Forest growth trends in the eastern United States

by Craig Loehle¹

ABSTRACT

Changes over the past century in factors such as temperature, precipitation, fire regimes, ozone, atmospheric CO₂, and nitrogen deposition naturally lead to questions about forest growth over this same time period. Determining changes in forest growth over long intervals is complicated by constantly changing growth conditions due to tree maturation, stand self-thinning, disturbance, fires, and other factors. Because a comprehensive review is lacking, results were evaluated from publications examining forest growth trends in the eastern United States over the past 100 years. Available studies used multiple sources of data, including permanent plots, growth models, and tree-ring analysis to evaluate forest growth trends. Reviewed publications (n = 19) reported medium to strong growth enhancement based on a variety of data types over periods exceeding 100 years in some cases. Model-based analyses, which mostly did not include CO₂ and nitrogen fertilization effects, had lower estimates of growth enhancement. Results were consistent for different study lengths and data types. No study reported forest-scale growth declines. Factors identified as the cause of enhanced growth varied by study, but included rising CO₂ concentrations, N deposition, increased precipitation, and warming temperatures.

Key words: climate change, environmental factors, forest growth and yield, forest growth trends, inventory data, eastern United States

RÉSUMÉ

Les changements survenus au cours du dernier siècle dans des facteurs comme la température, les précipitations, le régime des feux, l'ozone, le CO₂ atmosphérique, et les dépôts azotés soulèvent naturellement des questions sur la croissance de la forêt au cours de la même période. Il est par ailleurs difficile d'évaluer le changement dans la croissance de la forêt sur de longues périodes en raison des changements continuels des conditions de croissance dus à la maturation des arbres, à l'éclaircie naturelle des peuplements, aux perturbations, aux incendies forestiers et aux autres facteurs. À défaut d'une étude globale sur le sujet, nous avons tenté d'obtenir des résultats à partir des publications scientifiques qui se sont penchées sur les tendances de la croissance forestière aux États-Unis au cours des 100 dernières années. Les études à notre disposition s'appuient sur différentes sources d'informations comme des placettes permanentes, des modèles de croissance et des études d'anneaux de croissance pour évaluer les tendances de la croissance forestière. Les publications que nous avons consultées (n = 19) rapportent une augmentation moyenne à forte de la croissance basée sur divers types de données qui, dans certains cas, couvrent des périodes dépassant les 100 ans. Les études réalisées à partir de modèles de prédiction qui, le plus souvent, faisaient abstraction des effets de la fertilisation au CO₂ ou à l'azote avaient des estimations plus faibles des gains en croissance. Les résultats allaient dans le même sens, peu importe la durée de l'étude ou le type de données. Aucune étude n'a par ailleurs conclu à un déclin de la croissance à l'échelle de la forêt. Ce sont des facteurs comme la hausse des concentrations de CO₂, les dépôts azotés, l'accroissement des précipitations ainsi que le réchauffement des températures qui expliqueraient l'augmentation de la croissance.

Mots-clés : changement climatique, facteurs environnementaux, croissance et rendement des forêts, tendances de la croissance forestière, données d'inventaire, Est des États-Unis

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Introduction

Forest productivity is of critical interest to the public, forest landowners, and the forest products sector. There are reported changes over the past century in climate-related and other environmental factors that have the potential to influence forest growth, such as ozone levels, nitrogen deposition, atmospheric CO₂ concentrations, temperature, and precipitation (Peñuelas *et al.* 2013). The magnitude and pattern of reported changes in some of these factors have varied regionally. For example, Bishop *et al.* (2019) reported rising precipitation across most of the eastern US, with varying sub-regional trends by season. Kim *et al.* (2012) detected

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increasing non-frozen seasons for soils in the Northern Hemisphere during 1979 to 2008. Various authors (e.g., Anderegg *et al.* 2015; McDowell and Allen 2015; McDowell *et al.* 2016) have predicted that changing conditions will lead to widespread forest mortality and/or dieback and may already be doing so.

