Age class, longevity and growth rate relationships: protracted growth increases in old trees in the eastern United States

SARAH E. JOHNSON1,2 and MARC D. ABRAMS1

1 School of Forest Resources, Forest Resources Building, The Pennsylvania State University, University Park, PA 16802, USA
2 Corresponding author (sej141@psu.edu)

Received April 17, 2009; accepted August 1, 2009; published online 4 September 2009

Summary

This study uses data from the International Tree-Ring Data Bank website and tree cores collected in the field to explore growth rate (basal area increment, BAI) relationships across age classes (from young to old) for eight tree species in the eastern US. These species represent a variety of ecological traits and include those in the genera Populus, Quercus, Pinus, Tsuga and Nyssa. We found that most trees in all age classes and species exhibit an increasing BAI throughout their lives. This is particularly unusual for trees in the older age classes that we expected to have declining growth in the later years, as predicted by physiological growth models. There exists an inverse relationship between growth rate and increasing age class. The oldest trees within each species have consistently slow growth throughout their lives, implying an inverse relationship between growth rate and longevity. Younger trees (< 60 years of age) within each species are consistently growing faster than the older trees when they are of the same age resulting from a higher proportion of fast-growing trees in these young age classes. Slow, but increasing, BAI in the oldest trees in recent decades is a continuation of their growth pattern established in previous centuries. The fact that they have not shown a decreasing growth rate in their old age contradicts physiological growth models and may be related to the stimulatory effects of global change phenomenon (climate and land-use history).

Keywords: basal area increment, dendrochronology, global change, old-growth trees, sigmoidal growth model.

Introduction

Trees undergo physiological changes as they age, including lower photosynthetic rates, decreased growth rates, shifting of carbon resources to different parts of the plant and reductions in foliar efficiency, leaf size and gas exchange rates (Kaufmann 1996, Ryan and Yoder 1997, Carrer and Urbainati 2004, Martínez-Vilalta et al. 2007). The larger size and the structural complexity usually associated with tree aging increase the maintenance respiration costs and reduce the efficiency of water transport; these both tend to reduce growth (Weiner and Thomas 2001, Carrer and Urbainati 2004, Mencuccini et al. 2005, Pennisi 2005). Old Quercus rubra L. trees, for example, had moderate to high growth rates for the first 50–100 years, followed by a persistent, slow growth over the subsequent 200 years (Orwig et al. 2001). This growth trend may be related to an increasing tree canopy during early age, a constant canopy volume during middle age and then a physiological decline in old trees (Spiecker et al. 1996). This is expected with changing resource allocation in older trees, which maximizes life expectancy by focusing the energy on defense and maintenance rather than on growth (Loehle 1988, Herms and Mattson 1992). Weiner and Thomas (2001) and Weiner (2004) discuss a sigmoidal model in which the size of a plant increases slowly at an early age, becomes exponential during middle age and plateaus during old age. The latter phase is attributed to age- and size-related growth declines. In this study, we adopt a slightly revised version of the sigmoidal model (referred to here as the 'sigmoidal growth model') to include a late stage decline in tree growth rate after it plateaus in old age (as predicted in the physiological growth models). Thus, we are interested in testing whether the sigmoidal growth model applies to a variety of trees where there exists a large amount of dendrochronological data.

Vegetation is highly dynamic because the environment in which it grows is constantly altered by natural and anthropogenic factors. Anthropogenic disturbances such as aboriginal burning, land clearing for agriculture, widespread logging, introduction of exotic species and catastrophic wildfire followed by fire suppression have dramatically altered the structure and function of forests (Bazzaz 1990, Boisvenue and Running 2006, Abrams and Nowacki 2008). In the United States, it is thought that the European settlement legacy or ecological footprint is very large, typified by intensive logging practices and subsequent slash wildfires (Williams 1982, Abrams 2003, Nowacki and Abrams 2008). After European settlement, a period of resource exploitation produced changes in
community composition and structure. Anthropogenic and naturally caused disturbance events are discernable in the dendrochronological record as they produce large increases in radial growth in residual and newly established trees (Baker 1995, Nowacki and Abrams 1997). In contrast, the impacts of greenhouse gases and the corresponding, often subtle, changes in climate are not as easily detectable in the tree-ring record (Jacoby and D’Arrigo 1997, Mann et al. 1999). Some studies have shown increased radial growth in response to the global change factors such as nitrogen fertilization and increased CO$_2$ levels (Briffa et al. 1998, Voelker et al. 2006). Thus, changes in land-use history and climate may be impacting long-term growth trends in trees. However, this impact may vary by species and age class.

