The global terrestrial carbon cycle

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THE GLOBAL TERRESTRIAL CARBON CYCLE*

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Abstract. There is great uncertainty with regard to the future role of the terrestrial biosphere in the global carbon cycle. The uncertainty arises from both an inadequate understanding of current pools and fluxes as well as the potential effects of rising atmospheric concentrations of CO_2 on natural ecosystems. Despite these limitations, a number of studies have estimated current and future patterns of terrestrial carbon storage. Future estimates focus on the effects of a climate change associated with a doubled atmospheric concentration of CO_2. Available models for examining the dynamics of terrestrial carbon storage and the potential role of forest management and landuse practices on carbon conservation and sequestration are discussed.

1. Introduction

Although representing only a small fraction of the oceanic C pool, the annual flux of C between the terrestrial surface and atmosphere is of the same order as the flux between the ocean and atmosphere (Figure 1). Previous work has addressed the impacts of changing landuse patterns on the storage and flux of C from the terrestrial biosphere (Houghton *et al.,* 1983; Emanuel *et al.,* 1984), however, the potential impacts of rising concentrations of atmospheric CO_2 (and other greenhouse gases) on patterns of terrestrial C storage and the consequent flux between terrestrial and atmospheric pools has yet to be quantified. In combination with future changes in landuse patterns, the increasing atmospheric concentrations of CO_2 represent a major uncertainty in projecting the future dynamics of the global C cycle, both in terms of the direct effects of CO_2 on ecosystems, as well as the potential impacts of rising atmospheric concentrations of greenhouse gases on the global climate system (i.e., global warming) (Houghton *et al.,* 1992).
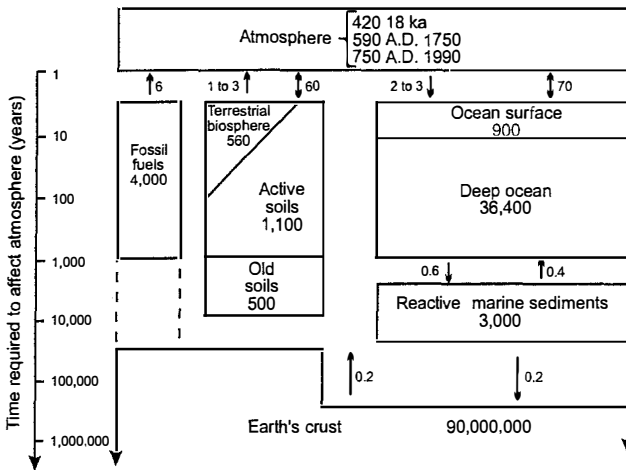
Figure 1. Principal reservoirs and fluxes (arrows) in the global carbon cycle. Vertical placements relative to scale on left show approximate time scales required for reservoirs and fluxes to affect atmospheric CO_2. Double arrows represent bidirectional exchange. Single arrows to and from the atmosphere are approximate estimates of anthropogenic fluxes for 1990. Terrestrial uptake of anthropogenic CO_2 is likely but not shown because of large uncertainties (from Sundquist, 1993).

The processes controlling C storage and release from the terrestrial biosphere are not documented well enough to accurately estimate and balance current exchanges (for discussion see: Sundquist, 1993). Measurements of C storage and release under present conditions are currently being undertaken in many places in the world, however, extrapolation of these estimates in time and space are dependent on a detailed understanding of the biological and

physical processes involved in the flux of C between the atmosphere and biosphere. To predict the current and future patterns of C flux from the terrestrial surface will require the development of detailed models of these processes within a geographical framework as well as improved estimates of C pools.

The objectives of this manuscript are to: 1) examine estimates of past and present C fluxes from the terrestrial surface, 2) define the processes we feel are most important in controlling future patterns of C storage and net flux from the terrestrial surface, 3) review global-scale vegetation models which are currently being used to examine the dynamics of terrestrial C storage and exchange with the atmosphere, 4) assess the strengths and weakness of current and future estimates of terrestrial C dynamics, and research required to improve them.

2. Global Carbon Budget

2.1 PAST

The global budget of C pools and fluxes at the end of the Pleistocene is not well defined. The most complete historic record is atmospheric CO_2 concentrations derived from ice-core samples collected in Antarctica (Sundquist, 1993). Atmospheric CO_2 concentration climbed from 200 to 280 ppm from 18,000 to 10,000 BC. The terrestrial biosphere was probably a net sink during period but historical data describing vegetation and soil system C pools and flux are highly variable. During the past 1000 yrs the atmospheric CO_2 concentration was relatively stable, ranging from 270 to 290 ppm (Stauffer and Oescheger, 1985).

Human activities began to significantly influence atmospheric CO_2 in the late 1700s. Between 1750 and 1850, up to 40 Pg C was released due to deforestation and land cultivation (Sundquist, 1993). With the advent of the industrial revolution combustion of fossil fuels became a significant factor in the global C cycle. Fossil fuel emissions released over 200 Pg C during the past 250 years. The Antarctic ice core record revealed that atmospheric CO_2 concentrations rose from 280 to 290 ppm from 1750 to 1850. From 1850 to 1950 atmospheric CO_2 rose to 310 ppm.

