Response of a Deciduous Forest to the Mount Pinatubo Eruption: Enhanced Photosynthesis

Lianhong Gu,[1]* Dennis D. Baldocchi,[2] Steve C. Wofsy,[3] J. William Munger,[3] Joseph J. Michalsky,[4] Shawn P. Urbanski,[3] Thomas A. Boden[1]

Volcanic aerosols from the 1991 Mount Pinatubo eruption greatly increased diffuse radiation worldwide for the following 2 years. We estimated that this increase in diffuse radiation alone enhanced noontime photosynthesis of a deciduous forest by 23% in 1992 and 8% in 1993 under cloudless conditions. This finding indicates that the aerosol-induced increase in diffuse radiation by the volcano enhanced the terrestrial carbon sink and contributed to the temporary decline in the growth rate of atmospheric carbon dioxide after the eruption.

The growth rate of atmospheric CO_2 concentration experienced a sharp decline in the early 1990s, an observation that was unprecedented since CO_2 monitoring began in the late 1950s (*1*, *2*). This perturbation is of great interest to the global carbon cycle community because it coincided with the eruption of Mount Pinatubo (15.1°N, 121.4°E) on 15 June 1991. Studies using inversions of atmospheric CO_2, O_2/N_2 ratios, and $\delta^{13}CO_2$ measurements have indicated that an enhanced terrestrial carbon sink explains this decline (*3*–*6*). However, there is debate about the mechanism, because an increase in global photosynthesis or a reduction in global respiration can both explain a greater carbon sink.

The simultaneous occurrence of the eruption and the decline in the growth rate of atmospheric CO_2 is not exceptional. The eruption of Mount Agung (8.34°S, 115.5°E) in February 1963 was also followed by a decrease in the growth rate of atmospheric CO_2 (*2*). The same pattern was identified for the eruption of El Chichón in March 1982 (17.33°N, 93.2°W), when compounding effects of the powerful 1982–83 El Nino event on the atmospheric CO_2 were removed (*7*). Thus, it appears that large volcanic eruptions cause substantial perturbations to the global carbon cycle, particularly its terrestrial component. Understanding how volcanoes affect the global carbon cycle can lead to valuable insights into the dynamics of atmospheric CO_2 concentration and its relation to climate and the responses of ecosystems to chronic aerosol loading.

The Mount Pinatubo eruption was the largest during the last 100 years (*8*), injecting about 14 to 20 Tg (1 Tg = 10^{12} g) of SO_2 into the stratosphere (*9*–*12*). The sulfate aerosol layer, which formed in the aftermath of the eruption, longitudinally circled the globe in about 3 weeks (*9*) and stretched to the Polar Regions in late 1991 and early 1992 (*10*). This aerosol envelope led to a decrease in global (diffuse plus direct) solar radiation (*11*, *13*–*16*), an increase in diffuse solar radiation (*8*, *17*–*20*), warming in winter, cooling in summer (*8*, *21*, *22*), drying of the atmosphere (*23*), and modification of global cloudiness (*24*).

Although the eruption caused multiple global environmental changes, most previous evaluations have focused only on the global cooling (*25*, *26*) to explain the apparent enhancement of the terrestrial carbon sink after the eruption (*2*, *27*, *28*). It is possible that the cooling reduced terrestrial respiration, but several considerations led us to question whether this factor alone could account for the noted drop in the atmospheric CO_2 growth rate. First, long-term records of CO_2 and temperature generally show that there is a time lag between fluctuations in CO_2 and those in temperature (*2*). However, the response of atmospheric CO_2 after the eruption appears to be rapid. Second, the magnitude of the global surface cooling [up to 0.5°C in mid-1992 (*26*)] is within the range of annual temperature swings since the 1950s (*29*). Previous cooling of this magnitude did not cause a drop in the atmospheric CO_2 growth rate as large as the one observed after the eruption. Third, modeling of the effects of the eruption on atmospheric CO_2 using a coupled general circulation climate–carbon cycle model showed that the cooling stops short of fully accounting for the observed atmospheric CO_2 anomaly (*7*). Therefore, it is likely that multiple mechanisms are responsible for the atmospheric CO_2 behavior in the aftermath of the eruption.

