3. M. J. Tegner, P. K. Dayton, P. B. Edwards, K. L. Riser, *Calif. Coop. Oceanic Fish. Invest. Rep.* **37**, 111 (1996).
4. R. R. Veit, P. Pyle, J. A. McGowan, *Mar. Ecol. Prog. Ser.* **139**, 11 (1996).
5. K. L. Smith Jr., *Limnol. Oceanogr.* **32**, 201 (1987).
6. ———, R. J. Baldwin, P. M. Williams, *Nature* **359**, 313 (1992).
7. F. L. Sayles, W. R. Martin, W. G. Deuser, *ibid.* **371**, 686 (1994).
8. K. L. Smith Jr., R. S. Kaufmann, R. J. Baldwin, *Limnol. Oceanogr.* **39**, 1101 (1994).
9. K. L. Smith Jr. and E. R. M. Druffel, *Deep-Sea Res. Part II* **45**, 573 (1998).
10. Sinking POC was collected in sediment traps with a sampling resolution of 10 days moored at 600 and 50 mab (3500 and 4050 m depth, respectively) and serviced every 4 months over the duration of the study. Each trap consisted of a Teflon-coated fiberglass funnel with an effective mouth opening of 0.25 m² and 13 sequencing collection cups, each poisoned with 3.0 mM $HgCl_2$ (*8, 11*). Upon recovery, cup samples were frozen after removal of swimmers (mobile fauna) and later analyzed in duplicate for total carbon, with a Perkin-Elmer elemental analyzer, and inorganic carbon, with a Coulometrics carbon analyzer with corrections for salinity (*8*). Organic carbon was calculated as the difference between total and inorganic carbon.
11. R. J. Baldwin, R. C. Glatts, K. L. Smith Jr., *Deep-Sea Res. Part II* **45**, 643 (1998).
12. J. C. Drazen, R. J. Baldwin, K. L. Smith Jr., *ibid.*, p. 893.
13. SCOC was measured with an FVGR on seasonal cruises throughout the study (*6, 8, 12*). On each deployment SCOC was measured with polarographic oxygen sensors during 2-day incubations within four FVGR grabs, each enclosing 413 cm⁻² of sediment surface (*5*). Sensor calibration followed procedures described in (*5*), with the resulting SCOC converted to organic carbon utilization (mg C m⁻² day⁻¹) assuming a respiratory quotient of 0.85 [K. L. Smith Jr., *Deep-Sea Res.* **36**, 1111 (1989)]. Thirty-nine measurements of SCOC were collected with TCRs placed by the submersible Alvin and incubated for 24- to 141-hour periods during August and September 1994 and April 1995 (*15*). Each TCR enclosed a surface area of 38.5 cm² and measured SCOC with the same sensors as in the FVGR. High–temporal resolution measurements of SCOC were made with an autonomous bottom-transecting vehicle (ROVER) from January through May 1996 at 17 sites. Individual measurements were made by enclosing 670 cm² of the sediment surface for 152.3 hours in each of two benthic chambers equipped with a polarographic oxygen sensor (*14*). Synchronous measurements of SCOC by the FVGR, TCRs, and ROVER were not significantly different (*14, 15*).
14. K. L. Smith Jr., R. J. Baldwin, R. C. Glatts, R. S. Kaufmann, E. C. Fisher, *Deep-Sea Res. Part II* **45**, 843 (1998).
15. K. L. Smith Jr. *et al.*, *Limnol. Oceanogr.* **42**, 1601 (1997).
16. E. R. M. Druffel, S. Griffin, J. E. Bauer, D. M. Wolgast, X.-C. Wang, *Deep-Sea Res. Part II* **45**, 667 (1998).
17. W. R. Martin and M. L. Bender, *Am. J. Sci.* **288**, 561 (1988).
18. D. Roemmich, *Science* **257**, 373 (1992).
19. R. W. Eppley and B. J. Peterson, *Nature* **282**, 677 (1979).
20. J. P. Barry, C. H. Baxter, R. D. Sagarin, S. E. Gilman, *Science* **267**, 672 (1995).
21. R. R. Veit, J. A. McGowan, D. G. Ainley, T. R. Wahls, P. Pyle, *Global Change Biol.* **3**, 23 (1997).
22. Macrozooplankton volumes were calculated from net tows carried out during California Cooperative Oceanic Fisheries Investigations (CalCOFI) cruises between March 1990 and October 1996. Data were averaged from tows on lines 77, 80, 83, 87, 90, and 93 at stations 70 through 100, all of which are located at least 30 miles offshore. Macrozooplankton were collected in oblique net tows from 210 m depth to the surface. A summary of the procedures used to determine macrozooplankton volume can be found at www-mlrg.ucsd.edu/calcofi.html and in D. Kramer, M. J. Kalin, E. G. Stevens, J. R. Thrailkill, J. R. Zweifel, *NOAA Technical Report NMFS CIRC-370* (1972).
23. T. J. Shaw, J. M. Smoak, L. M. L. Lauerman, *Deep-Sea Res. Part I* **45**, 763 (1998); S. E. Beaulieu and K. L. Smith Jr., *ibid.*, p. 781.
24. L. M. L. Lauerman, R. S. Kaufmann, K. L. Smith Jr., *Deep-Sea Res. Part I* **43**, 1075 (1996); L. M. L. Lauerman, R. S. Kaufmann, *Deep-Sea Res. Part II* **45**, 817 (1998).
25. T. S. Bianchi, J. E. Bauer, E. R. M. Druffel, C. D. Lambert, *Deep-Sea Res. Part II* **45**, 715 (1998); R. M. Sherrell, M. P. Field, Y. Gao, *ibid.*, p. 733.
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# Net Primary Production of a Forest Ecosystem with Experimental CO₂ Enrichment