2.2 PRESENT

In the latter half of the 20th century atmospheric CO_2 continued to rise exceeding 350 ppm in 1990. Currently, the global C budget can not be balanced as the amount of CO_2 produced by landuse change and fossil fuel combustion is greater than known terrestrial and marine sinks (Houghton *et al.*, 1992; Sundquist, 1993; Tans *et al.*, 1990). The budget imbalanced is due to the so-called "missing CO_2". Atmospheric CO_2 data and global simulation models suggest that the southern hemisphere is a weak C sink and the northern hemisphere is a major C source and sink. The enhanced northern hemisphere sink is attributed to both marine and terrestrial C accretion (Tans *et al.*, 1990; Keeling *et al.*, 1989). Despite significant release of CO_2 due to landuse change (eg., deforestation) most analyses suggest the biosphere is a net sink of CO_2. Research continues to define the magnitude of the terrestrial and marine C sinks of the northern hemisphere.

Estimates over the past 20 years suggest that terrestrial vegetation and soils contain 1500 to 2000 Pg C, with approximately two-thirds in soils (Dixon and Turner, 1991). Boreal, temperate

and tropical forests are estimated to contain approximately two-thirds of the total, cycling 70 to 90 Pg C annually via photosynthesis, respiration and decomposition (Orr, 1993; Dixon *et al.,*1993). However, these estimates are based on a very course resolution definition of vegetation or ecosystem types (eg., boreal forest) and a very limited number of studies to determine C pools within each type. Recent regional-based estimates suggest global vegetation and soil C pools have been overestimated by 20 to 30% (Botkin and Simpson, 1993). These differences in estimates have largely been attributed to changes in forest area and forest destruction and degradation. Land-use changes, primarily deforestation within tropical latitudes, is currently releasing 1.2 to 3.2 Pg C annually (Brown, 1993). However, geographic variation do to climate, soils and species composition within any one vegetation or ecosystem type also introduces a large source of potential error. Research is needed to further define terrestrial C pools and fluxes within a geographic context, particularly in forest systems.

3. Estimating Future Trends in Terrestrial Carbon Dynamics :
Processes Influencing Future Patterns of Terrestrial Carbon Storage

We can identify a number of critical processes which are likely to significantly modify the current distribution of above and below-ground C stocks. These processes include: 1) direct effects of increasing CO_2 on plants (eg., CO_2 fertilization), 2) response of plants to changing climate patterns, and 3) forest conservation and management including landuse practices such as afforestation and reforestation. We will briefly discuss these processes and then examine current attempts to incorporate these processes into a predictive framework for estimating future terrestrial C dynamics.

3.1 DIRECT EFFECTS OF CO_2

Numerous experimental studies have shown that enhanced atmospheric concentrations of CO_2 have the short-term effect of increasing both rates of photosynthesis and water-use efficiency (C fixed per unit of water transpired) at the level of the individual plant (Mooney *et al.,* 1991; Norby *et al.,* 1992; and see Bazzaz, 1990; Eamus and Jarvis, 1989 for reviews). If this short-term individual-level "fertilization" affect extrapolates to patterns of ecosystem net primary productivity, it would represent a large potential for increased terrestrial C storage. However, recent studies have shown that with prolonged exposure (eg., >1 year) some species acclimate to the higher CO_2 concentrations, with photosynthetic rates returning to values corresponding to those observed prior to treatment (eg., Oberbauer *et al.,* 1985; Smith *et al.,* 1987; Tissue and Oechel, 1987; Williams *et al.,* 1986). Secondly, data on ecosystem level response to elevated CO_2 from open-top chambers and free-air experiments are not consistent across different ecosystems (Curtis *et al.,* 1989; Ochel and Strain, 1985; Prudhomme *et al.,* 1984; see Bazzaz, 1990 for review), suggesting an interaction with other limiting factors (eg., N availability). Given the potential effects of elevated CO_2 on net primary productivity and terrestrial C storage, this area of research is critical to future projections and should represent a major focus in ecology over the next decade.

3.2 CLIMATE CHANGE

Rising atmospheric concentrations of CO_2 (and other greenhouse gases) over the next century have the potential to influence global climate patterns. Changes in global climate patterns as predicted by general circulation models (GCM's) for a doubled CO_2 atmosphere would have a major impact on the current global distribution of vegetation and soils (Emanuel *et al.*, 1985; Smith *et al.*, 1992a,b). Estimates of the changes in global patterns of vegetation and associated patterns of C storage for various GCM-derived climate change scenarios have been made and are discussed in detail in latter sections. These estimates represent equilibrium analyses, and a detailed analysis of the transient response of vegetation to changing climate patterns has yet to be undertaken. However, the qualitative nature of the transient response of terrestrial C storage can be estimated by examining the time scales associated with the basic ecological processes involved with the predicted shifts in vegetation distribution and associated patterns of C storage (Smith and Shugart, 1993a,b). Processes such as forest dieback resulting from increased aridity will occur on a time scale corresponding to the changes in climate conditions (decades to a century). Forest dieback and the associated increase in frequency of fire would represent a major net positive flux to the atmosphere (Neilson, 1993). In contrast, the increase in terrestrial C storage associated with natural forest expansion (eg., boreal forest into the current tundra region) will be limited by rates of species immigration into currently unforested areas. Estimates of forest migration rates from paleo-studies suggest a time-scale of centuries (Davis, 1984, 1989; Davis and Botkin 1985) for predicted shifts based on current analyses (eg., Emanuel *et al.*, 1985; Smith *et al.*, 1992a, b).