Drawing on principles developed by agricultural and forest meteorologists, two groups of scientists have recently proposed that the increase in diffuse radiation caused by the injected stratospheric sulfate aerosols could have enhanced terrestrial photosynthesis (*30*, *31*). The rationale for this proposition stems in part from work by crop scientists who have shown that plant canopies use diffuse radiation more efficiently than they use direct beam radiation in photosynthesis (*32*). This hypothesis is also bolstered by recent observations from a variety of plant canopies that diffuse radiation leads to radiation use efficiencies (RUE) (*33*) two or more times higher than direct beam radiation (*34*). In practice, greater canopy photosynthesis can be produced under a moderately turbid sky, even though global solar radiation is reduced compared with clear sky conditions, because of the shift in RUE [supporting online material (SOM) text; figs. S1 and S2].

Here, we used two independent and direct methods to examine the photosynthetic response of a northern hardwood forest (Harvard Forest, 42.5°N, 72.2°W) to changes in diffuse radiation caused by Mount Pinatubo's volcanic aerosols. The first method couples eddy covariance flux tower measurements and an empirical model to detect and quantify the eruption signal. The second method, which resorts to long-term averages from statistical analyses, uses flux measurements only and provides an independent check on the first method. The Harvard Forest flux tower site was established around the time of the eruption (*35*), and its data provide a rare opportunity to test the hypothesis that the Mount Pinatubo eruption produced aerosols that increased diffuse radiation and enhanced terrestrial ecosystem productivity.

Mount Pinatubo effects estimated with flux measurements and an empirical model. In our first method, we evaluated how canopy photosynthesis of Harvard Forest responds to two sky conditions: (i) the perturbed cloudless solar radiation regime with volcanic aerosols present, and (ii) the normal cloudless solar radiation regime after the aerosols had been deposited from the

[1]Environmental Sciences Division, Building 1509, Oak Ridge National Laboratory, Oak Ridge, TN 37831–6335, USA. [2]Ecosystem Science Division, Department of Environmental Science, Policy and Management, University of California, Berkeley, CA 94720, USA. [3]Division of Engineering and Applied Science and Department of Earth and Planetary Sciences, Harvard University, Cambridge, MA 02138, USA. [4]Atmospheric Sciences Research Center, University at Albany, State University of New York, Albany, NY 12203, USA.

*To whom correspondence should be addressed. E-mail: lianhong-gu@ornl.gov

atmosphere and the normal atmospheric radiative transfer condition had resumed. We based our analyses on cloudless conditions to avoid confounding effects of clouds, which also diffuse solar beam radiation. Cloudless radiation regimes for the perturbed and normal states were established (*36*) from long-term hourly observations of diffuse and direct beam solar radiation at a nearby location (Albany, New York, 42.7°N, 73.83°W, about 120 km west of Harvard Forest). At Albany, measuring of diffuse and direct beam radiation was initiated about 3 months after the eruption. Such measurements were not available at Harvard Forest for the period under this investigation.

Cloudless radiation data from the summer periods were used to develop regressions against the solar elevation angle (Fig. 1). Direct beam radiation in 1992 and 1993 was reduced relative to 1995, 1996, and 1997, with lower values in 1992 (Fig. 1A). The reduction in direct beam radiation was accompanied by an increase in diffuse radiation, particularly in 1992 (Fig. 1B). In 1992, diffuse radiation was almost twice as high as in 1995, 1996, and 1997 for the same solar elevation angle. The perturbation of the radiation regime waned considerably by 1994. These results are consistent with findings from previous studies (*8*, *17–20*). We considered the perturbed cloudless solar radiation regime to span 1992, 1993, and 1994. Data from 1997 were used to represent the normal cloudless solar radiation regime; using measurements from 1995 or 1996 did not produce much difference in our analyses.

