Einstein condensate gave rise to superradiance based on coherent external motion. The extremely low threshold in light intensity (~ 1 mW/cm^2 for our conditions) should be taken into account in BEC experiments that use optical probing and manipulation with off-resonant light. The simultaneous superradiant emission of light and atoms emphasizes the symmetry between atom lasers and optical lasers.

References and Notes

1. M. H. Anderson, J. R. Ensher, M. R. Matthews, C. E. Wieman, E. A. Cornell, *Science* **269**, 198 (1995); K. B. Davis *et al.*, *Phys. Rev. Lett.* **75**, 3969 (1995); C. C. Bradley, C. A. Sackett, R. G. Hulet, *ibid.* **78**, 985 (1997); D. G. Fried *et al.*, *ibid.* **81**, 3811 (1998).
2. M. R. Andrews *et al.*, *Science* **275**, 637 (1997); D. S. Hall, M. R. Matthews, C. E. Wieman, E. A. Cornell, *Phys. Rev. Lett.* **81**, 1543 (1998); B. P. Anderson and M. A. Kasevich, *Science* **282**, 1686 (1998).
3. J. Stenger *et al.*, *Phys. Rev. Lett.* **82**, 4569 (1999).
4. M. G. Moore and P. Meystre, *Phys. Rev. A* **59**, R1754 (1999).
5. N. E. Rehler and J. H. Eberly, *ibid.* **3**, 1735 (1971).
6. R. H. Dicke, in *Proceedings of the Third International Congress on Quantum Electronics*, P. Grivet and N. Bloembergen, Eds. (Columbia Univ. Press, New York, 1964), pp. 35–54.
7. M.-O. Mewes *et al.*, *Phys. Rev. Lett.* **77**, 416 (1996).
8. One can emphasize the symmetry of the atomic and optical fields by describing the process in the moving frame of the excited atoms that have absorbed one laser photon. Because the total momentum is zero in this frame, photons and atoms are emitted into opposite directions, preferentially along the long axis of the elongated cloud. Transforming back into the laboratory frame results in preferential emission of light still along the long axis but of atoms at 45°.
9. H.-J. Miesner *et al.*, *Science*, **279**, 1005 (1998).
10. The probability for reabsorption of scattered light was less than 3% and could be neglected. Optical amplification is accounted for by treating all the atoms as a single quantum mechanical system.
11. N. Skribanowitz, I. P. Herman, J. C. MacGillivray, M. S. Feld, *Phys. Rev. Lett.* **30**, 309 (1973); R. Bonifacio and L. A. Lugiato, *Phys. Rev. A* **11**, 1507 (1975); Q. H. F. Vrehen and H. M. Gibbs, in *Topics in Current Physics 27*, R. Bonifacio, Ed. (Springer-Verlag, Berlin, 1982), pp. 111–147; M. Gross and S. Haroche, *Phys. Rep.* **93**, 301 (1982).
12. R. H. Dicke, *Phys. Rev.* **93**, 99 (1954).
13. In (*3*), the recoiling atoms propagated perpendicular to the long axis of the condensate. The "finite size" contribution to the Doppler broadening was therefore twice that of the present geometry.
14. Elastic collisions at a maximum rate of ~2 kHz do not contribute substantially to L_j, although they reduce the number of atoms in the superradiant peak by ~50%.
15. Stimulated Raman scattering and four-wave mixing between matter waves [see L. Deng *et al.*, *Nature* **398**, 218 (1999)] may couple the different recoil modes and further affect the momentum distribution.
16. C. K. Law and N. P. Bigelow, *Phys. Rev. A* **58**, 4791 (1998).
17. This is called the coherent atomic recoil laser. See R. Bonifacio and L. De Salvo, *Nucl. Instrum. Methods Phys. Res. A* **341**, 360 (1994); M. G. Moore and P. Meystre, *Phys. Rev. A* **58**, 3248 (1998); P. R. Berman, *ibid.* **59**, 585 (1999); M. G. Moore, O. Zobay, P. Meystre, http://xxx.lanl.gov/abs/cond-mat/9902293.
18. M. Olshanii, Y. Castin, J. Dalibard, in *Proceedings of the XII Conference on Laser Spectroscopy*, M. Inguscio, M. Allegrini, A. Sasso, Eds. (World Scientific, New York, 1995), pp. 7–12; H. M. Wiseman and M. J. Collett, *Phys. Lett. A* **202**, 246 (1995); U. Janicke and M. Wilkens, in *Topics on Ultracold Atoms and BEC 7*, K. Burnett, Ed. (Optical Society of America, Washington, DC, 1997), pp. 38–47.
19. We thank C. E. Kuklewicz for experimental assistance, D. A. Kokorowski for critical reading of the manuscript, and H. M. Gibbs, P. Meystre, J. H. Eberly, E. M. Wright, and M. S. Feld for helpful discussions. This work was supported by the Office of Naval Research, NSF, Joint Services Electronics Program (Army Research Office), NASA, and the David and Lucile Packard Foundation. A.P.C acknowledges support from NSF, D.M.S.-K. from the Joint Services Electronics Program Graduate Fellowship Program, and J.S. from the Alexander von Humboldt–Foundation.

