Radial growth response of eastern hemlock to infestation of hemlock woolly adelgid

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ABSTRACT

Hemlock woolly adelgid (*Adelges tsugae* Annand) is causing defoliation and mortality of eastern hemlock (*Tsuga canadensis* (L.) Carrière) in the eastern United States. The objectives of this study were to quantify changes in tree-ring width and wood anatomy for trees that survived adelgid infestation, and to contrast dendroclimatic relationships across a latitudinal gradient. Six sites spanning the current range of hemlock woolly adelgid (HWA) infestation were selected. At each site, 23 infested eastern hemlocks were cored and two trees were felled at the Virginia site and thin-sectioned using a sliding microtome for analysis of wood anatomy. Tree cores were cross-dated and ring widths were measured. For each site, t-tests were used to determine if there was a difference in radial growth pre- and post-HWA arrival. To compare differences in pre- and post-HWA cell properties, t-tests were used. For dendroclimatic analysis, Pearson correlation coefficients were calculated between radial growth and monthly climate variables. Three sites showed significant suppression in radial growth after HWA arrival and latewood produced post-HWA arrival had significantly smaller cells with reduced cell-wall thickness than latewood produced before HWA arrival. This indicates that HWA can reduce a tree's photosynthate production. The relationship between hemlock growth and climate also varied with latitude and site, with trees growing further south or on shallower soils being more sensitive to moisture levels. This sensitivity to drought can also partially explain the variation in hemlock response to adelgid feeding, as trees affected by moisture stress tend to be more sensitive to insect attack.

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I. Introduction

Hemlock woolly adelgid (*Adelges tsugae* Annand) a small, aphid-like insect originally from Japan, primarily feeds on the new-growth of eastern hemlock (*Tsuga canadensis* (L.) Carrière) and is having tremendous impacts on hemlock forests in the eastern United States. The insect reproduces asexually through parthenogensis and has two generations per year, allowing populations to build quickly. Mortality of infested trees can occur in as little as four years, although some trees persist for more than 15 years (Eschtruth et al. 2006; McClure 1991). Hemlock woolly adelgid (HWA) was first discovered in the eastern United States in the mid-1950s (Souto et al. 1996), and by 2004 was found in 16 states from Maine to Georgia (USDA-Forest-Service 2005). It is predicted to spread further north and west, but the rate of spread appears to be slowing (Evans and Gregoire 2007a). Mortality in infested stands is highly variable, ranging from 5% to over 95% (Orwig and Foster 1998). The decline of eastern hemlock across its range has serious consequences for ecosystem processes as well as reducing the quality of wildlife habitat and changing forest composition (Daley et al. 2007; Jenkins et al. 1999; Nuckolls et al. 2009; Spaulding and Rieske 2010).

Eastern hemlock radial growth has been shown to decrease following attack by HWA (Rentch et al. 2009). Maple (*Acer* L.) and oak (*Quercus* L.) trees have benefited from the overall decline of hemlock, showing corresponding radial growth increases (Orwig 2002). Trees are predicted to be more sensitive to environmental variables, such as climate, at the edges of their range (Fritts and Swetnam 1989). Therefore, eastern hemlock growing at the southern edge of its range may experience more severe reductions in growth than has been shown from studies from the middle of its range (Orwig 2002; Rentch et al. 2009).

At the southern edge of its range, hemlock is primarily restricted to moist coves and riparian areas, while it tends to be less topographically restricted in its distribution further north (Ellison et al. 2005). Dendroclimatic studies have been conducted at both the northern and southern edge of hemlock's range, and hemlock has been shown to respond differently based on latitude (Black and Abrams 2005; Hart et al. 2010; Tardif et al. 2001). Hemlocks growing further south are more sensitive to summer temperature and precipitation levels in both the previous and current year (Hart et al. 2010; Tardif et al. 2001), as high summer temperatures can limit photosynthesis (Adams and Loucks 1971) and available moisture.

The xylem of eastern hemlock consists of numerous, thin-walled, earlywood tracheids that transport water and nutrients from the roots, and lesser amounts of the thick-walled, latewood tracheids that serve as a tree's primary support and structure. Defoliation of eastern larch (*Larix laricinia* (Du Roi) K. Koch) due to larch sawfly (*Pristiphora erichsonii* (Htg.)) affected tracheid size and shape with cells produced immediately following a sawfly outbreak having smaller cell lumen and thinner latewood cell walls (Filion and Cournoyer 1995). Although HWA does not actually consume the needles of hemlock, unlike the sawfly, its feeding takes place at the base of the needles and causes desiccation and needle loss (Young et al. 1995). The reduced photosynthate produced due to premature needle drop could similarly affect xylem production.

Few studies have examined how hemlock decline varies across the full range of hemlock woolly adelgid infestation. A better understanding of what edaphic and climatic factors affect hemlock susceptibility will lead to more effective and targeted management of HWA. The objectives of this study were to (1) observe and quantify changes in radial growth patterns of eastern hemlock infested with hemlock woolly adelgid across a latitudinal gradient, (2) contrast dendroclimatic relationships across six study areas from Massachusetts to Georgia, (3) investigate how crown structure, soil properties and dendroclimatic response affect tree response to adelgid infestation and (4) observe and quantify changes in xylem cell-wall thickness and cell size of eastern hemlocks infested with hemlock woolly adelgid from a single site in Virginia.

II. Literature Review

The ecological role of eastern hemlock

Eastern hemlock is a slow-growing, late-successional species that is considered to be the most shade-tolerant tree species in North America (Godman and Lancaster 1990). It is able to survive and grow in as little as 5% of full sunlight, can withstand suppression for 400 years, and responds to release in both height and diameter growth (Godman and Lancaster 1990). The native range of eastern hemlock extends from New England west to northern Wisconsin and southern Ontario, and then follows the Appalachian Mountains south to northern Georgia. It is generally found on moist but well-drained sites throughout its range. In the southern portion of its range, it is found scattered across the landscape keeping to moist valleys, coves, and streamsides, but is often found in pure stands further north, especially on flats and near swamps (Godman and Lancaster 1990; Hough 1960). It exercises a great deal of control of the microclimate of a stand by casting deep shade and depositing highly-acidic litter. Understory herbs, ferns and shrubs frequently found in eastern hemlock stands include partridge berry (*Mitchella repens* L.), trilliums (*Trillium erectum* L. and *T. undulatum* Willd.), wood ferns (*Dryopteris* Adanson), mountain-laurel (*Kalmia latifolia* L.) and early azalea (*Rhododendron prinophyllum* (Small) Millais) (D'Amato et al. 2009).

Many organisms, both terrestrial and aquatic, depend upon the unique habitat provided by eastern hemlock. It provides the best winter shelter for white-tailed deer (*Odocoileus virginianus* Zimm.) of any conifer species and stands of eastern hemlock are frequently managed specifically for this purpose (Reay 2000). It also provides cover for other wildlife species, such as ruffed grouse (*Bonasa umbellus* L.) and wild turkey (*Meleagris gallopavo* L.) (Godman and Lancaster 1990; Griesemer et al. 1998). Approximately 96 bird species and 47 mammal species have been identified as using eastern hemlock stands in northern New England (Yamasaki 2000). Several bird species, such as the black-throated green warbler (*Dendroica virens* Gmelin), have a higher number of singing males in hemlock stands compared to other conifers, hardwood, or mixed stands. Mitchell (1999) showed that five species of northern birds preferred sites dominated by eastern hemlock for breeding purposes. Porcupines (*Erethizon dorsatum* L.) and other small mammals frequently use eastern hemlock stands for both foraging and wintering areas. Many carnivorous species, such as red fox (*Vulpes vulpes* L.) and black bear (*Ursus americanus* Pallas), prey on animals that frequent these stands (Yamasaki 2000).

Streams flowing though hemlock-dominated forests often have a unique assemblage of salamanders, fish, and freshwater invertebrates, many of which are intolerant of seasonal drying (Snyder et al. 2002). Eastern hemlock transpires approximately 50% less water during the summer compared to deciduous trees, and streams flowing through hemlock-dominated forests have more consistent stream-flow levels and decreased variation in temperature, resulting in these unique communities (Ellison et al. 2005). Eastern hemlock forests also support a diverse assemblage of arthropods. Twenty-nine arthropod orders and over 160 families have been found in association with eastern hemlock (Mallis and Rieske 2010; Rohr et al. 2009). Arthropods species from hemlock forests were more evenly spread among taxonomic classes compared to those found in deciduous forests (Rohr et al. 2009).

The economic value of eastern hemlock: its historic and current uses

Although its current uses are limited, eastern hemlock was once considered a very important commercial species in the eastern United States (Brisban 1970; Godman and Lancaster 1990; Hough 1960). In the late 19th and early 20th century, it was the main source of tannin for the leather industry. Tannins extracted from the bark of eastern hemlock were combined with the proteins of animal hides to produce strong and resistant but flexible leather that was frequently used in shoe soles, belts, and harness leathers (Whitney 1994). In 1900, approximately 4.1 million cubic meters of hemlock were consumed by the tanning industry in the United States, half of which was supplied by Pennsylvania's old-growth forests (Whitney 1994). However, by the mid-1920's, most of Pennsylvania's hemlocks were gone which, along with the advent of new tanning agents and an overall change in market demands, led to the end of the hemlock-based tanning industry.

The production of lumber from eastern hemlock peaked between 1890 and 1910, when it was between 7 and 8 million cubic meters, and declined from 1910 to 1930 (Brisban 1970; Godman and Lancaster 1990). Around 75% of eastern hemlock lumber was used for light framing, sheathing, roofing and subflooring, with minor uses being crates, pallets, signs, boxcars, and furniture (Brisban 1970; Godman and Lancaster 1990; Hough 1960). Eastern hemlock was also used for paper pulp in the early 1900s, with pulpwood production peaking at 296,000 cubic meters in 1927 (Brisban 1970). Most of the pulpwood production occurred in Michigan and Wisconsin, and was principally used for newsprint, wrapping paper and other low-quality pulps

(Brisban 1970; Godman and Lancaster 1990; Hough 1960). The hemlock-based leather industry is now defunct, having been replaced by chromium and other mineral-based tanning processes (Covington 1997). Eastern hemlock is still used for both pulp and lumber, albeit at a much lower rate. In 2005, the total amount of eastern hemlock cut from national forests was 36,500 cubic meters, valued at 75.1 thousand dollars, comprising less than 0.04% of the total volume of eastern softwood production (Howard 2007).

Hemlock woolly adelgid in the United States

Hemlock woolly adelgid was first discovered in the United States in the early 1900s in Oregon (Annand 1924), where it remains a minor pest of western hemlock (*Tsuga heterophylla* (Raf.) Sarg.). It was first found in the eastern United States in an ornamental garden near Richmond, Virginia in the mid-1950s; but, it did not become a serious pest until the 1980s when it spread to natural stands. Originally from Japan (Havill et al. 2006), HWA rarely causes mortality of hemlocks in its native range due to the presence of native predators and inherent host resistance (McClure 1996).