A multivariable nonlinear regression model called the generalized rectangular hyperbola (*34*, *36*) was used to evaluate the impact of radiation perturbation on Harvard Forest photosynthesis. This model uses parameters that explicitly and separately characterize canopy photosynthetic responses to incident diffuse and direct beam radiation. These parameters include the initial RUE and a coefficient that quantifies how close the rectangular hyperbola is to linearity (CLR) (*33*, *34*, *36*). Their values are affected by the canopy's structural and physiological properties (such as leaf area index, C_3 or C_4 photosynthetic pathway species composition, and leaf photosynthetic capacity), as well as environmental variables such as temperature and vapor pressure deficit (VPD). Diffuse radiation and direct beam radiation each have a separate set of parameters associated with them. The generalized rectangular hyperbola model has been tested rigorously for different vegetation ecosystems (*34*) and for Harvard Forest data (*37*). With the relations between the diffuse and direct beam radiation and the solar elevation angle that we obtained (Fig. 1) as inputs, we inferred the model parameters by fitting the model to the midgrowing season cloudless net ecosystem exchange (NEE) measurements in each year (Table 1). During this parameter inference process, the actual canopy gross photosynthetic rates under the perturbation by the volcanic aerosols were also determined.

We then used the inferred canopy parameters to compute canopy gross photosynthetic rates in 1992, 1993, and 1994, assuming that the canopy was under the normal radiation regime. The computed canopy gross photosynthetic rates were compared with the actual rates (under the perturbed radiation regime). Although the inferred canopy parameters changed from year to year (Table 1), any difference in the computed canopy gross photosynthetic rates between the two different radiation scenarios was the result of variations in the diffuse and direct radiation only because the same set of canopy parameters was used in the calculation in each year. In 1992, the perturbed radiation regime led to a much larger gross photosynthetic rate than the normal radiation regime (Fig. 2A). The photosynthetic difference between the two regimes was smaller in 1993 (Fig. 2B) and negligible in 1994 (Fig. 2C). The decreasing photosynthetic differences between the two regimes from 1992 to 1994 are expected as the atmosphere gradually returned to the normal condition. Around noontime (solar elevation angle = 70°) in the midgrowing season (day 200), the gross photosynthetic rate under the perturbed cloudless solar radiation regime was 23, 8, and 4% higher than that under the normal cloudless solar radiation regime in 1992, 1993, and 1994, respectively. Integrated over a day, the enhancement for canopy gross photosynthesis by the volcanic aerosols was 21% in 1992, 6% in 1993, and 3% in 1994.

To examine whether the forest was unusually sensitive to diffuse radiation in the first couple of years after the eruption, we also determined the initial RUE and CLR coefficients in 1995, 1996, and 1997 (table S1). We then used all six sets of canopy photosynthetic parameters (from 1992 to 1997) to run for the radiation conditions observed in 1992, 1993, 1994, and 1997, respectively. We