3.3 FOREST CONSERVATION AND MANAGEMENT FOR CARBON CONSERVATION AND SEQUESTRATION

Landuse changes, primarily deforestation within tropical latitudes, are currently releasing 1.2 to 3.2 Pg C annually (Brown, 1993). Future patterns of land-use, primarily forest clearing for agriculture in developing countries, could continue to be a major net positive flux of C to the atmosphere. However, these trends could be reversed through forest conservation and management for C conservation and sequestration. Forest ecosystems can be managed for the temporary storage of C (Harmon, 1990; Winjum *et al.*, 1992; Brown *et al.*, 1993). Forest and agroforest establishment and management practices can be grouped by three major functions: 1) maintain or 2) improve existing sinks and stores of C, and 3) expand forest areas that can serve as sinks of CO_2. We will briefly discuss these three groups of practices in a global context.

3.3.1 Maintenance of Existing Forest Carbon Sinks

Slowing deforestation within the tropical latitudes can conserve up to 1.6 Pg C annually. Although efforts to slow deforestation and degradation within the tropical latitudes have met with mixed success (Winterbottom, 1990), forest destruction in some regions of Brazil's Amazon basin dropped 20% in 1991 (Brown *et al.*, 1992). Replacement of shifting agriculture by one hectare of sustainable agroforestry could potentially offset 5 to 20 ha of deforestation and consequently conserve existing C reservoirs (Sanchez and Benites, 1991). Based on the direct cost of providing economic incentives to practice sustainable forest management within tropical

latitudes it has been estimated that C conservation can be achieved for $0.20 to 3.50 Mg C (Dixon *et al.,* 1993c; Winjum *et al.,* 1992; Schroeder and Ladd, 1991). For example, the Forest Village Project in Thailand, which provides incentives for shifting cultivators to establish agroforest systems and reforest degraded lands, has conserved or sequestered approximately 1 Pg C over the past 20 years.

Globally, temperate and boreal forest fires represent a significant source C to the atmosphere. Within Russia, 4 to 8 million ha of boreal forest burn annually, contributing 0.3 to 1.2 Pg of direct and indirect C emissions to the atmosphere (Krankina and Dixon, 1993). Over 40% of the boreal forests in the former Soviet Union have no fire monitoring or protection system. It is estimated that fire management and silvicultural practices could be employed to conserve C at a cost of $0.5 to 1.00 Mg.

Soils are significant reservoirs of C and conservation practices could be employed to reduce greenhouse gas emissions. Soil management can result in significant changes in soil C (Schlesinger, 1990). Management practices to conserve forest soil C include: 1) forestation to reduce erosion, 2) maintain or improve soil fertility using amendments, 3) concentrate tropical agriculture and reduce shifting agriculture, 4) remove marginal lands from agricultural production, and 5) retain forest litter and debris after silvicultural or logging activities.

3.3.2 Expansion of Forest Area and Potential Carbon Sinks

Several forest and agroforest establishment and management practices could be employed to expand forest C sinks in all latitudinal belts (Dixon *et al.,* 1993a,b,c). These practices include urban tree planting, implementing agroforestry and/or restoring forests on degraded lands and watersheds, establishing plantations on harvested or abandoned lands, and protection of existing forests from pathogens, insects and fires, or further degradation by humans. Within boreal, temperate and tropical latitudes C storage in plantations and natural forests range from approximately 25 to 250 Mg/ha, respectively. Carbon sequestration can initially be achieved via forestation and establishment of agroforestry systems for a median initial cost of $10 Mg C within tropical latitudes (Dixon *et al.,* 1993c). Agroforestry, a traditional land-use practices throughout the tropics, provides fuel, food, fiber, fodder, medicine and other goods and services. As a result of these benefits, the associated actual costs of C sequestration may be negative (Gregerson *et al.,* 1989). In boreal and temperate regions, establishment of forest plantations (poly or monocultures) can sequester C at $1 to 60 Mg C, with a median cost in Russia of $3 Mg C.

Expansion of the boreal, temperate and tropical forest systems is a large undertaking but national and international proposals have been developed (Winjum *et al.,* 1992). Various estimates have been made of land technically suitable for this effort, identifying its location and biophysical characteristics (Grainger, 1988; Houghton, 1990). An estimated 100 million ha of formerly harvested sites and abandoned lands are available for forestation in the former Soviet Union (Krankina and Dixon, 1993). Houghton (1990) identified 3,125 million ha available for forestation within the tropical latitudes. This land is climatically suitable, does not overlap with other productive land uses and includes: 625 million ha of degraded grazing land in Latin America, 625 million ha of degraded grasslands in south Asia and 1,875 million ha in Africa.

Grainger (1988) estimated that almost 5 billion ha of degraded tropical land is available for forest replenishment including: 544 million ha of deforested watershed, 2,068 million ha of

degraded drylands, 1,258 million ha of forest fallows, 848 million ha of logged rainforests. Almost 75% of the 5 billion ha are suitable for plantation or agroforestry with the land being almost equally divided between Asia, Africa and Latin America. The land area available is 30 to 40 times the area of tropical forest plantations established in 1990. Proposals have been developed to implement a 50 yr forestation program on technically suitable lands where obstacles are minimal, while technical, social and economic constraints are confronted in other regions (Winjum *et al.,* 1992).

