Evidence for a recent increase in forest growth

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Forests and their soils contain the majority of the earth’s terrestrial carbon stocks. Changes in patterns of tree growth can have a huge impact on atmospheric cycles, biogeochemical cycles, climate change, and biodiversity. Recent studies have shown increases in biomass across many forest types. This increase has been attributed to climate change. However, without knowing the disturbance history of a forest, growth could also be caused by normal recovery from unknown disturbances. Using a unique dataset of tree biomass collected over the past 22 years from 55 temperate forest plots with known land-use histories and stand ages ranging from 5 to 250 years, we found that recent biomass accumulation greatly exceeded the expected growth caused by natural recovery. We have also collected over 100 years of local weather measurements and 17 years of on-site atmospheric CO₂ measurements that show consistent increases in line with globally observed climate-change patterns. Combined, these observations show that changes in temperature and CO₂ that have been observed worldwide can fundamentally alter the rate of critical natural processes, which is predicted by biogeochemical models. Identifying this rate change is important to research on the current state of carbon stocks and the fluxes that influence how carbon moves between storage and the atmosphere. These results signal a pressing need to better understand the changes in growth rates in forest systems, which influence current and future states of the atmosphere and biosphere.

Results and Discussion

The Monod function effectively describes the increase in biomass of forests during recovery and thus, is appropriate to model patterns of resource use and limitation (10). The function for stand biomass in megagrams per hectare (Mg ha⁻¹) for stand i is (Eq. 1):

$$\text{AGB}_i = \beta_0 + \beta_1 \left( \frac{\text{SA}_i}{\text{SA}_i + \theta} \right),$$

where $\beta_0 + \beta_1$ is the asymptote for the maximum biomass that a stand can achieve, $\text{SA}_i$ is the age of the stand, and $\theta$ is the age at half-saturation of the function.

We estimated the parameters $\beta_0$, $\beta_1$, and $\theta$ across the plots using hierarchical Bayesian methods (modified from ref. 21). We estimated biomass using species-specific algorithms relating diameter at breast height (DBH) to total AGB. Stand age was estimated from tree-ring counts of cores of the 10 largest trees immediately outside of the stand-plot boundary (see ref. 22 for detailed methods) and historical photographs of the stand sites (Materials and Methods). Fig. 1 shows the fit of Eq. 1 for 55 sites in red and 50 sampled curves from the posterior distributions of the estimated parameters in light blue. The blue lines highlight variation in parameter fits and not process error, which is larger and encompasses all plots. This is intended to show uncertainty in expectation of growth rates, which are defined as the tangent of these lines, but not intended to show if some sites have overall different biomass estimates than the mean. For sites that had multiple censuses, we used mean biomass at the mean stand age of those censuses to estimate function parameters.

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These high biomass-rate increases across stand age must be a recent phenomenon. Extrapolating observed annual growth rates backward would lead either to dramatically lower than estimated stand ages or unrealistic biomass gain functions. Many potential mechanisms can influence the rate of biomass change. Table 1 lists six hypotheses that might explain the difference between the observed and expected values that we found. Increases in temperature, growing season, and atmospheric CO₂ have documented influences on tree physiology, metabolism, and growth, and likely, they are critical to changing the rate of stand growth observed across stands.

**Increased Temperature.** Temperature is critical to all metabolic processes involved in uptake, release, and storage of carbon. Rising temperatures, especially when coinciding with adequate precipitation and without resource limitation, can increase tree metabolic processes that, in turn, lead to higher biomass accumulation (6, 23). Temperate forest trees have shown a broader range of temperatures for optimal photosynthesis than have tropical forests, and they can likely respond quickly to increased temperatures (24). Observational studies correlating temperature to diameter growth across forest types have shown both increases (15, 25) and decreases (26, 27) in response to higher temperatures. Decreases are likely caused by water limitation of photosynthesis, which is not the case at the SERC stands. Mean and maximum temperatures near SERC have shown consistent long-term increases (Fig. 3A).

