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## Terrestrial Biotic Responses to Environmental Change and Feedbacks to Climate

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## SUMMARY

Terrestrial ecosystems and climate are closely coupled. Changes in climate and the carbon dioxide concentration of the atmosphere cause changes in the structure and function of terrestrial ecosystems. In turn, changes in the structure and function of terrestrial ecosystems influence the climatic system through biogeochemical processes that involve the land-atmosphere exchanges of radiatively active gases such as carbon dioxide ( $\text{CO}_2$ ), methane ( $\text{CH}_4$ ) and nitrous oxide ( $\text{N}_2\text{O}$ ), and changes in biogeophysical processes that involve water and energy exchanges. The combined consequences of these effects and feedbacks must be taken into account when evaluating the future state of the atmosphere or of terrestrial ecosystems.

### *The global carbon budget and net $\text{CO}_2$ exchange between the land and the atmosphere*

Analyses based on atmospheric  $\text{CO}_2$  and  $^{13}\text{CO}_2$  measurements suggest that the terrestrial biosphere is currently a net carbon sink. Such analyses quantify the strength of this sink as 0.5–1.9 GtC/yr during the 1980s, and as high as 2.6 GtC/yr during 1992–3; they also suggest that the tropics have been a net carbon source, implying even greater rates of carbon storage in mid- to high latitudes. Direct observations to establish the processes responsible for this carbon storage are, however, lacking. Possibilities include post-harvest regrowth of mid- and high latitude forests (0.5–0.9 GtC/yr according to IPCC WGII (1995), Chapter 24), enhanced vegetation growth due to physiological effects of increasing  $\text{CO}_2$  (0.5–2.0 GtC/yr) and nitrogen deposition (0.5–1.0 GtC/yr) (figures from model calculations), and, probably, a substantial range (0–2.0 GtC/yr) of interannual variation due to climatic anomalies. These processes are not additive: for example, the rate of carbon sequestration in mid-latitude forests may include effects of all of the other processes.

The future role of the terrestrial biosphere in controlling atmospheric  $\text{CO}_2$  concentrations is difficult to predict because we do not know which of these processes will dominate. As long as  $\text{CO}_2$  increases, the  $\text{CO}_2$  fertilisation effect is expected to play a role in enhancing terrestrial

carbon storage. However, this role will disappear if atmospheric  $\text{CO}_2$  is stabilised; also, plant growth may not continue to increase if the atmosphere's  $\text{CO}_2$  concentration rises above some level, perhaps around 1000 ppmv, because the  $\text{CO}_2$  fertilisation response is then saturated. Nitrogen fertilisation may continue to promote carbon storage in the forests of the Northern Hemisphere, but this effect would cease if the cumulative nitrogen inputs reach levels, yet to be defined, beyond which the impacts on plant growth become deleterious. Deforestation, which is already causing a net release of carbon from tropical lands to the atmosphere of  $1.6 \pm 1.0$  GtC/yr, may increase to meet the food needs of an expanding human population, and extensive deforestation could adversely affect the biosphere's continued capacity to act as a carbon sink.

Further uncertainties arise because changes in climate and atmospheric  $\text{CO}_2$  over the next decades to a century are likely to produce changes in the structure of natural and managed ecosystems. Structural changes include changes in the local abundance of species and genetic sub-groups (genotypes), and in the global geographic distributions of assemblages of species (biomes). There will be transient effects, varying according to the rate of climate change. With slow change, shifts in competitive balance among species might occur subtly with minor effects on terrestrial carbon storage. With rapid change, direct impacts on the growth and survival of particular types of plants could cause die back and carbon loss before better adapted types become established. This possible asymmetry of terrestrial carbon loss and accumulation under rapid climate change has led to the concern that climate-induced transient vegetation changes could release  $\text{CO}_2$  into the atmosphere, counteracting the biosphere's capacity to take up  $\text{CO}_2$ . The magnitude of this feedback is highly uncertain: it could be near zero or, with low probability, as much as 200 GtC over the next one to two centuries. The more rapid the climate change, the greater the probability of a large transient carbon release. The probability also depends on the extent, intensity and impact of mid-continental drought, which is a major discrepancy both among general

circulation models<sup>1</sup> (GCMs) and among ecosystem models. More reliable projections of drought and its impacts on ecosystems will require the incorporation of ecosystem dynamics in global carbon cycle models and the coupling of ecosystem models with GCMs.

#### *Methane (or CO<sub>2</sub>) release from wetlands*

Methane is produced in flooded organic soils as a result of the metabolic activities of micro-organisms in the absence of oxygen. Methane emissions from natural wetlands contribute about 20% to the global emissions of this gas to the atmosphere. Methane flux from wetlands could either increase due to rising temperatures and CO<sub>2</sub>, or decrease due to drying of the soils. If high latitude wetlands dry out, however, there will be a release of stored carbon as CO<sub>2</sub>. The rate of CO<sub>2</sub> release with drying is uncertain, but potentially large since as much as 450 GtC may be stored in high latitude wetlands.

#### *Nitrous oxide release from soils*

The global nitrous oxide budget is dominated by microbial processes in soils, especially those in the moist tropics. The major N<sub>2</sub>O-producing process is denitrification. Denitrification is promoted by high nitrate supply and low soil oxygen concentration. Warmer soils promote more

rapid nitrogen cycling and often more nitrate, while wetter soils lead to low soil oxygen levels. Where soils become warmer and wetter, the production of N<sub>2</sub>O will increase, but the global magnitude of this increase has not been estimated.

#### *Effects of land-surface changes on climate*

Vegetation mediates the exchange of water and energy between the land surface and the atmosphere, and thereby affects climate. As biomes shift, the climate will be affected. For example, high latitude warming is expected to cause forests to spread into tundra. This change would be expected to increase the warming in northern mid- to high latitudes by more than 50% over 50–150 years because of the lower albedo of forests during the snow season. Such feedbacks will, however, be modified by land-use changes such as deforestation.

As atmospheric CO<sub>2</sub> increases, stomatal conductance declines, so that the effectiveness of water conservation by plants is increased and the effects of drought on plant growth ameliorated. But declining stomatal conductance will also have feedback effects on climate. It has been estimated that a global halving of stomatal conductance, with no change in leaf area, would lead to an additional surface air warming of about 0.5°C averaged over the land.

<sup>1</sup> Throughout this chapter a GCM refers to an atmospheric general circulation model coupled to a mixed-layer ocean model.

## 9.1 Introduction

Terrestrial ecosystems can influence the climate system through biogeochemical and biogeophysical processes. Key biogeochemical effects and feedbacks of ecosystems on climate involve the land-atmosphere exchange of radiatively active gases, such as  $\text{CO}_2$ ,  $\text{CH}_4$  and  $\text{N}_2\text{O}$ . These gases exert a major control on the climate system. Their atmospheric content can be increased or decreased by changes in the structure and function of terrestrial ecosystems as these systems respond to environmental changes including changes in climate. Structural and functional changes in land ecosystems can also cause biogeophysical effects and feedbacks by altering the exchange of water and energy, leading to changes in surface temperatures, atmospheric circulation and precipitation patterns.

In this chapter we will consider major feedbacks between terrestrial ecosystems and the climatic system for three time intervals: (1) the present; (2) a future period of "climate transition" that is likely to range from decades to centuries; and (3) a hypothesised "new equilibrium condition" that is probably centuries into the future. We deal with feedbacks in the global carbon, methane and nitrous oxide budgets. We also discuss how changes in ecosystem structure and function affect climate through biogeophysical feedbacks.

The range of topics covered in this chapter is more restricted than the range covered in the first IPCC Scientific Assessment (Melillo *et al.*, 1990). This is because an extensive assessment of terrestrial impacts is given in IPCC WGII (1995).

## 9.2 Land-atmosphere $\text{CO}_2$ Exchange and the Global Carbon Balance: the Present

Land ecosystems of the Earth contain about 2,200 GtC; an estimated 600 GtC in vegetation and 1600 GtC in soils. These land carbon stocks are changing now and are likely to continue to change in the future in response to changes in any or all of the following factors: area of agricultural land, age structure of forests, climate, and chemistry of the atmosphere and precipitation.

### 9.2.1 Changes in the Area of Agricultural Land

Agricultural land occupies almost one fifth of the Earth's terrestrial surface (Olson, 1983). A substantial portion of this land was once forested and so contained relatively large carbon stocks in both trees and soils. The conversion of forests to agricultural lands releases carbon, mostly from

trees, to the atmosphere through burning and decay. Conversely, the regrowth of forests on abandoned lands withdraws carbon from the atmosphere and stores it again in trees and soil. The net flux of carbon from the land to the atmosphere primarily associated with agricultural expansion for 1980 has been estimated at between 0.6 and 2.5 GtC/yr (Houghton *et al.*, 1987; Hall and Uhlig, 1991; Houghton, 1991; Houghton, 1995). IPCC (1994) indicates that the net emission from changes in tropical land-use was  $1.6 \pm 1.0$  GtC/yr for the period 1980 through 1989 (Schimel *et al.*, 1995). Houghton (1995) estimated that in 1990 the net flux to the atmosphere, essentially all from the tropics, was 1.7 GtC/yr with an uncertainty of  $\pm 30\%$ .

### 9.2.2 Changes in the Age Structure of Forests

Young and middle-aged forests accumulate carbon, while old-growth forests accumulate little if any carbon. Forests of the Northern Hemisphere's mid-latitudes that were harvested in the early and middle parts of the 20th century are still regrowing and accumulating carbon (e.g., Kauppi *et al.*, 1992; Wofsy *et al.*, 1993). Estimates of rates of carbon accumulation related to forest regrowth in these regions range between 0.7 and 0.8 GtC/yr for the 1980s (Melillo *et al.*, 1988; Sedjo, 1992; Dixon *et al.*, 1994). Melillo *et al.* (1988) have argued that the fate of the cut wood must also be taken into account when evaluating the net effect of forest harvest and regrowth in the global carbon budget; that is, the rate at which the carbon in the cut wood is returned to the atmosphere as a result of burning and decay must be considered. When Melillo *et al.* did this, they concluded that the net effect of forest harvest and regrowth for the middle and high latitudes of the Northern Hemisphere on terrestrial net carbon storage was approximately zero in the 1980s. It must be recognised that there are considerable uncertainties associated with estimating the fate of cut wood, including wood left at the harvest sites, fire wood, and wood products such as paper and lumber (Melillo *et al.*, 1988; Harmon *et al.*, 1990). Because of these uncertainties, IPCC (1994) estimated that forest harvest and regrowth resulted in an accumulation on land of  $0.5 \pm 0.5$  GtC/yr during the 1980s (Schimel *et al.*, 1995).

Changes in the frequency of fires, insect outbreaks and other disturbances can also alter the age structure of forests and affect their capacity to store carbon. Disturbance regimes are affected by climatic conditions such as warming and drought. Kurz and Apps (1995) have reported that since 1970, the boreal forest regions of Canada have experienced increased rates of disturbance, especially spruce budworm outbreaks and fire. As a consequence, these forests have switched from being a sink for

atmospheric CO<sub>2</sub> (0.15 GtC/yr) to being a carbon source to the atmosphere (0.05 GtC/yr), albeit a small one. Kurz *et al.* (1995) consider warming to be one of several factors possibly responsible for the recent increase in fire frequency in Canada. While climate-related increases in disturbance frequencies may be occurring in other regions (Woodwell, 1995), we do not have a good global accounting of them or of their consequences for terrestrial carbon storage.

### 9.2.3 Changes in Ecosystem Metabolism

Each year, about 5% of the land's total carbon stock is exchanged with the atmosphere as a result of plant and soil metabolic activities. Through the process of photosynthesis, land plants take up on the order of 120 GtC/yr in the form of CO<sub>2</sub> from the atmosphere. This carbon uptake is approximately balanced by plant and soil respiration, which release carbon as CO<sub>2</sub> to the atmosphere. A change in the balance between photosynthesis and respiration will change the carbon stock on land and also has the potential to alter the CO<sub>2</sub> content of the atmosphere.

The relationships among the various metabolic processes in terrestrial ecosystems can be defined by three equations:

$$NEP = GPP - R_a - R_h \quad (9.1)$$

$$NPP = GPP - R_a \quad (9.2)$$

$$NEP = NPP - R_h \quad (9.3)$$

where, at an annual time step:

$\Sigma NEP$  is net ecosystem production, the yearly rate of change in carbon storage in an ecosystem. It can be either positive or negative. A positive  $NEP$  indicates that the ecosystem has accumulated carbon during the year, while a negative  $NEP$  indicates that it has lost carbon during the year.

$\Sigma GPP$  is gross primary production, the amount of carbon fixed through the process of photosynthesis by the ecosystem's green plants in a year.

$\Sigma R_a$  is autotrophic respiration, the amount of carbon released to the atmosphere as CO<sub>2</sub> by the ecosystem's green plants through respiration in a year.