There is some evidence that forest growth may have increased over the last 100 years. Using models and fixed land cover types, O'Sullivan *et al.* (2019) estimated a 17.4% net primary productivity (NPP) increase globally from 1901 to 2016, much of it in forests. Global surveys combining various types of data also suggest that forest growth is increasing on average (e.g., Boisvenue and Running 2006, although this study did not include much data specific to the eastern US). A complication with some broad-scale studies (not the O'Sullivan *et al.* 2019 study) is that global C uptake is influenced not just by tree growth rates *per se* but by forest regrowth such as following fire and afforestation (Pugh *et al.* 2019), by changes over time in species composition due to succession, and by disturbance rates. Because of the multiplicity of potential causal pathways and interactions, general discussions of effects of changing conditions on ecosystems (e.g., Peñuelas *et al.* 2013) have been unable to reach specific conclusions. An empirical approach seems warranted.

The contradiction between predictions that changing conditions should be having adverse effects on forests and evidence to the contrary needs resolution. It clearly affects determination of forest health, near-term future trends for forest resources, and provision of ecosystem services. Therefore, I synthesized information on historical trends in forest growth in a specific region (eastern US) to help resolve this uncertainty. The eastern US acts as a sort of natural experiment because climate is favorable for tree growth and historical climate data are available for comparison. Two companion reviews cover Canada (Loehle and Solarik 2019) and the western United States (Loehle 2020). The metric of interest is measured or simulated historical forest growth rates, not changes in acreage of forest or changes in forest age classes (i.e., not carbon stocks).

The metric of interest here is growth rate of existing stands in terms of site (stand) productivity rather than landscape-scale productivity, which can vary based on land use change and stand ages. Ideally, this can be captured as area-based net primary productivity (NPP). Flux tower measurements of CO₂ exchange capture whole canopy growth on a plot. All other growth estimates are necessarily based on measurements (or simulations) of individual trees, usually on a plot of defined area. Stand (plot) estimates of growth represent samples from the forest and thus provide an estimate of forest productivity. Stand basal area, when combined with height, is a good predictor of total stand biomass because individual tree biomass can be predicted from allometric equations. Growth models can likewise be used to predict stand biomass and NPP. Ring width will be greater under better growing conditions, but I next discuss cautions in using this metric. All of these metrics are roughly correlated indicators of growing conditions.

A frequently used metric for tree growth is detrended tree ring width. Detrending accounts for the normal decrease in ring width due to stem geometry and tree age. A problem with detrending arises if a gradual change occurs over time

due, for example, to slowly rising carbon dioxide, the effect of which will be correlated with tree age. The age detrending methods used (of which there are many) to adjust growth histories to account for tree aging and stem geometry can in many cases dampen the long-term growth signal (i.e., any historical trend) by confounding it with tree age (Esper *et al.* 2004, 2005a, 2005b, 2007; von Storch *et al.* 2004), though Franke *et al.* (2013) argued that such detrended series exaggerate low-frequency signals. When stand density can change over time (due to ingrowth or mortality), standardization is further compromised (Cherubini *et al.* 1998; Carrer 2011; Nehrbass-Ahles *et al.* 2014). Given this controversy and the complex interactions among stand structure, individual tree growth, and total productivity (Forrester 2019), it is prudent to avoid studies that used detrended ring data. An approach that overcomes these issues is to use age-matching to compare trees at the same age but different establishment dates. If old trees are available, an age-ring width model can be developed. Then, deviations in growth from this model can be examined over the period of interest for younger trees. This method removes concerns about standardization (i.e., no detrending is done) and allows one to evaluate trends, assuming that stand density was similar at the two times. One caution is that there may exist growth rate trade-offs with mortality, such that very old trees may be slower growing (Loehle 1988; Büntgen *et al.* 2019), creating a bias toward detecting recent increased growth with age-matching.