Hemlock woolly adelgid is a bivoltine (two generations per year) insect that reproduces completely asexually. Adult females of the winter generation (sistens) deposit eggs into woolly ovisacs starting in mid-February. Eggs from northern populations hatch by the middle of April while those further south begin hatching in early March (Joseph et al. 2011b), when the crawlers emerge. These crawlers are very important for dispersal and are commonly spread by wind, birds, deer and humans (McClure 1990). After settling, the adelgid goes through 4 instars, becoming an adult from May to June, depending on latitude (Gray and Salom 1996; Joseph et al. 2011b; McClure 1987). Adults of this generation (progrediens) soon lay eggs, which hatch between May and July. These nymphs enter dormancy until late September to October, when feeding begins (Parker et al. 1998). They continue feeding whenever temperatures are warm enough, until reaching adulthood (Figure 1). In addition to the wingless life form, which feeds on eastern hemlock, a winged form called sexuparae that does not feed on eastern hemlock can also be produced. Sexuparae develop alongside progrediens and upon molting to the adult stage will fly in search of its primary host.

Hemlock woolly adelgid has a primary and secondary host. Spruce (*Picea* Dietrich) is considered the primary host of all adelgids (Havill and Foottit 2007). However, experiments have shown that HWA is unable to survive on any native or naturalized spruce in the United States (McClure 1987, 1989). Therefore, all of the reproduction of HWA in the United States is asexual (through parthenogenesis). Population cycles of HWA have been shown to be density dependent, with the proportion of wingless to winged offspring fluctuating (McClure 1991). After the first year of heavy feeding, survival of the wingless form, progredien, drops substantially and the proportion of sexuparae increases noticeably, primarily in response to the near-complete loss of palatable new growth. This would ordinarily allow the insect to escape the deteriorating host but this is prevented by a lack of suitable spruce hosts.

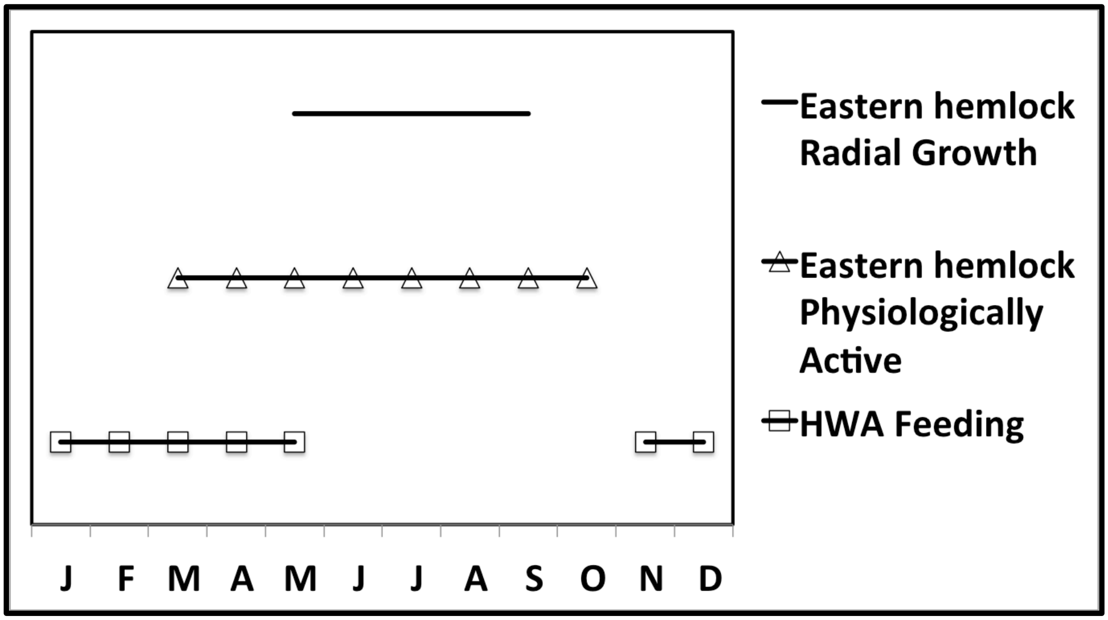

Figure 1. Timing of eastern hemlock radial growth, eastern hemlock being physiologically active, and hemlock woolly adelgid feeding (adapted from Skene 1971, Hadley 2000 and McClure 1987).

The hemlock woolly adelgid feeds on the new growth of eastern hemlocks by inserting a long stylet bundle into the underside of needles, where it feeds on stored nutrients found in the ray parenchyma (Young et al. 1995). These stored nutrients are critical for tree growth, and the removal of them by adelgid feeding hinders the tree's ability to produce new growth. The insect may also inject toxic saliva while feeding (McClure 1991). Trees infested with HWA have been shown to exhibit a hypersensitive response indicated by rapid cell death to adelgid feeding, and toxic insect salivary compounds can frequently induce such responses (Radville et al. 2011). This response also explains why HWA causes so much damage to eastern hemlock. Premature needle drop, discolored and thinning foliage, and branch tip dieback can result in tree morality in 4 to 10 years, with some trees persisting for 15 years or more (Eschtruth et al. 2006; McClure 1991; Orwig et al. 2002).

Ecosystem impacts of hemlock woolly adelgid in the United States

The threat of widespread eastern hemlock mortality could have serious impacts for many ecosystem processes, especially site hydrology, carbon and nutrient cycling and changes in species composition. In areas impacted by hemlock woolly adelgid, hemlock is frequently being replaced with many deciduous species, especially black birch (*Betula lenta* L.), red maple (*Acer rubrum* L.) and several oak species (Daley et al. 2007; Orwig et al. 2002). Black birch transpires approximately twice as much water during the growing season than eastern hemlock and an equal amount during the dormant season (Daley et al. 2007). This has the potential to severely impact ecosystem water balance and affect both terrestrial and aquatic organisms and processes. Small streams that drain from deciduous stands are more likely to dry up during the summer than streams that are associated with eastern hemlock (Evans 2004). The amount of throughfall under infested canopies can be twice as high and frequently contains higher concentrations of nitrogen and organic carbon (Stadler et al. 2005).

Hemlock woolly adelgid induced mortality also has serious effects on nutrient cycling. Net nitrogen mineralization, nitrification, and turnover significantly increased after mortality (Jenkins et al. 1999). These changes increase the amount of nitrogen that may be leached from a system. Total nitrogen pools have also been shown to increase, due to a combination of increased decomposition and reduced nitrogen uptake (Orwig et al. 2008). Soil carbon has also been shown to decrease rapidly after mortality due to the loss of fine root production. Carbon and nutrient dynamics are likely to change further as a large amount of organic matter will be added in dying hemlock stands (Nuckolls et al. 2009). Soil surface-temperature is generally lower in riparian hemlock forests compared to hardwood forests and the decline of hemlock basal area and shift to a hardwood-dominated overstory will likely lead to increases in soil temperature (Knoepp et al. 2011). These increases will alter soil biological and chemical properties, such as increasing decomposition and available nutrients. The higher amounts of mobile nutrients may simply be leached out of the system, especially in the southern Appalachians, as hemlock understories are often dominated by rosebay rhododendron (*Rhododendron maximum* L.), a shrub that can form a thick canopy and significantly reduce overstory regeneration (Krapfl et al. 2011; Phillips and Murdy 1985).

Species composition changes with hemlock mortality. In addition to the replacement of eastern hemlock by deciduous trees, the amount of shrubs and herbaceous cover frequently increases (Orwig et al. 2002; Small et al. 2005; Spaulding and Rieske 2010). The average amount of light reaching the forest floor can double, often resulting in a large increase in plant abundance and richness (Eschtruth et al. 2006). Elevated light levels can also increase the susceptibility of forests to exotic invasive plants. For example, no invasive plants were detected in two stands in the Delaware Water Gap National Recreation Area that were surveyed in 1994, before infestation of hemlock woolly adelgid. However, when resurveyed in 2003, 35% of plots contained invasive species, primarily tree-of-heaven (*Ailanthus altissima* (Miller) Swingle), multiflora rose (*Rosa multiflora* Thunberg), Japanese barberry (*Berberis thunbergii* DC.) and Japanese stiltgrass (*Microstegium viminium* (Trinius) A. Camus).

The loss of overstory hemlock trees due to HWA also affects fish, bird and amphibian assemblages. Increased light levels due to defoliation and mortality of riparian hemlocks would increase stream temperatures, and these increased temperatures negatively impact brook trout (*Salvelinus fontinalis* Mitchill), a species where the populations are already threatened due to habitat loss (Siderhurst et al. 2010). Many bird species depend on eastern hemlock and frequently decline following HWA induced mortality. The Acadian flycatcher (*Empidonax virescens* Vieillot), the black-throated green warbler, and the hermit thrush (*Catharus guttatus* Pallas) were found to be much more abundant in hemlock forests with little to no HWA mortality when compared to heavily impacted stands (Becker et al. 2008; Tingley et al. 2002). These hemlock specialists tend to be replaced by more generalist species, such as the eastern wood-pewee (*Contopus virens* L.) and the wood thrush (*Hylocichla mustelina* Gmelin). Populations of the eastern redback salamanders (*Plethodon cinereus* Green) decreased sharply following hemlock mortality, but their numbers tended to recover in a few years as other vegetation replaces dead hemlocks (Brannon and Rogers 2005).

Management and biological control of hemlock woolly adelgid

Chemical control of HWA has been shown to be effective in certain situations, especially for ornamental and urban trees. Foliar application of various insecticides can eliminate 100% of HWA populations (McClure 1987). Infested branches must be completely saturated for the insecticide to be effective and repeat applications are often necessary because new HWA populations can arrive. Soil application and direct trunk-injection of insecticides have also been shown to be effective in killing HWA (Cowles et al. 2006; Joseph et al. 2011a). Unfortunately, insecticides are only practical at small scales and alternative methods must be found to effectively manage HWA populations in hemlock forests.

Several potential biological control agents of HWA have been identified and two insect species in particular have been extensively studied. *Sasajiscymnus tsugae* Sasaji & McClure is a lady beetle that was discovered preying upon HWA in Japan in 1992 (McClure 2000). The beetle has two generations per year that are synched with HWA's life cycle during the spring and summer, and both larval and adult stages prefer to feed upon adelgids (Cheah 2004b). *Sasajiscymnus tsugae* has been successfully reared in the lab and populations were free-released in 1995 in the United States. Laboratory studies have shown that the beetle will also feed and complete its life cycle on another invasive species, the balsam woolly adelgid (*Adelges picea* Ratzeburg), but had a higher success rate on HWA (Jetton et al. 2011).

