Growth enhancement due to global atmospheric change as predicted by terrestrial ecosystem models: consistent with US forest inventory data

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Abstract

Small reported growth enhancement factors based on analyses of forest inventory data from the eastern USA (Caspersen *et al.* 2000, Science, 290, 1148–1151) have been interpreted as evidence against CO₂ fertilization in natural forests. We show to the contrary that growth enhancement in response to rising CO₂, as found in ecosystems with experimental CO₂ enrichment and implemented in terrestrial ecosystem models, is consistent with the data that have been presented within their uncertainties. Comparing forest inventory data with results of an empirical model of age-dependent biomass accumulation, we find that growth enhancement of plausible magnitude could not be detected in these data, even if it were present. Although forest regrowth due to land-use change is recognized as an important cause of carbon uptake by eastern US forests, forest inventory data do not provide a basis for eliminating environmentally induced growth enhancement as a substantial contribution to the global terrestrial carbon sink.

Keywords: carbon, CO₂, ecosystem models, fertilization, forest inventory, growth enhancement

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Introduction

Enhancement of tree growth, in response to globally rising atmospheric CO2 concentration and regional increases in the input of reactive N, is a key issue in understanding the fate of anthropogenic CO₂ and the location of the global terrestrial carbon sink (Prentice et al. 2001). Caspersen et al. (2000) used forest inventory data from five states of the eastern USA to estimate growth enhancement over the past century. They obtained estimates in the range of +0.001 to +0.01% per year. Such values are smaller than the CO₂-induced enhancement of net primary production by ca +0.1% per year, typically simulated by global terrestrial ecosystem models over the same period (Kicklighter et al. 1999; Cramer et al. 2001; Joos et al. 2001; McGuire et al. 2001). The small growth enhancement factors reported by Caspersen et al. (2000) have been interpreted as evidence against CO₂ fertilization in natural forests (e.g. Sarmiento 2000; Davidson & Hirsch 2001; Scholes & Noble 2001).

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In Caspersen *et al.* (2000), aboveground carbon accumulation since stand establishment was investigated by analysing data from the US Forest Inventory and Analysis (FIA) database. These data were derived from a sample of > 20~000 plots, sampled around 1980 and again in the early 1990s. Two main findings were presented by Caspersen *et al.* (2000).

- First, the overwhelming majority of carbon accumulation on previously cleared plots is due to forest regrowth. Biomass stored in living trees, and the annual increment in tree biomass, depend on age. In other words: the main mechanism of carbon storage in a growing forest is growth.
- More importantly, Caspersen *et al.* (2000) estimated how much tree growth and mortality rates have changed during the past century. They obtained statewide averages of biomass by age class, growth as a function of stand age (or biomass), and mortality rates (assumed constant with age) for the 1980s. They applied a simple empirical model for biomass accumulation with age. Past growth enhancement, changes in mortality rates, and biomass at age zero were

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determined so as to minimize the deviations between simulated biomass and the statewide-averaged biomass estimated from the inventory data for each age class, allowing growth and mortality rates to vary linearly in time. Changes in mortality estimated in this way were between -0.007 and +5% per year, and changes in growth between +0.001 and +0.01% per year, for the period up to 1980.

Here we present results obtained using the growth model of Caspersen *et al.* (2000) in a prognostic way to simulate forest biomass development with or without growth enhancement, and we compare the results with forest inventory data obtained from the same source. We chose parameter values to yield illustrative results: our approach did not require fine-tuning the model to fit the data. Our goal was to re-assess the overall interpretation of the data presented by Caspersen *et al.* (2000), and to evaluate their implications for current understanding of the global carbon cycle.

Data and methods

Biomass and stand age were extracted from the FIA database (http://www.srsfia.usfs.msstate.edu/) for Michigan, excluding plots in one of the database categories 'planted stands', 'nonforested land', 'census water', and trees with a nonliving status, from the calculation. The biomass (dry weight) of each plot was computed using data and conversion factors as given in the FIA database. A factor of 2.1 was used to convert mass of green biomass into dry weight (R. Birdsey, pers. comm.). Area-weighted average biomass at each age was calculated. We note that the estimated biomass at young stand ages can be inflated due to extant trees in the measured plots being older than regenerating trees.

