The Terrestrial Biosphere and Global Change: Implications for Natural and Managed Ecosystems

A Synthesis of GCTE and Related Research

The International Geosphere-Biosphere Programme (IGBP): A Study of Global Change
of the International Council of Scientific Unions (ICSU)
Stockholm, Sweden
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IGBP Science: Executive Summary

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The Terrestrial Biosphere and Global Change: Implications for Natural and Managed Ecosystems

A Synthesis of GCTE and Related Research

Edited by
Brian Walker and Will Steffen

With Contributions from

The International Geosphere-Biosphere Programme (IGBP): A Study of Global Change of the International Council of Scientific Unions (ICSU)
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Foreword

The International Geosphere-Biosphere Programme (IGBP) and its partners, the World Climate Research Programme (WCRP), and the International Human Dimensions Programme (IHDP), provide an international, interdisciplinary framework for the conduct of Global Change science. They add value to nationally funded activities through the identification and agreement of research priorities, the development of standardized research methodologies, the co-ordination of major multi-national field campaigns and research efforts, and the exchange of data and results. After approximately one decade of activity, they can point to an ever broadening pool of new Earth System knowledge and understanding, and a vastly enhanced international, interdisciplinary network of researchers, directly attributable to their existence and success.

An especially important characteristic of the programmes is their unique capacity to draw on the world’s front-ranking research expertise to synthesise “state of the art” summaries of new Earth System results. The Global Change and Terrestrial Ecosystems (GCTE) project is the first of IGBP’s projects to do so. Following a very substantial effort, including two major workshops, much energetic “electronic” debate and a major writing and editing task, the GCTE researchers have produced an account of the outcome of their work to date covering both basic research and policy-relevant issues. The former deal with the response of terrestrial ecosystems to predicted Earth System changes and associated feedbacks, whilst the latter address critical issues such as the future capacity of terrestrial ecosystems to provide food for the world’s growing population, and their ability to absorb the carbon emissions resulting from humankind’s exploitation of fossil fuels. The latter insights, in particular, constitute critical steps on the path to “Sustainability”.

I am delighted to commend the GCTE researchers on their impressive and very substantial achievement, which sets the standard for future publications in this new IGBP series.

Chris Rapley
Executive Director, IGBP
This executive summary presents the major findings of the synthesis of the first six years of the Global Change and Terrestrial Ecosystems (GCTE) Core Project of the IGBP (see Appendix I). It begins by identifying the major components and drivers of global change. It then outlines the important ecosystem interactions with global change, focusing on the functioning of ecosystems and the structure and composition of vegetation.

The executive summary then discusses the implications of these ecosystem interactions with global change in terms of impacts in three key areas: managed production systems, biodiversity and the terrestrial carbon cycle.

The full synthesis results and conclusions, with a complete reference list, are presented as a volume in the IGBP Book Series No. 4, published by Cambridge University Press (Walker et al. [In Press]). Here key references only are included.
The accelerating changes to the Earth’s environment are being driven by growth in the human population, by the increasing level of resource consumption by human societies and by changes in technology and socio-political organizations. Four aspects of large-scale environmental perturbations are considered here under the term “global change”: (i) changes in land use and land cover; (ii) the world-wide decline in biodiversity; (iii) changes in atmospheric composition, especially the increase in CO₂ concentration; and (iv) changes in climate (see Figure 1).

From the perspective of terrestrial ecosystems, the most important component of global change over the next three or four decades will likely be land-use/cover change. It is driven largely by the need to feed the expanding human population, expected to increase by almost one billion \((10^9)\) people per decade for the next three decades at least. Much of this increase will occur in developing countries in the low-latitude regions of the world. To meet the associated food demand, crop yields will need to increase, consistently, by over 2% every year through this period.

Despite advances in technology, increasing food production must lead to intensification of agriculture in areas which are already cropped, and conversion of forests and grasslands into cropping systems. Much of the latter will occur in semi-arid regions and on lands which are marginally suitable for cultivation, increasing the risk of soil erosion, accelerated water use, and further land degradation.

Concurrent with the expanding population, technological and economic advances will lead to an increase in per capita consumption of resources, with the most likely scenario being the continued strong increase in all four global change drivers.
Some components of global change: (a) increase in human population; (b) increase in atmospheric CO₂ concentration; (c) anthropogenic alteration of the nitrogen cycle; (d) modelled and observed change in global mean temperature; (e) change in global land cover; and (f) increase in extinction of birds and mammals. From: Vitousek (1994); Houghton et al. (1995); Klein Goldewijk and Battjes (1995); and Reid and Miller (1989).
Terrestrial Ecosystem Interactions with Global Change

The Functioning of Ecosystems

Global change is affecting the functioning of terrestrial ecosystems in complex ways. Given the certainty of atmospheric CO₂ increase and its importance for the growth and functioning of vegetation, much of GCTE’s initial work on ecosystem physiology has focused on the ecosystem-level effects of elevated CO₂ and its interactions with other factors (Figures 2 and 3).

- Most whole ecosystems exposed to a step increase of atmospheric CO₂ by a factor of two compared to current or preindustrial concentrations show higher peak season net carbon uptake than those growing at ambient CO₂ concentration. For grasslands, above-ground productivity increased by an average of about 15%, although the responses of individual grassland communities varied widely (some being negative) (see Figure 4). The variation in community responses reflects variation in their component species, the interactive effects amongst species, and the highly interactive nature of the CO₂ response with other environmental factors, such as water, nutrient availability and temperature. For example, low temperature systems, such as tundra and alpine grassland, are the least responsive to elevated CO₂ in some cases showing no growth response and complete acclimation of peak season gas exchange after a few years. Faster growth in juvenile trees does not indicate whether forest as a whole will sequester more carbon or not.
• Two earlier predictions about responsiveness to elevated CO₂ were that: (i) C₄ species will respond less than C₃ species (because of their chemically different photosynthetic pathways); and (ii) species with nitrogen-fixing symbionts will show a larger biomass response. Neither of these predictions has been consistently confirmed in ecosystem studies.