$\Sigma R_h$  is heterotrophic respiration, the amount of carbon released to the atmosphere as CO<sub>2</sub> by the ecosystem's animals and micro-organisms through respiration in a year.

$\Sigma NPP$  is net primary production, the difference between gross primary production ( $GPP$ ) and plant respiration ( $R_a$ ) in a year.

As we face the prospect of climate change, an important question to ask ourselves is: how will the relationship between  $NPP$  and  $R_h$  change as the Earth warms in response to the accumulation of carbon dioxide and other heat-trapping gases in the atmosphere? An answer to this question is complicated by the fact that both positive and negative metabolic feedbacks may be simultaneously involved.

The major positive metabolic feedback is associated with warming. The suggestion is that an increase in temperature will increase rates of both plant and microbial respiration and speed the release of carbon into the atmosphere from plants and soils (Woodwell, 1983, 1989, 1995). Negative feedbacks have been proposed that are associated with an increase in atmospheric CO<sub>2</sub> and with warming. The increase in atmospheric CO<sub>2</sub> may cause a stimulation in rates of photosynthesis and an increase in carbon storage (e.g., Oechel and Strain, 1985). In nutrient-limited forests, warming may increase terrestrial carbon storage by relieving plant nutrient limitations (McGuire *et al.*, 1992; Shaver *et al.*, 1992).

In addition to the possibility of simultaneous feedbacks of opposite sign, there are other aspects of global change that may affect terrestrial ecosystem metabolism and carbon storage. Some of the major effects are associated with the burning of fossil fuels, which causes changes in the chemistry of the atmosphere and precipitation. Fossil fuel burning can lead to the production of air pollutants such as sulphur dioxide and ozone that are toxic to plants. These air pollutants can decrease  $NPP$  and carbon storage (Allen and Amthor, 1995). The burning of fossil fuels can also lead to increases in nitrogen in precipitation. Up to some cumulative level, increased nitrogen inputs to nitrogen-limited ecosystems, such as many temperate and boreal forests of the northern hemisphere, can cause increases in  $NPP$  and carbon storage. Nitrogen inputs beyond the threshold level can lead to decreases in  $NPP$  and carbon storage (Aber *et al.*, 1989; Schulze *et al.*, 1989).

#### 9.2.3.1 Climate change

Climate changes may affect  $NPP$  in a variety of ways. Elevated temperature may increase  $NPP$  by enhancing photosynthesis (Larcher, 1983) or through increased nutrient availability if decomposition and nutrient mineralisation are enhanced (Bonan and Van Cleve, 1992; McGuire *et al.*, 1992; Melillo *et al.*, 1993, 1995a). It may



decrease *NPP* by decreasing soil moisture which may reduce photosynthesis through decreased stomatal conductance (Hsiao, 1973; Gifford, 1994) or decreased decomposition and mineralisation (McGuire *et al.*, 1992, 1993; Pastor and Post, 1988; Parton *et al.*, 1995). Elevated temperature may also increase plant respiration and so reduce *NPP* (McGuire *et al.*, 1992, 1993; Running and Nemani, 1991), although this effect may have been overestimated (Gifford, 1993). The effects of precipitation and cloudiness on *NPP* can also be positive or negative in different situations. In dry regions, lower precipitation or lower cloudiness may decrease *NPP* by lowering soil moisture. In moist regions, increased cloudiness may decrease *NPP* by reducing the availability of photosynthetically active radiation (PAR). Climate changes may further influence *NPP* by affecting leaf phenology in deciduous vegetation (Long and Hutchinson, 1991).

Climate affects carbon storage in terrestrial ecosystems because temperature, moisture, and radiation influence both carbon gain through photosynthesis and carbon loss through respiration. Soil respiration is generally accelerated by higher temperatures, producing an increase in the release of  $\text{CO}_2$  from terrestrial ecosystems (Houghton and Woodwell, 1989; Melillo *et al.*, 1990; Shaver *et al.*, 1992; Townsend *et al.*, 1992; Oechel *et al.*, 1993; Peterjohn *et al.*, 1993, 1994; Lloyd and Taylor, 1994; Schimel *et al.*, 1994; Kirschbaum, 1995). It is thought that in many ecosystems the increase of soil respiration with temperature is steeper than any increase of *NPP* with temperature, so that the net effect of warming is to reduce carbon storage. Lloyd and Taylor (1994), however, caution that valid conclusions regarding the effects of possible changes in temperatures on soil carbon pools cannot yet be made because we lack a detailed knowledge of the temperature sensitivity of carbon input into the soil via *NPP*.

Oechel *et al.* (1993) report that the recent general pattern of warming of the north slope of Alaska and the Canadian Arctic may have led to a reduction of carbon storage in tundra ecosystems of the region. At a set of sites in the tundra of the north slope of Alaska, they measured whole ecosystem  $\text{CO}_2$  flux over five summers between 1983 and 1990, and found a net flux of carbon from the land to the atmosphere. Extrapolating their results from the Alaskan tundra to the circumpolar Arctic, Oechel *et al.* (1993) estimate that regional warming could have caused a net flux from the land to the atmosphere of about 0.2 GtC/yr during the 1980s.

Warming may not always lead to a reduction of carbon storage in terrestrial ecosystems. It has also been suggested

#### The Link Between Carbon Storage and Nitrogen Distribution in Terrestrial Ecosystems

Changes in the distribution of nitrogen between plants and soil can change the amount of carbon stored in an ecosystem. Plant and detrital tissues in terrestrial ecosystems vary widely in their stoichiometric ratios of C and N (Melillo and Gosz, 1983; Schindler and Bayley, 1993; Gifford, 1994; Kinzig and Socolow, 1994; Schulze *et al.*, 1994). If warming of the Earth accelerates mineralisation of N from soil organic matter, where the C:N ratio usually ranges from 10 to 25, and if the N is taken up by plants and used to produce more woody biomass with a C:N ratio between 40 and 400, then the ecosystem would experience a net increase in carbon storage (Gifford, 1994; Peterjohn *et al.*, 1994; Melillo, 1995; Melillo *et al.*, 1995a). On the other hand, if the processes of microbial mineralisation of soil organic matter and plant uptake of mineral N are decoupled in space or time, then N might be lost from the ecosystem via leaching or denitrification, resulting in a net loss of both C and N from that ecosystem.

that in nutrient-limited forests, particularly in cold climates, warming may increase carbon storage through a two-step mechanism (McGuire *et al.*, 1992; Shaver *et al.*, 1992; Melillo *et al.*, 1993; see Box on The Link Between Carbon Storage and Nitrogen Distribution). First, warming may increase the decay rate of low carbon-to-nutrient ratio soil organic matter which may release nutrients to soil solution and some  $\text{CO}_2$  to the atmosphere (Peterjohn *et al.*, 1994; Melillo *et al.*, 1995a). Second, there may be increased nutrient uptake by trees which store nutrients in woody tissues which have a high carbon-to-nutrient ratio.

By differentially affecting *NPP* and  $R_h$ , climate variations in temperature, precipitation and cloudiness on the annual to decadal time-scale may have affected terrestrial carbon storage. Dai and Fung (1993) and Keeling *et al.* (1995) have suggested that these variations could have resulted in a substantial terrestrial carbon sink in recent years. Ciais *et al.* (1995a) suggested that cooling arising from the effects of Mt. Pinatubo's eruption in June, 1991, may have increased terrestrial carbon storage and contributed to the observed reduction in atmospheric growth rate during the 1991 to 1992 period. The magnitude of the effect of these climatic variations on global terrestrial carbon storage is highly uncertain, but may be between 0 and 2.0 GtC/yr. Terrestrial carbon storage

caused by climate anomalies may be spatially complex due to the potential for a spatial mosaic structure of the anomalies. In the near term, some regions may experience increases in carbon storage and others decreases.

### 9.2.3.2 Carbon dioxide fertilisation

#### Results of laboratory and field studies

A short-term increase in  $\text{CO}_2$  concentration causes an increase in photosynthesis at the level of individual leaves (e.g., Idso and Kimball, 1993). Leaves may acclimate to increased  $\text{CO}_2$  such that long-term increases in  $\text{CO}_2$  result in smaller increases in leaf-level photosynthesis (Wong, 1979; Tissue and Oechel, 1987; Fetcher *et al.*, 1988; Sage *et al.*, 1989); but this does not always occur (e.g., Masle *et al.*, 1993; Gunderson and Wullschlegel, 1994; Luo *et al.*, 1994; Sage, 1994). At the level of the whole plant, feedbacks from non-leaf organs can influence leaf photosynthetic responses to  $\text{CO}_2$ . If photosynthesis increases to a greater extent than the rate at which carbon assimilated during photosynthesis can be used in additional growth, photosynthesis can be slowed by negative metabolic feedbacks in plants (Arp, 1991; Bowes, 1991; Luo *et al.*, 1994; Sage, 1994). On the other hand, an increased carbohydrate supply which is allocated below ground may help to alleviate nutrient limitations on photosynthesis by enhancing biological nitrogen fixation and/or increasing mycorrhizal activity leading to greater uptake of phosphorus (Norby, 1987; O'Neill *et al.*, 1987; Arnone and Gordon, 1990; Lewis *et al.*, 1994; O'Neill, 1994).

Studies of both crop and non-crop plants grown in doubled  $\text{CO}_2$  have shown increased growth responses often in the range of 15 to 71%. The total range is from a negative response of 43% to a positive response of up to 375% (Kimball, 1975; Kimball and Idso, 1983; Eamus and Jarvis, 1989; Poorter, 1993; Ceulemans and Mousseau, 1994; Idso and Idso, 1994; McGuire *et al.*, 1995a; Wullschlegel *et al.*, 1995). Across the tissue, plant and ecosystem levels the experimental evidence shows that the proportional response of *NPP* to elevated  $\text{CO}_2$  is greater when soil moisture is depleted. Elevated  $\text{CO}_2$  generally decreases stomatal conductance and hence transpiration, enhancing *NPP* by promoting greater water use efficiency (Gifford, 1979; Wong, 1979; Morrison and Gifford, 1984; Polley *et al.*, 1993). There is some evidence that nitrogen-limited plants are less responsive to increases in  $\text{CO}_2$  level (McGuire *et al.*, 1995a), but a recent review suggests that this is not always true (Lloyd and Farquhar, 1995).

Increased  $\text{CO}_2$  may lead to increased carbon storage, but the magnitude of this effect is highly uncertain. Carbon

sequestration at the ecosystem level depends not only on plant photosynthesis, respiration and growth, but also on the fluxes of carbon out of litter and soil carbon pools. At equilibrium, plant *NPP* would be balanced by these microbially mediated soil fluxes ( $R_h$ ). However, if there is a progressive change in *NPP* such as a progressive increase in *NPP* due to the effect of rising  $\text{CO}_2$ , the system will not be in equilibrium. In general the soil  $\text{CO}_2$  flux ( $R_h$ ) is proportional to the size of the decomposing carbon pools, whereas *NPP* is determined by the activity of the leaves. If  $\text{CO}_2$  increases, *NPP* may therefore increase immediately while the size of the decomposing pools takes time to build up. If *NPP* were to stop increasing (e.g., due to  $\text{CO}_2$  stabilisation), the sink would weaken, with a decay time determined by the residence times of the pools to which carbon has been added. This is the theoretical explanation for why rising  $\text{CO}_2$  is thought to be producing a carbon sink, and why the sink may be a transient one (Taylor and Lloyd, 1992).

A number of  $\text{CO}_2$ -enrichment field experiments have been conducted on intact ecosystems (Drake, 1992a; Nie *et al.*, 1992; Owensby *et al.*, 1993; Oechel *et al.*, 1994; Jackson *et al.*, 1994; Körner and Diemer, 1994). When the *NEP* responses to  $\text{CO}_2$  increases were measured, the results ranged from relatively large increases in a temperate wetland (Drake, 1992a,b), to a small increase in a tundra (Oechel *et al.*, 1994). There have been no comparable experiments on forests and this has resulted in an important gap in our understanding of how terrestrial ecosystems respond to increased atmospheric  $\text{CO}_2$ . Carbon dioxide fertilisation studies in forests are a high research priority.

