Using Dendrochronology to Examine the Growth Patterns of Eastern Hemlock Following Hemlock Woolly Adelgid Infestation

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by
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To all of my parents and sisters

I would like to thank the following people:

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Contents

Abstract

Eastern hemlock is experiencing widespread mortality across its range in the eastern United States due to hemlock woolly adelgid infestation. Although the patterns of decline of this important coniferous species have been studied, many questions about predictive factors and characteristics of mortality remain unanswered. I used dendrochronology to investigate the declines of two different groups of trees — one group that was dead by 2002, and another group that is still alive. I found significant differences in growth, size, and age between the two groups of trees. While the hemlock woolly adelgid infestation significantly affected the growth of both groups, it did not have a different effect on the two groups. However, prior research and examination of the data suggest a possible difference in the declines of these two groups. In particular, moisture availability seemed to be a predictor of damage incurred, as did overall tree performance. I was unable to separate location and demographics as possible causative agents, so future work should focus on isolating these two factors.

Introduction

Hemlock woolly adelgid (*Adelges tsugae* Annand), an invasive pest species, was first reported in the eastern United States in 1951 as a minor issue in a Richmond, Virginia ornamental garden (Gouger 1971; Souto et al. 1996). The adelgid has now spread throughout most of the eastern United States, impacting hemlock (*Tsuga canadensis* (L.) Carriere) populations from North Carolina to Maine (Orwig and Foster 1998; USDA Forest Service 2012). Hemlocks are a late-successional tree species that dominates many east coast forests (Rogers 1978). The widespread effects of hemlock decline have been extensively researched and reported, but there are many questions that remain only partially answered.

Forests are an essential part of the carbon cycle on earth and are valued for their contributions to human life – both in terms of resources and aesthetics (Pan et al. 2011). As trees grow, they use carbon to build their own structures, thereby storing carbon (Luyssaert et al. 2008). While the perceived value of forests has changed throughout history, at this point in time the significance of forests to humans can be thought of as economic/utilitarian, life support, aesthetic, and moral/spiritual (Bengston and Xu 1995). The importance of forests cannot be overstated – therefore major factors impacting their health are worth investigating.

Hemlock woolly adelgids feed only on hemlock trees in the United States, so all other tree species stay healthly or even benefit in the midst of an infestation (McClure 1987*a*; Orwig 2002; Eschtruth et al. 2006). Why, then, is it significant for one tree species to be largely replaced by another? One school of thought might say that it is not cause for concern and that nature should be left to its own mechanisms. Perhaps human introduction of invasive species could be considered natural. Though hemlock forests will eventually stabilize and come to be dominated by another tree species, that transition will be slow, and the rapid decline of hemlock could leave forests without important structural and ecological aspects for some time.

Hemlocks can live for more than 800 years, with some of the biggest specimens measuring over 1.9 meters in diameter and 53 meters in height (Burns and Honkala 1990). European colonists found hemlocks that were up to 160 feet tall, 6 feet in diameter, and upwards of 500 years old (Quimby 1996). Though these particular specimens have all been cut, these findings indicate that hemlocks have been dominant in the eastern United States for many centuries. Because hemlock is shade-tolerant and able to thrive in a variety of soil types, it often comes to dominate stands after growing up through the understory (Rogers 1978). Through the nineteenth century, hemlocks were quite valuable economically. They were used in leather tanneries for the tannins in their bark, and by the lumber industry for their wood (Burns and Honkala 1990). As the old-growth hemlocks became depleted and better methods were introduced for leather-making, the species' use tapered off (Quimby 1996).

Despite the end of its economic utility, hemlock remains important to eastern forests for both ecological and aesthetic reasons. Ninety-six avian species and 47 mammal species use hemlock as a nesting site, food source, or general habitat (Yamasaki et al. 2000). Indirectly, hemlock is the framework for ecosystems that support many shrubs and understory growth, such as leatherwood (*Dirca*), rattlesnake plantains (*Goodyera pubescens*), bunchberry (*Cornus canadensis*), goldthread (*Coptis*), bluebead (*Clintonia borealis*), Canada mayflower (*Maianthemum canadense*), and wood sorrel (*Oxalis*) (Quimby 1996). Hemlock is also linked to lower stream temperatures, an important factor in maintaining habitats for fish such as brook trout (Evans 2002). As for the visual impact of hemlock in eastern forests, John Quimby of the Department of Conservation and Natural Resources states, "Aesthetically, the hemlock has no equal in the east" (1996). There is no doubt that he is not alone in this sentiment, and in general Americans tend to feel that beauty is worth protecting – especially beauty as it exists in nature. The hemlock is also prevalent in many state and national parks, although it is hard to say whether this is due to chance. In other words, were parks built around hemlock's beauty, or was hemlock's dominance in the east just represented by its inclusion in many forests? Regardless, hemlock characterizes many eastern United States parks, and its demise would not be favorable to the patrons of these parks.

From the vantage point of a human lifetime, forests often appear to be places of great stability, but this is only partly true. While some forests shift and grow very slowly, in long cycles, they are never stagnant. But there are also circumstances that can bring about rapid change. For example, many forests – notably those in the western United States – are constantly plagued by fire (Agee 1998). Fire regimes vary in severity and frequency, based on the fire tolerance of the dominant species. For instance, Ponderosa Pine (*Pinus ponderosa*) forests have a low-severity fire regime, because the frequency of the fires prevents fuel buildup and the characteristics of the trees make the overstory fireproof (Agee 1998). Pest outbreaks are also common in forests, and vary widely in severity due to differences in host specificity, host resistance, and pest features (Lovett et al. 2006). Whether due to natural cycles of succession, natural disturbances, or clear-cutting, stress and disturbance are always found in forests.

In hemlock forests in the eastern United Staes, the hemlock woolly adelgid beetle is becoming a major disturbance. HWA is native to Japan, where it lives, feeds, and reproduces on the trees of the *Tsuga* and *Picea* genera (McClure 1987*a*). Its impact is checked by host resistance and natural enemies in its native habitat (McClure et al. 1999). In the United States, neither of these controls exists, allowing HWA populations to grow rapidly and quickly decimate hemlock stands (McClure 1987*b*). HWA is self-limiting on an individual tree level; adelgids feed on new needle growth, and they quickly reproduce to the extent that they exceed the carrying capacity of the branch (McClure 1991). Their presence is so taxing on the hemlock that not enough new growth is produced to sustain the same HWA population the next season (McClure 1991). But, because of rapid reproduction and spread, HWA mortality has not stopped the spread of the infestation. Due to lack of resistance and an absence of natural predators, HWA population dynamics are mostly controlled by climate patterns and density-dependent feedback (McClure et al. 1999).

HWA has a polymorphic life cycle with two generations annually (McClure 1987*a*). In mid-February, adult females from the overwintering generation begin laying eggs. Each lays about 50 eggs in a spherical woolly sac over a roughly 16-week period (McClure 1987*b*). In mid-April these eggs begin hatching into crawlers. Crawlers are the first instar, or nymph developmental stage, and they are mobile, as their name suggests. After three more instars, the nymphs become either winged or wingless adults, both originating from the same batch of eggs (McClure 1987*b*). The winged adults are a migratory form, a generation that leaves for a different host, in this case spruce (*Picea*). In native Japan, spruce is the primary host and hemlock is the secondary host. However, since there are no spruce species in the Northeastern United States that HWA can survive on, this winged contingent flies off in search of a nonexistent host and subsequently dies (McClure 1987*a*). The wingless adults of the spring generation lay about 25 eggs each into ovisacs, and these eggs hatch in June or in the first half of July (McClure 1987*b*). The crawlers settle onto young branches, and then are dormant until October, when they resume maturing, becoming adults by February (McClure 1987*b*).

Crawlers, once on the selected needle, attach to the underside of the base of the needle with their legs, and prepare for feeding (Shields et al. 1996). The hemlock woolly adelgid feeds by inserting a stylet bundle into the proximal needle stem (Shields et al. 1996). The stylet bundle consists of two mandibular stylets and two sheathed inner maxillary stylets, the latter of which can extend or retract in the grooves of the former. The stylets are inserted intracellularly, just promixal to the abscission zone of the needle, where the final segment of the needle attaches to the stem. Once inside the needle, the maxillary stylets locate a parenchyma cell to puncture and feed on, secreting saliva with unknown properties in the process (Shields et al. 1996). Parenchyma are cells responsible for transfer and storage of nutrients, and also contain photosynthate (Shields et al. 1996).

