one was tested, all reaction mixtures were supplemented with an appropriate amount of ethanol (5% v/v), because the menadione was dissolved in ethanol as a stock solution. The reaction was initiated by the addition of [γ-^{32}P]ATP. Samples were withdrawn at the indicated time intervals, mixed with an equal volume of 2× SDS sample buffer, and immediately subjected to SDS–polyacrylamide gel electrophoresis on 12.5% polyacrylamide gels. The radioactivity of ArcB was revealed by exposure to X-Omat AR films, and the amount of protein-P was quantitated with a PhosphorImager.

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35. We dedicate this work to Bernard D. Davis, who demonstrated the existence of the tricarboxylic acid cycle in bacteria and, in 1968, encouraged E.C.C.L. to study its genetic regulation. We thank R. Meganathan for discussions and R. Poole for strain RKP4152. Supported by U.S. Public Health Service grant GM40993 from the National Institute of General Medical Sciences.

29 January 2001; accepted 14 May 2001

Consistent Land- and Atmosphere-Based U.S. Carbon Sink Estimates

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For the period 1980–89, we estimate a carbon sink in the coterminous United States between 0.30 and 0.58 petagrams of carbon per year (petagrams of carbon = 10^{15} grams of carbon). The net carbon flux from the atmosphere to the land was higher, 0.37 to 0.71 petagrams of carbon per year, because a net flux of 0.07 to 0.13 petagrams of carbon per year was exported by rivers and commerce and returned to the atmosphere elsewhere. These land-based estimates are larger than those from previous studies (0.08 to 0.35 petagrams of carbon per year) because of the inclusion of additional processes and revised estimates of some component fluxes. Although component estimates are uncertain, about one-half of the total is outside the forest sector. We also estimated the sink using atmospheric models and the atmospheric concentration of carbon dioxide (the tracer-transport inversion method). The range of results from the atmosphere-based inversions contains the land-based estimates. Atmosphere- and land-based estimates are thus consistent, within the large ranges of uncertainty for both methods. Atmosphere-based results for 1980–89 are similar to those for 1985–89 and 1990–94, indicating a relatively stable U.S. sink throughout the period.

Despite widespread consensus about the existence of a terrestrial carbon sink of 1 to 2 Pg of C (Pg C) year^{-1} in the Northern Hemisphere, the size, spatial distribution, and cause of the sink remain uncertain (*1–3*). Information about the sink comes from two primary sources: (i) atmosphere-based methods that determine the combination of carbon sources and sinks in an atmospheric transport model that gives the best match to a global set of atmospheric CO_2 data (the tracer-transport inversion method) and (ii) land-based approaches incorporating direct inventories of carbon on the ground, reconstructions of land use change, and ecosystem models.

The size of the sink in temperate North America has been estimated with both approaches, with diverse results. One set of inverse modeling studies estimates a large North American sink of 1.7 Pg C year^{-1} for 1988–92, with 1.4 Pg C year^{-1} south of 51°N (*4*), whereas others estimate a much smaller sink (i.e., 0.5 Pg C year^{-1} for the entire continent) (*5–7*). Land-based analyses for the United States in the 1980s suggest a sink of 0.08 to 0.35 Pg C year^{-1}, with virtually all of this in the coterminous United States (the United States minus Alaska and Hawaii) (*8–12*). Although these land-based values are at least fourfold smaller than the Fan *et al.* estimate (*4*) for temperate North America, comparisons between existing land- and atmosphere-based estimates are not straightforward.

To make a direct comparison, atmospheric and land-based estimates should correspond to (i) the same time period, (ii) the same land area, and (iii) the same set of biogeochemical fluxes.

1) Inverse modeling studies show that global and North American sinks fluctuate among years by up to 100% of their long-term means (*2*, *3*). This makes it essential to compare land- and atmosphere-based estimates from the same time period.

2) The portion of the atmosphere-based estimate in (*4*) attributable to the coterminous United States is only 48% of 1.7 Pg C year^{-1} or 0.81 Pg C year^{-1}. This adjustment is based on the area of the coterminous United States as a fraction of North America (32%) and the assumption in (*4*) that the spatial distribution of the sink in any region matches the spatial

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distribution of net annual primary productivity from (*13*). With the same adjustment, the estimated North American sink of 1.4 Pg C year^{-1} south of 51°N translates to a sink in the coterminous United States of 0.84 Pg C year^{-1}. Comparing estimates for the same land area reduces the discrepancy between (*4*) and the land-based range, but 0.81 to 0.84 Pg C year^{-1} is still more than twice the largest published land-based estimate (*8*).