4. Estimating Future Trends in Terrestrial Carbon Dynamics : Available Models for Examining The Dynamics of Terrestrial Carbon Storage

The flux of C between the terrestrial and atmospheric pools is largely a function of the uptake of CO_2 in photosynthesis by terrestrial plants and the release of CO_2 by plant and microbial respiration. Rates of photosynthesis and microbial decomposition are directly influenced by climate and substrata and therefore the rates of C sequestration and residence times differ geographically. These geographical relationships between climate and C storage form the fundamental basis for estimating current pools and predicting future C dynamics. It is our belief that predictive models of the terrestrial C cycle must begin with geographic specificity. We can then evaluate the impacts of various processes on the current patterns of storage.

There have been a wide variety of models developed to explore the response of vegetation and soils to environmental variation. These models range from purely statistical to models which simulate basic ecophysiological and demographic processes. Any number of these models have been used to examine patterns of C dynamics for a given site or region, but in this review we will focus solely on those models which have been used (or can easily be used) to provide global coverage.

4.1 BIOGEOGRAPHICAL MODELS

Perhaps the simplest of models for relating vegetation pattern to climate at a global scale is the approach of climate-vegetation classification. Assuming that the broad-scale patterns of vegetation (eg., biomes) are essentially at equilibrium with present climate conditions, one can relate the distribution of vegetation or plant types with biologically important features of the climate. Global bioclimatic classification schemes (von Humbolt, 1867; Grisebach, 1838; Koppen, 1900, 1918, 1936; Thornthwaite, 1931, 1933, 1948; Holdridge, 1947, 1959; Troll and Paffen, 1964; Box, 1981; Prentice, 1990) are essentially climate classifications defined by the large-scale distribution of vegetation. Although similar in concept, the wide variation in both the terminology used to describe categories of vegetation and the climate variables defined as important in influencing plant pattern make comparison among the models difficult. Bioclimatic classification models have a history of application in simulating the global distribution of vegetation under changed climate conditions, both past climatic conditions associated with the last glacial maximum (Manabe and Stouffer 1980; Hansen *et al.,* 1984; Prentice and Fung, 1990) and predictions of future climate patterns under conditions of doubled CO_2 (Emanuel *et al.,* 1985; Prentice and Fung, 1990; Smith *et al.,* 1992a,b).

One of the most widely used of the bioclimatic classifications at a global scale is the model of Holdridge (1947, 1967). The Holdridge Classification is a bioclimatic classification relating the distribution of major ecosystem complexes (referred to as life zones) to the climate indices of biotemperature, annual precipitation and a ratio of potential evapotranspiration to annual precipitation (PET ratio). The classification has proven useful in estimating the potential impacts on vegetation distribution resulting from changes in global climate patterns as predicted by general circulation models of the earth's atmosphere for a doubling of CO_2 (Emanuel *et al.,* 1985; Smith *et al.,* 1992a,b). The model has also been combined with estimates of C storage in both soils and vegetation to estimate current patterns of potential C storage under both current and changed climate condition (Smith *et al.,* 1992a). Prentice and Fung (1990) used a modified version of the Holdridge model to estimate both past and future patterns of potential C storage based on global climate patterns simulated by the GCM developed at the Goddard Institute for Space Studies (Hansen *et al.,* 1988).

A difficulty with zonal concepts like the Holdridge Classification is that the vegetation is defined as an aggregate vegetation type or association. As such, the vegetation type responds to changes in climate patterns as a single unit. However, terrestrial ecosystems are composed of numerous species which can respond individualistically to changing environmental conditions (Davis, 1984) and whose distributions often cover more than one ecosystem or zone. Although it is currently impossible to construct bioclimatic models at a global scale where the species forms the basic unit of vegetation description, a number of efforts have been made to define classifications based on a functional scheme for aggregating species into groupings based on similarity in ecology and physiognomy.

Box (1981) developed a classification of "plant functional types" based on a combination of ecology and taxonomy. The classification defines 87 plant types whose potential global distribution is defined by correlating eight climatic indices to their current distributional limits. Using a rule based system which defines patterns of dominance for a given location (and climate), the model achieves a considerable detail in describing ecosystem structure as related to climate. However, the complexity of this scheme has also imposed a limit on its potential to be parameterized appropriately for all plant types and climatic indices. Some of these problems have been overcome by dramatically reducing the number of plant types defined and the selection of climatic variables whose influence on plant distribution have a more mechanistic interpretation. Two such models are BIOME (Prentice *et al.,* 1992) and MAPSS (Neilson, 1993).

