9   WG1 Summary: Natural and anthropogenically-induced variations in terrestrial carbon balance

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INTRODUCTION

Combustion of fossil fuels and changes in land use have caused a substantial increase in atmospheric CO_2 over the past century, yet the actual atmospheric change is only about half of total fossil fuel emissions alone. This difference is accounted for by carbon (C) uptake into terrestrial and oceanic systems (Table 9.1). CO_2 dissolves into surface waters of the ocean, and can then be stored for centuries via transport into deep waters. Terrestrial ecosystems act as a sink for CO_2 when their net ecosystem productivity (NEP) is positive, in other words when net primary productivity (NPP) exceeds heterotrophic respiration. Recent estimates suggest that significant C sinks are operating in both land and ocean systems (Tans et al. 1990; Keeling et al. 1993; Siegenthaler and Sarmiento 1993), but considerable uncertainty exists about the relative sizes of these sinks, about the mechanisms behind terrestrial storage, and about the potential for the terrestrial biosphere to continue moderating the accumulation of CO_2 in the atmosphere.

Resolution of these uncertainties is critical to projections of future CO_2 concentrations and climate. Storage of C in the oceans is likely to be more stable and persistent than storage on land (IPCC 1990). In turn, alternative mechanisms for terrestrial sinks have very different implications for the biosphere's long-term response to change. For example, C fixed into leaves and easily decomposable litter will return to the atmosphere in a matter of months, whereas C in wood and recalcitrant soil organic matter (SOM) can remain on land for centuries, therefore equal increases in gross C uptake into wood versus leaves will result in very different changes in net C uptake.

This chapter draws upon the individual papers of Working Group 1 (WG1), and summarises some of the group discussions. We discuss ways in which forested biomes may respond to and influence anthropogenic perturbations to the global C cycle, with a focus on "natural" processes in the C cycle and on the response of those processes to "indirect" anthropogenic perturbations. By indirect, we mean human-induced changes such as elevated atmospheric CO_2, climate change, and high rates of N deposition. The "direct" effects of land use changes are discussed in Part II of this volume.

There is roughly 1.5 times more C in the vegetation and soils of the world's forests than is in the atmosphere—ca. 1000 Pg C versus ca. 700 Pg C (Schlesinger 1991; Dixon et al. 1994)—and annual exchanges of CO_2 between forest ecosystems and the atmosphere are several times larger than yearly fossil fuel emissions. Thus, a relatively small imbalance in the global fluxes of C to and from forests could have significant effects on atmospheric CO_2 levels, and where that imbalance is due to changes in wood or SOM, the effects may last for decades to centuries. We discuss several factors which could cause variability in global forest NEP, including:

Table 9.1. Average annual budget of CO_2 perturbations for 1980–1989 (Pg C yr^{-1}). Reprinted from Schimel et al. (IPCC 1995) with author's permission.

| RESERVOIR	MEAN ANNUAL RESERVOIR CHANGE (Pg C yr^{-1})
Emissions from fossil fuel combustion and cement production	-5.5 ±0.5
Storage in atmosphere	3.2 ±0.2
Oceanic uptake	2.0 ±0.8
Emissions from changes in tropical land use	-1.6 ±1.0
Uptake by Northern Hemisphere forest regrowth	0.5 ±0.5
Additional net terrestrial sinks	1.4 ±1.5

fire, insect and other pest outbreaks, climate, atmospheric CO_2 levels, and the deposition of N from the atmosphere. We also devote separate sections to the role of carbon-rich peatlands, and to the potential changes in C storage caused by the movement of forest biomes in response to a changing environment.

Natural *versus* anthropogenic effects on global C balance

A host of modelling studies exist in the literature in which quantitative ranges are given for terrestrial C gain or loss in response to a given anthropogenic perturbation (Jenkinson et al. 1991; Townsend et al. 1992; Melillo et al. 1993; Schimel et al. 1994). One uncertainty in all of these estimates, though, is that they assume the C cycle is in steady state prior to the perturbation being investigated. In contrast to the modelled estimates, recent field data on changes in C stocks (Kauppi et al. 1992; Sedjo 1992; Dixon et al. 1994) represent the combined effects of human perturbation *and* natural "background" variability. If background fluctuations in regional to global exchanges of C are non-trivial, then they must be quantified to allow comparisons of modelled and data-based estimates of human perturbations to the C cycle (Fung, Chapter 2).

The key question is: how large and frequent are these background departures from steady state? Fluctuations in the global environment and in terrestrial C pools have occurred throughout the history of the planet (Webb and Bartlein 1992); northern peatlands, for example, have been accumulating C since the end of the last ice age (Schlesinger 1991). Recent attention to global change phenomena is due to concern that human activities may alter the earth at a rate and/or magnitude that is unmatched over, at the very least, human history. For atmospheric CO_2, that appears to be the case (Figure 9.1). Ice core records show that CO_2 has varied by more than 80 ppm over the last 160 000 years (Barnola et al. 1987), rising and falling several times, but the recent rate of increase and current concentration appear greater than at any other point in the record. This change in CO_2 is predicted to change climate, but the evidence for a human-induced shift in climate is much less clear than that for CO_2. A long-term reconstruction of climate for the same period as the ice core records of CO_2 does not show as clear a departure in recent decades from background variability (Figure 9.1).