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The concentration of atmospheric carbon dioxide was increased by 200 microliters per liter in a forest plantation, where competition between organisms, resource limitations, and environmental stresses may modulate biotic responses. After 2 years the growth rate of the dominant pine trees increased by about 26 percent relative to trees under ambient conditions. Carbon dioxide enrichment also increased litterfall and fine-root increment. These changes increased the total net primary production by 25 percent. Such an increase in forest net primary production globally would fix about 50 percent of the anthropogenic carbon dioxide projected to be released into the atmosphere in the year 2050. The response of this young, rapidly growing forest to carbon dioxide may represent the upper limit for forest carbon sequestration.

Combustion of fossil fuels and deforestation, particularly in tropical regions, are rapidly increasing the concentration of $CO_2$ in the atmosphere (*1, 2*). Trees that use the $C_3$ mechanism of photosynthesis are carbon-limited at the current atmospheric $CO_2$ concentration (*3*); therefore, the stimulation of photosynthesis by elevated $CO_2$ may increase the capacity of forests to store carbon in wood and soil organic matter. Because of their imposing contribution to global productivity (*2*), forests have the potential to reduce the anthropogenic increase in atmospheric $CO_2$.

Seedlings or saplings exposed to two times the current atmospheric concentration of $CO_2$ in growth chambers, greenhouses, or open-top chambers have ~54% greater photosynthesis and ~31% greater biomass (*4*). These enhancements are considerably reduced when plants receive suboptimal amounts of other important resources such as nitrogen (*5*). Most studies of tree rings (*6*)

show no increase in growth rate in response to the increase in atmospheric $CO_2$ that has occurred from the pre-industrial concentration of ~280 µl liter⁻¹ to the current 360 µl liter⁻¹. Resource limitations in natural ecosystems and other ecological interactions including competition (*7*) may constrain the potential for forests to respond to increasing concentrations of $CO_2$.