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The U.S. Carbon Budget: Contributions from Land-Use Change

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The rates at which lands in the United States were cleared for agriculture, abandoned, harvested for wood, and burned were reconstructed from historical data for the period 1700–1990 and used in a terrestrial carbon model to calculate annual changes in the amount of carbon stored in terrestrial ecosystems, including wood products. Changes in land use released 27 ± 6 petagrams of carbon to the atmosphere before 1945 and accumulated 2 ± 2 petagrams of carbon after 1945, largely as a result of fire suppression and forest growth on abandoned farmlands. During the 1980s, the net flux of carbon attributable to land management offset 10 to 30 percent of U.S. fossil fuel emissions.

The rate at which carbon is accumulating in terrestrial ecosystems in the United States is uncertain, as are the mechanisms responsible for the current sink. Estimates based on measured changes in wood volumes (forest inventories) (*1–3*) range between 0.079 and 0.280 petagrams of carbon per year (Pg C year^{-1}). An estimate, based on atmospheric and oceanic data and models, and including southern Canada, calculated a sink of 1.7 ± 0.5 Pg C year^{-1} (*4*). Neither of these approaches identifies the mechanisms responsible for the sink (*5*). In contrast, although the changes in carbon associated with land-use change do not define the total net flux of carbon between land and atmosphere, they represent the portion of the flux that can be attributed to direct human activity, and it is this portion that is addressed by the United Nations Framework Convention on Climate Change and by the Kyoto Protocol. In this report, we estimate the annual flux of carbon in the United States attributable to changes in land use.

Our approach is based on two types of information: rates of land-use change and changes per hectare in carbon that follow a change in land use. We considered the conversion of natural ecosystems to croplands (cultivated) and pastures (not cultivated), the abandonment of croplands and pastures, harvest of industrial wood and fuel wood, and fire management, that is, the area annually burned by wildfires. Rates of agricultural clearing and abandonment and rates of wood harvest were obtained directly from the U.S. Department of Agriculture (USDA) for the period since 1945 (*6*) and largely from the U.S. Bureau of Census (*7*) for the period between 1700 and 1945. Areas burned each year were obtained from wildfire statistics of the U.S. Forest Service (*8*) for the period after 1930 and from pre-European burning rates (*9*) modified by settlement and logging practices for the years 1700–1930 (*10*). A more detailed description of the data, sources, and assumptions can be found elsewhere (*11*, *12*).

We divided the United States into seven geographic regions (each region including two to five natural ecosystems) for a total of 13 different ecosystems, not including croplands and pastures. The areas and carbon stocks of ecosystems in 1700 were determined from both natural areas (*13*) and current ecosystems (*14*). The fractions of vegetation left alive, killed, and burned as a result of human activity and fire were defined for each type of land use and ecosystem. The efficiency of industrial wood harvest increased through time, so that more wood was removed per hectare and less left as slash (dead vegetation) (*15*, *16*). Rates of forest growth after harvest, fire, and agricultural abandonment and rates of decay of organic matter for each ecosystem were obtained from the ecological literature (*17*). Changes in soil carbon included only the losses that resulted from cultivation and the reaccumulations that followed abandonment of cultivated land. These per hectare rates of carbon loss and accumulation after changes in land

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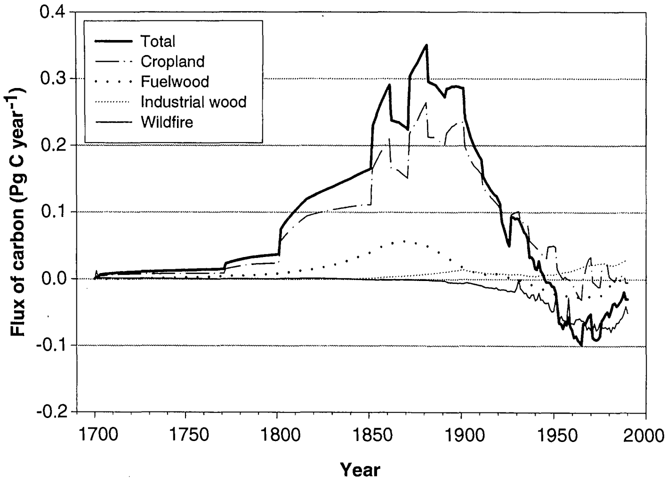

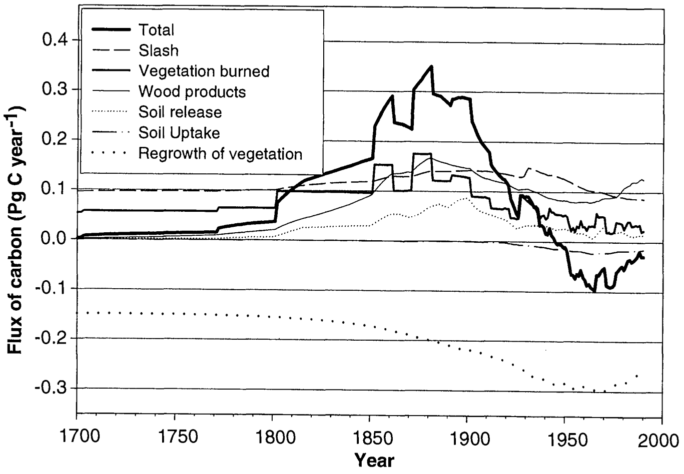

Fig. 1 (Left). Annual net sources and sinks of carbon resulting from different types of land use in the United States. **Fig. 2 (Right).** Annual losses and accumulations of carbon in different terrestrial pools as a result of land management in the United States.