The atmospheric CO_2 record also shows that land and/or ocean systems have taken up and stored roughly half of anthropogenic emissions (Fung 1993). However, there is considerable uncertainty over how the total sink is partitioned among land and ocean, in part because of potential variations in natural sources and sinks (Fung 1995). A variety of inherently variable environmental factors can alter the balance between NPP and respiration, including fire, pest outbreaks, and climate (both short- and long-term). Soils, for example, have been accumulating C since the last deglaciation at a rate of about 0.04 Pg yr^{-1} (Schlesinger 1991).
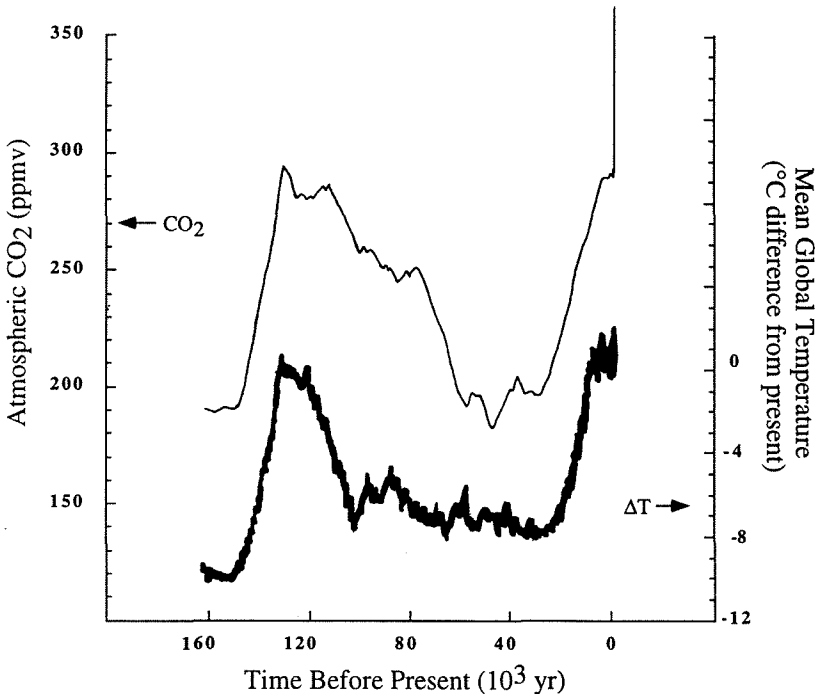
Figure 9.1. Atmospheric CO_2 concentrations and mean global temperatures over the last 160 000 years. CO_2 concentrations are determined by analyses of air bubbles trapped in the Vostok ice core (Antarctica) and from direct measurements at the Mauna Loa Observatory, and temperatures are deduced from ^{18}O values in the core. Redrawn from Barnola et al. (1987).

Fung (Chapter 2) gives a quantitative summary of the current global C budget from the perspective of the atmosphere. She clearly illustrates how background variability in atmosphere–biosphere C exchange could confuse our understanding of how much anthropogenic CO_2 may be stored on land. The "missing" terrestrial sink is commonly thought of as simply an increased flux of C into land ecosystems "induced" by human activity, but Fung points out that the complete equation for the missing sink must include not only this induced flux, but also any imbalance in the background state (see Equation 11, Chapter 2).

Fire

The net effect of fire on the C balance of a forested region is the balance between short term losses of C during and just after burning and gains of C during forest regrowth. In any one year, this is a difference in the dynamics of two very different areas: relatively small C gain for much of the region minus large losses from a small fraction of the area. If integrated over hundreds of years, the net exchange may be a slight sink due to the formation of highly recalcitrant charcoal, but at shorter time scales, a region must vary between net uptake and loss of C. Variability in total C uptake should be small, since it is the product of small gains over a large area, therefore short-term departures from a regional NEP equal to zero will be

over a large area, therefore short-term departures from a regional NEP equal to zero will be driven by variations in fire frequency. In particular, a series of intense fire years could cause the region to be a relatively large short-term source of C to the atmosphere, followed by a longer period in which it is a C sink. See Chapter 14 (Kurz and Apps) for a Canadian example.