**Increased Growing Season.** Higher temperatures are also correlated with longer growing seasons (Fig. 3B). A steady lengthening of the growing season has been documented worldwide (7), and even a shift in the seasonal phase of surface temperatures has been detected (28). Growing degree days correlate with the speed of forest recovery from pasture in the Amazon (9, 29) and increased plant growth in boreal forests (11, 25). Fig. 3B shows that last frosts of winter have come earlier and first frosts of fall have come later in the SERC region over the last century, significantly increasing the length of the growing season.

**Increased CO₂.** Atmospheric CO₂ can increase tree growth through carbon fertilization (30). Trees have shown species-specific increases in growth under elevated CO₂, but nutrient and
were sweet gum (Liquidambar styraciflua) occurred recently. On the western shore of the Chesapeake Bay, atmospheric deposition or groundwater enrichment have not to disturbance (33). In our forest stands, however, systematic in runoff. Magnani et al. (32) estimate that N is responsible for agricultural and expanding urban areas have lead to increased N limited. In temperate forests, increases in soil nitrogen caused by fluctuations and feedbacks are expected to drive growth when nutrients, such as N or P, and water are not limiting.

Nutrient Fertilization. Phosphorous fertilization is primarily thought to be possible in the tropics, where P and N are not limited. In temperate forests, increases in soil nitrogen caused by agricultural and expanding urban areas have lead to increased N in runoff. Magnani et al. (32) estimate that N is responsible for significant temperate forest growth above background response to disturbance (33). In our forest stands, however, systematic increases in soil nutrients (e.g., available N and P) caused by atmospheric deposition or groundwater enrichment have not occurred recently. On the western shore of the Chesapeake Bay, data on atmospheric deposition of NO3 and NH4 show that although this region has higher levels of nutrient deposition than the national average, measured deposition has declined since 1983 (34). Nutrient fertilization through groundwater can also be ruled out, because the agricultural history of these sites is well-documented; additionally, no increase in nearby farming occurred (fields have actually consistently been removed from agricultural use in the region).

Community Composition. Different species can correlate with different stages of recovery from disturbance. Differential species growth rates, therefore, could potentially influence biomass-accumulation rates (35, 36). In our forest stands, the most prevalent pioneer species that could influence stand growth rates were sweet gum (Liquidambar styraciflua) and tulip poplar (Liriodendron tulipifera). Neither species showed a positive relationship with the difference between observed and expected biomass growth (Fig. 2B).

Demographic Stochasticity. Forest stands can respond to gaps created by the death of large trees with rapid regrowth. If our censuses consistently sampled forest growth directly after a large mortality event, then we could have recorded the accelerated growth response to gap formation. However, this explanation does not hold, because we witnessed few gap events (only 8% of all interval estimates showed biomass losses), far fewer than would be expected if death and recovery explained the observed growth rates. Furthermore, our growth rates were observed in stands of many different ages, the younger of which (<60 years old) would not be expected to have large mortality events. Overall, we found that the recent accelerated growth in our forest stands cannot be explained by random sampling after mortality events. Changes in community species composition also failed to explain changing growth rates. Most likely, a combination of long-term temperature increases, longer growing seasons, and CO2 fertilization have combined to increase the recent rate of biomass gain in these forest stands above their long-term trend.

State and Rate of Terrestrial Carbon Stocks. Forests form a critical component of the terrestrial carbon cycle. Trees absorb carbon, store carbon, and release carbon through abscission and decomposition. Calculating the amount of carbon stored in forests (37, 38) guides predictions of how much potential carbon could move from storage (sinks) into the atmosphere (6). Just as deforestation constitutes an important cause of carbon leaving terrestrial stocks, regrowth of forests after land-use change has been recognized as critical to the removal of carbon from the atmosphere (39, 40). This sequestration of carbon from the atmosphere into recovering forests can continue even for forests over 800 years old (41).

