural) and a drought-induced reduction in photosynthesis.

On a longer time-scale, it is likely that the terrestrial carbon sink will diminish in magnitude as the CO_2 fertilization effect decreases in magnitude and structural factors limit the amount of new carbon that can be stored in forest biomass. What the most important limiting factors will be and when they will become important is still

unknown. Furthermore, it is possible that climatic warming will enhance plant respiration and the decomposition of soil organic matter, leading to natural ecosystems becoming net sources of carbon and accelerating climate change. Measurements of CO_2 fluxes suggest that in tundras and high latitude boreal forests, where climatic warming is greatest, the enhanced carbon sink in biomass is being offset by the release of soil carbon caused by the thawing of biomass (Goulden *et al.* 1998; Oechel *et al.* 1993, 2000). There is currently little evidence of a similar effect (net loss of soil carbon) in tropical regions, although some climate-biosphere simulations suggest that the warming and drying of eastern Amazonia may result in a dieback of forest and a major release of carbon to the atmosphere (Cox *et al.* 2000).

(*d*) *Implications for ecology and biodiversity*

The biosphere is not like to be a purely passive sink for carbon: the changes contributing to the terrestrial carbon sink are likely to be causing profound changes in the ecological balance of ecosystems, with consequences for ecosystem function and species diversity. Laboratory studies show that responsiveness to high CO_2 varies between species (Norby *et al.* 1999); for example, at the most basic level, the CO_2 response is much higher in plants with a C3 photosynthetic mechanism (all trees, nearly all plants of cold climates, and most temperate crops including wheat and rice) than it is in those with a C4 mechanism (tropical and many temperate grasses, some desert shrubs and some important tropical crops including maize, sorghum and sugar cane). This has the potential to alter the competitive balance between trees and grasslands. Certain functional groups such as pioneers or lianas may also benefit disproportionately. There have been only a few systematic field studies that have looked for long-term trends in forest composition. For example, in the RAIN-FOR project (Malhi *et al.* 2002), field researchers are re-censusing old-growth forest plots across the Amazon basin to look for evidence of shifts in forest biomass and composition.

5. The future

In the short term at least, anthropogenic CO_2 emissions are set to accelerate. The evidence that this will affect climate is now almost unequivocal. Learning how to minimize these emissions and deal with their consequences is likely to be one of the great challenges of the 21st century. A variety of strategies will need to be adopted, including shifting to renewable energy sources, increasing carbon use efficiency, and possibly sequestering CO_2 in deep sediments or the deep ocean (IPCC Working Group III 2001).

One of the most immediate options, and the one that is the focus of this theme issue, is the option of locking up carbon in the terrestrial biosphere. Biosphere management options could include:

(i) the prevention of deforestation;

(ii) the reduction of carbon loss from forests by changing harvesting regimes, converting from conventional to reduced-impact logging, and controlling other disturbances such as fire and pest outbreaks;

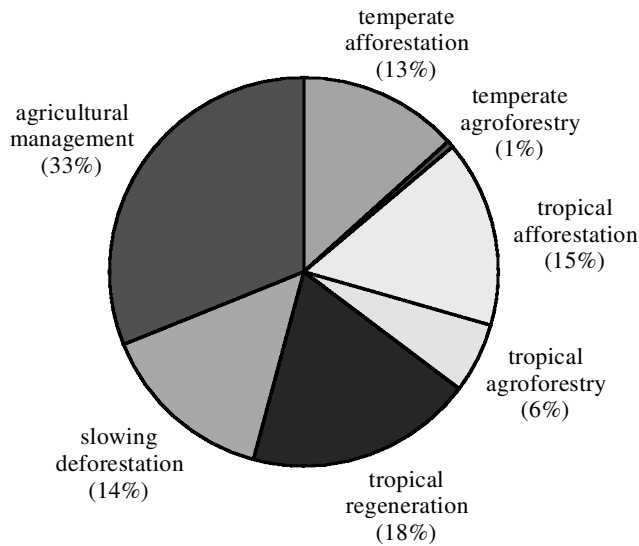(iii) reforestation/afforestation of abandoned or degraded lands;

Figure 12. The potential of various land-management activities to mitigate global emissions of CO_2 by increasing the carbon-sink potential of forestry and agriculture or reducing emissions at source (reducing deforestation). Estimates provided by the IPCC suggest that a maximum mitigation of 100 PgC could be achieved between 2000 and 2050. (Reproduced from The Royal Society (2001).)