3) Published land-based studies include only a part of the net atmosphere-to-ground flux estimated by atmospheric inversions. Table 1 itemizes eight fluxes that contributed to the net atmosphere-to-ground flux in the coterminous United States during the 1980s. Each published land-based study has, by design, included only a subset of the terms in Table 1. The most complete such analysis (*8*) included five of the eight terms [see Houghton *et al.* (*8*) in Table 1], whereas the U.S. Forest Service (USFS) estimate (*12*) included three [see Birdsey and Heath (*12*) in Table 1]. In addition, Houghton *et al.* (*8*) attempted to estimate only part of the accumulation of carbon in forests—the portion caused by land use. In contrast, Birdsey and Heath (*12*) attempted to estimate all changes in forest carbon. Estimates from ecosystem models present similar challenges. The models in the recently published VEMAP study estimated a small sink in the coterminous United States (0.08 ± 0.02 Pg C year^{-1}) for the period from 1980 to 1993 (*14*). However, these models excluded four of the eight terms in Table 1 (rows 5 to 8), as well as processes such as agricultural abandonment, fire suppression, and forest harvesting that play a dominant role in land-based analyses of the remaining terms (rows 1 to 4).

Collectively, the first six rows in Table 1 give the annual change in the total carbon inventory: the mass of carbon inside the coterminous United States in 1990 minus that in 1980, divided by 10. Carbon may accumulate in forests as living (row 1) or nonliving (row 2) organic matter, in agricultural soils (row 3), and in other ecosystems (row 4, i.e., the response of western rangelands to fire suppression). Carbon may also accumulate in wood products both in use and in landfills (row 5) and in sediments of reservoirs and rivers (row 6, including alluvium and colluvium). The final two terms (rows 7 and 8) account for surface exports and imports: the mass of atmospheric carbon fixed by U.S. ecosystems and then exported by rivers and commerce, minus the amount imported and released to the atmosphere (e.g., consumption of imported food inside the United States). These last two terms affect the net atmosphere-to–United States flux estimated by an inversion, but not the size of the global carbon sink.

To make a direct comparison of flux estimates for the same time period, land area, and set of biogeochemical fluxes, we compared the comprehensive land-based analysis in Table 1 with a corresponding suite of atmosphere-based inverse estimates [Peylin *et al.* (*15*)]. The atmospheric inverse analyses were designed to span a range of techniques currently used (*15*). We include 81 cases: 3 atmospheric models × 3 spatial resolutions × 3 temporal resolutions × 3 time periods. To assess the temporal variability of the U.S. sink, we provide atmospheric inverse estimates for 1985–89 and 1990–94, in addition to 1980–89.

Land- and atmosphere-based estimates broadly agree, but the land-based estimates have a narrower range of uncertainty (Fig. 1). We now itemize the estimation of each of the eight rows in Table 1.

1) We used the USFS estimates of carbon accumulation in forest trees for the 247 million ha of commercial and noncommercial forest in the coterminous United States during the 1980s (*16*). USFS estimates were issued in 1977, 1987, and 1992, and the lower bound in Table 1 is an interpolation for 1980–89 (*12*). The flux is positive because regrowth exceeded harvest in the eastern half of the United States, as it has for the past 50 years (*12*). The raw measurements include tree diameter and species every 5 to 13 years for literally millions of trees (*16*). Allometric equations convert these to carbon content, which are then differenced to produce a flux. The upper bound in Table 1 reflects uncertainty about allometric relations (*16*).

2) Because the USFS forest survey program has not historically included systematic measurements of litter, woody debris, slash, and mineral soil, land-based analyses rely on models to estimate changes in nonliving forest carbon. The idea is to model the historical production of dead organic matter caused by harvesting, land use change, fire, other natural mortality, and tissue death and to predict its decomposition with an ecosystem model. Although published estimates of changes in dead organic matter in forests cover a very wide range (values of −0.01, 0.01, and 0.18 Pg C year^{-1}), we think that the first two of these values are underestimates, whereas the third is an overestimate (*16*). We thus supplemented published estimates using two recent models, an updated version of the USFS

Table 1. Sinks of carbon for 1980–90 in the coterminous United States (Pg C year^{-1}).