Both BIOME and MAPSS rely on relatively simple methods to derive bioclimatic "envelopes" from long-term meteorological records. Both models define a set of plant types rather than vegetation complexes, allowing for the ecosystem or biome type to be defined by the set of plant types which can occur at any location. These models depend on calculating an index of plant moisture deficit based on a seasonal solution to potential and actual evapotranspiration. In addition they use a number of indices of seasonality, as well as values for absolute temperature tolerances for the plant types. Both models produce global patterns of vegetation cover which agree well statistically with the actual vegetation map of Olson *et al.* (1983). Like the Holdridge Classification, both BIOME and MAPSS have been used to estimate current C stocks for terrestrial vegetation and soils (Cramer and Solomon, in press; Prentice *et al.,* in press; Neilson, 1993)

Biogeographical models often have been, but do not need to be, limited to potential natural vegetation. There is a convincing body of data about the potential distribution of anthropogenically derived ecosystems, such as agronomic and forest crops, as a function of bioclimatic constraints. This type of information can be embedded into a predictive model of potential natural vegetation, thereby giving the potential for human land use as well (Cramer and Solomon, in press; Leemans, 1993). Ecosystems which are affected by slight or severe human impact cannot be described by biogeographical models alone, but need the inclusion of a specific landuse models which must be driven by socioeconomic variables such as population growth.

One major problem in the application of most bioclimatic models to assessing the potential response of vegetation to a CO_2-induced climate change is their inability to address the direct response of CO_2 on vegetation (Norby *et al., 1992*; Mooney *et al.,* 1991). Models that do not simulate stomatal processes must find indirect, empirical approaches for incorporating the effects, as is done in BIOME. Models, such as MAPSS can incorporate increased WUE directly through manipulation of stomatal conductance. It is not yet certain which of these approaches produces accurate results.

The use of bioclimatic models to estimate terrestrial C dynamics is a two step process since the models do not directly simulate C pools. The models are used to define potential patterns of vegetation and associated soil properties based on simple climate indices. The calculation of C pools are done by multiplying the areal extent of each cover type (eg., vegetation type, ecosystem type, biome, life zone) by some estimate of C storage in vegetation and soils (see: Prentice and Fung, 1990, Smith *et al.,* 1992a). Generally these estimates are solely dependent on the vegetation or biome type and do not vary geographically within any one type (eg., all tropical rain forests have the same value). This approach is in contrast to process-based ecosystem models which simulate patterns of net primary productivity for a given vegetation and climate.

4.2 MODELS OF NET PRIMARY PRODUCTIVITY

Several global productivity models have been developed and are being used to examine potential effects of both increasing atmospheric concentrations of CO_2 and associated prediction of climate change on global patterns of net primary productivity and biogeochemical cycles. Three examples are the Terrestrial Ecosystem Model (TEM) (Raich *et al.,* 1991), the General Ecosystem Model (GEM) (Melillo *et al.,* in press; Rastetter *et al.,* 1991), and CENTURY (Parton *et al.,* 1988). These models simulate the processes of plant energy and C balance at the canopy level. Given data on the site vegetation type (and characteristic physiological parameters), leaf area and soil water status, these models can predict vegetation growth and soil C and nutrient dynamics. The explicit consideration of ecosystem C dynamics in these models allows them to simulate the changes in net C flux for a given location, providing estimates of change in net primary productivity under changing climate conditions.

Melillo et al. (1993) recently employed GEM to estimate global patterns of net primary productivity for current and future climate conditions. GEM estimated that over half of global net primary productivity occurs in the tropical latitudes, mostly in tropical evergreen forests. Future responses of tropical and temperate biomes are predicted to be strongly influenced by CO_2, ambient temperature and nutrient availability (eg., N).

The explicit consideration of photosynthesis and transpiration allows this class of models to include estimates of the direct effects of CO_2 on net primary productivity and water use

efficiency. However, they are not able to simulate changes in the composition and structure in response to changing environmental conditions. This is a major limitation to the use of these models for long term projections. Over the long term, changes in net primary productivity might be accompanied by a change in vegetation structure and composition comparable to those predicted by the biogeographical models.

4.3 OVERVIEW

In general, the two classes of models (i.e., biogeographical and net primary productivity) are addressing two sets of processes operating at different temporal scales. The models of net primary productivity require input defining the current cover of vegetation, the characteristics of which interact with climate and site conditions to determine the net flux of CO_2 with the atmosphere. The advantage of these models is that they are able to explicitly simulate the short-term dynamics of CO_2 flux from the terrestrial surface in response to CO_2 and changing climate patterns. The major constraint of these models is that they do not consider processes which define the longer-term response of vegetation structure and composition to these variables (CO_2 and climate). These longer-term changes in structure and composition are both a function of the changing patterns of net primary productivity as well as a constraint on future patterns of net CO_2 flux.

In contrast to the models of net primary productivity, the biogeographical models function as correlations between climate and vegetation/soils. The biogeographical models do not address the temporal dynamics of vegetation change or the processes by which those changes come about. In that respect they represent equilibrium solutions. Models which are able to examine both the short-term patterns of net primary productivity and the longer-term changes in vegetation and composition as a function of climate have been developed for a variety of ecosystems (eg., forest gap models: see Shugart, 1984). However, their utility to provide even region coverage is currently limited (Prentice *et al.,* 1992), because of the spatial scale at which they operate and problems with parameterization.