#### Modelling studies

The first model-based analyses of the current effects of  $\text{CO}_2$  increase on terrestrial carbon storage were performed with simple models in which the terrestrial biosphere was represented by one or a few boxes. In one such analysis, Gifford (1993) worked within a plausible range of values (10, 25 and 40%) for the increase in *NPP* at doubled  $\text{CO}_2$ . Assuming that the terrestrial biosphere was in equilibrium in pre-industrial times, he forced his model with the historical record to give an idea of the extent to which the  $\text{CO}_2$  increase would produce an imbalance of carbon uptake and release. The resulting terrestrial carbon storage rates due to this mechanism were 0.5, 2.0 and 4.0 GtC/yr during the 1980s. Rotmans and den Elzen (1993) showed, in an analogous model experiment, that  $\text{CO}_2$  fertilisation was stimulating carbon storage at a rate of 1.2 GtC/yr. A new version of a global biogeochemistry model, the Terrestrial Ecosystem Model (TEM), (McGuire *et al.*,



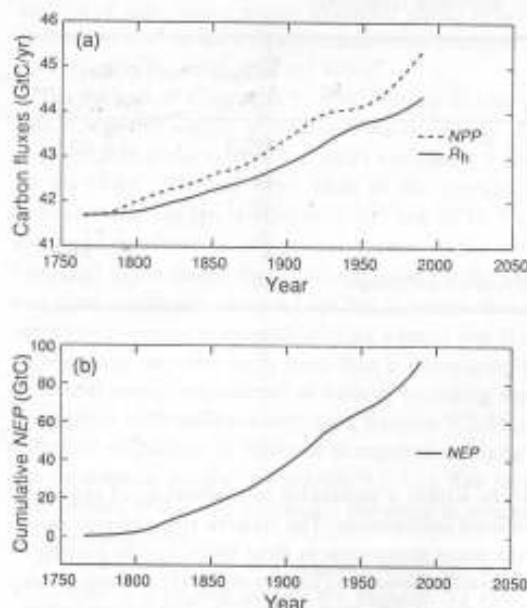


Figure 9.1: Simulated development of a terrestrial biosphere carbon sink due to  $\text{CO}_2$ -induced increases in net primary production (NPP), as simulated with the Terrestrial Ecosystem Model (Melillo *et al.*, 1995b). The biosphere was assumed to be in equilibrium before 1750. Climate was kept constant (as present). (a) Simulated time course of net primary production (NPP) and heterotrophic respiration ( $R_h$ ). (b) Cumulative net ecosystem production (NEP), i.e., sink strength.

1995b) was used by Melillo *et al.* (1995b) in the transient mode to explore the effects of  $\text{CO}_2$  enrichment, taking into account the variety of responses by different ecosystems. The model indicated that the mean  $\text{CO}_2$ -stimulated carbon storage (NPP minus  $R_h$ ) during the 1980s was 0.9 GtC/yr, and that it reached almost 1.0 GtC/yr in 1990 (Figure 9.1). Based on our current knowledge from laboratory, field and modelling studies, we consider a plausible range of the  $\text{CO}_2$  fertilisation effect to be 0.5–2.0 GtC/yr for the 1980s.

#### 9.2.3.3 Air pollution

The world's two major phytotoxic air pollutants are ozone ( $\text{O}_3$ ) and sulphur dioxide ( $\text{SO}_2$ ). They are spread throughout the industrial and agricultural regions (Heck, 1984). Experimental studies have documented significant effects of ozone on a variety of plant processes. It can reduce photosynthesis, increase respiration and promote early leaf senescence. These effects, either singly or in combination, can lead to reduced plant growth (Allen and

Amthor, 1995). Chameides *et al.* (1994) have presented evidence that the growth of urban and industrialised areas and intensive agriculture, through their production of tropospheric ozone, are reducing agricultural yields and, presumably, plant growth in adjacent non-agricultural ecosystems. Sulphur dioxide's main effect appears to be to reduce photosynthesis, which leads to reduced plant growth (Allen and Amthor, 1995). In combination, ozone and sulphur dioxide can interact to magnify the negative effects of either pollutant alone on plant growth (Ormrod, 1982). While it is not disputed that ozone and sulphur dioxide pollution have the potential to reduce both NPP and carbon storage in terrestrial ecosystems, there is little basis for making global estimates of these effects (Chameides *et al.*, 1994).

#### 9.2.3.4 Nitrogen fertilisation associated with acid rain

Those mid-latitude ecosystems of the Northern Hemisphere that are near or downwind of industrial and agricultural areas are receiving large inputs of nitrogen, mostly from fossil fuel burning. Forests in western and central Europe and eastern North America receive up to 50 kg N/ha/yr (Melillo *et al.*, 1989; Schulze *et al.*, 1989) or more. These nitrogen inputs may be enhancing NPP and terrestrial carbon storage. For example, Kauppi *et al.* (1992) suggested that increases in the growth rates of European forests observed between 1950 and 1980 were due to nitrogen fertilisation, although other mechanisms such as  $\text{CO}_2$  fertilisation, climate variability and management changes may also be involved.

Experimental evidence supports the nitrogen-stimulation mechanism for increasing carbon storage in mid-latitude forests. In a field study in which 50 kg N/ha/yr has been added to large plots of healthy evergreen and deciduous forests for several years, carbon storage in aboveground woody tissue has increased by 10–20%/yr (Aber *et al.*, 1993). However, this increase in carbon storage is expected to reach a threshold level beyond which further additions of nitrogen are likely to result in NPP reduction, tree death, and carbon loss (Aber *et al.*, 1989; Schulze *et al.*, 1989).

Many terrestrial ecosystems, especially those in middle and high latitudes, are nitrogen limited; that is, added nitrogen will produce a growth response and additional carbon storage (e.g., Melillo and Gosz, 1983; Vitousek and Howarth, 1991; Schimel *et al.*, 1994; Melillo, 1995). Nitrogen deposition from fertilisers and oxides of nitrogen released from the burning of fossil fuel during the 1980s is estimated to amount to a global total of 0.05–0.08 GtN/yr (Peterson and Melillo, 1985; Duce *et al.*, 1991; Galloway *et al.*, 1995; Melillo, 1995), spatially concentrated in the

Table 9.1: Recent estimates of nitrogen-stimulated carbon storage in terrestrial ecosystems.

	Region(s) considered	N input TgN/yr	C store GtC/yr
Kohlmaier <i>et al.</i> , 1988	30 – 60°N	21 ± 7	up to 0.7
Schindler and Bayley, 1993	globe	13	~ 0.7 – 2.0
Hudson <i>et al.</i> , 1994	Northern Hemisphere	30	~ 0.7
Townsend <i>et al.</i> , 1994	global (excluding cultivated areas)	7†	0.2 – 1.2*
Melillo, 1995	temperate and boreal forests of North America and Europe	18	0.6 – 0.9†

† NO<sub>3</sub> only.

\* Best estimate 0.3 – 0.6.

† Lower end of range more likely.

northern mid-latitudes. The carbon sequestration which results from this added nitrogen is estimated to be 0.2–2.0 GtC/yr (see Table 9.1), depending on assumptions about: (1) the proportion of nitrogen that remains in ecosystems; (2) the relative distribution of nitrogen between vegetation and soil; and (3) the C:N ratios of the vegetation and soil. Estimates higher than 1 GtC/yr seem unrealistic because they assume that all of the N would be stored, and in forms with high C:N ratios, which is improbable. Recent studies of the fate of nitrogen added to forest ecosystems suggests that between 70 and 90% ends up in the soil, which has a relatively low C:N ratio (Aber *et al.*, 1993; Nadelhoffer *et al.*, 1995). In addition, much atmospheric nitrogen is in reality deposited on grasslands and agricultural lands where storage occurs in soils with low average C:N ratios. A more plausible range for this effect is therefore 0.5–1.0 GtC/yr.

Model calculations have not yet considered the fact that CO<sub>2</sub> and nitrogen fertilisation are likely to be interacting. The additional nitrogen may enhance photosynthesis and plant growth (Bazzaz and Fajer, 1992; Diaz *et al.*, 1993; McGuire *et al.*, 1995a – see Section 9.2.3.1), and possibly lead to increased carbon storage.

#### 9.2.4 Estimates of Current Terrestrial Carbon Sinks from Atmospheric Measurements

Observations at stations monitoring background concentrations of CO<sub>2</sub> indicate that only a portion of the fossil fuel-derived CO<sub>2</sub> remains airborne, while the remainder is absorbed by the oceans and the terrestrial biosphere. A first order estimate of the global distribution of sinks by latitude can be made using CO<sub>2</sub> concentration data from networks of monitoring stations (Denning *et al.*, 1995), but the distinction between land and ocean sinks and

sources within a particular latitudinal band requires additional information. The relative roles of terrestrial versus ocean ecosystems in these bands can be estimated with several approaches (Tans *et al.*, 1995), including ones that use the <sup>13</sup>C/<sup>12</sup>C ratio of the CO<sub>2</sub>. The carbon isotope ratio of CO<sub>2</sub> is useful because terrestrial uptake discriminates strongly against <sup>13</sup>C while the ocean uptake shows little discrimination (Keeling *et al.*, 1989, 1995; Francey *et al.*, 1995). Francey *et al.* (1995), using a terrestrial discrimination value of 18 parts per thousand, estimated a net terrestrial storage over the last decade of 1 to 3 GtC/yr.

Lloyd and Farquhar (1994) pointed out that the magnitude of <sup>13</sup>C discrimination among land plants depends on the biochemical pathway they use in photosynthesis and that this affects the analysis of atmospheric observations. The C<sub>3</sub> pathway results in a discrimination of 18 parts per thousand, while the C<sub>4</sub> pathway results in very little discrimination.<sup>1</sup> Considering the distribution of C<sub>3</sub> and C<sub>4</sub> plants and their share in global NPP, Lloyd and Farquhar (1994) estimated that the global average terrestrial discrimination factor is about 15 parts per thousand. This means that Francey *et al.* (1995) may have underestimated the net terrestrial uptake by up to 25%. Ciais *et al.* (1995b) included the C<sub>4</sub> effect in an

<sup>1</sup> C<sub>3</sub> photosynthesis is the normal biochemical pathway of carbon fixation in plants. C<sub>4</sub> photosynthesis is a more complex pathway, found for example in tropical grasses, which includes a mechanism for concentrating CO<sub>2</sub> at the sites of carbon fixation. The C<sub>4</sub> pathway accounts for a substantial fraction of total NPP in tropical grasslands and savannahs. Some tropical crops, including sugar cane, also use this pathway.

analysis of data from a greatly expanded global network. They found that the net terrestrial carbon sink averaged 2.6 GtC/yr during the years 1992 and 1993.

The analyses of Ciais *et al.* (1995b) indicate that for the land ecosystems outside of the equatorial band from 30°S to 30°N, net carbon storage (i.e. *NEP*) averaged 4.3 GtC/yr for the years 1992 and 1993. Most of this storage, an average of 3.5 GtC/yr, was between 30° and 60°N. These are large numbers in the global carbon cycle when compared to the annual fossil fuel emissions for the same two years, which was about 6.1 GtC/yr. It follows that the terrestrial biosphere is currently playing a major role in the carbon cycle, in some years more than compensating for terrestrial ecosystem sources of carbon, including those associated with deforestation (see Section 9.2.1) and enhanced respiration in response to regional warming in the circumpolar tundra (see Section 9.2.3.1). The future maintenance of this role is crucially important to scenarios of CO<sub>2</sub> stabilisation.

A major complication in developing future scenarios of CO<sub>2</sub> stabilisation that accurately include the role of terrestrial ecosystems in the global carbon cycle is that the magnitude of the extra-tropical sink appears to vary substantially through time (see Table 9.2, Keeling *et al.*,

1989; Tans *et al.*, 1990; Ciais *et al.*, 1995b; Francey *et al.*, 1995) and may be responding to climatic variations on the scale of years to decades (Dai and Fung, 1993; Keeling *et al.*, 1995). The magnitude of the response to climatic anomalies is highly uncertain but may be in the range of  $\pm 2.0$  GtC/yr.

Longer time-series with information on carbon isotope composition of CO<sub>2</sub> will provide us with a better idea of how much the extra-tropical carbon sink changes through time. Refined estimates of the role of terrestrial ecosystems in the global carbon balance will likely soon come from data on the oxygen isotope composition of CO<sub>2</sub> (Francey and Tans, 1987; Farquhar *et al.*, 1993) which can also be obtained from the global network. Further information will come from measurements of the atmospheric concentration of oxygen and its spatial variation (Keeling and Shertz, 1992).

While various pieces of evidence support a substantial terrestrial carbon sink in the Northern Hemisphere, direct observations to confirm the hypothesis and to establish the processes for this carbon storage are lacking. Expanding our understanding of the processes responsible for net annual storage of carbon by the terrestrial biosphere is among our greatest challenges.

**Table 9.2:** Estimated global carbon budgets based on atmospheric observations, obtained using a range of methods for various years during the 1980s and 1990s (modified from Tans *et al.*, 1995).

Reference	Year(s)	Global net flux GtC/yr	Tropical net flux <sup>§</sup> GtC/yr	Extra-tropical net flux GtC/yr	Primary constraints
Keeling <i>et al.</i> , 1989	1984	-0.5 <sup>§</sup>	+0.3 <sup>§</sup>	0.7 <sup>†</sup>	history of atmospheric [CO <sub>2</sub> ], and its <sup>13</sup> C/ <sup>12</sup> C ratio
Tans <i>et al.</i> , 1990	1981–1987	-1.9	+0.5	-2.4 <sup>†</sup>	observed latitudinal gradient of atmospheric [CO <sub>2</sub> ], and its global annual rate of increase
Ciais <i>et al.</i> , 1995a	1992–1993	-2.6	+1.7	-4.3*	observed latitudinal gradient of atmospheric [CO <sub>2</sub> ], and its <sup>13</sup> C/ <sup>12</sup> C ratio

§ The net tropical flux term represents both the release of carbon from the land to the atmosphere due to deforestation and any storage occurring in undisturbed forests associated with processes such as CO<sub>2</sub> fertilisation.