• Contrary to earlier prediction, litter from plants grown under elevated CO₂ does not necessarily decompose more slowly. The ratio of carbon to nitrogen in litter generally is not higher under elevated CO₂, as is observed in green tissue, although there is a great deal of variation among species.

• Elevated CO₂ generally increases the allocation of photosynthate to roots, which increases the capacity and/or activity of below-ground carbon sinks. Models suggest that some of the increased capacity of below-ground sinks may lead to increased long-term soil carbon sequestration, although strong empirical evidence is still lacking.

• Herbaceous plants exposed to elevated CO₂ show a reduction in stomatal conductance, which commonly results in reduced loss of soil moisture. This increase in water availability is the dominant driver for increased net carbon uptake in water-limited grassland systems. There is also a reduction in stomatal conductance in tree-seedlings exposed to elevated CO₂, but this does not seem to be the case for mature trees (forests), based on current experimental datasets.

• In some forests nitrogen deposition is associated with increased Net Primary Production (NPP). However, continuous nitrogen loading will lead, in the long term, to changes in species composition which may or may not be associated with increased carbon sequestration at the ecosystem level. Continuous nitrogen loading, along with other associated pollutants, could lead in many cases to soil acidification with a subsequent decrease in NPP.

• Model results suggest that the combined effect of elevated CO₂, higher temperatures and nitrogen deposition is to increase nitrogen mineralization and NPP, while carbon storage is decreased by increasing soil temperature.

• Tropospheric ozone has negative effects on ecosystem NPP, but elevated CO₂ could potentially ameliorate plant ozone injury for those species that show decreased stomatal conductance at elevated CO₂. There is also the potential for increased UV-B radiation to decrease NPP.

• In general, wherever human activities have a direct, significant impact on water and nutrient cycles and on disturbance regimes, this impact will override any direct CO₂ effects on ecosystem functioning.
In summary, the work so far in GCTE and related programmes shows that the extrapolation from experiments on single plants to the responses of whole ecosystems to global change must be done with considerable care (e.g., Körner 1995). In addition, ecosystem functioning and composition/structure are intricately linked, albeit at different time scales. In the short term (years to decades), changes in ecosystem physiology and species performance will dominate the response to altered atmospheric composition and climate. In the long term (decades to centuries), changes in the composition and structure of ecosystems, together with the changed physiological properties associated with them, will dominate the response (see The Terrestrial Carbon Cycle section of this report).

Changes to the Structure and Composition of Vegetation

The first generation of models of vegetation change at regional and global scales was based on the assumption that vegetation is in equilibrium with its abiotic environment. These “equilibrium” models quickly found applications in a wide range of impact studies, but such use often led to a misleading concept of vegetation change based on a rearrangement of present biomes, resulting in a sharp transition from one equilibrium distribution of biomes to another.

The reality is quite different. Impacts on vegetation composition and structure, at scales from the patch to the globe, are occurring now, are continuous, will likely accelerate, and have no identifiable or predictable end point. These non-equilibrium, transient dynamics of changing vegetation composition and structure include several important features:

- Biomes will not shift as intact entities. Species respond differently in competitive abilities (e.g., growth rates), migration rates, recovery from (response to) disturbance, and in other ways. Thus, new combinations of species will arise.

- Changes in vegetation over the next hundred years projected by the new, transient Dynamic Global Vegetation Models are significantly different from those suggested by the equilibrium models (see Box 1).

- Palaeo studies and model simulations suggest that many plant species can migrate fast enough to keep up with projected climatic change, but only if they can migrate through continuous, relatively undisturbed natural ecosystems. This emphasizes the important consequences of fragmentation of natural ecosystems as a global change phenomenon (Pitelka et al. 1997).

- Invasion of non-native species into natural ecosystems is an increasing problem. It will likely be exacerbated by the trends in land-use/cover change, by increased globalization of trade, and by increased disturbance.

- Disturbances (e.g., fire, dieback due to insect attacks) appear to be increasing in some regions (e.g., boreal forest), leading to more ecosystems in early successional states (Kurz et al. 1995, Figure 5), whereas in other regions (e.g., northern Europe) changes in management have tended to reduce the area of forests in early successional states.

Figure 5

The average area of Canadian boreal forest annually disturbed by forest fires, insect-induced stand mortality and clear-cut logging in the period 1920 to 1989. From Kurz et al. 1995.
• Within individual landscapes, local effects of climate change may differ strongly, due to the effects of soil, land use and topographic variability.

Taking all these factors together, some generalizations about vegetation dynamics in the 21st century begin to emerge:

• Given the increasing demand for food and fibre and its consequences for land use and land cover, the terrestrial biosphere of the 21st century will likely be further impoverished in terms of species richness and substantially “reorganized” in terms of species composition, with as yet unknown consequences for ecosystem functioning (see Box 2 and Biodiversity section of this report).

• Disturbance and dieback will likely increase as more long-lived organisms (trees) are further from their optimal environmental ranges and subject to increasing pressure from land-use change.

• More natural ecosystems will be in an early successional state, given the projected increase in disturbance, or will be converted into human-dominated terrestrial production systems. These trends will result in a generally “weedier”, structurally simpler biosphere with fewer systems in a more ecologically complex old-growth state.
The recognition that the world’s biomes will not shift as homogeneous entities in response to changing climate and land use has led to the development of a new class of global biosphere models, which aim at capturing the dynamics of land vegetation over time-scales of decades to centuries. This time-scale is critical, since earlier results have shown that competition within vegetation, modified disturbance regimes (e.g., fires, wind storms) and migration of species all lead to significant time lags in biospheric response. If, for example, mortality due to increased disturbance occurred faster than re-growth of other vegetation, then the result could be a carbon pulse to the atmosphere. To quantify this process, DGVMs are necessary.