use were used in a bookkeeping model (*18*) to calculate annual changes in carbon for each type of ecosystem, land use, and region. The areas of forest burned each year, together with the total area of forest in each region and the rate of forest growth, constrained the average biomass that could be burned per hectare in a region's forests (*19*).

According to our analysis, changes in land use released about 25 Pg C to the atmosphere over the period 1700–1990, largely from the conversion of forests to agricultural lands and from cultivation of prairie soils (Fig. 1). The net release, overall, included a net uptake of 2.4 Pg C after 1945 as both the area and biomass of forests increased in response to fire suppression, reduced harvest of fuel wood, and the abandonment of farms. It also included an uptake in eastern forests, largely offset by releases of carbon from western regions where rates of industrial wood harvest increased.

The net flux resulted from accumulations of carbon in regrowing vegetation and, to a lesser extent, soils and from releases of carbon from burning and decay (Fig. 2). Before European settlement, fires accounted for the largest sources (immediate burning and delayed decay) and sinks of carbon, although the net flux from fire was nearly zero as long as rates of burning were about constant. As wood harvest and agricultural clearing increased in the 18th century, emissions from fire, soil, and wood products increased, but annual accumulations also increased as the areas of forests recovering from fire and harvesting increased. Replacement of wood fuels with fossil fuels midway through the 19th century began to reduce the emissions from fuel wood harvesting, and fire suppression after 1930 further reduced the areas burned. Despite the recovery of forests in the east, increasing rates of industrial wood harvests in the west and south increased the generation of slash and wood products and hence emissions of carbon. The largest annual accumulations of carbon occurred in the 1950s and 1960s. By the 1970s, as a result of aging (slower growing) forests and a resurgence of fuel wood use, the net flux from land-use change was close to zero.

The errors resulting from uncertainties in rates of land-use change, from aggregated estimates of biomass, growth, and decay, and from simplifying assumptions in the structure of the model may be estimated by comparing the results of successive analyses (Fig. 3). For the three analyses in which changes in land use are reasonably well documented, estimates of the long-term (1700–1990) carbon flux range between 24 and 30 Pg C. For shorter intervals, the errors are larger. The difference between our estimate that includes fire and an earlier estimate for North America that did not include fire (*18*) is as large as 0.2 Pg C year^{-1} before 1900. A comparison of our estimates with and without fire shows that including fire and fire suppression changed estimates of flux by as much as 0.05 Pg C year^{-1}. Surprisingly, fire reduced the estimated emissions during the 1800s. The reduction occurred because the biomass of forests cleared for agriculture was less if fire was included in the analysis. The errors are estimated to be less than ±0.1 Pg C year^{-1} in recent decades (*20*). The analysis that shows a large sink for carbon beginning in 1920 is based on generous assumptions about woody encroachment (*21*) and early fire exclusion (*22*). Although detailed site-specific data document these processes, the aerial extent and the historical pattern of the changes are unknown. The curve represents an upper limit for the sink strength of U.S. ecosystems.

Most other estimates of flux available for comparison pertain to the 1980s and 1990s. Our analysis for the 1980s shows an average annual accumulation of 0.037 Pg C (Fig. 4). This net uptake results from the uptake of carbon by growing vegetation (0.280 Pg C year^{-1}) and emissions from the decay of wood products (0.104 Pg C year^{-1}) and slash (0.091 Pg C year^{-1}), some of which had accumulated before 1980. The uptake of 0.280 Pg C year^{-1} occurred on 200 × 10^6 ha of recovering forest and woodlands (about 65% of the U.S. forest areas). The average rate of growth (1.4 Mg C ha^{-1} year^{-1}) was low, indicating that many of the forests and woodlands were aging and their rates of growth were declining. For comparison, net annual uptake in a 55- to 75-year-old New

Table 1. Average annual changes in the amount of carbon held in forests and wood products during the 1980s (petagrams of carbon per year). Positive values indicate an accumulation on land.

	Method		
	Forest inventory (*2*)	Forest inventory (*3*)	Land-use change (this study)
Trees and understory vegetation	0.098	0.063	0.020
Wood products (*37*)	−0.072	0.027	0.027
Woody debris and forest floor	0.021	0.016	−0.012
Soils (*38*)	0.155	0	0.002
Net accumulation	0.202	0.106	0.037

England forest varied between 1.4 and 2.8 Mg C ha^{-1} year^{-1} (*23*).