Category	Low	High	Land area 1980–90 (10^6 ha)	Houghton *et al.* (*8*)	Birdsey and Heath (*12*)
Forest trees	0.11	0.15	247–247	0.06*	0.11
Other forest organic matter	0.03	0.15	247–247	−0.01	0.18
Cropland soils	0.00	0.04	185–183	0.14	–
Nonforest, noncropland (woody encroachment)	0.12†	0.13†	334–336‡	0.12	–
Wood products	0.03	0.07	–	0.03	0.03
Reservoirs, alluvium, colluvium	0.01	0.04	–	–	–
Exports minus imports of food, wood	0.04	0.09	–	–	–
Fixed in United States but exported by rivers	0.03	0.04	–	–	–
Apparent§ U.S. sink without woody encroachment	0.25	0.58	766	0.15–0.23‖	0.31
Apparent§ U.S. sink including woody encroachment	0.37	0.71	766	0.15–0.35‖	–
Sink¶	0.30	0.58	766	0.15–0.35‖	0.31

*Assumes that the 0.05 Pg C year^{-1} estimated in (*8*) to be accumulating in western pine woodlands as a result of fire suppression is assigned to forest instead of row 4. †These numbers are not bounds, but rather the only two existing estimates. ‡ Total area for all lands other than forest and croplands. Possible woody encroachment because of fire suppression on up to about two-thirds of this land (*10*, *16*). §By "apparent" sink, we mean the net flux from the atmosphere to the land that would be estimated in an inversion. It includes all terms in the table. ‖Lower bound reflects uncertainty in the estimates for the effects of fire suppression. ¶Excludes sinks caused by the export/import imbalance for food and wood products and river exports because these create corresponding sources outside the United States.

FORCARB model (*17*, *18*) and the Ecosystem Demography (ED) model (*16*, *19*). The FORCARB model uses the USFS forest inventory data to drive the historical inputs of dead organic matter, but the model does not explicitly account for the effects of the large reduction in fire frequencies before the USFS inventories were initiated (*17*). ED is a mechanistic ecosystem model with a simple model of fire that reproduces approximately the historical sequence of fire frequencies (*16*, *19*). We forced ED with a reconstruction of land use for the coterminous United States from 1700 to the present (*16*). The two models provided consistent upper bounds for the accumulation of nonliving forest carbon (*16*). The lower bound in the Table 1 combines convergent estimates for the accumulation of slash and woody debris (*11*, *16*, *17*, *20*) with minimum estimates for the accumulation of soil carbon (*16*).

3) Three recent trends may have led to increases in carbon storage on U.S. agricultural soils: the Conservation Reserve Program (i.e., conversion of unproductive croplands to perennial grassland), expanded use of no-till agriculture, and improved productivity caused by new plant varieties and increased fertilizer inputs (*8*). The upper bound in Table 1 was obtained by spatially extrapolating the results from a modeling study of increased crop productivity and field studies of no-till agriculture and the Conservation Reserve Program (*16*). We view the much larger value reported in (*8*) as an overestimate (*16*). The lower bound in Table 1 was obtained from recent studies with the CENTURY model in which warm temperatures and droughts during the 1980s offset the comparatively small increases in carbon storage caused by no-till agriculture and the Conservation Reserve Program (*14*).

4) Before the middle of the 19th century, about 80 million ha of land burned annually, mostly in unforested parts of the western United States (*10*). The area burned has now been reduced by more than 95%, and woody plants that were historically excluded by recurrent fire are now encroaching over large areas. Field studies report accumulations of more than 1 Mg of C ha^{-1} $year^{-1}$ in nonforested biomes that are usually used for grazing, such as juniper woodland, mesquite savanna, and oak savanna (*16*). Because the extent of this woody encroachment is not known, we cannot estimate reliable upper and lower bounds. The values in Table 1 represent the only two large-scale estimates that we know of for the coterminous United States. The value of 0.12 Pg C $year^{-1}$ was obtained by multiplying observed rates of carbon uptake caused by woody encroachment by an estimate of the land area experiencing encroachment (*8*), whereas the value of 0.13 Pg C $year^{-1}$ was predicted by the ED model (*16*). Of the eight separate items in the budget in Table 1, there is a substantial likelihood that the correct value lies outside of the reported range only in the case of woody encroachment.