The long-term pattern of biomass accumulation after stand-initiation events allows one to distinguish recovery caused by disturbance from other factors, such as changes in climate (13, 42). Our direct test of observed biomass gains given known stand histories shows that forest systems can change long-term patterns because of widely recorded climate changes. Furthermore, our study quantifies this rate change. This finding casts estimates of carbon flux in a new light, as it indicates that in this forest, carbon is being absorbed at a new, higher rate than it was in the past. Additionally, although our evidence suggests no change in these rates over the past 20 years, we expect them to decline when nutrients or water become limiting factors (2, 6). Our study also supports the growing understanding that climate change is not just changing features of the environment but changing the systems that drive feedback to the atmosphere.

We found that the recent increase in growth was unrelated to stand age (r = −1.08; P = 0.28), averaging 3.4 Mg ha−1yr−1 (2.8–4.2) across all measurement intervals, even those with catastrophic tree death. The proportion of total biomass accumulation represented by the increased growth we describe depends on stand age. In stands younger than about 50 years, the observed rate increase can be as little as one-third of total growth, but in older stands, it can be the majority of growth; under the expectation of the ensemble function, old forests should grow very little as they approach equilibrium. The accelerated growth we have documented raises two key questions. First, how widespread is the accelerated growth that we

Table 1. Hypotheses to explain accelerated recent growth of forest stands

<table>
<thead>
<tr>
<th>Hypothesis</th>
<th>Description</th>
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<tbody>
<tr>
<td>Increased temperature</td>
<td>Higher temperatures over the growing season (or growing degree day sums) can increase metabolic rates and therefore, lead to more rapid carbon sequestration.</td>
</tr>
<tr>
<td>Increased growing season</td>
<td>Longer growing seasons (especially earlier springs) has been observed in many systems. A longer growing season would allow stands earlier leaf-flush and therefore, increased carbon sequestration.</td>
</tr>
<tr>
<td>Increased CO2 fertilization</td>
<td>Higher atmospheric CO2 can increase photosynthesis and lead to higher biomass accumulation.</td>
</tr>
<tr>
<td>Nutrient fertilization</td>
<td>Nitrogen and phosphorus fertilization from agricultural and urban runoff can increase tree growth. Atmospheric deposition of nitrogen has increased in urban and industrial regions in the United States in recent decades and could lead to soil fertilization as well.</td>
</tr>
<tr>
<td>Community composition</td>
<td>Some pioneer species tend to grow faster than others, especially sweet gum (Liriodendron styraciflua) and tulip poplar (Liquidambar tulipifera). An influx of these species into a plot or a preponderance of fast-growing species recently becoming dominant could lead to an increase in biomass accumulation.</td>
</tr>
<tr>
<td>Demographic stochasticity</td>
<td>Although a stand may follow the ensemble biomass-accumulation pattern, random deaths of large trees can lower the stand biomass, and rapid regeneration will quickly increase the biomass as if the plot were, through a death, moved to a younger state.</td>
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</table>
have measured? Although our plot censuses have offered a rare replication of biomass trends across centuries of stand regeneration, there are likely other sources of similar data. Forest stands at SERC are not very different in composition or climate from the secondary forests that cover the eastern United States, making broad comparisons with similar datasets relevant. Dendrochronological analyses of historical growth, forest stands with known land-use history, and forests exposed to periodic storms could help determine the scope of current forest biomass response to climate change. We encourage forest ecologists to match recent census data against long-term trends in regeneration.

Second, which specific mechanisms are driving the observed change in growth rate of the SERC forest sites? It is possible that temperature, CO$_2$ fertilization, and growing-season length interactively contributed to recent growth-rate increases, but a finer understanding of these processes is important. When in the growing season does the response occur? Which are the essential nutrients that allow growth increases? When are these rate increases likely to level off? With the advent of more aggressive and fine-scale monitoring of forest–atmosphere boundaries (e.g., the National Ecological Observatory Network), we should soon gain important new data relevant to these questions. Continuing to monitor and analyze how forests behave in the context of changing climate is important to better understand and predict long-term ecosystem dynamics.