5. Estimating Potential Carbon Storage under Present and Future Climates

A critical question regarding the role of the terrestrial surface in the global C cycle is "How will patterns of terrestrial C storage respond to elevating atmospheric concentrations of CO_2 and associated changes in global climate patterns?" A number of studies have examined the sensitivity of terrestrial C storage to changes in global climate, both past and future (Lashof, 1987; Sedjo and Solomon, 1989; Prentice and Fung, 1990; Smith *et al.,* 1992a; King and Neilson, 1992; Prentice *et al.,* in press; Cramer and Solomon, in press; Smith and Shugart, 1993; Neilson, 1993). All of these studies share a common methodology, combining a mapping system for global patterns of vegetation with C density estimates for vegetation and soils relating to the classification units (i.e., vegetation or ecosystem types). The global distribution of vegetation is mapped by applying one of the biogeographical modelling approach outlined above to global databases of climate, soils and topography. By overlaying the predicted patterns of climate change as simulated by various global circulation models for past and future conditions (eg., 2XCO_2 atmosphere) on the current global climate databases, the potential global distribution of

vegetation and associated soils is mapped for the new climate conditions (eg., Emanuel *et al.,* 1985; Smith *et al.,* 1992a, b). Carbon density for each vegetation type and associated soil (i.e., classification unit) are estimated from published sources (eg., Olson *et al.,* 1983; Post *et al.,* 1982) and these densities are multiplied by the areal estimates for each of the vegetation types (classification units) as predicted by the biogeographical models.

5.1 CURRENT ESTIMATES

Current estimates of potential C storage in terrestrial vegetation and soils based on the approach discussed above are presented in Table 1. All three studies (Prentice and Fung, 1990; Smith et al., 1992; Cramer and Solomon, in press) use estimates of C in above-ground biomass from Olson *et al.* (1983) and estimates of soil C from Post *et al.* (1982). Although the three studies use different biogeographical models for mapping vegetation and soils distribution as a function of climate, the estimates of total C storage in vegetation and soils are in close agreement. Prentice and Fung (1990) used a modified version of the Holdridge Model (see Biogeographical Models) which defines 14 biome or ecosystem types (Prentice 1990). The study by Smith *et al.* (1992a) used the complete 39 class Holdridge Life Zone Classification. The estimates of Cramer and Solomon (in press) are based on the BIOME model of Prentice *et al.* (1992) which defines 14 biome or ecosystem types.

The studies by Prentice and Fung (1990) and Smith *et al.* (1992a) consider only potential C storage, in that the global vegetation maps which form the basis of the estimates (define areal coverage of ecosystems) consider only natural vegetation. These estimates therefore do not take into account lands in agricultural production, and in general overestimate C storage in terrestrial vegetation when compared to the values presented by Olson *et al.* (1983) (see Table 1). Cramer and Solomon (in press) provide estimates for conditions of natural vegetation only

Table 1. Estimates of current terrestrial carbon storage (Values in Gt).

Study	Vegetation	Soils	Total
[1]Olson et al. (1983)	561.3 (461-665)[3]		
[1]Post et al. (1982)		1308.6	
[2]Prentice and Fung (1990)	748	1143	1891
[2]Smith et al. (1992)	737.2	1158.5	1895.7
[2]Cramer and Solomon (in press)	754 (457-574)[4]	1367	2121

[1] Based on field based estimates from various ecosystem studies
[2] Based on estimates from Olson et al. (1983) and Post et al. (1982) combined with potential vegetation maps from biogeographical model (see text)
[3] Range for estimates
[4] With extensive and sparse agriculture

(i.e., potential cover) and with sparse and extensive agronomic cultivation. Their estimate of carbon storage without agronomic cultivation is similar to the other two studies. Estimates with agronomic cultivation agree well with the range of values presented by Olson *et al.* (1983).

Although the estimates of total terrestrial C storage are rather robust across mapping systems (i.e., biogeographical mode used), this does not speak for the quality or accuracy of the estimates, nor is landuse considered. As stated above, the estimates of C content for the various classification units used to describe vegetation and soils were all derived from Olson *et al.* (1984) and Post *et al.* (1982). Although these estimates represent some of the only data available at a global scale, they are based on a limited number of samples and geographical regions. A great deal of work is needed to provide more suitable estimates on a regional basis.

5.2 ESTIMATES UNDER FUTURE CLIMATES

A number of studies have used the approach outlined above to examine the potential impacts of a global climate change resulting from a doubling of atmospheric CO_2 on the potential of the terrestrial surface to store C. Lashof (1987) developed a classification system of 14 ecosystem types based on the vegetation classification of Olson *et al.* (1983). The global distribution of these types were then related to mean winter and summer temperature and precipitation. The resulting model was used to examine potential shifts in the distribution of ecosystems and associated changes in terrestrial C storage under climate change scenarios from the National Center for Atmospheric Research (NCAR) (Washington and Meehl, 1984), Geophysical Fluid Dynamics Laboratory (GFDL) (Wetherald and Manabe, 1986) and Goddard Institute for Space Studies (GISS) (Hansen *et al.*, 1984) general circulation models.

The GISS scenario predicted a 28 Gt increase in C storage. In contrast, C storage declined in both the GFDL (-64 Gt) and NCAR (-40 Gt) scenarios. Soil C declined under all three scenarios as a result of the transition from boreal forest to grassland. For the GISS scenario, this decrease was offset by a significant increase in forest cover in the tropics. Above-ground C decreased in the other two scenarios as a result of forest decline in the warm temperate, subtropical and tropical zones.