Inventory plots can be used to estimate growth of either wood volume or NPP (aboveground or total) using various methods (Talbot *et al.* 2014; Searle and Chen 2017; Kohyama *et al.* 2019). To estimate growth rate changes, at least three inventory-based estimates are needed (e.g., 1995, 2000, 2005), where each pair (e.g., 1995–2000) gives an estimate of growth rate to compute a change of rate. Various complications exist, but most are not critical in eastern forests. High turnover during long sample intervals, for example, is a larger problem in tropical forests where trees can grow into a plot, die, and decay before being sampled. In this study, however, I am concerned with net stand level biomass accumulation, ignoring such fine scale mortality turnover. Size thresholds (e.g., 5-cm dbh) for sample inclusion may bias NPP down slightly, but this problem is only significant where growth is very rapid (e.g., tropical forest). Other inaccuracies in estimating growth, per above, are minor or are minimized if the same methods are used over time, as I am interested in growth rate changes rather than absolute rates.

Comparison of stand growth rates over time must account for stand age. The net effect of stand dynamics for even-aged stands is an area-based pattern of accelerating growth, a peak shortly after crown closure, and a long decline period (Girardin *et al.* 2011; Boisvenue *et al.* 2016; Hogg *et al.* 2017). This dynamic can be captured using Hoerl's function (Eq. 1):

$$(1) \quad \Delta AGB = \beta_0(age)^{\beta_1}e^{\beta_2(age)}$$

where β_0 , β_1 , β_2 are fitted parameters that change curve height and shape to reflect species and growing conditions, and ΔAGB is above ground live biomass increment per year per ha, usually live only.

In Fig. 1, a typical curve as estimated (their Fig. 6) by Boisvenue *et al.* (2016) is shown. Other functional forms

Fig. 1 Typical growth curve (Hoerl's function) for trees in even-aged stands on a unit area basis (based on Boisvenue *et al.* 2016); other functional forms (e.g., McMahon *et al.* 2010) give similar results.

(e.g., McMahon *et al.* 2010) can also be used. The decline phase is partially due to increased mortality resulting from crowding and tree aging (Hogg *et al.* 2017) and reduced hydraulic efficiency with age or height (Baret *et al.* 2018). Growth response of older stands could thus be misleading if a reduction in growth resulted from maturation rather than changes in environmental conditions. In northern Minnesota, growth variations due to climate were 92-95% smaller than those due to tree size and age (Foster *et al.* 2014).

Height growth rate of dominant trees, commonly used to construct site index metrics, is less affected by competition (Bontemps *et al.* 2011) and could provide a useful approach for estimating growth trends. In plantations, where spacing and age are uniform, height at a given age for older and younger stands could be compared either from inventory data or from tree dissections, although similar sites should be compared (Lieffers *et al.* 2018). For plantations on similar sites, yield tables from past harvests or tree sizes (height or biomass) at given ages can be validly compared. Planting density must be the same, as should treatments (e.g., thinning, fertilization), for such comparisons to be valid. Genetic improvement of planting stock over time could also confound results.

Finally, short- versus long-term data may show different trends. A region that is experiencing increased growth over the past 100 years due to changing climate factors (e.g., precipitation, temperature) and/or rising CO₂ might nevertheless show a recent short-term decline in growth due to drought, pests, or stand aging. A recent period could also have abnormally good growing conditions. It is therefore

important to consider multiple sites and the longest time periods possible.

Remote sensing data are widely used for estimating leaf area and productivity. However, based on strong contradictions found between temporal forest productivity trends using remote sensing vs. other methods (e.g., Marchand *et al.* 2018) and signal saturation at high leaf area, such studies are not used in this review.

Alterations in forest growth caused by human land use are not considered here. Area in forest may change due to farm abandonment, for example, which would affect carbon stocks. However, the focus here is on productivity of forest stands, not landscape carbon pools. Thus, studies that simulate combined historical effects of the environment and land use change (e.g., Tian *et al.* 2010, 2012) are not informative about stand-level NPP unless land use is considered separately. The long-term effects of agricultural land abandonment and succession on species composition and consequent productivity (Nowacki and Abrams 2015) is mostly at longer time-scales than the studies reviewed here, but were considered in interpreting reviewed studies if relevant. Also not considered are changes in forest carbon stocks caused by disturbances (e.g., Kautz *et al.* 2018). These factors would need to be considered for assessing carbon pools but not for growth rate *per se*. Long-term inventory data do encompass small-scale disturbances (e.g., insect attack) but not stand-replacing disturbances.