The area burned in boreal and temperate regions can fluctuate dramatically on an annual basis. In some regions fire suppression policies are likely to have changed the frequency and variability of fire, but year-to-year variability for the entire region is primarily due to short term weather (Stocks et al., Chapter 8). Based on 1980s data, the area burned in northern temperate and boreal latitudes varied between about 3–12 Mha (Stocks and Simard 1993). Assuming a combustion loss of 1.5 kg C m^{-2} (which is somewhat conservative), this translates into a range in C efflux of 0.14 Pg. This is a rough estimate at best of the potential variability in NEP that is due to fire, and the added contribution of tropical regions is unknown, but it suggests that "natural" variability in global fire frequency could at most cause a short term (several years) source of no more than a few tenths of a Pg. Periods of net uptake should last longer than those of net release, but account for a smaller per year departure from steady state.

More detail on forest fires and the global C cycle is provided by Stocks et al. in Chapter 8. They point out that any attempt to estimate the effects of a naturally varying fire regime are confounded recently by fire management. This effect is much larger in southern boreal and temperate zones, where industrial forestry dominates. The longer past is also confounded by land use change, especially in the U.S. and southern Canada. In general, they state that we can assume much more burned in the past in the temperate zone, and that for the boreal region, the area burned seems to be primarily driven by shifts in climate (see also Working Group 2 summary).

Stocks et al. also suggest that in the future, economic constraints will likely translate into larger burned areas in the boreal, and that a climate change toward warmer and drier conditions would mean increases in boreal fires. Fire management agencies with decreasing budgets would protect only high-value regions, allowing more fire over a larger area. Climate change may also shorten fire return intervals, altering the forest age-class structure and therefore C storage. Finally, they point out that fire may accelerate biome migration.

Pest outbreaks

Periodic outbreaks of forest pests such as jack pine budworms (*Choristoneura pinus*) or spruce budworms (*C. fumiferana*) also cause the release of forest C to the atmosphere. In the circumpolar boreal zone, the average area per year affected by pest outbreaks is roughly equivalent to the area burned (Kurz et al. 1995). Like fire, the effects on NEP come from balancing C lost during infestation against C gained during regrowth. Although a severe outbreak may cause the release of as much C as a fire, the average loss per area is much lower, and any release of C will occur much more slowly than during combustion. As a result, short-term variability in C balance due to insect outbreaks should be less than that for fire. Based on Canadian data for C losses (Volney 1988), we derived a rough estimate of variability in NEP of the circumpolar boreal zone of 0.01–0.03 Pg yr^{-1}.

A couple of major unknowns, however, limit our ability to estimate the full effects of pest outbreaks. One, the quantitative estimates of area affected and C lost for boreal and temperate zones are for insects only; the regional effects of chronic diseases such as root rot are poorly understood. Two, very little is known about pest outbreaks in tropical forests. Therefore, values for C fluctuations based on the northern insect data alone may underestimate the global variability induced by all forest pests. Finally, although natural variability in pest outbreaks may not appear significant to large scale C balance, human activities may cause pronounced

increases in pest outbreaks, and as Kurz and Apps (Chapter 14) point out, it is "easier to kill than grow". In other words, an increase in the frequency of disturbance is likely to cause a decrease in the capacity for C storage.

Volney (Chapter 7) outlines the interactions between forest pests and C balance in Chapter 7. He proposes that the impacts of pests on forests will increase dramatically if changes in climate result in lower soil moisture regimes. This speculation is based on observations of conditions in areas increasingly affected by pests. Historically, the most intense pest outbreaks were restricted to the southern portions of the boreal forest, but Volney points out that a changing climate could allow intense outbreaks to spread to all productive forests in the biome. In addition, he suggests that the introduction of exotic pest species into forested areas will certainly increase the frequency and intensity of outbreaks, and that C losses from these introductions could be large unless managed by effective biological control programs.

Climate

It is quoted widely that the 1980s were the warmest years on record, while the 1950s, 1960s and 1970s were relatively cool; the range in mean global temperature across this period is more than 0.5 °C (Folland et al. 1990). At the same time, global precipitation was somewhat above average in the 1950s and the 1970s, while the 1980s were relatively dry (Eischeid et al. 1991). How do these relatively short-term variations in climate affect terrestrial NEP? Using simple relationships between climate, soil respiration and NPP, Dai and Fung (1993) estimate that climate variability over the last 60 years may have caused the biosphere to alternate between net uptake and release of C, with a total range of more than 1 Pg and an annual variability of 0.3 Pg yr^{-1}. They suggest that the effects of climate alone may account for about half of the unexplained residual in the C budget between 1950 and 1984.