HWA can cause hemlock mortality within two years, so it was initially hypothesized that the adelgid injected toxic saliva and removed sap when it fed (McClure 1987*b*, 1990). Newer studies explain the rapid mortality by suggesting how the adelgid is likely affecting plant defense mechanisms. Hemlock is having a defensive hypersensitive response to HWA, in which it releases H_2O_2 and causes its own localized tissue death at the site of attack, in order to prevent the pest from feeding (Radville et al. 2011). Additionally, a systemic hypersensitive response is likely, because increased levels of H_2O_2 were found in parts of the trees that had no local threat (Radville et al. 2011). In addition to taking nutrients from hemlocks, HWA may be causing cell death by provoking this defensive response in the trees it feeds on (Shields et al. 1996; Radville et al. 2011).

Hemlock woolly adelgid was first found in the United States in 1928, in Eugene, Oregon (Gouger 1971). The insect was found in California later in 1928 and in Washington in 1968, but it was not of consequence in forests in the West, perhaps due to differences between western hemlock (*Tsuga heterophylla*) and eastern hemlock (Gouger 1971; Furniss and Carolin 1977). It was, however, quite injurious on the eastern coast of the United States, where it was found in Virginia in 1951 and Pennsylvania in 1969 (Gouger 1971). In 1985, Hurricane Gloria blew the HWA into Connecticut from Long Island, where it had been for several years (McClure 1987*b*). By 1998, HWA was established in ten states from North Carolina to Massachusetts (Orwig and Foster 1998). In 2011, HWA was established in 18 states, from Georgia to Maine (USDA Forest Service 2012). Although winter temperatures currently limit HWA spread, climate change could make the entire Northeast habitable to HWA by the end of the century (Paradis et al. 2008).

In the Connecticut College Arboretum, the total basal area of hemlocks has dropped 70% from 1982 to 2002 (Small et al. 2005). During that same time period, black oaks (*Quercus velutina, Q. coccinea, Q. rubra*) have gone from 28% of the canopy basal area to 41%, suggesting that other species are using the resources that hemlock once used (Small et al. 2005). In Shenandoah National Park, mortality of infested hemlocks ranged from 8% in 1991 to 48.7% in 2001 (Bair 2002). Hemlock mortality in infested sites is variable, but in some Connecticut stands it surpasses 95% (Orwig and Foster 1998). Unfortunately, hemlock has shown no ability to refoliate or sprout following defoliation (Orwig and Foster 1998). Small et al. (2005) did not think it was likely that a hemlock population rebound would occur in the twenty-first century.

Many different strategies can be used to study forests, trees, and their histories. Satellite imaging, composition and size surveying, visual inspection, and nutrient monitoring are all used to assess both trees and ecosystems as a whole (Bair 2002; Young and Morton 2002; Orwig et al. 2008; Schuster et al. 2008). Every method has its benefits and shortcomings, and for this reason they are often used in tandem (Orwig et al. 2003). Dendrochronology is an area of study that is particularly useful for historical reconstructions, because it is the study of the growth rings in a tree, which provides a history for each tree (Cook et al. 1987). The most basic use of dendrochronology is simply assessing the growth patterns of a tree through time, but because many factors affect growth, the growth response of a tree can be unpacked to reveal climate, disturbances, and other ecosystem conditions at play throughout time. Fire, climate, and insect outbreaks have all been studied using a dendrochronological approach (Pohl et al. 2006; Cook et al. 1987; Swetnam 1987).

Also using this approach, a 1940 Connecticut study found that precipitation had no significant correlation with basal growth in hemlocks (Avery et al. 1940). They pointed out that in the approximately 130 years that their sample hemlocks lived, while ring width decreased, basal area increment actually increased due to the growing circumference of the tree (Avery et al. 1940). The study compared trees growing in ravines versus on ridges and found consistently different amounts of growth, despite correlated cyclical patterns of growth (Avery et al. 1940). The trees in the ravine had a mean ring width greater than the trees on the ridge for all but 11 of the last 63 years of their lives (sample trees were uprooted in a 1938 hurricane) (Avery et al. 1940). This illustrates that while there may not have been a strong precipitation signal, it is possible to pick up consistent growth patterns in different groupings of hemlocks.

In 2008, Rentch et al. used dendrochronology to study the effects of HWA on hemlock growth and vulnerability. They found that trees in decline (three consecutive years of below-average growth) had lower crown density. Trees in decline had a significantly different mean age, with declining trees being on average younger. They also found that dieback increased dramatically after 2000. HWA was first noticed in the Delaware Water Gap National Recreation Area, where the study was conducted, in 1989. By 1992, decline in hemlock health was evident

(Rentch et al. 2008). In one of their test sites, the percentage of trees in decline rose from 41% in 1998 to 96% in 2001. They noted that regardless of the infestation, the ring widths of the trees decline with age, as is usual in hemlocks (Rentch et al. 2008). Another recent study spanning six mid-Atlantic sites found significant differences in mean pre- and post-infestation ring width for half of the sites (Walker 2012).

I studied hemlocks at the Black Rock Forest Consortium (BRF), a scientific preserve in Cornwall, New York (www.blackrockforest.org). While the forest has a long history of management, the consortium wasn't founded until 1989. Before the turn of the twentieth century, land use was mixed between homesteads, farms, and orchards, with the more severe terrain remaining undeveloped. Human presence couldn't yet be termed management, with the inhabitants' behaviors, including numerous fires, responsible for largely degrading the quality of the forest (Maher 2004). Fortunately, around the turn of the century all of the land was purchased and consolidated by a single owner: the Stillman family (Maher 2004). In 1928, Dr. Ernest G. Stillman declared Black Rock Forest a "research and demonstration forest." At this time, forest management began in earnest, albeit with the nascent methodology of the early twentieth century. By 1989, deliberate management had the forest once again flourishing. BRF had been used for numerous scientific experiments, but the overall health of the forest was good, although by this point it had a long history of human presence, dating back to Native American use (Maher 2004).

Black Rock Forest is a 1550 ha oak-dominated forest preserve. It is rocky and mountainous, with many streams, slopes, and ravines, ranging from 110 m to 450 m above sea level (Schuster et al. 2008). The mean annual precipitation is 1190 mm, and temperature varies seasonally, with monthly mean temperatures ranging from -2.7˚C to 23.4˚C (Turnbull et al.

2001). Soil is loamy forest soil, formed in glacial till over bedrock, going from 25 cm deep in steeper, higher elevation sites to over 1.5 m in lower, gentler sites (Olsson 1981; Turnbull et al. 2001). Drainage can be excessive in the shallower soils, and it is well drained in the deeper soil (Olsson 1981).

In 2002, a study of Black Rock Forest investigated whether there was a correlation between distance from stream and intensity of infestation. Kimple and Schuster (2002) focused on three hemlock dominated stands: Black Rock Brook, Canterbury Brook, and Mineral Springs, where the hemlock woolly adelgid arrived in 1992, 1994, and 1996, respectively. In the Black Rock Brook and Mineral Springs stands, hemlocks farther from the stream had decreased damage from HWA. Damage was also significantly more severe towards the forest boundary. However, they found no correlations between spatial measures and damage in the Canterbury Brook stand (Kimple and Schuster 2002).

A patch of hemlocks was cut down in the upper part of the Canterbury Brook Stand in 2002. In the words of John Brady, the BRF forest manager, the hemlocks were “defoliated, totally dead” (John Brady, personal communication). An area was established for the purpose of building an exclosure to test for successional species after hemlocks were wiped out, and all hemlocks in the predefined space were cut to begin the simulated succession.

I was interested in growth responses of hemlocks to HWA, how long their declines lasted, what characterized their declines, and if there was any chance of a comeback. For my project, dendrochronology seemed to be the best approach for several reasons. We had access to rare evidence — cross sections from trees cut down in the past. These cross sections came from a specific time and place, and by themselves were an interesting record of particular trees, from sapling to death. By combining these data with cores obtained from living trees, I could compare the growth patterns of trees that died from HWA and trees that have survived the infestation so far.

Methods

Study Area

I sampled at the Black Rock Forest Consortium (BRF), a nearly 4,000 acre scientific preserve in Cornwall, New York (www.blackrockforest.org; Fig. 1). I collected cores between June and August 2012 from living hemlock trees in the Canterbury Brook stand at BRF.

Field Methods

I cored every relatively healthy tree I could find in the Canterbury Brook stand that was at least 30 cm in diameter at breast height (DBH) (n = 10 trees). Coordinates and elevation for each tree were obtained using a Garmin GPS unit. Aspect was determined to quadrant using a compass on an individual tree basis. Slope was measured one meter downslope of the tree, using a Suunto clinometer. Tree health was estimated using the following scale:

1. Most needles present
2. Needles in crown present
3. Few needles present
4. No needles present

Trees that were obviously dead due to missing branches or abundant fungal presence were avoided. DBH was measured using a circumference to diameter conversion tape, with accuracy to the nearest centimeter. Outer bark depth was determined by measuring how deeply a thin stick went into the furrows of the bark. This measure was repeated four times on each tree, evenly spaced. Coring was done at breast height (1.37 m) using Haglof 10-100-1028 and 10-100-1038 increment borers. Core height was checked afterwards by measuring the distance from the core opening directly down to where the tree met the soil. Each of the cores was taken perpendicular to the slope that the tree was on in order to avoid compression wood (Walker 2012). Compression wood — growth on the downhill side of a tree — is a reaction by the tree used to maintain a vertical orientation (Speer 2010). Core bearing was approximated using a compass. Photographs were taken of each tree.