The current set of DGVM prototypes are based on the above structure (adapted from Foley et al., 1996):

**Carbon Balance**
Photosynthesis and canopy respiration are driven by weather conditions with short time steps (potentially coupled interactively with a climate model); the net results are then summarised for the main plant functional types by an annual growth model.

**Vegetation Dynamics**
Plant types compete for basic growth resources, such as light and water. Since biomass is accumulated over time, with different capacities of plant types to attain height, the competitive relationships between them can be calculated at annual time-steps. Competition thereby inhibits growth of some types, and the outcome is the overall structure of the canopy, including total biomass.

**Phenology**
Different DGVMs simulate seasonal leaf developments in different ways. The leaf area index (LAI) is a critical variable for the estimation of feedbacks to the atmosphere, since it influences albedo and thereby the energy flux back to the atmosphere. Seasonal LAI is also important for water balance calculations. Results of recent DGVM simulations, using climate model output as driving variables for four prototype models1, have been compared for the present synthesis. They show that the general processes of vegetation dynamics, such as replacement of species during changing environmental conditions, are modelled appropriately. The left half of the diagram (opposite page) indicates the differential increase in biomass for the tropical and boreal zone. The right half shows the component of this change which involves major vegetation redistribution. It must be noted that migration currently is considered to involve no time lags in these models—a feature which will likely change in further developments. Due to the warming (particularly at Northern high latitudes), trees encroach northwards, but these may be deciduous or evergreen, depending on the models’ sensitivity to climatic variables. Two models (IBIS and Lund DGVM) simulate a strong reduction in deciduous trees in the tropics—nevertheless, the overall biomass of these types increases, due to enhanced growth in the remaining areas.
These results must be considered initial. For better quantitative analyses, however, improved formulations of disturbance, competition and migration are necessary. Then, DGVMs could be used in connection with scenarios or models of changing human land use, to provide an interactive biosphere component for realistic Earth System models.

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1 Lund DGVM (I.G. Prentice, Lund University, Lund, Sweden), HYBRID-4 (A. Friend, Institute for Terrestrial Ecology, Edinburgh, UK), IBIS-1 (J. Foley, University of Wisconsin, Madison, USA) and SDGVM (F.I. Woodward, Sheffield University, Sheffield, UK)
Temporal & spatial dynamics of the 3 PFTs
Simplification and Homogenization of the Terrestrial Biosphere.

The conversion of natural ecosystems into systems managed for the production of food and fibre, and the intensification of production on existing managed systems, will be an increasing trend over the next several decades. The conversion of natural primary rainforest into “jungle rubber” production systems and the conversion of both into oil palm plantations in Jambi Province, Sumatra, is an example of such a conversion and intensification process.

The initial conversion of primary forest to “jungle rubber”, in which the secondary regrowth following a slash and burn operation is seeded with rubber trees, has a relatively small effect on biodiversity; about 70% of the original vascular plant species are retained in the rubber production system (A. Gillison, personal communication). However, the further intensification of production, from rubber to oil palm, requires the complete clearing of the forest and its conversion to a monospecies row “crop” of oil palm trees. This process results in a drastic loss of both plant and animal species.

Similar processes of modification, conversion and intensification of natural ecosystems for production are occurring throughout the world, primarily in developing countries (the conversion of mangrove forests to prawn farms is a widespread example in the coastal zones of Southeast Asia). These processes almost always lead to a sharp loss of biodiversity, at least on a local level, and very often require the introduction of one or more alien species as part of the production system (e.g., rubber trees, which are native to South America) with the inadvertent introduction of additional alien species. Given the scale and rate of such conversions and intensifications, the terrestrial biosphere of next century will likely be further impoverished in terms of species richness and substantially “reorganized” in terms of species composition.
The need to meet a 2% per annum or greater increase in food demand will put enormous stresses on managed production systems. Climatic change will likely further stress these systems. Extreme weather events, such as back-to-back droughts in one, or simultaneous droughts in two or more, of the world’s major grain producing areas would create severe food shortages. (The extended drought in the mid-US grain region in the 1930s caused massive environmental and economic damage).

One response to the food supply issue is technology: the development of improved cropping systems and/or crop varieties. There is no doubt that improved varieties, such as genetically engineered crops with in-built insecticides and short season varieties with high water use efficiencies, will offset some of the increased demand. However, biotechnology has not yet succeeded in improving our capability to cope with complex, system-level problems, such as drought and salinity. A sustained increase in global production of the required 2% per year may well be achieved, but it will have considerable impact on land use and on ecosystems in general. Climate change makes the task of producing the additional food and fibre more uncertain.

The availability of resources will continue to constrain agricultural development in many regions. For example, water availability, already a major problem, is likely to become increasingly limiting as agricultural, industrial and urban demands for water compete more directly with the need to maintain river flows for conservation and waste removal and purification purposes.

In terms of the impacts of global change on terrestrial production systems, and the implications for regional and global food supply, work over the past six years has highlighted the following major issues:

**Crop Production**

Crop production will be affected by global change very differently in different parts of the world (as already highlighted by other recent assessments). Recent estimates indicate increases in yield at mid and high latitudes but decreases at low latitudes, where food demand will be greatest:

- Under ideal field conditions, wheat yields are unlikely to increase by more than about 10% for a doubled current CO₂ concentration; a 5-7% increase is more realistic for average management conditions. (Pinter et al. 1996)
- Major wheat models are being rapidly refined but caution is still needed in spatial extrapolation using any single model (see Table 1)
- Temperatures above 32°C reduce rice yields due to spikelet sterility. This relationship is unaffected by elevated CO₂. Major rice models agree across a wide range of potential yields; and suggest a ca. 5% reduction in yield per °C rise for temperatures above 32°C (see Figure 6)
- Global change will likely exacerbate the already significant impacts of pests, diseases and weeds on crop production (see Box 3).
Table 1

Maximum and minimum estimates of wheat yield by eight models from the GCTE Wheat Network. Models simulated the growth of hypothetical wheat crops using common weather datasets and the same time course of leaf area index (LAI) development. From Goudriaan et al. 1994.