5) Wood products create a carbon sink because they accumulate both in use and in landfills. Although the flow of carbon into this pair of pools is relatively easy to estimate from wood production data, the outflow is more uncertain. Previous estimates of the wood products sink include two for the 1980s of 0.03 Pg C $year^{-1}$ from entirely different models [(*8*) and (*12*)], one of 0.05 Pg C $year^{-1}$ (*21*), and one of 0.07 Pg C $year^{-1}$ (*22*). Our lower bound in Table 1 is from (*8*) and (*12*), and the upper bound is from (*22*).

6) We estimate that 0.01 to 0.04 Pg C $year^{-1}$ is buried in U.S. reservoirs, alluvium, and colluvium. We derive this estimate using a subset of the reservoir sedimentation data in (*23*), extrapolated to a nationwide inventory of about 68,000 dams (*24*) and combined with a range of estimates for net carbon burial in alluvium and colluvium. At the upper end of this range, carbon accumulation in alluvium and colluvium is about equal to accumulation in reservoir sediments. At the lower end, the accumulation in reservoir sediments is partially offset by a net release of carbon

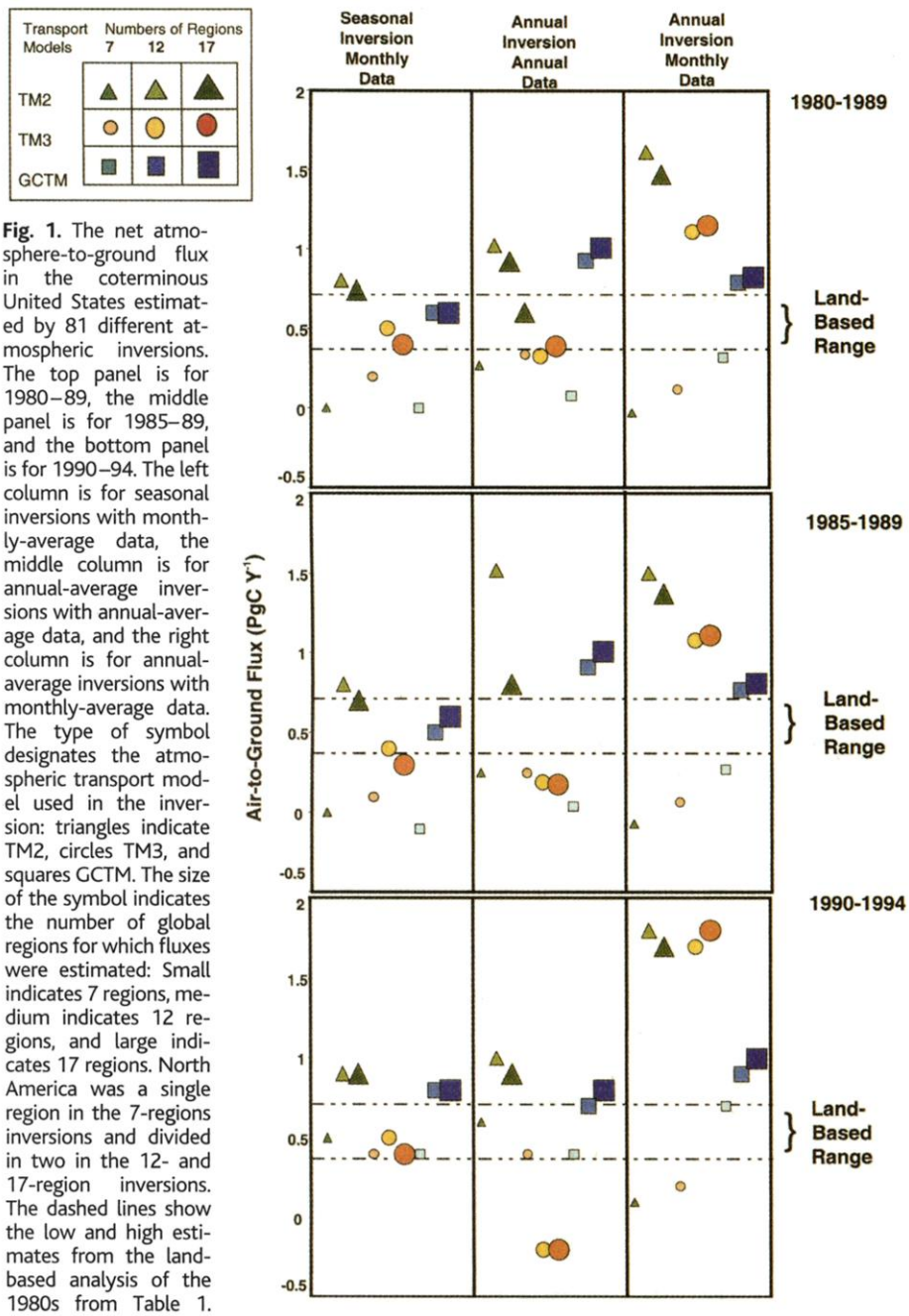

Fig. 1. The net atmosphere-to-ground flux in the coterminous United States estimated by 81 different atmospheric inversions. The top panel is for 1980–89, the middle panel is for 1985–89, and the bottom panel is for 1990–94. The left column is for seasonal inversions with monthly-average data, the middle column is for annual-average inversions with annual-average data, and the right column is for annual-average inversions with monthly-average data. The type of symbol designates the atmospheric transport model used in the inversion: triangles indicate TM2, circles TM3, and squares GCTM. The size of the symbol indicates the number of global regions for which fluxes were estimated: Small indicates 7 regions, medium indicates 12 regions, and large indicates 17 regions. North America was a single region in the 7-regions inversions and divided in two in the 12- and 17-region inversions. The dashed lines show the low and high estimates from the land-based analysis of the 1980s from Table 1. See supplementary material (*16*) for a complete description of the inversion methods.

from oxidation and erosion of previously deposited alluvium and colluvium.

7) The United States exports more carbon in agricultural and wood products than it imports. Agricultural products and especially grains, oilseeds, and oilseed cakes dominate this imbalance. Trade statistics from the Food and Agriculture Organization and the U.S. Department of Agriculture (USDA) (*16*) indicate that carbon exports exceeded imports by 0.03 to 0.05 Pg C year^{-1}. Together with the wood products imbalance of 0.004 to 0.005 Pg C year^{-1}, this provides the lower bound of 0.04 Pg C year^{-1} in Table 1. An independent analysis (*25*) of the USDA data places the agricultural trade imbalance for North America at up to 0.1 Pg C year^{-1} and leads to our upper bound of 0.09 Pg C year^{-1}.

