

Carbon Pools and Flux of Global Forest Ecosystems

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Forest systems cover more than 4.1×10^9 hectares of the Earth's land area. Globally, forest vegetation and soils contain about 1146 petagrams of carbon, with approximately 37 percent of this carbon in low-latitude forests, 14 percent in mid-latitudes, and 49 percent at high latitudes. Over two-thirds of the carbon in forest ecosystems is contained in soils and associated peat deposits. In 1990, deforestation in the low latitudes emitted 1.6 ± 0.4 petagrams of carbon per year, whereas forest area expansion and growth in mid- and high-latitude forest sequestered 0.7 ± 0.2 petagrams of carbon per year, for a net flux to the atmosphere of 0.9 ± 0.4 petagrams of carbon per year. Slowing deforestation, combined with an increase in forestation and other management measures to improve forest ecosystem productivity, could conserve or sequester significant quantities of carbon. Future forest carbon cycling trends attributable to losses and regrowth associated with global climate and land-use change are uncertain. Model projections and some results suggest that forests could be carbon sinks or sources in the future.

The emission of the greenhouse gas CO_2 to the atmosphere by fossil fuel combustion and land-use change continues to escalate, and its global dynamics and regulation are inadequately understood (1). Recent estimates for annual emissions of CO_2 by fossil fuel combustion and land-use change for 1980 to 1989 are 5.4 ± 0.5 Pg of C per year ($1 \text{ Pg} = 10^{15} \text{ g} = 1 \text{ Gt}$) and 1.6 ± 1.0 Pg of C per year, respectively (1). Global oceans are estimated to absorb 2.0 ± 0.8 Pg of C per year, and $\sim 3.2 \pm 0.1$ Pg of C per year remains in the atmosphere. This calculation leaves an amount of 1.8 ± 1.4 Pg of C per year unaccounted for. Low-latitude and mid-latitude terrestrial ecosystems, particularly forests, have both been proposed to be significant repositories of this missing C or the imbalance in the C budget (2).

Globally, forests cover ~ 4.1 billion hectares of the Earth's land surface with $\sim 13\%$ of the forests protected by governments and less than 10% actively managed (Table 1). The largest area of forests (42%) is in low latitudes, where more than half are in tropical America. Mid-latitude forests make up $\sim 25\%$ of the global total. Russia has the largest area of forests, $\sim 21\%$ of the global forest area. Brazil is next with $\sim 10\%$ of the total (3). The world's forests have been estimated to contain up to 80% of all above-ground C and $\sim 40\%$ of all below-ground (soils, litter, and roots) terrestrial C (4–7). Furthermore, changes in forest land use have

been estimated to produce a net C flux to the atmosphere of 0.4 to 2.5 Pg year^{-1} in 1980, mostly from low-latitude forests (8–11).

Since the last IPCC (Intergovernmental Panel on Climate Change) assessment, there has been considerable research on the role of terrestrial ecosystems, particularly forests, in the global C cycle. Our objectives for this article were to (i) analyze these recent studies to produce a new global estimate of C pools and emissions from changes in forest land use, (ii) determine if there is evidence for C sinks in forest

landscapes, (iii) examine the potential to expand and manage forests to conserve and sequester C, and (iv) consider future forest C pools and flux in changing climate and land-use scenarios. We did not examine the influence of CO_2 enrichment on forest systems, as it has been reviewed (12).

Recently, forest C budgets, calculated on the basis of national forest inventory data, have helped improve estimates of forest C content and flux in mid- and high-latitude regions (13–15). New estimates of forest C density [C in biomass per unit area; Mg ha^{-1} (10^6 g ha^{-1})] are as low as one-third of earlier estimates for high-latitude forests (16, 17) and one-half of those in low-latitude forests (18, 19). Progress has also been made in estimating recent rates of land-use change, particularly in low latitudes (20). These new data have not been integrated to revise estimates of global forest C pools and flux. Studies which quantify C flux in soil systems (21), C assimilation and partitioning in vegetation (22), the influence of environmental stresses on C cycling (6, 23), and forest management and utilization practices that conserve C and reduce greenhouse gas emissions (24–31) are considered in our analysis.

Table 1. Area of forests, protected forests, and plantations by latitudinal zone [in 1987–90 (see text)]. Changes of forest area by latitudinal belts are estimated from multidecade analysis, spanning 1971–90. Protected forests include parks, preserves, and other forest land uses in which tree cutting, removal, degradation, or human-linked disturbance is prohibited or minimal (for example, biosphere reserves).

Latitudinal belt	References	Area (10 ⁶ ha)			Change in forest area (10 ⁶ ha year ⁻¹)
		Current forests	Protected forests	Plan-tations	
<i>High</i>					
Russia	(28, 74, 76)	884	178	43	-0.2
Canada	(13, 16, 76)	436	9	3	-0.5
Alaska	(15)	52	2	1	trace
Subtotal		1372	189	47	-0.7
<i>Mid</i>					
Continental U.S.A.	(15)	241	14	2	-0.1
Europe*	(32)	283	40	1	+0.3
China	(77, 78)	118	trace	31	+0.6
Australia	(78, 79)	396	18	1	-0.1
Subtotal		1038	72	35	+0.7
<i>Low</i>					
Asia	(20, 78)	310	49	22	-3.9
Africa	(20, 78)	527	113	2	-4.1
Americas	(20, 78)	918	105	6	-7.4
Subtotal		1755	267	30	-15.4
Total		4165	528	112	-15.4

*Includes Nordic nations.

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Our approach for producing current forest C pool and flux estimates was to analyze and integrate new studies on regional and national forest resource and C pool and flux data to reach globally comprehensive estimates. We divided the world's forests into three latitudinal belts: low-, mid-, and high-latitude forests that occur between 0° to 25°, 25° to 50°, and 50° to 75° latitude, respectively. Both open (including woodlands) and closed forest systems were evaluated. Nations or regions were grouped by latitude on the basis of the approximate geographic location of their forests. This approach accounts for the inherent differences in forest C pools and land-use changes between continents and countries. In contrast, previous estimates depended largely on model projections and average point estimates of C densities by forest type distributed across landscapes and summed for the world (4, 5).