<table>
<thead>
<tr>
<th>Location</th>
<th>Day of Year - Anthesis</th>
<th>Day of Year - Maturity</th>
<th>LAI (m²/m²)</th>
<th>Total Above-Ground Dry Weight (t/ha)</th>
<th>Grain Dry Weight (t/ha)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Crookston, MN, USA (Spring Wheat)</td>
<td>Prescribed</td>
<td>183</td>
<td>216</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>Minimum</td>
<td>182</td>
<td>215</td>
<td>4.5</td>
<td>10.6</td>
</tr>
<tr>
<td></td>
<td>Maximum</td>
<td>187</td>
<td>216</td>
<td>4.5</td>
<td>16.1</td>
</tr>
<tr>
<td>Lelystad, The Netherlands (Winter Wheat)</td>
<td>Prescribed</td>
<td>166</td>
<td>207</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>Minimum</td>
<td>164</td>
<td>204</td>
<td>7.5</td>
<td>13.5</td>
</tr>
<tr>
<td></td>
<td>Maximum</td>
<td>166</td>
<td>207</td>
<td>7.5</td>
<td>26.4</td>
</tr>
</tbody>
</table>

Figure 6

Relative changes in rice yield due to changes in temperature, as simulated by five rice growth models. From Mitchell 1996.

Pastures and Rangelands

The crop/rangeland boundary will encroach on grazing lands in developing countries due primarily to population pressure. Changes to rangeland livestock production will be dominated by a reduction in land area due to cropping and to changes in evapotranspiration and precipitation. Doubled current CO₂ will increase production in different pastures and rangelands by 0-20%, depending on temperature, water and nutrient limitations. A sensitivity analysis for a subtropical pasture indicates that a 5% increase in pasture growth due to CO₂ would lead to a 3% increase in long-term mean liveweight gain in cattle, by reducing the variability of NPP between years.

Managed Forests

Short-term studies of elevated CO₂ in managed forests show an increase in plant biomass production by young trees grown under fertile conditions. This increase, however, will be reduced in the longer term as an effect of increased respiration. This reduction may be substantially compensated for by the interactive effects of CO₂ and atmospheric nitrogen deposition; the net effect is uncertain.
Pests, diseases and weeds cause significant impacts on the world’s food production under current climatic conditions. Current losses caused by pests, diseases and weeds to the harvests of the world’s four most important crops are summarised in the table below, with the totals estimated on the assumption that the losses to each agent are sequential.

<table>
<thead>
<tr>
<th>Crop</th>
<th>Pests</th>
<th>Diseases</th>
<th>Weeds</th>
<th>TOTAL</th>
</tr>
</thead>
<tbody>
<tr>
<td>Maize</td>
<td>15</td>
<td>11</td>
<td>13</td>
<td>34</td>
</tr>
<tr>
<td>Rice</td>
<td>21</td>
<td>15</td>
<td>16</td>
<td>44</td>
</tr>
<tr>
<td>Wheat</td>
<td>9</td>
<td>12</td>
<td>12</td>
<td>30</td>
</tr>
<tr>
<td>Potatoes</td>
<td>16</td>
<td>16</td>
<td>9</td>
<td>36</td>
</tr>
<tr>
<td>Average</td>
<td>15</td>
<td>14</td>
<td>13</td>
<td>36</td>
</tr>
</tbody>
</table>

Climate change is likely to cause a spread of tropical and sub-tropical species into temperate areas and to increase the numbers of many temperate species currently limited by low temperatures at high latitudes. For example, the geographical range of the Colorado Potato Beetle in Europe is expected to increase with a climate change scenario that assumes a 2°C increase in temperature and a 10% decrease in summer rainfall. The potential expansion of geographical ranges of pest species will be disruptive to quarantine barriers and is likely to result in increased costs to agriculture in previously pest-free areas. Similarly, an increase in temperature will lead to more opportunity for population growth in areas already affected by a pest.

An integration of impact assessments on pests with assessments of crop impacts is essential to gain a full picture of the likely effect of climate change on agriculture.

Disease-affected maize in Brazil.
Soils

The main controls on soil organic matter (SOM) levels and erosion over the next few decades will continue to be land management, but changes in vegetation cover due to near-term changes in climate variability will be significant, especially in semi-arid regions. A longer-term increase in mean temperatures will accelerate SOM oxidation, especially where it allows new land to be brought into cultivation. Climate change will also affect soil erosion, which increases linearly with mean precipitation but nonlinearly with wind speed, with a threshold for rapid and significant increase in wind erosion at about 5.5 m s\(^{-1}\) (see Figure 7).

Figure 7

Sensitivity of soil erosion in the US corn belt to climate change as estimated using the model Erosion Productivity Impact Calculator (EPIC). Each point represents the 100-year average of 100 randomly selected sites.
A recent analysis of future biodiversity trends in the major biomes of the world (Sala and Chapin, In prep.) identified the main cause of biodiversity loss in the coming decades as land-use change, mainly loss of habitat and landscape fragmentation. The next most important factor identified was invasion of alien species. Although trends are less certain here, the general conclusion is that alien species will be an increasing problem, given: (i) the globalization of economies, and hence the movement of people and materials; and (ii) the susceptibility of disturbed ecosystems to invasions. Changes in atmospheric composition and climate are regarded as longer term factors, increasing in relative importance over time (Figure 8). However, changes in nitrogen deposition have important impacts in shorter timeframes on species diversity, especially in the developed world.