Simple relationships between climate, NPP and decomposition tend to show that warming will cause a net loss of C, while cooling will cause net C uptake (Woodwell 1990; Townsend et al. 1992; Dai and Fung 1993). The effects of climate on NEP, however, may be more complex than these relationships suggest. Increasing decomposition rates not only cause greater respiratory C losses, they also cause an increase in N mineralization, and N limitation of plant growth is widespread in forest ecosystems (Vitousek and Howarth 1991). Because of a dynamic equilibrium between vegetation and soil processes, about 80–90% of forest N is in SOM and litter, and only 10–20% is in vegetation. Rastetter et al. (1992) suggest that this equilibrium distribution will shift as the rate of N cycling changes. If the rate of turnover is increased, the dynamic equilibrium will shift so that a higher percentage of the N will be in vegetation. Thus, a shift toward more optimal temperature and moisture for soil processes will result in a redistribution of N from soils to vegetation. Because the C:N ratio of forest vegetation is about an order of magnitude higher than that of soils (100–200 *vs.* 10–20), any redistribution of N from soils to vegetation will result in a net increase in total ecosystem C. That is, any loss of C resulting from SOM decomposition should be more than made up by the stimulation of vegetation growth at a much higher C:N ratio.

This mechanism for increasing total ecosystem C will work as long as NPP is limited by N or some other nutrient that is supplied largely through the decomposition of SOM (e.g., P). In forests where NPP is limited by light or water, an increase in nutrient availability resulting from an increase in SOM decomposition will not stimulate production and therefore will not stimulate C storage. Under such conditions, nutrients released from the SOM will likely be lost from the ecosystem altogether. Thus, C released by the increased decomposition will not be made up by production in the vegetation and there should be a net loss of C from the ecosystem as a whole.

The Dai and Fung analysis did not account for these potential nutrient effects on NEP. In fact, if most terrestrial systems are primarily nutrient limited (rather than by moisture or light), then the warming period during the eighties might be expected to increase terrestrial net C uptake, rather than shift the biosphere towards the net source suggested by Dai and Fung. If, however, this nutrient effect dominates the terrestrial response, then climate variability should have caused the net C flux in recent decades to oppose, rather than track, temporal estimates of the missing sink.

The effects of a warmer climate on both C and nutrient cycles, and the overall effect on forest C balance, are discussed by Townsend and Rastetter (Chapter 3). For a given biome, whether warming leads to C gain or loss should depend on the response of vegetation growth rates to increasing rates of nutrient mineralization balanced against the increases in respiration. Townsend and Rastetter suggest that net uptake of atmospheric C should prevail, at least in the short term, although Fung (1995) points out that a positive feedback, in which warming leads to C loss from the biosphere, is more consistent with the recent C budget. The interactive effects of changes in moisture add to the uncertainty, as does the likelihood that a warmer climate will initiate biome redistribution.

Summary of background variability in carbon balance

There is still much uncertainty over how the net C flux of an undisturbed biosphere might vary both in magnitude and in time. Of the factors discussed above, variations in climate appear to produce the greatest potential range in NEP, but the net effects of climate are still unclear, as are the total potential influences of fire, pest outbreaks and other disturbances in forested regions.

Estimates of global variability derived from scaling up regional data are subject to large errors; it may be that the range decreases significantly with greater area considered. None of the numbers given in the preceding sections are robust; instead they are meant to show the potential importance of natural variability in terrestrial ecosystems—especially in forests—to estimates of recent anthropogenic influences on C balance. It does appear that total background fluctuations in the biosphere may be of the same order of magnitude as the missing C sink, therefore the typical baseline assumption of zero net C exchange prior to human disturbance may introduce significant errors into the current C budget (see also WG2 summary, Chapter 17). On the other hand, it seems unlikely that natural variability in the global C cycle could have been predominantly responsible for the apparent steady increase in terrestrial C storage over the last two centuries.

Atmospheric CO_2

In contrast to the climate record, it is clear that atmospheric CO_2 concentrations are much higher today than they were in the centuries preceding the industrial revolution (Figure 9.1). In addition, decadal variability in CO_2 was a tiny fraction of the change brought on by human activities (Keeling et al. 1989). Therefore, any recent changes in terrestrial C storage due to changes in CO_2 may be safely attributed to human influence. These changes, however, are extremely difficult to estimate, as the effects of CO_2 have been shown to vary substantially with plant species, resource availability, and time (Mooney et al. 1991; Bazzaz and Fajer 1992; Comins and McMurtrie 1993). Based on the immediate response and several model computations, Kellomaki and Karjalainen (Chapter 5) suggest that boreal forest growth should be enhanced under the combination of elevated temperature and CO_2. The duration of this response, however, is not certain. They describe field experiments which indicate that the photosynthetic response of coniferous species subjected to long-term doubled CO_2 is much smaller than the initial change. Similarly, they suggest that long term temperature elevation will reduce C

uptake. Finally, any enhancement of growth will speed successional processes, thereby causing an earlier reduction in a forest's capacity to sequester C than under pristine conditions. In the long run, Kellomaki and Karjalainen propose that the C uptake by boreal forest ecosystems subjected to higher temperatures and CO_2 concentrations will probably not be higher than current levels.