In this study, we explore the long-term growth patterns for tree species of the eastern US to assess the relationship between growth rate and age class, and whether trees in varying age classes are following or deviating from the sigmoidal growth model. We take the approach of examining basal area increment (BAI) changes over time across all age classes from young to old trees, rather than just studying the oldest individuals of each species where sample biases may exist (Cherubini et al. 1998, Voelker et al. 2006). Eight tree species were chosen for this study to encompass a range of ecological and life history attributes in the eastern forest biome: bigtooth aspen (Populus grandidentata Michx.), black oak (Quercus velutina Lam.), red oak (Q. rubra), chestnut oak (Quercus Montana L.), white oak (Quercus alba L.), pitch pine (Pinus rigida Mill.), hemlock (Tsuga canadensis L. Carr.) and blackgum (Nyssa sylvatica Marsh.; Table 1). The primary objectives of this study are to examine the following:

1. The relationships between growth rate, longevity and age class for contrasting tree species both within and between sites.

Table 1. Maximum lifespan (Burns and Honkala 1990) and oldest recorded individuals (Pederson 2009) of the study species according to successional status.

<table>
<thead>
<tr>
<th>Successional Stage</th>
<th>Species</th>
<th>Typical maximum age (years)</th>
<th>Oldest recorded (years)</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Early successional</strong></td>
<td>Bigtooth aspen</td>
<td>70–100</td>
<td>113</td>
</tr>
<tr>
<td></td>
<td>Pitch pine</td>
<td>200–300</td>
<td>375</td>
</tr>
<tr>
<td><strong>Mid-successional</strong></td>
<td>Black oak</td>
<td>150–200</td>
<td>257</td>
</tr>
<tr>
<td></td>
<td>Chestnut oak</td>
<td>300–400</td>
<td>427</td>
</tr>
<tr>
<td></td>
<td>Red oak</td>
<td>200–250</td>
<td>326</td>
</tr>
<tr>
<td></td>
<td>White oak</td>
<td>400–450</td>
<td>464</td>
</tr>
<tr>
<td><strong>Late successional</strong></td>
<td>Blackgum</td>
<td>500 +</td>
<td>679</td>
</tr>
<tr>
<td></td>
<td>Hemlock</td>
<td>500 +</td>
<td>555</td>
</tr>
</tbody>
</table>

2. The role of shade tolerance and site class (e.g., rock outcrop and bog) in growth rate and longevity.

3. Whether BAI trends in trees are following the sigmoidal growth model.

**Methods**

The International Tree-Ring Data Bank (ITRDB; Grissino-Mayer and Fritts 1997) was used to compile tree-ring chronologies for eight eastern North American tree species (bigtooth aspen, blackgum, black oak, chestnut oak, hemlock, pitch pine, red oak and white oak; see Table 2 for tree-ring series used). Further details pertaining to specific sites can be found in appendix of Johnson (2007). The majority of the contributing investigators were personally contacted to ensure that they posted complete chronologies extending from the bark to (or very near) the pith of the trees recorded. Both young and old trees were obtained from the ITRDB.

When faced with the decision of which measurement type to use for this study, raw-ring widths, ring-width index (RWI) and BAI were considered. The BAI is typically used in forest growth and modeling studies because it provides an accurate quantification of wood production due to the ever-increasing diameter of a growing tree (Rubino and McCarthy 2000). In contrast, RWI is typically used in dendroclimatological studies to standardize ring widths into indices to highlight above- or below-average periods of growth through time in relation to climate (Esper et al. 2002). The RWI was calculated for the 20 oldest trees of four of the study species at individual study sites. Raw-ring widths were fitted with negative exponential curves using the subtraction method in the program ARSTAN (Cook and Holmes 1984). A comparison of BAI and RWI data for two of these species revealed obvious long-term growth trends evident in the BAI data that are masked in the RWI (Figure 1). Because the focus of this study is on ecological growth trends by age class in relation to the sigmoidal growth model, rather than climate impacts on growth indices, we chose to use BAI, in addition to raw-ring width, rather than RWI (Stan 2008).