To examine the response of an intact forest ecosystem to projected elevated concentrations of $CO_2$, we installed a gas-delivery system in a 13-year-old loblolly pine (*Pinus taeda* L.) plantation in the Piedmont region of North Carolina (35°97′N 79°09′W) (*8*). The free-air $CO_2$ enrichment (FACE) system (*9*) increases the concentration of atmospheric $CO_2$ in 30-m-diameter experimental plots nested within this continuous pine forest (Fig. 1). Each FACE ring (plot) consists of a large circular plenum that delivers air to an array of 32 vertical pipes. The pipes extend from the forest floor through the 14-m-tall forest canopy and contain adjustable ports at 50-cm intervals. These ports are tuned to control the atmospheric concentration of $CO_2$ ([$CO_2$]) through the entire volume of forest. In the three elevated $CO_2$ plots, $CO_2$ was injected to maintain the atmosphere at ambient [$CO_2$] plus 200 µl liter⁻¹ (~560 µl liter⁻¹); three ambient $CO_2$ plots were treated identically

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but without the addition of $CO_2$ (*10*). Unlike closed growth chambers or open-top chambers, the FACE system controls atmospheric $[CO_2]$ without changing other variables. Moreover, its size permits the experimental manipulation of an entire forest ecosystem, including vegetation and soil components. The injection of $CO_2$ was initiated on 27 August 1996.

At monthly intervals beginning in March



**Fig. 1.** Free-air $CO_2$ enrichment (FACE) rings in a pine plantation in North Carolina, USA. Each ring is 30 m in diameter and circumscribes about 100 trees. The distance from the single ring in the southwest (top right) to the two rings in the north (bottom) is ~500 m. The single ring in the background is a prototype. There are six experimental rings; three rings receive ambient air and three receive ambient plus 200 μl liter$^{-1}$ $CO_2$ (photo: Will Owens).
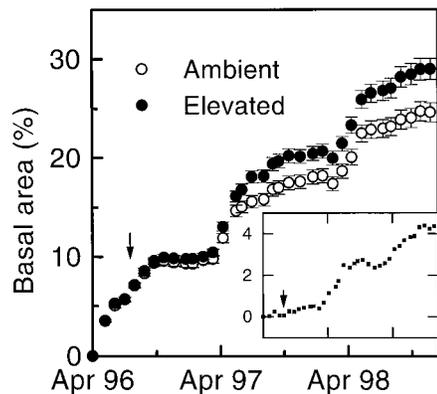


**Fig. 2.** Average basal area (±1 SE) for loblolly pine trees growing in ambient ($N = 102$) and elevated ($N = 101$) $CO_2$. Values are expressed as the percentage of the initial basal area. The insert shows the absolute difference between the basal area of elevated and ambient trees, and the arrows indicate when the $CO_2$ fumigation was initiated.

1996 we measured the diameter of 203 canopy pine trees distributed across the ambient and elevated plots (*11*). In 1997 and 1998 we made additional measurements of 112 subcanopy hardwood trees. Before the fumigation was initiated, the seasonal increase in basal area was similar for canopy trees in the ambient and elevated plots (Fig. 2). The basal area increment began to diverge soon after the fumigation started in August 1996, and by 1997 and 1998 the average basal areas for trees in the elevated plots were ~2.6 and 4.5% larger, respectively, than those in the ambient plots.

Diameters at the beginning and the end of each growing season were used to calculate the relative basal area increment of each tree [RBAI = (BA$_{December}$ − BA$_{January}$)/BA$_{January}$, where BA is basal area] (*12*). A mild drought in 1997 and a severe drought during the summer

of 1998 [modified Palmer drought index: −3 (*13*)] caused lower RBAI in the ambient plots relative to 1996 (Table 1). The addition of $CO_2$ to the experimental plots in the late summer and fall of 1996 produced no statistical effect on RBAI between ambient and elevated plots (0.094 compared with 0.098 cm$^2$ cm$^{-2}$ year$^{-1}$) in that year. During the two full years of exposure, however, elevated $CO_2$ caused significant increases in RBAI. The ~26% stimulation in RBAI was similar to the growth stimulation observed for potted loblolly pine seedlings maintained at two times $[CO_2]$ but with suboptimal soil N and P, and considerably less than the maximum response observed for this species under optimal growth conditions (*14, 15*). For the subcanopy hardwood species, a stimulation in RBAI by elevated $CO_2$ was statistically detectable only in *Ulmus alata* (for 1997: ambient = 0.055, elevated = 0.072 cm$^2$ cm$^{-2}$