Because of changes in precipitation, nitrogen deposition, temperature, CO₂, and other factors, attribution of forest growth changes can be complex and often requires evalua-

tion of several types of evidence. In the studies described next, more than one environmental factor often could have caused observed changes in forest growth. In such cases, the authors of these studies sometimes made inferences from historical data to help clarify causation.

Methods

I searched the scientific literature for references to long-term growth trends of forests in the eastern US. I selected studies if they covered any part of the eastern US, defined as forested areas east of the Great Plains (i.e., starting in the states just west of the Mississippi River). As an initial entry to the literature, I manually searched (i.e., contents read) the complete contents of *Forest Science* (2015–2018), *Canadian Journal of Forest Research* (2012–2018), *Forest Ecology and Management* (2012–2018), *Global and Planetary Change* (2014–2017), and *Global Change Biology* (2012–2018). This search included over 6000 articles. I also searched the literature with Google Scholar using “tree-ring chronologies”, “forest history”, “NPP”, “growth reconstruction”, “forest greening”, “forest browning”, “forest growth decline”, “forest growth acceleration”, “forest growth trends”, “forest carbon dynamics”, and “carbon sequestration” as keywords. I also searched the International Tree-Ring Data Bank (ITRDB) for relevant studies. I then searched cited literature in each publication. To be included in the analysis, studies needed to use age-matching, stand-scale metrics, or models of stands to avoid complications documented in the introduction. Studies needed to consider a single species or fixed forest type such as northern hardwoods. For example, a study in which aspen forest transitioned to spruce would not give consistent results. Growth rates estimated at least at two times were needed for a study to be included as measures of biomass at two times only yield a single rate, not two. While studies differed in their metrics (ring width vs. NPP, for example), species studied, and geographic coverage, they can all be considered independent rate of change estimates. For some of the studies, I used conservative values where there were uncertain age, scale, or metric values. I was unable to use many additional studies because their focus was on growth responses to seasonal weather factors or estimation of historical climate from tree rings, for example, and growth trends could not be extracted from their data. Many studies I retrieved with key words did not document changes in growth rates *per se*, but only metrics such as biomass at two different times or growth rate at a single time and could thus not be used. Some entries in the ITRDB did not contain meta-data. Other studies did not separate forest growth rates from regional or national ecosystem totals that included non-forest lands (e.g., Chen *et al.* 2012).

Results

I found nineteen publications that quantified forest growth trends in the eastern US over time (Table 1). Four additional studies provided qualitative results. Reviewed studies estimated forest growth rates over periods ranging from 10 years to the century scale. I used modeling studies and those based on various types of long-term data (inventories, tree-ring reconstructions, flux towers, plot data) in this review. Most studies used in what follows either sampled multiple stands or simulated many plots to obtain their growth estimates and can thus be considered forest-level estimates of growth. The

basic types of studies found were modeling ($n = 7$), age-matching ($n = 4$) and plot-based data ($n = 7$), where Twine and Kucharik (2009) calculated trends for broadleaf and conifer separately. See the Supplemental Information for details of cited studies.

I found seven modeling studies (Joos *et al.* 2002; Del Grosso *et al.* 2008; Pan *et al.* 2009; Twine and Kucharik 2009; Motew and Kucharik 2013; Rollinson *et al.* 2017; O’Sullivan *et al.* 2019). An advantage of modeling studies is that the forest age and composition can be held constant, eliminating tree age and successional effects on productivity. Joos *et al.* (2002), Del Grosso *et al.* (2008), Rollinson *et al.* (2017), O’Sullivan *et al.* (2019), and found positive growth trends across the entire region. Twine and Kucharik (2009) found positive trends for broadleaf forest over the entire region but no trend for coniferous species, though they held CO_2 constant in their analysis. Rollinson *et al.* (2017) found positive trends in New England and the Upper Midwest. Pan *et al.* (2009) found increased growth in the Mid-Atlantic States (Virginia north to New York). The studies with fixed CO_2 (Del Grosso *et al.* 2008; Twine and Kucharik 2009; Motew and Kucharik 2013) may have underestimated growth enhancement based on Loehle (2018). The modeling studies variously ascribed increased growth to rising CO_2 , N deposition, warming, increased precipitation, or a combination of these. Only Pan *et al.* (2009) modeled ozone effects and found an 8% growth reduction over the period 1895–2000, but with other factors more than compensating for this detriment.