Lab Methods

I mounted cores on wooden troughs cut to roughly the length of the core. I glued the cores using Elmer's wood glue, and wrapped thin string around the glued cores until they were dry. Most of the cores experienced some breakage as they were removed from the increment borer, so mounting required reassembly of the cores prior to gluing. Once cores were dry, I flattened the mounted cores with a belt sander and then sanded with progressively finer grit sandpaper, stopping at 1500. The mounts were labeled with site name, tree species, tree number, core number, and diameter at breast height.

Mounted cores were dated by hand under a microscope, using pencil to mark decades, centuries, and years. I measured the cores at the Lamont-Doherty Tree Ring Laboratory, in Palisades, New York. Mounted cores were measured using Velmex 0904 measuring stage with an optical linear encoder accurate to 0.001 mm. Measurements were recorded on an Apple Imac with Measure J2x. An Olympus SZ51 stereozoom microscope supported by a boom stand and equipped with a Mikelite 7000 was used to take the measurements. Cores were measured starting at the ring closest to the pith, with the hand-measured date used as the preliminary initial ring age. Core measurements were exported from Measure J2x in raw decadal format.

Measurements were run in COFECHA, a tree ring quality-control computer program (Grissino-Mayer 1997). COFECHA cross-dates 50-year segments of measurements to form a master chronology, taking successive segments every 25 years (Rentch et al. 2008). The cores were initially run as undated samples, and cross-dated by checking for agreement in segments of the cores. The cores that showed strong agreement ($r > 0.4$, $p < 0.05$) were used as a small master chronology, against which a few of the trees were adjusted. This meant shifting the initial ring year back 1–2 years for these trees, and resulted in correlations between all the trees that were satisfactory, based on prior dendrochronology work ($r > 0.3281$, $p < 0.05$; Rentch et al. 2008).

I obtained additional data from Bill Schuster at Black Rock Forest about the group of trees cut in 2002 in Canterbury Brook. The hemlocks cut to clear out the exclosure area were cross-sectioned in and sanded for measuring. The measuring was done in 2002 in the Black Rock Forest tree ring lab on a Velmex system, using Measure J2x. Data came in dated, spreadsheet format.

Calculations and Data Analysis

For the cores, ring width measurements were summed to get the radius of the core. Annual ring width was then divided by the core radius to get the annual proportion of total tree growth. To get working field radius measurements, I subtracted the external bark depth, along with the depth of cored bark, from the measured DBH, and divided in half. The field diameter at breast height was achieved by doubling this number. Multiplying the yearly proportion by the field radius yielded a more accurate yearly ring width, because the cores usually aren't perfect radii of the tree (Bakker 2005). From this, I calculated the radius through each year, adding the ring widths for each year to the sum of the years before. This radius through each year was used to calculate basal area of the tree through each year using the formula $\pi \cdot r^2$, assuming that each tree was circular (Bakker 2005). I subtracted basal area of prior years from each year to get the amount of wood added each year, or the basal area increment (BAI).

For the cross sections, ring width measurements were added to get the radius through each year, and the total radius of the core. The total radius was doubled to get the diameter for each tree. The yearly radius was used to calculate basal area and basal area increment, as was done with the cores.

I calculated means and standard errors in Microsoft Excel. I compared basal area increment through time between the two groups of trees using a repeated measures ANOVA, with two treatments (cut, uncut) and four time periods (1991–1993, 1994–1996, 1997–1999, 2000–2002) as factors. The ANOVA and Welch's T-tests were done using JMP statistical software.

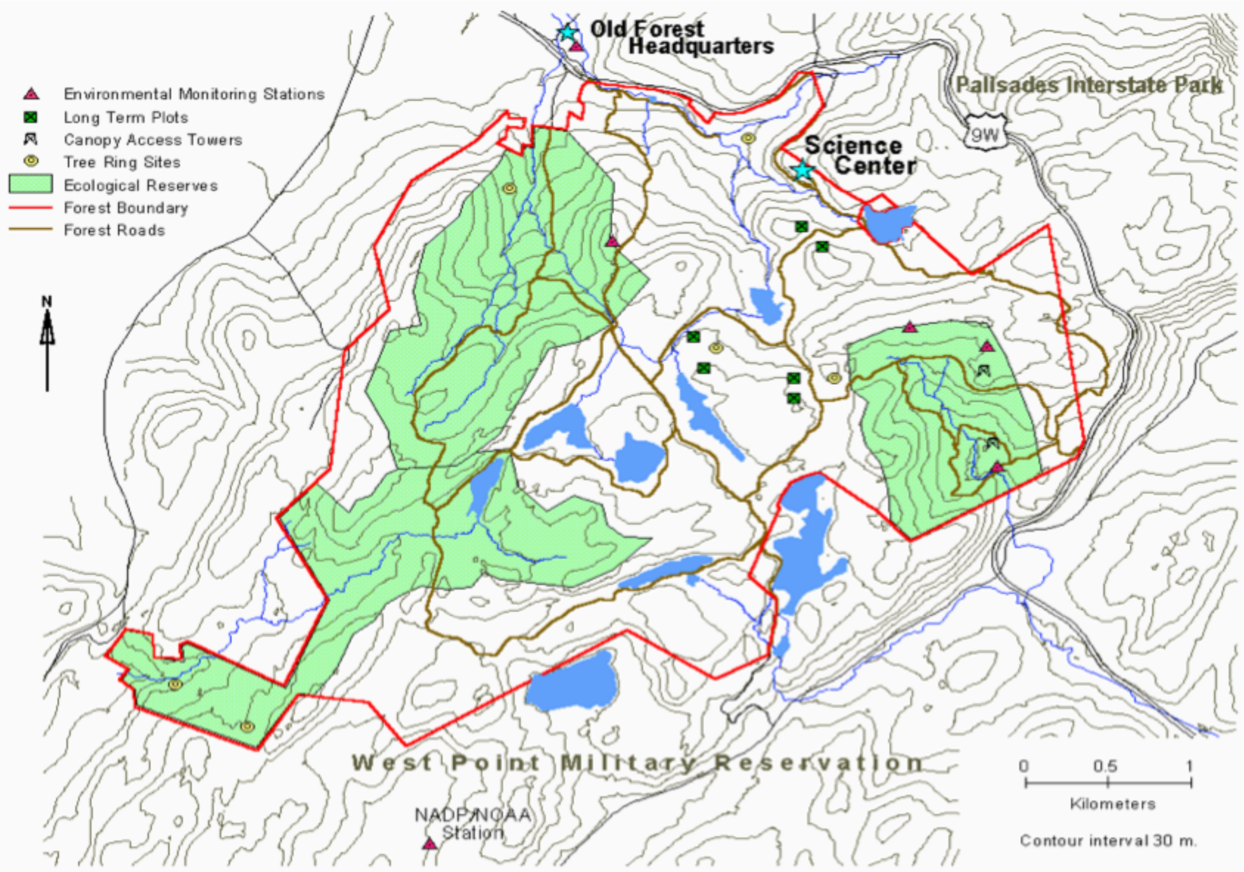


Figure 1. Map of Black Rock Forest Consortium, Cornwall, New York (map from www.blackrockforest.org). The Canterbury Brook stand is located around the stream in northwest part of the forest.

Results

Trees that were cut in 2002 (hereafter: cut) had a mean age of 80.6 ± 9.3 years, while trees that were cored in 2012 (hereafter: uncut) had a mean age of 121.1 ± 9.6 years in 2002 (Welch's $T_{1,19} = 3.361$, $p = 0.0033$; Fig. 2). The 2002 mean diameter excluding bark of uncut trees was twice that of cut trees (uncut: 40.6 ± 2.8 cm; cut: 20.8 ± 3.8 cm; Welch's $T_{1,24} = 4.263$, $p < 0.001$; Fig. 3). Uncut trees had a mean average lifetime growth rate more than double that of cut trees (uncut: 1059.8 ± 96.8 mm^2/year; cut: 488.2 ± 162.4 mm^2/year; Welch's $T_{1,24} = 3.555$, $p = 0.0016$; Fig. 4). There was no definitive trend in ring width over time; however, uncut trees had a consistently higher mean basal area increment than cut trees, which makes sense considering the former's larger mean diameter (Fig. 5).