Another potential biological control agent is *Laricobius nigrinus* Fender, a beetle species that is endemic to western North America, where it was observed feeding on HWA (Cheah 2004a). Although *L. nigrinus* only has one generation per year, its dormancy phase has been shown to occur concurrently with that of HWA (Zilahi-Balogh et al. 2003b). The beetles have also been shown to be active during the winter making them good predators of HWA's winter generation (sistens) (Zilahi-Balogh et al. 2003a). Colonies of *L. nigrinus* have been reared successfully in the lab and field studies have been promising. Over 50% of adult beetles survived the winter in field cages and the beetles significantly reduced HWA populations compared to areas with no predators (Lamb et al. 2005). Large-scale releases have also been conducted and the beetle appears to have successfully established across a wide geographic range (Mausel et al. 2010). Studies evaluating competitive interactions between the two proposed biological control agents (*S. tsugae* and *L. nigrinus*) showed that they can coexist in the same area and have additive predatory effects on HWA populations, indicating that the two beetles can be used in concert (Flowers et al. 2006).

Salvage logging is also used as a tool for managing the effects of HWA and logging of hemlock forests has significantly increased since its arrival (Orwig et al. 2002). However, salvage logging generally results in more shade-intolerant regeneration, higher soil pH and nitrification rates, and a reduction in forest floor mass when compared to stands that have simply been infested (Kizlinski et al. 2002). Therefore, salvage logging may lead to greater changes in nutrient dynamics, such as nitrogen leaching, and site hydrology. Also, because HWA is a poor self-disperser, salvage logging has the potential to speed the spread to uninfested areas. Egg masses become firmly attached to the bark of both hemlock and other species growing in association, and can survive up to 15 days (McClure 1990). Transport of infested material is believed to have been a significant factor in previous rates of spread by creating outlying populations outside the general infestation front (Morin et al. 2009). These smaller colonies then coalesce and eventually combine with the general front, leading to faster rates of spread (Shigesada et al. 1995).

Use of tree rings to understand forest decline

Fungal diseases often cause reduction in radial growth. Trees infected by two root-pathogenic fungi, *Armillaria* Staude and *Heterobasidion irregulare* Garbelotto & Otrosina (Annosus root rot) had significantly lower growth rates compared to pre-infestation levels and to concurrent growth rates of healthy trees (Cherubini et al. 2002). The two pathogens affected growth rates differently, with *H. irregulare* abruptly decreasing growth and *Armillaria* gradually decreasing growth. The canker-causing fungi *Cryphonectria parasitica* (Murrill) Barr. has also been shown to reduce basal area growth, with scarlet oaks (*Quercus coccinea* Muenchh.) infected with the fungus growing approximately 2 cm^2 less per year compared to uninfected trees (Davis et al. 1997). Many plant diseases are caused by phytoplasmic bacteria. These organisms cause defoliation and death, and are frequently vectored by piercing-sucking insects (Edmonds et al. 2000). Ash yellows is a disease associated with a phytoplasm that has been linked to dieback and death of ash trees throughout the northeastern and midwestern United States. Radial growth of white ash (*Fraxinus americana* L.) infected with ash yellows was shown to have significantly narrower ring widths compared to uninfected white ash (Ying et al. 1991). Foliar diseases, which are caused by multiple groups of fungi, can disrupt the normal functions of leaves by decreasing photosynthesis and reducing plant vigor, leading to lower radial growth rates (Edmonds et al. 2000). Slash pines (*Pinus eliottii* var. *elliottii* Engelm.) infected by pine-needle cast (*Lophodermella cerina* Darker) had significantly lower radial growth rates compared to uninfected trees (Van Deusen and Snow 1991).

The use of tree rings to measure the impacts of insect attack on radial growth was first used in 1866 by Ratzeburg, who matched growth declines with defoliating caterpillar outbreaks (Speer 2010). Tree rings have since been used to quantify the effects of insect feeding on the radial growth of many tree species. Defoliating insects consume part or all of a plant's leaves, and severe or persistent defoliation can result in severe growth loss or mortality. Douglas-fir (*Pseudotsuga menziesii* Mirb.) defoliated by the western false hemlock looper (*Nepytia freeman* Munroe) grew significantly less than non-defoliated trees, with heavily infested trees recovering more slowly than less impacted ones (Alfaro and MacDonald 1988). Radial growth of western larch (*Larix occidentalis* Nutt.) attacked by the larch casebearer (*Coleophora laricella* Huebner) decreased significantly compared to Douglas-fir growing in the same area (Alfaro et al. 1991). These growth reductions often persist past the initial infestation, with radial growth rates being as much as 81% lower 10 years after defoliation (Alfaro and Shepherd 1991; Brubaker 1978).

Wood-boring insects, such as bark beetles, damage trees by disrupting the tree's vascular tissue. They can attack both healthy and weakened trees, and outbreaks of bark beetles can kill hundreds of hectares of forests (Edmonds et al. 2000). Northern red oaks (*Quercus rubra* L.) severely infested with red oak borers (*Enaphalodes rufulus* Haldeman) were shown to grow approximately 20% less than lightly infested and uninfested trees (Haavik et al. 2008), while outbreaks of the spruce bark beetle (*Dendroctonus rufipennis* Kirby) were shown to significantly reduce the growth of Engelmann spruce (*Picea engelmannii* Parry ex Engelm.) in northwestern Colorado (Eisenhart and Veblen 2000). Root parasites, such as the periodic cicada (*Magicicada* Davis), can reduce the growth of trees during oviposition, but often increase growth by providing a large pulse of nutrients due to decomposing carcasses after a mass emergence (Speer 2010).

Aphids, a type of piercing-sucking insect, feed on trees by inserting their mouthparts into the vascular tissue of the foliage or branches, and extracting sugars. Defoliation induced by aphid feeding significantly reduced the growth of Sitka spruce (*Picea sitchensis* (Bong.) Carrière) when compared to healthy trees (Halldorsson et al. 2003). Similar to the feeding habits of aphids, HWA inserts its stylet bundle into the xylem ray parenchyma, where it extracts nutrients (Young et al. 1995). The radial growth of eastern hemlock has been shown to decrease following attack by HWA (Rentch et al. 2009), and eastern hemlocks with heavy infestations of the adelgid experienced large reductions in radial growth, while maple and oak species benefitted from the HWA induced decline because of reduced competition for resources (Orwig 2002).

Changes in wood anatomy due to defoliation

Defoliation of conifers often results in changes in wood anatomical structure and characteristics. In addition to reductions in overall radial growth, jack pines (*Pinus banksiana* Lamb.) defoliated by the jack pine budworm (*Choristoneura pinus* Freeman) were shown to have reduced latewood production when compared to an unaffected stand (Gross 1992). Eastern white pines (*Pinus strobus* L.) attacked by the pine false webworm (*Acantholyda erythrocephala* L.) also showed significant reductions in latewood production compared to non-defoliated trees

(Mayfield et al. 2005). Severe and prolonged defoliation, similar to what would be seen with HWA attacks, reduces carbon availability for new needle production, which results in less latewood formation.

Defoliation also affects earlywood production and tracheid cell-wall thickness. Larches defoliated by the larch budmoth (*Zeiraphera improbana* Walker) have been shown to produce fewer latewood cells, while cell wall thickness is also reduced (Schweingruber 2007). Similarly, tracheids formed by eastern larches defoliated by the larch sawfly had thinner latewood cell walls compared to healthy trees (Liang et al. 1997). As well as changes in the number and size, the structure of cells can also be affected, with tracheids produced after the first year of defoliation being irregularly shaped (Schweingruber 2007). Wood produced the year before death can contain rows of traumatic resin canals (Schweingruber 2007; Schweingruber et al. 2006).

III. Methods

Site descriptions

Six study sites spanning the current range of HWA infestation and covering a significant portion of eastern hemlock's natural range, from northern Georgia to southern Massachusetts, were selected (Figure 1, Table 1). The first site is located in the Chattahoochee National Forest, west of Crandell, Georgia, in Murray County (34°53'N, 84°39'W). The average temperature for January was 5.2 °C, and July was 25.8°C. Site elevation is approximately 600 m asl, and the average total annual precipitation is 1,332 mm. Overstory vegetation is mixed hardwood-hemlock, consisting mainly of northern red oak, chestnut oak (*Quercus prinus* L.), tulip-poplar

(*Liriodendron tulipifera* L.) and black gum (*Nyssa sylvatica* Marshall). The site is located in the Ridge-and-Valley physiographic region and soils are Ultisols in the Edneytown series.

The second site is located along the Davidson River in the Pisgah National Forest, near the town of Brevard, North Carolina in Transylvania County (35°17'N, 82°43'W). The average temperature for January was 3.7 °C, and July was 20.9 °C. Site elevation ranges from 660 to 680 m asl, and the average total annual precipitation is 1,393 mm. Overstory vegetation is mixed hardwood-hemlock, consisting mainly of eastern hemlock, American beech (*Fagus grandifolia* Ehrhart), black gum and sycamore (*Platanus occidentalis* L.). The site is located in the Blue Ridge physiographic region and soils are Inceptisols in the Rosman-Reddies complex.

The third site is located in the Fishburn Forest, near Blacksburg, Virginia in Montgomery County (37°11'N, 80°29'W). The average temperature for January was 0.8°C, and July was 21.9°C. The average total annual precipitation is 1,095 mm, and the approximate elevation of the site is 570 m asl. The overstory vegetation is mixed hardwood-hemlock, consisting mainly of eastern hemlock, red maple, eastern white pine and northern red oak. The site is located in the Ridge-and Valley-physiographic region and soils are Inceptisols in the Berks and Weikert complex.

The fourth site is located in the Monongahela National Forest, just North of Durbin, West Virginia, in Pocahontas County (38°37’N, 79°47’W). Average temperature for January was -1.8°C, and July was 20.2°C. Site elevation is approximately 900 m asl and average total annual precipitation is 1,265 mm. Overstory vegetation is a mixed hardwood-hemlock-red spruce (*Picea rubens* Sargent), consisting mainly of eastern hemlock, red spruce and black cherry (*Prunus serotina* Ehrhart). The site is located in the Ridge-and-Valley physiographic region and soils are Udifluvents-Fluvaquents.

The fifth site is located in the Buchanan State Forest, outside of McConnellsburg, Pennsylvania, in Franklin County (40°00’N, 77°48’W. Average temperature for January was -1.4°C, and for July was 23.6°C. The average total annual precipitation is 1,010 mm and elevation is approximately 500 m asl. The overstory vegetation is mixed hardwood-hemlock, mainly containing eastern hemlock, yellow birch (*Betula alleghaniensis* Britt.), red maple and tulip-poplar. The site is located in the Ridge-and-Valley physiographic region and soils are Ultisols in the Andover series.

The sixth site is located at the Quabbin Reservoir, near Belchertown, Massachusetts, in Hampshire County (42°21’N, 72°22’W). Average temperature for January was -4.0°C, and July was 21.6 °C. The average total annual precipitation is 1,100 mm and elevation ranged from 170 to 190 m asl. The overstory vegetation consists mainly of eastern hemlock with scattered black birch, river birch (*Betula nigra* L.), and red maple. The site is located in the New England physiographic region and soils are Inceptisols in the Charlton-Hollis complex.