**Table 1.** The mean (±1 SD) relative basal area increment (RBAI; cm$^2$ cm$^{-2}$ year$^{-1}$) for loblolly pine trees growing in ambient and elevated atmospheric $CO_2$ plots. The average RBAI was calculated for 30 to 40 trees in each plot. The RBAI for ambient and elevated plots for each year was compared with a paired-sample *t* test (one-tailed, $N = 3$).

| Year | Mean RBAI (cm$^2$ cm$^{-2}$ year$^{-1}$) | | Percent $CO_2$ effect | P |
|------|---------|----------|---------|---|
| | Ambient | Elevated | | |
| 1996 | 0.094 ± 0.024 | 0.098 ± 0.011 | 4.2 | 0.342 |
| 1997 | 0.076 ± 0.020 | 0.095 ± 0.010 | 25.0 | 0.044 |
| 1998 | 0.054 ± 0.011 | 0.068 ± 0.012 | 25.9 | 0.007 |

**Table 2.** Net primary production (production of dry matter; g m$^{-2}$ year$^{-1}$) for a pine ecosystem under ambient or elevated atmospheric $CO_2$ during fumigation in 1997 and 1998. Subcanopy hardwoods are trees with a diameter ≥2.5 cm. The "sapling" category includes trees (<2 m tall), shrubs, and vines. Litterfall is the amount of dead biomass in foliage, branches, and reproductive structures falling to the ground annually. Net primary production ("Production") is the sum of all components. For years where data were not available for one or more components, they were not included in the calculation of NPP (for example, fine roots in 1996 and 1997 and subcanopy hardwoods and sapling production in 1996). The "Percent $CO_2$ effect" is the percentage difference between the elevated and ambient plots. Values for ambient and elevated plots were compared with a paired-sample *t* test (one-tailed, $N = 3$).

| Category | Year | NPP (g m$^{-2}$ year$^{-1}$) | | Percent $CO_2$ effect | P |
|----------|------|---------|----------|---------|---|
| | | Ambient | Elevated | | |
| *Increments* | | | | | |
| Canopy pines | 1996 | 976 | 1002 | 3 | 0.40 |
| | 1997 | 879 | 1087 | 24 | 0.14 |
| | 1998 | 685 | 857 | 25 | 0.09 |
| Subcanopy hardwoods | 1997 | 75 | 105 | 40 | 0.14 |
| | 1998 | 118 | 155 | 31 | 0.16 |
| Saplings, shrubs, and vines | 1997 | 8 | 4 | −100 | 0.26 |
| | 1998 | 9 | 7 | −22 | 0.29 |
| Fine roots | 1998 | 43 | 80 | 86 | 0.02 |
| *Turnover* | | | | | |
| Litterfall | 1996 | 660 | 588 | −11 | 0.13 |
| | 1997 | 529 | 533 | 1 | 0.45 |
| | 1998 | 613 | 739 | 21 | 0.08 |
| Fine roots | 1998 | 195 | 245 | 26 | 0.21 |
| *Production* | | | | | |
| | 1996 | 1637 | 1590 | −3 | 0.30 |
| | 1997 | 1491 | 1727 | 16 | 0.11 |
| | 1998 | 1662 | 2082 | 25 | 0.01 |

year$^{-1}$, $P = 0.07$, $N = 24$; for 1998: ambient = 0.09, elevated = 0.118 cm$^2$ cm$^{-2}$ year$^{-1}$, $P = 0.027$).