Raw-ring-width chronologies of the selected species were used to calculate tree age and average yearly growth rates in BAI (expressed as mm$^2$ year$^{-1}$). The BAI measurements were calculated for each tree using the tree radius and the formula for circle area. Cores of each species of interest previously collected in our laboratory were reanalyzed for age and growth rate by measuring the annual growth increments on a TA Unislide Velmech machine (0.002 mm precision; Velmech Inc., Bloomfield, NY). This data was used in conjunction with the chronologies obtained from the ITRDB. Many of these cores represented the oldest individuals used for this study. These cores were taken as low as possible on each tree above buttreeing, mounted on wood blocks and sanded with increasingly finer grit.
sandpaper (60–3200 grit in some cases, i.e., blackgum cores) in preparation for measurement with the Velmex machine. The cores were crossdated by hand using skeleton plotting to check for missing and false rings using the identification of signature years (Stokes and Smiley 1968). A skeleton plot evaluates the tree-ring width in relation to the rest of the rings of each tree in a stand. Signature years are consistently small or large rings indicative of extreme climatic or disturbance events that allow for the crossdating of trees. We used the computer program COFECHA for crossdating (Holmes 1983, Grissino-Mayer 2001), which analyzes each measured ring-width series individually. COFECHA bases its analysis on a master chronology of all the cores compiled and calculates a correlation coefficient indicating how well the interannual variability in ring widths correlates with the other ring-width series. Ring-width chronologies obtained from the ITRDB have been subjected to rigorous crossdating standards and checked with COFECHA. The raw-ring widths recorded for remeasured and newly collected core sets were converted to BAI in the same manner as ring widths collected from the ITRDB (see the above procedure).

The relationship between growth rate and age class was analyzed based on 30-year age classes for the entire life of the trees. Each tree was assigned to a 30-year age class

<table>
<thead>
<tr>
<th>Species</th>
<th>30–60 years</th>
<th>60–90 years</th>
<th>90–120 years</th>
<th>120–150 years</th>
<th>150–180 years</th>
<th>180–210 years</th>
<th>210–240 years</th>
<th>240–270 years</th>
<th>270–300 years</th>
<th>300+ years</th>
</tr>
</thead>
<tbody>
<tr>
<td>Bigtooth aspen</td>
<td>8</td>
<td>37</td>
<td>4</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Black oak</td>
<td>10</td>
<td>15</td>
<td>14</td>
<td>9</td>
<td>4</td>
<td>4</td>
<td>3</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Red oak</td>
<td>6</td>
<td>28</td>
<td>19</td>
<td>20</td>
<td>12</td>
<td>16</td>
<td>5</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Chestnut oak</td>
<td>39</td>
<td>55</td>
<td>35</td>
<td>24</td>
<td>24</td>
<td>44</td>
<td>29</td>
<td>41</td>
<td>29</td>
<td>3</td>
</tr>
<tr>
<td>White oak</td>
<td>14</td>
<td>55</td>
<td>99</td>
<td>139</td>
<td>133</td>
<td>221</td>
<td>239</td>
<td>239</td>
<td>136</td>
<td>11</td>
</tr>
<tr>
<td>Pitch pine</td>
<td>13</td>
<td>56</td>
<td>30</td>
<td>17</td>
<td>12</td>
<td>7</td>
<td>8</td>
<td>5</td>
<td>7</td>
<td>3</td>
</tr>
<tr>
<td>Hemlock</td>
<td>4</td>
<td>10</td>
<td>27</td>
<td>39</td>
<td>58</td>
<td>78</td>
<td>87</td>
<td>87</td>
<td>13</td>
<td></td>
</tr>
<tr>
<td>Blackgum</td>
<td>3</td>
<td>33</td>
<td>16</td>
<td>8</td>
<td>9</td>
<td>4</td>
<td>3</td>
<td>6</td>
<td>7</td>
<td>2</td>
</tr>
</tbody>
</table>

Table 2. Number of tree-ring series used in each age class for each of the study species.