Precipitation varied from a high of 144.2 cm in 1871 to a low of 54.7 cm in 1964 (Fig. 6). Annual variation in basal area increment of both cut and uncut trees was not significantly correlated with annual precipitation (cut: $p = 0.107$, $R^2 = 0.022$; uncut: $p = 0.575$, $R^2 = 0.002$; Fig. 7). Growth of cut trees was highly correlated with growth of uncut trees (ring width: $p << 0.001$, $R^2 = 0.267$; basal area increment: $p << 0.001$, $R^2 = 0.525$; Fig. 8).

When I compared basal area increment through time between the two groups of trees using a repeated measures ANOVA, uncut trees had a higher basal area increment than cut trees through all time periods ($F_{1,24} = 4.401$, $p = 0.0466$; Fig. 9b). Basal area increment of both cut and uncut trees significantly declined through time ($F_{3,22} = 9.057$, $p < 0.001$; Fig. 9b). There was no interaction between time and treatment; time affected both treatment groups in the same way ($F_{3,22} = 0.468$, $p = 0.7075$; Fig. 9b).

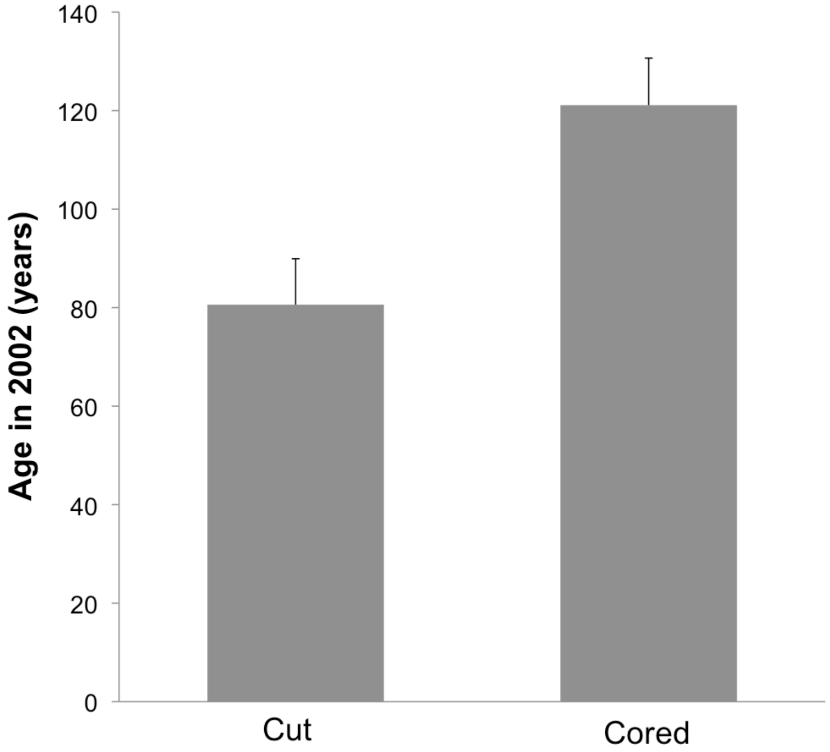


Figure 2. Mean age of trees + standard error (SE) in the two sample groups. “Cut” trees were cut down in 2002; “cored” trees were cored in 2012.

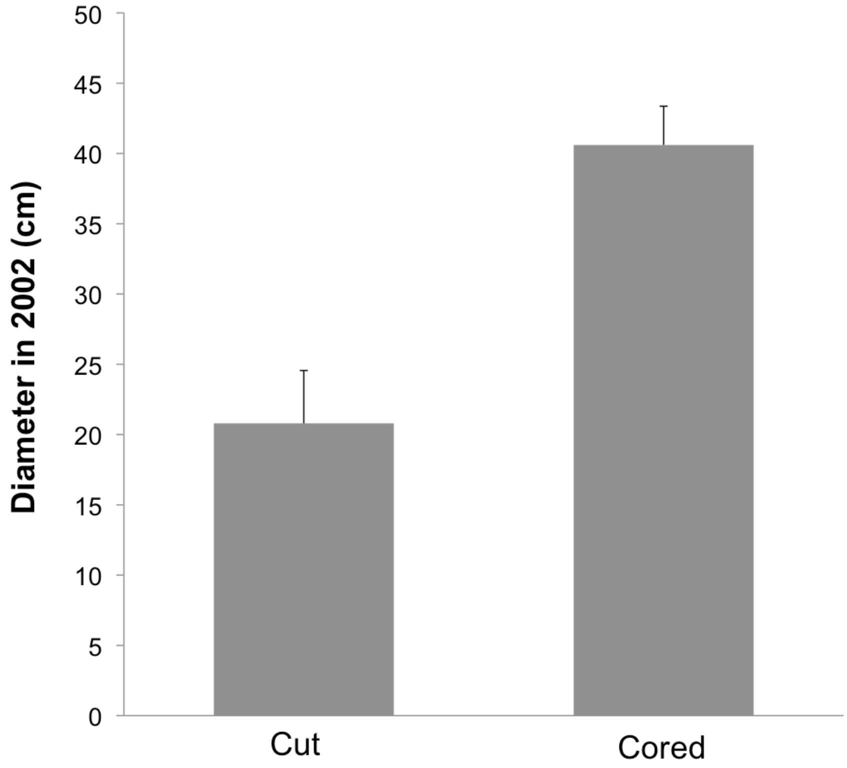


Figure 3. Mean diameter in 2002 + SE of the two groups of trees. "Cut" trees were cut down in 2002; "cored" trees were cored in 2012. Diameter was determined by measuring cross sections from the cut trees, and by measuring tree cores taken at breast height (1.37 m) from the cored trees.

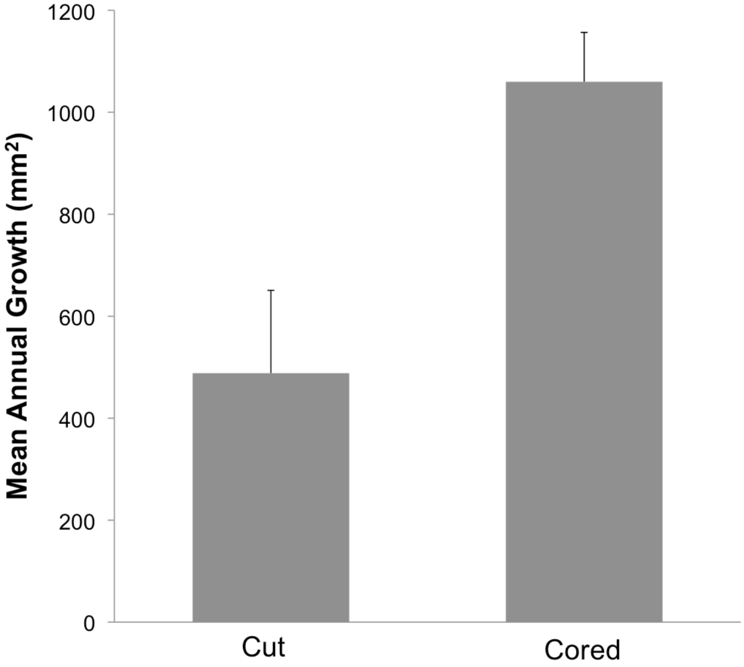


Figure 4. Mean lifetime growth rate + SE of the two groups of trees. “Cut” trees were cut down in 2002; “cored” trees were cored in 2012. Lifetime growth rate was calculated by dividing total lifetime growth by tree age.

