Forest response to elevated CO_2 is conserved across a broad range of productivity

Richard J. Norby[a,b], Evan H. DeLucia[c], Birgit Gielen[d], Carlo Calfapietra[e], Christian P. Giardina[f], John S. King[g], Joanne Ledford[a], Heather R. McCarthy[h], David J. P. Moore[i], Reinhart Ceulemans[d], Paolo De Angelis[e], Adrien C. Finzi[j], David F. Karnosky[k], Mark E. Kubiske[l], Martin Lukac[m], Kurt S. Pregitzer[k], Giuseppe E. Scarascia-Mugnozza[n], William H. Schlesinger[b,h], and Ram Oren[h]

[a]Environmental Sciences Division, Oak Ridge National Laboratory, Oak Ridge, TN 37831-6422; [c]Department of Plant Biology and [i]Program in Ecology and Evolutionary Biology, University of Illinois, Urbana, IL 61801; [d]Department of Biology, University of Antwerp, B-2610 Wilrijk, Belgium; [e]Department of Forest Environment and Resources, University of Tuscia, I-01100 Viterbo, Italy; [f]U.S. Department of Agriculture Forest Service, North Central Research Station, Houghton, MI 49931; [g]Department of Forestry and Environmental Resources, North Carolina State University, Raleigh, NC 27695; [h]Nicholas School of the Environment and Earth Sciences, Duke University, Durham, NC 27708-0328; [i]Department of Biology, Boston University, Boston, MA 02215; [k]Ecosystem Science Center, School of Forest Resources and Environmental Science, Michigan Technological University, Houghton, MI 49931; [l]U.S. Department of Agriculture Forest Service, North Central Research Station, Rhinelander, WI 54501; [m]School of Agricultural and Forest Sciences, University of Wales, Bangor LL57 2UW, United Kingdom; and [n]Institute of Agro-Environmental and Forest Biology, Consiglio Nazionale delle Ricerche, 05010 Porano (TR), Italy

Climate change predictions derived from coupled carbon-climate models are highly dependent on assumptions about feedbacks between the biosphere and atmosphere. One critical feedback occurs if C uptake by the biosphere increases in response to the fossil-fuel driven increase in atmospheric $[CO_2]$ ("CO_2 fertilization"), thereby slowing the rate of increase in atmospheric $[CO_2]$. Carbon exchanges between the terrestrial biosphere and atmosphere are often first represented in models as net primary productivity (NPP). However, the contribution of CO_2 fertilization to the future global C cycle has been uncertain, especially in forest ecosystems that dominate global NPP, and models that include a feedback between terrestrial biosphere metabolism and atmospheric $[CO_2]$ are poorly constrained by experimental evidence. We analyzed the response of NPP to elevated CO_2 (≈ 550 ppm) in four free-air CO_2 enrichment experiments in forest stands. We show that the response of forest NPP to elevated $[CO_2]$ is highly conserved across a broad range of productivity, with a stimulation at the median of $23 \pm 2\%$. At low leaf area indices, a large portion of the response was attributable to increased light absorption, but as leaf area indices increased, the response to elevated $[CO_2]$ was wholly caused by increased light-use efficiency. The surprising consistency of response across diverse sites provides a benchmark to evaluate predictions of ecosystem and global models and allows us now to focus on unresolved questions about carbon partitioning and retention, and spatial variation in NPP response caused by availability of other growth limiting resources.

CO_2 fertilization | global change | leaf area index | net primary productivity

Analysis and prediction of the effects of human activities, particularly the combustion of fossil fuels, on climate and the biological, physical, and social responses to changing climate require an integrated view of the complex interactions between the biosphere and atmosphere. Carbon cycle models are now being coupled to atmosphere–ocean general circulation climate models to achieve a dynamic analysis of the relationships between C emissions, atmospheric chemistry, biosphere activity, and climatic change (1–3).