We used a forest C budget methodology (13–16), which quantifies all major pools and fluxes, to achieve global estimates. A global forest C budget was constructed with recently completed national C budgets and national or regional databases of C densities and forest areas (data sources are referenced in Tables 1, 2, and 3). All estimates of C pools were made within the period 1987–90. Estimates of C flux were made for periods of various lengths, from 1970–90 for Europe and Russia (28, 32), to 1981–90 for Canada, to a single year of 1987 for the United States (15), and annually back to the 1800s for the low latitudes (we report the values for 1990) (33). We made no attempt to standardize these multidecade estimates to the same base year as their variability is relatively small. A single-year global forest C inventory has not been completed to date.

The primary forest C budget pool components included all above- and below-ground tree biomass, biomass of nontree vegetation, soil organic matter to a depth of 1 m (including peat), coarse woody debris, and fine litter. The primary budget sources for C pools in vegetation of low-latitude forests did not include estimates for below-ground biomass, nontree biomass, and woody debris because these budgets are incomplete; thus, we estimated these values on the basis of regional databases (see notes to Table 2). We did not include in the inventories the long-term C pools in durable wood products (for example, houses and furniture) because this is an insignificant component of the global total. For example, total global wood production for the last 30 years amounted to 20 Pg of C, about half of which was used as fuelwood and the other half was used for such things as sawlogs, veneer, and pulp (35). Changes in the pools of wood products were included in calculations of C flux.

Estimates of C flux were made on the

basis of measured and simulated changes in forest C pools caused by (i) shifts in land use (for example, deforestation, logging, and vegetation regrowth), (ii) changes in forest status and successional state (for example, aggrading versus degrading), and (iii) ecosystem C assimilation and respiration (mid- and high-latitude forests). A complete description of the net forest flux estimation method is as described (10, 13–15, 33, 34). These net flux estimates are distinct from projections of net ecosystem productivity (NEP), because they do not include changes in C pools associated with a changing environment. This accounting procedure for estimating global C pools and flux is not (static C density) × (changes in landscape area) because of dynamic factors introduced by complex vegetation and soil C cycling processes and shifting land uses. Net C emissions are reported that account for the rate of accumulation of C in vegetation, soils, litter, and wood products; emission of C from burning and decay of vegetation after disturbance; and oxidation of wood products and soil C. Net C emissions from naturally occurring forest fires, where important in the landscape, were also included (36).

The forest C budget methodology for estimating C pools and flux is subject to random and systematic errors which cannot always be quantified. Errors (difference be-

tween true value and calculated or observed value) may occur in the (i) primary databases (such as land-use change, C densities, and forest volumes), (ii) conversions of primary data to quantities of interest (for example, volumes to C densities), (iii) spatial extrapolations (for example, small-scale assessments to regions), and (iv) assumptions regarding the components of the forest C budgets. Where possible, we give a range of mean values to reflect the uncertainties caused by the errors.

Current biologic potential and land technically suitable to conserve and sequester C were estimated with national and global forest C budget methodology and databases described above (26, 27). Future forest C pools and flux were projected by the BIOME model which simulates the transient and nontransient responses of forests to projected climate change, changes in land cover, and conversion to agriculture (37–40). We evaluated future forest C pools and flux under two climate change scenarios, GISS and GFDL, with forest C pool data in Table 2 (41).

Carbon Pools in Forest Ecosystems

Our analysis of the recent studies indicates that, globally, forest vegetation and soils contain 359 and 787 Pg of C, respectively,

Table 2. Estimated C pools and area-weighted C densities (C pool per forest area in Table 1) in forest vegetation (above- and below-ground living and dead mass) and soils (O horizon, mineral soil to a depth of 1 m and colocated peatlands) in forests of the world. The date of the estimate varies by country and region but covers the period 1987–90. The estimates of forest C pools are calculated on the basis of complete C budgets in all latitudes (see text for methods).

Latitudinal belt	References	C pools (Pg)		C densities (Mg ha ⁻¹)		
		Vegetation	Soils	Vegetation	Soils	
<i>High</i>						
Russia	(28, 74, 76)	74	249	83	281	
Canada	(13, 16)	12	211	28	484	
Alaska	(15)	2	11	39	212	
	Subtotal	88	471	Mean	64	343
<i>Mid</i>						
Continental U.S.A.	(15)	15	26	62	108	
Europe*	(32)	9	25	32	90	
China	(77)	17	16	114	136	
Australia	(79)	18	33	45	83	
	Subtotal	59	100	Mean	57	96
<i>Low</i>						
Asia	(20, 80)	41†–54	43	132–174	139	
Africa	(20)	52†	63‡	99	120	
Americas	(20)	119†	110‡	130	120	
	Subtotal	212	216§	121	123	
Total		359	787	Mean	86	189

*Includes Nordic nations. A factor of 1.75 was used to convert stem to total vegetation biomass (32). For soil C, an average of 9 kg m⁻² for temperate forests was used (43) and forest area in Table 1. †Estimated as the product of C densities by ecoclimatic zone and areas of forest in each zone (20), corrected for roots, nontree components, and woody debris (3, 44). ‡Estimated as the product of forest area (Table 1) and an average of 12 kg m⁻² of soil organic C (derived as total tropical pool minus Asia divided by area of forests in Africa and America). §From (43) for mineral soil of all tropical forest life zones and from (81) for O horizon, with total area adjusted according to Table 1. Another recent estimate gives 184 Pg in mineral soil only (82).

for a total of 1146 Pg (Table 2). Earlier projections ranged from 953 to 1400 Pg (5, 6, 42, 43). We estimate that soils and peat contain ~69% and vegetation 31% of the total forest C pool, whereas earlier analyses reported an almost even split between soils and vegetation. These differences could reflect (i) changes in forest area during the last decade or so, (ii) extensive forest degradation and formation of secondary forests at the global scale, but particularly in low latitudes (18, 19), (iii) that earlier investigators assumed that most forests were mature and used data from ecological field studies that were not necessarily collected from the population of interest and tended to overestimate forest biomass C densities (4, 15, 44), and (iv) use of different soil data, which excluded peatlands colocated with forest zones, at high latitudes [we report a total of 471 Pg of C for these forest zones compared with 179 to 182 Pg reported earlier (6, 42, 43)].