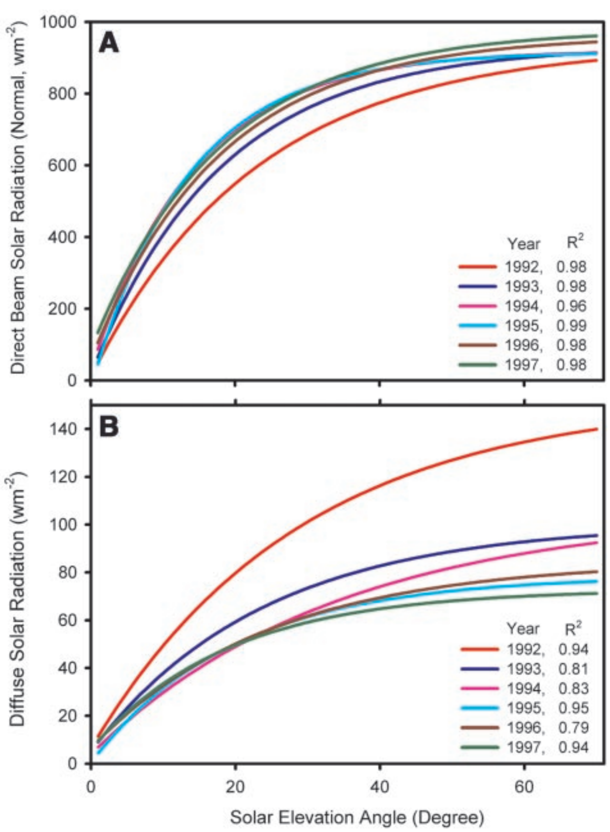

Fig. 1. Regression between the cloudless solar radiation and the solar elevation angle for the 6 years (1992 to 1997) after the Mount Pinatubo eruption. The regression relation is $I = c_0 + c_1*[1 - \exp(-c_2*\theta)]$. I is the direct beam or the diffuse solar radiation. c_0, c_1, and c_2 are regression coefficients. θ is the solar elevation angle. Diffuse radiation and direct beam radiation were measured independently. Because of this, some minor mismatch between diffuse and direct radiation in the year-to-year variations existed, but it was not found to affect the final results considerably (SOM text; figs. S3 and S4). (**A**) Direct beam solar radiation on the normal plane. (**B**) Diffuse solar radiation.

Table 1. Inferred canopy parameters in 1992, 1993, and 1994 from hourly NEE measurements under cloudless conditions. Parameters associated with diffuse radiation are larger than those associated with direct beam radiation, indicating advantages of diffuse radiation over direct beam radiation for canopy photosynthesis (*33*, *34*, *36*).

	1992	1993	1994
Initial diffuse RUE (μmol/J) × 100	11.82	7.39	10.18
Initial direct RUE (μmol/J) × 100	3.94	6.17	3.78
Diffuse CLR (μmol m^{-2} s^{-1})	139.60	169.07	146.93
Direct CLR (μmol $m^{-2}s^{-1}$)	19.33	18.95	28.66

found that Mount Pinatubo aerosols would have enhanced canopy photosynthesis in each and every year during the 6-year period (SOM text; figs. S5 and S6).

Mount Pinatubo effects estimated with flux measurements only. We normalized cloudless NEE measurements with a representative long-term value computed from a regression relation between the pooled cloudless NEE data from 1992 to 2001 and the solar elevation angle (*38*). This normalization procedure removed the dependence of NEE on solar elevation. Then we combined the normalized NEE from 1995 to 2001 together to form a reference sample. Statistical tests were conducted to compare the normalized cloudless NEE in 1992, 1993, and 1994 with the reference sample.

The means of the normalized cloudless NEE in 1992 and 1993 were significantly larger than that of the reference sample, with P values less than 0.01 (Table 2). No significant difference was detected in 1994. The relative difference between the means of the normalized cloudless NEE after the eruption and the reference sample decreased from 1992 to 1994, which is consistent with the results from the first approach. However, there are differences in the magnitudes produced by the two methods. The relative difference between the means of 1992 and the reference sample is about 18%, close to the daytime-integrated 21% enhancement that was estimated with the first method. With respect to the analysis of data in 1993, the two methods produced diverging estimates of photosynthesis enhancement. The relative difference between the means of the normalized cloudless NEE in 1993 and the reference sample is about 15%, whereas a 6% daytime-integrated enhancement in photosynthesis is obtained by the first approach. The relatively large difference between the two approaches in the estimated effects of the eruption in 1993 can be explained partly by changes in temperature and, therefore, ecosystem respiration. In 1993, the soil surface temperature was consistently lower than the average soil surface temperature from 1995 to 2001 (Fig. 3A). A cooler soil may have reduced soil respiration and contributed to the increase in net absorption of CO_2 under cloudless conditions in 1993, as compared with the average of 1995 to 2001 (SOM text). Although the global surface temperature reached the minimum in mid-1992 after the eruption (*26*, *29*), the soil surface in the second half-year of 1992 was actually warmer than the average of 1995 to 2001 at Harvard Forest. The warmer soil could have led to higher soil respiration. The soil surface was cooler than the average only in the springtime of 1992. The air temperature showed similar patterns, although they were less distinct (Fig. 3B). This effect may have led to late leafout and possibly reduced leaf area index at this site, as suggested by broad-area satellite observations (*28*, *39*). Evidently, these adversarial factors did not completely offset the effect of increased diffuse radiation on photosynthesis.