Exchanges between the terrestrial biosphere and atmosphere are represented in models using empirical and theoretical expressions of net primary productivity (NPP), the net fixation of C by green plants into organic matter, or the difference between photosynthesis and plant respiration. Because the photosynthetic uptake of carbon that drives NPP is not saturated at current atmospheric concentrations (4), NPP should increase as fossil-fuel combustion adds to the atmospheric $[CO_2]$. Increased C uptake into the biosphere in response to rising $[CO_2]$ ("CO_2

fertilization") can create a negative feedback that slows the rate of increase in atmospheric $[CO_2]$ (3, 5). Hence, assumptions regarding CO_2 fertilization of the terrestrial biosphere greatly affect predictions of future atmospheric $[CO_2]$ (3). The response of NPP to $[CO_2]$ in models can be prescribed (1) or calculated through a mechanistic representation (3, 5). In either case, the predicted responses of net ecosystem production (or NPP minus heterotrophic respiration), net C exchange with the atmosphere, and the climatic responses to atmospheric $[CO_2]$ will be incorrect if the magnitude of the CO_2 fertilization effect is not represented accurately.

Experimental data should provide useful guidance to models, thereby increasing our confidence in model predictions. Experiments have unequivocally shown that plants can grow faster and larger in a CO_2-enriched atmosphere (6–8), and the mechanisms of response are well understood (4). The relevance of this evidence to prediction of global C budgets over decadal time frames, however, may be limited. As spatial and temporal scales increase beyond what can be captured in experiments, modifying influences of resource availability and biogeochemical feedbacks within the ecosystem become increasingly important, and these tend to diminish the simple response to elevated $[CO_2]$ observed in small-scale experiments. The problem is especially severe with forests because of the inherent difficulty in conducting relevant experiments at appropriate spatial and temporal scales with large and long-lived organisms and complex ecosystems. Nevertheless, the potential responses of forests to rising $[CO_2]$ cannot be ignored in global C cycling analyses and predictions of climatic change because forest ecosystems contribute $\approx 50\%$ of global NPP and $\approx 80\%$ of terrestrial NPP (9). With the development of Free-Air CO_2 Enrichment (FACE) technology (10, 11), it is now possible to elevate atmospheric $[CO_2]$ in large plots in intact forest ecosystems without altering other microclimatic and biotic variables (12). Recognizing that the results from any single experiment may not be broadly representative, here we provide the an analysis of NPP data from the four FACE experiments operating in forest stands.

Materials and Methods

The forest stands examined in the FACE experiments (Table 1) represent a broad range of productivity, climatic and soil con-

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Table 1. Characteristics of the four FACE experiments

Characteristic	DukeFACE	AspenFACE	ORNL-FACE	POP-EUROFACE
Location	Durham, NC	Rhinelander, WI	Oak Ridge, TN	Tuscania (Viterbo), Italy
Latitude, longitude	35°58′N, 79°05′W	45°40′N, 89°37′W	35°54′N, 84°20′W	42°22′ N, 11°48′E
Mean annual precipitation, mm	1,140	810	1,390	818*
Mean annual temperature, °C	15.5	4.9	14.2	14.1
Growing season,[†] days	200	150	190	247
Soil classification (U.S.)	Ultic Hapludalf	Alfic Haplorthod	Aquic Hapludult	Pachic Xerumbrept
Soil texture	Clay loam	Sandy loam	Silty clay loam	Loam and silt loam
Total soil N, g·kg^{-1}	0.79	1.20	1.12	1.1–1.4
Overstory vegetation	*Pinus taeda* L.	*Populus tremuloides* Michx., *Acer saccharum* Marsh., *Betula papyrifera* Marsh.	*Liquidambar styraciflua* L.	*Populus alba* L., *P. nigra* L., *P. × euramericana* Dode Guinier
Peak leaf area index,[‡] m²·m^{-2}	3.4	2.7–3.4	5.5	4.6–7.4
Year planted	1983	1997	1988	1999
Year treatment initiation	1996	1997	1998	1999

*The POP-EUROFACE experiment used irrigation to avoid drought, so inferences regarding precipitation should be avoided for this site.

[†]For deciduous stands, the growing season is the duration that trees have leaves; for the evergreen system, it is the period of active stem growth.

[‡]Values of leaf area index are expressed as leaf area per ground area; the range in values describes portions of experimental plots occupied by different species after LAI was no longer increasing.

ditions, stand developmental history, and life history characteristics of the dominant species, although all four are young stands in the temperate zone. Two experiments were initiated in established monoculture plantations that had fully occupied the sites: an evergreen loblolly pine (*Pinus taeda*) stand at Duke-FACE and a deciduous sweetgum (*Liquidambar styraciflua*) stand at ORNL-FACE. The other two experiments, Aspen-FACE and POP-EUROFACE, comprise simple multispecies assemblages dominated by *Populus* spp. that were initiated on previously bare ground.

