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Evidence of Accelerated Growth of Old Trees in Eastern U.S. Forests

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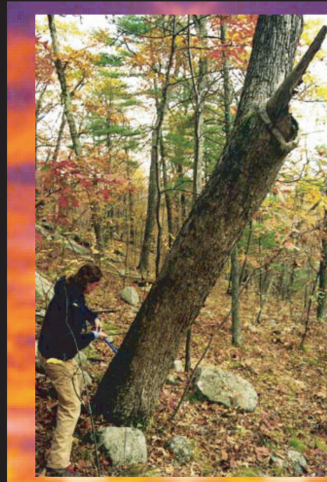
ABSTRACT

Many ecological, forestry and carbon sequestration models operate under the assumption that growth declines as trees age. Tree-ring studies at latitudinal and altitudinal treeline locations suggest that this may not always be true, especially over the last 150 years. Increment cores from > 1200 southern temperate trees were used to test the age-related decline hypothesis in the eastern U.S. Trees in this database range in age from 70 to 463 years, are comprised of four species (*Querucs alba, Q. prinus, Liriodendron tulipifera, Chameacyparis thyoides*) and include the oldest individuals documented by dendrochronology for *Q. alba* (463 years), *Q. prinus* (426 years), and *L. tulipifera* (335 years). *Quercus* trees were combined and grouped into six periods (1851-1900, 1801-1850,…pre-1651) to avoid a potential bias in growth trend by younger trees. Because age structure of *L. tulipifera* and *C. thyoides* forests are generally much younger, unique age classes were created for each species. The oldest trees for all species had periods of statistically significant, above average ring-width during the 20th century. The current trend of increased growth started in the mid- to late-1800s for *Quercus* and *L. tulipifera* while it started in the 1920s for *C. thyoides*. Using allometric equations to convert all chronologies to carbon increment reveals strong, positive trends in growth over the last century. These results show that even the oldest trees are taking much up more carbon today than in the past. Because *L. tulipifera* and *C. thyoides* are less shade tolerant and have considerably different life-history traits than *Quercus*, it seems less likely that stand dynamics is the most important factor of these trends. Though old-growth forests are rare in temperate zones, our data can serve as a model for the large number of forests 100-180+ years old. It may not necessarily be true that forests in the eastern US will slow down in growth at ages 200 year and beyond. If ecosystem productivity declines with increasing tree age, changes in stand structure, environmental growth conditions or tree size may be the primary causes. Regardless, our results support treeline location studies to show that tree-scale productivity does not necessarily decline with age.

Coring chestnut oak at Montgomery Place, NY



Coring a 300+ yr old white oak in the southeastern Adirondacks Mountains in NY State.

Purpose:

Most ecological, forestry and carbon sequestration models operate under the assumption that forest productivity declines as trees age

Recent research, however, suggests that age may not limit short or long-term tree growth.

To test the hypothesis that tree growth declines with age we examine the productivity of >1200 old trees over nearly 400000 km $_2$ in the eastern United States. We also test an alternative hypothesis that predicts that tree growth declines with size.

Data Set:

- four species (white oak (*Quercus alba*), chestnut oak (*Q. prinus*), yellow-poplar (*Liriodendron tulipifera*), Atlantic white-cedar (*Chameacyparis thyoides*));
- includes the oldest known individuals for 3 of the 4 species: white oak (464 years), chestnut oak (427 years), and yellow-poplar (336 years)

Methods:

- 1-2 increment cores collected per tree and processed following standard dendrochronological techniques. Cores were averaged to create average radial increment per tree.