The allocation of C between vegetation and soils differs by latitude. A large part of the vegetation (25%) and soil (59%) C pools are located in the high-latitude forests (Table 2). Significant peat deposits are colocated with forests at high latitudes, and many of these peats are covered with sparse forest cover, particularly in Canada. Sparsely vegetated lands partly explain the low area-weighted average C density for forest vegetation in Canada. In contrast, Russian forests have the highest C densities in vegetation, partly because they contain relatively large quantities of standing and lying dead wood. The forests of Russia contain the largest proportion of the high-latitude pools (58% of total) (Table 2); thus, any future change in these forests

(21% of the world's forest land area), particularly conversion to nonforest use, has the potential to significantly affect the global C storage.

Mid-latitude systems account for a small part of the global forest C pools (16 and 13% of the vegetation and soil, respectively) (Table 2). The European forest C pool is about one-half that of the other regions in this latitudinal belt, and European forests have the lowest average C density. China has a relatively large forest vegetation C pool and the smallest forest area among mid-latitude nations. The implementation of an intensive program of forestation and management to enrich the forest resource base of China may explain its high C density forests. Australia, often considered to be mostly a semi-arid country, has forests with an average C density that is only 25% less than that for forests in the continental United States. Although mid-latitude forests are a small proportion of the global forest area (~25%), they are relatively young, are expanding in area (Table 1), and have the capability to accumulate C in future decades (15, 32).

Low-latitude tropical forests are relatively heterogeneous and contain 59 and 27% of global forest vegetation and soil C, respectively (Table 2). Weighted C densities for forest vegetation range from 99 Mg ha⁻¹ in tropical Africa to 174 Mg ha⁻¹ in tropical Asia, although smaller regions (for example, in Indonesia and Malaysia) may contain more than 250 Mg ha⁻¹ (18, 19). Brazil's Amazon basin, containing the largest area of tropical forest, accounts for 49 Pg of C in forest vegetation or ~23% of the total tropical vegetation C pool (3). Soil C densities in the low-latitude forests are gen-

erally higher than those for the mid-latitude forests (5, 43).

Carbon Sources and Sinks

The net C flux to the atmosphere from the world's forests caused by changes in land use, forest status, and forest C cycling processes was approximately -1.3 to -1.5 Pg year⁻¹, with a midpoint of -0.4 Pg year⁻¹ (Table 3). This is ~15% of global fossil fuel-based C emissions. Deforestation in low latitudes (currently, a net loss of forest area of 15.4 million ha year⁻¹) (Table 1) produced 1.6 ± 0.4 Pg of C per year. This source was partially offset by a net sink of 0.7 ± 0.2 Pg of C per year in mid- to high-latitude forests (Table 3). The conclusion that mid- and high-latitude forests are a sink is different from the results of other analyses which estimated that these forests were approximately in balance in 1980 (10, 34).

Our estimate of a net release of 0.9 ± 0.4 Pg of C per year from global forest ecosystems to the atmosphere substantially reduces the imbalance in the global C budget. Substituting this new estimate for the terrestrial source into the global C budget given in (1) results in a total source to the atmosphere of 6.3 ± 0.6 Pg year⁻¹. The sink value remains the same at 5.2 ± 0.8 Pg year⁻¹, and the imbalance (sources - sinks) now equals -1.1 ± 1.0 Pg year⁻¹. However, this reduction in the imbalance is still not consistent with estimates of the total net terrestrial C flux obtained from geophysical data and modeling (1). Geophysical data imply that the net terrestrial flux of C is near zero over the last decade. That is, emissions of C from fossil fuel combustion are accounted for by the observed increase in atmospheric C and the modeled uptake of C by oceans. Thus, the release of C from changes in forest land use must be balanced by the accumulation of C elsewhere. Using latitudinal gradients in atmospheric CO₂ concentration, relative abundance of ¹³CO₂, and precise measurements of atmospheric O₂ (45), investigators have suggested that C is accumulating on land, particularly in the low- or mid-latitude forests (2). Because we have shown that changes in land use in the low-latitude forests are a significant C source (Table 3), any accumulation on land would have to be over and above that being released by changes in land use, that is, in previously disturbed and regrowing forests (34, 46).

If the imbalance in the global carbon budget were to be explained by the accumulation of C in northern mid-latitude forests, the required rate of accumulation would average ~1.5 Mg ha⁻¹ year⁻¹ or 2 to 3% of their present standing stock in vegetation. Although this rate is within the range of values reported for intensively studied plots

Table 3. Estimated annual C fluxes to (–) and from (+) the atmosphere by the world's forests. The incipient influence of CO₂ enrichment on vegetation may be expressed in flux data but has not been quantified. The reporting period varies by country (see text for further details).

Latitudinal belt	References	C flux (Pg year ⁻¹)
<i>High</i>		
Russia	(28, 74)	+0.30 to +0.50
Canada	(13, 16)	+0.08
	Subtotal (mean ± range)	+0.48 ± 0.1
<i>Mid</i>		
Continental U.S.A. and Alaska	(15)	+0.10 to +0.25
Europe*	(32)	+0.09 to +0.12
China	(77)	–0.02
Australia	(79)	trace
	Subtotal (mean ± range)	+0.26 ± 0.09
<i>Low</i>		
Asia	(33)	–0.50 to –0.90
Africa	(33)	–0.25 to –0.45
Americas	(33)	–0.50 to –0.70
	Subtotal (mean ± range)	–1.65 ± 0.40
Total		–0.9 ± 0.4

*Includes Nordic nations.