Each experiment used FACE technology to control the CO_2 concentration in the atmosphere in replicated 25- to 30-m-diameter plots in the tree stands. The DukeFACE, ORNL-FACE, and AspenFACE experiments used similar technology, whereby pure CO_2 was mixed with a turbulent air-stream in a plenum and released through vertical vent pipes at the up-wind side of each plot (10). In the POP-EUROFACE experiment, pure CO_2 was released at supersonic velocity directly into the atmosphere from pipes on the up-wind side of each plot (11). The average atmospheric [CO_2] in current-CO_2 plots across all years of these experiments was 376 ppm, and the FACE systems (10, 11) provided additional CO_2 sufficient to maintain an average concentration (across all experiments) in the elevated-CO_2 plots of 550 ppm (13). These CO_2 treatments were chosen on the basis of current projections of atmospheric [CO_2] anticipated for 2050 (14). Detailed descriptions of the exposure systems and the CO_2 concentration dynamics are provided for DukeFACE (10), ORNL-FACE (15), AspenFACE (16, 17), and POP-EUROFACE (11).

Our analysis of NPP was based on all years and subplots for which data were available and canopy development was complete. Our goal was to understand the response of closed-canopy forests. We therefore excluded data from stands with an expanding canopy, which would not be informative of the response of the global forest (7). For ORNL-FACE and DukeFACE, the CO_2 treatments were initiated after canopy development was complete, and 5–6 years of data were used (1999–2003 and 1997–2002, respectively). The plots in the AspenFACE experiment were planted half with a monoculture of trembling aspen (*Populus tremuloides*), one fourth with an equal mixture of trembling aspen and paper birch (*Betula papyrifera*), and one fourth with a mixture of trembling aspen and sugar maple (*Acer saccharum*). On the basis of our canopy closure criterion, 1 year (2003) of data from the aspen stand and 3 years (2001–2003) from the aspen–birch stand were included in the analysis; the

aspen–maple stand was not included because the canopy was still open. Six of the 12 plots in AspenFACE received elevated concentrations of ozone; these were not included in the analysis. The plots in the POP-EUROFACE were split into subplots, each occupied by a different *Populus* species; data from all subplots from 2000–2001 were used.

NPP, expressed as grams of C per square meter of land surface per year, was calculated as annual carbon increments (I_{wood} + I_{leaf} + $I_{coarse\ root}$ + $I_{fine\ root}$), plus the major inputs to detritus, litterfall, and fine root turnover ($D_{litterfall}$ + $D_{fine\ root}$) (18), although different approaches were used in the four experiments. The annual increments of stem wood (I_{wood}) and coarse woody root ($I_{coarse\ root}$) were estimated by applying site-specific allometric equations to periodic measurements of the diameter of trees in current and elevated CO_2 plots. Harvest data from the POP-EUROFACE (19) and AspenFACE experiments (20); and the tree height–diameter relationship for trees at DukeFACE (21) indicate that exposure to elevated [CO_2] did not affect the allometric relationships between plant parts. The allometric equation used at ORNL-FACE incorporated basal area, height, taper, and wood density to reduce the possibility of the allometry being altered by elevated [CO_2] (15). In the pine forest at DukeFACE, I_{leaf} also was estimated from allometric regression (22) applied at different intervals (18); I_{leaf} = 0 for the deciduous forests. The production of leaf litter ($D_{litterfall}$) was estimated from litter baskets at all sites (23–25). In most cases biomass measurements were converted to C units by using the measured C content of different tissues, which varied between 0.4 and 0.5 (26, 27); when measured values were not available, C content was assumed equal to 0.5.