The rate of carbon accumulation attributed to land-use change in our study is somewhat less than that determined from direct measurement of wood volumes in forests (forest inventories) (*24*) (Table 1). Despite the relatively high variability of estimated changes for soil carbon and wood products, the absolute differences between analyses based on forest inventories are <0.2 Pg C year^{-1}, about the error estimated for our analysis.

The approaches based on land-use change and on forest inventories are largely independent, and differences in their results may suggest the importance of management in determining the accumulation of carbon in forests (*25*). Carbon accumulations in our analysis are calculated by applying growth rates to forest areas previously harvested. Carbon accumulations obtained from forest inventories, on the other hand, are based on measured rates of growth, which include both recovery from earlier harvests and other factors. If CO$_2$ fertilization, climatic change, or N deposition were responsible for an enhanced rate of growth, for example, one would expect analyses based on forest inventories to show higher rates of growth (and a greater rate of carbon accumulation) than the analysis based on land-use change (in which rates of growth were held constant over time) (*26*). This difference in accumulation rates is observed. The growth attributable to recovery from previous harvests accounts for only 20 to 30% of the growth measured (Table 1). The other 70 to 80% may be attributable to other factors. Remarkably, the uptake of carbon calculated recently with a process model including variations in temperature, precipitation, and increased CO$_2$ accounts for the rest of the difference (0.078 Pg C year^{-1}) (*27*). The agreement is fortuitous given the errors associated with the estimates, but it suggests that both changes in land use and the responses of ecosystems to environmental changes are important in explaining the uptake of carbon observed in U.S. forests during the 1980s.

Table 2. Average annual emissions (+) and accumulations (−) of carbon (petagrams of carbon per year) during the 1980s from forestry and changes in land use. Changes in soil carbon are included in cultivation and abandonment of croplands. Wood products are included in the emissions from harvests.

	Emissions from burning and decay	Accumulations in recovering ecosystems	Net flux
Croplands	0.092	−0.090	0.002
Pastures	0.025	−0.025	0
Wildfires	0.081	−0.144	−0.063
Industrial harvests	0.094	−0.067	0.027
Fuel wood harvests	0.022	−0.025	−0.003
Subtotal	0.314	−0.348	−0.037
Woody encroachment			−0.122
Continued "thickening" of western pine woodlands from early fire suppression			−0.052
Recent gains in soil carbon from changing agricultural practices			−0.138
Total			−0.350

The estimates of uptake of carbon from direct measurements of forest growth and from changes in land use are both considerably lower than the annual sink of 1.7 ± 0.5 Pg C year^{-1} inferred from atmospheric data and models (*4*). That estimate includes Canadian lands south of 51°N, so the sink for the United States alone is presumably less. Some of the difference may also be explained by the time periods included in the analyses. Our estimate and those based on forest inventories were for the 1980s. The analysis based on atmospheric data and models was based on a shorter interval, 1988–1992, that included the eruption of Mt. Pinatubo and anomalously low growth rates of atmospheric CO$_2$. Thus, the large sink may have been transient. Other estimates of a terrestrial carbon sink in northern mid-latitudes, based on analyses of atmospheric gradients in CO$_2$, ^{13}CO$_2$, and O$_2$, vary between 2 and 3.5 Pg C year^{-1} (*28*) and suggest a U.S. sink of 0.3 to 0.5 Pg C year^{-1} if the sink is assumed to be distributed evenly over northern lands (*29*).

The accumulations of carbon estimated from forest inventories and land-use change may be low. The analyses do not consider all lands. Forest inventories, in addressing only forests, ignore 70% of the land surface, and natural ecosystems not directly harvested, cleared, or burned were ignored in our analysis. Could such ecosystems be accumulating substantial carbon? It seems unlikely. The total area of these unmanaged lands was only 220×10^6 ha (24% of the land area of the United States) in our analysis, too small to account for much of the difference between 0.2 Pg C year^{-1} (from land-use change or forest inventories) and ~1 Pg C year^{-1} [from (*4*)]. The sink would have to average 3.6 Mg C ha^{-1} year^{-1} or 85% of the average net

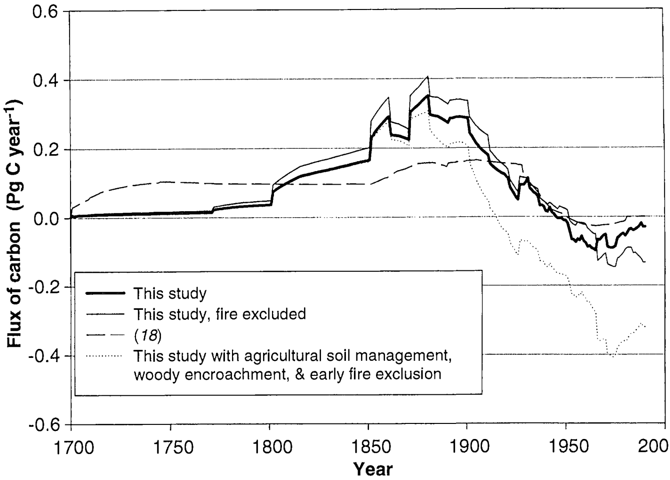

Fig. 3. Annual net flux of carbon in the United States as a result of changes in land use.