(iii) sequestration in agricultural soils through change in tilling practices; and

(iv) the increased use of biofuels to replace fossil-fuel combustion.

How much potential does the biosphere-management option have?

We noted above that by the end of 2000 *ca.* 190 PgC had been released from the biosphere by human activity. Thus, if *all* agricultural and degraded lands were reverted back to original vegetation cover (an extremely unlikely scenario), a similar amount of carbon would be sequestered.

Slightly more realistically, the IPCC Third Assessment Report (Kauppi *et al.* 2001) confirms previous estimates (Brown *et al.* 1996) that the potential avoidance and removal of carbon emissions that could be achieved through the implementation of an aggressive programme of changing forestry practices over the next 50 years is *ca.* 60–87 PgC. About 80% of this amount could be achieved in the tropics. Changes in agricultural practices could result in a further carbon sink of 20–30 Pg over the same period (Cole *et al.* 1996), resulting in a maximum land-management carbon sink of 80–120 Pg, and a mean annual sink of *ca.* 2 PgC yr^{-1}. Figure 12 shows how this potential sink is distributed between various activities.

It is important to emphasize that here we are discussing an *additional, deliberately planned land-carbon sink* that would complement the 'natural' sink mentioned previously. The two sinks are sometimes confused in discussion. For example, although the natural carbon sink may reduce with climatic warming and possibly become a net source, intact, well-managed forests will almost always contain more carbon than degraded forests or agricultural lands. Therefore, improved carbon-focused forest management will almost always result in net carbon sequestration.

How does this land-management sink potential compare with expected carbon emissions over the 21st century? The IPCC 'business as usual' scenario suggests that that *ca.* 1400 PgC would be emitted by fossil-fuel combustion and land-use change over the 21st century. More detailed recent emissions scenarios suggest that, without conscious environment-based decision making, emissions will total between 1800 PgC (scenario A2, a regionalized world) and 2100 PgC (scenario A1F, a fossil-fuel-intensive globalized world) over the 21st century (Nakicenovic *et al.* 2000). With more environmentally focused policies, total emissions are expected to vary between 800 and 1100 PgC. Whatever the details of the scenario, it is clear that even an extensive land carbon-sink programme could only offset a fraction of likely anthropogenic carbon emissions over the coming century. Fossil-fuel emissions alone (not considering any further emissions from ongoing tropical deforestation) over the 21st century may exceed by 5–10 times even the maximum possible human-induced forest-carbon sink. Using the simplistic conversion factor outlined above (3 PgC emissions = 1 ppm atmospheric CO_2 = 0.01 °C temperature rise), *a managed land-use sink of* 100 PgC *over the 21st century would reduce projected CO_2 concentrations in 2100 by ca.* 33 ppm*, and reduce the projected global mean temperature increase by* 0.3 °C: a modest but significant effect. Using a similar calculation for historical CO_2 emissions, Prentice *et al.* (2001) estimated that a complete reversion of agriculture to forest would reduce atmospheric CO_2 concentrations by 40 ppm, a comparable figure.

Absorbing carbon in trees clearly cannot 'solve' the global warming problem on its own. Where forest-carbon absorption can be effective, however, is in being a significant component in a package of CO_2 mitigation strategies, and providing an immediate carbon sink while other mitigation technologies are developed. Carbon absorbed early in the century has a greater effect on reducing end-of-century temperatures than carbon absorbed late in the century. The immediate potential of forestry is illustrated in figure 13. Suppose that a global carbon emissions goal for the 21st century is to move our emissions pathway from the IPCC 'business-as-usual' scenario (IS92a) to a low-emissions scenario (SRES scenario B1), as illustrated in figure 13*a*. The required carbon offset is the difference between these two emissions curves. Now let us suppose that an ambitious forest-carbon-sink programme can be implemented immediately, aiming to absorb 75 PgC by 2050, at a uniform rate of 1.5 PgC yr^{-1}. Figure 13*b* illustrates the proportional contribution that such a carbon sink could make to the required total carbon offset. *For the next decade, such a land carbon sink would on its own be sufficient to move us onto the low-emissions pathway, and for the subsequent two decades it could provide about half of the required carbon offsets.* Thus even a less ambitious carbon offset programme could play a significant role over the next few decades. As the century progresses and the magnitude of the required carbon reductions increases, the relative potential of forest-carbon sinks declines. A forest-carbon offset programme implemented in 2050 would only be able to produce between 10 and 30% of the required offsets. Thus, to be relevant, a forest-carbon sequestration programme has to absorb most of its carbon within the next few decades. Tropical ecosystems have the highest productivities, and are therefore likely to be the most effective sinks at this short time-scale.