Research on the consequences of these changes to biological diversity for the functioning of terrestrial ecosystems is in its infancy. Some possible trends which appear to be emerging from this early work include:

- Relatively short-term experiments (a decade or less) show a positive, saturating relationship between species richness (one aspect of biological diversity) and various ecosystem processes, such as primary productivity. Possible explanations include: (i) addition of species increases the probability of there being at least one species present that is productive under various environmental conditions; and (ii) additional species may be able to tap resources that are not captured by other species, due to differences in rooting depth, phenology, form of nitrogen utilized, etc.

- Over long time periods species richness may buffer ecosystem functioning against extreme events or unanticipated effects of global change. One mechanism is through the different responses of functionally similar species to variation in environment. Thus, genetic diversity within species and diversity among functionally similar species provides insurance against large changes in ecosystem functioning in the face of environmental change, and in the event of species loss.

- Species likely to have particularly strong impacts on ecosystem functioning include those that modify: (i) resource availability; (ii) trophic structure; or (iii) disturbance regime. In these cases, introduction or loss of a single species could have profound ecosystem effects.

- The probability of species extinctions in fragmented landscapes is increasing, as a consequence of smaller population size and decreased connectivity between the subpopulations.
The Terrestrial Carbon Cycle

The potential for terrestrial ecosystems to absorb significant amounts of CO₂, thus slowing the build-up of CO₂ in the atmosphere and reducing the rate of climate change, is a key issue in the debate on CO₂ emission controls. The current understanding of the global carbon cycle, based on a budget of the known sources and sinks of CO₂ for the decade of the 1980s, is shown in Table 2. This analysis suggests that the terrestrial biosphere was about in balance with regard to the emission and absorption of CO₂ for that period, a conclusion supported by recent measurements of atmospheric O₂ concentrations (e.g., Heimann 1997). An estimated 1.6 billion tonnes of carbon per year were released through land-use change in the tropics, while about 2.1 billion tonnes of carbon per year were absorbed by terrestrial ecosystems, through the combined effects of forest regrowth, CO₂ fertilization and nitrogen deposition. This increase in the size of some terrestrial carbon pools has been demonstrated for a number of locations, but has not been proven at a global scale, nor over the full vegetation disturbance cycle. It is likely that the increase is thinly distributed over a wide range of ecosystems, and is thus hard to detect. The crucial question is whether this current capability of the terrestrial biosphere to absorb CO₂ can be maintained or increased in the future.

Prediction of future scenarios is difficult because the terms in Table 2 cannot be projected reliably into the future. It is important to note also that the terms in Table 2 are average annual estimates and that, due to interannual climate variability, the terrestrial biosphere can fluctuate from being a source to a sink from year to year. The budget is finely balanced around zero. Despite the uncertainties and the effects of climate variability, it is possible to assess the likely trends in the terms of the budget – whether they will increase or decrease in relative importance – so that an overall trend can be projected. The magnitude of the terms will be determined by trends in three main processes: land-use/cover change, ecosystem structural change, and ecosystem physiology.

**Table 2**

<table>
<thead>
<tr>
<th>CO₂ Sources</th>
<th>Gt C y⁻¹</th>
</tr>
</thead>
<tbody>
<tr>
<td>Emissions from fossil fuel combustion and cement production</td>
<td>5.5 ± 0.5</td>
</tr>
<tr>
<td>Net emissions from changes in tropical land use</td>
<td>1.6 ± 1.0</td>
</tr>
<tr>
<td>Total anthropogenic emissions</td>
<td>7.1 ± 1.1</td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>CO₂ Sinks</th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td>Storage in the atmosphere</td>
<td>3.2 ± 0.2</td>
</tr>
<tr>
<td>Oceanic uptake</td>
<td>2.0 ± 0.8</td>
</tr>
<tr>
<td>Uptake by Northern Hemisphere forest regrowth</td>
<td>0.5 ± 0.5</td>
</tr>
<tr>
<td>CO₂ fertilization</td>
<td>1.0 ± 0.5</td>
</tr>
<tr>
<td>N deposition</td>
<td>0.6 ± 0.3</td>
</tr>
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</table>

**Land-Use/Cover Change**

With the human population rising by almost a billion a decade over the next three decades at least, sustained increases in food production are required. According to projections from the Integrated Model for Assessment of the Greenhouse Effect (IMAGE model) (Alcamo 1994) and from other analyses, this will result both in further conversion of natural ecosystems to agriculture, especially in Africa and Asia (Figure 9), and in intensification of production on currently cropped lands. Both of these processes almost always accelerate release of carbon to the atmosphere, so the overall rate of emission from this source will at least be maintained at current levels, or, more likely, will increase. In addition, as more land is converted to agriculture, there is less area of natural ecosystems able to act as a carbon sink, thereby reducing the potential sink strength of the terrestrial biosphere.
Ecosystem Structural Change

Changes in the composition and structure of ecosystems are driven by a combination of management practices and changes in climate and atmospheric composition. For example, the biomass increases currently observed in many forested areas largely reflect successional changes due to past changes in forest management. Future global change effects will be superimposed on these present trends. In particular, the current trend of biomass increases may be reversed in some areas as the effects of global change become increasingly important. Under global change, present vegetation assemblages will likely change through increased mortality of some of their components, followed by establishment and growth of new assemblages, rather than shift as intact biomes. Mortality of the present vegetation, which releases carbon to the atmosphere, is a fast process, while the growth of a new assemblage of vegetation, which absorbs carbon from the atmosphere, is slower. Thus, the processes by which ecosystem structure and composition will change will probably release a transient pulse of carbon to the atmosphere on a timescale of decades to centuries, irrespective of whether the new theoretical equilibrium biome distribution (assuming some stable future climate) eventually stores more or less carbon than the present distribution.