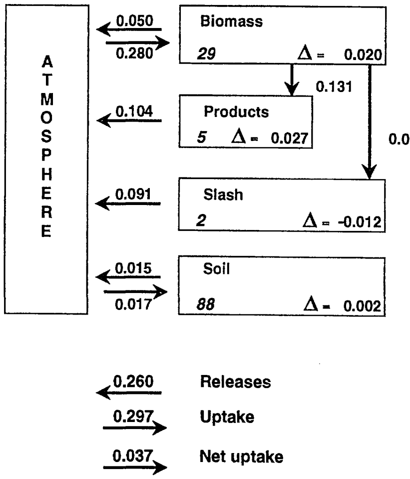

Fig. 4. The amount of carbon in terrestrial carbon pools of the United States in 1990 (petagrams of carbon), changes in these pools (petagrams of carbon per year), and exchanges between these pools and the atmosphere during the 1980s (petagrams of carbon per year).

primary production of terrestrial ecosystems in the contiguous United States (*27*). Furthermore, forest inventories include the accumulation of carbon in unmanaged as well as managed forests, thus reducing further the area not considered in either analysis.

Perhaps forest soils, which are not measured in forest inventories, are accumulating carbon. We have already noted the large uncertainty in estimates of change in soil carbon (Table 1). In our analysis, we included the accumulation of carbon in soils recovering from abandoned agriculture but not the possible loss (and subsequent recovery) of carbon in forest soils affected by logging. Although some studies have reported such a loss, the data are not consistent (*30*). Furthermore, a recent analysis of soils in a 55- to 75-year-old New England forest found that soils accounted for only 7 to 15% of the net sink measured for the stand (*31*). If the estimate is representative, the accumulation of carbon in forest soils is intermediate between those calculated from forest inventories (*2*, *3*) (Table 1).

The evidence is more compelling that carbon is accumulating in agricultural soils as a result of changes in management, but our bookkeeping model did not consider these changes. We calculated that the net loss of soil organic carbon from cultivation and abandonment accounted for about 23% of the long-term net flux attributable to land-use change. Each hectare cultivated lost about 25% of its initial carbon to a depth of 1 m, and during the 1980s, soils were a net sink of 0.002 Pg C year^{-1} as a result of agricultural abandonment (Fig. 4). However, increased crop productivity since 1960 and, more recently, conservation tillage and the Conservation Reserve Program are likely to have increased further the storage of carbon in agricultural soils. Using the estimates of Donigian *et al.* (*32*), we calculated an additional rate of accumulation of 0.107 Pg C year^{-1} for the 1980s. Adding conservation tillage (*33*) and the Conservation Reserve Program (*34*) increased the estimated sink in managed soils to 0.138 Pg C year^{-1} (Table 2).

We also estimated the amount of carbon that might have accumulated as a result of woody encroachment in nonforest ecosystems (*21*) and the "thickening" of western pine forests that began with fire suppression initiated before systematic collection of data on wildfires (*22*). All of these processes together (changes in agricultural soils, woody encroachment, and early fire suppression) give an upper estimate for carbon sequestration of 0.35 Pg C year^{-1} for the entire United States (Table 2). Two of the largest sinks (woody encroachment and early fire suppression) are also the most uncertain, whereas the sinks best documented (from changes in agricultural areas and wood harvests) are small. It is quite possible that the total terrestrial sink during the 1980s averaged only 0.15 Pg C year^{-1}, and thus it is difficult for us to imagine that an additional sink three to ten times larger (*4*) has been overlooked. A possible increase in the carbon buried in sediments as a result of human-induced erosion (*35*) might increase the terrestrial carbon sink further, but the magnitude of carbon burial through erosion is unknown. In contrast to these terrestrial carbon sinks attributable to management of the landscape, the annual release from fossil fuels in the United States averaged 1.230 Pg C year^{-1} during the 1980s and was 1.447 Pg C in 1996 (*36*). Management of terrestrial ecosystems appears to have offset only 10 to 30% of the carbon released from fossil fuels.