(47) and less than an estimate of $3.7 \text{ Mg ha}^{-1} \text{ year}^{-1}$ based on ecosystem CO_2 exchange in a successional forest in the north-eastern United States (48), the required rate is more than the average rates determined for U.S. forests ($1.4 \text{ Mg ha}^{-1} \text{ year}^{-1}$) (15) and European forests (0.4 to $0.6 \text{ Mg ha}^{-1} \text{ year}^{-1}$) (32). More importantly, the estimates of C accumulation in U.S. and European forests are based on observed rates of growth over large areas. The observed rates are the basis for the C flux reported here and they helped define the global C imbalance. If the missing C was to be accumulating in these forests, the observed rates of growth must have been an underestimate of the actual rates by a factor of up to 4, which is unlikely. Many forest ecosystems are likely not accumulating C at high rates in vegetation because of poor site conditions, anthropogenically induced stresses, or successional stage (6, 32, 34). Accumulation of C in forest soils could account for an additional C sink, especially in second-growth forests at mid- and high latitudes (49). Similarly, global accumulation rates of C in woody detritus of forests may also be underestimated (14). However, we expect these additional sinks to be small compared with the C accumulation rates in vegetation.

In our estimates of C flux, uncertainties exist for all forests but are largest in low-latitude forests. Many of the mid- or high-latitude forests are covered by permanent national forest inventories, on relatively homogeneous landscapes, and currently subject to less modification by humans than low-latitude systems (13–16). Much of the uncertainty in estimates for mid- and high-latitude forests results from differences in accounting for the C in wood products and in organic matter left in the forest after harvest (34). In low latitudes, uncertainties in estimated rates of forest area change (deforestation and reforestation) are high and may vary by 10 to 30%. Moreover, spatial variation in vegetation C density estimates may be up to 90% of mean values (18, 50). Although estimates of biomass C densities have been improved (18, 19), these estimates are in need of constant refinement because of forest degradation. Losses due to degradation are not from clearing of forests but a gradual reduction in biomass C density by nonsanctioned removal of wood for timber or fuel (9, 18, 19, 51). For example, primary forests of peninsular Malaysia lost ~35% of their biomass C density during 1972–82 from removal of large-diameter trees as the forests became more fragmented (51).

National forest inventories and continuous forest monitoring systems are not uniformly available, particularly in most low-latitude nations. Thus, there is no consistent method to measure and detect changes

(degradation or accumulation) in the C stored in forests. In models of land-use change used for estimating C flux, forests that have not been cut or cleared within the past 100 years or so are assumed to be in C steady state (10), which cannot be supported by recent work (46). Uncertainties in balancing the C flux from forest landscapes will remain until a coordinated global network of permanent forest inventory plots and the application of remote sensing technology to measure changes in area and condition of forests, including “mature” forest, is undertaken.

Forest Carbon Conservation and Sequestration

Although forests are continuously recycling C (photosynthesis and decomposition), the period of C sequestration by net storage in vegetation and soil can range from years to centuries with the time scale dependent on species, site conditions, disturbance, and management practices. Estimates of unrealized global forest C conservation and sequestration potential, calculated on the basis of C budget methodology, suggest a biologic capability of 1 to 3 Pg of C annually for as much as a century (26–28). Forest management practices to conserve and sequester C can be grouped into four major categories: (i) maintain existing C pools (slow deforestation and forest degradation), (ii) expand existing C sinks and pools through forest management, (iii) create new C sinks and pools by expanding tree and forest cover, and (iv) substitute renewable wood-based fuels for fossil fuels. Management of forests as C reservoirs often complements other environmental goals including protection of biologic, water, and soil resources (52).

Maintenance of existing forest C pools. Slowing forest loss and degradation can significantly affect C flux across all forest biomes (Tables 1 and 3). International and national efforts are being proposed and mounted to reduce deforestation, particularly in low latitudes. For example, deforestation in Brazil's Amazon basin dropped 40% between 1988 and 1991 (3, 53). In Thailand, incentives for shifting cultivators to establish agroforest systems to offset deforestation and reforest degraded lands has conserved or sequestered ~1 Pg of C over the past 20 years (54). Establishment of biosphere reserves, extractive reserves, national parks, and other forest conservation and management programs maintains forest C pools even though they were not specifically designed for that purpose (Table 1) (30, 56, 57). Our analysis (58) projects that cumulative deforestation (on the basis of past and ongoing trends) could be slowed by 138 million ha by the year 2045 from a base

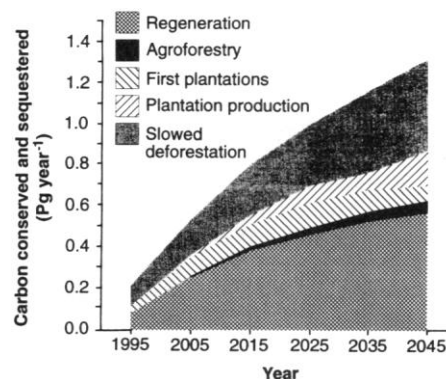


Fig. 1. Carbon conserved and sequestered through implementation of forest management in low latitudes (58).

line projection of 650 million ha under future scenarios, thus conserving up to 0.5 Pg of C per year (Fig. 1).

Similar opportunities to maintain forest C pools also exist at high latitudes. For example, 40% of forests in the former Soviet Union have no fire monitoring or protection system. Implementation of a comprehensive fire management system could increase the near- and long-term C sinks in Russia by up to 0.1 and 0.6 Pg year⁻¹, respectively (28).

Expansion of existing C sinks and pools. Large areas of forest (vegetation and soils) at all latitudes are not at maximum C storage (26, 28, 32). Most of what has been considered to be primary tropical forests are secondary forests that could accumulate C over many decades if they were protected (26, 46, 59, 60). Areas of tropical Asian forests continue to lose biomass because of log poaching and fuelwood gathering (9, 18, 19). In some regions C accretion is occurring (for example, in managed forests), but it is not a widespread phenomenon (46, 51). In the United States and other mid-latitude nations, net C accumulation of commercial timberland, on average, is below its biologic capacity, and these forests can store more C in future decades (15, 32).