Ecosystem Physiology

Specific physiological factors likely to affect the long-term carbon balance of terrestrial ecosystems include:

Soil Emissions
As noted earlier, oxidation of soil organic matter is predicted to increase with rising temperatures. Observations from the high latitudes, where continental areas have been subjected to a temperature increase over the past three decades, suggest that some tundra ecosystems in Alaska and Siberia have gone from being a carbon sink to a source, or are in approximate balance, largely due to increasing decomposition of soil carbon. However, much more work, such as a coordinated set of warming experiments across several biomes, is required before the potential significance of soil emissions as an emerging source of CO$_2$ can be confirmed.
**CO₂ Fertilization/N Deposition**

As summarized earlier, the most recent ecosystem-level CO₂ research indicates that the effect of CO₂ on ecosystem functioning, although still potentially significant, is not as large as often portrayed in global biogeochemical analyses (there is an unavoidable lag in the incorporation of experimental/observational results into simulation and analytical tools). The interactive effects of land-use change (abandonment of agriculture to forests), N deposition and CO₂ fertilization have led to strong growth in many European forests, with evidence that N deposition has played a major role (e.g., Auclair and Bedford 1995). However, the N deposition effect has a definite maximum, and it appears that it is being exceeded for some European forests (Schulze 1989).

**Nutrient Limitations**

The carbon cycle is closely and necessarily linked, at multiple time scales, to the cycles of other nutrients, particularly nitrogen, phosphorus and sulphur (Rastetter et al. 1997). Insufficient nutrient supply limits ecosystem-level carbon uptake and storage in many systems (as demonstrated by the nitrogen deposition effect), thus attenuating the effects of increasing atmospheric CO₂ and changing climate. In some biomes increasing temperatures will result in increased nitrogen mineralization which, on its own, would lead to enhanced CO₂ uptake, at least in the short term.

**Physiological “Saturation”**

The net uptake of carbon from the atmosphere through ecosystem physiology is a balance between the assimilation of CO₂ via photosynthesis and the release of CO₂ through respiration and decomposition. These processes occur at different rates. Carbon assimilation responds positively and almost instantly to increased atmospheric CO₂, whereas the process of decomposition responds only indirectly, through changes in temperature, moisture and litter quality - all of which include long delay components. In addition, there are nonlinearities in these processes. While carbon assimilation increases with increasing atmospheric CO₂, it does so at a diminishing rate. Respiration, on the other hand, is an exponentially increasing function of temperature. Thus, as global change proceeds, the rate of increase of CO₂ assimilation by terrestrial ecosystems will slow, while rates of both respiration and decomposition will increase. In the short-term there will be a positive effect on growth and therefore on CO₂ uptake, but over longer timeframes (centuries) the net effect is that the ability of the terrestrial biosphere to absorb CO₂ will decrease.

**Overall Trend**

The terms in the terrestrial carbon budget do not operate independently nor on the same time scales, features which make it difficult to extrapolate from knowledge of the dynamics of one budget term over short time scales to long-term trends in carbon storage. The concept of Net Biome Productivity, (NBP) (Schulze and Heimann 1997, see Box 3), is a useful tool to integrate the effects of several processes over multiple time scales.

In addition, the terms in the budget do not operate with the same strength in all regions of the world. In some regions, such as sub-Saharan Africa and large parts of Asia, the land-use change component will likely dominate and these regions will be net sources of carbon. For others, such as parts of North America and Europe, the carbon sequestration processes may dominate and these regions may remain or become significant carbon sinks on a decadal or century timeframe, unless disturbed.

Given the difficulty in estimating the future (or even present) magnitudes of processes which sequester carbon (e.g., N deposition, CO₂ fertilization) versus those which release carbon (soil organic matter oxidation, ecosystem structural change), there are many possible scenarios for the terrestrial carbon cycle at a global scale over the next 100 years. However, there is little doubt that for the next several decades at least, more areas of natural ecosystems will be converted to agriculture, simultaneously emitting carbon and reducing the amount of land on which significant amounts of carbon can be sequestered. Thus, the overall conclusion of the GCTE synthesis is that the present rate of absorption of carbon from the atmosphere, on a global scale, will be difficult to maintain. It is more likely that the terrestrial biosphere as a whole (that is, including land converted or modified for production of food and fibre) will become a net source. This projection has significant implications for the development of strategies to stabilize the concentration of greenhouse gases in the atmosphere.
A cascade of effects on increasing time and space scales describes the interaction of ecosystem physiology and structure in the carbon cycle. Photosynthesis (Pn, sometimes called Gross Primary Production, GPP), at the cellular level is enhanced by increasing CO₂ concentrations. Net Primary Production (NPP), the net amount of carbon uptake by vegetation (carbon fixed through photosynthesis minus carbon emitted through plant respiration), is affected by CO₂ temperature and the state of other factors, such as nitrogen. Net Ecosystem Production (NEP), the net amount of carbon gained or lost by the ecosystem as a whole, usually measured over a growing season on a single patch/stand (NPP minus all carbon losses not accounted for in NPP [largely heterotrophic respiration]), is strongly affected by temperature. Net Biome Production (NBP), the net amount of carbon gained or lost over several successional cycles at a landscape or larger scale, is NEP modified to account for changes in individuals (mortality and establishment of new individuals), and is therefore strongly dependent on disturbance regimes. It is possible, and even likely for some biomes, for Pn and NPP to be strongly enhanced in response to global change, for NEP to be positive (net-carbon uptake for a patch over a season), but for NBP to be negative (net carbon emission for a landscape over a decade) due to changes in disturbance regimes. NBP is the most appropriate concept in analysing long-term changes to the terrestrial carbon cycle over large spatial scales.