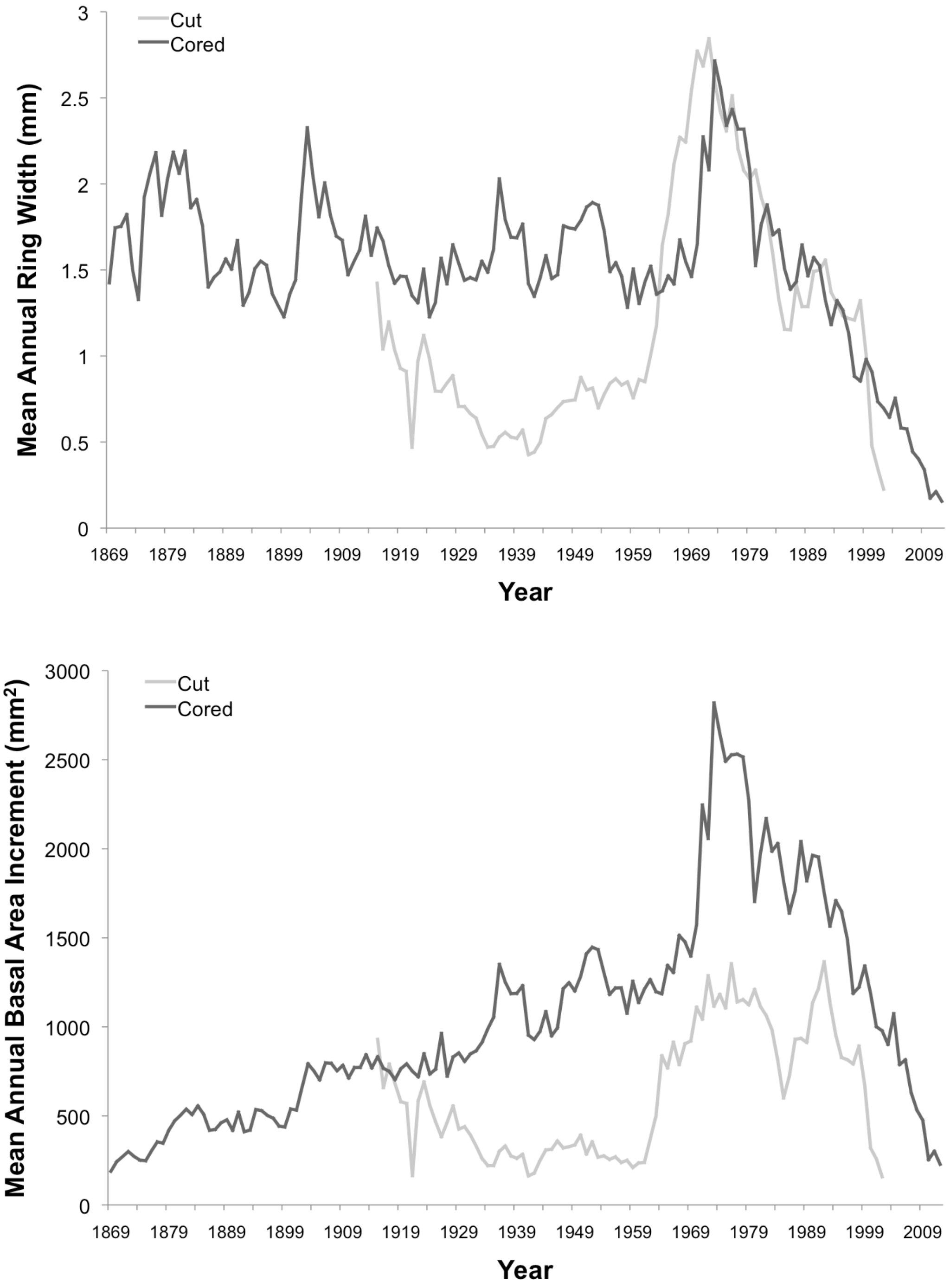


Figure 5. a) Mean annual ring width of the two groups of trees. “Cut” trees were cut down in 2002; “cored” trees were cored in 2012. Each series begins when the sample size is five. b) Mean annual basal area increment of the two groups of trees. Cut trees were cut down in 2002, and cored trees were cored in 2012. Series begin when the sample size is five. Basal area was determined by treating the ring widths as radii of a circle and calculating circular area. Basal area increment was achieved by subtracting previous basal area from each successive year.

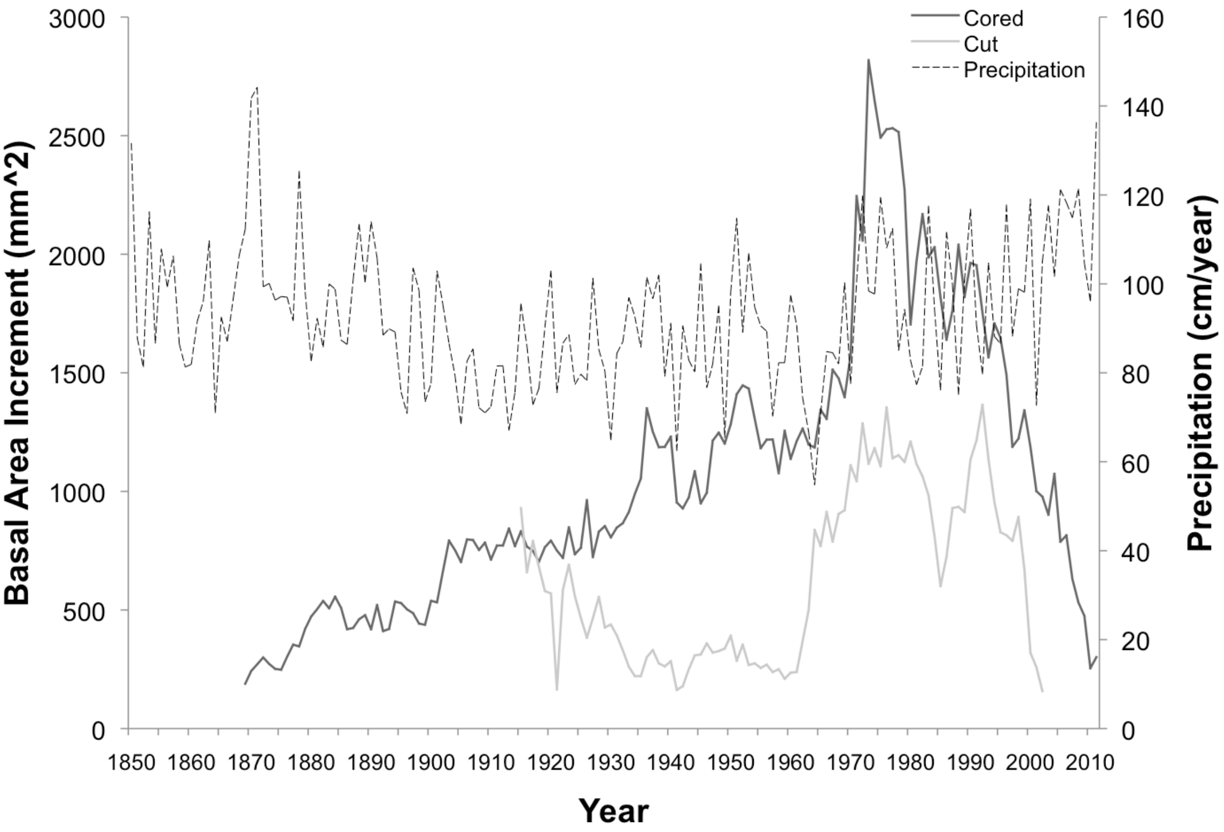


Figure 6. Annual precipitation (right y-axis) and basal area increment (left y-axis). Cut trees were cut down in 2002, and cored trees were cored in 2012. Tree series start when the sample size is five. Precipitation data from NOAA Albany, NY.