Figure 1. A comparison of RWI (Figure 1A and C; calculated by calendar year of growth) and BAI (Figure 1B and D) for the 20 oldest trees of chestnut oak from Detweiler Run in central Pennsylvania (Figure 1A and B) and of blackgum from Mohonk State Park, New York (Figure 1C and D).
(e.g., 30–60 years, 61–90 years, etc. to 300+ years; based on tree age at sampling, not calendar year of growth). Tree growth (both raw-ring width and BAI) was measured as the average of 10-year intervals across all trees in each age category. A repeated-measures analysis of covariance was used to compare each tree’s decadal mean growth rates both between age classes of a single species and among species. Adjusted $P$ values were generated for each age class comparison ($\alpha = 0.05$).

Results

Bigtooth aspen and pitch pine, both shade intolerant and considered early successional, showed very different growth rates as well as different maximum ages (120 and 300+ years, respectively). Overall, both bigtooth aspen and pitch pine trees showed an inverse relationship between growth rate and increasing age class (Figure 2A and C). Even so, in both species older trees continued to increase in average BAI throughout their life. For the first 50 years of aspen growth, trees in the 30–60 year age class grew faster than the trees in the 60–90 and 90–120 year age classes ($P = 0.004$ and 0.017, respectively). Pitch pine trees 30–90 years old exhibited the fastest growth rates, peaking at BAI at nearly $1400 \text{ mm}^2 \text{ year}^{-1}$. Significant differences in pitch pine BAI growth rates exist between disparate age classes. For example, trees 30–150 years of age grew significantly ($P < 0.05$) faster than the trees over 150 years of age. The youngest pitch pine trees peaked at around $1400 \text{ mm}^2 \text{ year}^{-1}$, whereas even though the youngest bigtooth aspen trees also peaked at around this value, older trees continued to increase in growth rate until leveling off occurred in very old specimens. Bigtooth aspen trees aged 90–120 years and pitch pine that lived to be over 300 years showed the slowest growth rates overall, indicating that maximum longevity is obtained through slow growth. Young bigtooth aspen and pitch pine trees grew significantly faster than did the older trees at the same respective age. For example, when bigtooth aspen trees in the 90–120 year age class were 30 years old, they grew at $\sim 200 \text{ mm}^2 \text{ year}^{-1}$. In contrast, trees in the 30–60 year age class were growing at about $1000 \text{ mm}^2 \text{ year}^{-1}$ when they were 30 years old. In terms of raw-ring data (mm year$^{-1}$), aspen trees in the 30–60 year age class showed a growth decline over their lives, whereas trees in the 61–120 year age class had an increasing growth (Figure 2B). Pitch pine raw growth rates increased with age in younger trees, but were fairly constant throughout the older age classes (Figure 2D).

![Figure 2](attachment:image.png)

Figure 2. Bigtooth aspen decadal average growth rates in BAI (A) and raw-ring widths (B), and pitch pine decadal average growth rates in BAI (C) and raw-ring widths (D) for each age class. Each decade indicates a 10-year period of averaged growth over all trees in each data set.
The four intermediately shade tolerant oak species were separated based on family groups (red oak family versus white oak family). In the red oak group, black oak trees in the four youngest age classes (30–150 years old) had a significantly greater BAI over time than the trees in the oldest age classes (150 years old and above; Figure 3A). Young trees exhibited large increases in growth rate with increasing age. Growth increased over time in older black oak, but in a much less dramatic fashion (~200% in the youngest four age classes compared to <50% in the oldest four age classes). Black oak in older age classes grew much more slowly than the younger black oak, both at the same respective age and throughout the lives of these older trees (i.e., growth rates of 200 mm² yr⁻¹ in older black oak versus 2000–3000 mm² yr⁻¹ in younger black oak; P < 0.05). Black oak raw-ring growth declined over time in the two youngest age classes, but was highly variable (with no significant trend) in trees in the older age classes (>90 years; Figure 3B). It is important to note that constant raw-ring growth over time results in an increasing BAI (i.e., it takes more wood to produce the same size tree ring as the diameter of a tree increases). In northern red oak, BAI increased significantly from past to present in all age classes (Figure 3C). Northern red oak trees between 30 and 120 years of age typically had the fastest growth rates (P < 0.05), although trees 120–150 years of age ultimately produced the highest growth rate of about 5000 mm² yr⁻¹. The youngest northern red oak trees had increasing raw-ring growth over time, whereas the older age classes had variable, but overall flat growth trends (Figure 3D).