Materials and Methods

Site and Census Methods. Biomass was estimated from DBH measurements of trees over 2 cm DBH at or near the Smithsonian Environmental Research Center, which is about approximately 15 km south of Annapolis, MD (38°53′ N, 76°33′ W) on the western shore of the Chesapeake Bay. The stands are all of the tulip-poplar association (43) or yellow-poplar cover type (44), and we chose them as representative of the stages in a successive sequence. The tulip-poplar association is a common upland forest type in the mid-Atlantic coastal plain and piedmont (43, 45). For several decades after timbering or abandonment from agriculture, this forest type was dominated by dense populations of sweet gum (Liquidambar styraciflua L.) or tulip poplar (Liriodendron tulipifera L.). Understory species like ironwood (Carpinus caroliniana Walter) and dogwood (Cornus florida L) then appear in these areas, as do additional overstory species, such as oaks (Quercus spp.) and hickories (Carya spp.). In the mature stages, the canopy is composed of oaks, hickories, beech (Fagus grandifolia Ehrhart), and some tulip poplar with a diverse complement of mid- and subcanopy species. L. tulipifera, although not always dominant, occurs at most stages (46). All of the stands were on level (slope = 0−7.5°), upland, well-drained sites of the Marr–Westphalia–Sassafras soil association (47) within 5 km of each other. It should be noted that dogwood anthracnose, the fungal disease Discula destructiva, killed many of the understory dogwoods at these sites over the past decade, and although they do not contribute high proportions of biomass to these sites, these deaths, if anything, would lower our observed growth rates.

We defined the successive age of a stand as the number of years since it was cut over or abandoned from agriculture. We determined this interval from two sources. Aerial photographs covering most of the study sites were available for the years 1938, 1951, 1952, 1957, 1960, 1963, 1970, 1980, 1981, and 1988. These provided a finite possible range of ages and a finite possible error for each of the younger plots. We adjusted some of the age estimates up or down (within the possible range) after some further, somewhat more subjective examination of the photographs. We also took wood cores from the 10 largest individuals outside of the plots and determined their age, adding 5 years to account for pre-ring growth to estimate the age of the original cohort. In older stands, where the oldest trees may have already died, this method underestimates stand age. In these cases, the older stands would further support a biomass asymptote at younger ages and lead to an expectation of even lower growth that we estimate here.

To estimate biomass, all woody plants with 2 cm and greater DBH were measured. Although our plot censuses have offered a rare replication of biomass trends across centuries of stand regeneration, there are likely other sources of similar data. Forest stands at SERC are not very different in composition or climate from the secondary forests that cover the eastern United States, making broad comparisons with similar datasets relevant. Dendrochronological analyses of historical growth, forest stands with known land-use history, and forests exposed to periodic storms could help determine the scope of current forest biomass response to climate change. We encourage forest ecologists to match recent census data against long-term trends in regeneration.

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To estimate biomass, all woody plants with 2 cm and greater DBH were identified in every stand, measured, and assessed for condition. Species-specific allometric equations from the tabulation of Jenkins et al. (48) were used to estimate biomass. We de...
used to estimate AGB from live tree-stem DBH. For species where equations were unavailable, we used the general equations of Jenkins et al. (49).

Bayes Monod Model. The Monod function in Eq. 1 was estimated by taking advantage of the linear transformation of the alternate parameterization (Eq. 2)

\[ AGB = G \left( \frac{SA_i}{SA} - \frac{SA_0}{SA} + \theta \right). \]  

[2]

Here, the asymptote \( G = \beta_1 + \beta_2 \) in Eq. 1 and \( SA_0 = -\beta_2/\beta_1 \) are the minimum stand ages that register positive stand biomass. When made linear as in Eq. 1, we model biomass with error, such as \( E(biomass) = AGB + e \) where \( e \sim N(0, \sigma^2) \). In the Bayesian model, we used uniform priors in logical ranges on the parameters to facilitate convergence. \( \sigma^2 \) was estimated with a scaling factor for age to account for increasing variance with increasing stand age. This absorbed uncertainty in stand differences that would otherwise be wrongly attributed to parameter estimates. Ten chains beginning from random draws of the parameters were run for 50,000 iterations each in the hybrid Gibbs, Metropolis–Hastings sampling algorithm. The chains were highly similar (mixed), and therefore, they were thinned and combined to provide the posterior distributions shown in Table 2.

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