The second method is less robust than the first method because the former is based on NEE, the net difference between canopy photosynthesis and ecosystem respiration. Also, many factors could have changed systematically from 1992 to 2001. Examples include forest regrowth and variations in soil moisture, VPD, atmospheric CO_2, nitrogen deposition, and temperature. These factors could confound the analyses on effects of Mount Pinatubo aerosols and diffuse radiation with the second method. Some of them, such as forest regrowth (Harvard Forest is relatively young) and an increase in atmospheric CO_2, may lead to an underestimation of diffuse radiation effects by the second method. Other

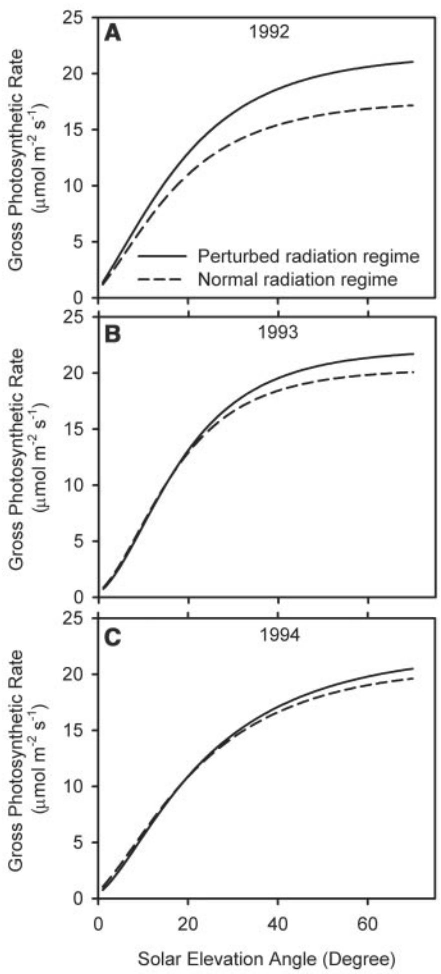

Fig. 2. The canopy gross photosynthetic rate versus the solar elevation angle under the perturbed cloudless solar radiation regime (solid lines) and the normal cloudless solar radiation regime (dashed lines) in (**A**) 1992, (**B**) 1993, and (**C**) 1994. The canopy gross photosynthetic rate was calculated from the parameters in Table 1 and the relations between the diffuse radiation and direct beam radiation and the solar elevation angle (Fig. 1) using the generalized rectangular hyperbola model (*34*).