The contribution of fine roots ($I_{fine\ root}$, $D_{fine\ root}$) to NPP typically was low in these forests ($\approx$3% in AspenFACE, 6% in DukeFACE, 7% in POP-EUROFACE, and 16% in ORNL-FACE) and was estimated differently among sites. At ORNL-FACE (28) and PopFACE (29), fine-root production was measured directly by using minirhizotrons and in-growth cores. The DukeFACE experiment used a compartment flow model for estimating fine-root production (30); AspenFACE calculated fine-root turnover from published rates of aspen fine-root production and mortality (31) that were then applied to allometrically determined peak standing fine-root biomass (20). Other components of NPP (e.g., losses to herbivory and root exudation) were not included in our analysis because data were not available. The combined contribution of herbivory and dissolved organic C in the DukeFACE experiment was only 3%
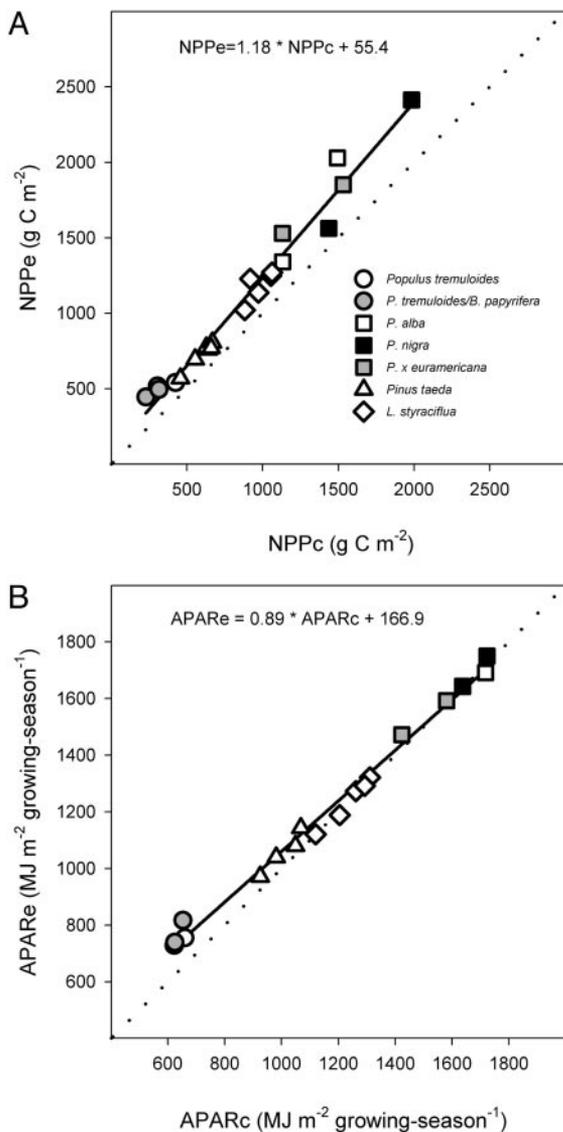
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Fig. 1. Responses of NPP and APAR to elevated [CO_2] in four FACE experiments in forests. (*A*) Regression of NPPe (550 ppm) as a function of NPPc (376 ppm). The coefficient of determination (R^2) of regression is 0.97, $P < 0.001$. The intercept is not significantly different from 0; the slope is significantly different from 1. (*B*) Regression of APAR in elevated vs. current [CO_2]. The coefficient of determination (R^2) of regression is 0.99, $P < 0.001$. The intercept is significantly different from 0, and the slope is significantly different from 1. Sources of data are given in Table 1; data are included only from years after LAI was no longer increasing. Data were analyzed by using error-in-variables (EIV) regression (SAS Proc NLP). The dotted line represents the 1:1 relationship.

of NPP (18), so it is unlikely that their exclusion would alter our results.

Absorbed photosynthetically active radiation (APAR, or the light energy in megajoules absorbed by the canopy) was estimated from the difference between quantum sensor measurements of down-welling radiation (400–700 nm) and the amount reaching the forest floor (POP-EUROFACE and ORNL-FACE) (19, 25) or by applying a Beer's Law approximation to measurements of leaf area index (LAI) (21). Values of APAR were integrated over the growing season.