Prentice and Fung (1990) used a modified version of the Holdridge Classification (Prentice 1990) to examine the impacts of perturbed climates on the distribution of global vegetation and associated changes in terrestrial C. Using predicted climate patterns from the Goddard Institute for Space Studies (GISS) general circulation model (Hansen *et al.*, 1988) for conditions of $2XCO_2$, Prentice and Fung found a 235 Gt increase in terrestrial C storage, resulting in a strong negative feedback on elevated atmospheric CO_2 (128 ppm). The increase in C storage was primarily associated with a large increase (75%) in the extent of tropical rainforest under the changed climate conditions.

Smith *et al.* (1992a) examined the potential impacts of CO_2 induced climate change on terrestrial C storage using the Holdridge Life Zone Classification and four climate change scenarios derived from general circulation models: GISS (Hansen *et al.*, 1988), GFDL (Manabe and Wetherald, 1987), UKMO (Mitchell, 1983) and OSU (Schlesinger and Zhao, 1988). All four scenarios showed an increase in potential terrestrial C storage ranging from a 0.4% to 9.5%: GISS (147 Gt), GFDL (38 Gt), UKMO (8.5 Gt) and OSU (180 Gt). Carbon storage in above-ground biomass rose in all four scenarios, but soil C declined under the GFDL and UKMO scenarios. The increases in C storage were primarily a function of the poleward shift of the forested zones, with an increase in the areal extent of tropical forests and a shift of the boreal forest zone into the region currently occupied by tundra.

Neilson (1993) used the MAPSS model (Biogeographical Models above) to examine the potential changes in terrestrial C storage under four GCM scenarios based on 2XCO$_2$ simulations (GISS, GFDL, UKMO and OSU). In contrast to the results of Prentice and Fung (1990) and Smith *et al*. (1992), Neilson found a decrease in potential C storage under the four scenarios investigated. This decline in C is a result of predicted patterns of forest decline, primarily in the subtropical and tropical regions.

Cramer and Solomon (in press) used the BIOME model (Prentice *et al.,* 1992) discussed above (Biogeographical Models) to examine potential changes in terrestrial C storage under a climate change scenarios based on the GFDL and OSU general circulation models. Unlike the above analyses which examined only potential vegetation cover, Cramer and Solomon included agroecosystems in their classification. Their results were similar to Smith *et al*. (1992), predicting an increase in potential C storage under the two GCM scenarios (OSU 16 Gt, GFDL 76 Gt) when agricultural lands were excluded. In contrast to Smith *et al*., Cramer and Solomon predict a decline in soil C under the OSU scenario. However, as with the GFDL scenario, increases in above-ground C more than offsets this decline giving a net positive gain in total C storage. In the case where agricultural lands are included in the classification, potential C storage declined under both scenarios.

With the exception of Neilson (1993), all of the analyses discussed above agree qualitatively in their predictions of an increase in potential terrestrial C storage under the climate change scenarios investigated. However, the quantitative predictions differ significantly. There are a number of sources of variation responsible for the differences in predicted future C stores in the above analyses. First, the differences among scenarios are a direct result of the differences in predicted global climate patterns and associated predictions for vegetation distribution. The largest difference among the scenarios is the greater degree of warming and associated mid-continental drying predicted by the GFDL and UKMO scenarios.

The second source of variation is in the differences among the models in their classification systems (for vegetation) and the associated estimates of C densities (above-ground biomass and soils). These two are interrelated in that the C densities have to be interpreted from the original sources (and classifications) for the specific vegetation classification system included in the model. As shown earlier (Table 1), despite the differences in the classifications associated with the different biogeographical models, the estimates of current potential C pools do not vary to a large degree. The differences arise from the predicted patterns of vegetation change under the climate change scenarios. The proportion and direction of vegetation change predicted for a given climate change will vary dependent on the classification system used and is particularly sensitive to the number of categories included in the classification (Smith *et al.,* 1992a). In general, the fewer the number of categories the greater the change in climate necessary to produce a shift in classification, and given a shift there will be a larger associated change in C density.

The analyses discussed above all represent equilibrium patterns of potential C storage resulting from a changed global climate pattern. As was noted in the discussion of biogeographical models, these models do not address the temporal or spatial dynamics of the transitions in vegetation and soils required to achieve the new equilibrium conditions. These transitional dynamics would be dependent on the rate of climate change and the rates of key ecological processes controlling the vegetation and soils dynamics associated with the predicted shift in cover (eg., tundra to boreal forest). These processes include vegetation dieback,

successional replacement, species immigration, decomposition and soil formation. Despite the limitations presented by these equilibrium analyses, initial estimates of the transient dynamics of terrestrial C storage have been made by categorizing the shifts in vegetation and soils predicted by the equilibrium analyses and examining the rates associated with the ecological processes required for those shifts to occur (Smith and Shugart, 1993a,b). Initial results suggest that although the equilibrium analyses predict a net increase potential C storage, the transient dynamics necessary for those new equilibria to be achieved would result in a significant net flux of C from the terrestrial surface following a climate change.

5.3 ESTIMATES OF C FLUX UNDER FUTURE LANDUSE SCENARIOS

The timing and magnitude of future impacts of terrestrial C pools and flux will depend on both landuse and natural resource management policies, and environmental variables such as climate change and biogeochemical cycling. Future changes in landuse patterns could overwhelm any change in terrestrial C dynamics associated with CO_2 fertilization and climate change (eg., warming and drying). Demographic projections of human populations during the next few decades suggest forest and agroecosystem disturbance will be significant (Brown *et al.,* 1993).