§ A negative sign represents uptake of carbon by terrestrial ecosystems from the atmosphere, a positive sign represents a release of carbon by terrestrial systems to the atmosphere.

† Extra-tropical region includes all land outside of a band between 15°N and 15°S.

\* Extra-tropical region includes all land outside of a band between 30°N and 30°S.

### 9.3 Possible Effects of Climate Change and Atmospheric Carbon Dioxide Increases on Ecosystem Structure

Changes in climate and atmospheric carbon dioxide concentration affect the species composition and structure of ecosystems because the environment limits both the types of organisms that can thrive and the amounts of plant tissues that can be sustained. Compositional and structural changes, in turn, affect ecosystem function (Schulze, 1982; Schulze and Chapin, 1987; Schulze, 1994). Compositional and structural changes will occur over a longer period than functional changes and these may not keep pace with rapid environmental change, so complex transient effects may result.

Experimental approaches have shown strong effects of climate change on vegetation composition and structure (Harte and Shaw, 1995). However, longer-term changes cannot be investigated experimentally, so much of what we understand about these changes is based on modelling and palaeodata.

#### 9.3.1 Environmental Controls on Vegetation Structure: Ecophysiological Constraints on Plant Types

The ecosystems of the world are usually classified into 15–20 “biomes”, each characterised by the dominance of one or more structural/functional types of plant. The global distributions of biomes are determined by ecophysiological constraints on the dominant plant types of each biome (Schulze, 1982; Woodward, 1987). The main constraints are related to temperature and water.

Cold tolerance in woody plants ranges from tropical trees, some damaged by temperatures of less than 10°C, to boreal deciduous trees which in their leafless, cold-hardened state have apparently unlimited tolerance (Sakai and Weiser, 1973; Larcher, 1983; Woodward, 1987). Warmer winters would cause an expansion of more diverse woody plant types towards the poles and continental interiors. Warmer summers, and/or longer growing seasons, would also allow some cold-adapted trees to spread poleward (Emanuel et al., 1985; Pastor and Post, 1988) especially at the polar tree-line where growing-season warmth is limiting. Cold-tolerant woody plants have, however, evolved mechanisms to delay spring budburst until day length is adequate, and/or a long enough chilling period has occurred. These mechanisms insure against the possibility of premature budburst in a mild period during winter. Premature budburst would be damaging because the leaves could be killed by a subsequent frost. Chilling requirements keep continental

woody plants out of maritime climates. Warmer winters will force such species to retreat from their low latitude and maritime limits (Dahl, 1990; Overpeck et al., 1991; Davis and Zabinski, 1992).

Plants vary enormously in their ability to tolerate drought, ranging from rain forest trees that can tolerate only a few weeks without rain unless they have access to deep water, to succulents that store water, and other hot desert species that can persist in a dry state. Some evergreen trees survive drought by reducing transpiration to near zero, while drought deciduous trees lose their leaves. As water availability declines further, trees give way to fire-adapted grasses and/or shrubs, then ultimately to the low shrubs, forbs and other drought-adapted life forms characteristic of steppes and deserts. Changes in water availability, whether positive or negative, will lead to shifts along this continuum.

#### 9.3.2 Environmental Controls on Vegetation Structure: Resource Availability

Vegetation structure is determined not only by the types of plants present but also by the height and foliage cover they attain. Foliage cover, often expressed as leaf area index (LAI), is constrained by resource availability (water, carbon, nitrogen). LAI decreases as water availability declines. Along moisture gradients, vegetation composition and structure change due partly to replacement of drought-sensitive by drought-tolerant (or more deep-rooted) plant types, and partly to reductions in the LAI of each type (Walter, 1979). Values for LAI are typically low enough to prevent drought damage in most years (Specht, 1972; Woodward, 1987; Neilson, 1995), so maintaining annual *NPP* near maximal for the environment (Eagleson, 1978; Haxeltine et al., 1996). Changes in water availability will therefore affect LAI (Smith et al., 1993), but the response may be modified by changes in  $\text{CO}_2$ . In particular, increasing  $\text{CO}_2$  (by reducing transpiration) would be expected to compensate for the effect of reduced water availability on LAI (Jarvis, 1989; Woodward, 1992; VEMAP Members, 1995).

Vegetation structure also changes with light availability, summer temperature and growing season length. From boreal forest to high-arctic tundra, trees are gradually replaced by shrubs and grasses as *NPP* declines. Comparable vegetation gradients occur at high elevations in all latitudes (Walter, 1979). In these cold environments warming should generally increase *NPP* and therefore LAI. Rising  $\text{CO}_2$  may also increase LAI in so far as  $\text{CO}_2$  fertilisation can increase *NPP* (see Section 9.2.3.2). *NPP* in cold climates today may be further limited by the slow rate

of nitrogen mineralisation (see Section 9.2.3.1). The combination of warming with  $\text{CO}_2$  increase could therefore increase LAI especially in high latitudes.

The ecophysiological and resource-availability constraints that determine the natural distribution of biomes also closely determine potential (non-agricultural) land-use, for example, suitability for forestry or grazing, the types of tree which can be exploited for forestry, sustainable density of grazing animals. Changes in these constraints strongly affect both natural and managed ecosystems.

### 9.3.3 Environmental Mediation of the Competitive Balance

The physical environment also contributes to determining the natural competitive balance among those plant types that can co-exist in a given environment. For example:

- (1) Wet tropical climates support evergreen rain forest; longer dry seasons favour drought-deciduous trees in seasonal and dry forests (Chabot and Hicks, 1982; Haxeltine *et al.*, 1996). Any change in monsoon duration would shift the natural boundaries among these forest types.
- (2) Savannas represent an equilibrium of trees and grasses. In seasonal tropical climates, grasslands are favoured by summer rainfall and slow-percolating clay soils, woodlands by winter rainfall and sandy soils (Walter, 1979; Walker and Noy-Meir, 1982; Lauenroth *et al.*, 1993). Natural savannas occur in intermediate situations, where the combination is favoured (Eagleson and Segarra, 1985; Haxeltine *et al.*, 1996). Changes in rainfall seasonality, as well as changes in land management, would affect the tree-grass balance.
- (3) Seasonal shifts between  $\text{C}_3$  and  $\text{C}_4$  grass dominance (Groves and Williams, 1981) occur because  $\text{C}_4$  plants have a higher light use efficiency than  $\text{C}_3$  plants wherever temperatures exceed a threshold of about  $22^\circ\text{C}$ , at current  $\text{CO}_2$  concentration (Ehleringer and Monson, 1993). An increase in atmospheric  $\text{CO}_2$  raises this temperature threshold (Drake, 1992b; Arp *et al.*, 1993; Johnson *et al.*, 1993). Warming should therefore favour  $\text{C}_4$ , but increasing  $\text{CO}_2$  may favour  $\text{C}_3$ . Increasing  $\text{CO}_2$  might have caused the recent invasion of some  $\text{C}_4$  grasslands by  $\text{C}_3$  woody plants (e.g., Johnson *et al.*, 1993), although other factors such as land-use changes may be involved as well (Archer *et al.*, 1995).

- (4) In temperate and cold climates, evergreen woody plants are favoured over winter-deciduous woody plants wherever carbon and/or nutrient costs of replacing leaves annually exceed the costs of maintaining leaves during winter (Chabot and Hicks, 1982; Reich *et al.*, 1992; Chapin, 1991; Mooney *et al.*, 1991; Shaver and Chapin, 1991; Arris and Eagleson, 1994; Chapin *et al.*, 1995). Changes in the seasonality of either temperature or precipitation could alter the balance between evergreen and deciduous trees.

### 9.3.4 Global Biome Model Projections

Global models for ecosystem dynamics, that can simulate the transient response of vegetation structure to changes in climate and atmospheric  $\text{CO}_2$ , are being developed by several groups but none has yet been published. Simple biome models project equilibrium distributions of broad vegetation types ("potential natural vegetation") from ecophysiological constraints, but without consideration of  $\text{CO}_2$  effects on plant physiology. The BIOME model (Prentice *et al.*, 1992) reproduces well the present vegetation as mapped by Olson *et al.* (1983), except where intensive agriculture predominates. BIOME has been applied to various  $2 \times \text{CO}_2$  equilibrium climate scenarios developed using outputs from atmospheric general circulation models (GCMs) (Solomon *et al.*, 1993; Claussen, 1994; Claussen and Esch, 1994; Prentice and Sykes, 1995). Consistent results include poleward shifts of the northern-hemisphere taiga, temperate deciduous, and warm-temperate evergreen/warm mixed forest belts, a northward shift of the Eurasian taiga, and a slight expansion of tropical seasonal and rain forests into areas of warm-temperate evergreen forests (IPCC WG II, 1995). Differences among GCM scenarios in the extent of these changes are consistent with the GCMs' different climate sensitivities. Some scenarios (not all) show reductions of temperate forests in the continental interiors.

These results differ from analyses based on earlier, empirical models, e.g., in the tropics where the Holdridge (Prentice and Fung, 1990; Smith *et al.*, 1992, 1993) and Budyko (Tchebakova *et al.*, 1992) models showed greater expansions of tropical rain forest. Such expansions are probably an artefact, due to ignoring rainfall seasonality. The Holdridge model also showed a smaller northward and eastward shift of the Eurasian taiga than other models (including Tchebakova *et al.*, 1992; Monserud *et al.*, 1993), because temperature seasonality is ignored.

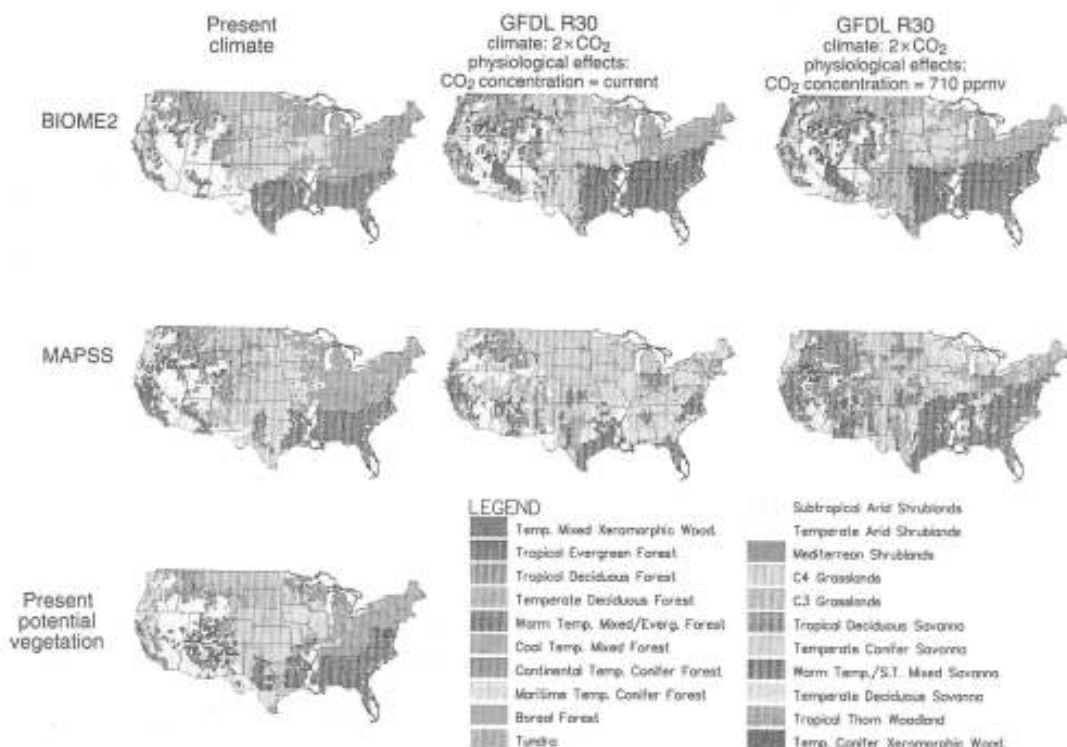
Comparisons with past biome distributions are instructive. At 6000 yr bp (before present) there was more



insolation than today in the Northern Hemisphere summer, and more total annual insolation (leading to warmer year-round temperatures) at high latitudes. 6000 yr bp is not an analogue for the future, because the Earth's orbital configuration was different from present, while the CO<sub>2</sub> concentration was similar to pre-industrial (Mitchell *et al.*, 1990; Monserud *et al.*, 1993). Palaeoecological data for 6000 yr bp show that climate change alone does indeed cause major biome shifts. GCM simulations (e.g., Kutzbach and Guetter, 1986) driven by the insolation changes ("orbital forcing") capture the general direction of these shifts (COHMAP Members, 1988; Wright *et al.*, 1993; Foley, 1994). Their magnitude tends to be underestimated, however, possibly because the GCM modelling procedure disregards biogeophysical feedback (Henderson-Sellers and McGuffie, 1995; Section 9.7).