8) The export of carbon by rivers to the sea is another small but important cause of the net atmosphere-to-land carbon flux. From published data, combined with an analysis of recent data from the U.S. Geological Survey (*16*), we estimate the export of dissolved organic carbon and particulate organic carbon each to be somewhat less than 0.01 Pg C year^{-1} and the export of dissolved inorganic carbon to be about 0.03 to 0.04 Pg C year^{-1}. Assuming that about one-half of the dissolved inorganic carbon flux is derived from carbonate minerals rather than from atmospheric CO_2, we estimate the atmosphere-to-ground flux of CO_2 due to river export to be 0.03 to 0.04 Pg C year^{-1}.

The 81 atmospheric inversions were arranged in a 3 × 3 × 3 × 3 design of three time periods, three atmospheric transport models, three spatial resolutions, and three temporal resolutions. See Peylin *et al.* (*15*) and (*16*) for a complete description of the methods. In all cases, the CO_2 concentration data came from a global network of flask sampling stations (*16*, *26*). The three atmospheric models were GCTM, which uses model-derived climatological winds (*27*), and TM2 and TM3, which are forced with winds calculated from meteorological data (*28*). The three spatial resolutions were 7, 12, or 17 global regions, with separate surface flux estimate(s) for each region. North America was a single region in the 7-region inversions and divided into two parts in the 12- and 17-region inversions [see the map in the supplemental material (*16*)]. Within a terrestrial region, the spatiotemporal pattern of the estimated flux was given by the CASA biosphere model in the GCTM inversions (*13*) and by the SiB2 model in the TM2 and TM3 inversions (*16*). This allows us to calculate the fraction of the estimated sink occurring within the coterminous United States. The three temporal resolutions were (i) annual-average inversion with annual-average data, (ii) annual-average inversion with monthly-average data, and (iii) seasonal inversion with monthly-average data. In the first, we averaged over the seasonal cycle in the data and estimated only a single average CO_2 flux per region. In the second, we retained the seasonal cycle in the data but still estimated only the average flux for each region. In the third, we both retained the seasonal cycle in the data and estimated the seasonal cycle of the fluxes in each region [additional details in (*16*)].