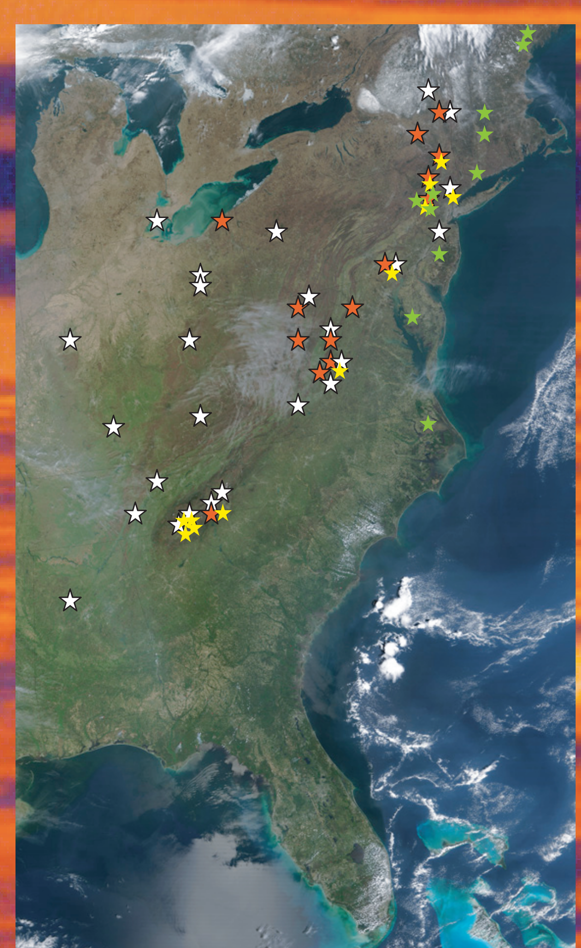
- Oaks were grouped into six periods (pre-1651 A.D., 1651-1700 A.D. , ...1851-1900 A.D.) to exclusively examine ring width and growth trends of the oldest trees.
- unique age classes were created for yellow-poplar and Atlantic white-cedar because of smaller smaple size and younger age structure

- differences in average radial growth between the 1st and 2nd collections for some oaks were removed by standardizing growth with a straight-line fit
- *there was no removal of long-term growth trends!!*

- tree-level radial growth was averaged for each age class: - indices of ring widths for each age class were re-scaled to create time series of ring width in mm
- time series of ring width were placed into published allometric equations to create time-series of annual carbon increment

- oak and yellow-poplar from recent collections were grouped into size classes to test the size-related decline hypothesis (following the same techniques as above)

Study Area



Site Locations:

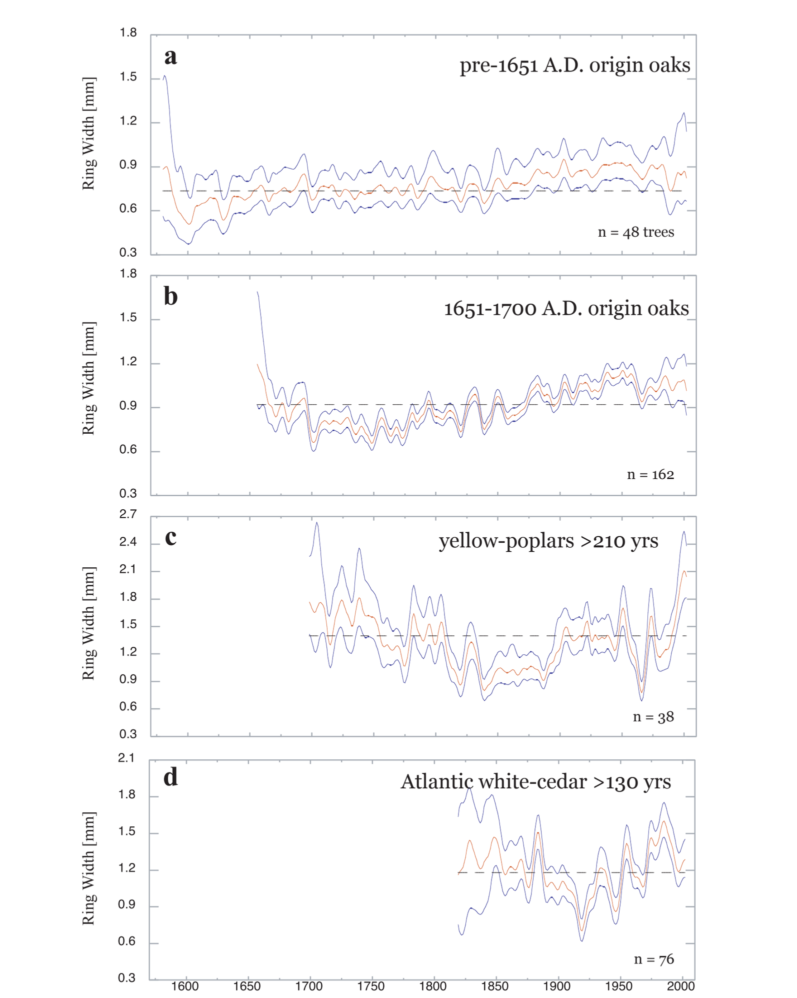
☆ = white oak

★ = chestnut oak

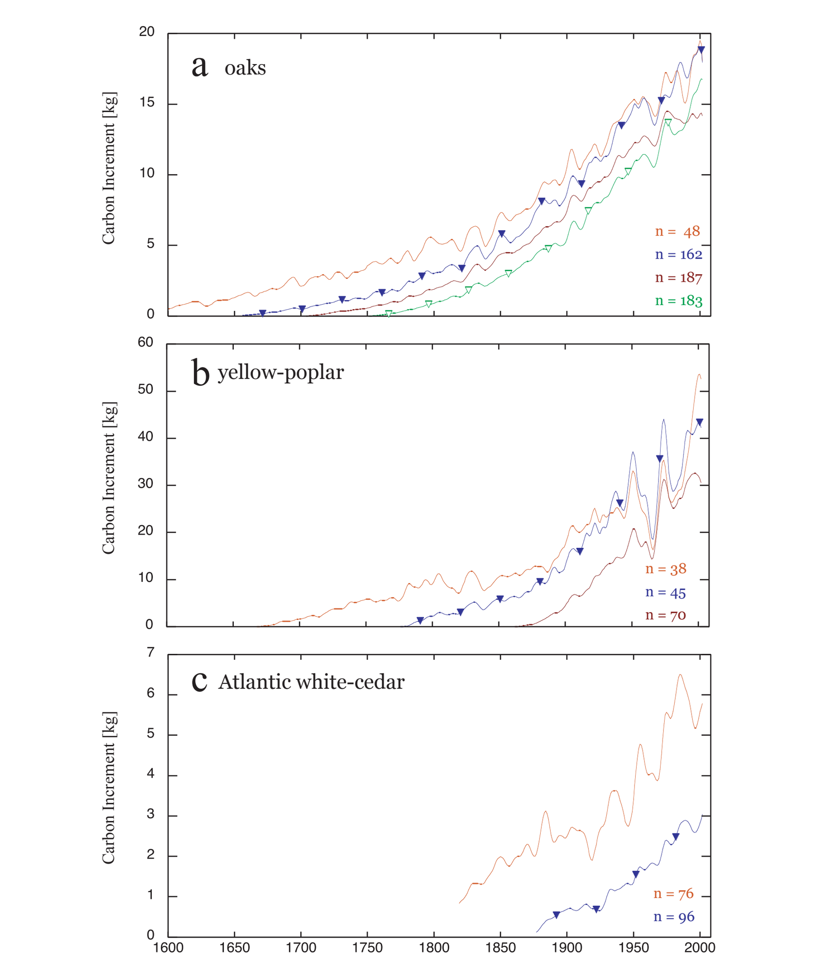
★ = yellow-poplar

★ = Atlantic white-cedar

Age-Related Growth Results



Average raw ring widths for the two oldest oaks [a = pre-1651 A.D., b = 1651-1700 A.D.], yellow-poplars [c = > 210 yrs old] and and Atlantic white-cedar [d = > 130 yrs old]. The oldest oaks show significantly above average ring widths since the late-1880s. After below-average growth through much of the 1800's, yellow-poplar show ring widths equal to or above the long-term mean throughout the 1900's. Atlantic white-cedar has different temporal trends in ring width than oak and yellow-poplar. However, average ring width is significantly above the long-term mean since the early 1970's. The dashed line represents the long-term mean; Orange line represents population mean; Blue lines represent the upper and lower 95% confidence limit as calculated by the bootstrap method. All time-series are smoothed with a 10-yr spline to emphasize decadal-scale variations and centennial trends.