Nitrogen deposition

Like atmospheric CO_2, recent effects of anthropogenic activity on the N cycle are much larger than background variability; human activity has caused the global rate of N_2 fixation to more than double in just three decades (Vitousek 1994; Figure 9.2). Such disturbance of the N cycle has led to much higher rates of N deposition on to land and ocean. Galloway et al. (1994) estimate that deposition has increased by more than an order of magnitude in parts of the temperate zone, and since most temperate ecosystems appear to be N limited, it has been suggested that this increase may stimulate C uptake and storage (Peterson and Melillo 1985; Schindler and Bayley 1993; Hudson et al. 1994; Townsend et al. 1985). However, the magnitude and duration of such a sink are not well known.

In Chapter 3, Townsend and Rastetter suggest that forests are likely to dominate the global response to N deposition due to their capacity to produce woody tissue with both high C:N ratios and long turnover times. They also point out that a global estimate of the effects of N deposition must take into account a number of factors which vary strongly in time and space.
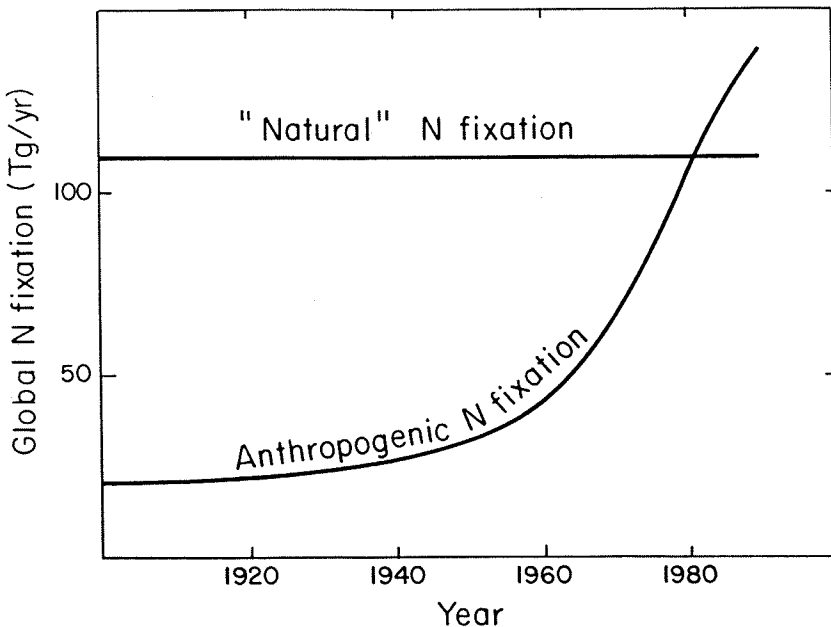
Figure 9.2. Natural and anthropogenic N fixation over the twentieth century. The natural line is biological fixation in natural terrestrial systems plus fixation by lightning; the anthropogenic line is the sum of fixation for fertilisers, fossil fuel combustion and leguminous crops. Reprinted from Vitousek (1994) with permission of the author.

Uptake in any given year will be equal to the net primary production stimulated by the current year's deposition minus the respiration from excess C fixed in previous years. In other words, C storage in the present depends upon N inputs in the past. In addition, deposition is not evenly distributed across the terrestrial landscape; it varies by more than an order of magnitude among world biomes (Penner et al. 1991), and different ecosystem types will vary greatly in their response to that N. For example, N which falls on cultivated areas will not contribute significantly to any terrestrial sink.

Townsend and Rastetter identify three major variables as critical in determining the global effects of N deposition on C storage. The first is the distribution of N-limited forest ecosystems relative to the distribution of N deposition. The second is the fraction of N inputs which are allocated to the production of woody tissue. Finally, both current and future C storage will depend on the fraction of N inputs which are retained in the ecosystem. Aber et al. (1989) suggest that as elevated N inputs continue, the extent of N limitation will decline and therefore that N retention will decline. In the extreme case, N inputs may become so high that they are damaging, causing ecosystem decline and C loss. Forest dieback in some areas of Europe and the north-eastern United States has been attributed to long-term exposure to high N and sulphur inputs (Schulze 1989). Townsend and Rastetter propose that even if these inputs do not prove harmful, the global extent of N limitation must be declining, and therefore the long-term persistence of any N-derived sink is inherently limited.

Peatlands

Peatlands are a large reservoir of C, and we address them here for several reasons. Firstly, many of the world's peatlands also have a significant amount of tree biomass. Secondly, the rate of C accumulation in peatlands may be important in establishing the natural variability of terrestrial NEP. Finally, changes in climate may cause large scale conversion of open and sparsely wooded peatlands to more dense forest.