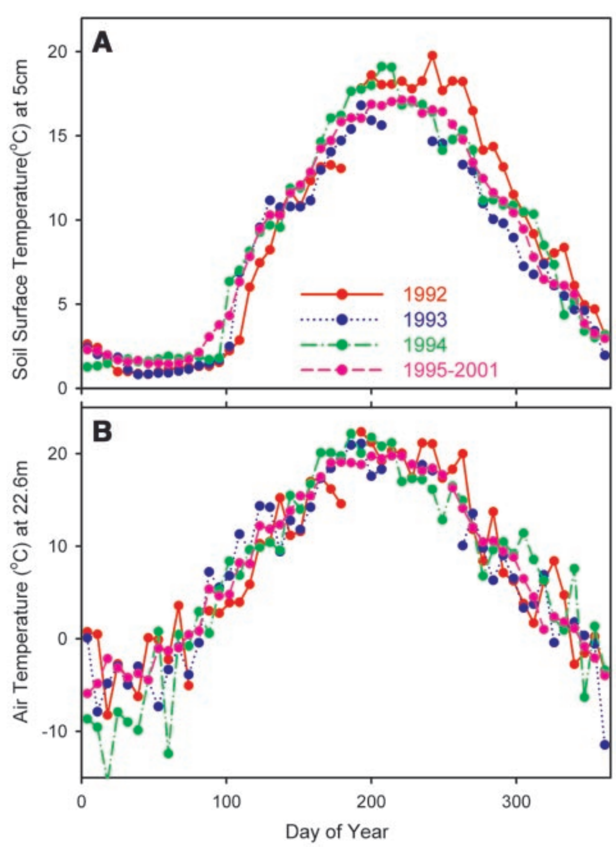

Fig. 3. Seasonal variations of the weekly mean soil surface temperature at 5 cm (**A**) and the air temperature at 22.6 m (**B**) at Harvard Forest. The average for the years from 1995 to 2001 was obtained from the hourly measurements directly (not from the average of means).

factors (such as VPD and temperature) can affect the results in both directions.

Two sensitivity tests were conducted to assess the uncertainties associated with temperature and VPD (SOM text). In the temperature sensitivity test, we hypothetically "warmed" the soil surface by 2°C in 1992 and 1993 and estimated the additional amount of respiration (ΔR_e) that would be produced by this warming. ΔR_e, which depended on the actual soil surface temperature, was then used to shift the measured NEE in 1992 and 1993 to a lower level (indicating less uptake). We analyzed the shifted data using the second method. It was found that even if the soil surface were 2°C warmer, the NEE in 1992 and 1993 would still have been significantly larger than the mean from 1995 to 2001 (table S2). In the VPD sensitivity test, we removed the highest VPD points from the 1995 to 2001 data set so that for each and every 1-hour interval, the mean VPD of the 1995 to 2001 data was no more than the mean VPD of the 1992 data (fig. S7). A reanalysis was then conducted using the second method. We found that the obtained estimates of photosynthesis enhancement in 1992 and 1993, although slightly reduced, were still statistically significant (table S3). Overall, these sensitivity analyses indicate that the first and second methods agree with each other.

Conclusions. The increase in diffuse radiation caused by volcanic aerosols enhanced Harvard Forest photosynthesis under cloudless conditions for the two years after the Mount Pinatubo eruption. Because of substantial increases in diffuse radiation worldwide after the eruption (*8*, *17–20*) and strong positive effects of diffuse radiation for a variety of vegetation types (*30–32*, *34*), it is likely that our findings at Harvard Forest represent a global phenomenon. Here, we examined cloudless conditions only. Some researchers have suggested that Mount Pinatubo aerosols might have enhanced the terrestrial carbon sink on an annual time scale (*30*, *31*). A comprehensive assessment of the effects of the eruption on the global carbon cycle will require knowledge of how the volcanic aerosols affected the type, frequency, distribution, and amount of cloud cover over the globe, as sulfate aerosols can increase cloudiness (*40*). There is evidence indicating that Mount Pinatubo aerosols increased high cloudiness, particularly in the middle latitudes (*24*). Variations in cloudiness can influence the global carbon cycle, because clouds are effective producers of diffuse radiation and can also change many meteorological variables that affect plant activities (*41*, *42*). The observation that forest ecosystems often absorb more CO_2 under cloudy conditions than under cloudless conditions (*41–45*) supports this idea.

Around noontime at the Harvard Forest site, diffuse radiation increases with cloud cover and reaches maximum when cloud cover is about 60%. Because of this, Harvard Forest photosynthesis also increases with cloud cover, with a peak at about 50% cloud cover (SOM text; fig. S8). Improved moisture condition and reduced solar heating may further enhance carbon uptake under cloudy conditions (*42*). If Mount Pinatubo aerosols increased global cloudiness moderately (without overly reducing global solar radiation), this would be an additional pathway for global terrestrial photosynthesis to be enhanced by the eruption, further contributing to a larger terrestrial carbon sink and the decline in the observed growth rate of atmospheric CO_2. Our study suggests that long-term trends and interannual variability in cloudiness and aerosol concentrations (*46*) may play important roles in the dynamics of the global carbon cycle.