Notes and References

1. R. A. Birdsey, A. J. Plantinga, L. S. Heath, *For. Ecol. Manage.* **58**, 33 (1993).
2. R. A. Birdsey and L. S. Heath, in *Productivity of America's Forest and Climatic Change, General Technical Report RM-GTR-271*, L. A. Joyce, Eds. (U.S. Department of Agriculture, Forest Service, Rocky Mountain Forest and Range Experiment Station, Fort Collins, CO, 1995), pp. 56–70.
3. D. P. Turner, G. J. Koerper, M. E. Harmon, J. J. Lee, *Ecol. Appl.* **5**, 421 (1995).
4. S. Fan *et al.*, *Science* **282**, 442 (1998).
5. The exception to this statement is the ability of forest inventory data to identify the importance of past disturbances to current rates of growth [W. A. Kurz and M. J. Apps, *Ecol. Appl.* **9**, 526 (1999)].
6. *Major Land Uses 1945–1992, Stock #89003* (USDA, Economic Research Service, Washington, DC, 1996).
7. *Historical Statistics of the United States from Colonial Times to 1970* (U.S. Bureau of the Census, Washington, DC, 1977).
8. *Forest Service Cooperative Fire Protection Program Wildfire Statistics 1926–1990* (USDA, U.S. Government Printing Office, Washington, DC, 1926–1990).
9. H. A. Mooney *et al.*, Eds., *Proceedings of the Conference: Fire Regimes and Ecosystem Properties, USDA Forest Service General Technical Report WO-26* (USDA, U.S. Forest Service, Washington, DC, 1981).
10. S. J. Pyne, *Fire in America: A Cultural History of Wildland and Rural Fire* (Princeton University Press, Princeton, NJ, 1982; reprinted by the University of Washington Press, Seattle, WA, 1997); *Introduction to Wildland Fire: Fire Management in the United States* (Wiley, New York, 1984).
11. R. A. Houghton and J. L. Hackler, *Global Ecol. Biogeogr.*, in press.
12. ———, K. T. Lawrence, *ibid.*, in press.
13. Current (1990) areas, together with changes in land use between 1700 and 1990, determined the starting (1700) areas for each ecosystem [R. G. Bailey, *Description of the Ecoregions of the United States, Miscellaneous Publication Number 1391* (USDA, Forest Service, Washington, DC, ed. 2, 1995)].
14. R. A. Birdsey, *Carbon Storage and Accumulation in the United States Forest Ecosystems, Forest Service General Technical Report WO-59* (USDA, Washington, DC, 1992); S. Brown, P. Schroeder, R. Birdsey, *For. Ecol. Manage.* **96**, 37 (1997); P. Schroeder, S. Brown, J. Mo, R. Birdsey, C. Cieszewski, *For. Sci.* **43**, 424 (1997); IGBP 1-km land cover classification database (generated by the U.S. Geological Survey, the University of Nebraska–Lincoln, and the European Commission's Joint Research Centre), available at http://edcwww.cr.usgs.gov/landdaac/glcc/glcc.html.
15. M. E. Harmon, S. L. Garman, W. K. Ferrell, *Ecol. Appl.* **6**, 641 (1996); I. K. Wernick, P. E. Waggoner, J. H. Ausubel, *J. Ind. Ecol.* **1**, 125 (1998).
16. Harvested wood products decayed at rates of 1 year^{-1}, 0.1 year^{-1}, and 0.01 year^{-1}, corresponding to burned material (including fuel wood), paper, and lumber, respectively.
17. Slash generated during harvests decayed exponentially at rates that varied between 0.02 and 0.06 year^{-1}. Regrowth ranged between 0.3 and 3.0 Mg C ha^{-1} year^{-1} depending on the type of forest and its age [G. L. Ajtay, P. Ketner, P. Duvigneaud, in *The Global Carbon Cycle*, B. Bolin, E. T. Degens, S. Kempe, P. Ketner, Eds. (Wiley, New York, 1979), pp. 129–182; D. E. Reichle, Ed., *Dynamic Properties of Forest Ecosystems* (Cambridge Univ. Press, New York, 1981); J. S. Olson, J. A. Watts, L. J. Allison, *TR004* (U.S. Department of Energy, Washington, DC, 1983)].
18. R. A. Houghton and J. L. Hackler, *ORNL/CDIAC-79, NDP-050* (Oak Ridge National Laboratory, Oak Ridge, TN, 1995).
19. The areas of forest burned each year were too large to allow recovery of biomass if the fires were assumed to be stand-replacing (high mortality) fires. We used the combination of burned areas, total areas of forest, and regrowth rates to define a burning cycle in which the same (young) forests were burned repeatedly and older, high-biomass forests were burned only when rates of burning increased. The cycle is consistent with the observation that recently burned forests are more likely to burn than mature forests [G. G. Whitney, *From Coastal Wilderness to Fruited Plain. A History of Environmental Change in Temperate North America from 1500 to the Present* (Cambridge Univ. Press, Cambridge, 1994)] and with the fact that certain low-biomass ecosystems (savannas and woodlands) burn more frequently than dense forests (*9*, *10*). When rates of burning decreased through fire suppression, our analysis allowed young, repeatedly burned forests to escape from the burn cycle and accumulate carbon. Although the burning cycle underestimates gross emissions and accumulations of carbon (*12*), it captures the net flux of carbon associated with changes in burning, that is, the net releases of carbon from increased rates of burning and the net accumulations from decreased rates.
20. The annual flux of carbon calculated by the bookkeeping model is most sensitive to the rates of land-use conversion and to the biomass of ecosystems converted. The errors (and net fluxes) from wood harvest and fires are smaller than those associated with land conversion because the emissions from harvest and fires are offset by the accumulations of carbon in recovering forests. The bookkeeping analysis is least sensitive to rates of decay and growth. For example, if rates of regrowth are overestimated, the uptake per hectare will be too high, but fewer hectares will be regrowing (forests disturbed earlier will have regrown and will no longer be accumulating carbon). If rates of growth are underestimated, rates of accumulation per hectare will be too low, but more hectares will be recovering. On the other hand, if rates of regrowth per hectare have systematically increased over the 290-year period of analysis, as they might have through CO_2 fertilization, the errors in the estimated flux will be larger, especially toward the early years, because most data on rates of growth have been obtained in recent decades of research [see (*26*)].
21. Assuming that fire exclusion and grazing in western grasslands and savannas resulted in woody encroachment [R. T. Coupland, *J. Ecol.* **49**, 135 (1961); W. S. Phillips and H. L. Shantz, *Vegetational Changes in the Northern Great Plains, Agricultural Experiment Station Report 214* (College of Agriculture, University of Arizona, Tucson, AZ, 1963); J. W. Burkhardt and W. W. Tisdale, *Ecology* **57**, 472 (1976); S. H. Sharrow and H. A. Wright, *J. Range Manage.* **30**, 266 (1977); D. R. Streng and P. A. Harcombe, *Am. Midl. Nat.* **108**, 278 (1982); S. Archer, *Am. Nat.* **134**, 545 (1989); H. D. Grover and H. B. Musick, *Clim. Change* **17**, 305 (1990); J. N. Mast, T. T. Veblen, M. E. Hodgson, *For. Ecol. Manage.* **93**, 181 (1997); P. A Knapp and P. T. Soule, *Global Change Biol.* **4**, 347 (1998)] on 220 × 10^6 ha [the area neither forested nor cultivated (*12*)], we estimated that woody encroachment might have accumulated as much 0.122 Pg C year^{-1} in the 1980s. The rate is an upper limit. Loss of soil carbon in the replacement of grasslands with shrubs may offset completely the increased woody biomass in some ecosystems [W. H. Schlesinger and A. M. Pilmanis, *Biogeochemistry* **42**, 169 (1998)].
22. We assumed that the elimination of fire before 1926 [and thus not captured by (*8*)] in many pine ecosystems of the west [R. Guyette and E. A. McGinnes,