Field methods

At each site, 23 dominant or codominant eastern hemlock trees infested with HWA were selected and cored approximately 0.5 m above the ground using an increment borer. Trees were categorized as being infested if HWA was detected on any living branches (Costa and Onken 2006). Two cores were extracted from each tree on opposite sides of the trunk. Where appropriate, cores were taken parallel to the slope in order to minimize distortion due to compression wood. The total height and diameter at breast height (DBH) of each tree were also measured. To develop a competition index, the distance from each cored tree to the nearest living tree was measured. That nearest tree’s DBH and species were also recorded (Appendix A). The average soil depth for each site was measured using a bucket auger and soil from the B-horizon of each site was hand textured. At the Virginia site, 2 trees were felled and cross-sections were removed for wood anatomy analysis.

The crowns of selected trees were rated using the Forest Service's Visual Crown Rating Methods (Montgomery et al. 2006). Crown rating provides a simple and easy to understand score of infested hemlock health. Live-crown ratio (LCR), foliage density (a percentage of the fullness of the crown based on the amount of light blocked by foliage, twigs, branches and stem), crown transparency (an estimate of the amount of light seen through the foliage), and crown dieback were recorded (Appendix B).

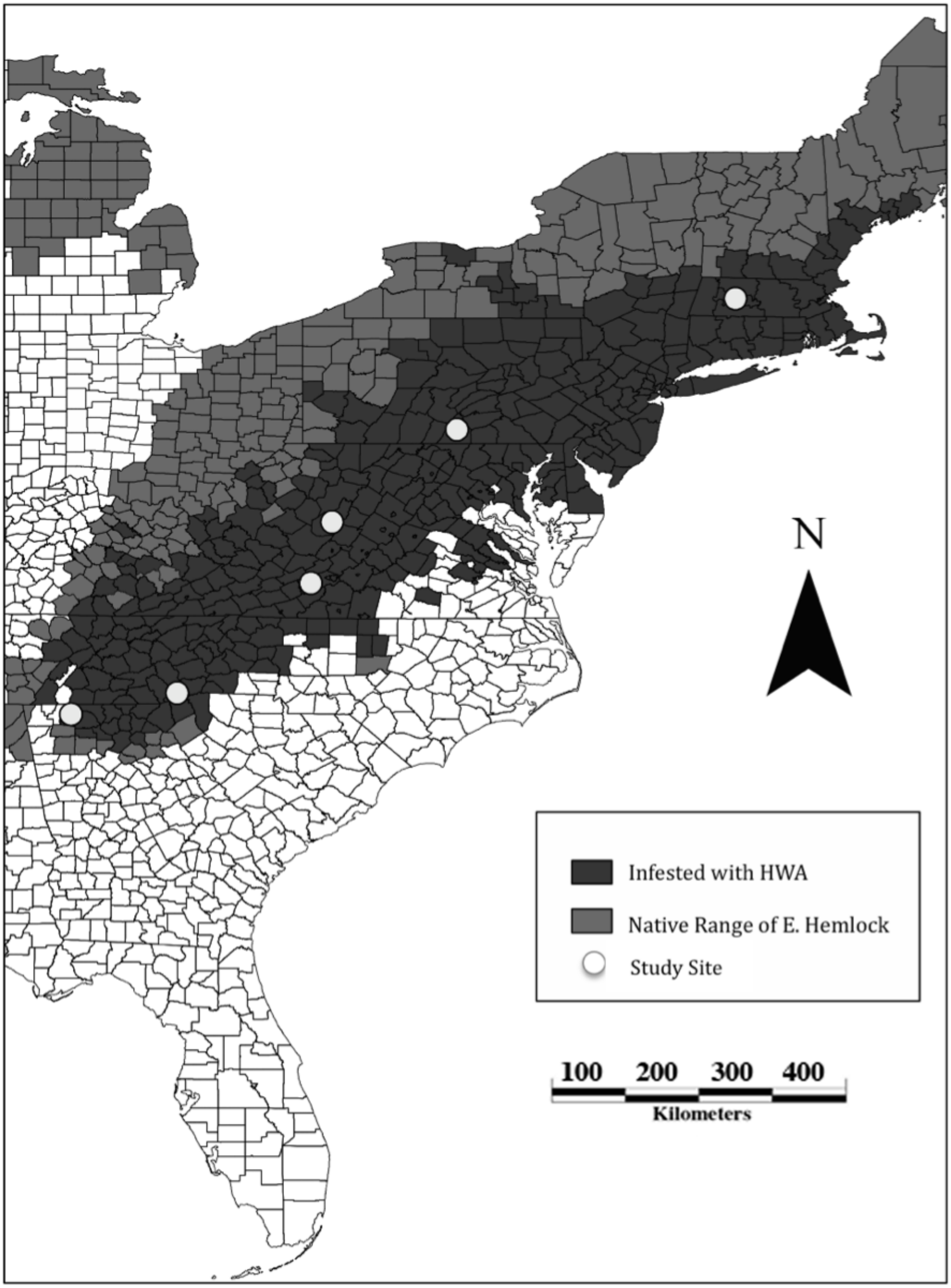

Figure 2. Map showing study site locations, range of eastern hemlock and current range (as of 2011) of hemlock woolly adelgid. Adapted from 2011 Forest Service hemlock woolly adelgid infestation map.

Table 1. Summary of study site information. Climate data from the National Climatic Data Center for the period of 1895-2011.

Site Name	Latitude	Longitude	Approximate Elevation (m)	Average Temperature (°C)		Total Annual Precipitation (mm)
				January	July	
Georgia	34°53'N	84°39'W	600	5.2	25.8	1,332
North Carolina	35°17'N	82°43'W	670	3.7	20.9	1,393
Virginia	37°11'N	80°29'W	570	0.8	21.9	1,095
West Virginia	38°37'N	79°47'W	900	-1.8	20.2	1,265
Pennsylvania	40°00'N	77°48'W	500	-1.4	23.6	1,010
Massachusetts	42°21'N	72°22'W	180	-4.0	21.6	1,100

Lab methods

After air drying, collected increment cores were glued on wooden blocks and sanded with progressively finer grit sandpaper until a smooth surface was achieved and cells were clearly differentiated under a microscope. All cores from individual sites were then cross-dated using the list method, where narrow rings present in each core were recorded (Yamaguchi 1991). All cores were then measured using either a TA Unislide Measurement System (Velmex, Inc., Bloomfield, NY) with the software Measure J2X (Voor Tech Consulting, Holderness, NH), or a Lintab 5 with TSAP-Win software (Rinntech, Heidelberg, Germany). Cross-dating was then statistically verified using the computer program COFECHA (Holmes 1986, Appendix C). Cores that did not cross-date well were re-measured and re-evaluated using COFECHA. Any cores that still did not meet standards were removed from further analysis. This left a minimum of 20 trees per site.

Cross-sections from the trees felled at the Virginia site were cut into 10 small cubes, 5 containing wood produced post-HWA arrival, and 5 containing wood produced pre-HWA arrival. The blocks were then soaked in water for 24 hours. Using a sliding microtome (GSL 1 sledge microtome, Swiss Federal Institute, Birmensdorf, Switzerland), cross-sections approximately 40 μm thick of each piece were taken. Sections were stained using a 0.5% Safranin O solution and mounted to microscope slides which were then sealed using nail polish. Using a light microscope (Zeiss Axioscope 40A Pol) equipped with a digital camera (Nikon DS-Fi2) and the computer program Nikon Image Systems – BR (Nikon Instruments Inc., Tokyo, Japan), the radial tracheid diameter and cell-wall thickness of 30 latewood and 30 earlywood cells were measured per thin section. Cell-wall thickness (CW) was computed using the following formula:

$$CW = \frac{(CW_1 + CW_2)}{2}$$

where CW_1 is the thickness of one cell wall and CW_2 is the thickness of the adjacent cell wall (Filion and Cournoyer 1995). Both cell walls were measured and the value was divided by two due to the inability to accurately discern the boundaries between cells. Cell-wall thickness was measured in the radial direction. This yielded 300 cells of pre-HWA wood measured (150 latewood, 150 earlywood), and 300 cells of post-HWA wood measured (150 latewood, 150 earlywood).

Data analysis

At each site, paired t-tests were used to determine if there was a difference in radial growth pre- and post-HWA arrival. Paired t-tests were chosen because the radial growth pre- and post-HWA arrival of each tree is a natural pairing. We used an equal number of annual rings in pre- and post-HWA analysis, thus the number of years analyzed at each site depended on the date of HWA arrival, with Georgia having 4 years pre-HWA and 4 years post-HWA arrival, North Carolina (5 years), Virginia (13 years), West Virginia (18 years), Pennsylvania (17 years), and Massachusetts (15 years). Because the analysis computes the differences in the measurement pairs, the distribution of differences was plotted to determine the shape. The Georgia, North Carolina, Virginia, Pennsylvania and Massachusetts sites were normally distributed and a $\log_{10}$ transformation was used to normalize the West Virginia site.

To compare differences in pre- and post-HWA cell properties (latewood cell-wall thickness, latewood radial cell diameter, earlywood cell-wall thickness, and earlywood radial cell diameter) t-tests were used. Distributions of the cell-property data were plotted. Latewood cell diameter, latewood cell-wall thickness and earlywood cell diameter were normally distributed, and a square-root transformation was used to normalize the earlywood cell-wall thickness data. Levene's test was used to determine if the variances were equivalent for each cell property. Latewood cell-wall thickness ($F = 0.51, p = 0.475$), latewood cell diameter ($F = 3.05, p = 0.082$), earlywood cell-wall thickness ($F = 0.34, p = 0.557$), and earlywood cell diameter ($F = 1.14, p = 0.231$) all had equal variances, so a two-sample t-test was used.

An analysis of variance (ANOVA) was used to determine differences in average growth post-HWA arrival among sites. The last 4 years of growth was used to maintain equal sample sizes. Four years was chosen because it was the minimum amount of time all the sites had been affected by HWA. A distribution of ring-width values was plotted and a square-root transformation was used to normalize the data. Levene's test was used to examine the homogeneity of variance. The variances were unequal ($F = 27.19, p = <0.001$), so a Welch's ANOVA, which does not assume equal variances, was used. For post-hoc comparison of means, Tukey's Honestly Significant Difference (HSD) was used.

Simple, distance-dependent competition indices are reliable in predicting the effect of tree-to-tree competition on growth (Mugasha 1989). The following equation was used to measure competition:

$$CI = \frac{D_j / D_i}{DIST_{ij}}$$

where the competition index (CI) is equal to the DBH (measured in cm) of the neighboring tree (D_j) divided by the DBH of the tree of interest (D_i) divided by the distance (measured in m) between the two trees (Lorimer 1983). The higher the index value the greater the competition experienced by the tree of interest.