### 9.3.5 Regional Biome Model Projections

"Second-generation" biome models include resource limitation and competitive balance effects. Examples are MAPSS (Neilson, 1995; Neilson and Marks, 1995) and BIOME2 (Haxelme *et al.*, 1996). In an application to the continental USA both models produced good simulations of potential natural vegetation (VEMAP Members, 1995; Figure 9.2). Temperature-controlled biome boundaries responded to  $2 \times \text{CO}_2$  climates in a similar way to the earlier BIOME results. Moisture-controlled boundaries (e.g., the forest-grassland boundary) responded differently, due to different evapotranspiration parametrizations, in the two models. In the central and eastern USA, some climate scenarios without corresponding CO<sub>2</sub> doubling caused partial replacement of forests by grasslands. This effect was more extensive in MAPSS, but the effect was



**Figure 9.2:** Changes in potential natural vegetation of the conterminous USA, simulated with the BIOME2 and MAPSS vegetation models. Left: simulations based on present climate. The actual distribution of potential natural vegetation types is shown for comparison. Centre: simulations based on " $2 \times \text{CO}_2$ " climate scenario. This scenario was derived by using an equilibrium simulation from the GFDL R30 atmospheric/mixed-layer ocean model to modify the climate data. Right: simulations based on the same climate scenario, but including the physiological effects of a CO<sub>2</sub> concentration of 710 ppmv. After VEMAP Members (1995).

mitigated in both models by the physiological effects of  $\text{CO}_2$ . This mitigation was more effective in MAPSS. Note that the mitigation is an effect of  $\text{CO}_2$  only; it does not apply to the other greenhouse gases.

BIOME2 also simulates the differential effects of  $\text{CO}_2$  on photosynthesis in  $\text{C}_3$  and  $\text{C}_4$  plants. Warming alone pushes the area of potential  $\text{C}_4$  grasslands northwards, but  $\text{CO}_2$  doubling overwhelms this effect, favouring  $\text{C}_3$  grasses down to the subtropics. The competition between  $\text{C}_4$  grasses and woody plants is determined mainly by the climate change and only slightly by  $\text{CO}_2$ , according to this model. MAPSS simulates only the differential effects of  $\text{CO}_2$  on water use, which in combination with greater simulated drought produces the opposite effect favouring  $\text{C}_4$  plants up to the boreal zone.

BIOME2 and MAPSS probably bracket the plausible range for the sensitivity of moisture-related biome boundaries to temperature and  $\text{CO}_2$ , and for the response of  $\text{C}_3$  versus  $\text{C}_4$  plants to changes in  $\text{CO}_2$ . More realistic treatment of the coupling between carbon and water fluxes should help to resolve the discrepancies. These discrepancies represent an important uncertainty about the ecosystem impacts of climate change, comparable in magnitude with the uncertainty due to differences in the regional climate anomalies predicted by GCMs.

### 9.3.6 Changes in Biome Distribution Since the Last Glacial Maximum

Climatically controlled changes in biome distributions are well documented for the recent glacial-interglacial cycle, especially from the last glacial maximum (LGM, 21,000 yr bp) to the present (Wright *et al.*, 1993). Atmospheric  $\text{CO}_2$  increased by about 90 ppmv to the pre-industrial value of 280 ppmv after the LGM (Chapter 2). Large changes occurred in global climate and vegetation patterns (Overpeck and Bartlein, 1989; Webb, 1992).

Climate simulations of the LGM are based mainly on the ice sheet distributions, sea level, sea surface temperatures and  $\text{CO}_2$  (Kutzbach and Guetter, 1986; Broccoli and Manabe, 1987); the Earth's orbital configuration was also slightly different from present. BIOME results derived from the LGM climate simulation by Lautenschlager and Herterich (1990) agree qualitatively with palaeoclimatic and palaeoecological data (COHMAP Members, 1988; Street-Perrott *et al.*, 1989; Prentice *et al.*, 1993a). Thus, major changes in biome distribution after the LGM can be explained as a result of changes in climate. Direct effects of low  $\text{CO}_2$  may also have been involved, due to reduced carbon assimilation or low water-use efficiency of  $\text{C}_3$  plants at the LGM (Beerling and Woodward, 1993; Giresse *et al.*, 1994).

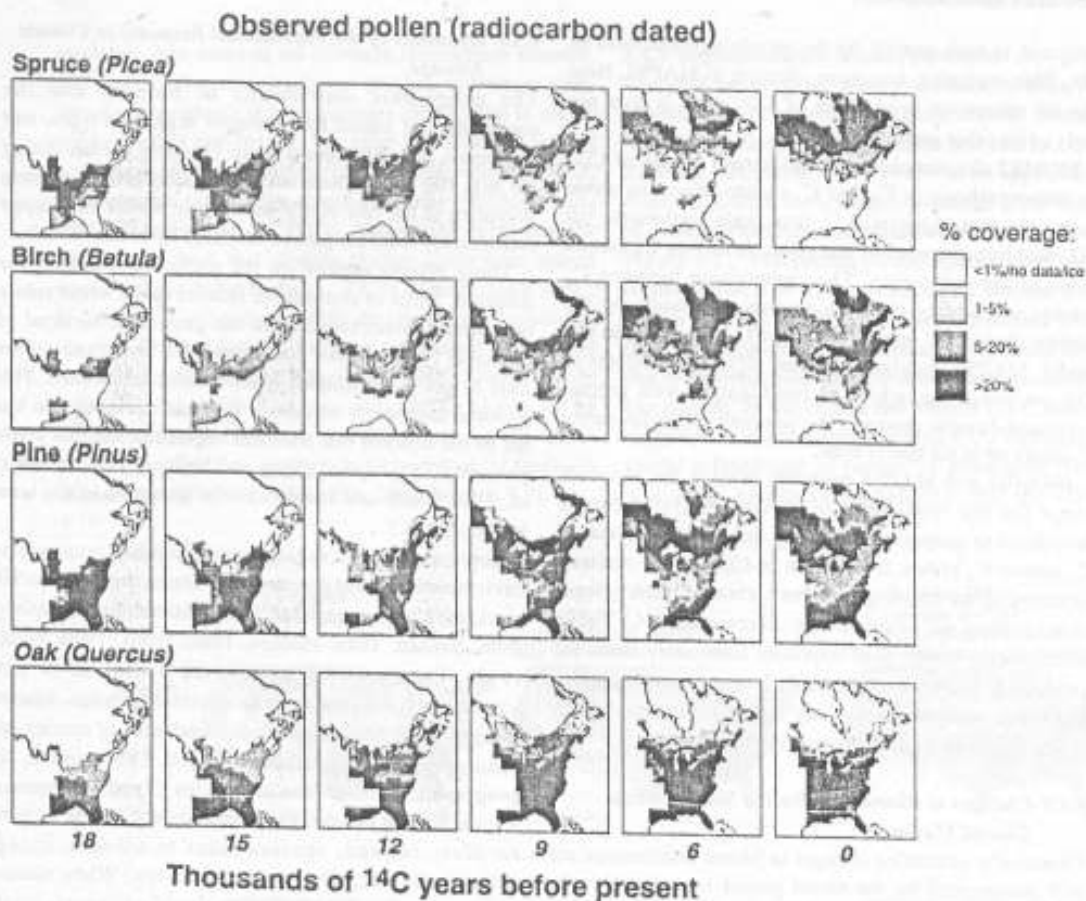
### 9.3.7 Dynamics of the Vegetational Response to Climate Change

The geographic distribution of biomes, and the composition of natural and managed vegetation types, will not remain in equilibrium with the changing climate during the next 100 years. There will be transient effects, varying according to the rate of climate change, which may depart considerably from the pattern indicated by biome models.

These effects depend on the particular mechanisms involved. Shifts in competitive balance might occur subtly over time. Direct impacts on the growth or survival of particular types of plant could cause die back (and carbon loss) before better-adapted types become established. This possible asymmetry of carbon loss and accumulation has led to the concern that transient vegetation changes could produce a  $\text{CO}_2$  "spike" (King and Neilson, 1992; Smith *et al.*, 1992; Smith and Shugart, 1993). We return to this issue in Section 9.4.1.

Some aspects of vegetation's dynamic response to environmental changes, on time-scales from 10 to  $10^4$  years, have been established from palaeoecology (Prentice, 1986; Bennett, 1986; Huntley, 1988; Davis, 1990; Webb, 1992). For perennial plants, the evolution of new adaptations is too slow to be an effective response. Instead, changes occur both in the local abundances of species and genotypes (Type A response, Webb, 1986) and in the geographic distributions of species (Type B response) (Figure 9.3). In this process biomes do not change or move *en bloc*; instead, species react to climate change individually according to their biology. When climate changes to produce novel regional climates, novel associations of plants arise (Webb, 1992). Successive interglacial periods have therefore been characterised by different vegetation assemblages (Watts, 1988). The general directions of change are predictable from a knowledge of the climate change and the present-day climatic tolerances (realised niches) of the species.

Type A vegetation responses are caused primarily by the differential effects of climate on the growth and regeneration of different taxa and plant types. These responses can occur at different rates depending on the rate of climate change. In periods of rapid climate changes, Type A vegetation responses have been reported to occur within 150 yr (MacDonald *et al.*, 1993), 50–100 yr (Mayle and Cwynar, 1995) and even within 30 yr (Gear and Huntley, 1991; Zackrisson *et al.*, 1995). Type A vegetation responses can be modelled with vegetation-dynamics models such as forest succession models (Botkin *et al.*, 1972; Shugart, 1984). These represent regeneration, growth and mortality of statistical populations of individual plants



**Figure 9.3:** Postglacial changes in the distribution and abundance of some major tree types in eastern North America, based on pollen analysis data. After Webb *et al.* (1993).

on a plot whose size reflects the scale of competition. With no environmental change, such models simulate the natural cyclical behaviour of ecosystems (Shugart, 1984; Prentice and Leemans, 1990). Climate effects modify the growth and regeneration functions. Applied to the past, such models have shown responses of forest composition to climate change that agree well with changes shown in pollen records (Solomon and Bartlein, 1992; Campbell and McAndrews, 1993).

When driven by climate-change scenarios, forest succession models can describe the interaction of climate and natural cycles (Solomon, 1986; Prentice, *et al.*, 1991a). Various transient effects have appeared, including transient die backs of species whose growth becomes reduced (Solomon and Bartlein, 1992). However, many succession

models assume stylised climatic responses (e.g., dome-shaped responses of total annual growth to annual growing degree days) which have no physiological basis and may give misleading results (Bonan and Sirois, 1992). The growth equation used in many such models is also physiologically unrealistic (Moore, 1989), producing too sudden mortality in large trees. Because of these and other uncertainties, including the potential significance of short-lived climatic extremes, the structure of vegetation dynamics models is undergoing re-examination (Bugmann, 1993; Prentice *et al.*, 1993b).

Climate change may further alter ecosystem structure and composition by affecting the disturbance regime (Grimm, 1983; Torn and Fried, 1992; Clark, 1993). Natural disturbances generally facilitate plant migration and the

attainment of compositional equilibrium with climate (Davis and Botkin, 1985; Bradshaw and Hannon, 1992). But climatically induced transitions between biomes may also show hysteresis, due to positive feedbacks that tend to maintain vegetation structure (Grimm, 1983). Such effects can cause delays of up to 100 yr (Grimm, 1984). The total response time of vegetational composition (combined Type A and B responses) has been estimated as between 300 and 1500 yr; fast enough to track the "envelope" of climate changes since the LGM (Overpeck and Bartlein, 1989; Prentice *et al.*, 1991b), but too slow to track interdecadal climate variability without considerable lag (Davis and Botkin, 1985; Campbell and McAndrews, 1993).

Faced with climate change, species presumably can (in the right conditions) spread at least as fast as they have done before. Species spread (migration) involves a number of factors including dispersal, regeneration on a suitable site, growth to maturity and seed production. Dispersal seems not to have been a major limitation in the past, at least to the major species detected over the long time-periods represented in the palaeo-record (see Biogeographic Dynamics Box). The mechanisms of rapid spread as observed in the Holocene may involve coalescence of many populations, each starting from an "infection centre" which could either be a pre-existing small population in a favourable microhabitat, or a new population founded by long-distance seed dispersal (birds, mammals and tornadoes are possible vectors; see references in Box). This way, species distribution ranges could expand orders of magnitude faster than they would if they advanced along an orderly front.