Collectively, the land- and atmosphere-based estimates in Table 1 and Fig. 1 indicate a large carbon sink in the coterminous United States. The sink, which stores between one-third and two-thirds of a billion tons of carbon annually, is about evenly divided between the forest and nonforest sectors. Additional data are essential to refine the estimates, especially for nonforested regions experiencing woody encroachment and for soils in all ecosystems.

Comparing estimates for the same land area and set of biogeochemical fluxes eliminates much of the discrepancy between land-based and atmospheric estimates. Inversion and land-based estimates are consistent because the former contain the latter's range (Fig. 1). However, this conclusion is weakened by the large variation among inversions, especially when one considers that each atmospheric estimate is itself highly uncertain, with a standard deviation averaging 0.25 Pg C year^{-1} (*15*). As indicated previously (*29*), the longitudinal resolution of the inverse modeling methods in this study must be improved to provide practically useful estimates of carbon sources and sinks for individual countries or continents. Nonetheless, some inverse modeling methods appear to be more consistent with the land-based estimates than others. First, annual-average inversions with monthly-average data yield much more variable estimates for the United States than the other methods (Fig. 1) (*15*). Annual-average inversions with annual-average data are intermediate, and seasonal inversions with monthly-average data appear to be the least variable (Fig. 1) (*15*). Second, in 1980–89 and 1985–89, the 7-region seasonal inversions (left column in Fig. 1, two upper panels) produce fluxes consistently beneath the land-based range, whereas the 12- and 17-region inversions are in better agreement with it. In the remaining cases, the 7-region inversions also tend to be lower than the others. The reason for this pattern appears to be that boreal North America is estimated as a strong source in the 12- and 17-region inversions in 1980–89 and 1985–89 (*15*, *16*). The counteracting sink in temperate North America and source in boreal North America produce a lower average flux when they are estimated together, as in our 7-region inversions with a single North American region. The seasonal inversions with 12 or 17 regions appear to be consistent with the land-based range over all time periods. As discussed by Peylin *et al.* (*15*), it is possible that the seasonal cycle or the relatively short correlation lengths associated with estimation of monthly fluxes provide the signal necessary for robust estimation of terrestrial fluxes.

Comparison of the results for different time periods reveals a remarkably steady net atmosphere-to-ground flux in the coterminous United States from 1980–94 (Fig. 1) [Web tables 3, 4, and 5 in (*16*)]. Although this is in part the result of taking 5- or 10-year averages over the interannual fluctuations (*3*), the relative constancy of the U.S. sink is surprising because the early 1990s were, relative to the 1980s, a period of reduced growth in atmospheric CO_2 and large global terrestrial carbon sink (*2*, *3*). Our inversion estimates imply that terrestrial regions outside the United States, particularly in the tropics, were responsible for the large observed fluctuations in the global sink (*15*, *16*).

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30. This research grew out of a workshop in March 1999 at Princeton University supported by the National Oceanic and Atmospheric Administration Office of Global Programs. Additional support came from the NSF-supported National Center for Ecological Analysis and Synthesis in Santa Barbara, through its support of a working group on the carbon budget of Eurasia and North America.

9 November 2000; accepted 29 May 2001

Changes in Forest Biomass Carbon Storage in China Between 1949 and 1998

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The location and mechanisms responsible for the carbon sink in northern mid-latitude lands are uncertain. Here, we used an improved estimation method of forest biomass and a 50-year national forest resource inventory in China to estimate changes in the storage of living biomass between 1949 and 1998. Our results suggest that Chinese forests released about 0.68 petagram of carbon between 1949 and 1980, for an annual emission rate of 0.022 petagram of carbon. Carbon storage increased significantly after the late 1970s from 4.38 to 4.75 petagram of carbon by 1998, for a mean accumulation rate of 0.021 petagram of carbon per year, mainly due to forest expansion and regrowth. Since the mid-1970s, planted forests (afforestation and reforestation) have sequestered 0.45 petagram of carbon, and their average carbon density increased from 15.3 to 31.1 megagrams per hectare, while natural forests have lost an additional 0.14 petagram of carbon, suggesting that carbon sequestration through forest management practices addressed in the Kyoto Protocol could help offset industrial carbon dioxide emissions.