Multiple linear regression (MLR) was used to determine the value of crown variables and the CI as predictors of average growth of the last 4 years. The data were analyzed by site due to differences in topography, climate and stand history. Stepwise variable selection, which is a combination of the forward selection and backward elimination procedures, was used to determine which variables were included in the models. This procedure alternates adding and removing variables using an *F* test. A significance level of $\alpha \leq 0.15$ was used for the *F*-to-include criterion and $\alpha \leq 0.15$ was used for the *F*-to-remove criterion.

At the Georgia, North Carolina, Virginia, Pennsylvania, and Massachusetts sites the cross-dated tree-ring measurements were detrended using a smoothing spline 50% of the length of the series in order to enhance the climatic signal in the data. If a spline was inappropriate for a particular series, linear regression was used. Trees from the West Virginia site were much older than the other sites, so a spline 30% of the length of the series was used because it better fit the data. These detrended series were combined into a stand-level master chronology to use in dendroclimatic analysis using the computer program ARSTAN (Cook and Holmes 1996). Three chronologies were produced by ARSTAN: standard, residual, and ARSTAN. The standard chronology is an average of the standardized indices produced through detrending and may contain autocorrelation. The residual chronology is built by averaging the residuals produced through detrending, resulting in no autocorrelation in the final chronology. The ARSTAN chronology is built by reincorporating only autocorrelation that is common among most series back into the residual chronology, and is intended to contain the strongest climatic signal (Cook and Holmes 1996).

ARSTAN was also used to determine the expressed population signal (EPS), which is a measure of chronology reliability in dendroclimatology analysis (Wigley et al. 1984). Only the segment of each chronology that had an EPS above 0.85 was used for analysis because the common signal above this cutoff is appropriate for dendroclimatic analysis. The following years were used: Georgia 1972 - 2011; North Carolina 1942 - 2010; Virginia 1920 – 2010; West Virginia 1918 – 2010; Pennsylvania 1922 – 2010; Massachusetts 1922 – 2010.

Pearson correlation coefficients were then calculated between the ring–width indices (RWI) developed and both the current and previous year’s monthly precipitation, temperature and the Palmer Drought Severity Index (PDSI) for each site. The previous year’s climate was included to test for a lag effect, where the previous year’s climate would affect the current year’s growth. Palmer Drought Severity Index is the most widely used regional drought index, and it serves to quantify the duration and intensity of the drought (Alley 1984). Values in the index range from approximately -4 (extreme drought) to +4 (extreme wetness). All climate data were obtained from the National Climate Data Center (NCDC). Divisional data, rather than single station data, were used because the regional values have been shown to have stronger relationships to radial growth and are less influenced by microclimate conditions that are often found with single station data (Kimball and Keifer 1988). The following divisions were used: Georgia Northwest Division (01), North Carolina Southern Mountain Division (01), Virginia Southwestern Mountain Division (06), West Virginia Central Division (04), Pennsylvania Lower Susquehanna Division (04), and Massachusetts Central Division (02).

IV. Results

The West Virginia site had the highest series intercorrelation, while the Georgia site had the lowest (Table 2). Series intercorrelation measures the strength of the common stand-level signal and is representative of the common tree-to-tree variation in growth. West Virginia was also the oldest site, both in terms of maximum tree age (241 years) and average tree age (115), and can be classified as old growth (Lorimer et al. 2001). Georgia was the youngest site, with a maximum tree age of 65 years. Mean sensitivity, a measure of year-to-year variation in ring-width, was highest at the Virginia site and lowest at the Georgia and Pennsylvania sites.

Table 2. General statistics characterizing the six tree-ring chronologies used in this study.

Site	Number of trees	Mean ring-width (mm)	Series intercorrelation	Mean sensitivity	Maximum tree age (years)	Average tree age (years)
Georgia	21	2.97	0.46	0.20	65	49
North Carolina	20	1.93	0.51	0.25	101	58
Virginia	21	2.02	0.52	0.27	142	70
West Virginia	20	1.70	0.57	0.22	241	115
Pennsylvania	20	1.67	0.50	0.20	115	92
Massachusetts	21	2.11	0.54	0.22	124	86

Three of the 6 sites (North Carolina, Virginia, and Pennsylvania) had significantly narrower mean ring-widths post-HWA arrival compared to pre-HWA (Table 3). These 3 sites were centrally located in eastern hemlock's range. The 3 sites also had multiple trees where either no annual ring was produced for a given year or only a partial ring was produced (Figure 3). North Carolina had 21 cores with missing rings (all either 2009 or 2010), Virginia had 9 cores with missing rings (2004, 2008, 2009 or 2010), and Pennsylvania had 9 cores with missing rings (2008, 2009 or 2010). Georgia and West Virginia had statistically equal mean ring-width pre- and post-HWA arrival, while Massachusetts had significantly wider ring-widths post-HWA arrival compared to pre-HWA. The largest difference in mean ring-width pre- and post-HWA arrival was North Carolina (0.97 mm less); in contrast, at West Virginia, the difference was only 0.01 mm.

Table 3. Mean ring-width values pre- and post-HWA arrival by site ($\alpha = 0.05$). The full number of years with hemlock woolly adelgid (HWA) and a matching number from before HWA's arrival were used at each site (Georgia 4 years pre-HWA and 4 years post-HWA arrival, North Carolina [5 years], Virginia [13 years], West Virginia [18 years], Pennsylvania [17 years], and Massachusetts [15 years]).

Site	Mean ring-width Pre-HWA (mm)	Mean ring-width with HWA (mm)	t-value	p-value
Georgia	2.71	2.83	-0.72	0.473
North Carolina	2.20	1.23	-7.24	<0.001
Virginia	2.58	1.72	-6.17	<0.001
West Virginia	1.02	1.01	-0.51	0.612
Pennsylvania	1.42	1.01	-6.45	<0.001
Massachusetts	1.65	1.87	2.08	0.044

There was high variability in individual tree response; however, three common trends were noted at all sites: (1) a decline in growth shortly after HWA arrival (Figure 4), (2) a gradual decline in growth starting before HWA arrival (Figure 5), and (3) no apparent change in growth post-HWA arrival (Figure 6). North Carolina, Virginia and Pennsylvania all had over 50% of the individual cores showing a decline in growth shortly after HWA arrival (Table 4). The Georgia and Massachusetts sites, representing the southern and northern edge of HWA's current range, each showed unique trends. The Georgia site showed an increase in growth near the time of HWA arrival (Figure 7). The Massachusetts site showed either a decline or no change followed by a growth release (Figure 8), or a rapid increase in growth followed by a decline (Figure 9). Although all sites have been growing at lower than average rates the past few years, only North Carolina is experiencing an unprecedented low growth-rate (Figure 10).

There was a significant difference in the mean ring width from the last 4 years of growth by site ($F = 127.38$, $p < 0.001$, Table 4). Tukey's HSD identified Georgia with the widest mean ring-width (2.71 mm) and Pennsylvania with the lowest (0.57 mm). The sites at the northern and southern edge of HWA's current range had the widest mean ring-width, with Massachusetts significantly narrower than Georgia. Three of the centrally located sites, Pennsylvania, Virginia, and North Carolina had the narrowest mean ring-width.

The mean latewood (LW) cell-wall thickness of tracheids produced post-HWA arrival was significantly thinner compared to tracheids produced pre-HWA arrival ($t = 6.87$, $p <0.001$). The mean radial cell diameter of LW tracheids produced post-HWA arrival was also smaller ($t = 3.33$, $p = 0.001$). The post-HWA mean LW cell-wall thickness was 0.86 mm thinner compared to pre-HWA arrival. The mean diameter of LW tracheids produced post-HWA arrival was 1.08 mm smaller than tracheids produced pre-HWA. The mean earlywood cell-wall thickness and radial diameter of tracheids produced post-HWA arrival were statistically equal to those produced pre-HWA (Table 5).

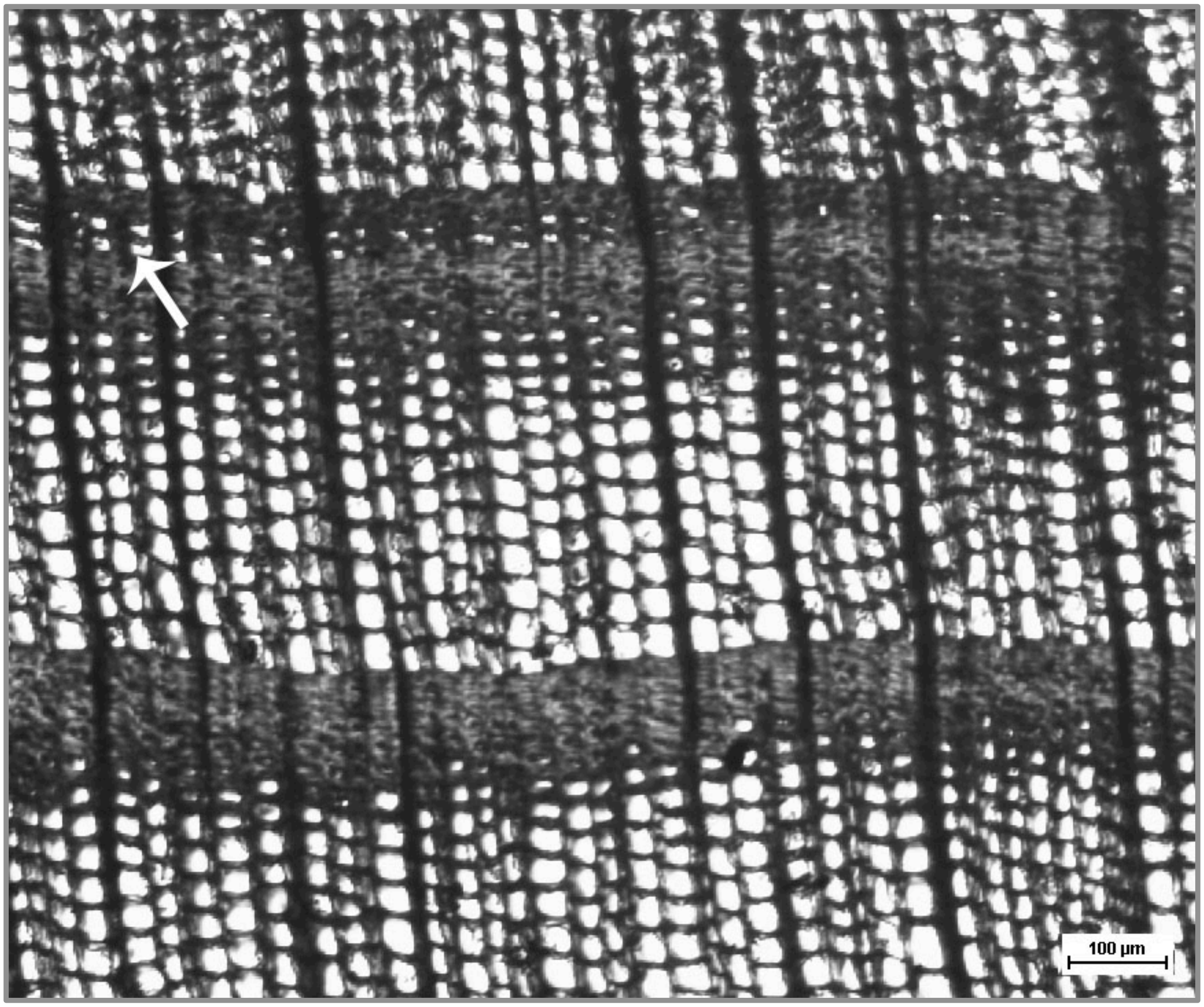

Figure 3. Partial growth ring produced in 2009 from an eastern hemlock growing at Virginia. Note white arrow on left indicating earlywood cells, which are not present on right side of image.