The present average accumulation of C in northern peatlands is estimated at 29 g C m^{-2} yr^{-1} (Zoltai and Martikainen, Chapter 4). This value leads to an annual C sink of about 0.1 Pg yr^{-1} in all northern peatlands (330 Mha). Total C in this region has been estimated to be between 192–455 Pg, and NPP averages about 300 g m^{-2} yr^{-1}, thus roughly 8% of annual NPP is accumulated as peat. The ~0.1 Pg yr^{-1} rate of accumulation appears to be relatively stable, at least in recent centuries. Peatlands are therefore unlikely to have caused any significant inter-decadal variability in the terrestrial C budget, but their steady C uptake should be accounted for when establishing a background against which recent perturbations are to be measured. The additional influence of the large area of tropical peatlands is not well known.

Zoltai and Martikainen (Chapter 4) outline how the effects of peatlands on the C cycle and climate depend not only on CO_2 exchange, but also on the production and emission of methane. For example, a drying of peatlands may increase CO_2 efflux, but it may also decrease CH_4 production, and since on a per molecule basis CH_4 has a greater impact on radiative balance than does CO_2, the net effect could be a negative feedback to warming (Billings et al. 1984; Oechel et al. 1993). On the other hand, they point out that a warmer climate will both increase microbial activity and allow greater emissions in fall and spring by shortening the number of months in which surface water is frozen. Finally, they propose that the practice of converting peatlands to forested areas via draining will result in a net loss of C, due to an increase in decomposition rates as conditions switch from anaerobic to aerobic that exceeds any C gain from the accretion of woody biomass.

Biome migration

Present day ecosystem types, or biomes, are not fixed in space, nor have they been at any time in the past (Prentice and Fung 1990; Friedlingstein et al. 1995). Changes in both the composition of the biomes and in their distribution over the globe have been driven by changes in climate. In the past, changes in climate have been relatively slow, so that the movement of biomes has usually occurred on the time scale of centuries. Future changes, however, are predicted to occur at an unprecedented rate, which may well lead to rapid changes in the present boundaries of biomes, and even to complete breakdown of some biomes and a consequential reduction in their ability to store C.

Possible equilibrium changes in the distribution of biomes and C storage under an altered climate have been examined both on a global scale (Prentice and Sykes 1994) and on a regional scale (Sykes and Prentice, Chapter 6) using the equilibrium model of potential vegetation, BIOME 1 (Prentice et al. 1992). The model uses a small number of plant functional types, a dominance hierarchy and five environmental parameters to project the distribution of biomes. Prentice and Sykes (1994) used the model to project changes in biome distribution and C storage under doubled CO_2 scenarios from two general circulation models GFDL (Manabe and Wetherald 1987) and OSU (Schlesinger and Zhao 1989). Generally, their projections show a poleward shift of the taiga, cool conifer, cool mixed, temperate deciduous and warm temperate evergreen/warm mixed forest belts in northern high- and mid-latitudes, an eastward shift of forests in Western Eurasia, and a poleward shift of warm (C_4 dominated) grass and shrublands. They also a project a slight increase in tropical rain and seasonal forests. However, there are regional variations to this general pattern.

On a global scale, the net change in C is not clear as there are both regional gains and losses, and large differences depending on the climate scenario used (Prentice and Sykes 1994; Friedlingstein et al. 1995). In the Prentice and Sykes study, the OSU scenario estimated that terrestrial C storage would increase by 90 to 100 Pg C, while the GFDL scenario produced an increase of only 50 Pg C down to no change at all. Prentice and Sykes (1994) also suggested that the terrestrial biosphere may respond in a non-linear fashion to rapid changes in climate, and that beyond a certain point the shifts in biomes may turn the biosphere from a sink into a source of C if taiga and tundra regions are reduced sufficiently. All current estimates of C storage under a new biome distribution are equilibrium simulations, and the transient responses may be much different, but a dynamic vegetation model is yet to be developed which could answer these questions on a global scale. Sykes and Prentice discuss the effects of biome shifting in Chapter 6, and describe some regional attempts at estimating transient changes in C storage through the use of a dynamic simulation model.

SUMMARY

In summary, the members of WG1 discussed several factors which influence the C balance of the terrestrial biosphere. These discussions focused on the role of forest ecosystems, as we felt that forest dynamics may dominate the terrestrial response to many current and future changes in the environment. The potential effects of fire, forest pests, climate, atmospheric CO_2, N deposition, and biome redistribution were all addressed, and each is presented in some detail by individual members of WG1 in the following chapters. Finally, we identified five major unknowns that arose during the group discussions:

- How much of recent net C uptake into terrestrial systems might be due to natural variability?
- How important are tropical regions in all of the factors discussed?

- What is the long-term persistence of any current C sinks stimulated by elevated N deposition and atmospheric CO_2?
- What is the most likely net effect of a warmer climate on terrestrial C pools?
- What are the transient responses of biome areas and C pools to climate and atmospheric change?

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REFERENCES

Aber JD, Nadelhoffer KJ, Steudler P, Melillo JM (1989) Nitrogen saturation in northern forest ecosystems. *BioScience* 39(6): 378–386. .