The estimates of terrestrial C flux resulting from projected climate change do not consider the role of improved land management in mitigating C sources. If global climate change occurs, the boreal and temperate zone forest and agroecosystem vegetation will be in transition. The potential to manage and adapt terrestrial ecosystems to help minimize greenhouse gas emissions is significant (NAS, 1991; Sampson *et al.,* 1993). Simulation modes which consider landuse patterns, resource management options and climate change are needed to develop and test strategies for greenhouse gas mitigation options.

6. Integrating a Dynamic Terrestrial Surface Into Global Carbon Models

Traditionally, global C models have specified the dynamics between different compartments (atmosphere, oceans, and biosphere) and simulated the fluxes by balancing the different budgets globally (eg., Bolin *et al.,* 1981; Emanuel *et al.,* 1984; Goudriaan and Ketner, 1984). These C models are currently being used to project future trajectories of GHGs' emissions (eg., Rotmans, 1990). Recently, the major limitations of this traditional budget approach has been reviewed (Post *et al.,*1992; Solomon and Shugart, 1993). The major criticism of these highly aggregated budget models is that they do not account for significant regional differences within the terrestrial biosphere. The inclusion of geographic variation should yield better estimates of fluxes, sources and sinks, as well as improve our understanding of feedbacks. Recently several geographically explicit models have been developed (e.g. Raich *et al.,* 1991; Janecek *et al.,* 1989; Kohlmaier, 1993). However, these models do not take changes in landuse into account.

The earliest global C model to considered the dynamics of landuse was the Osnabrück model (Esser, 1991). Changes in landuse in the Osnabruck model are driven mainly by prescribed demographic processes. In contrast, in the more recent IMAGE 2.0 model (Alcamo *et al.,* 1993), landuse dynamics are lined to socio-economic developments with respect to energy, industrial and agriculture. The objective of the model is to evaluate a large array of policy and scientific global change issues. The model consist of three main components (Figure 1 of Vloedbeld and

Leemans, 1993): 1) the energy-industry component simulates regional specific energy and industrial demands, which results in the annual emissions of GHGs; 2) the terrestrial biosphere component simulates regional specific demands for agricultural products, like fibre, timber and food; and 3) the third component simulates the interactions between the atmosphere and oceans. The processes that are included are atmospheric chemistry, heat transport and C uptake by the oceans, and atmospheric circulation. It uses the emissions of GHGs from the other components and some specific land cover characteristics, like albedo, as inputs. It simulates a transient climate change, including several system feedbacks, but can also be run with climate-change results from different GCMs. The climatic change and final GHGs concentration immediate feedforward into the two other components and influence energy demand (heating/cooling) and land cover. Socio-economic impacts are therefore an intrinsic part of this model.

Initial results with the IMAGE 2.0 framework show the importance of combinations of different feedback mechanisms (Vloedbeld and Leemans, 1993). The magnitude and both positive and negative feedbacks are considered. The net result of all direct CO_2-effects (C fertilization, WUE) and climatic change (temperature response on growth and soil respiration, vegetation shifts) are significantly positive. The biosphere acts as a small sink under these conditions and until 2050 12.4 Gt can be sequestered. However, this additional C storage is not preserved, when changing land cover is taken in to account according to the IPPC business -as-usual scenario (Houghton, 1992), the biosphere act as a strong additional source.

7. Conclusions

The lack of consistent data on current patterns of terrestrial C storage (both pool sizes and current fluxes) presents a major limitation on our present understanding of the role of the terrestrial surface in the global C cycle. Landuse patterns and their current influence on terrestrial C pools and fluxes are difficult to estimate. The development and application of simulation models which can address the impacts of future landuse patterns on terrestrial C dynamics have only recently been initiated at a continental to global scale (Brown *et al.,* 1993; Hall *et al.,* 1993). Moreover, our limited understanding of the potential impacts of rising concentrations of atmospheric CO_2, both through direct effects on net primary productivity and indirectly through its influence on the global climate system, further limits our ability to make predictions of the future role of the terrestrial surface in the global C cycle. Given the overwhelming importance of understanding the global C cycle in the face of rising atmospheric CO_2 concentrations, research towards reducing these uncertainties is urgent.

Current analyses of the potential impacts of a global climate change resulting from increasing atmospheric concentrations of GHG's on patterns of terrestrial C storage suggest that in the equilibrium case, there is a potential for increased storage. This increase in potential C storage in the earth's vegetation and soils would represent an important negative feedback to rising atmospheric concentrations of CO_2. However, transient analyses designed to examine the dynamics of terrestrial C storage associated with achieving the new equilibrium conditions (i.e., changes in vegetation distribution and associated soils) suggest that the terrestrial surface may act as a major C source for a period following a climate change. A source of the same magnitude as that from current fossil fuel emissions. One of the major uncertainties with these analyses is that they do not address the possible direct effects of CO_2 on ecosystem dynamics. The potential for increased net primary productivity and water-use efficiency under rising levels of CO_2 could

offset some of the predicted declines in forest distribution responsible for the net positive flux from the terrestrial surface in these transient analyses. An understanding of the direct effects of increasing landuse and CO_2 on natural ecosystems is essential to predicting the response of the earth's vegetation to possible changes in climate and the resulting future patterns of terrestrial C storage.

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