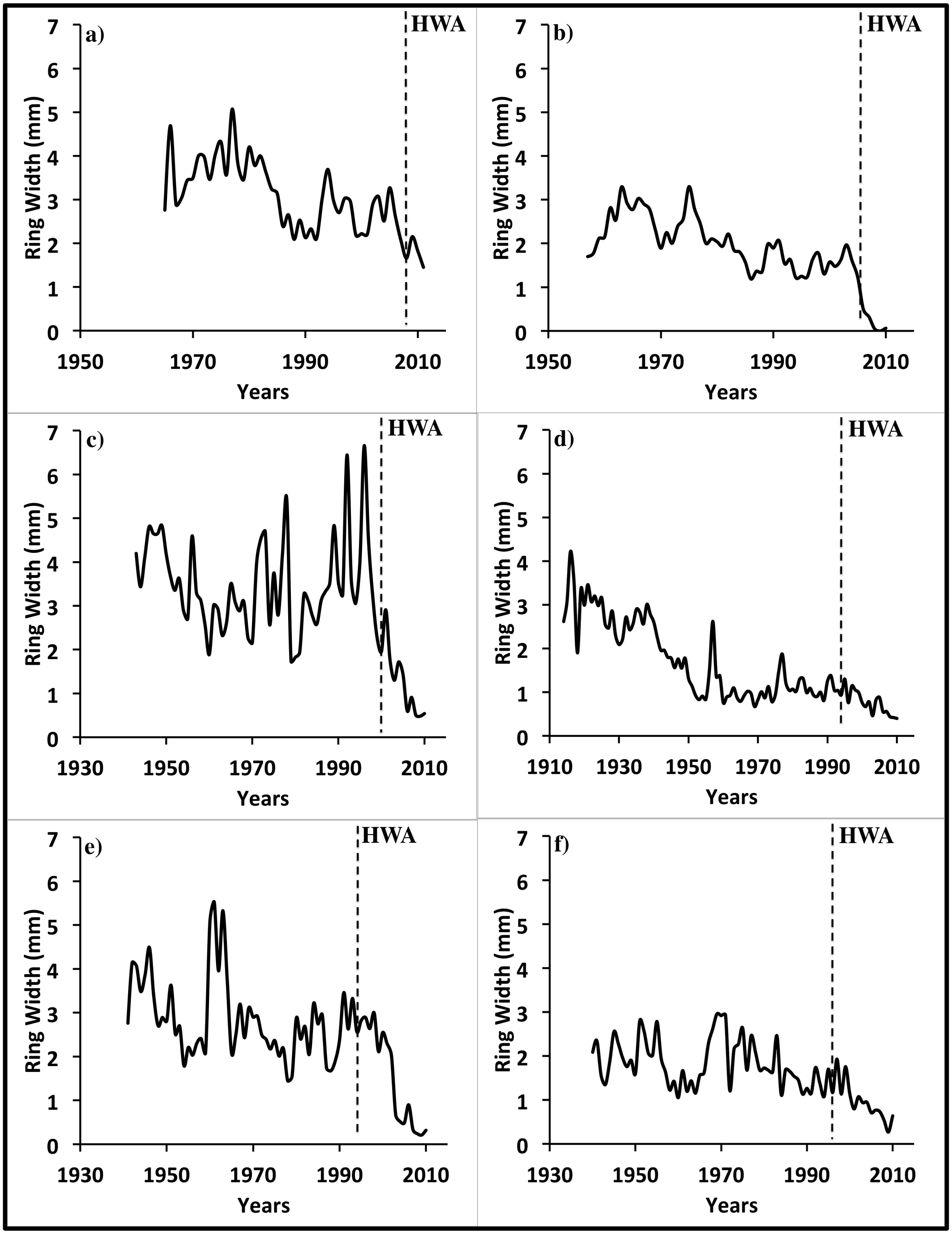

Figure 4. Individual series (tree cores) from the six sites showing a decline in growth shortly after hemlock woolly adelgid (HWA) arrival (a) Georgia, b) North Carolina, c) Virginia, d) West Virginia, e) Pennsylvania, and f) Massachusetts. Dashed line indicates arrival of HWA. Note different scales on x-axis of each panel.

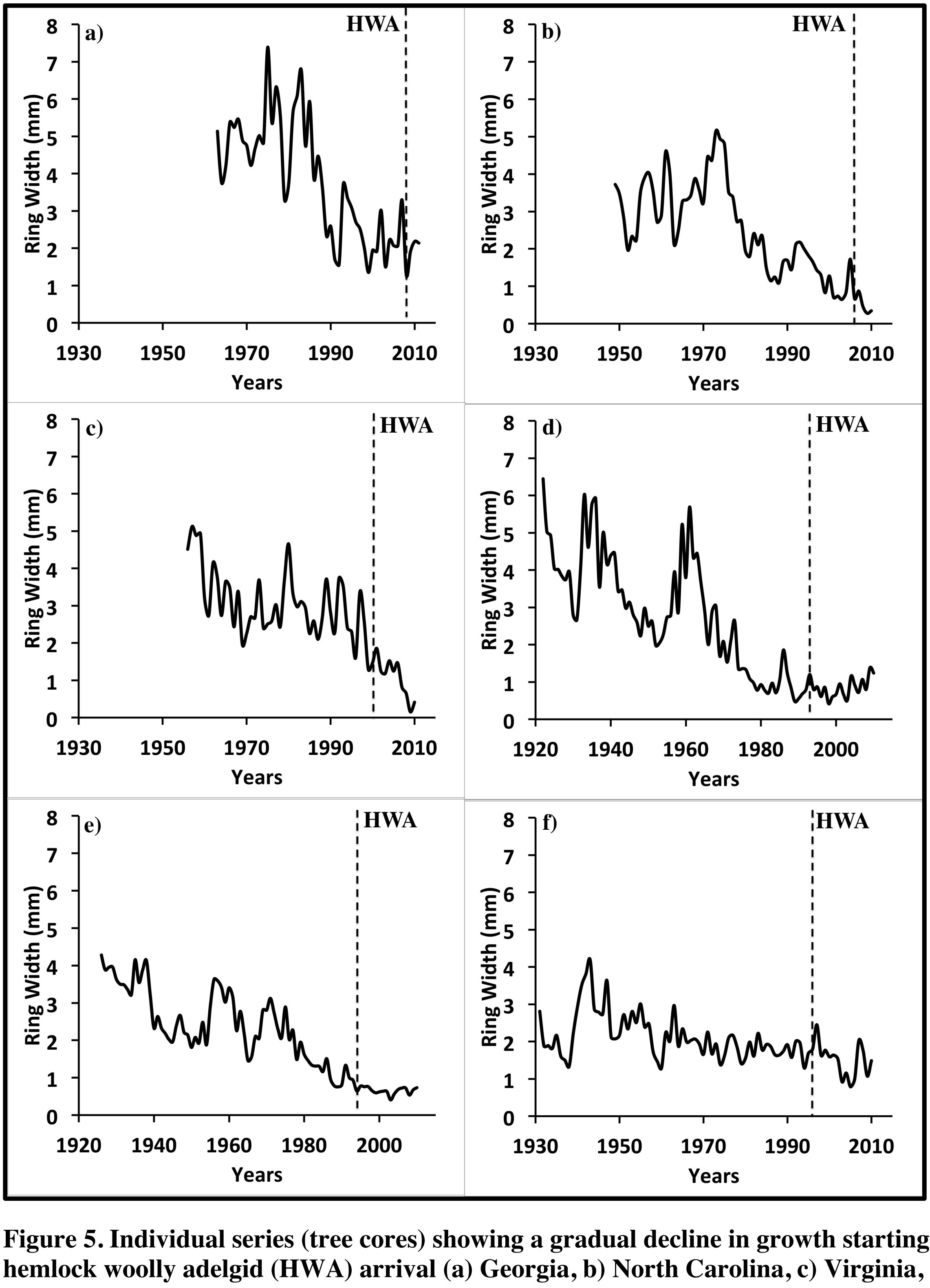

Figure 5. Individual series (tree cores) showing a gradual decline in growth starting before hemlock woolly adelgid (HWA) arrival (a) Georgia, b) North Carolina, c) Virginia, d) West Virginia, e) Pennsylvania, and f) Massachusetts). Dashed line indicates arrival of HWA. Note different scales on x-axis of each panel.