Species in the white oak group, chestnut oak and white oak, displayed slower growth rates overall than the species of the red oak family, except in the youngest chestnut oak (Figure 4). Chestnut oak trees in the 30–60 and 60–90 year age classes grew significantly faster in terms of BAI than trees 120 years of age and older (P < 0.05), peaking near 8000 mm² yr⁻¹ (Figure 4A). Chestnut and white oak trees of all age classes had a variable but an increasing BAI growth over time; however, white oak trees in the 300+ age class exhibited a growth plateau after 200 years of age (Figure 4C). Young chestnut oak trees grew much faster than did the older trees at the same respective age (P < 0.05); young white oak showed a similar trend; however, the growth rates were less disparate when compared with other oak species. Both chestnut oak and white oak raw growth rates showed fairly constant trends; however, chestnut oak 300+ years of age had a decline in raw-ring growth over time (Figure 4B and D). Nonetheless, this was enough to result in an increasing BAI curve in all age classes. The decline in raw growth of white oak is more

---

**Figure 3.** Black oak decadal average growth rates in BAI (A) and raw-ring widths (B), and red oak decadal average growth rates in BAI (C) and raw-ring widths (D) for each age class. Each decade indicates a 10-year period of averaged growth over all trees in each data set.
apparent in the 300+ year old trees until the most recent years when growth abruptly increased (Figure 4D).

Late-successional shade tolerant species (hemlock and blackgum) displayed the slowest overall BAI growth rates of the species studied (Figure 5A and B). Hemlock trees exhibited a significantly increasing BAI growth over time in all age classes, except 300+ year old trees; these trees reached a growth plateau after 200 years. Blackgum trees in all age classes exhibited an increasing BAI with increasing age, including trees over 300 years old. The growth plateau seen in the oldest trees of some of the study species was not evident in blackgum even after 400 years of age. Fast-growing hemlock trees were seen in the four youngest age classes (90–210 years old), whereas slow-growing hemlock trees were in the four oldest age classes (210–300+ years old). Significant differences in hemlock BAI growth rates were seen between these younger versus older age classes (P < 0.05), whereas significant differences in blackgum growth rates were seen only between disparate age classes, e.g., 30–60 versus 300+ years old (P < 0.05). Hemlock and blackgum trees in the older age classes also grew significantly slower than the younger trees at the same respective age. Both species had a highly variable raw growth in younger age classes (~ 30–120 years old; Figure 5C and D). Hemlock trees in the 120–300 year age classes typically had flat raw growth curves, whereas trees in the 300+ year age class had a slightly declining raw growth in the later years. Raw-ring growth in blackgum was variable but tended to be flat over time, although trees in the oldest age classes (240+ years) had a trend of increasing raw growth.

A comparison between the BAI growth rate and the tree age for the highest age class of each species indicates that old pitch pine, blackgum and hemlock trees are the slowest growing of the eight study species (Figure 6). Hemlock trees typically grew faster than pitch pine and blackgum at younger ages, although a large decline in hemlock growth occurred after age 300. The oldest blackgum, hemlock and pitch pine are growing significantly slower than the four oak species (P < 0.05). Bigtooth aspen in the highest age class typically had the highest growth rate and the fastest increase in growth as trees aged (P < 0.05). The oldest trees of the four oak species were intermediate in growth, but had some spikes in growth that equaled or exceeded that of bigtooth aspen. Among the oldest oaks, chestnut oak typically had a slower growth than the others, whereas black and northern red oak displayed higher growth rates.