Four studies used age-matching. With this method, individual tree growth (ring width, basal area increment, or height) is compared between young trees and older trees when they were that same age. This method controls for both age and competition effects. Two studies evaluated longleaf pine (*Pinus palustris* Mill.), in southern Georgia using ring widths (West *et al.* 1993) and in southern Alabama using height metrics (Boyer 2001) and both found substantial growth increases in recent decades. Voelker *et al.* (2006) found a doubling of oak (two *Quercus* spp.) growth over the period 1840 to 1980. Cole *et al.* (2010) found a 60% growth enhancement of quaking aspen (*Populus tremuloides* Michx.) in Wisconsin over roughly 1950 to 2000. Authors attributed growth enhancements to N deposition and CO_2 (West *et al.* 1993), CO_2 (Voelker *et al.* 2006), and CO_2 plus precipitation (Cole *et al.* 2010).

The remaining studies were based on long-term plot data. Dragoni *et al.* (2011) and Keenan *et al.* (2012) used CO_2 flux data in south-central Indiana and the Harvard Forest, respectively, with both finding large recent increases in C uptake at decadal scales. Plot-based studies across the Northeast (Hornbeck *et al.* 1988; Thomas *et al.* 2009; McMahon *et al.* 2010; Dye *et al.* 2016; Pontius *et al.* 2016) found increased growth at the stand level and for many species. These growth enhancements were variously attributed to N deposition, warming, longer growing seasons, and rising CO_2 .

Red spruce (*Picea rubens* Sarg.) decline has historically been of concern. Both Engel *et al.* (2016) and Mathias and Thomas (2018) found red spruce growth to have fluctuated due to weather and pollution episodes, with a recent increase in growth. Hornbeck *et al.* (1988), Battles *et al.* (2003), and Gavin *et al.* (2008), found historic (1960s to 1980s) decline and mortality of red spruce in New England followed by recovery.