Practices to expand or conserve forests also influence soil C pools, including (i) forestation to reduce erosion, (ii) addition of amendments to improve soil fertility, (iii) concentration of intensive tropical agriculture and reduction of shifting cultivation, (iv) removal of marginal lands from agricultural production that is followed by forestation, and (v) retention of forest litter and debris after silvicultural or logging activities. Accumulation of soil C in mature forests occurs over decades to centuries (49), but C aggradation on relatively young, disturbed or degraded soils, particularly in low latitudes, can range from 0.5 to $2.0 \text{ Mg ha}^{-1} \text{ year}^{-1}$ (54, 61, 62).

Creation of new C sinks and pools. Humans have cleared over 750 million hectares of

land within low latitudes (60, 63), and more than 90% of this land is inefficiently managed, is in marginal agricultural uses, has been degraded, or has been abandoned (59–61, 63). Hundreds of millions of additional hectares in high- and mid-latitude regions fall into similar land-use categories. There may be 100 million hectares of formerly harvested sites and abandoned lands available for forestation in the former Soviet Union (28). Similarly, more than 100 million hectares of economically and technically marginal lands in Europe and the United States could support forest cover (54, 55, 64).

Expansion of forests at all latitudes could sequester significant quantities of C (54–56, 60–62, 65). Estimates of forest C sequestration suggest a biological potential of up to 1 to 2 Pg annually over a period of decades to centuries (30, 56–58, 65). On the basis of technical suitability of land and biological potential of forest growth, the low latitudes offer the greatest potential for C conservation and sequestration (26). Natural regeneration of previously disturbed forests will significantly increase C sequestration. Establishment of plantations and agroforestry appear to be less important tools to sequester C (Fig. 1), but without these management options, protection and regeneration of existing forests is highly unlikely.

Substitution of wood fuels for fossil fuels. Although forest C conservation and sequestration could help mitigate some greenhouse gas emissions in the future, currently available options could offset ~5 to 15% of current fossil fuel emissions (1, 30, 56, 57, 65). Substitution of sustainable woody biomass energy, a renewable source, for fossil fuel combustion is an alternative method of C conservation in all forest nations (25, 30, 31, 52, 54, 56). Short-rotation woody crops have the potential, with advances in energy conservation and crop yield, to reduce global fossil fuel emissions by up to 20% (25, 30, 31).

Global Forest C Cycling: Prognosis

The timing and magnitude of future changes in forest C cycling will depend on (i) environmental factors such as changing climate, accumulation of atmospheric CO₂, and increased global mobilization of nutrients such as N and S (12, 66), and (ii) human factors such as demographics, economic growth, technology, and resource management policies (52). The interactive effects of all these factors on the world's forest regions are complex and not intuitively obvious and are likely to differ among geographic regions.

High- and mid-latitude forests will probably be more strongly influenced by environmental factors than low-latitude regions. Of particular concern are the lagged, or transient effects of climate change that may

increase C flux to the atmosphere or alter current C storage, including increasing soil C oxidation (67), changing productivity of forests in an increasingly exotic climate (68), shifts in the occurrence of C-dense trees (for example, late-successional species) (69), and the local absence of climatically appropriate tree species because of delays in immigration to newly available habitats (70–72). Those processes that decrease C storage under a changed climate could be compensated by responses that increase C sequestration in forests; for example, young forests have high rates of net C accretion (15, 32), increased soil C decomposition may increase rates of soil nutrient mobilization (8), and the increase in atmospheric CO₂ may increase above- and below-ground forest productivity (12, 66), particularly in the ever-increasing area of secondary forests. Results from a global biogeochemical model, which considers only environmental factors, project that net primary productivity of forests may increase up to 25%. Improvements in productivity were attributed to warmer ambient conditions, mineralization of soil N, and CO₂ enrichment (66). Although large-scale field experiments at the ecosystem level are needed to evaluate the long-term impacts of changes in future environmental conditions on C cycling, current trends from field studies point toward changes in patterns of C accumulation in the system in response to increases in CO₂ enrichment (12).

Future changes in low-latitude land-use patterns, particularly continued deforestation, could overwhelm changes in C pools and flux caused by future environmental conditions (37, 38, 63, 73). Demographic projections of increases in low-latitude human population and associated agricultural and industrial development in future decades suggest that these pressures will be great (52). To assess the potential impacts of the combined effects of human and environmental factors on forests, we used the BIOME model (40). Potential transient and nontransient changes in forest C pools under moderate (GISS) and intense (GFDL) climate change scenarios (41) were projected. Nonirrigated agriculture was assumed to replace 50% of the native vegetation in regions where it becomes climatically suitable in the future (37, 38). Thus, the combined effect of changing climate and atmospheric composition on native forest vegetation (39) and on agricultural area (37, 38) was simulated.

The GISS nontransient climate scenario simulation showed a net decrease in forest C storage of 27 Pg and GFDL of 176 Pg, both primarily from soil C losses at high latitudes. Other C cycling response projections (37–39, 70–72, 75) are not comparable with our results because they used higher estimates of forest C density (4, 5) and

did not include future expansion of agriculture (37, 38). On the basis of BIOME output (40), the transient projection of total future C emissions from forest lands, without emission from land-use change, annualized over a 100-year period was 4.1 Pg of C per year for the moderate and 4.2 Pg of C per year for the intense scenario. Projected total future forest C emissions with climate-induced land-use change is 4.4 to 6.0 Pg year⁻¹ without implementation of adaptation or mitigation practices.

In summary, large uncertainty exists with our ability to project future forest distribution, composition, and productivity (70–72). Moreover, global models have not been developed that consider the role of improved forest management in mitigating C flux to the atmosphere under transient or nontransient climate change scenarios (25, 30, 31, 54–56, 58). The potential to adapt forest ecosystems to help minimize greenhouse gas emissions is considerable in mid-latitude forests given current infrastructure and technology (30, 54–57). However, the effects most responsible for future C emissions, such as decline in forests and expansion of agriculture, should be considered in development of forest C conservation and sequestration options.