There exists the possibility that some of these patterns of growth could be the result of tree age and site quality interactions, for example, older trees are typically growing on poorer (rock outcrops with thin soils or bogs/swamps with organic soils), inaccessible sites. Therefore, we analyzed age
and BAI growth rate relationships for chestnut oak, white oak, pitch pine, hemlock and blackgum trees growing on the same site (Figure 7). Chestnut oak trees near Detweiler Run in central Pennsylvania (Figure 7A) and white oak at Lake Ahquabi, Iowa (Figure 7B) had increasing growth as trees aged (with the exception of the oldest white oak), decreasing growth with increasing age class and younger trees grew faster than older trees at the same respective age. Pitch pine trees on the Shawangunk Ridge, New York, were highly variable in their BAI growth rates both within and between age classes (Figure 7C). Nonetheless, pitch trees typically grew faster up until about 200 years of age and younger pitch pine trees had higher growth rates than older trees, including a higher growth at the same respective

Figure 5. Hemlock decadal average growth rates in BAI (A) and raw-ring widths (B), and blackgum decadal average growth rates in BAI (C) and raw-ring widths (D) for each age class. Each decade indicates a 10-year period of averaged growth over all trees in each data set.

Figure 6. Decadal average BAI growth trends of the highest age classes of each of the study species.
age as the older trees. Hemlock trees growing at Ramseys Draft, Virginia (Figure 7D) as well as blackgum growing at Mohonk State Park, New York (Figure 7E) showed increasing growth with age within each age class, decreasing growth from young to old age class and younger trees growing faster than older trees at the same respective age. Therefore, similar tree age, longevity and growth rate relationships exist for these five species when trees of a species grew on the same site as well as when the trees grew across different sites throughout their range. A complete listing of all statistical results can be found in Johnson (2007; Tables 3–10). Also included are figures containing standard error bars for each decadal data point across all age classes and species (Figures 2, 4, 6, 8, 10, 12 and 14).

**Discussion**

The major results of this study are that (1) BAI is a robust measure of long-term growth trends for contrasting tree species.
species and age classes; (2) an inverse relationship exists between BAI and increasing age class for all species (both within and between sites); (3) trees in the oldest age class for each species grew at the slowest rate throughout their life, implying an inverse relationship between growth rate and longevity; (4) the majority of trees in all age classes had increasing BAI throughout their life, including most of the oldest trees, which represents a continuation of their established growth patterns and a deviation from the sigmoidal growth model; (5) over the last 50–100 years, younger trees within a species grew faster than did the older trees when they were of the same respective age; and (6) highly shade tolerant trees and trees growing on poor sites (e.g., rock outcrops and bogs) have an inherently slow growth, implying a relationship among tree life history, site quality and growth rate.

The BAI measurements in this study consistently increased over the life of the trees, including all age classes from young to old. However, BAI plateaued in the oldest trees (240–300+ years) of black oak, chestnut oak, white oak and hemlock over their last 50–150 years of growth. The increase in growth in young trees is expected from the sigmoidal growth model because BAI should increase as young trees produce an increasingly larger leaf canopy (Spiecker et al. 1996). However, a remarkable finding of this study is that even the oldest trees of several species had slow but increasing BAI values, which continued throughout the life of most trees. This contradicts the sigmoidal growth model that predicts growth rate should plateau and then decline, as middle age trees approach old age (Ryan and Yoder 1997, Weiner and Thomas 2001). Patterns of continued carbon sequestration have been noted in old-growth forests, indicating a continued biomass accumulation (Luyssaert et al. 2008); these results may provide substantiation for such findings. The increasing BAI exhibited by both young and old trees in this study is also indicated by a quasi-constant raw-ring-width trend, rather than decreasing over time. The latter case is expected when a constant amount of wood is distributed over an increasingly larger tree diameter. A constant raw-ring width over time means that the tree is producing an increasingly larger amount of wood (BAI) each year.

Fast growth in young trees versus old trees when they were of the same age is intriguing yet confounded by several factors. It is important to note that trees can only reach the maximum longevity for a species by having slow growth (i.e., grow slow, live long, or the converse-grow fast, die young; cf. Schulman 1954, Mäkelä 1986, Kelly