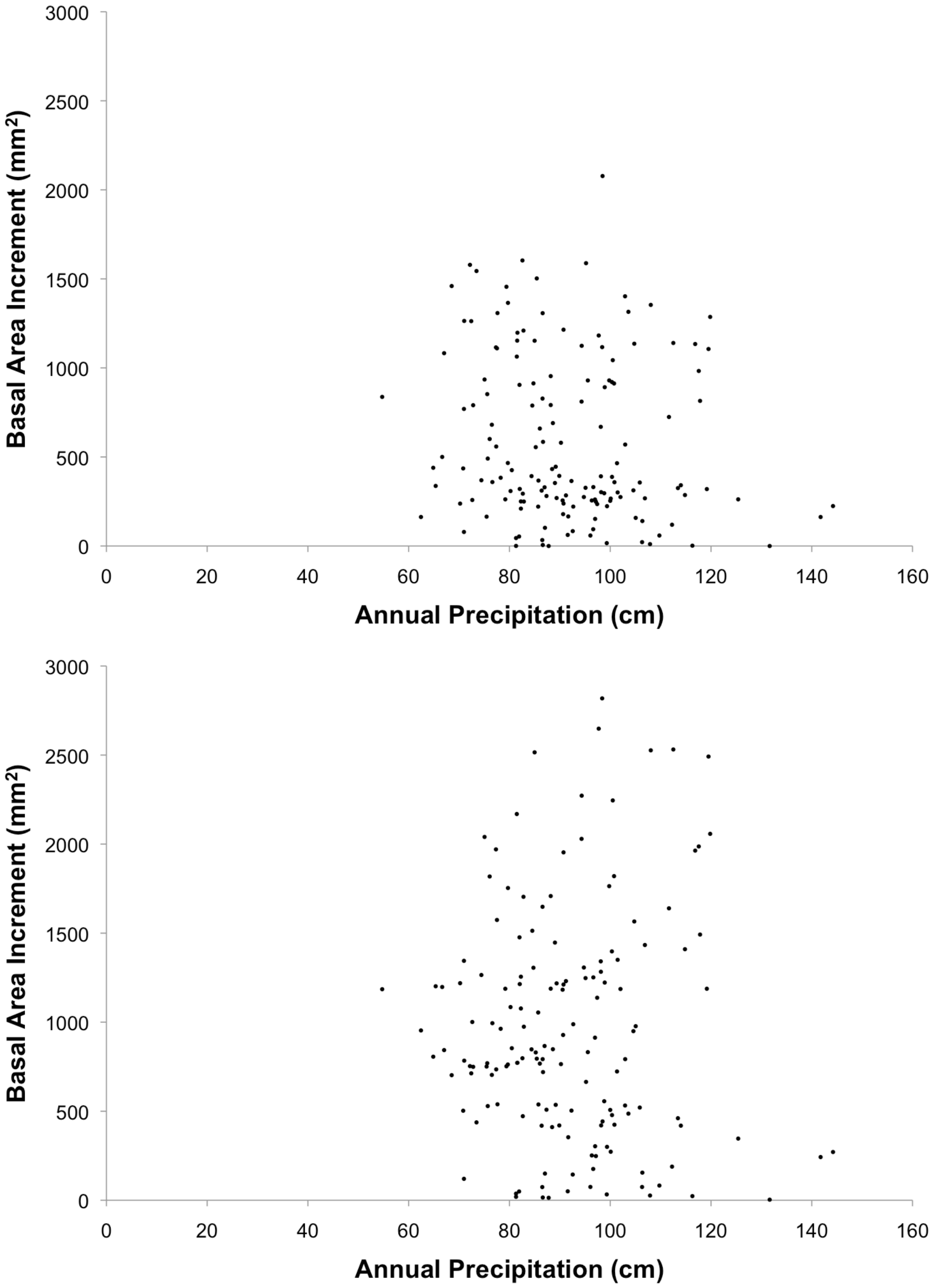
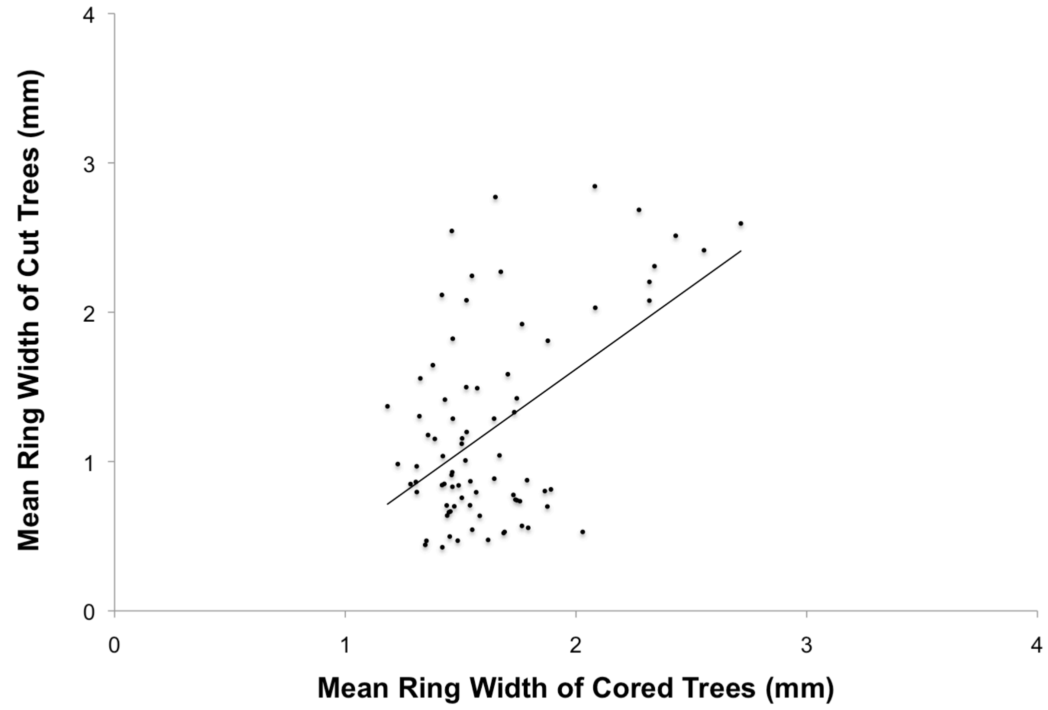


Figure 7. a) Correlation between basal area increment of trees cut in 2002 and precipitation ($y = -11.263x + 990.27$; $R^2 = 0.0217$, $p = 0.107$). b) Correlation between basal area increment of trees cored in 2012 and precipitation ($y = -4.4965x + 1098.6$; $R^2 = 0.00197$, $p = 0.575$).



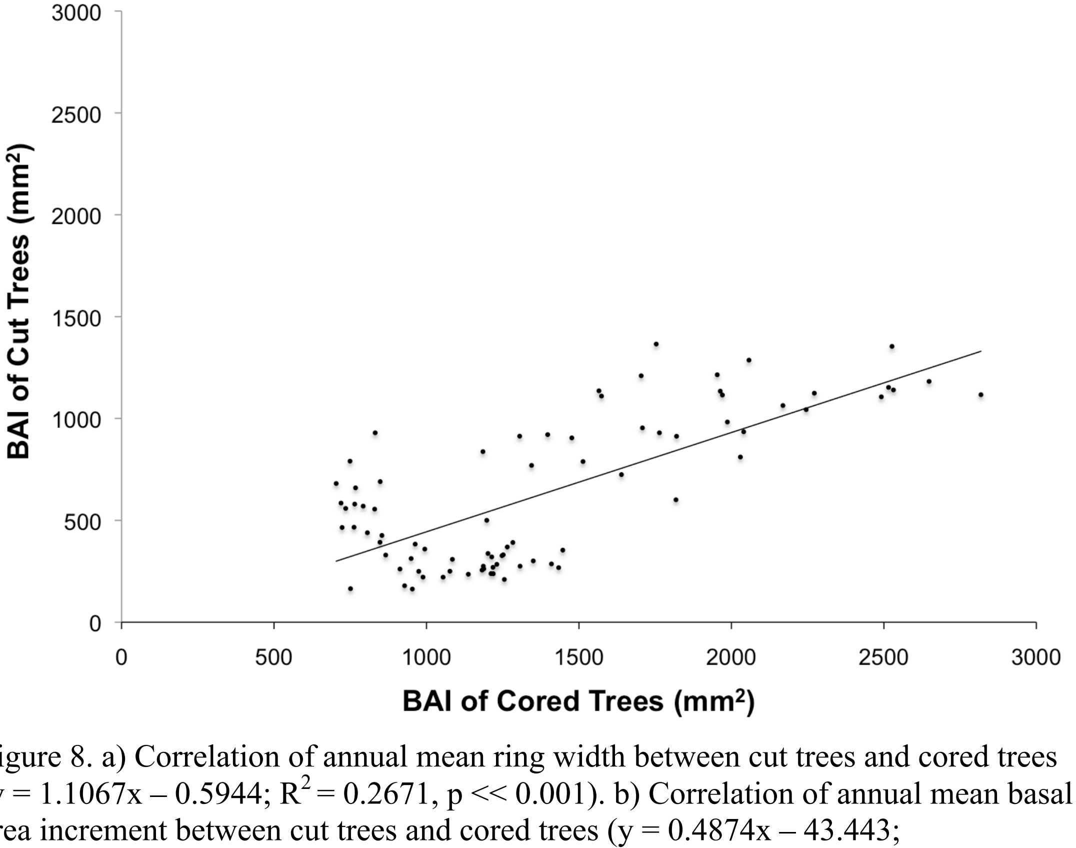


Figure 8. a) Correlation of annual mean ring width between cut trees and cored trees (y = 1.1067x – 0.5944; $R^2 = 0.2671$, $p << 0.001$). b) Correlation of annual mean basal area increment between cut trees and cored trees (y = 0.4874x – 43.443; $R^2 = 0.52464$, $p << 0.001$). "Cut" trees were cut down in 2002; "cored" trees were cored in 2012. Data shown is from 1915 through 1994, the time before infestation when both tree groups have sample sizes of at least five.