Barnola J-M, Raynaud D, Korotkevitch YS, Lorius C, (1987) Vostok ice core provides 160,000 year record of atmospheric CO_2. *Nature* 329: 408–414.

Barnola J-M., Pimenta P, Raynaud D, Korotkevich TS (1991) CO_2-climate relationship as deduced from the Vostok ice core: a re-examination based on new measurement and on a re-evaluation of the air dating. *Tellus* 43B: 83–90.

Bazzaz FA, Fajer ED (1992) Plant life in a CO_2-rich world. *Scientific American* 266: 68–74.

Billings WD, Lukeen JO, Mortensen DA, Peterson KM, 1984. Arctic tundra: a source or sink for atmospheric carbon dioxide in a changing environment? *Oecologia* 53: 7–11.

Comins HN, McMurtrie RE (1993) Long-term response of nutrient limited forests to CO_2 enrichment: equilibrium behavior of plant–soil models. *Ecological Applications* 3: 666–681.

Dai A, Fung IY (1993) Can climate variability contribute to the "missing" CO_2 sink? *Global Biogeochemical Cycles* 7: 599–609.

Dixon RK, Brown SA, Houghton RA, Solomon AM, Trexler MC, Wisniewski J (1994) Carbon pools and flux of global forest ecosystems. *Science* 263: 185–190.

Eischeid JK, Bradley RS, Jones PD (1991) A comprehensive precipitation data set for global land areas. Tech. Report TR051, DOE ER-69017T-H1, US Dept. of Energy CO_2 Research Division, Washington, DC, 81 pp.

Folland CK, Karl TR, Vinnikov KY (1990) Observed climate variations and change. In: Houghton JT, Jenkins GJ, Ephraums JJ (eds) Climate Change, the IPCC Scientific Assessment WMO/UNEP, Cambridge University. Press, New York, pp 201–238.

Friedlingstein P, Prentice KC, Fung IY, John JG, Brasseur GP (1995) Carbon-Biosphere-Climate interactions in the LGM climate. *J. Geophys Res.* (In press).

Fung IY (1993) Models of oceanic and terrestrial sinks of anthropogenic CO_2: A review of the contemporary carbon cycle. In: Oremland R (ed) Biogeochemistry of global change: radiatively active trace gases: selected papers from the Tenth International Symposium on Environmental Biogeochemistry, San Francisco, 19–24 August, 1991. Chapman and Hall, New York.

Fung IY (1995) Perturbations to the biospheric carbon cycle: uncertainties in the estimates. In: Woodwell GM, MacKenzie FT (eds) Biotic Feedbacks in the Global Climate System: Will Warming Speed the Warming? Oxford University Press, New York, 416 pp.

Fung IY (1995) The global carbon cycle and the atmospheric record: "the problem definition". (Chapter 2, this volume).

Galloway JN, Levy II H, Kasibhatla PS (1994) Year 2020: consequences of population growth and development on deposition of oxidized nitrogen. *Ambio* 23(2): 120–123.

Hudson RJM, Gherini SA, Goldstein RA (1994) Modeling the global carbon cycle: nitrogen fertilization of the terrestrial biosphere and the missing CO_2 sink. *Global Biogeochemical Cycles* 8(3): 307–333.

IPCC (1990) Climate change: the IPCC scientific assessment. Cambridge University Press, Cambridge, UK, 365 pp. .

Jenkinson DS, Adams DE, Wild A (1991) Model estimates of CO_2 emissions from soil in response to global warming. *Nature* 351: 304–306.

Kauppi PE, Mielikäinen K, Kuusela K (1992) Biomass and carbon budget of European forests, 1971–1990. *Science* 256: 70–74.

Keeling CD, Bacastow RB, Carter AF, Piper SC, Whorf TP, Heimann M, Mook WG, Roeloffzen H (1989a) A three-dimensional model of atmospheric CO_2 transport based on observed winds: 1. Analysis and observational data. In: Peterson DH (ed), Aspects of Climate Variability in the Pacific and Western Americas. *Geophysical Monograph* 55, American Geophysical Union, Washington, DC, pp 305–363.

Kellomaki S, Karjalainen T (1995) Sequestration of carbon in the Finnish boreal forest ecosystem managed for timber production. (Chapter 5, this volume).

Kurz WA, Apps MJ (1995) Retrospective assessment of C flows in Canadian boreal forests. (Chapter 14, this volume).

Kurz WA, Apps MJ, Beukema SJ, Lekstrum T (1995) Twentieth century carbon budget of Canadian forests. *Tellus* 47B: 170–177.

Manabe S, Wetherald RT (1987) Large scale changes in soil wetness induced by and increase in carbon dioxide. *J. Atmos. Sci.* 44: 1211–1235.