Net primary production represents the flux of carbon into ecosystems. Some of this carbon is returned to the atmosphere by respiration from soil microbes and herbivores—the remaining carbon is stored as net ecosystem production. Net primary production (NPP; gross photosynthesis minus plant respiration) for the ambient and elevated $CO_2$ plots was calculated as the summation of the annual increment in standing biomass of trees (including roots), saplings, shrubs, and vines, plus the turnover of foliage (litterfall) and fine roots [16]. We calculated the biomass of the dominant pine trees from diameter using site-specific allometric equations [17], and equations from the literature were used to convert diameter to total biomass for the subcanopy hardwoods [18]. Herbivory was not included in our estimates, but losses by herbivory from forest ecosystems typically are <10% [19].

Net primary production for the entire ecosystem in 1998 was 1662 g of dry matter per square meter per year in control plots and 2082 g m$^{-2}$ year$^{-1}$ in experimental plots (Table 2). Our estimates of biomass increment for the canopy pines (685 to 1087 g m$^{-2}$ year$^{-1}$) are within the range reported for other loblolly pine forests [20]. The annual biomass increment in canopy pines plus litterfall accounted for 78% of NPP (1998), followed by contributions from fine roots, subcanopy hardwoods, and saplings, shrubs, and vines. Elevated $CO_2$ caused a consistent increase in NPP during the two full years of treatment (1997 and 1998). There was a trend of higher fine-root turnover and a significant increase in fine-root increment (86%) in the elevated-$CO_2$ plots in 1998. Higher fine-root turnover under $CO_2$ enrichment is consistent with higher rates of $CO_2$ efflux from the soil in fumigated compared with ambient plots [1066 ± 46 g of C per square meter per year in 1997 and 928 ± 19 gC m$^{-2}$ year$^{-1}$ in 1998 in ambient plots; 1183 ± 8 gC m$^{-2}$ year$^{-1}$ in 1997 and 1175 ± 132 gC m$^{-2}$ year$^{-1}$ in 1998 in elevated plots; paired $t$ test within each year: $P = 0.04$ for both years, $N = 3$ [21]]. Model simulations of terrestrial ecosystems predict an 8% increase in NPP for the contiguous United States [22] and a ~9% increase for temperate coniferous forests with a doubling of $CO_2$ [23]. It was therefore striking to find 25% stimulation in NPP with only a 1.5-fold increase in $CO_2$.

It is unclear if the response of this young, fast-growing southeastern forest will be sustained over many years or if other vegetation types will respond similarly. In simulations with process-based models [24], the initial increases in forest NPP after a step doubling of $CO_2$ declined dramatically with time as tree growth exceeded the rate of soil nitrogen mineralization. Similarly, individual trees ex-

posed for long periods to elevated $CO_2$ [25] and forests near natural $CO_2$ sources [26] show a rapid attenuation of the $CO_2$ growth response with age. Thus, the growth stimulation observed for this pine ecosystem under $CO_2$ enrichment may represent the maximum response. If it applies to forests globally, the 25% increase in NPP that we observed suggests that enhanced uptake of $CO_2$ by forests will not exceed 50% of the $CO_2$ emitted from fossil fuel combustion in the year 2050, when the atmospheric [$CO_2$] is expected to reach 560 μl liter$^{-1}$ [1, 27].