The palaeo-record tells us mainly about migration in a natural matrix. Future migrations may be very different. For example, the modern landscape provides fewer regeneration sites. Migrating species in the past exploited recently disturbed sites, whereas now natural vegetation is often fragmented (Peters, 1992) and confined to undisturbed sites. On the other hand, humans are already spreading many species beyond their natural ranges both deliberately and accidentally. Outlier populations spread by humans could be future infection centres even if they are not regenerating now (Davis and Zabinski, 1992). The net effect of human activities on plant species' ability to migrate is unclear.

Climate changes implied by the IS92 emission scenarios (see Chapter 6) call for migration rates up to ten times faster than historically observed for many taxa, so vegetation composition may be out of equilibrium with the changing climate (Davis, 1989, 1990; Davis and Zabinski, 1992). Non-equilibrium vegetation types could take many

forms. At one extreme, an existing vegetation type might persist until gradually invaded by other species, with minimal implications for the atmosphere. At the other extreme, large areas of forests might die (e.g., due to heat stress, drought and fire; Auclair and Carter, 1993) and be temporarily replaced by shrublands. This would result in different structural and functional properties, the transition being accompanied by changes in albedo, canopy roughness and rooting depth, reductions in NPP, and losses of plant and soil carbon to the atmosphere (Neilson, 1993; Section 9.4.1). The larger and more rapid the climate change, the greater the chance that effects of the latter type will occur.

#### Biogeographic Dynamics: The Issue of Dispersal Rate

Rates of species spread in response to Holocene climate changes have been reconstructed by mapping pollen data from networks of  $^{14}\text{C}$ -dated sediment cores. They range from 50–2000 m/yr for most woody species in Europe and North America (Davis, 1976; Huntley and Birks, 1983; Huntley, 1988). The puzzle is how species could spread so fast. Several explanations have been offered. For example, the rapid spread of *Picea glauca* into interior Canada immediately after deglaciation has been attributed to long-distance dispersal aided by strong anticyclonic winds (Ritchie and MacDonald, 1986). Migrations into already-vegetated regions that appear instantaneous over hundreds of kilometres, such as the spread of *Tsuga* into the Great Lakes region in response to precipitation and winter temperature increases ~7000 yr bp (Prentice *et al.*, 1991b), may be better described as infilling by the expansion of scattered "advance populations" (Clark, 1993; Davis, 1983; MacDonald *et al.*, 1993).

Rates of spread of different species within genera (e.g., *Picea*, *Fagus*) were similar regardless of whether the migration route lay in mountain regions or lowlands (Davis, 1983; Bennett, 1986). Species spread at comparable rates whether their seeds are adapted to wind- or animal transport (Davis, 1983). Migrating species were not stopped by water bodies such as Lake Michigan or the Baltic (Davis *et al.*, 1986; Huntley and Webb, 1989). The lesson for the future is that dispersal as such will not necessarily limit species migration rates. Other factors, such as the availability of sites for regeneration, may well provide greater barriers.



## 9.4 Effects of Climate Change and Carbon Dioxide Increases on Regional and Global Carbon Storage: Transient and Equilibrium Analyses

### 9.4.1 Possible Transient Effects of Climate Change on Global Carbon Storage

While biome shifts may have a major effect on terrestrial carbon storage during the climate transient, many other things may be happening at the same time that have the potential to affect terrestrial carbon storage. Continued forest clearing for agriculture to meet the food needs of a growing human population combined with an expansion and intensification of air-pollution stress on terrestrial ecosystems could further reduce carbon storage on land. Alternatively, mechanisms such as  $\text{CO}_2$  fertilisation may continue to result in enhanced carbon storage in land areas not involved in biome shifts. Improved quantification of these transient processes is a research priority.

### 9.4.2 Equilibrium Analyses: Regional Ecosystem Model Projections

In a rapidly changing environment, there may be complex transient effects including possible releases of carbon due to climate-change-induced forest die back as mentioned in Section 9.3.7. At the present time there is no consensus on the likely magnitude of such releases. In a modelling study, Smith and Shugart (1993) began to explore how large they might be. In Smith and Shugart's model, climate-induced vegetation redistribution initially led to a large transient release of about 200 GtC during 100–200 years due to die back of forests. While an important conceptual advance, this transient analysis contains many crude assumptions such as very long lags due to slow migration. This estimate probably represents an upper bound to the effect of biome shifts alone in causing a transient loss of carbon from the terrestrial biosphere. Such losses would be expected to depend strongly on the rate of climate change; that is, the faster the rate of climate change, the greater the likelihood of large carbon losses from terrestrial ecosystems due to biome shifts during the transient (Woodwell, 1995).

A number of terrestrial biogeochemistry models are now capable of evaluating how terrestrial carbon storage might change with shifts in climate and atmospheric  $\text{CO}_2$  concentrations from one equilibrium condition to another. Examples are BIOME-BGC (Hunt and Running, 1992; Running and Hunt, 1993), CENTURY (Parton *et al.*, 1987, 1988, 1993) and TEM (Raich *et al.*, 1991; McGuire *et al.*, 1992; Melillo *et al.*, 1993). In an application to the continental United States, these models were run for a range of future equilibrium climates at doubled  $\text{CO}_2$ . The

BIOME-BGC model projected terrestrial carbon losses up to 33% relative to the current condition, and CENTURY and TEM projected carbon gains of between 6 and 16% (VEMAP Members, 1995).

As part of the VEMAP activity, these three biogeochemistry models were coupled with three biogeography models<sup>1</sup> (see Section 9.3.5); BIOME2 (Haxeltine *et al.*, 1996), DOLY (Woodward and Smith, 1994; Woodward *et al.*, 1995), and MAPSS (Neilson, 1995; Neilson and Marks, 1995). Each of the model pairs was then run with three GCM-generated climate scenarios for doubled  $\text{CO}_2$ . The terrestrial carbon storage response ranged from a loss of 39% for the BIOME-BGC/MAPSS pair with a UKMO-GCM climate, to a 32% gain for the TEM/MAPSS pair with an OSU-GCM climate (Figure 9.4). The BIOME-BGC/MAPSS response for the UKMO climate scenario was primarily caused by decreases in forested area and temperature-induced water stress. The TEM/MAPSS response for the OSU climate was largely attributable to forest expansion and temperature-enhanced nitrogen cycling. This range of responses represents the pooled uncertainty for structural and functional ecosystem responses and for the regional climate anomalies inferred from three GCMs.

### 9.4.3 Equilibrium Analyses: Global Ecosystem Model Projections

Several process-based ecological models including TEM and IMAGE2 (Alcamo *et al.*, 1994) have been used to evaluate the effects of equilibrium climate and atmospheric carbon dioxide shifts on global terrestrial carbon storage. Melillo *et al.* (1995b) used a new version of TEM (McGuire *et al.*, 1995b) to assess the equilibrium response of global ecosystem carbon storage to a  $\text{CO}_2$  doubling alone, with no climate change and no change in vegetation distribution. Under these conditions, terrestrial carbon storage was projected to increase by 360 GtC (Figure 9.5).

The TEM model was also used to simulate the response of terrestrial carbon storage with constant  $\text{CO}_2$ , but with  $\text{CO}_2$ -induced climate changes inferred from equilibrium simulations with the GFDL-GCM. The result was a projected net loss of terrestrial carbon of 130 Gt (Figure 9.5). This result was obtained under the assumption of no vegetation redistribution. When TEM was coupled to a modified version of BIOME (Prentice *et al.*, 1992), the

<sup>1</sup> Terrestrial biogeochemistry models simulate carbon, water and nutrient fluxes through ecosystems, assuming a prescribed vegetation structure. Thus they contrast with biome (or biogeography) models, which simulate the geographic distributions of vegetation structural types (biomes).



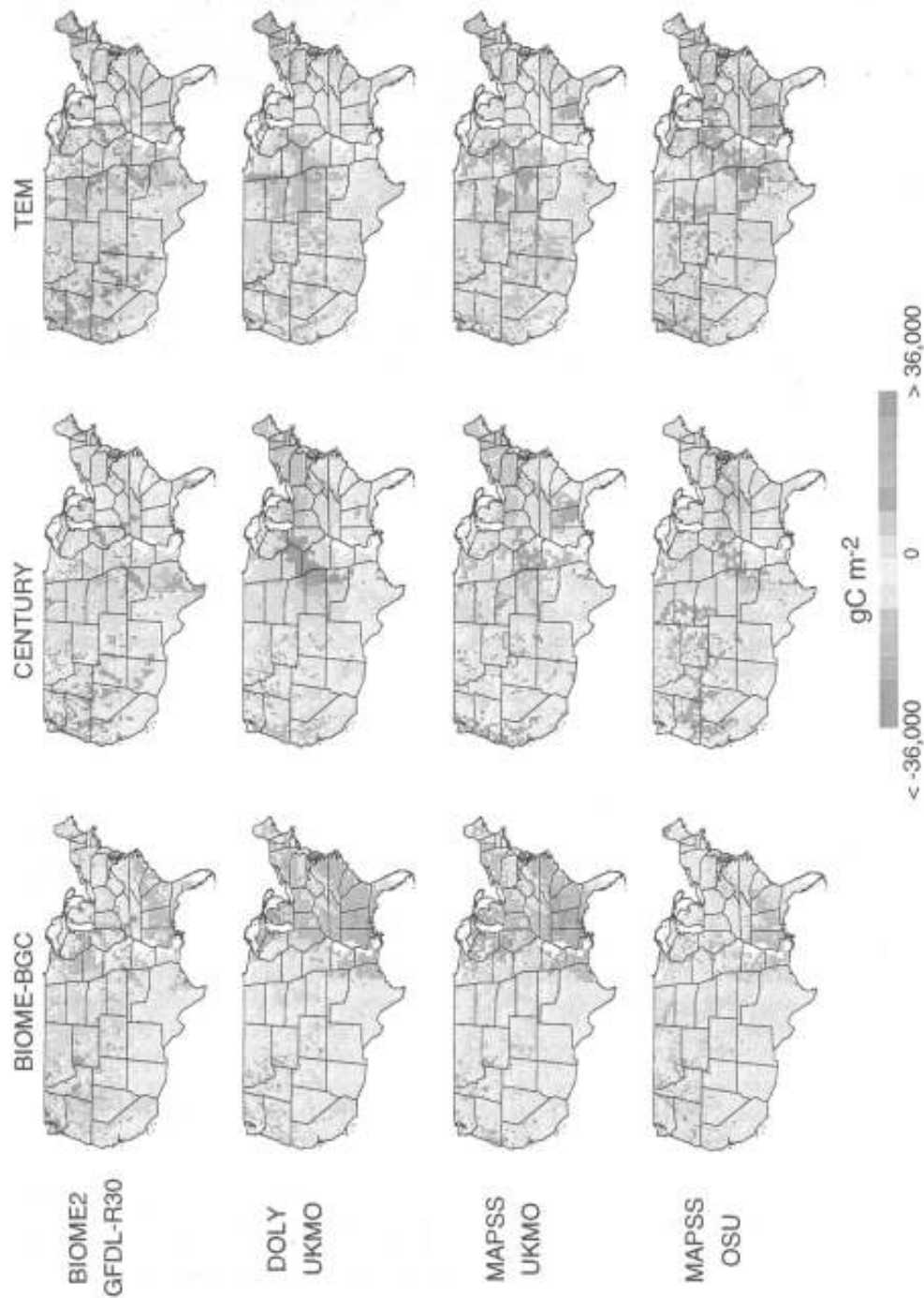
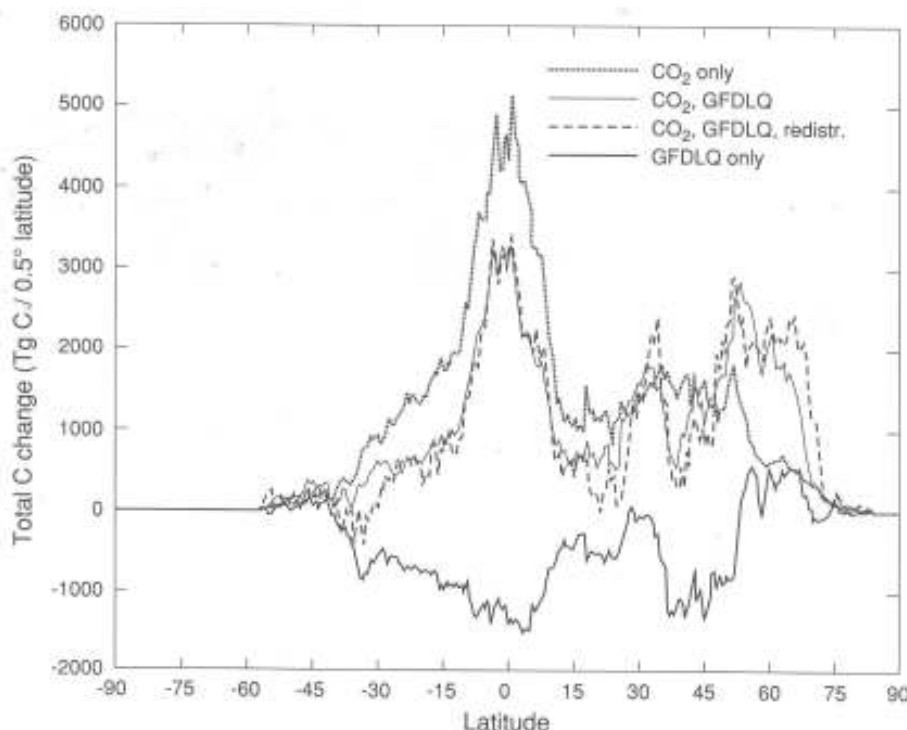


Figure 9.4: Simulated changes in equilibrium terrestrial carbon storage for the conterminous USA (VEMAP Members, 1995). Biogeochemistry models (BIOME-BGC, CENTURY and TEM) are run with the vegetation distributions of biogeography models (BIOME2, DOLY and MAPSS) for particular climate scenarios (GFDL-R30, UKMO and OSU).



