Age-Related Decline in *Quercus rubra*: A Physiological test of the hydraulic limitation hypothesis

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Robert Carson

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Graduate School of Arts and Sciences
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Abstract

The study of age-related decline in forest primary productivity has been the focus of recent work on coniferous forest species from the western United States. This study seeks to address the paucity of literature on the subject with respect to eastern deciduous forest species. Research indicates that two promising explanations for age-related decline: imbalance between photosynthesis and respiration; and increasing nutrient limitation may not be sufficient to explain the observed declines. Much recent work has been focused on the third hypothesis of hydraulic limitation restricting the physiology of the hydraulic, and photosynthetic pathway. This study seeks to document changes in the physical structures of the hydraulic pathway in individual *Quercus rubra* L. trees from stands ranging from 35-135+ years old in a temperate deciduous forest. No evidence for reduced leaf area with tree age was observed, a linear regression with positive slope was fit to the leaf area data (R^2=0.7861). Analysis of growth rings from increment cores provide historical carbon sequestration rate data, and reveals a significant decline in relative growth rate between the youngest individuals (35-years old) and the next age groups (70- and 91-years), as well as between the 91-year old individuals and the oldest individuals (137-years old). Total carbon accumulation rate is positive in all stands, with the steepest positive slope in the oldest individuals.

Introduction

Age-related decline in primary productivity of forests has been the focus of considerable recent research. It is a paradigm that is often accepted, but lacks a clear mechanistic explanation. Aside from a basic understanding of forest form and function, this paradigm is clearly important to current efforts to assess the role of forests as carbon sinks, and to construct mechanistic models that could be used to predict the response of forests to climate change (Ryan et al, 1997). Shifts in theoretical framework, and advances in technology and methods have led to refinements of the physiological models. (Gower et al 1996, Murty et al 1996, Ryan et al 1997, Bond 2000, McDowell et al, 2002a). Gower et al (1996) reviewed the status of the field by delineating three physiological hypotheses for age-related decline in above ground net primary production associated with stand age:

1. Photosynthesis-respiration imbalance
2. Decreased nutrient supply (nutrient limitation)
3. Increased hydraulic resistance

In addition, some authors have suggested that genetic changes associated with meristem age may also contribute to growth constraints (Ryan and Yoder 1997, Day et al 2001). Although recent advances have been made in documenting and testing the hypotheses, the pattern of the responsible mechanisms is not clearly applicable across sites and species.

To date, nearly all of the studies of age-related decline have focused on coniferous species, primarily from the western US where old growth forests are more common. Very little research has addressed this issue through studies on deciduous species that dominate the forests of the North East. In this study, I explore the third hypothesis from Gower et al (1996), that age-related decline in primary productivity is due to increased hydraulic resistance resulting from increased path length of water from bulk soil to stomata. The water balance of a forest ecosystem has important implication for primary productivity (Eamus, 2003) and for canopy hydraulic properties (Engel et al 2002). Indeed, the limits of height growth in trees appears t be limited by the ability to transport water to the crown (Koch, 2004, Midgley 2003).

That there is an allometric relationship between stem sapwood area and leaf area has been recognized in plant literature since Huber (1928). It was Shinozaki et al. (1964) who suggested a formal conceptualization of this relationship in the pipe model: interpreting tree form as “an assemblage of unit pipes each supporting a unit amount of photosynthetic organs”. The assumptions of this model include a constant ratio of leaf area to sapwood area (A_l:A_s) throughout plant development. Using this relationship the leaf area of a specific tree, or of a stand can be estimated from knowledge of the species’ Huber value (A_l:A_s ratio) and the sapwood area (Grier and Waring 1974, Whitehead 1978, Waring et al 1982). Recent studies suggest, however, that the A_l:A_s varies according to the water balance of a particular site. White et al (1998) found that A_l:A_s declined with decreasing soil water availability at constant evaporative demand. In addition, A_l:A_s declined along gradients from low to high evaporative demand (Menuccini and Grace 1995). Whitehead et al (1984) refined a hydraulic model for the mechanism by which reductions in the Huber value could compensate for increased evaporative demand. This compensation would be the key to avoiding cavitation from excessive water potential gradients and maintaining canopy conductance (McDowell et al 2002a).

Additional recent work has focused on the precise relationship between sapwood area and leaf area in a variety of species (Meadows and Hodges 2002, Mokany et al 2003). Studies have shown that changes in the hydraulic architecture of trees occur along gradients of water availability (Magnani et al 2002), and that acclimation to hydraulic constraints plays a role in age-related decline (Magnani et al 2000).