Melillo JM, McGuire AD, Kicklighter DW, Moore III B, Vorosmarty CJ, Schloss AL (1993) Global climate change and terrestrial net primary production. *Nature* 363: 234–240.

Mooney HA, Drake BG, Luxmoore RJ (1991) Predicting ecosystem responses to elevated CO_2 concentrations. *BioScience* 41: 96–104.

Oechel WC, Hastings SJ, Vourlitis G, Jenkins M, Riechers G, Grulke N (1993) Recent change of Arctic tundra ecosystems from a net carbon dioxide sink to a source. *Nature* 361: 520–523.

Penner JE, Atherton CS, Dignon J, Ghan SJ, Walton JJ, Hameed S (1991) Tropospheric nitrogen: a three-dimensional study of sources, distributions, and deposition. *J. Geophys. Res.* 96: 959–990.

Peterson BJ, Melillo JM (1985) The potential storage of carbon caused by eutrophication of the biosphere. *Tellus* 37B: 117–127.

Prentice KC, Fung IY (1990) The sensitivity of terrestrial C storage to climate change. *Nature* 346: 48–51.

Rastetter EB, McKane RB, Shaver GR, Melillo JM (1992) Changes in C storage by terrestrial ecosystems: how C–N interactions restrict responses to CO_2 and temperature. *Water, Air, and Soil Pollution* 64: 327–344.

Schimel DS, Braswell Jr BH, Holland EA, McKeown R, Ojima DS, Painter TH, Parton WJ, Townsend AR (1994) Climatic, edaphic and biotic controls over storage and turnover of carbon in soils. *Global Biogeochemical Cycles* 8(3): 279–293.

Schindler DW, Bayley SE (1993) The biosphere as an increasing sink for atmospheric carbon: estimates from increased nitrogen deposition. *Global Biogeochemical Cycles* 7: 717–734.

Schlesinger ME, Zhao ZC (1989) Seasonal climate change introduced by doubled CO_2 as simulated by the OSU atmospheric Gcm/mixed-layer ocean model. *J. Climate* 2: 429–495.

Schlesinger WH (1991) Biogeochemistry: An Analysis of Global Change. Academic Press. San Diego, CA, 443 pp.

Schulze ED (1989) Air pollution and forest decline in a spruce (*Picea abies*) forest. *Science* 244: 776–783.

Sedjo RA, (1992) Temperate forest ecosystems in the global carbon cycle. *Ambio* 21: 274–277.

Sellers P, Schimel D (1993) Remote sensing of the land biosphere and biogeochemistry in the EOS era: science priorities, methods and implementation—EOS land biosphere and biogeochemical cycles panels. *Global and Planetary Change* 7: 279–297.

Siegenthaler U, Sarmiento JL (1993) Atmospheric carbon dioxide and the ocean. *Nature* 365: 119–125.

Stocks BJ, Simard AJ (1993) Forest fire management in Canada. *Disaster Management* 5: 21–27.

Stocks BJ, Lee BS, Martell DL (1995) Some potential carbon budget implications of fire management in the boreal forest. (Chapter 8, this volume).

Sykes MT, Prentice IC (1995) Carbon storage and climate change in Swedish forests: a comparison of static and dynamic modelling approaches. (Chapter 6, this volume).

Tans PP, Fung IY, Takahashi T (1990) Observational constraints on the global atmospheric CO_2 budget. *Science* 247: 1431–1438.

Townsend AR, Vitousek PM, Holland EA (1992) Tropical soils could dominate the short-term carbon cycle feedbacks to increased global temperatures. *Climatic Change* 22: 293–303.

Townsend AR, Braswell BH, Holland EA, Penner JE (1995) Spatial and temporal patterns in potential terrestrial carbon storage due to deposition of fossil fuel derived nitrogen. *Ecological Applications* (In press).

Townsend AR, Rastetter EB (1995) Nutrient constraints on carbon storage in forested ecosystems. (Chapter 3, this volume).

Vitousek PM, Howarth RW (1991) Nitrogen limitation on land and in the sea: how can it occur? *Biogeochemistry* 13: 87–115.

Vitousek PM (1994) Beyond global warming: ecology and global change. *Ecology* 75(7): 1861–1876.

Volney WJA (1988) Analysis of historic jack pine budworm outbreaks in the Prairie provinces of Canada. *Can. J. For. Res.* 18: 1152–1158.

Volney WJA (1995) Climate change and management of insect defoliators in boreal forest ecosystems. (Chapter 7, this volume).

Webb TL, Bartlein PJ (1992) Global changes during the last three million years: climatic controls and biotic responses. *Ann. Rev. Ecology and Systematics* 23: 141–174.

Woodwell GM (1990) The effects of global warming. In: Leggett J (ed) Global Warming, The Greenpeace Report. Oxford University Press, New York.

Zoltai SC, Martikainen PJ (1995) Estimated extent of forested peatlands and their role in the global carbon cycle. (Chapter 4, this volume).