Changes in the Canadian boreal forests over the past few decades illustrate this cascade of effects. There is good evidence from remote sensing data that photosynthesis (Pn) has increased significantly over the 1981-1991 decade in the high latitudes, including Canada, primarily due to a lengthening of the growing season (Myneni et al. 1997; Fung 1997). Detailed process-level studies of gas exchange between Canadian boreal forests and the atmosphere suggest that net carbon uptake (NEP) is positive over the growing season, although there is much variation from site to site (measurements vary from 350 g C m⁻² yr⁻¹ for aspen, an early successional species, to about 50 g C m⁻² yr⁻¹ for jack pine to near 0 for the northern Boreal Ecosystem Atmosphere Study (BOREAS) stand of black spruce (Black et al. 1996; Baldocchi et al. 1997; P.G. Jarvis, personal communication). However, a continental-scale analysis over the last 100 years of disturbance frequencies in the Canadian boreal forests (Kurz et al. 1995) suggests that they have gone over the last few decades from being a sink of about 0.2 Gt C yr⁻¹ to being about neutral in terms of carbon exchange. Thus, for recent years estimates of Pn and NEP for the Canadian boreal forest are positive (net carbon up-take at the patch scale over a season) while an estimate of NBP is near zero (no net carbon uptake by the biome on a decadal time scale).
Global change is occurring now, will continue for the foreseeable future and is likely to intensify in many aspects. It is an emerging reality that will increasingly impact on the political process, on regional strategic planning and on the daily lives of resource managers. Learning to live with global change, to avoid the worst of the hazards and capitalize on opportunities as they arise, requires creative and innovative strategies. These must be built upon a sound scientific understanding of terrestrial ecosystem interactions with global change. Although GCTE and similar efforts have made good progress in the last six years, large challenges remain, both in the basic understanding of the science and in the development of research tools to improve that understanding (see Box 5).

How can, or should, society use current scientific understanding in responding to global change? An example of this difficulty is the current debate on the “take action now vs. take action later (or take no action)” proposals to limit greenhouse gas emissions. There are global processes which have lag times of decades or even centuries. The consequences of not taking action now may therefore not be felt until the middle of next century, but when these consequences do occur, they could be serious and very difficult to address. An example of such a lag effect is the diminishing ability of the terrestrial biosphere to absorb carbon as both atmospheric CO$_2$ concentration and temperature increase; a lack of action now could lead to a large, unavoidable, additional CO$_2$ release a century or so from now, through increasing decomposition of soil organic matter (about twice as much carbon is stored below-ground than above in terrestrial ecosystems).

The bottom line is that we will probably never be able to predict, with a high degree of certainty, precisely how terrestrial ecosystems will interact with accelerating environmental change. Thus, the analogy that ecosystems can be “managed” in the same way that much simpler human-designed industrial systems can is misleading and dangerous. In terms of terrestrial ecosystem interactions with global change, we must expect the unexpected (and unpredictable), and keep open as many response options as possible. There is an inescapable trade-off between resilience and production in managed agro-ecosystems: the most productive systems are often the simplest, but they are the least resilient to disturbance and perturbation. Highly productive systems are required to feed an expanding population; complex, resilient systems are required to be able to respond to future shocks and disturbances, and to continue providing the ecosystem “goods and services” we need. Learning to strike the right balance in this dichotomy is the biggest environmental challenge facing humanity in the 21st century.
Box 5

*Emerging Questions and Challenges.*

**The Integration of Natural and Social Sciences**
How can closer collaboration between the natural and social sciences improve understanding of the complex impact-feedback loops involving socio-economic and political systems and institutions and the natural environment? In the immediate future, closer collaboration is needed to improve our capability to undertake integrated assessments of global change impacts.

**Sustainable Development and Global Change**
Sustainable development and global change are closely related. The continuing build-up of anthropogenically generated trace gases in the atmosphere and the rapid loss of biodiversity suggest that past and present rates of development are not sustainable in a biophysical sense. These global environmental changes are now producing biophysical constraints on sustainable development strategies for the future. How can we more effectively merge these closely related research-applications efforts to deliver more effective outcomes for policy and resource management?

**Rates of Change**
The Earth's environment is constantly changing, but anthropogenically driven global change appears to be much more rapid than natural, “background” change, causing serious problems for terrestrial ecosystems to adapt without human intervention. What are “safe” rates of global change that avoid dangerous disruption of natural ecological processes and cycles, and what needs to be done to slow global change to these rates?

**Interactive Effects of Global Change Drivers**
The components of global change are not independent but interact strongly. How can we devise more appropriate methodologies for studying the interactions of terrestrial ecosystems with combinations of global change drivers, as opposed to the linear “driver-response-impact” chain of reasoning?

**Climate Scenarios**
Although much progress has been made in our ability to model climate processes, the present capability still falls well short of what is required to study impacts on ecological systems. Can climate prediction capability be improved to produce realistic regional-scale scenarios of the nature and frequencies of extreme events?

**The Interaction Between Physiology and Structure**
Failure to include the interactive effects of ecosystem physiology and structure continues to confound much global change research. How can we better integrate these two strands of research to gain a whole ecosystem perspective of global change interactions, over multiple space and time scales?

**Landscape Processes**
Much of the “action” in terms of disturbance dynamics and direct human impacts on terrestrial ecosystems occurs at the landscape scale. How can we improve our understanding of these phenomena, both to assist resource managers to “live with global change” and to facilitate the scaling between patch and globe?