It should be noted that this model is an oversimplification of hydraulics of trees in many respects. One example is that the model is best applied to cylinders of uniform material. Another example is that tree height is used as a surrogate for the actual path-length of water from the bulk soil to the stomata that includes not only height, but also tortuosity and branch length. But, because tree height comprises the majority of this path-length, and is an easy and common measurement made in the field, it provides a useful variable for the purposes of the model.

McDowell et al (2002a) tested hydraulic constraints to tree height and age in a coniferous forest using 30, 50- and 450-year-old stands. Their findings suggest that A_l:A_s declines substantially with tree height (and age). In a meta-analysis of published data sets, they explored the generality of their results, and found the trend was exhibited in *most* species. Their conclusion was that the decrease in A_l:A_s with increasing height observed in the majority of species may be a homeostatic mechanism that partially compensates for decreased hydraulic conductance as trees grow in height.

The decrease in A_l:A_s with age in stands has been documented in a number of species (Gower et al 1996, Barnard and Ryan 2003), while some species have exhibited an increase in A_l:A_s with age or height (Phillips et al 2003, McDowell et al 2002b). Because an understanding of the physiological responses of different forest types is necessary to more accurately predict the carbon dynamics under climate change, an accurate assessment of variable characteristics across landscapes is crucial. This study seeks to provide an understanding of the effect of hydraulic limitations on the growth, and physical characteristics of the hydraulic pathway in red oaks (*Q. rubra*).The measurement and analysis of physiological properties of the hydraulic pathway, such as sapwood area, leaf area and canopy characteristics will allow a regression analysis with tree age and will allow the assessment of the hydraulic limitation hypothesis in a temperate, deciduous forest. In addition, the assessment of carbon uptake through each tree's history will address the patterns of carbon storage in this system. This information can provide useful calibrations for global carbon budgets in the framework of senescence.

Materials and Methods:

Study site

Black Rock forest is a 1500 ha preserve in the Hudson Highlands region of New York (41˚24'N, 74˚01'W). Elevations in the forest range from 110 – 450 m above sea level with average seasonal temperatures from –2.7˚C in January to 23˚C in July. The medium texture soils are typically very thin, ranging from 10-15 cm in upland areas to greater than 1 m in the depressional areas. Lumber extraction in the forest ceased in 1934 and the forest has been managed as a preserve without significant disturbance since that time. The forest is dominated by oaks of various species (*Quercus* spp.) which is typical of the secondary growth forest that characterizes the North-Eastern United States. There are approximately 734 trees per hectare throughout the forest with an average basal area of 21.0m2 ha-1 (Friday and Friday, 1985, W. Schuster, unpublished data). *Q. rubra* is the dominant species in Black Rock forest, and represents 42.3% of the total basal area. *Quercus prinus* is the next most dominant species and represents 23.8% of the total basal area, followed by *Acer rubrum* (7.6%).

This research was conducted on five neighboring stands situated in compartment IV of the forest (near the intersection of Bog Meadow and Carpenter Roads). Sites were selected with the help of historical records of forest management, and the expertise of the forest manager. An attempt was made to select sites to represent 5 distinct age classes (35, 70, 95, 115 and 150+ years old) in stands where *Q. rubra* dominates. In each site, twelve trees were selected for inclusion in the study. This research was part of a larger study to quantify physiological characteristics of *Q. rubra* across age classes. Additional research addressed the capacity for carbon fixation, stem and foliar respiration rates, leaf chemical and physical properties, and standing biomass (K. Griffin, unpublished).

Site Measurements

Measurements taken directly for this study included stand-level leaf area index (LAI), specific tree age, height, relative growth rate (RGR), and sapwood area. From the LAI measurements, tree-specific leaf area was calculated.

Age, RGR and Sapwood Area

Increment cores were taken from each tree, including at least one core taken from the trunk at breast height (~1.3m) to determine both bark thickness, and sapwood radii. The sapwood-heartwood boundary (defined as: total sapwood area) was determined by marking the point of visual translucence when holding the fresh core up to the sunlight. Cores were sealed in straws and kept cool until return to the laboratory. The total sapwood radius marked in the field was measured with calipers. Additionally, the current sapwood radius, defined as the early-wood portion of the current year, plus the entire previous year, (Meadows and Hodges 2002, White 1993, Rogers and Hinckley 1979,) was measured. These radii, along with the diameter at breast height (dbh), and bark depth were used to determine the total and current sapwood areas. Bark depth was measured directly from sapwood cores, but because coring technique tends to underestimate bark depth, calculations were also made using allometric equations from Martin (1981).