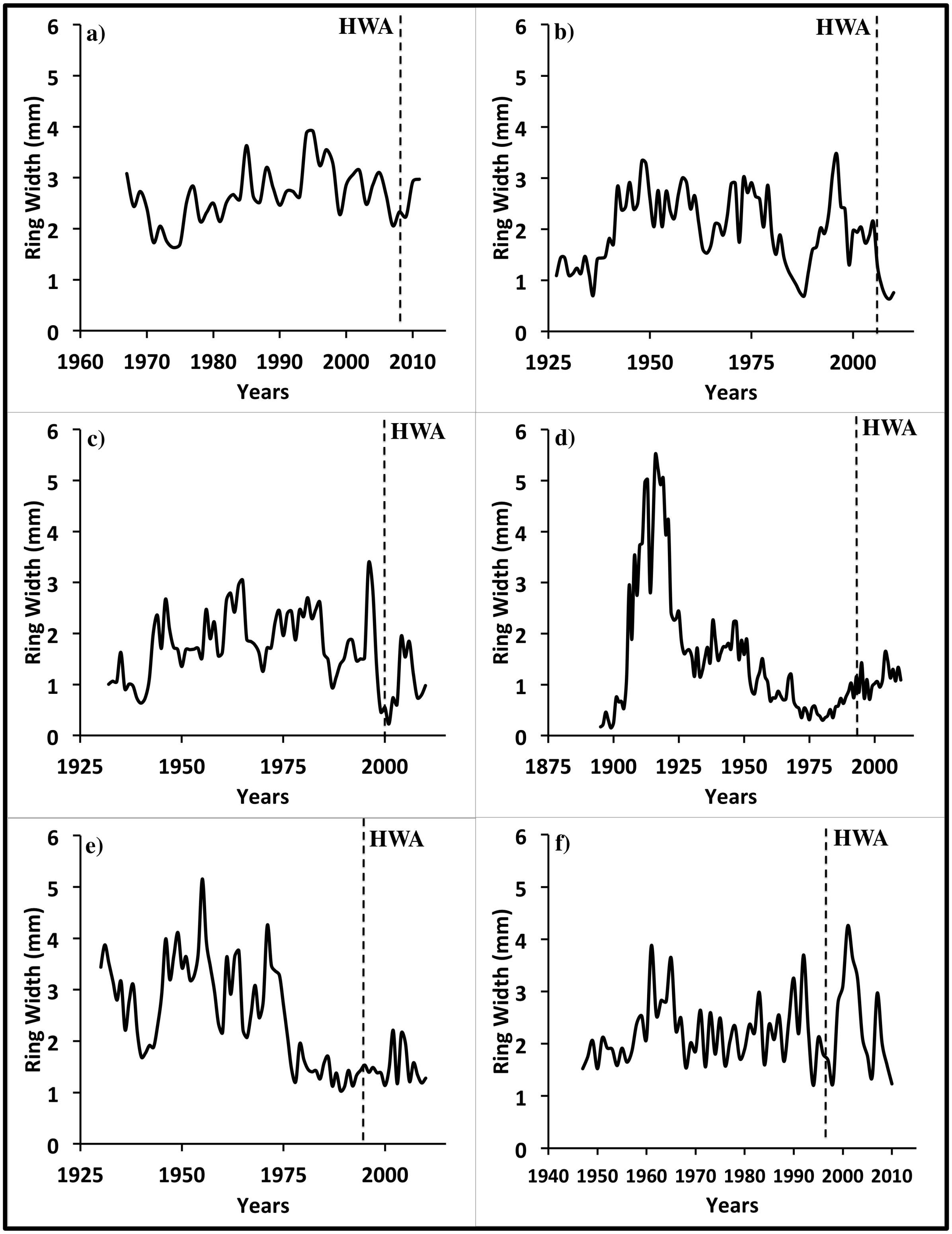

Figure 6. Individual series (tree cores) showing no immediate change in growth post-hemlock woolly adelgid arrival (HWA) arrival (a) Georgia, b) North Carolina, c) Virginia, d) West Virginia, e) Pennsylvania, and f) Massachusetts). Dashed line indicates arrival of HWA. Note different scales on x-axis of each panel.

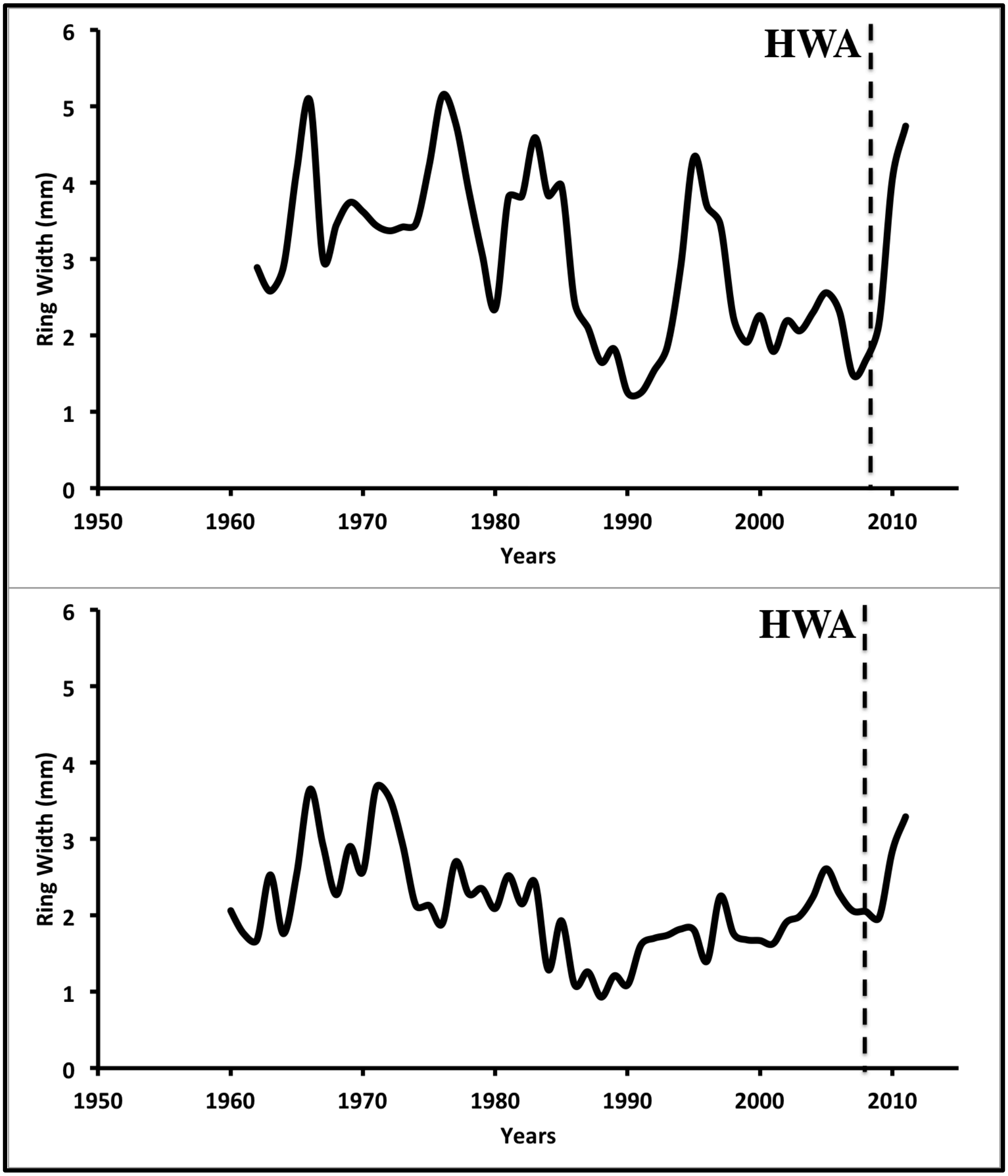

Figure 7. Two individual series (tree cores) showing increase in growth following hemlock woolly adelgid arrival, a trend unique to the Georgia site.

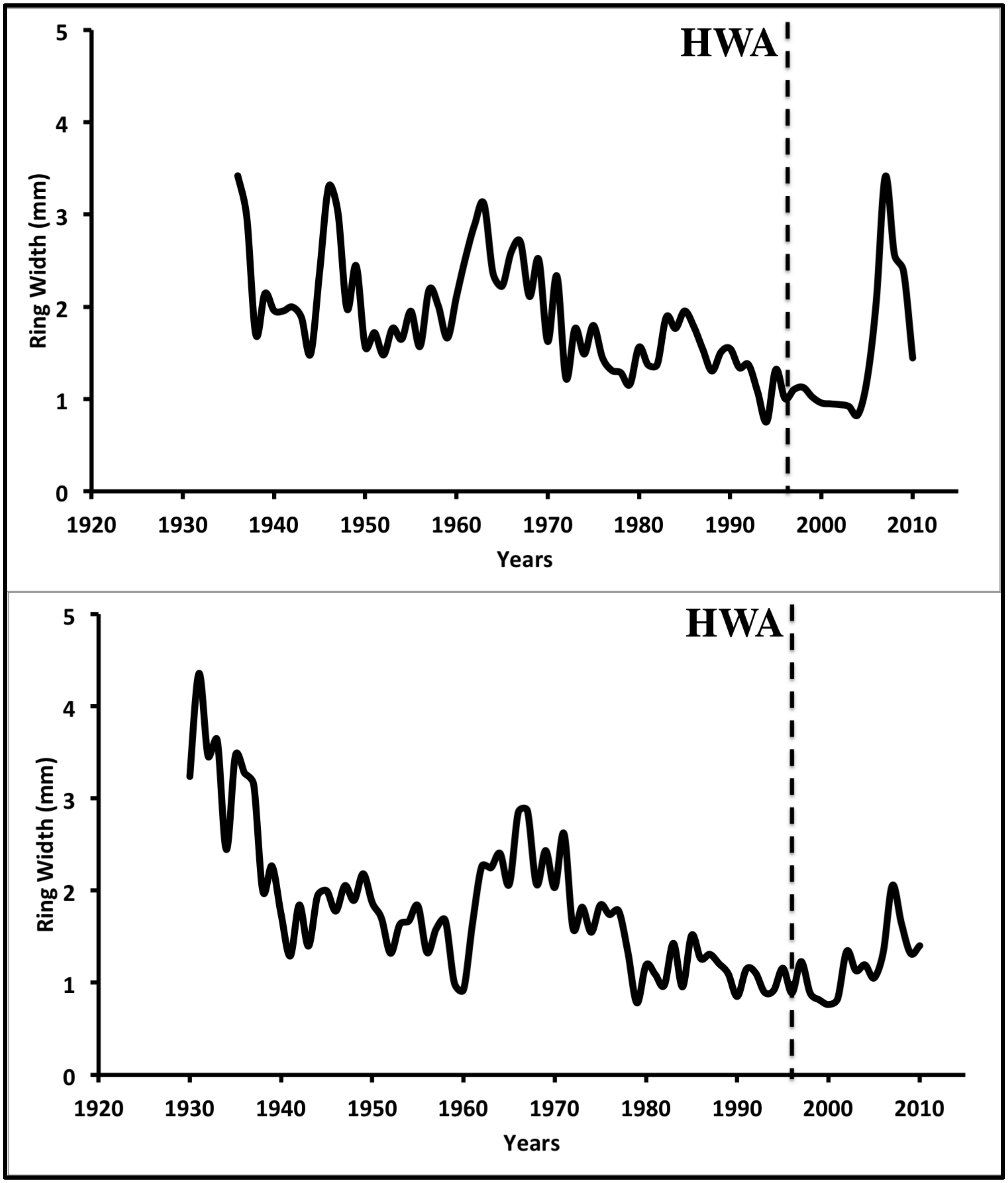

Figure 8. Two individual series (tree cores) showing a slight decline followed by a growth release after hemlock woolly adelgid arrival, a trend unique to the Massachusetts site.