Trans. Mo. Acad. Sci. **16**, 85 (1982); G. E. Gruell, *Northwest Sci.* **59**, 97 (1985); E. M. Steinauer and T. B. Bragg, *Am. Midl. Nat.* **118**, 358 (1987); T. W. Swetnam, *Science* **262**, 885 (1993); W. W. Covington and M. M. Moore, *J. For.* **92**, 39 (1994); B. E. Cutter and R. P. Guyette, *Am. Midl. Nat.* **132**, 393 (1994); P. Z. Fule, W. W. Covington, M. M. Moore, *Ecol. Appl.* **7**, 895 (1997)] resulted in an increased density of trees throughout the entire range of ponderosa pine forests (22×10^6 ha) [*Forest Type Groups of the United States* (USDA, Forest Service, Washington, DC, 1993), available at http://www.srsfia.usfs.msstate.edu/rpa/rpa93.htm] and an accumulation of 0.052 Pg C year^{-1} over the past 90 years. These processes are well documented for individual sites, but their spatial extent is largely unknown. The calculated rates of carbon uptake are exaggerated and may be attributable more to changes in climate than to changes in management [T. W. Swetnam and J. L. Betancourt, *J. Clim.* **11**, 3128 (1998)].

23. M. L. Goulden, J. W. Munger, S. M. Fan, B. C. Daube, S. C. Wofsy, *Science* **271**, 1576 (1996).
24. *Forest Service Resource Inventories: An Overview* (USDA, Forest Service, Forest Inventory, Economics, and Recreation Research, Washington, DC, 1992).
25. It should be clear that we use the term "management" broadly. Much of the current sink attributed to management is a recovery from past use rather than a consequence of skillful environmental management.
26. Attributing growth to management, as opposed to environmental factors, is complicated because preindustrial rates of growth are not known. For our analysis, we obtained rates of growth from the literature (*17*), and, because most of the measurements were made after 1950, they may already include an enhanced rate of growth. If rates of growth have increased substantially over time, the emissions attributed to land-use change may have been underestimated in the early years of the analysis, whereas sinks may have been underestimated in recent decades.
27. H. Tian, J. M. Melillo, D. W. Kicklighter, A. D. McGuire, J. Helfrich, *Tellus*, in press.
28. P. Ciais *et al.*, *J. Geophys. Res.* **100**, 5051 (1995); R. F. Keeling, S. C. Piper, M. Heimann, *Nature* **381**, 218 (1996).
29. Land area of the United States is about 15% of the land area between 30° and 70°N.
30. D. W. Johnson, *Water Air Soil Pollut.* **64**, 83 (1992).
31. J. B. Gaudinski, S. E. Trumbore, E. A. Davidson, S. Zheng, *Biogeochemistry*, in press.
32. A. S. Donigian *et al.*, in *Advances in Soil Science. Soil Management and Greenhouse Effect*, R. Lal, J. Kimble, E. Levine, B. A. Stewart, Eds. (CRC Press, Boca Raton, FL,1995), pp. 121–135. Using the CENTURY model, these authors calculated that soil organic carbon increased over 60 to 70% of U.S. croplands, largely as a result of increased productivity between the years 1960 and 1990. They estimate that about 25% of the carbon initially lost through cultivation had been recovered.
33. P. Smith, D. S. Powlson, M. J. Glendining, J. U. Smith, *Global Change Biol.* **4**, 679 (1998); R. Q. Cannell and J. D. Hawes, *Soil Tillage Res.* **30**, 245 (1994).
34. D. L. Gebhart, H. B. Johnson, H. S. Mayeux, H. W. Polley, *J. Soil Water Conserv.* **49**, 488 (1994).
35. R. F. Stallard, *Global Biogeochem. Cycles* **12**, 231 (1998).
36. G. Marland, R. J. Andres, T. A. Boden, C. Johnston, A. Brenkert, Global, regional, and national CO_2 emission estimates from fossil fuel burning, cement production, and gas flaring: 1751–1996 (revised March 1999; 1950–1996 estimates are preliminary), available at http://cdiac.esd.ornl.gov/ndps/ndp030.html.
37. We reduced the carbon sink in forests estimated in (*2*) to account for the net effect of wood products. Birdsey and Heath (*2*) reported an accumulation of 0.027 Pg C year^{-1} in new wood products and emissions of 0.099 Pg C year^{-1} from oxidation of products, for a net release of 0.072 Pg C year^{-1}. Turner *et al.* (*3*) reported 0.124 Pg C year^{-1} removed from the forest. Assuming the same distribution of these removals as in (*2*), we calculated that 0.097 Pg C was released and 0.027 Pg C was stored in long-lasting products, thus increasing the reported net sink by 0.027 Pg C year^{-1}.
38. Soil carbon is not measured in forest inventories. Turner *et al.* (*3*) assumed soils to be in balance (net flux = 0); Birdsey and Heath (*2*) assumed that soils accumulated carbon in proportion to growth in aboveground biomass.
39. We are grateful to two anonymous reviewers whose comments helped improve the precision and clarity of the paper. Research was supported through the Joint Program on Terrestrial Ecology and Global Change, grant number NAGW-4748 from the Terrestrial Ecology Program in NASA's Office of Earth Science.