An additional core was taken from as low on the trunk as possible. This core was used to correctly age the tree, and determine the tree's relative growth rate through time. All cores were dried, mounted and sanded to prepare for age, and growth analysis. Measurement of growth rate, and age determination was conducted using MeasureJ2X® software (VoorTech Consulting 1998) and a standard microscope and sled system. Each core was analyzed twice to minimize error. In order to determine age in the cases where the center (pith) of the tree was not included in the core, the inside radius of the earliest growth ring was measured, and average growth, compared with allometric equations (Martin 1981; Martin et al 1998), was used to determine the number of interior rings.

Tree Height and Canopy Volume

Measurement of tree height and canopy height was determined using an optical hypsometer. The device uses a stationary reflector placed at breast-height and a remote optical device that is alternately pointed at the stationary reflector, and at points of interest. In this case, the top of a top-canopy branch, and the trunk at the lowest canopy branch was used to determine tree height, and height of tree canopy, respectively.

Measurements were initially made in July, and some were duplicated in March to compare with- and without-leaf determinations. Canopy size was determined by measurements taken in the four cardinal directions from the base of the tree to the drip-line. The area of the ellipse connecting these four points provided a value for canopy area. Canopy volume was then calculated using this area and the canopy depth.

Leaf Area Index (LAI), and Leaf Area

Determination of stand LAI and tree-specific leaf area was made using both indirect and direct methods. The direct method included the placement of ten litter traps in each stand. The litter traps consisted of plastic bins with fine mesh netting inside to keep the leaf litter out of standing water. Collections of leaf litter were made weekly during leaf fall to minimize decomposition and wind-throw. Fresh leaves were separated by species and their petioles were removed. A sub-sample was scanned (LI-3000, LiCor Incorporated, Lincoln NE, USA) to determine one-sided surface area. The sorted and separated leaves were then dried in a 70° C oven until all moisture had evaporated. Each sample was then weighed to the nearest 0.01g. A weight:area ratio was determined for each species in each stand using the scanned sub-sample. This ratio was then used to estimate leaf area index (m^2/m^2) in each stand, and the relative contribution of each species. This method is a relatively good indicator of total leaf area, and has been used to calibrate and interpret results from indirect methods (Bréda 2003, Jonckheere et al 2004).

Indirect determination of both stand-level and individual tree leaf area was made using hemispheric photography. Standard methods of image capture and analysis were followed, for a discussion see (Jonckheere et al 2004). High-resolution digital photos were taken at the drip-line in each of the four cardinal directions around each tree, and bracketing exposures were taken to ensure an analyzable image. Each point was photographed once during mid-late summer, and again during the winter to enable correction for stem and branch area. The images were analyzed using Gap Light Analyzer (GLA) software (Frazer et al 1999) to determine canopy properties including stand-level LAI. Individual tree leaf area was determined by manipulating each of the four images to exclude all but the subject tree, running the analysis to get an average 4-ring LAI value, then multiplying this value by the ground area covered by the stand height and azimuth angle. In all cases, a similar procedure was used with the winter images, and the output value was subtracted from the summer output value to determine the leaf area index corrected for stem and branch areas.

Carbon accumulation was assessed using the ring-width data from the basal increment core and allometric relationships to determine aboveground biomass and carbon accumulation. The general equation ($M=aD^b$; where M is the dry weight of the biomass component; a and b are parameters which must be calibrated depending on species or biomass component of interest. A review of this method from Ter-Mikaelian and Korzukhin (1997) provided useful calibration values for *Q. rubra* biomass components from a variety of sources, including studies of red oak in New Hampshire and West Virginia (Kinerson and Bartholomew 1977, Hocker and Earley 1983, Brenneman et al. 1978). Additional allometric equations for the species can be found in a review by Martin et al (1998). A regression approach was used to analyze the physical parameters in the hydraulic pathway for evidence of compensation for hydraulic limitation. Data were also analyzed by age class to determine general patterns of these variables across stands.