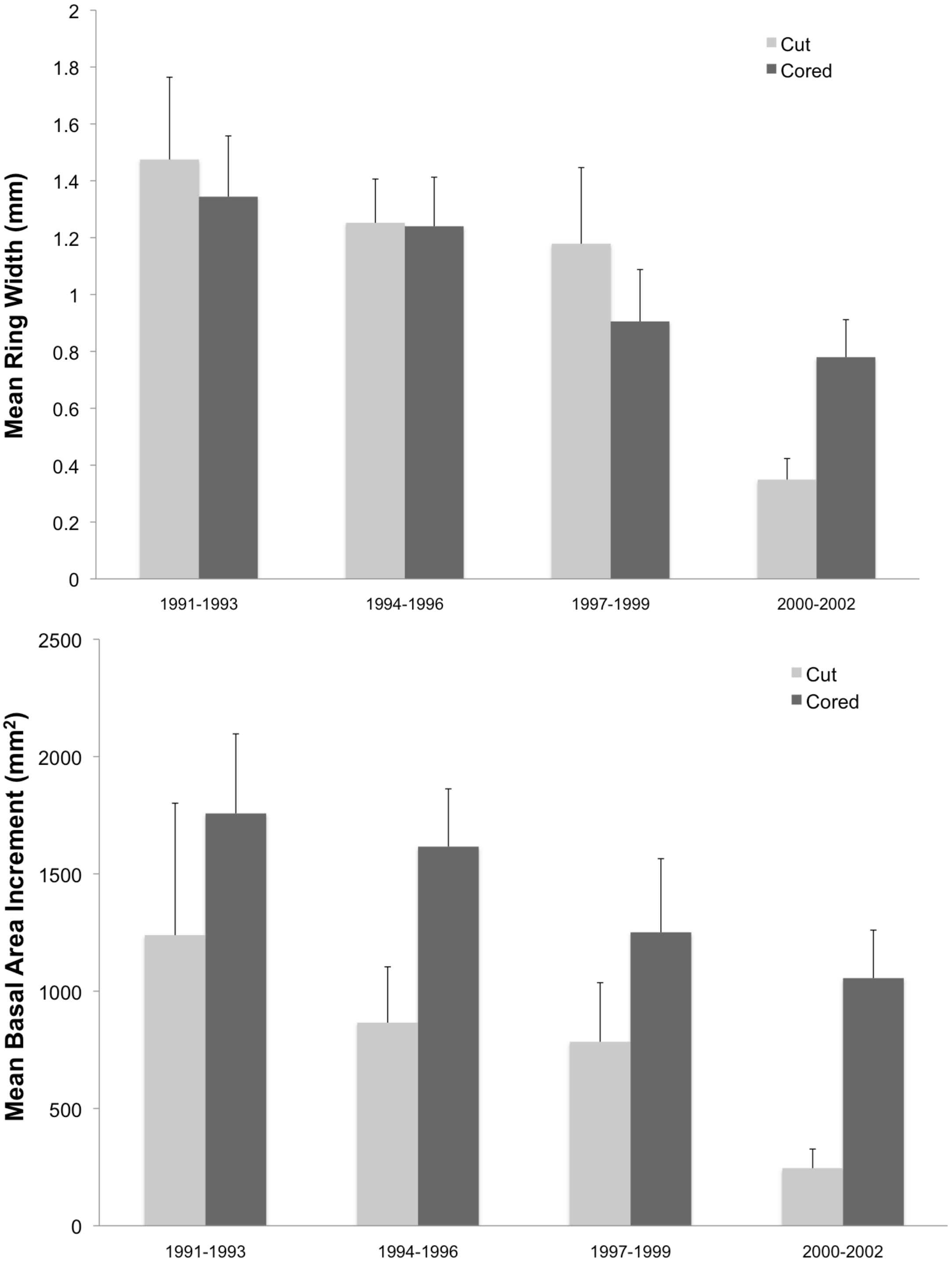


Figure 9. a) Mean ring width by time period ± SE. “Cut” trees were cut down in 2002; “cored” trees were cored in 2012. Ring width of the cut trees declined precipitously in the final three years. b) Mean basal area increment by time period ± SE. Cut trees were cut down in 2002, and cored trees were cored in 2012. Basal area of cored trees decreased steadily over time, whereas basal area of cut trees seemed to decrease only after the first and third time periods.

Discussion

Live trees that I cored in 2012 were 50% older, 95% larger, and had a 117% higher lifetime growth rate than trees that were cut in 2002 (Fig. 2; Fig. 3; Fig. 4). In other words, cored trees were generally higher performing trees that had been established for longer than the trees that were cut in 2002. Precipitation did not predict variation in tree growth for either of the groups. The growth of cored trees predicted the growth of trees cut in 2002; so although precipitation didn’t predict growth, there seem to be some factors that both sets of trees have in common. According to all measures, these groups of trees are different, but why and how did these differences relate to each group’s reaction to the hemlock woolly adelgid is the important question.

The growth of both groups of trees was significantly reduced following HWA infestation (Fig. 9b). Although the two groups of trees had different lifetime growth patterns, the HWA infestation did not affect the growth of the two groups in a significantly different way (Fig. 5; Fig. 9). Despite this lack of statistical difference, these groups of trees differ in a major way: one group survived the infestation, while the other did not. I found no statistically significant difference in the declines of the groups, but they appear to follow different patterns (Fig. 9b).

I might have missed this difference between the groups by sampling insufficiently. I took one core out of each of ten sample trees, which is less than would have been ideal, but still acceptable (Orwig 2002; Rentch et al. 2008). It would have been better to have more than one core per tree: this would not increase the sample size, but it would make the sampling more robust and less susceptible to measuring errors.

Another possible source of error is the difference in sampling methods between the two groups. Cores were taken at breast height (1.37 m). Cross sections were taken from bottoms of the trees cut in 2002, putting them somewhere below breast height. Because of this, I probably estimated the ages of the trees unequally. However, this discrepancy was biased towards making the cut trees look older, so it did not add to the trend I found. This should not affect growth measurements, because trees grow from the inside out, so new growth is on the outside of the entire length of the tree.

When I learned of the existing data from trees cut down in 2002, I was curious about why they had been cut down. According to Brady, hemlocks that were cut were defoliated and totally dead. Since I have no way of going back to 2002, all I can do is assume that this account is accurate, and speculate on what any possible errors might mean with regards to the interpretation of my results. Although these trees were totally defoliated, they still could have been alive. Hemlocks prioritize their needs, so it might be possible for a tree to be needleless but still marginally alive. However, total defoliation has been used as the definition of mortality in prior work on HWA (Mayer et al. 2002; Kimple and Schuster 2002). This is noteworthy because the trees that are alive in 2012 are certainly not in prime condition; in fact they look like they have been struggling to stay alive for a number of years. If the trees cut down in 2002 were indeed alive, at least some of them might have made a partial recovery.

I compared two groups of trees from two different locations within one hemlock stand. The cored trees were mostly from the ravine, while the cut trees were from the hillside. One piece of prior research gave me confidence that this would be a fair comparison, at least with regards to the locations of the two sets of trees. Kimple and Schuster (2002) looked at the relationship between hemlock woolly adelgid damage class and spatial measures. After doing a Spearman rank order correlation, Kimple and Schuster found a significant correlation between damage class and both distance from stream channel and distance from forest exterior for two stands, Mineral Springs and Black Rock Brook. Damage class was determined by estimating the percent of needles present, with 100% defoliation being synonymous with mortality. Spatial measures were the distance from the tree to the forest exterior and the distance from the tree to the stream channel, as all three stands sampled (Mineral Springs, Black Rock Brook, Canterbury Brook) are more or less bisected by streams. The basis for this comparison was the thought that infestation should be most severe where the adelgid first lands. Stream channels and forest edges — which interact with wind from outside of the forest — are likely places for the adelgid to first land, because HWA is largely transported by wind. The main trend they saw was that the farther trees were from both the stream channel and the forest edge, the less severe their damage was. However, they found no such correlations for the Canterbury Brook stand.

Kimple and Schuster had two possible explanations for this lack of correlation. First, they thought that because Canterbury Brook stand had been infested longer than the Mineral Springs stand, the trend might have gradually disappeared. This shouldn't be discounted, but Black Rock Brook, another BRF location, was infested in 1992 and still shows a significant correlation. The infestation dates should be treated with some caution, because although Black Rock Forest is well monitored, the adelgid could have gone unseen by human eyes for a number of years. Their second explanation for the lack of correlation was that because the Canterbury Brook stand was sampled less extensively than the Black Rock Brook stand, a correlation may not have been found when one existed. Although their findings gave me confidence to compare trees from different parts of the Canterbury Brook stand, the implications of these two distinct locations must be reconsidered in light of my results.

Because trees are rooted in particular environments, any differences in trees are difficult to separate from differences in environment. The cored trees and the cut trees were from the ravine and the hillside of Canterbury Brook, respectively. A stream runs through the ravine, so it is closer in proximity to water than the hillside. The ravine is farther downslope than the hillside, so it gets more runoff water. There are differences in soil between the ravine and the hillside. Additionally, there might be differences in light availability, competition, or animal activity. The patterns we see in the two groups of trees may not be differences in the trees themselves, but rather differences in their respective environments causing differences in the trees.