REFERENCES AND NOTES

1. J. T. Houghton, B. A. Callander, S. K. Varney, Eds., *Climate Change 1992* (Cambridge Univ. Press, Cambridge, 1992); E. T. Sundquist, *Science* **259**, 934 (1993); J. L. Sarmiento and E. T. Sundquist, *Nature* **356**, 589 (1992).
2. P. P. Tans, I. Y. Fung, T. Takahashi, *Science* **247**, 1431 (1990); J. A. Taylor and J. Lloyd, *Aust. J. Bot.* **40**, 47 (1992).
3. P. Fearnside, *Carbon Emissions and Sequestration in Forests: Case Studies from Seven Developing Countries: vol. 2: Brazil* (Lawrence Berkeley Laboratory, University of California, Berkeley, CA, 1992).
4. R. H. Whittaker and G. E. Likens, in *Primary Productivity of the Biosphere*, H. Leith and R. H. Whittaker, Eds. (Springer-Verlag, New York, 1975), pp. 305–328; G. L. Atjay, P. Ketner, P. Duvigneaud, in *Scope 13—The Global Carbon Cycle: Measurement by Remote Sensing*, G. M. Woodwell, Ed. (Cambridge Univ. Press, Cambridge, 1984), pp. 129–182.
5. J. S. Olson, J. A. Watts, L. J. Allison, *Carbon in Live Vegetation of Major World Ecosystems* (Rep. ORNL-5862, Oak Ridge National Laboratory, Oak Ridge, TN, 1983); P. J. Zinke *et al.*, *Worldwide Organic Soil Carbon and Nitrogen Data* (Rep. ORNL-TM-8857, Oak Ridge National Laboratory, Oak Ridge, TN, 1984).
6. R. H. Waring and W. H. Schlesinger, *Forest Ecosystems: Concepts and Management* (Academic Press, New York, 1985); W. H. Schlesinger, in *The Role of Terrestrial Vegetation in the Global Carbon Cycle: Measurement by Remote Sensing*, G. M. Woodwell, Ed. (Cambridge Univ. Press, Cambridge, 1984), pp. 11–127.
7. R. K. Dixon and D. P. Turner, *Environ. Pollut.* **73**, 245 (1991).
8. R. A. Houghton and D. L. Skole, in *The Earth as Transformed by Human Action*, B. L. Turner *et al.*, Eds. (Cambridge Univ. Press, Cambridge, 1990), pp. 393–408.
9. E. P. Flint and J. F. Richards, in *Effects of Land Use Change on Atmospheric CO₂ Concentra-*

