

Evidence for a recent increase in forest growth is questionable

In a recent article, McMahon et al. (1) examined forest-plot biomass accumulation across a range of stands in the mid-Atlantic United States and suggest that climate change and trends in atmospheric CO₂ explain an increase in forest growth. To show this increase, they fit a simple model to live above-ground forest biomass (AGB) as a function of stand age, and then propose that the derivative of this model is the expected rate of ensemble biomass change (ΔAGB). They conclude that biomass changes within census plots that exceed the ensemble expectation constitute recent increases in growth rates.

We disagree with this conclusion, and instead, we suggest that (i) ΔAGB is incorrectly equated with forest growth, because it ignores past mortality that could explain the difference in rates, (ii) stated trends in plot-species composition could account for plot AGB trajectories that differ from ensemble-model expectations, and (iii) the authors' model and confidence bounds (CIs) are overly conservative (2), making overlap of rates unlikely.

McMahon et al. (1) equate the derivative of their model with annual growth, but a more complete definition of ΔAGB is described by Caspersen et al. (3) as

$$\Delta AGB = +Biomass(Growth) - Biomass(Mortality).$$

Biomass change within plots may deviate from the median expectation because of differences in growth or mortality rates (Fig. 1). Either rate can vary among plots and through time because of species composition, age structure, herbivory, defoliation, competition, developmental stage, disturbances, etc. Based on ΔAGB data alone, there is no way to determine if growth rates were higher, as the authors assert, or if mortality rates were lower than expected over the last 22 years (Fig. 1). Excluding plots with significant mortality ($-\Delta AGB$) (1) only exacerbates this problem.

Mortality also factors into the authors' assumed succession sequence from young stands dominated by tulip poplar to older oak-hickory stands (1). Because tulip poplar grows very fast, gets very large, and is long-lived (~250 years), young tulip poplar stands cannot transition to oaks over the time frame discussed

without experiencing significant biomass loss. In the classic ecosystem-development context (5), aggrading forest stands do accumulate biomass faster than an asymptotic model would suggest, precisely because old stands in the model experienced substantial past mortality before measurement.

Thus, although simple models such as the Monod function (1) can approximate the median relationship in AGB data, they are considered inadequate to fully capture the dynamics of forest-biomass accumulation (5). Furthermore, Clark et al. (2) recommend wider Bayesian CIs that would encompass most of the plot-level variability in AGB and ΔAGB observed in ref. 1. Instead, the authors described applying CIs from parameter estimation to plot-level $\Delta AGBs$ (figure 2b in ref. 1) when much wider prediction intervals were necessary. We suspect that more appropriate CIs and a complete accounting of uncertainty in plot AGB and stand-age estimation may eliminate the difference between observed and expected $\Delta AGBs$ that is attributed to recent increases in growth.

The evidence cited by McMahon et al. (1) is unconvincing and certainly does not prove an actual change in recent forest-growth rates; thus, their subsequent speculation on causes including possible CO₂ fertilization, although interesting, is premature.

Jane R. Foster^{a,1}, Julia I. Burton^a, Jodi A. Forrester^a, Feng Liu^a, Jordan D. Muss^a, Francesco M. Sabatini^b, Robert M. Scheller^c, and David J. Mladenoff^a

^aDepartment of Forest and Wildlife Ecology, University of Wisconsin, Madison, WI 53706; ^bDepartment of Plant Biology, Sapienza, University of Rome, 00185 Rome, Italy; and ^cDepartment of Environmental Sciences and Management, Portland State University, Portland, OR 97207

1. McMahon SM, Parker GG, Miller DR (2010) Evidence for a recent increase in forest growth. *Proc Natl Acad Sci USA* 107:3611–3615.
2. Clark JS, Mohan J, Dietze M, Ibanez I (2003) Coexistence: How to identify trophic trade-offs. *Ecology* 84:17–31.
3. Caspersen JP, et al. (2000) Contributions of land-use history to carbon accumulation in U.S. forests. *Science* 290:1148–1151.
4. Jenkins JC, Birdsey RA, Pan Y (2001) Biomass and NPP estimation for the Mid-Atlantic region (USA) using plot-level forest inventory data. *Ecol Appl* 11:1174–1193.
5. Bormann FH, Likens GE (1979) *Pattern and Process in a Forested Ecosystem* (Springer, New York), pp 164–191.

Author contributions: J.R.F. performed research; J.R.F. analyzed data; and J.R.F., J.I.B., J.A.F., F.L., J.D.M., F.M.S., R.M.S., and D.J.M. wrote the paper.

The authors declare no conflict of interest.

¹To whom correspondence should be addressed. E-mail: jrfoster@wisc.edu.

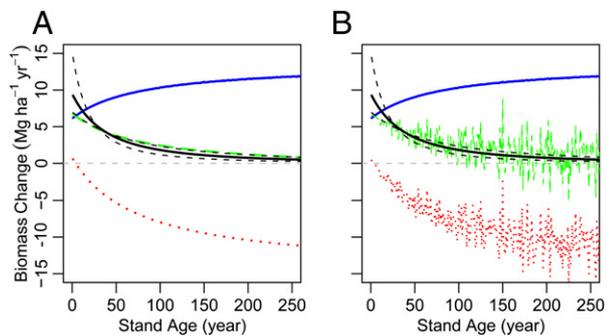


Fig. 1. (A) Derivative of McMahon et al.'s (1) AGB model (black) with 95% CIs (black dashes) (table 2 in ref. 1). We calculated above-ground net primary productivity (growth; blue) as a function of AGB using equations derived from Forest Inventory and Analysis plot data for the Mid-Atlantic states region (figure 9 in ref. 4). We estimated biomass lost to mortality assuming a constant annual mortality rate of 2.1% (3) of ensemble AGB (red dotted line). The sum of growth and mortality gives us an estimate of biomass change (green dashes), which corresponds with the authors' model and confirms the definition of ΔAGB (1). We note that temporal variability in either mortality or growth rates could cause point estimates of ΔAGB from census plots to deviate from the model CIs. (B) To illustrate this, we allow the mortality rate to vary randomly over time, assuming that it is $\sim N(0.021, 0.005)$. We find that varying mortality rates (red) cause the observed ΔAGB (green) to frequently fall outside of the model expectations (black lines). If mortality rates decline to 1% for remeasurement intervals similar to those cited by McMahon et al. (1), the resulting $\Delta AGBs$ exceed the upper confidence bound by approximately the amount observed by the authors (3–4 Mg·ha⁻¹·yr⁻¹).