### References and Notes

1. Technical Summary, in *Climate Change 1995*, J. T. Houghton *et al.*, Eds. (Cambridge Univ. Press, Cambridge, 1996), pp. 9–49.
2. W. H. Schlesinger, *Biogeochemistry: An Analysis of Global Change* (Academic Press, New York, ed. 2, 1997).
3. T. D. Sharkey, *Bot. Rev.* **51**, 507 (1985); C. A. Gunderson and S. D. Wullschleger, *Photosynth. Res.* **39**, 369 (1994); B. G. Drake, M. A. González-Meler, S. P. Long, *Annu. Rev. Plant Physiol. Plant Mol. Biol.* **48**, 609 (1997).
4. P. S. Curtis and X. Wang, *Oecologia* **113**, 299 (1998).
5. R. J. Norby *et al.*, *Nature* **357**, 322 (1992).
6. L. J. Graumlich, *Ecology* **72**, 1 (1991); J. L. Innes, *Holocene* **1**, 168 (1991); P. C. Van Deusen, *Can. J. For. Res.* **22**, 660 (1992); R. J. Luxmore, S. D. Wullschleger, P. J. Hanson, *Water Air Soil Pollut.* **70**, 309 (1993).
7. F. A. Bazzaz, *Annu. Rev. Ecol. Syst.* **21**, 167 (1990).
8. Three control and three treatment plots were installed in a loblolly plantation that was planted in 1983 on formerly agricultural land. The clay-rich, ultic Alfisols in this region are of the Enon series and are low in available nitrogen and phosphorus. The density of pine trees is 1733 stems ha$^{-1}$, and the forest has not yet initiated rapid self-thinning [R. K. Peet and N. L. Christensen, *BioScience* **37**, 586 (1987)]. Silvicultural practices have not been applied, and several hardwood species including sweetgum (*Liquidambar styraciflua* L., 620 stems ha$^{-1}$), yellow poplar (*Liriodendron tulipifera* L., 68 stems ha$^{-1}$), winged elm (*Ulmus alata* Michx., 226 stems ha$^{-1}$), and red maple (*Acer rubrum* L., 207 stems ha$^{-1}$) have established in the forest understory. Pine trees represent more than 98% of the total basal area. To control for topographic variation between plots (~5 m) and potential gradients in site fertility, we arranged the three ambient and three elevated $CO_2$ plots in a blocked design (three pairs).
9. Y. He, X. Yang, D. R. Miller, G. R. Hendrey, K. F. Lewin, J. Nagy, *Trans. ASAE* (*Am. Soc. Agric. Eng.*) **39**, 1551 (1996); G. R. Hendrey, D. S. Ellsworth, K. F. Lewin, J. Nagy, *Global Change Biol.* **5**, 293 (1999); A. R. McLeod and S. P. Long, *Adv. Ecol. Res.* **28**, 1 (1999).
10. The elevated $CO_2$ plots were fumigated for 81% and 79% of 1997 and 1998, respectively. Most of the nontreatment periods were to accommodate ancillary experiments and during extreme weather. The system provided reliable control of [$CO_2$] for ≥99% of the period of fumigation in 1997 and 1998. The annual average $CO_2$ enrichment at the center of each plot varied from 199 to 203 μl liter$^{-1}$ above ambient concentrations, and the maximum standard deviation of the annual mean $CO_2$ enrichment observed in any fumigated plot was 84 μl liter$^{-1}$.
11. Stainless steel dendrometer bands [R. C. Hall, *J. For.* **42**, 742 (1944); B. D. Keeland and R. R. Sharitz, *Can. J. For. Res.* **24**, 2454 (1993)] were installed on stems 1.4 m above the soil surface on 30 to 40 trees in each plot. The populations of sample trees in ambient and elevated $CO_2$ plots were normally distributed, and the mean (±1 SD) basal area per tree at the beginning of the experiment was not significantly different between ambient and elevated plots (ambient: 179.8 ± 92.7 cm$^2$; elevated: 186.5 ± 92.6 cm$^2$; $P = 0.57$).
12. Within the elevated and ambient groups, RBAI changed ≤0.2% over the entire range of basal areas and therefore was considered independent of tree size.
13. Regional estimates of drought, expressed as the modified Palmer drought index, were obtained from the National Oceanic and Atmospheric Administration, National Climate Data Center.