- tions. *Southeast Asia as a Case Study*, V. H. Dale, Ed. (Springer-Verlag, New York, 1994), chap. 6.
10. R. A. Houghton *et al.*, *Ecol. Monogr.* **53**, 235 (1983); R. A. Houghton *et al.*, *Tellus* **39B**, 122 (1987); J. M. Melillo, J. R. Frucci, R. A. Houghton, B. Moore, D. L. Skole, *ibid.* **40B**, 116 (1988).
 11. R. P. Detwiler and C. A. S. Hall, *Science* **239**, 42 (1988).
 12. H. A. Mooney, B. G. Drake, R. J. Luxmoore, W. C. Oechel, L. F. Pitelka, *BioScience* **41**, 96 (1991); C. Korner and J. A. Arnone, *Science* **257**, 1672 (1992); R. M. Gifford, *Aust. J. Bot.* **40**, 527 (1992).
 13. M. J. Apps and W. A. Kurz, *World Resour. Rev.* **3**, 333 (1991).
 14. M. E. Harmon, W. K. Ferrell, J. F. Franklin, *Science* **247**, 699 (1990).
 15. R. A. Birdsey, A. J. Plantiga, L. S. Heath, *For. Ecol. Manage.* **58**, 33 (1993); R. A. Birdsey, *Carbon Storage and Accumulation in United States Forest Ecosystems* (Rep. WO-59, Department of Agriculture Forest Service, Washington, DC, 1992); D. P. Turner, G. Koerper, M. Harmon, J. J. Lee, *Ecol. Applic.*, in press.
 16. W. A. Kurz and M. J. Apps, *Water Air Soil Pollut.* **70**, 163 (1993); ———, T. M. Webb, P. J. McNamee, *The Carbon Budget of the Canadian Forest Sector: Phase I* (Rep. NOR-X-326, Forestry Canada, Edmonton, 1992).
 17. D. B. Botkin and L. G. Simpson, *Biogeochemistry* **9**, 161 (1990).
 18. S. Brown, A. J. R. Gillespie, A. E. Lugo, *Can. J. For. Res.* **21**, 111 (1991).
 19. S. Brown and L. R. Iverson, *World Resour. Rev.* **4**, 366 (1992).
 20. K. D. Singh, *Unasylva* **44**, 10 (1993); *Forest Resources Assessment 1990 Program: Tropical Countries* (Food and Agriculture Organization Forestry Pap. 112, Rome, Italy, 1993).
 21. K. Harrison and W. Broecker, *Global Biogeochem. Cycles* **7**, 69 (1993); ———, G. Bonani, *Science* **262**, 725 (1993); W. E. Schlesinger, *Nature* **348**, 232 (1990).
 22. R. J. Norby, C. A. Gunderson, S. D. Wullschleger, E. G. O'Neill, M. K. McCracken, *Nature* **357**, 322 (1992).
 23. A. M. Solomon and H. H. Shugart, Eds., *Vegetation Dynamics and Global Change* (Chapman and Hall, New York, 1993); F. A. Bazzaz, *Annu. Rev. Ecol. Syst.* **21**, 176 (1992); R. L. Graham, M. G. Turner, V. H. Dale, *Bioscience* **40**, 575 (1990).
 24. E. S. Rubin *et al.*, *Science* **257**, 148 (1992).
 25. D. O. Hall, H. E. Mynick, R. H. Williams, *Nature* **353**, 11 (1991).
 26. S. Brown, A. E. Lugo, L. R. Iverson, *Water Air Soil Pollut.* **64**, 139 (1992); L. R. Iverson, S. Brown, A. Grainger, *Clim. Res.* **3**, 23 (1993); J. D. Unruh, R. A. Houghton, P. A. Lefebvre, *ibid.*, p. 39.
 27. J. K. Winjum, R. K. Dixon, P. E. Schroeder, *Water Air Soil Pollut.* **64**, 213 (1992); R. Sedjo and A. M. Solomon, in *Greenhouse Warming: Abatement and Adaptation*, N. S. Rosenberg, W. E. Easterling, P. R. Crosson, J. Darmstadter, Eds. (Resources for the Future, Washington, DC, 1989), pp. 105–119; S. Kellomaki, H. Hanninen, T. Kolstrom, *Silva Fenn.* **22**, 293 (1988); R. Sedjo, *J. For.* **87**, 12 (1989).
 28. O. N. Krankina and R. K. Dixon, *World Resour. Rev.*, No. 6, in press; R. K. Dixon and O. N. Krankina, *Can. J. For. Res.* **23**, 700 (1993).
 29. C. Row and R. B. Phelps, in *Forests in a Changing Climate*, A. Quereshi, Ed. (Climate Institute, Washington, DC, 1992), pp. 208–219.
 30. R. N. Sampson *et al.*, *Water Air Soil Pollut.* **70**, 139 (1993).
 31. R. L. Graham, L. Wright, A. F. Turhollow, *Clim. Change* **22**, 223 (1992).
 32. P. E. Kauppi, K. Mielikainen, K. Kuusela, *Science* **256**, 70 (1992).
 33. R. A. Houghton, in *Biotic Feedbacks in the Global Climate System*, G. M. Woodwell, Ed. (Oxford Univ. Press, London, in press).
 34. ———, *Global Biogeochem. Cycles* **7**, 611 (1993); E. B. Rastetter and R. A. Houghton, *Science* **258**, 382 (1992).
 35. Food and Agriculture Organization, *Yearbook of Forest Products* (Food and Agriculture Organization, Rome, Italy, 1962–90).
 36. Gross C emissions from naturally occurring forest fires do not account for regrowth of burned ecosystems and, therefore, are not appropriate flux estimates for use in this analysis [R. A. Houghton, in *Global Biomass Burning: Atmospheric, Climate Biospheric Implications*, J. Levine, Ed. (MIT Press, Cambridge, MA, 1991)].
 37. W. P. Cramer and A. M. Solomon, *Clim. Res.* **3**, 97 (1993).
 38. A. M. Solomon, I. C. Prentice, R. Leemans, W. P. Cramer, *Water Air Soil Pollut.* **70**, 595 (1993).
 39. I. C. Prentice *et al.*, *J. Biogeogr.* **19**, 117 (1992).
 40. The BIOME model was developed specifically for assessing geographic responses of vegetation zones to climate change (39). Unlike other static models, BIOME uses physiological thresholds to temperature and water stress to predict regional plant functional types which are assembled into biomes on the basis of a dominance hierarchy. BIOME is more accurate in simulating current vegetation distribution than other models (37, 70, 72). Currently, no other static models simultaneously consider global climate change and agricultural expansion impacts on forests. Soil C emissions were based on earlier analyses [C. V. Cole, K. Flach, J. Lee, D. Sauerbeck, B. Stewart, *Water Air Soil Pollut.* **70**, 111 (1993)].
 41. GISS (Goddard Institute of Space Sciences) refers to the scenario described in J. Hansen *et al.* [*J. Geophys. Res.* **93**, 9341 (1988)] and GFDL (Geophysical Fluid Dynamics Laboratory) refers to the scenario described in S. Manabe and R. T. Wetherald [*J. Atmos. Sci.* **44**, 1211 (1987)].
 42. T. M. Smith *et al.*, *Water Air Soil Pollut.* **70**, 19 (1993); W. M. Post *et al.*, *Am. Sci.* **78**, 310 (1990).
 43. W. M. Post, W. R. Emanuel, P. J. Zinke, A. G. Strangenberg, *Nature* **298**, 156 (1982).
 44. S. Brown and A. E. Lugo, *Interciencia* **17**, 8 (1992).
 45. R. Keeling and S. R. Shertz, *Nature* **358**, 723 (1992).