Results

The results from the age analysis of the basal increment cores showed that 10 trees in stand four were not significantly different in age from those in stand 3, while two trees in stand 4 were as old as those in stand 5. The age consistency within stands 1, 2, and 3 (M=35, 70 and 91-years old respectively) was excellent, with most trees falling within three years of one another. Some variation existed in stand 5, with most trees falling between 130- and 150-years old. As a result, the age-class analysis was conducted using the following categories: stand 1(35-years old, stand 2 (70-years old), stands 3 and 4 (91-years old), and stand 5 (131 years old) (Table 1). The values shown in the stand-level averages demonstrate a general trend toward higher leaf area and sapwood area in older stands. The two older trees from stand four exhibit characteristics that are consistent with the trees in the oldest stand, but were not included in stand-level analyses.

The regression approach was used to explore the relationship between leaf area, sapwood area and tree age or height. In both cases, a linear regression with tree age provided a better fit than with tree height. The results from the regression approach show a linear increase in leaf area with age (R^2=0.7861) (Figure 1a), sapwood area shows a linear increase with age in *Q. rubra* (R^2=0.5304)(Figure 1b). A linear regression fit for leaf area vs. current sapwood area (figure 1c) (R^2=0.4869) showed a better fit that leaf area to total sapwood area. Tree-height, and dbh were poor predictors of leaf area, (data not shown).

The tree height and tree age regression exhibited a logarithmic trend (Table 2a) (R^2=0.4182) demonstrating that height growth rate was not substantial after 70 years.

Canopy volume showed a linear increase with tree age (Figure 2b), particularly between the two youngest stands. The regression of tree age and canopy volume (R^2=0.6021) showed little deviation from the trend for tree canopy volumes in stands 1 and 2, but greater deviation from the trend particularly in the oldest stand.

Total aboveground biomass was calculated from diameter and incremental ring width. Comparison of calibration values showed little relative variation; so two values (a=0.1130 and b=2.4572) were chosen a study of red oaks with the greatest range of diameter values (Ter-Mikaelian and Korzukhin 1997, Brenneman et al 1978). Incremental carbon gain was calculated by multiplying total AB by 0.454 g C g^{-1}. Patterns of carbon uptake were assessed using the average individual tree carbon accumulation (figure 4a,b) from each stand. The average total carbon storage in individual trees in different-aged stands shows that the oldest stand is, unsurprisingly, holding the largest amount of carbon per tree. Normalizing carbon accumulation curves by age (figure 4b), reveals that the average carbon accumulation value from stand 5 (131+years old), is as high or higher than the rates expressed by overlapping ages from other stands. It also reveals some variation in accumulation rates when stands are/were 10-30-years in age, these differences are likely to have long-lasting impacts on the total carbon storage in each stand

Relative growth rate, in terms of incremental carbon gain relative to existing aboveground biomass reveals decreasing primary productivity with age (figure 5a,b). Normalization of the RGR data with age (figure 5a) reveals that trees in the two ~91 year-old stands exhibit very similar patterns of RGR decline, and that trees in the 35-year old stand appear to be closely following the trend exhibited by older trees during the first four decades of *their* growth. Looking at the past five full-years of growth (1998-2003) (figure 5b), average individual RGR declines across the age progression, with the exception of a small increase noted between stands two and three. This increase was due entirely to the inclusion of one fast-growing tree in stand 3. As noted on the figure, exclusion of this tree from the stand average reduced the stand 3 average RGR to within the standard error value of stand 2. There is little difference between the average individual RGR from the 70-year stand, and that from the first stand of 91-year-old individuals. There is a slight decline in RGR between individuals in stands three and four, and a notable decrease between these and the oldest individuals (stand 5, figure 5b).

Discussion

The evidence from this study suggests that any hydraulic limitations experienced by these trees were not expressed through a reduction of leaf area with age. Indeed, the ratio between leaf area and current sapwood area showed little discernible change with age (R^2=0.0252). It should be noted, however, that because stand 4 turned out to have the same median age as stand 3, rather than intermediate between the 91-, and 130+-year-old stands the desired age-progression was not captured. But, the strong linear fit between the estimated leaf area of each tree and its age does suggest that the leaf area of trees in these stands is not decliningThe variation in sapwood area that was not explained by the regression with age (R^2=0.5304) may be due to changes in the sapwood permeability of individual trees (Shelburne and Hedden 1996; Chen 1991), or due to variation in the amount of actual conducting sapwood (Mäkelä 2002).