We implemented the growth model of Caspersen *et al.* (2000) with variation in the parameters representing time-dependent changes in growth β , and mortality rate α . Growth G was computed as a function of chronological time t, and stand age A, as follows:

$$\begin{split} G(t,A) &= 2.4 \text{ tons ha}^{-1} \text{yr}^{-1} \\ &\quad \cdot \left\{ 0.12 + 0.88 \cdot \left(1 - \exp \frac{-A}{4 \text{yr}} \right) \right\} \\ &\quad \cdot \left\{ 1 - \beta \cdot (1980 - t) \right\}. \end{split} \tag{1}$$

The growth enhancement parameter β was varied between zero and 0.1% year⁻¹. Mortality M was calculated as a function of biomass B, age, and time:

$$M(t,A) = 0.021 \text{yr}^{-1} \cdot B(t,A) \cdot \{1 + \alpha \cdot (1980 - t)\}.$$
 (2)

The mortality trend parameter α was varied between +0.19% year⁻¹ (as estimated for Michigan by Caspersen *et al.* 2000) and -0.19% year⁻¹.

By definition, the biomass in 1980 is the integral of the difference between growth and mortality over the period since stand establishment. This integral over age was solved for different stand ages A (t = 1980), substituting the chronological time t, in Equations 1 and 2 by:

$$t = 1980 - A(t = 1980) + A. (3)$$

Biomass at stand age zero was taken to be 15 tons ha⁻¹. Biomass at stand age zero can be considerable in the FIA database due to either a few large residual trees in a regenerating plot or when a few trees from a neighbouring old stand are included in the sample.

We emphasize that the constants in Equations 1 and 2 and biomass at age zero were chosen to yield illustrative results and that our conclusions do not depend on their exact values. Similarly, growth *G* may be formulated as a function of biomass instead of age as shown in Equation 2. Random variables used by Caspersen *et al.* (2000) in their optimization procedure (see their supplementary material), are not required for our illustrative calculations and omitted in the above equations.

Results and discussion

Figure 1 illustrates the simulated dependence of 1980 stand biomass on stand age. The simulated biomass was found to vary by less than 3% for variations in the growth enhancement factor between zero and +0.1% per year. This last value is typical for present ecosystem models when forced by the observed changes in CO2 concentration over the same period. The sensitivities of simulated biomass to a unit change in the growth enhancement parameter β or in the mortality trend parameter α are similar. For young stands, the deviations due to variations in β are larger than those due to variations in α , but the deviations for both factors are very small. Varying biomass at stand age zero, B(t, A = 0), which was determined by Caspersen *et al.* (2000) together with α and β in their optimization procedure, around its standard value of 15 tons ha⁻¹ causes additional deviations in the simulated biomass around the time of the first forest inventory B(t = 1980, A) (not shown in Fig. 1). These results imply that it is problematic to determine α , β , and biomass at stand age zero precisely, and to disentangle small changes in growth from small changes in mortality rates using forest inventory data in the manner of Caspersen et al. (2000).

Further, biomass stored in living trees varies considerably among plots, independent of age class (Fig. 2). It is instructive to compare the very small variations in

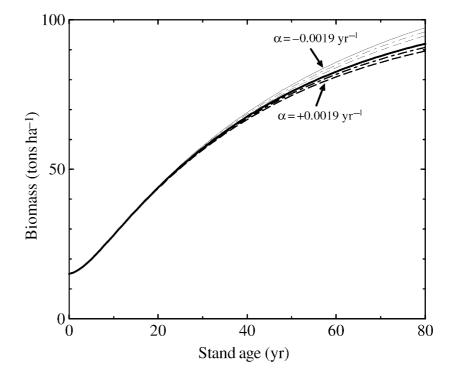


Fig. 1 Simulated biomass at year 1980 as a function of stand age for different growth enhancement factors β , and different factors for changes in mortality rates α , as calculated applying the growth model of Caspersen et al. (2000). Solid lines: $\beta = 0$, dot-dashed lines: $\beta = 0.05\% \text{ year}^{-1}$, dashed $\beta = 0.1\% \text{ year}^{-1}$. Thick lines: $\alpha = 0.19\%$ year⁻¹, thin lines: $\alpha = -0.19\%$ year⁻¹.

biomass obtained by varying the model parameters (Fig. 1) with the very large variability shown in the forest inventory data themselves (Fig. 2). Phillips et al. (2000) estimated standard errors for tree volume calculations from the FIA data for individual states in the southeastern US to be in the range of 1-2% for state-wide total growing-stock volume and of 1-4% for state-wide net growth (G-M). The errors in biomass, growth, and mortality for a particular age class, as used to determine growth enhancement by Caspersen et al. (2000), must necessarily be larger than the uncertainty for state-wide averages that include all age classes, and thus larger than the effects of varying growth enhancement or mortality through plausible ranges (Fig. 1). It follows that uncertainties in the forest inventory data as used by Caspersen et al. (2000) do not allow discrimination between the null hypothesis of no growth enhancement, and the alternative of growth enhancement as implemented in current global ecosystem models.