 46. A. E. Lugo and S. Brown, *For. Ecol. Manage.* **54**, 23 (1992); S. Brown, A. E. Lugo, J. Wisniewski, *Science* **257**, 11 (1992); A. E. Lugo and J. Wisniewski, *Water Air Soil Pollut.* **64**, 455 (1992).
 47. C. F. Jordan and P. G. Murphy, *Am. Midl. Nat.* **99**, 415 (1978).
 48. S. C. Wofsy *et al.*, *Science* **260**, 1314 (1993).
 49. D. W. Johnson, *Water Air Soil Pollut.* **64**, 83 (1992).
 50. S. Brown, A. J. R. Gillespie, A. E. Lugo, *For. Sci.* **35**, 881 (1989).
 51. S. Brown, L. R. Iverson, A. E. Lugo, in (9), pp. 117–143.
 52. H. Gregerson, S. Draper, D. Elz, Eds., *People and Trees: The Role of Social Forestry in Sustainable Development* (World Bank, Washington, DC, 1989); N. P. Sharma, Ed., *Managing the World's Forests* (Kendall Hunt, Dubuque, IA, 1992).
 53. The Brazilian Institute for the Environment and Renewable Natural Resources reports that deforestation was 0.3% of the existing forests in the Brazilian Amazon region, the third year in a row that forest destruction declined. D. Skole and C. Tucker, *Science* **260**, 1905 (1993); V. H. Dale, R. V. O'Neill, M. Pedlowski, F. Southworth, *Photogram. Eng. Remote Sensing* **59**, 997 (1993).
 54. R. K. Dixon, J. K. Winjum, K. J. Andrasko, J. J. Lee, P. E. Schroeder, *Clim. Change*, in press.
 55. J. K. Winjum, R. A. Meganck, R. K. Dixon, *J. For.* **91**, 38 (1993); P. E. Schroeder, R. K. Dixon, J. K. Winjum, *Unasylva* **44**, 52 (1993).
 56. R. K. Dixon, K. J. Andrasko, F. A. Sussman, M. C. Trexler, T. S. Vinson, *Water Air Soil Pollut.* **70**, 561 (1993); G. Marland and S. Marland, *ibid.* **64**, 181 (1992).
 57. D. H. Alban and D. H. Perala, *Can. J. For. Res.* **22**, 1107 (1992).
 58. M. C. Trexler and C. A. Haugen, *Keeping It Green: Using Tropical Forestry to Mitigate Global Warming* (World Resources Institute, Washington, DC, 1993). Five forest management options to conserve and sequester C were considered in the analysis. regeneration of forest vegetation, establishment of agroforestry systems, establishment of first-time plantations, management of plantations to ensure flow and storage of C into long-term wood products, or bioenergy production.
 59. S. Brown and A. E. Lugo, *J. Trop. Ecol.* **6**, 1 (1990).
 60. R. A. Houghton, J. D. Unruh, P. A. Lefebvre, *Global Biogeochem. Cycles* **7**, 305 (1993).
 61. A. E. Lugo and S. Brown, *Plant Soil* **149**, 27 (1993).
 62. P. A. Sanchez and J. R. Benites, *Science* **238**, 1521 (1987).
 63. V. H. Dale, R. A. Houghton, A. Grainger, A. E. Lugo, S. Brown, in *Sustainable Agriculture and the Environment in the Humid Tropics* (National Academy Press, Washington, DC, 1993), pp. 215–262; A. Grainger, *Int. Tree Crops J.* **5**, 31 (1988).
 64. R. N. Sampson, *Water Air Soil Pollut.* **64**, 157 (1992).
 65. R. K. Dixon, J. K. Winjum, P. E. Schroeder, *Global Environ. Change* **3**, 159 (1993); T. D. Bekkering, *Ambio* **21**, 414 (1992).
 66. J. M. Melillo *et al.*, *Nature* **363**, 234 (1993). Other analyses also suggest that high-latitude forest productivity will initially increase in a changing climate [G. B. Bonan and K. Van Cleve, *Can. J. For. Res.* **22**, 629 (1992)].
 67. W. D. Billings, K. M. Peterson, J. O. Luken, D. A. Mortenson, *Oecologia* **65**, 26 (1984); W. C. Oechel *et al.*, *Nature* **361**, 520 (1993).
 68. M. B. Davis and C. Zabinski, in *Global Warming and Biological Diversity*, R. L. Peters and T. E. Lovejoy, Eds. (Yale Univ. Press, New Haven, CT, 1992); A. M. Solomon and P. J. Bartlein, *Can. J. For. Res.* **22**, 1727 (1992); N. J. Rosenberg, *Clim. Change* **4**, 239 (1982); ———, W. E. Easterling, P. R. Crosson, J. Darmstadter, Eds., *Greenhouse Warming: Abatement and Adaptation* (Resources for the Future, Washington, DC, 1988).
 69. A. M. Solomon, *Oecologia* **68**, 567 (1986).
 70. T. M. Smith and H. H. Shugart, *Nature* **361**, 523 (1993).
 71. K. C. Prentice and I. Fung, *Nature* **346**, 48 (1990).
 72. G. A. King and R. P. Neilson, *Water Air Soil Pollut.* **64**, 365 (1992).
 73. S. Brown *et al.*, *ibid.* **70**, 71 (1993).
 74. T. P. Kolchugina and T. S. Vinson, *Global Biogeochem. Cycles*, in press; *Can. J. For. Res.* **23**, 81 (1993); K. I. Kobak, *Biotic Compounds of the Carbon Cycle* (Hydrometeorological Publications, Leningrad, 1988).
 75. T. M. Smith, H. H. Shugart, G. B. Bonan, J. B. Smith, *Adv. Ecol. Res.* **22**, 93 (1992); W. R. Emanuel, H. H. Shugart, M. L. Stephenson, *Clim. Change* **7**, 29 (1985).
 76. M. Apps *et al.*, *Water Air Soil Pollut.* **70**, 39 (1993).
 77. X. Deying, *Carbon Emissions and Sequestration in Forests: Case Studies from Seven Developing Countries: vol. 3: India and China* (Lawrence Berkeley Laboratory, University of California, Berkeley, CA, 1992).
 78. World Conservation Monitoring Centre, *Global Biodiversity, Status of the Earth's Living Resource* (Chapman Hall, London, 1992).
 79. R. M. Gifford *et al.*, in *Australia's Renewable Resources: Sustainability and Global Change* (Commonwealth Scientific and Industrial Research Organization Division of Plant Industry, Canberra, Australia, 1992), pp. 151–187.
 80. S. Brown, L. R. Iverson, A. Prasad, D. Liu, *Geocarto Int.*, in press.
 81. S. Brown and A. E. Lugo, *Biotropica* **14**, 161 (1982).
 82. M. Esawaran, E. VanDenBerg, P. Reich, *Soil Sci. Soc. Am. J.* **57**, 192 (1993).
 83. Support for this work to S.B. was provided by grant DFG902-90ER61081 from the Department of Energy and Cooperative Agreement PNW 91-0115 from the Department of Agriculture Forest Service to the University of Illinois. Support for this work to R.H. was provided by Cooperative Agreement CR-818636 from the Environmental Protection Agency (EPA). Support to J.W. was provided by Cooperative Agreement CR-820797 from EPA. We offer thanks to multiple colleagues for review comments and helpful suggestions and to V. Robinson for manuscript preparation.