**Figure 9.5:** Simulated changes in equilibrium terrestrial carbon storage as a function of latitude due to: direct effects of a doubling of  $\text{CO}_2$  (dotted line); effects of climate change, from the GFDL  $2 \times \text{CO}_2$  scenario (thick solid line); combined effects of  $\text{CO}_2$  and climate without vegetation redistribution (thin solid line); combined effects of  $\text{CO}_2$  and climate with vegetation redistribution (dashed line). After Melillo *et al.* (1995b).

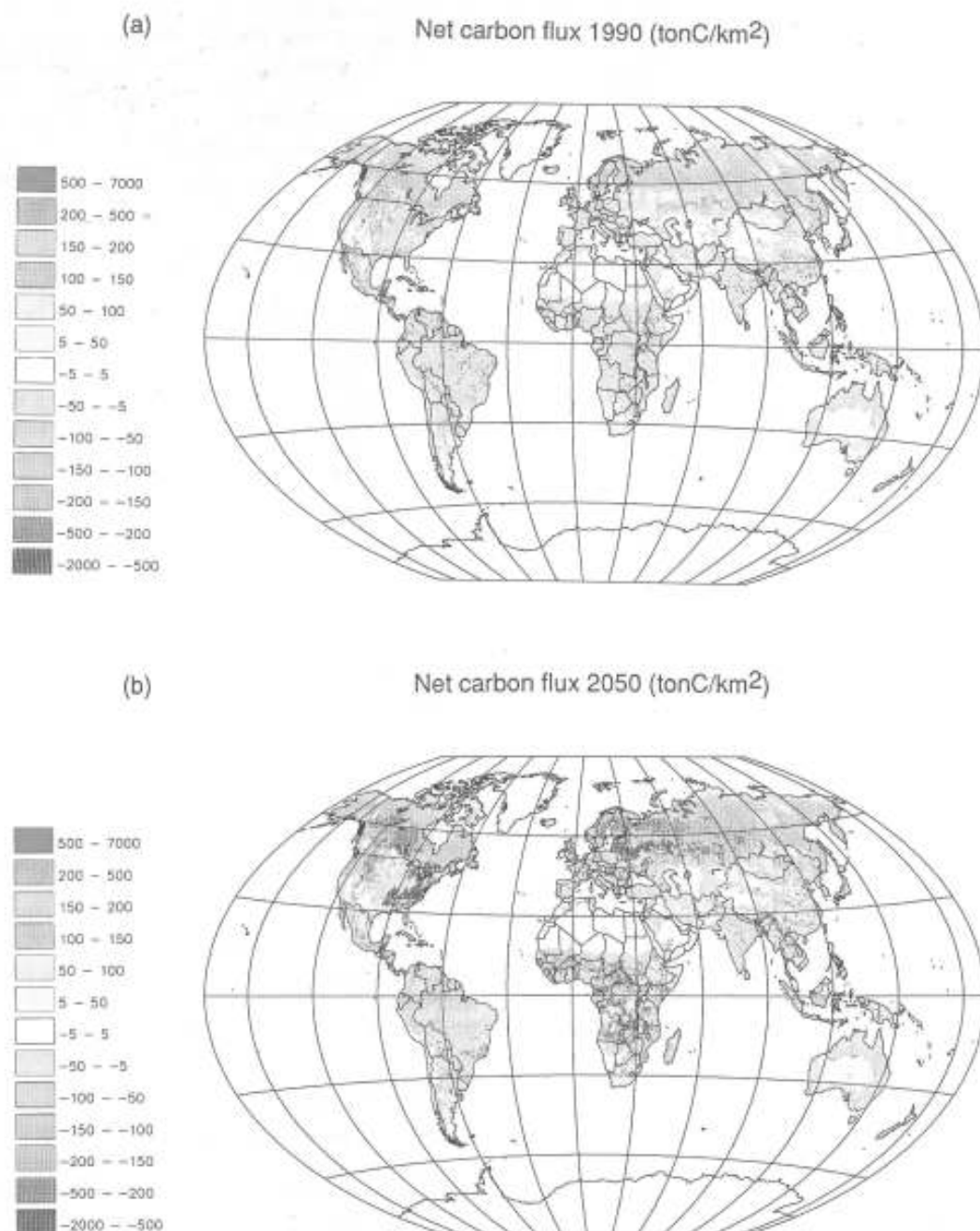
projected carbon loss was of a similar magnitude (Figure 9.5). Although some other modelling studies have projected long-term increases in carbon storage of up to about 100 GtC over several hundred years (Cramer and Solomon 1993; Smith and Shugart 1993; Prentice and Sykes 1995), due to climate change alone, these results are probably unrealistic. The TEM-BIOME result (Figure 9.5) includes the effects of both biogeochemistry and biogeography; the other results included only biogeographical changes, assuming fixed carbon densities in each biome.

Ecosystem models have also been used to evaluate the combined response of terrestrial carbon storage to  $\text{CO}_2$  fertilisation and climate change. TEM (Melillo *et al.*, 1995b) projected a net increase of 290 GtC (Figure 9.5). The gain due to  $\text{CO}_2$  fertilisation outweighed the loss due to warming. Again, allowing vegetation redistribution did not appreciably change this result (Figure 9.5). Alcamo *et al.* (1994) used the IMAGE2 model to assess the combined effects of  $\text{CO}_2$  fertilisation and climate change plus various scenarios of land-use change. Their study projected an

increase in terrestrial carbon storage, in the range 200–250 Gt depending upon future land-use assumptions (Figure 9.6). These equilibrium model results suggest that the effect of  $\text{CO}_2$  in increasing carbon storage could dominate over any warming-induced reduction in carbon storage, but this result must be considered as preliminary.

#### 9.4.4 The Palaeo-record and Implications for a Future Climate Equilibrium: Increasing Terrestrial Carbon Storage with Increases in Atmospheric Carbon Dioxide and Global Mean Temperature after the Last Glacial Maximum

Between the last glacial maximum and the start of the present (Holocene) interglacial there were large increases both in atmospheric greenhouse gas concentrations and global mean temperature.  $\text{CO}_2$  increased by about 90 ppmv. There may have been several causes of the increase in atmospheric  $\text{CO}_2$ , but they probably all included an ocean source (Siegenthaler, 1989; Heinze *et al.*, 1991; Peltier *et al.*, 1993; Archer and Maier-Reimer 1994;



**Figure 9.6:** Net carbon flux from the terrestrial biosphere to the atmosphere simulated by the IMAGE2 integrated assessment model for (a) 1990 and (b) 2050 under a “conventional wisdom” scenario. The net flux includes deforestation and forest regrowth as well as climate and CO<sub>2</sub> effects. The large sinks shown in the northern temperate regions for 2050 are due to abandonment of agricultural land. After Alcamo *et al.* (1994).

Ganeshram *et al.*, 1995; Chapter 10). Along with the atmospheric  $\text{CO}_2$  increase, global mean temperature increased by 4–7°C according to climate model estimates (Kutzbach and Guetter, 1986; Broccoli and Manabe, 1987; Kutzbach *et al.*, 1995). Palaeodata indicate local temperature increases on the order of 5°C or more in both temperate and tropical regions (Wright *et al.*, 1993; Stute *et al.*, 1995; Thompson *et al.*, 1995). Over the same period, global terrestrial carbon storage increased by 310–550 Gt (Duplessy *et al.*, 1988; Bird *et al.*, 1994).

For several reasons this is not a strict analogy for future  $\text{CO}_2$  and climate changes. The detailed time courses of change in global mean temperature,  $\text{CO}_2$  and especially carbon storage are not known. The increase in temperature was partly due to the disappearance of the ice sheets, and was about twice as large as would be expected due to the radiative-forcing changes alone (Lorius *et al.*, 1990). Deglaciation increased the area available for vegetation; however, a similar area of the exposed continental shelf was flooded. The increase in unglaciated land area from the LGM to the present was, at most, 2% (Prentice *et al.*, 1993b). The lesson is that a combined  $\text{CO}_2$  increase and global warming can lead to a substantial (in this case, about 25%) increase in the amount of carbon stored in terrestrial vegetation and soils.

### 9.5 Methane: Effects of Climate Change and an Increase in Atmospheric $\text{CO}_2$ on Methane Flux and Carbon Balance in Wetlands

Methane ( $\text{CH}_4$ ) is produced in flooded organic soils as a result of anaerobic respiration (methanogenesis), and  $\text{CH}_4$  emissions from natural wetlands are estimated to contribute about 20% to the global emissions of this gas to the atmosphere (Chapter 2; Prather *et al.*, 1995). Climate change could either increase or decrease  $\text{CH}_4$  flux from wetlands. Factors increasing  $\text{CH}_4$  flux would include northward spread of peat-forming areas into the high latitudes (enhanced by increased precipitation) and faster carbon turnover due to warmer temperatures (Crill *et al.*, 1988; Christensen and Cox, 1995) and/or higher  $\text{CO}_2$  (Hutchin *et al.*, 1995). Factors decreasing  $\text{CH}_4$  flux would include drier conditions (lower water table) in extant peatlands (Whalen and Reeburgh, 1990; Roulet *et al.*, 1992), and drying-out and/or permafrost melting leading to loss of peat-forming areas in the continental interiors (Lachenbruch and Marshall, 1986; Oechel *et al.*, 1993; Oechel and Vourlitis, 1994; Gorham, 1995).

However, if  $\text{CH}_4$  flux declines in some regions due to drying, this would imply an additional flux of  $\text{CO}_2$  to the atmosphere due to enhanced aerobic respiration and,

perhaps, large-scale oxidation of the peat by erosion and fire (Hogg *et al.*, 1992). This scenario is of concern because as much as 450 GtC may be stored in high latitude peats (Gorham, 1991; Botch *et al.*, 1995). It has been suggested that the large warming that climate models predict for the high latitudes could thus threaten the integrity of this carbon store (Gorham, 1991, 1995). Like the possible carbon “spike” due to transient vegetation changes, this possible source of carbon to the atmosphere represents a potential positive feedback that has not been adequately quantified (Nisbet and Ingham, 1995).

Analysis of the palaeo-record of  $\text{CH}_4$  support the idea that the net  $\text{CH}_4$  flux from wetlands could either increase due to warming and  $\text{CO}_2$  increase, or decline due to drying. Atmospheric  $\text{CH}_4$  concentration increased (by 300 ppbv) after the LGM, and closely tracked global climate changes through the deglaciation (Stauffer *et al.*, 1988; Chapellaz *et al.*, 1990; Chapellaz *et al.*, 1993a). The increase in  $\text{CH}_4$  concentration contributed to the global warming that followed the LGM (Lorius *et al.*, 1990; Lorius and Oeschger, 1994). In contrast to  $\text{CO}_2$ , the increase in  $\text{CH}_4$  is thought to represent a positive feedback involving the terrestrial biosphere (Schimel *et al.*, 1995).

Model calculations suggest that the low  $\text{CH}_4$  concentration at the LGM was primarily due to low  $\text{CH}_4$  production by terrestrial ecosystems (Chapellaz *et al.*, 1993b), rather than to high OH concentrations in the atmosphere (Pinto, 1991; Thompson *et al.*, 1993; Crutzen and Bruhl, 1993; Martinerie *et al.*, 1995). Low  $\text{CH}_4$  production would be expected at the LGM, because tropical and high latitude wetlands were less extensive (implying a reduced source area: Petit-Maire *et al.*, 1991) and temperatures and  $\text{CO}_2$  were lower, both factors implying slower carbon turnover in the source area.