Results

The relationship between NPP in elevated [CO_2] (NPPe) and NPP in current [CO_2] (NPPc) (Fig. 1*A*) was remarkably consis-
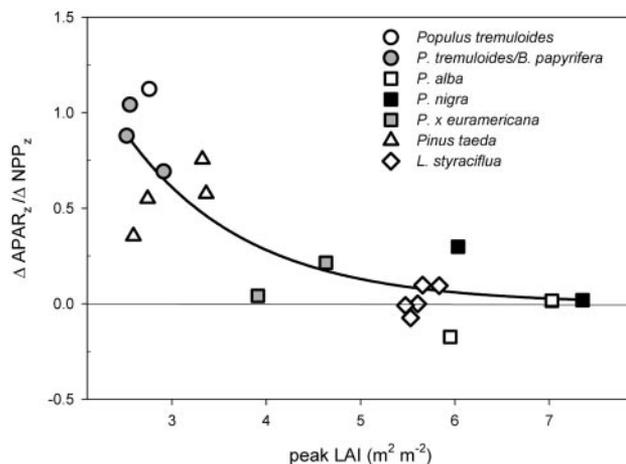

Fig. 2. Fraction of gain in NPP attributable to a gain in APAR declines as peak seasonal LAI increases. ΔNPP and ΔAPAR were normalized to the maximum values observed. Regression equation is: $\Delta APAR_z/\Delta NPP_z = 6.19 \times \exp(-0.77 \times LAI)$; $R^2 = 0.73$, $P < 0.001$.

tent across a broad range of productivity. Although many important forest types are missing in this analysis (e.g., boreal and tropical forests, in which FACE experiments have not been conducted), the range in NPP comprises much of the range observed among forests globally (9) and represented in models (32). The linear relationship between NPPe and NPPc is different from the 1:1 line ($P < 0.0001$), indicating a significant effect of [CO_2] on NPP. The positive intercept implies that as NPP increases, the CO_2 response declines, but this response was defined primarily by a single experimental forest stand, and the intercept is not significantly different from zero. Rearranging the regression equation gives the CO_2 response ratio as NPPe/NPPc = 1.18 + 55/NPPc, with NPPc expressed as g of C per m^{-2} yr^{-1}. At the median of the range of NPP in our data set, the CO_2 response ratio as predicted by the regression was 1.23 ± 0.02.

LAI in high LAI stands was generally similar in current and elevated [CO_2] (data not shown), so APAR in these stands also was similar (Fig. 1*B*). If APAR did not increase, then the response of NPP derived not from increased energy capture but primarily from higher efficiency by which light energy is converted to organic matter (light-use efficiency, ε). We assessed this by calculating the fraction of the normalized gain in NPP attributable to a gain in APAR (Fig. 2). In the lower LAI stands, 60–90% of the gain in NPP with CO_2 fertilization was associated with increased APAR, whereas in high LAI stands there was little gain in APAR even when CO_2 enrichment caused higher LAI.

Discussion

Our analysis indicates a 23% increase in forest NPP as atmospheric [CO_2] increases to 550 ppm over the next few decades. The logarithmic biotic growth factor (β-factor) formulation, which expresses the response as a function of the relative [CO_2] increase (8, 33), calculated from these data are 0.60. A 23% enrichment response is less than that of previous syntheses of tree growth (not NPP) responses, which ranged from 29% in an analysis dominated by short-term seedling studies (6) to 55% (median value) for field-grown trees (7). However, these older analyses considered higher CO_2 concentrations, generally 300 ppm higher than ambient, and often only aboveground biomass increment, so the results are not directly comparable. The wide variation among these older values has resulted in substantial uncertainty as to the true response, and they could not be used with confidence because, in experiments with individual, fast-growing seedlings and saplings, growth responses are confounded with ontogeny (7).

A useful analytical tool for interpreting plant responses that are confounded with ontogenetic or stand development has been to separate the response into structural and functional components (25), which also is an important analytical framework used in ecosystem models (34) and remote sensing analysis (32). Here, the structural component is leaf area by which light is absorbed, and the functional component is the conversion of light energy to organic matter. Our analysis suggested that at low LAI, elevated [CO_2] was causing structural changes and increased APAR even after LAI in current [CO_2] had reached a maximum. At higher LAI, there was no additional gain in light absorption even if elevated [CO_2] increased LAI (a consequence of Beer's Law), and increased NPP in elevated [CO_2] was primarily or wholly attributable to increased ε.