In conclusion, the managed absorption of carbon in forests has the potential to play a significant role in any carbon-emissions-reduction strategy over the next few decades. Such a strategy can be viewed as partly undoing the negative effects of pre-
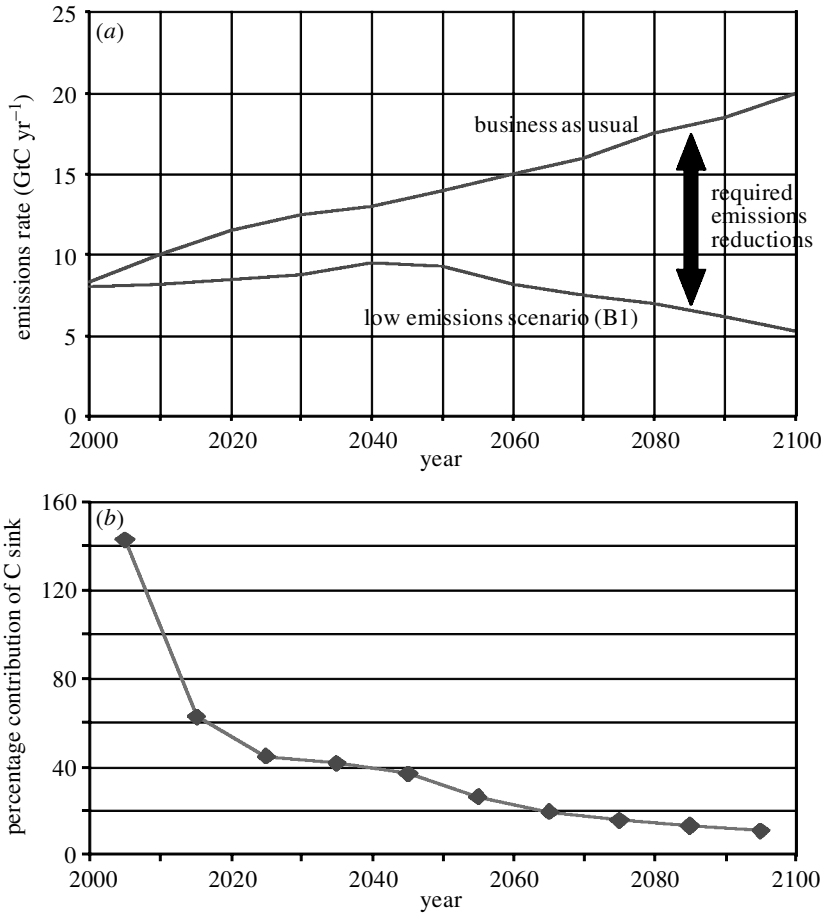
Figure 13. (*a*) A 'business as usual' carbon emissions scenario (IS92a) and a low-emissions scenario for the 21st century (IPCC 2001). (*b*) The percentage contribution that a human-induced land carbon sink of 1.5 PgC yr^{-1} could make towards a move from the 'business-as-usual' pathway to a low-emissions pathway.

vious centuries of forest clearance, both in climatic and biological terms. The relative potential contribution of a forest-carbon sink declines later in the century, and therefore forest-carbon absorption cannot be viewed as a long-term solution to the global warming problem. It can only be a useful stopgap. As a stopgap, however, it is essential that carbon sinks are not allowed to divert resources and attention from required developments and changes in technology, energy use, and energy supply, the only developments that can provide a long-term solution to the great carbon disruption.

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