Recent studies have shown that the mid- and high-latitude forests in the Northern Hemisphere are functioning as a significant sink for C (*1–4*). These findings have been confirmed by several studies, mainly from North America and European countries using forest inventories (*5–8*). A long history of agricultural exploitation, forest management practice, and changing land use and forestry policies suggest that China, too, plays an important role in the global C cycle (*9, 10*). China has 133.7 million hectares of forested land (*11*) that range from tropical forests in the south to boreal forests in the north. Nationwide afforestation and reforestation programs have been in effect since the 1970s. To reduce the uncertainty in estimating C sinks, well-designed and statistically sound national forest inventories over the long term, combined with direct field measurements of C stocks from local sample plots, may provide the best data sources for accurately quantifying C sinks and their dynamics at large scales.

Here, we used the National Forest Resource Inventory database for China collected from 1949 to 1998 for 5- to 10-year periods (*11, 12*) and a forest biomass database obtained from direct field measurements (*13, 14*) to estimate forest biomass C storage and its spatiotemporal distributions. The forest inventory database is based on the Forest Resource Inventory of China (FRIC), which spans seven periods: 1949, 1950–62, 1973–76, 1977–81, 1984–88, 1989–93, and 1994–98 (*11, 12, 15*). These inventories, excluding FRIC from 1949 which was derived from an assessment report (*11, 16*), were compiled from more than 250,000 plots (160,000 permanent sample plots plus 90,000 temporary sample plots) across the country. Systematic sampling with a grid of 2 km by 2 km or 4 km by 4 km and an area of 10 m by 10 m was used depending on forest region. Forest area and timber volume by age class as well as by forest type were documented at provincial levels. Unfortunately, these forest inventories do not provide detailed information about forest biomass; only the commercial portion (such as timber volume) is available. To use timber data to estimate all forest biomass, a biomass expansion factor (BEF, defined as the ratio of all stand biomass to growing stock volume), which converts timber volume to mass and accounts for noncommercial components, such as branches, roots, and leaves, must be calculated. The forest biomass database obtained from direct field measurements (*17*) was used to determine BEF values for each forest type using a literature review of forest biomass studies in China (*14*).

Recent studies (*8, 13, 18, 19*) suggest that BEF is not constant, but varies with forest age, site class, stand density, and other biotic and abiotic factors that are closely associated with relative stand density, and can be expressed as a function of timber volume. Here, we used a function expressed as $BEF = a + b/x$, to obtain a variable BEF value for each forest type, where x is timber volume and a and b are constants for a forest type (*13*) (Table 1). Using the method published by Fang *et al.* (*13*), forest inventory data, and parameters listed in Table 1, forest biomass (including all living trees and shrubs) for each forest type was calculated at both provincial and national levels for all seven periods (*20*).

Total forest biomass C (Table 2) decreased from 5.06 Pg of C (Pg C) in 1949 to 4.38 Pg C in 1977–81, and then increased by 4.75 Pg C over the period 1980–98, mainly due to changes in land use, population growth, and economic policy changes. Since the new social system was established in 1949, rapidly increasing population and economic development have resulted in increased forest exploitation across the country (*11*). By 1949, Chinese forests accumulated the largest C storage (5.06 Pg C) and area-weighted mean C density (49.45 Mg ha^{-1}), due to a larger area of primary forests that have high biomass density. Since then, forest C storage has significantly decreased by 0.68 Pg C, with a mean rate of 0.022 Pg C $year^{-1}$ (ranging from 0.01 to 0.04 Pg C $year^{-1}$) from 1949 to the end of the 1970s. For this period, the policy of forest exploitation led to soil erosion, widespread desertification, loss of biodiversity, land degradation, and catastrophic flooding (*21*). Since the 1970s, however, the Chinese government has implemented several ecological restoration projects, including the Three-North Protective Forest Program, South China Timber Production Program, Rivers Pro-

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