Annual carbon increment (ACI) for oaks with rings prior to 1801 [a], all yellow-poplar age classess [b] and two oldest Atlantic white-cedar classes [c]. Oaks (orange line = pre-1651 A.D., blue line with inverted triangles = 1651-1700 A.D., red line = 1701-1750 A.D., green line with hollow triangles = 1751-1800 A.D.) have had increasing biomass production rates through the 1900s except for the 1701-1750 A.D. group. Yellow-poplar (orange line => 210 yrs old, blue line with inverted triangles = 140-209 yrs, red line = 70-139 yrs) experienced increasing rates of biomass production with a sharp increase starting around the beginning of the 1900s. Atlantic white-cedar (orange line => 130 yrs old, blue line with inverted triangles = 100-129 yrs old) shows accelerated growth with the sharpest increase starting in the 1920s. To estimate ACI, we used published allometric equations for white oak, yellow-poplar and yellow cedar for AWC [it is lacking an allometric equation]. All time-series are smoothed with a 10-yr spline to emphasize decadal-scale variations and centennial trends.

Age does not seem to be the primary limiting factor of individual tree growth. Seperating trees into age classes or time periods did not diminish long-term growth trends. In fact, we observe significantly increased growth rates among the oldest trees. Tree physiology models term cambial growth as secondary growth. Carbon allocation models suggests that allocation to cambial growth follows allocation to new foliage, buds, roots and non-structural storage. If these are met prior to radial growth, the oldest oak and yellow-poplar trees could be considered as growing vigorously.

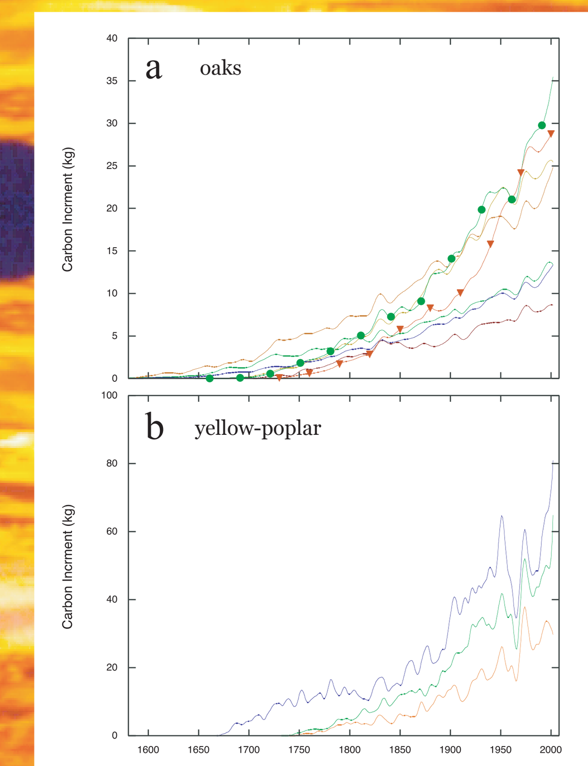
Also, our results support a controlled study showing that old trees can respond to improved growth conditions ((Latham and Tappeiner, 2002). Trees that can persist for centuries while being capable of vigorous growth or responding to improved growth conditions has evolutionary advantages.

Results of the age-related and size-related hypotheses (see figure to the right) lend support to the single-tree hypothesis. First, older trees, and actually, all trees sampled, increased in growth over the last 150 years, attaining their highest growth rates in recent decades. Old trees with accelerated growth rates suggests that if forest productivity declines with age, the decline may be caused by stand structure or forest development rather than individual tree growth. Second, our results suggest that large trees can gain and use resources to sustain or increase growth rates more efficiently than smaller trees. Increased growth as trees age and differences in growth rates between small and large trees follow predictions of the single-tree hypothesis.

Most studies showing an age-related decline in forest productivity are outside of our study region, coniferous, short-lived early successional hardwood species or are from even-aged forests (Gower et al., 1996, Ryan et al., 2004). The oak and yellow-poplar data, representative mixed-mesophytic species of the eastern deciduous forest, represent new data for long-term productivity studies. It is possible that expected long-term growth trends of conifers are different than long-lived, shade tolerant hardwoods. Research on temperature-sensitive treeline trees, however, would suggest otherwise.

Our data are the first indicating increased growth over a large area of the temperate zone of eastern North America. This region has a large and dynamic aboveground carbon pool (Myneni et al., 2001). The increased growth in our study area is similar temporally to several regions globally: high elevation forests of the Pacific northwest of the United States, Europe, Mongolia, Northern Hemisphere latitudinal and mountain treelines and South America. Increased growth in these regions was most often associated with warming over the last 150 years. Accelerated growth of Atlantic white-cedar is strongly associated with warming along the east coast (Hopton and Pederson, accepted). Determining what is driving increased growth in the eastern U.S. is beyond the scope of this study as many factors could be playing a role, however.