Table 2. Statistical analysis (*t* test) of the normalized hourly NEE under cloudless conditions. The normalization function for NEE was the polynomial regression (cubic) of the hourly cloudless NEE pooled together for all years from 1992 to 2001 against the solar elevation angle (*38*). Only data with solar elevation angles greater than 10° were included in the statistical analysis to avoid distortion by unusually high normalized fluxes from early morning or late afternoon, when NEE approaches zero. The reference for the percentage difference was the mean for the 1995 to 2001 data. Values in parentheses are 95% confidence intervals. It was assumed that the two samples had unequal variances.

	1992	1993	1994	1995–2001
Mean (95%)	1.15 (0.05)	1.12 (0.07)	0.96 (0.08)	0.97 (0.03)
% difference	18.3	14.6	−1.3	
t test against 1995–2001				
t stat	6.33	3.77	−0.32	
$t_{0.05}$	1.97	1.98	1.98	
P value	0.00	0.00	0.75	

References and Notes

1. T. J. Conway *et al.*, *J. Geophys. Res.* **99**, 22831 (1994).
2. C. D. Keeling, T. P. Whorf, M. Wahlen, J. van der Plicht, *Nature* **375**, 666 (1995).
3. P. Ciais *et al.*, *Science* **269**, 1098 (1995).
4. R. F. Keeling, S. C. Piper, M. Heimann, *Nature* **381**, 218 (1996).
5. P. Bousquet *et al.*, *Science* **290**, 1342 (2000).
6. M. Battle *et al.*, *Science* **287**, 2467 (2000).
7. C. D. Jones, P. M. Cox, *Global Biogeochem. Cycles* **15**, 453 (2001).
8. A. Robock, *Rev. Geophys.* **38**, 191 (2000).
9. G. J. S. Bluth *et al.*, *Geophys. Res. Lett.* **19**, 151 (1992).
10. A. Herber *et al.*, *J. Geophys. Res.* **101**, 3921 (1996).
11. L. L. Stowe, R. M. Carey, P. P. Pellegrino, *Geophys. Res. Lett.* **19**, 159 (1992).
12. A. J. Baran, J. S. Foot, *J. Geophys. Res.* **99**, 25673 (1994).
13. E. G. Dutton, J. R. Christy, *Geophys. Res. Lett.* **19**, 2313 (1992).
14. C. R. Trepte, R. E. Veiga, M. P. Mccormick, *J. Geophys. Res.* **98**, 18563 (1993).
15. P. Minnis *et al.*, *Science* **259**, 1411 (1993).
16. G. L. Stenchikov *et al.*, *J. Geophys. Res.* **103**, 13837 (1998).
17. M. Blumthaler, W. Ambach, *Tellus* **46B**, 76 (1994).
18. J. J. Michalsky, R. Perez, R. Seals, P. Ineichen, *Sol. Energy* **52**, 205 (1994).
19. B. Molineaux, P. Ineichen, *Sol. Energy* **58**, 91 (1996).
20. F. J. Olmo, F. J. Batlles, L. Alados-Arboledas, *Sol. Energy* **57**, 433 (1996).
21. A. Robock, J. Mao, *J. Climate* **8**, 1086 (1995).
22. A. Robock, *Science* **295**, 1242 (2002).
23. D. Randel *et al.*, *Bull. Am. Meteorol. Soc.* **77**, 1233 (1996).
24. N. H. Song, D. O. Starr, D. J. Wuebbles, A. Williams, S. M. Larson, *Geophys. Res. Lett.* **23**, 2657 (1996).
25. M. P. McCormick, L. W. Thomason, C. R. Trepte, *Nature* **373**, 399 (1995).
26. D. E. Parker, H. Wilson, P. D. Jones, J. R. Christy, C. K. Folland, *Int. J. Climatol.* **16**, 487 (1996).
27. D. S. Schimel *et al.*, *Global Biogeochem. Cycles* **10**, 677 (1996).
28. W. Lucht *et al.*, *Science* **296**, 1687 (2002).
29. J. Hansen, R. Ruedy, M. Sato, R. Reynolds, *Geophys. Res. Lett.* **23**, 1665 (1996).