Table 1. Summary of Growth Trend Results^a

Reference	Years	Region	Methods	Trend
Boyer 2001	1964–2000 AL (~44 yr difference)	Longleaf pine site index	+28% age 50 site index	(+6.4%/decade) (+30–35% wood volume)
Cole <i>et al.</i> 2010	1935–2003	WI	Aspen ring width	+60% for young trees over 50 yr period (+12%/decade)
Del Grosso <i>et al.</i> 2008	1901–2000	US & Canada	Simulated NPP with fixed CO ₂	+ 3% to 7.7% tNPP increase (+0.3–0.77%/decade)
Dragoni <i>et al.</i> 2011	1998–2008	South-Central Indiana	Flux tower measurements	38% NEP increase (38%/decade)
Dye <i>et al.</i> 2016	1970–2010	Three sites in ME, MA, WV	Permanent plots & tree-ring data	No NPP trend but data highly variable
Engel <i>et al.</i> 2016	1951–2010	Vermont & New Hampshire	BAI of dominant, co-dominant red spruce	Zero trend 1951–1999; 33% increase 2000–2010 (33%/decade)
Keenan <i>et al.</i> 2012	1992–2009	Harvard Forest	Eddy-covariance data	Doubling of NEE (59%/decade)
Mathias and Thomas, 2018	1960–2014	Central Appalachians	Basal area increment of dominant red spruce	Net zero growth rate
McMahon <i>et al.</i> 2010	1987–2005	Maryland	Compared resurvey periodic increment on stands of multiple ages to expected trend from biomass vs age curve	All ages were growing faster than predicted, up to twice as fast, 50% increase conserva- tively used in analyses (no time period)
Motew and Kucharik 2013	1948–2007	MN, WI, MI	Simulated NPP	+8% NPP (1.4%/decade)
O'Sullivan <i>et al.</i> 2019	1901–2016	E US	Used simulated climate, N deposition, CO ₂ histories to model NPP	+50–100 g C/m ² /yr increase (from map) (+4.3–8.6 g C/m ² /decade increase)
Pan <i>et al.</i> 2009	1895–2000	US Mid-Atlantic	Used simulated climate, N deposition, CO ₂ histories to model NPP	NPP increased 29% (2.8%/decade) due to net N, CO ₂ , O ₃ effects, +4% due to simulated climate change alone
Pontius <i>et al.</i> 2016	1931–2001	New Hampshire	Long-term plot data	90% higher 10-year NPP increments for most recent survey
Rollinson <i>et al.</i> 2017	1880–2010	Upper Midwest and NE	Models calibrated to tree- ring data	+37.5% NPP increase, mainly due to CO ₂ , 32% after 1940 (+4.6%/decade)
Thomas <i>et al.</i> 2009	Pre-industrial vs recent	Midwest & NE US	Based on FIA data & N depo- sition, estimated N effect on growth	+40% biomass growth enhancement but CO ₂ effect could not be separated
Twine and Kucharik 2009	1950–2002	Eastern US	Modeled forest NPP growth by vegetation type (CO ₂ constant)	+5% deciduous forest (+0.96%/decade) 0% conifer forest
Voelker <i>et al.</i> 2006	1840–1980	MO	Tree rings	+100% (+7.1%/decade)
West <i>et al.</i> 1993	1940–1987	South GA	Tree rings	+44.5% ring index (+9.5%/decade)

^aSome model study results interpreted from color-coded maps. In case of ambiguity, lower bounds on estimates were chosen. Twine and Kucharik (2009) provided rates separately for conifer and broadleaf types and both were used. Trends are over the reported time period. See Supplemental Information for details of analysis.

Another species of concern is sugar maple (*Acer saccharum* Marsh.). Aside from a decline at one site in Vermont (Gavin *et al.* 2008) and enhanced growth across New England from the 1960s to 1980s (Hornbeck *et al.* (1988), the plot-level and modeling studies did not detect a significant maple growth decline signal.

We can summarize these results by several categories: models (n = 7), age match (n = 4), plots (n = 7), and all (n = 18). Data were converted to percent change for comparisons (Fig. 2). O'Sullivan *et al.* (2019) could not be converted from g C/m²/yr increase to a percent and was not included. Keenan *et al.* (2012) produced a 33% increase over just 10 years, which is probably an outlier due to either methods or local weather fluctuations and was also left out. Age matching had the highest mean increase per century (85%) compared to plots (69%), models (16%), and all sources (52%). These values are conservative because positive model and plot-based results were not included (as noted above). Models showed a much reduced positive response compared to data studies, perhaps due to factors such as CO₂ and N deposition being inadequately represented. The lowest percent change over all the data is zero. No study found a growth decline.

Discussion

Quantifiable growth enhancements, some large, over up to 100-year time-frames are evident in the eastern half of the US (Table 1). The mean growth enhancements over all studies fall mostly in the range of 20% to 90% per century, with growth enhancements being variously ascribed by investiga-

tors to CO₂, N deposition, precipitation, warming, or some combination of these. A few studies did not detect a trend but no study showed declining growth. No study quantified or implicated ozone as a damaging agent, except Pan *et al.* (2009), who found an 8% growth reduction that was more than compensated by growth enhancements from other causes. While periodic mortality or declines of, for example, sugar maple, would seem to be negative indicators, overall negative trends at the forest level were not detectable with any of the data available, and even sugar maple showed increasing trends in some studies. Red spruce decline trends observed prior to the 1980s would seem to have been reversed. The trends detected are despite a detectable shift toward more shade-tolerant, slower-growing species due to successional changes and other factors over the centennial scale (Knott *et al.* 2019). Low rates of increase found in several modeling studies were probably underestimates because leaving CO₂ out of models reduces simulated growth trends (Loehle 2018). Growth trends seem consistent across the region and for the forest types studied, but formal tests were precluded by small sample sizes.