Size-Related Growth Results



Annual carbon increment for oaks [a] and yellow-poplars [b] of different size classes. All oaks have increased biomass production rates (size classes (DBH) are: dark red line = <39 cm (n=37), green line = 40-49 cm (n=66), blue line = 50-59 cm (n=84), orange line = 60-69 cm (n=62), mustard yellow line = 70-79 cm (n=47); green line with dotted circles = 80-89 cm (n=17), orange line with inverted triangles = 90+ cm (n=9)). Yellow-poplar experienced increasing rates of biomass production across all size classes (size classes are: orange line = <59 cm (n=24), green line = 60-79 cm (n=37), blue line = 80+ cm (n=25)).

Coring old-growth chestnut oak [left] and yellow-poplar [below] in George Washington National Forest in the Blue Ridge Mountains of Virginia

Larger trees tended to increase in growth more rapidly than smaller trees. For example, oaks in the 60-69 cm DBH class had significantly more ACI than trees < 59 cm DBH. Differences between oaks >90 cm DBH and those <39 cm were not related to age structure. The oldest trees in each class dated to the early 1700s and ~ 90% of the trees were present by 1840 in each size class. While this database is limited, it does indicate that trees do not necessarily experience a decline in growth as they increase in size, contrary to the size-related decline hypothesis.

Conclusions:

Our results show that tree-scale productivity does not necessarily decline with age. They also represent the first evidence of increased growth in temperate eastern North America, a region with a large and dynamic aboveground carbon pool. Though old-growth forests are rare in temperate zones, our data can serve as a model for the increasingly common 100-180+ year old forests in temperate eastern North America. It may not necessarily be true that trees will slow down in growth at old ages. If ecosystem productivity declines with increasing tree age, changes in stand structure, environmental growth conditions or tree size may be the primary causes.

Because our results are in opposition to the long-held tenet that growth declines as trees age, they suggest that old-growth forests could be active carbon sinks. The potential for old trees to respond to improved growth conditions will have important implications for carbon sequestration, forest development models, ecosystem management and evolution.

References:

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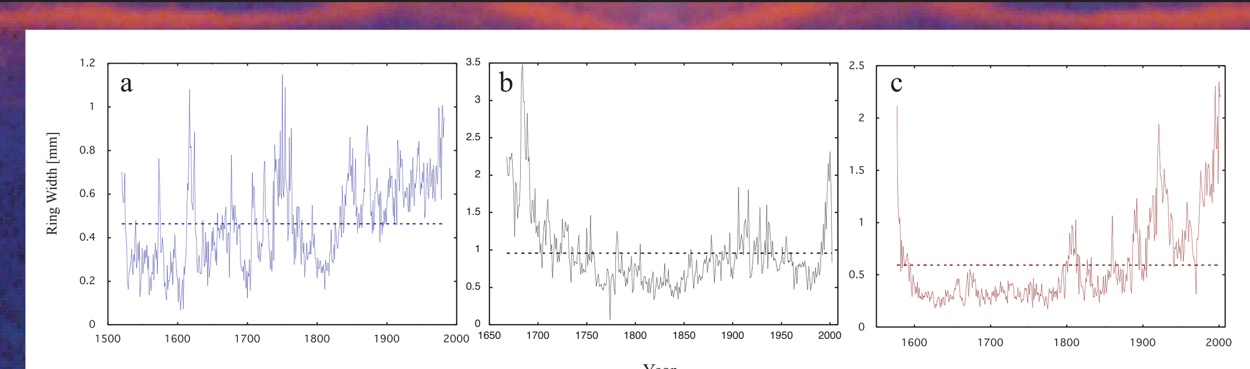
Chestnut oak in a mixed oak-pine-northern hardwood forest in Uttertown, NJ. This stand contains the oldest known chestnut oak [426 yrs] as well as a second tree >420 years old and two others approaching 400 years.

Despite their great age, the old oak [and old-growth yellow-poplar!!] are growing at rates subsstantially higher today than at any other time in the past.



Raw ring widths of the oldest known white oak [a], yellow-poplar [b] and one of the oldest chestnut oaks [c].

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