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An Adhesin of the Yeast Pathogen *Candida glabrata* Mediating Adherence to Human Epithelial Cells

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Candida glabrata is an important fungal pathogen of humans that is responsible for about 15 percent of mucosal and systemic candidiasis. *Candida glabrata* adhered avidly to human epithelial cells in culture. By means of a genetic approach and a strategy allowing parallel screening of mutants, it was possible to clone a lectin from a *Candida* species. Deletion of this adhesin reduced adherence of *C. glabrata* to human epithelial cells by 95 percent. The adhesin, encoded by the *EPA1* gene, is likely a glucan–cross-linked cell-wall protein and binds to host-cell carbohydrate, specifically recognizing asialo-lactosyl–containing carbohydrates.

Candida species are responsible for more than 8% of all hospital-acquired infections (*1*); the two most frequently encountered species are *C. glabrata* and *C. albicans* (*2*). *Candida albicans* is asexual and diploid, which complicates genetic analysis in this organism because both copies of a gene must be knocked out to uncover a recessive phenotype. Analysis of virulence in *C. albicans* has, therefore, been limited largely to reverse genetic approaches in which both copies of individual cloned genes are deleted and the resulting phenotype is assessed. *Candida glabrata*, although asexual, is haploid (*3*), which facilitates genetic analysis. In *C. glabrata*, it is possible to generate random mutants and screen for phenotypes of interest (*4*). Here, we demonstrate that this forward genetic approach can be used to analyze the host-pathogen interaction in *C. glabrata* and use this approach to identify an adhesin mediating adherence of *C. glabrata* to host epithelial cells.

The adherence of *Candida* to host cells has been the subject of intense investigation, and in the case of *C. albicans*, the yeast expresses a number of adhesins capable of interacting with a variety of ligands, including proteins [reviewed in (*5*)] and carbohydrates (*5*–*8*). Recently, it has also been shown that Hwp1p, a hypha-specific protein, is a substrate for mammalian transglutaminases and mediates covalent attachment of *C. albicans* to human buccal epithelial cells (*9*).

We found that *C. glabrata* adheres strongly to human epithelial cells in culture. In our assay (*10*), with a multiplicity of infection (MOI) of 1:1, between 10 and 20% of added yeast adheres to a monolayer of the human laryngeal carcinoma cell line HEp2 compared with 0.1% of added yeast for *Saccharomyces cerevisiae* (*11*). Scanning electron micrographs of *C. glabrata* bound to the surface of the monolayer show a marked and intimate interaction between the epithelial cell filopodia and the yeast cell (Fig. 1) (*12*). In transmission electron micrographs (*13*), a similar tight association is seen between the surface of the yeast cell and the surface of the epithelial cell, suggesting that the host ligand is broadly distributed on these tissue culture cells. This interaction is dependent on Ca^{2+} because adherent yeast can be removed with EGTA or with EGTA titrated with Mg^{2+} but not with EGTA titrated with Ca^{2+} (*13*).

To identify the yeast gene mediating the interaction of *C. glabrata* with epithelial cells, we undertook a mutant screen. We implemented a number of genetic tools to facilitate this analysis. First, we used a *ura3* deletion strain congenic with a virulent clinical isolate (*4*). Second, we used a variation

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