The modelled effect of rising CO2 during the forest growth period is small, in part because the rate of CO₂ increase during this interval was relatively modest. If we approximate the growth enhancement effect of CO2 conventionally by:

$$G(t) = G(t_0) \cdot \left\{ 1 + \beta' \cdot \ln \frac{\text{CO}_2(t)}{\text{CO}_2(t_0)} \right\},$$
 (4)

then a growth enhancement of 0.1% year⁻¹ during the period of interest corresponds to a fertilization factor β' of

0.36. This value implies that a doubling of atmospheric CO₂ concentration would produce a 25% increase in growth. However, Caspersen et al. (2000) used as an example (their Figs 1 and 2) a hypothetical growth enhancement factor of 0.5% per year ($\beta' = 1.8$). Such an enhancement is three to four times larger than has been found in the Free Air CO2 Enrichment (FACE) experiment at Duke Forest (e.g. DeLucia et al. 1999), which has been suggested to represent an upper bound of the likely sustainable CO2 effect in natural ecosystems (DeLucia et al. 1999; Oren et al. 2001). Yet even relatively small growth enhancements have potentially large implications for terrestrial carbon storage. The mechanisms by which enhanced growth can translate into a (transient) carbon sink in vegetation and/or soils under conditions of continuously rising atmospheric CO₂ concentration are well known and have been summarized by Prentice et al. (2001). A growth enhancement of 0.08% year⁻¹ $(\beta' = 0.287)$ applied in a simplified four-box model of the terrestrial biosphere (Joos et al. 1996) yielded a carbon uptake of 1.3 PgC year⁻¹ by 1990. The simulated integrated terrestrial carbon uptake of 69 PgC up to 1990 obtained by Joos et al. (1996) is similar to values of 74 and 90 PgC obtained with process-based, spatially explicit global simulations with the Terrestrial Ecosystem Model (TEM: Kicklighter et al. 1999) and the Lund-Potsdam-Jena Dynamic Global Vegetation Model (LPJ: Cramer et al. 2001; Joos et al. 2001), respectively. Such an enhancement is sufficient to explain the residual

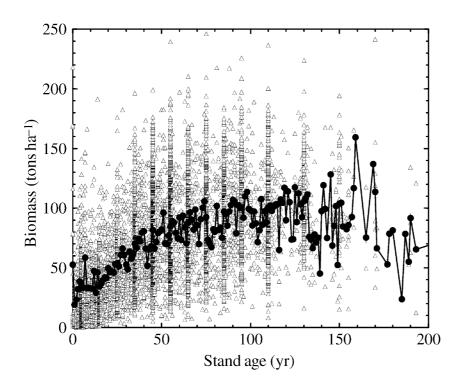


Fig. 2 Biomass vs. stand age for managed, regrowing forest plots in Michigan state (triangles). The data are from the US Forest Inventory and Analysis (FIA) database and sampled around 1980. The circles connected by the solid line represent area-weighted averages for each year since stand establishment.

terrestrial sink implied by the global atmospheric CO₂ budget (Prentice *et al.* 2001).

Finally, we note that the FIA data cannot in principle give information about whole-ecosystem carbon balance. Plausible changes in the allocation of carbon to leaves or roots vs. stems, and possible increases in carbon stored in woody detritus and soils (see, e.g. Ceulemans *et al.* 1999; Allen *et al.* 2000), could not be detected. Thus, even if stem biomass growth and mortality trends could be characterized with sufficient precision, definitive information on trends in ecosystem carbon storage would still be lacking.

Our analysis implies that any plausible degree of growth enhancement in response to rising CO₂ is consistent within the uncertainties with forest inventory data from the eastern USA. Growth enhancement due to rising CO₂ and/or reactive N deposition may be contributing substantially to the present global terrestrial carbon sink (Prentice *et al.* 2001) and to carbon uptake by eastern US forests. This conclusion does not conflict with the idea that land-use change has promoted additional carbon storage in areas of secondary forest regrowth, as proposed by Caspersen *et al.* (2000), McGuire *et al.* (2001), and others.

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