Atmospheric  $\text{CH}_4$  concentration stood at 700–750 ppbv in the early Holocene, had fallen to < 600 ppbv by the mid-Holocene, then rose gradually in the late Holocene to once again reach the “pre-industrial” level of 700–750 ppbv. These variations may reflect a trade-off between the extent of tropical and high latitude wetlands (Blunier *et al.*, 1995). Tropical wetlands were most extensive in the early Holocene due to increased monsoonal precipitation (Petit-Maire *et al.*, 1991; Street-Perrott, 1992). High latitude wetlands have increased in extent during the late Holocene due to decreasing temperatures and evaporation (Ovenden, 1990; Zoltai and Vitt, 1990; Gorham, 1991; Botch *et al.*, 1995). The lesson is that warming in high latitudes can either increase or decrease natural  $\text{CH}_4$  production, depending on the extent to which increased temperatures are matched by increased precipitation and/or  $\text{CO}_2$ .

## 9.6 Nitrous Oxide

Our current understanding of the global budget of nitrous oxide ( $N_2O$ ) is reviewed in Chapter 2 and by Prather *et al.* (1995). The budget is largely controlled by microbial processes in soils. Today, the warm, moist soils of the tropical forests are probably the single most important source of  $N_2O$ . Land-use and the intensification of agriculture in the tropics appear to be increasing the size of the  $N_2O$  source from this region.

The microbial process responsible for the production of most of the  $N_2O$  is denitrification: the dissimilatory reduction of oxides of nitrogen that produces  $N_2$  as well as  $N_2O$ . The rate of denitrification is controlled by oxygen ( $O_2$ ), nitrate ( $NO_3^-$ ) and carbon. Moisture has an indirect effect on denitrification by influencing  $O_2$  content of soil. If other conditions are appropriate, then temperature becomes an important controller of denitrification.

Denitrifiers in natural environments are capable of producing either  $N_2O$  or  $N_2$  as end products. Numerous factors have been reported to affect the proportion of  $N_2O$  produced relative to  $N_2$ . Perhaps most important are the relative supplies of nitrate and carbon (Firestone and Davidson, 1989). The dominant product of denitrification may be  $N_2O$  in systems where, at least for a time, nitrate supply is high and carbon supply is low, but not excessively so.

Probably due to a combination of more extensive wetland areas and increased rates of nitrogen cycling in terrestrial ecosystems under warmer and/or moister climates after the LGM, atmospheric  $N_2O$  concentration increased from ~200 ppbv to ~270 ppbv (Leuenberger and Siegenthaler, 1992). In the future, a wetter climate may lead to increased  $N_2O$  production, although this potential positive feedback has not been adequately quantified.

## 9.7 Global-Scale Biogeophysical Feedbacks: Changes in Ecosystem Structure and Function Affect Climate

### 9.7.1 Effects of Vegetation Structure on Land-surface Characteristics

Vegetation mediates the exchange of water and energy between the land surface and the atmosphere (Rind, 1984; Sud *et al.*, 1990; Hostetler *et al.*, 1994). Land-atmosphere interactions are physically represented by land-surface models designed for implementation in current GCMs (see Chapter 5, Section 5.3.2). These models require a global vegetation type (biome) distribution to be prescribed. Most climate change analyses with GCMs have assumed no change in vegetation distribution. However, both land-use

change (e.g., deforestation and human-induced deforestation) and climatically induced natural vegetation change can significantly alter global vegetation distribution over decades to centuries.

The main land-surface parameters influenced by vegetation structure are surface albedo (normal and snow-covered), roughness length (affecting boundary-layer conductance), canopy conductance and rooting depth. Snow-free surface albedo for total short-wave radiation ranges from ~0.15 in closed forests to 0.4–0.5 in hot deserts (Henderson-Sellers and McGuffie, 1987). The largest effect of snow cover is on low vegetation types such as grasslands and tundra, where the snow-covered albedo can be up to 0.8. Roughness length increases with vegetation height: tall forests therefore present a boundary-layer conductance that is much larger than short grasslands. Canopy conductance is influenced by foliage density, plant nitrogen content, atmospheric  $CO_2$  content and drought stress (Schulze *et al.*, 1994). At present ambient  $CO_2$ , most natural vegetation types have a maximum stomatal conductance of 3–6 mm/s while field crops have a higher conductance, up to 12 mm/s (Kelliher *et al.*, 1993). Canopy conductance increases asymptotically with leaf area index, towards a value of about 3–4 times stomatal conductance for a closed canopy (Schulze *et al.*, 1994). Maximum stomatal conductance is lowered under increased ambient  $CO_2$ . Stomatal closure under midday conditions of high evaporative demand acts to restrict canopy conductance. This closure occurs sooner as soil moisture supply is reduced and vapour pressure deficit increases.

### 9.7.2 Effects of Land-surface Changes on Climate

The sensitivity of climate to changes in these different land-surface properties varies regionally. For example, albedo effects are important in controlling precipitation in climatic regimes where precipitation is controlled by large-scale dynamics or convection; canopy conductance and rooting depth are important in regimes where a large proportion of precipitation arises by recycling of evapotranspiration from the land surface (Rind, 1984).

Sensitivity analyses with GCMs have been used to estimate the response of climate to major changes in the land surface, such as tropical deforestation (Dickinson, 1989; Shukla *et al.*, 1990; Nobre *et al.*, 1991; Henderson-Sellers *et al.*, 1993; Polcher and Laval, 1994). Through raising albedo and/or lowering evapotranspiration, large-scale deforestation tends to reduce moisture convergence and precipitation. The potential area of tropical rain forests and seasonal forests is therefore reduced. More generally, albedo exerts a strong control over evapotranspiration and



precipitation in the tropics and subtropics (Charney, 1975; Charney *et al.*, 1977; Mylne and Rowntree, 1992).

Albedo changes in the high latitudes can also have major effects. Bonan *et al.* (1992) and Chalita and Le Treut (1994) examined the sensitivity of global climate to boreal deforestation (replacement of the boreal forests by tundra). The large increase in snow-covered albedo resulted in colder winters and a longer snow season. In Bonan *et al.*'s study, which included a mixed-layer ocean model, the thickness and duration of Arctic sea ice was increased and the cooling thereby extended from winter into summer. The total effect was felt across the Northern Hemisphere and summer temperatures became too cold for the persistence of boreal forests in their present range. Such sensitivity studies suggest that large biogeophysical effects of vegetation structure on climate could be brought into play by land-use change.

Climate-induced changes in biome distribution would presumably also cause feedbacks. Palaeoclimate simulations suggest that such feedbacks are important. Street-Perrott *et al.* (1990) showed that a GCM with surface boundary conditions kept as today could simulate the phenomenon, but not the extent and magnitude, of African monsoon expansion at 9000 yr bp. When a realistic expansion of vegetation across the present-day Sahara was included (via the albedo effect), precipitation increased by a further ~1 mm/day over large areas, including northern and western regions that were scarcely affected in the original simulation. Foley *et al.* (1994) showed that the warming-induced poleward expansion of boreal forests into what is now tundra at 6000 yr bp could have doubled the initial effects of orbital forcing (Figure 9.7). In both examples, biogeophysical feedbacks amplified the initial radiative forcing.

More detailed investigation of biogeophysical feedbacks requires coupling vegetation models with GCMs (Henderson-Sellers, 1993; Claussen, 1994). Claussen (1993) coupled the BIOME model asynchronously to an GCM, using an iterative procedure: 4–6 year ensembles of simulated climate were used to modify the biome distribution, which in turn modified the climate. The coupled system proved stable with respect to small perturbations of the biome distribution, as also found by Henderson-Sellers (1993). However a very large perturbation triggered a complex response in the atmospheric circulation and caused the coupled system to return to an alternative state in which the south-western Sahara remained wooded. With 6000 yr bp orbital forcing, the coupled system approached an even more extreme state in which most of the Sahara turned to savannah (Claussen

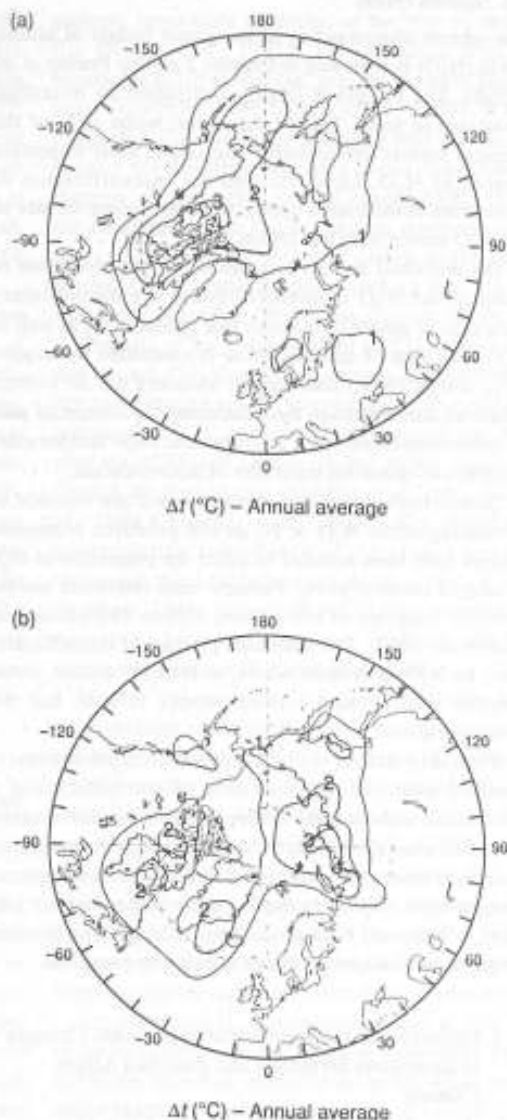


Figure 9.7: Amplification of 6,000 yr bp radiative forcing due to biogeophysical feedback, as simulated with the GENESIS atmospheric/mixed-layer ocean model. (a) Increase in annual mean temperature due to radiative forcing alone, (b) Additional increase due to northward extension of the boreal forest. After Foley *et al.* (1994).

and Gayler, 1995). This state is similar to the 6000 yr bp situation shown by palaeoecological data.

CO<sub>2</sub>-induced changes in canopy conductance are expected to have further feedback effects on climate

(Martin *et al.*, 1989; Field *et al.*, 1995). As ambient  $\text{CO}_2$  increases, stomatal conductance declines. GCM sensitivity studies indicate that a global halving of surface conductance, with no change in leaf area, would lead to reduced evapotranspiration rates, increased surface air warming about  $0.5^\circ\text{C}$  averaged over terrestrial areas, compared with  $1.1$  to  $2.5^\circ\text{C}$  which is predicted for the combined effects of radiative forcing and aerosols (Chapter 6), and in some regions increase soil moisture storage (Henderson-Sellers *et al.*, 1995; Pollard and Thompson 1995). This latter effect of  $\text{CO}_2$  could mitigate or even reverse the mid-latitude drying seen in some  $2 \times \text{CO}_2$  simulations with fixed surface conductance (Chapter 6). Compensatory increases in leaf area would work against the effect of  $\text{CO}_2$ -induced reductions in stomatal conductance. However, a study with a coupled (single column) model of the soil-ecosystem-atmosphere system, including interactive adjustment of leaf area in response to  $\text{CO}_2$ , suggested that the stomatal conductance response would dominate over the compensatory leaf area response (Friend and Cox, 1995). Thus, the net "physiological" effect of  $\text{CO}_2$  on climate would be to reduce evapotranspiration and increase soil moisture, relative to the scenarios based on radiative forcing alone.

Such studies underline the sensitivity of the simulated hydrological cycle to land-surface properties that are determined by ecosystem functional and structural responses to climate and  $\text{CO}_2$ . In particular, GCM simulations of regional changes in soil moisture in a high- $\text{CO}_2$  world are questionable because such simulations have not, as yet, taken into account changes in ecosystem structure and function that would have major feedback effects on the hydrological cycle. The uncertainty is compounded because most current GCMs do not resolve the vertical structure of the planetary boundary layer (PBL), which may limit the effect of changes in stomatal conductance on evapotranspiration (Jarvis and McNaughton, 1986; Martin, 1989; McNaughton and Jarvis, 1991; Monteith, 1995).

Proper representation of these feedbacks in models requires a physiologically based representation of the processes controlling canopy conductance (e.g., Collatz *et al.*, 1991; Friend and Cox, 1995), a sufficiently resolved representation of the PBL (e.g., Troen and Mahrt, 1986; MacNaughton and Jarvis, 1991; Jacobs and de Bruin, 1992), and these elements to be fully interactive in the GCM. Such a coupling of atmospheric and ecosystem processes appears to be a high priority because the potential for future drought is: (a) a key issue in assessing the biological and societal impacts of global change; and

(b) one of the main hypotheses underlying predictions of positive biogeochemical feedbacks leading to  $\text{CO}_2$  release and further warming, as discussed in Section 9.2.3.1 and in Woodwell and Mackenzie (1995).

In conclusion, biogeophysical feedbacks involve interactions between the atmosphere and biosphere which can only be assessed quantitatively through the further development of coupled models including the terrestrial biosphere as an integral component of the climate system. Model sensitivity studies (including palaeoclimate simulation) suggest that these feedbacks are potentially of similar magnitude to the direct effects of changes in radiative forcing.

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## Change and Feedbacks to Climate

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