The finding that age was a better predictor of sapwood area, leaf area, and Huber value than was height is contrary to the accepted doctrine (McDowell et al. 2002b; Mokany et al 2003). This may be due to the structural growth patterns of red oak trees. Perhaps because *Q. rubra* do not grow as tall as many coniferous species, and are rarely competing directly with coniferous species in the same habitat for light, they show a lateral branching pattern in the crown, which leads to a wide, rather than tall canopy with age. The contribution of height *per se* to the overall path-length from bulk soil to stomata is less than is observed in canopies of coniferous species that generally grow narrower with height. These data suggest that the red oak trees in Black Rock Forest reach their maximum height relatively early in life, and subsequent growth is generally observed as an increase in canopy volume. The variation in canopy volume in the older stands can perhaps be explained by the competitive interactions for light and canopy space as stands mature (Binkley 2004).

The canopy LAI measurements made by analysis of the hemispheric photographs showed a generally consistent pattern with the LAI estimated by direct collection of litter-fall. Both methods estimated a LAI increase with age, but the values estimated with the photos were consistently lower than direct measurements. This finding is consistent with a review of methods by Jonckheere et al. (2004), which suggests that hemispheric photographs underestimate actual canopy LAI because of light distortion around the edges of canopy leaves. The use of canopy photo analysis to determine both canopy LAI and the leaf area of specific trees is justified, particularly when the findings can be compared to results from direct measurement (Bréda 2003), and correction for stem and branch area can be accomplished. I would suggest that careful and standardized use of canopy hemispheric photos can be a useful indirect measurement of leaf area, but careful attention to sky-conditions, and camera position should be observed.

The assessment of the carbon dynamics of aboveground biomass in this study raises two interesting perspectives. Firstly, the total carbon accumulation patterns underline the potential importance of old stands at effectively storing and continuing to draw down atmospheric carbon (Law et al 2003). Current forest models may be seriously underestimating this capacity (Carey et al. 2001). The slope of the carbon accumulation line in Figure 4a for the oldest individuals is steeply positive, suggesting any eventual decline in the total carbon sequestration rate may be in the distant future. Evidence from a study of an old-growth oak forest indicates that the oldest red oak trees were between 200 and 225-years old (Rentch et al 2003). So, it is possible that the oldest cohort in this study may not yet be old enough to capture a decline in late-age growth patterns This individual tree perspective of carbon sequestration supports those who claim that any study of age-related decline must focus first on the emergent stand-level changes that occur with age, such as: declines in density (Smith and Long 2001); dominance and competition (Binkley 2004, Binkley et al 2002); genetically programmed growth patterns or reproductive effort (Becker et al 2000), or natural sigmoidal growth patterns (Weiner 2001).

The second perspective on carbon storage rates is offered by the relative growth rate information in Figure 5. This perspective focuses on the efficiency of increasing current standing biomass. This study clearly demonstrates the decline in the efficiency of older *Q. rubra* trees at adding large percentages of their current biomass on a yearly basis. Such patterns of relative growth demonstrates that while older forests may provide an important storehouse of carbon (Carey et al 2001), and invaluable habitat for wildlife, they harbor lower tree density (Smith and Long 2001, Ryan et al 1997), and are less effective at relative growth than fast-growing trees planted and harvested on short cycles. In terms of productivity, higher stand density in even-aged young stands, and the higher relative growth rates of young trees leads to a higher carbon gain per unit ground area than is observed in older stands with lower tree density. (Ryan et al 1997).

It should be noted that there is little evidence from this study, that climate change is having an impact on the relative growth rate of this forest. Because the relative growth rate and carbon accumulation curve for the average individual in the youngest stand show a close affinity with the pattern established by even the oldest individuals, these results provide little evidence for any current effects of CO_2 fertilization or increased evaporation which may occur with climate change. The impact of hydraulic limitation on carbon gain or plant morphology cannot be inferred from the physical properties collected in this study but this data should provide important calibrations for the scaling of canopy, leaf and stomata level physiological measurements.

Conclusions

Measurement of the physical components of the hydraulic pathway in red oak trees enables a proximate assessment of compensatory, structural effects of hydraulic limitation. Analysis of the relative growth rates (exhibited in ring-width) allows for an historical look at the accumulation of both biomass and carbon with age. The findings reported in this study would suggest that there were no changes to the structural pattern of the hydraulic pathway with age. This does not mean, however, that there has not been any. Other mechanisms that could compensate for hydraulic limitation include changes in conductance (Mencuccini 2003; Phillips et al 2002) that were not measured in this study. A more complete assessment of the physiology of structures (leaves, roots) and of processes (photosynthesis/respiration) involved in tree growth will allow for a more definitive conclusion on the question of age-related decline. Because of environmental variation, and evolutionary history, it is important that similar studies be undertaken on a variety of species in a variety of environments address the role of particular systems in the global carbon budget.

Appendix C: Referenced Literature

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