The question of scale needs to be considered. The modeling studies typically simulated many plots across their study area and are thus spatially extensive. Field studies sampled multiple multi-species plots, while a few focused on a single species (e.g., Cole *et al.* 2010). Only West *et al.* (1993) could be said to suffer from a small sample size but their results were corroborated by Boyer (2001). Given that studies that focused on different species and sub-regions all generally

Fig. 2 Box and whisker plot for percent growth change per century for 18 studies. X represents the mean. Keenan *et al.* (2012) was so large that it was left out and probably represents very short-term weather responses. O'Sullivan *et al.* (2019) could not be converted to percent and is not plotted. Twine and Kucharik (2009) provided trends for broadleaf and conifers separately.

agreed on trends, this supports the conclusion that regional growth has been generally increasing. Given the evidence for rising effective moisture across the region (Greve *et al.* 2014), N deposition, and rising CO₂, this response makes sense. Because the growth enhancing factors (N deposition, rising precipitation, and rising CO₂ plus perhaps warming) have all been increasing in concert in this region, it is not possible to separate their effects in general, though attempts were made to do so in a few of the studies cited here. Growth rate data were in general only available at two or a few periods so that correlations of growth with these factors is generally not possible.

Small-scale or non-catastrophic disturbances and mortality including insect/pathogen attack are present on most study plots and are thus factored into rate changes. If plots burned up or blew down, they obviously could not be remeasured. While this might affect extrapolation for regional carbon balance calculations, my concern here is with growth rates of existing stands. If disturbance rates were increasing, as with western fires in recent decades, this would bias my results upward, but there is little evidence for this in the eastern US (e.g., Cohen *et al.* 2016).

Several introduced insect pests and pathogens have been affecting multiple species. For example, exotic earthworm invasion of the Upper Midwest is quite recent and is affecting growth of sugar maple (Bal *et al.* 2018). However, some species sampled (e.g., longleaf pine) are not experiencing effects from introduced pathogens and cited modeling studies did not include their effects. Given that episodic weather events (storms, drought) and insect (and other) damage is always present, the extent to which new damage agents might be causing growth reductions is an open question. Results of this survey thus capture the baseline forest growth responses including normal climatic fluctuations and damage agents but not recent invasive pest effects, though some studies did avoid stands with major disturbances. Overall, the significant growth enhancements found here are consistent with other studies (e.g., Joos *et al.* 2002; Boisvenue and Running 2006; Pugh *et al.* 2019) which could not be directly compared to Table 1 entries due to scale or location differences.

The weight of evidence from reviewed studies indicates that, in the study area, growth relationships have been changing over time. An assumption underlying yield tables and site index curves in forestry is that short-term weather fluctuations will average out over the life of a stand, making growth projections mostly reliable. If conditions change radically over decades, however, such relationships could be altered. Numerous studies cited here found major increases in productivity over just the past few decades. Thus, indicators of growth such as yield tables and site index curves, even from the 1980s, might significantly underestimate growth. Impacts on stand economics of changing growth need not be in the distant future (*per* Johnston and Williamson 2005) to warrant consideration. A general ongoing effect is rising CO₂ which accelerates early tree growth (Loehle 1995; LaDeau and Clark 2001) thus potentially distorting yield tables, site index curves, and stand growth-density responses (Kubiske *et al.* 2019), while favoring some species more than others. Also, as CO₂ rises, trees become more fecund at an earlier age (LaDeau and Clark 2001), with implications for seed

orchards and natural regeneration. Finally, ongoing growth changes may require reassessment of seed zones for tree planting (McKenney *et al.* 2009).

Trends observed to date in this region obviously cannot be simply extrapolated into the future. While it is fairly predictable that CO₂ will continue to rise, other climatic changes are less certain. A recent synthesis of climate projections and consequent forest growth responses (Loehle 2018) indicates that, in this region, growth trends are likely to be generally positive in coming decades, with some local disruptions or southern ecotone range retractions possible.

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