**Ecological Complexity and Resilience**
How can we gain a better quantitative understanding of the relationships between ecological complexity (including biological diversity) and ecosystem resilience, and the ways in which global change will affect this relationship?
References


Appendix I

GCTE is an international scientific research effort with two major objectives:

• To predict the effects of changes in climate, atmospheric composition, and land use on terrestrial ecosystems, including: (i) agriculture, forestry, soils; and (ii) ecological complexity
• To determine how these effects lead to feedbacks to the atmosphere and the physical climate system.

The GCTE research programme is organized around four themes, or Foci:

• Ecosystem Physiology
• Change in Ecosystem Structure
• Global Change Impact on Agriculture, Forestry and Soils
• Global Change and Ecological Complexity.

GCTE’s strategy for implementing its research agenda is built around four key elements:

**GCTE Operational Plan**
This report (IGBP Report No. 21 [Steffen et al. 1992]), first published in 1992 and revised in 1997, describes in detail the scientific framework and implementation plan for executing the research agenda.

**Acceptance of Existing Research**
Existing research projects, funded by national or regional agencies, constitute the bulk of GCTE Core Research. They are normally submitted by individual scientists on behalf of the project, evaluated and accepted (or otherwise) by the GCTE Scientific Steering Committee (SSC), and join others to form networks designed to address particular Tasks.
**Initiation of New Research**
Where there are critical gaps in the programme, GCTE, in partnership with national and regional agencies, attempts to initiate new research projects.

**Research Coordination**
One or two scientists are invited to lead each of the specific Tasks within the GCTE Core Research Programme. Their role is to organize the individual projects contributing to their Task into a coherent programme through formation of networks and consortia and use of mechanisms such as common experimental protocols, standardized methodologies, model comparisons and synthesis workshops. The IGBP Terrestrial Transects and a set of terrestrial ecosystem impacts centres are also important coordinating mechanisms.

The implementation phase of GCTE began in 1992. At July 1997 its Core Research Programme consisted of 55 contributing projects involving over 1000 scientists and technicians from 44 countries. This research is supported by a large number of national and regional agencies; its current value on an annual basis is about $US 44.2 million.

GCTE is a component of a larger international global change research effort, the International Geosphere-Biosphere Programme (IGBP). The goal of IGBP is:

- To describe and understand the interactive physical, chemical and biological processes that regulate the total Earth system, the unique environment that it provides for life, the changes that are occurring in this system, and the manner in which they are influenced by human actions.

Other components address global change-related questions in atmospheric chemistry, biospheric aspects of the hydrological cycle, the coastal zone, land-use/cover change, oceanic carbon fluxes, marine ecosystems and palaeo-environmental sciences.

Further information on GCTE can be found on the homepage: [http://jasper.stanford.edu:80/GCTE/](http://jasper.stanford.edu:80/GCTE/)
GCTE Books

Copies of GCTE Books can be requested from the publisher


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<tr>
<th>Acronym</th>
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<tr>
<td>BAHC</td>
<td>Biospheric Aspects of the Hydrological Cycle (IGBP)</td>
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<td>BOREAS</td>
<td>Boreal Ecosystems Atmosphere Study (BAHC/GEWEX)</td>
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<td>CACGP</td>
<td>Commission on Atmospheric Chemistry and Global Pollution</td>
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<td>DGVM</td>
<td>Dynamic Global Vegetation Model</td>
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<td>(IGBP)-DIS</td>
<td>Data and Information System (IGBP)</td>
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<td>FACE</td>
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<td>GPP</td>
<td>Gross Primary Production</td>
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<td>International Human Dimensions Programme on Global Environmental Change</td>
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<td>IMAGE</td>
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Continental Land Cover Map 1 km AVHRR data (DIS-COVER Project).
Illustration credits

Cover Page: (Clockwise from right) Dry season fires, Kaoma, Zambia, courtesy of P.G.H. Frost; The CORINE Land Cover Project, courtesy of LUCC IPO; Primary rainforest, Jambi Province, Sumatra, Indonesia, courtesy of W. Steffen; Temporal and spatial dynamics of three Plant Functional Types (PFTs), courtesy of A. Bondeau and W. Cramer; Page 2: Open woodland, Katima Mulilo, Zambia, courtesy of D. Parsons; Page 5: Arid-zone savanna, Uluru-Katajuta National Park, Australia, courtesy of W. Steffen; Page 6: NASA MSS satellite (MESSR instrument) over Malaysia, courtesy of IGBP-DIS IPO; Page 7/Figure 1: Courtesy of Vitousek (1994), Houghton et al. (1995), Klein Goldewijk and Battjes (1995), and Reid and Miller (1989); Page 8/Figure 2: Courtesy of J. Canadell; Page 8/Figure 3: Courtesy of J. Canadell; Page 9/Figure 4: Courtesy of J. Canadell; Page 10/Figure 5: Courtesy of Kurz et al. 1995; Page 11: Clearing of forest for oil palm plantation, Jambi Province, Sumatra, Indonesia, courtesy of W. Steffen; Page 12 and 13: Box 1: Adapted from Foley et al. 1996; A. Bondeau and W. Cramer; Page 14/Box 2: Simplification and homogenization of the terrestrial biosphere - from Jambi Province, Sumatra, Indonesia, courtesy of W. Steffen; Page 16/Figure 6: Courtesy of Mitchell 1996; Page 17: Disease-affected maize, from near Ji Parana, Rondonia, Brazil, courtesy of W. Steffen; Page 18/Figure 7: Courtesy of Walker et al., in press; Page 18: courtesy of CSIRO Division of Wildlife and Ecology, Canberra, Australia; Page 19/Figure 8: Courtesy of Chapin et al. 1995; Page 21/Figure 9: Modified by J. Langridge from Alcamo et al. 1996. Page 23/Box 4: courtesy of Walker et al., in press; Appendix 1: Courtesy of GCTE IPO and IGBP Secretariat; Back cover: Courtesy of LUCC IPO.

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