A 2003 study found that sites on xeric aspects succumbed more rapidly than those in moister areas (Orwig et al. 2003). This is potentially relevant to our results, but we must consider how they determined the moisture level of their sites. They used the term "xeric aspects," which they derived from directional aspect. The association was between southwestern and western aspects and increased hemlock mortality, and because those aspects are generally warmer and drier than other aspects, the summation "xeric aspects" was used (Orwig et al. 2003). This association makes sense, because moisture is critical to trees, so decreased moisture puts strain on trees (Orwig et al. 2003). In our study, most of the cored trees are close to the stream, while the trees cut down in 2002 were from the same northwestern aspect, but came from farther away from the stream, and therefore farther from moisture. The level of moisture was estimated differently in the two studies, but in both cases moisture availability seems to predict the extent of hemlock decline.

In a 2002 study conducted in New Jersey, researchers found that in heavily infested stands, trees located at the bottom of a slope or near water had substantially more new growth and less mortality than trees on upper slopes or drier areas (Mayer et al. 2002). They found that water availability was related to the amount of new growth, which might also explain why the trees I cored had a higher lifetime growth rate than the trees that were cut down (Mayer et al.

2002). However, while surviving trees with access to water appeared healthier than those that didn’t, it looked as if trees would eventually succumb even under ideal growing conditions (Mayer et al. 2002). It remains to be seen how long the trees I cored in 2012 will remain alive, but it is important to consider their longevity and the possibility of recovery. Location — and therefore moisture availability — seems like a plausible explanation for the death of the cut trees, but it isn’t the only explanation.

The cut and cored trees have different locations, but they also have different demographics. Cut trees were on average 40 years younger and half the diameter of cored trees (Fig. 2; Fig. 3). I did not measure tree height, but it can be inferred that cut trees were shorter than cored trees. These demographics suggest a potential explanation for the results. In addition to stream channels and forest edges, the air above a forest should be a third wind-heavy location. Therefore, it might be that taller trees get infested on their crowns, while shorter trees don’t get infested until the adelgid spreads from taller trees or from elsewhere in the stand. This is a simple hypothesis, but it predicts that the trees cored in 2012 would be hit harder than the trees cut in 2002, which is the opposite of the trend we see. Another difference between the trees is their age, which might change the way they are able to defend themselves. Perhaps younger trees focus more on growing, while older trees are more established and can devote more resources to defense. Also, cut trees had a consistently lower basal area increment, and so were potentially less robust overall, and therefore less able to deal with the additional stress of an HWA infestation (Fig. 5b). It is imperative to keep in mind that location cannot be ruled out as a causative agent of any demographic differences between the two groups of trees.

In a 1998 study conducted in Connecticut, Orwig and Foster began to determine the factors of HWA-related hemlock mortality. They found that all sizes and ages of trees were attacked: every hemlock tree sampled was infested with the exception of those trees at the one site that the adelgid had not yet reached (Orwig and Foster 1998). On a stand-wide basis, they found no relationship between mortality and average tree size or age within a stand (Orwig and Foster 1998). That is, stands that had the same composition experienced different mortality. On an individual tree level, they found that there was a higher rate of mortality for trees that were overtopped or in the intermediate canopy, as opposed to trees that were classed as codominant or dominant (Orwig and Foster 1998). They didn’t link their finding that smaller trees experienced higher mortality to the way HWA spreads through a stand, but they did offer some possible explanations for this pattern. They posited that it could be due to the less extensive root systems, diminished ability to store and transport water, and the limited amount of stored carbohydrates that are inherent in smaller trees (Orwig and Foster 1998).

Although the interaction between time and tree group was not significant in the ANOVA, a visual inspection of Figure 9b suggests that the two groups may have responded differently to the infestation. Visually, the graph suggests a slow, steady decline in the cored trees, and a two-part decline in the cut trees. Following the first part of this decline, the cut trees appear to then have had a more precipitous decline than did the cored trees in the final time period of 2000–2002, though the difference was not significant. Statistical analysis of the relationship between tree group and decline did not yield significant results, but looking at past work may shed more light on the feasibility of this perceived trend.

Old-growth hemlock stands in Pennsylvania showed a relationship between hemlock growth rate and degree of infestation. In 2003, slower growing hemlocks were more infested than better growing hemlocks (Davis et al. 2007). While not quantified in the study, a graph of growth rates of both severely and lightly infested trees reveals the trend in growth discrepancy over time. In the two groups of trees I studied, there was a similar discrepancy in lifetime growth rates. We cannot know how infested the two groups were relative to each other, but this evidence suggests that the cut trees could have been more heavily infested. Before 2003, researchers observed an interesting interaction between growth and severity of infestation since the hemlocks became infested in the early 1990s. Between 1993 and 1997, growth in severely infested trees was greater than growth in lightly infested trees, despite the former having a lower lifetime growth rate (Davis et al. 2007). By 2003, 41% of heavily infested trees were dead, following a rapid decline starting after 1997 (Davis et al. 2007). This trend is similar to the trend we see in Figure 9, where after an initial decline, trees cut in 2002 seem to level off until a precipitous decline around 2000. While the cut trees don't surpass the growth of the cored trees during this early stage of infestation, the overall trend could be similar. The findings of Davis et al. (2007) suggest that the perceived difference in the declines of our two groups of trees is plausible.

One possible explanation for the staggered decline of trees hit the hardest is the density-dependent feedback discussed earlier. Because HWA prefers new growth, any reduction in new growth makes their environment less favorable (McClure 1991). The initial tide of HWA infestation can cause initial mortality in 5–6 years (Mayer et al. 2002). Once this first wave has severely impacted trees, even those that aren't dead have severely reduced new growth, thereby supporting fewer adelgids the following season (Mayer et al. 2002; McClure 1991). Because the infestation has lessened, trees have the opportunity to rebound or at least stabilize (Mayer et al. 2002). Once there is more new growth, the adelgid is quick to repopulate, and decline at that point can be precipitous (Mayer et al. 2002; McClure 1991). This scenario seems possible in the case of the trees that were cut in 2002.

The two sets of trees in my study have many differences, but the most important difference is that one group has survived the HWA infestation, at least until 2012. While it is a small group of trees in bad health, it has survived for 18 years. In previous studies, the time between the HWA infestation and the first dead hemlock tree ranges from two to ten years (McClure 1990; Davis et al. 2007). While many factors affect mortality, in the end it is predicted best by infestation time (Orwig et al. 2003). This relationship makes mortality the definite end; however, there is limited evidence that recovery is possible. Orwig and Foster reported that hemlocks had no ability to refoliate or sprout following defoliation, but elsewhere hemlocks that were 60% defoliated have shown ability to refoliate (Orwig and Foster 1998; Mayer et al. 2002). The cored trees could potentially refoliate, but only if the adelgid no longer had a strong presence, which is possible considering the dearth of favorable food for HWA in the Canterbury Brook stand. The cored trees will likely die in the near future, at which point in time a more direct comparison between the two groups of trees would be possible, and might be able to determine how different the trees really are.

In order to begin to solve the HWA problem, it is necessary to have a starting place. Because of the extensive range of hemlock in the eastern United States, finding out where to focus management efforts is often considered a first step. Figuring out the common characteristics of trees that survived the longest, recovered the best, or seemed most resilient could point forest managers towards the trees that stand to benefit the most from control efforts. In this study, we offer two possible explanations for the different declines of the trees on the hillside and the trees in the ravine. The difference in moisture availability could affect the way trees respond to HWA infestation. A tree in a drier area could experience the dryness as an additional stressor: a constant but minor hardship that is exacerbated by an HWA infestation.

Alternatively, increased moisture availability might aid trees in defense or facilitate growing under adversity more. The second possible explanation is that the tree’s demographic predicts its response to the HWA infestation. In this study and others, trees that were smaller, younger, shorter, and overall less robust tended to do worse in the face of an HWA infestation. One issue with this second explanation is that it cannot be separated from the moisture availability hypothesis — trees could be more robust because they were in a moister environment in the first place. In this way, moisture could have a twofold effect on how trees respond to HWA — the effect of moisture on lifetime tree performance, and the effect of moisture on the tree during the time of infestation. It would be very useful to be able to separate these two hypotheses, because then management efforts could be better focused. One management effort that would benefit from this separation is the search for an HWA-resistant variant of *Tsuga canadensis*. By isolating the features of the tree itself that predict performance against HWA, we may be able to get closer to finding the eastern hemlock with the most resistance. Future studies should focus on further exploring how site characteristics affect trees’ responses to HWA, in addition to isolating tree demographics by attempting to conduct experiments on stands with both uniform environments and a wide variety of hemlocks.

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