30. M. Roderick, G. D. Farquhar, S. L. Berry, I. R. Noble, *Oecologia* **129**, 21 (2001).
31. D. D. Baldocchi, K. B. Wilson, L. Gu, *Tree Physiol.* **22**, 1065 (2002).
32. J. Goudriaan, *Crop Micrometeorology and a Simulation Study* (Center for Agricultural Publication and Documentation, Wageningen, Netherlands, 1977).
33. Here, RUE is defined as the ratio of the CO_2 assimilation rate to the incident solar radiation above the canopy. RUE in general decreases with incident radiation intensity. When incident radiation intensity approaches zero, the RUE is the initial RUE. How RUE changes with incident radiation intensity depends on the shape of the photosynthetic response curve, which is characterized by the closeness to linear response (CLR) coefficient. If the response curve is linear, CLR is infinite. If the response curve levels off quickly as the incident radiation intensity increases, CLR is small. Initial RUE and CLR differ between diffuse and direct beam radiation. Detailed explanations can be found in (*34*) and in (*36*).
34. L. Gu *et al.*, *J. Geophys. Res.* **107(D6)**, 4050, doi: 10.1029/2001JD001242 (2002).
35. S. C. Wofsy *et al.*, *Science* **260**, 1314 (1993).
36. Materials and methods are available as supporting material on *Science* Online.
37. Intercept 0.16; slope = 1.01; $R^2 = 0.8$.
38. NEE = $3.75 - 44.5\sin\theta + 27.17\sin^2\theta - 4.05\sin^3\theta$, where θ is the solar elevation angle. $R^2 = 0.6$.
39. C. J. Tucker *et al.*, *Int. J. Biometeorol.* **45**, 184 (2001).
40. V. Ramanathan, P. J. Crutzen, J. T. Kiehl, D. Rosenfeld, *Science* **294**, 2119 (2001).
41. L. Gu *et al.*, *J. Geophys. Res.* **104**, 31421 (1999).
42. J. M. Freedman *et al.*, *J. Climate* **14**, 180 (2001).
43. D. T. Price, T. A. Black, *Agric. For. Meteorol.* **50**, 139 (1990).
44. D. Y. Hollinger *et al.*, *Ecology* **75**, 134 (1994).
45. D. D. Baldocchi, *Plant Cell Environ.* **20**, 1108 (1997).
46. J. T. Houghton *et al.*, Eds., *Climate Change 2001: The Scientific Basis* (Cambridge Univ. Press, Cambridge, 2001), available at www.grida.no/climate/ipcc_tar/wg1/index.htm.

47. We thank M. Post, M. Huston, T. West, A. King, G. Marland, F. Pan, and D. Fitzjarrald for commenting on the manuscript. D. Fitzjarrald contributed to the data used in this study. This paper was a contribution to Ameriflux and Fluxnet as well as the Oak Ridge National Laboratory's (ORNL's) Carbon Cycle Project (Principal Investigator, M. Post). The AmeriFlux and Carbon Cycle Project are sponsored by the U.S. Department of Energy, Office of Science, Biological, and Environmental Research, Terrestrial Carbon Program. Fluxnet is sponsored by NASA's Carbon Cycle Science Program. ORNL is managed by UT-Battelle, LLC, for the U.S. Department of Energy under the contract DE-AC05-00OR22725.

Supporting Online Material

www.sciencemag.org/cgi/content/full/299/5615/2035/DC1

Materials and Methods

SOM Text

Figs. S1 to S8

Tables S1 to S3

References

11 September 2002; accepted 28 January 2003