14. B. R. Strain and R. B. Thomas, *Water Air Soil Pollut.* **64**, 45 (1994).
15. D. T. Tissue, R. B. Thomas, B. R. Strain, *Plant Cell Env.* **20**, 1123 (1997).
16. Litterfall was collected at monthly intervals in 12 traps that were 0.16 m$^2$, randomly placed on the forest floor of each ring. The biomass increment for saplings, vines, and shrubs was calculated with species-specific allometric equations. The mass of living and dead fine roots (≤1 mm diameter) was measured in soil cores removed from the ambient and elevated plots (five cores per plot) at 2-month intervals; fine root increments were calculated from the regression of live root biomass versus time over the period of November 1997 to November 1998. Root turnover rates were calculated as annual mortality plus annual decomposition for the same period [H. Persson, *Vegetatio* **41**, 101 (1979); D. Santantonio and J. C. Grace, *Can. J. For. Res.* **17**, 900 (1987); K. A. Vogt, D. J. Vogt, J. Bloomfield, *Plant Soil* **200**, 71 (1998)].
17. Before initiating this experiment, we harvested 30 pine trees (3.5 to 35.6 cm in diameter) from nearby stands to generate allometric regressions equating bole diameter to whole tree dry mass {woody roots, bole, branches, and foliage [S. L. Naidu, E. H. DeLucia, R. B. Thomas, *Can. J. For. Res.* **28**, 1116 (1998)]}. The standing biomass of all trees in each plot at the beginning of the 1996 growing season was calculated from measured BA and these size-dependent allometric regressions. The values for all trees were summed to provide initial total standing biomass per plot. The diameter for all trees at the end of each year was calculated by multiplying the initial BA by the RBAI for sample trees, and the allometric regressions were again used to calculate the final standing crop for each year. Previous research indicates that $CO_2$ enrichment does not alter the allometric relations for loblolly pine [15] or the root/shoot ratio for other tree species [4].
18. The above-ground biomass of subcanopy trees was calculated from equations in C. D. Monk, G. I. Child, S. A. Nicholson, *Oikos* **21**, 138 (1970), and the coarse-root biomass was calculated from R. H. Whittaker and P. L. Marks, in *Primary Productivity of the Biosphere*, H. Lieth and R. H. Whittaker, Eds. (Springer-Verlag, New York, 1975), pp. 55–118.
19. M. J. Crawley, *Stud. Ecol.* **10**, 1 (1983); H. Cyr and M. L. Pace, *Nature* **361**, 148 (1993).
20. D. E. DeAngelis, R. H. Gardener, H. H. Shugart, in *Dynamic Properties of Forest Ecosystems*, D. E. Reichle, Ed. (Cambridge Univ. Press, Cambridge, 1981), pp. 567–672; S. G. McNulty, J. M. Vose, W. T. Swank, *For. Ecol. Manag.* **86**, 241 (1996).
21. Monthly measurements of the efflux of $CO_2$ from the forest floor over 24 hours were made in four random locations in each ring with enclosed soda-lime traps [N. T. Edwards, *Pedobiologia* **23**, 321 (1982); P. Grogan, *Ecology* **79**, 1467 (1998)]. The total annual $CO_2$ efflux from the soil was calculated by integrating the area beneath these plots of the monthly measurements.
22. Y. Pan *et al.*, *Oecologia* **114**, 389 (1998).
23. J. M. Melillo *et al.*, *Nature* **363**, 234 (1993).
24. H. N. Comins and R. E. McMurtrie, *Ecol. Appl.* **3**, 666 (1993); Y. Luo and J. F. Reynolds, *Ecology*, in press.
25. S. B. Idso, *Global Change Biol.* **5**, 493 (1999).
26. S. Hattenschwiler, F. Miglietta, A. Raschi, C. Körner, *ibid.* **3**, 463 (1997).
27. If we assume that half of global NPP (30 Gt of carbon per year) is in forests, then a 25% stimulation of NPP would capture 7.5 Gt of the projected 15 Gt of carbon emitted from fossil fuel combustion in 2050 [1].
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