![Fig 7. Continued.](http://www.treephys.oxfordjournals.org)
et al. 1994, Abrams and Orwig 1995, Larson 2001, Abrams 2007, Black et al. 2008). Age class-related growth declines in each species are likely due to a lower proportion of fast-growing trees with increasing age class. Very old trees are rare within a species, whereas younger trees are common for most species. Younger trees are represented by both fast-growing and slower-growing individuals, of which only a few slow growers will probably obtain old age. The proportion of fast-growing trees is higher in the younger age classes; this trend is reversed in the older age classes resulting in significant decreases in the average growth rate (cf. Abrams and Orwig 1995, Orwig et al. 2001, Black et al. 2008). A slow growth rate may come about from genetics, physiology or from site factors. Site factors such as poor site quality, deep shade, and intense competition will result in slow tree growth (Nowacki and Abrams 1997, Pederson 2005, Abrams 2007). Only a small percentage of young trees will have the right combination of genetics and site conditions (which may include inaccessibility to logging) to result in slow growth rates, and thus the opportunity to reach maximum potential lifespan. Our results suggest that growth rate and longevity relationships hold true for both between- and within-site comparisons (Figure 6); however, site conditions are certainly a factor in the analysis.

Ecophysiological differences between species also play a role in a variety of growth rates and longevities seen over the study species. For example, bigtooth aspen is an early successional, shade intolerant species that displays high growth rates and short lifespan. The oak species studied here are typically intermediate in shade tolerance and successional status, while blackgum and hemlock are highly shade tolerant and have among the slowest growth rates and the longest lifespan observed of the study species. Hemlock and blackgum also have the ability to occupy nutrient-poor, upper slopes and bogs, where they grow very slowly and may approach maximum longevity (Abrams et al. 2001, Abrams 2007). However, poor site quality resulting in a very slow growth can result in great longevity, even in early successional trees species such as pitch pine and northern white cedar (Abrams and Orwig 1995, Larson 2001). This phenomenon can be seen with this analysis, as the pitch pine and blackgum had slow growth rates on rock outcrops and bogs, respectively, resulting in a longer lifespan on these types of sites.

Intrinsic differences in growth are shown irrespective of the climate, as noted in previous studies, because tree growth rate data before the year 1800 still shows age class differences (Black et al. 2008). Very old age classes in this data also have a high proportion of very slow-growing trees even before the Industrial Revolution, suggesting that old trees exhibited slow growth throughout their entire life, as reported in this study. However, a surprising trend is that older trees in this study had slow but increasing BAI over the last century or more, which contradicts the sigmoidal growth model. We do not know the exact cause of the increasing BAI in the oldest trees; however, it seems reasonable to assume that it may be due to a stimulatory effect of anthropogenic global change defined in the broadest sense, i.e., including both land-use history (land clearing and changes in natural disturbance regimes) and atmospheric factors (cf. Innes 1991, Briffa et al. 1998, Voelker et al. 2006). Atmospheric factors include increased CO2 levels, warming temperatures, increased precipitation, and changes in precipitation chemistry (Aber et al. 1989, Bazzaz 1990). Yearly average temperatures, atmospheric CO2 and nitrogen levels have increased in the eastern US (as well as much of the rest of the world) over the last 50–100 years (Aber et al. 1989, Lindroth et al. 1993, Nadelhoffer et al. 1999, Korner 2000, Galloway et al. 2003, IPCC 2007). The fertilizing effect of these factors is present in many, but not all, tree-ring series as increases in radial growth (Briffa 1992, Hattenschwiler et al. 1996, Rathgeber et al. 2000, Esper et al. 2002, Voelker et al. 2006). The relationship between tree growth rates and these global change factors requires much more study to define the various factors associated with changing global climate and environments, and the effect that these may have on tree growth. It may be that global change phenomena, including land-use history, have increased the growth rate of old trees during the last century. This leads to the intriguing hypothesis that the continuation of global change factors that have a stimulatory effect on tree growth may act to reduce tree longevity in the future, as fast-growing trees are less likely to obtain the maximum longevity for the species.

Funding

Support was provided by the Department of Defense, Ft. Indiantown Gap National Guard Base and Pennsylvania State University.

Supplementary data

Supplementary data for this article are available at Tree Physiology Online.

Acknowledgments

The authors thank Drs. Charles Ruffner, Mary Ann Fajvan, Neil Pederson, Ed Cook, Bryan Black, Carolyn Copenheaver, Steve Signell and Rebekah Wagner for research advice and for providing the tree core sets; Drs. Margot Kaye, Kim Steiner and Jacob Weiner for ideas on data analysis and for a critical review of the manuscript; Christine Shook and Glenna Malcolm for field, statistical and graphical help.

References