Our experimental evidence provides a standard to evaluate models that generate predictions of a NPP response to CO_2 fertilization as an intermediate step in predicting a C cycle feedback between the biosphere and atmosphere. Six dynamic global vegetation models predicted increasing global NPP in response to rising [CO_2], with the forcing defined by the IS92a emissions scenario (14) and the response based on a standard photosynthesis model (5). The increase in NPP between 1999 and 2049 (the years corresponding to the current and elevated [CO_2] in our data set) ranged from 15% to 32%, indicating some substantial discrepancies between models and data. Nevertheless, the average of the six models was 22%, in close agreement with the mean response of 23% reported here. A coupled carbon-climate model (1), which prescribes the CO_2 fertilization response using a β-factor formulation (35), used a β of 0.65 as the "control" value, also in good agreement with our experimental results. Although there are other assumptions involved in the subsequent calculations of net ecosystem production and in the interactions between [CO_2] effects and climate change influences, the congruence of the NPP predictions with the experimental evidence we present here should add confidence in overall model results.

The concurrence across sites in the NPP response does not resolve all issues attending CO_2 fertilization. The mean response, while appropriate for global analyses, masks several sources of significant variation that could be especially important in determining how a specific site will respond to rising [CO_2]. At the DukeFACE, a wide range of response to CO_2 enrichment across replicate plots correlated with differences in soil N availability. Under low N availability, CO_2 enrichment increased NPP by 19%, whereas under intermediate and high N availability the percent CO_2 stimulation was 27% (36). Where soils are poor or prolonged water limitation occurs, represented only through within-site variation in our dataset, forests may have limited capacity to support any response to CO_2 enrichment (37). Concurrent increases in tropospheric ozone could negate the productivity increases from elevated [CO_2] (17, 20). In addition to controlling spatial variability in response, N availability may also be a factor in determining whether the responses observed here can be sustained for decades (38, 39). The data in our analysis all come from fast-growing, early successional stands, and there has been no evidence to date for a negative feedback on NPP through N availability in these stands (20, 40, 41).

NPP represents the amount of organic C entering an ecosystem; it does not address the fate of that C. Model comparisons demonstrate that whether additional C storage occurs in vegetation or in soil is crucial to understanding the future C cycle and its control of the climate system (2). Experimental results demonstrate that the partitioning of C between plant organs with different turnover rates determines the potential of an ecosystem to store additional C and whether the storage occurs in plant biomass or in soil. At Duke-FACE, increased NPP was associated with C sequestration in stem wood (18, 42), whereas at ORNL-FACE increased NPP was partitioned to production of fine roots (28). Fine roots decompose rapidly and add C to soil, where most is respired by microbes, but a fraction may be sequestered into soil organic matter pools (28). Although the two forests have a similar NPP response to CO_2 enrichment, and over the short term their net ecosystem production response was similar (42), the longer-term trajectory of C cycling will differ. In our four-site dataset, the percentage of NPP gain partitioned to wood varied from 11% to 93%, and there was no discernible pattern between forest types. Global productivity models vary nearly as much in the fraction of C stored in vegetation vs. soil: from 35% to 85% (2). Results from some of the DukeFACE plots showed that the enhancement in wood production under CO_2 enrichment was not sustained at levels observed during the first 3 years of the experiment, but the initial enhancement was reestablished in half a plot that was supplied with nitrogen (37). Imposing additional treatments on existing FACE experiments or designing experiments that account for multiple constraints will remove some of the uncertainty in the controls over partitioning. With the response of NPP to CO_2 fertilization better resolved, it becomes especially important to understand the controls on C partitioning as a priority challenge in relating NPP to C cycling and storage in forest ecosystems.

The effect of CO_2 fertilization on forest NPP is now firmly established, at least for young stands in the temperate zone. Recent observations of older and larger deciduous trees in a mature Swiss forest (43) demonstrated that physiological responses (e.g., photosynthesis, foliar N and nonstructural carbohydrate concentrations) were similar to those of younger trees, thereby increasing our confidence that our results are more generally relevant. NPP and stand-level growth responses could not be measured in the Swiss study, but stem basal area increment was not significantly stimulated by elevated CO_2. Although interpreted as an indication of C saturation (43), this conclusion was based on the stem growth response of only 10 CO_2-enriched trees with high variance, and it is not at odds with our conclusion about the response of NPP. While the ongoing FACE experiments will continue to provide data relevant to questions about the fate of additional C in CO_2-enriched forests, there is not a compelling reason for new, single-factor FACE experiments in young, temperate-zone forests. Rather, the limitations of our current data show the need for new experiments in mature forests and in unexplored biomes, particularly tropical forests that contribute much to global NPP.

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