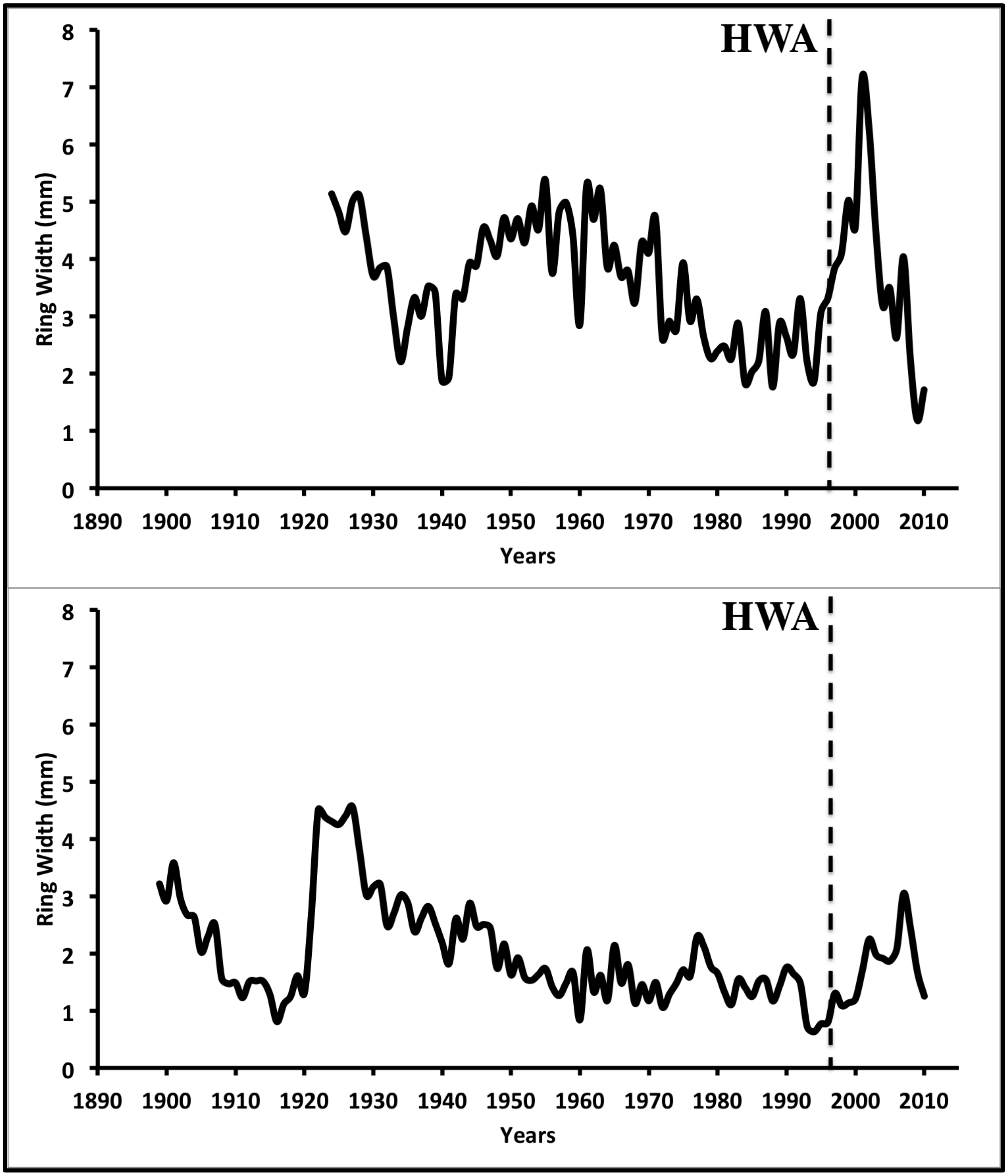

Figure 9. Individual series (tree cores) showing a rapid increase in growth followed by a decline after hemlock woolly adelgid arrival, a trend unique to the Massachusetts site.

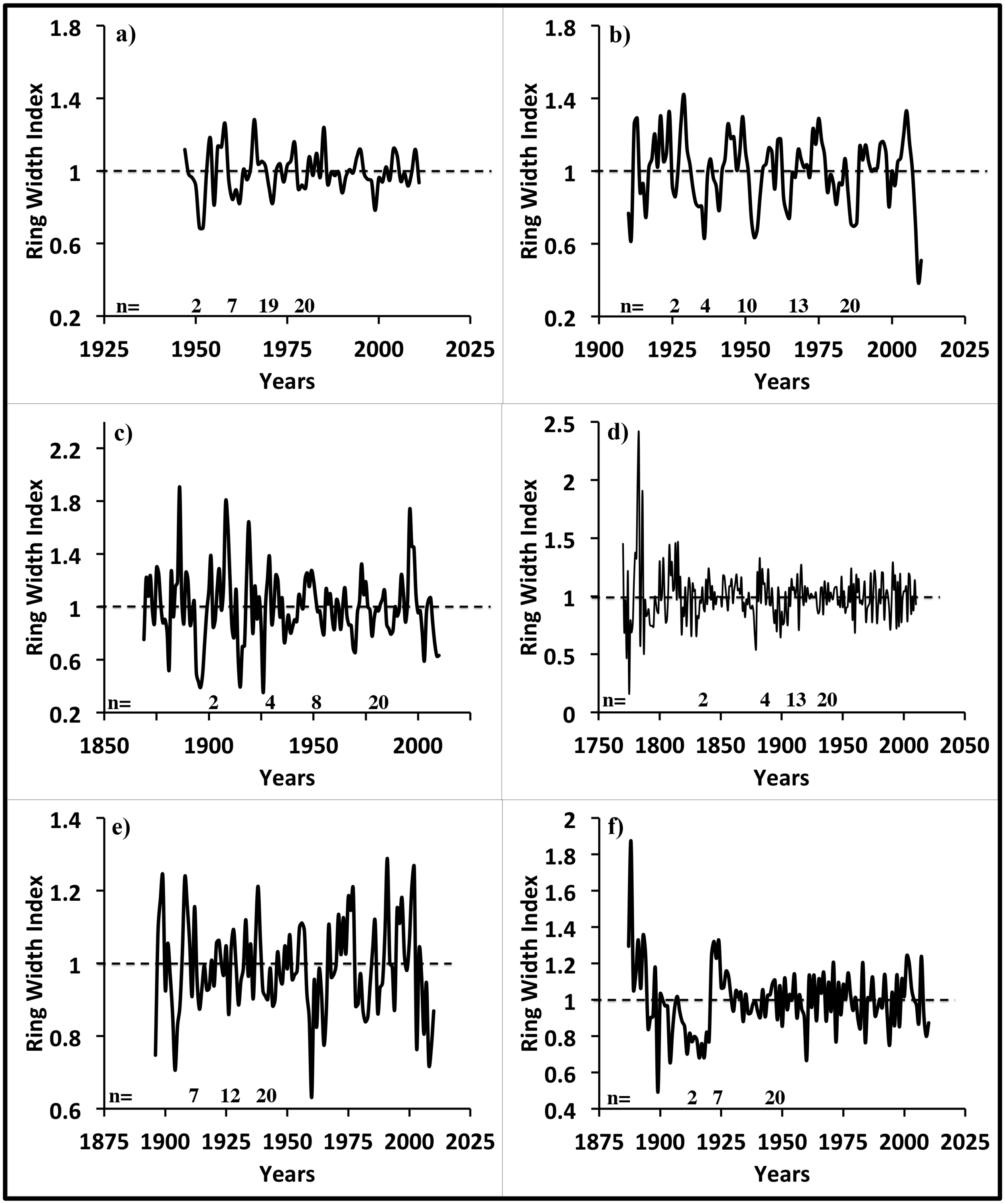

Figure 10. ARSTAN chronologies for Georgia (a), North Carolina (b), Virginia (c), West Virginia (d), Pennsylvania (e), and Massachusetts (f). The dashed line indicates a mean of 1. Note different scales for x- and y-axes in each panel.

Table 4. Percentage of tree cores that showed one of the three common trends observed at each site. 'Decline' is a decline in growth shortly after HWA arrival (see Figure 4), 'Gradual decline' is a gradual decline in growth starting before HWA arrival (see Figure 5), and 'No change' is no apparent change in growth post-HWA arrival (see Figure 6), and 'Other' is some other growth trend.

	Decline	Gradual decline	No change	Other
Georgia	20%	15%	33%	32%
North Carolina	62%	19%	11%	8%
Virginia	54%	26%	21%	0%
West Virginia	10%	28%	56%	6%
Pennsylvania	52%	14%	33%	1%
Massachusetts	10%	37%	27%	26%

Table 5. ANOVA of mean ring-width (last 4 years of growth) by site. Although the actual values are reported, mean separation was calculated on transformed data in order to meet the assumptions of the ANOVA. Means followed by different letters are significantly different ($\alpha = 0.05$; Tukey's HSD test).

Site	Mean ring-width (mm)	F	p
Georgia	2.71^{A}	127.38	<0.001
Massachusetts	1.73^{B}		
West Virginia	1.08^{C}		
North Carolina	1.08^{D}		
Virginia	0.81^{DE}		
Pennsylvania	0.57^{E}		

Table 6. Comparison of cell properties pre- and post-HWA arrival ($\alpha = 0.05$). LW stands for latewood and EW stands for earlywood.

Cell Properties	Pre-HWA Arrival	Post-HWA Arrival	t-value	p-value
Mean LW cell-wall thickness (μm)	5.51	4.65	6.87	<0.001
Mean LW radial cell diameter (μm)	15.90	14.82	3.33	0.001
Mean EW cell-wall thickness (μm)	2.24	2.34	-0.79	0.430
Mean EW radial cell diameter (μm)	50.36	51.17	1.48	0.141

The average live crown ratio was highest at Georgia and the lowest at Massachusetts (Table 6). The average crown density was greatest at Massachusetts and lowest at North Carolina. North Carolina also had the highest crown transparency and percent crown dieback, while Massachusetts had the lowest crown transparency and percent crown dieback. Multiple linear regression identified which crown variables were significant predictors of radial growth at each site (Table 7). Live crown ratio was a significant predictor in all models except Pennsylvania, while percent crown dieback was only identified as significant at North Carolina, Pennsylvania and Massachusetts. The competition index was also an important predictor of radial growth at 3 of the 6 sites. The regression models based on crown variables explained over 50% of the variance in radial growth at 5 of the 6 sites, but West Virginia (R^2=0.23) explained the least amount of variance.

Table 7. Average crown variable measurements by site (standard deviation in parenthesis).

Site	Live Crown Ratio	Crown Density	Crown Transparency	Percent Crown Dieback
Georgia	80 (13.87)	44 (9.86)	47 (9.42)	10 (5.58)
North Carolina	71 (20.08)	42 (14.07)	52 (14.98)	22 (15.60)
Virginia	70 (17.71)	49 (12.81)	41 (12.00)	15 (9.61)
West Virginia	70 (16.08)	44 (6.79)	43 (9.73)	13 (6.28)
Pennsylvania	57 (13.78)	52 (12.51)	40 (12.30)	15 (8.96)
Massachusetts	50 (12.95)	53 (10.67)	36 (12.58)	10 (4.98)

The relationship between monthly precipitation and radial growth differed among sites. Georgia showed only one significant relationship, a positive correlation between previous May precipitation and ring width (Figure 11a). Ring width at North Carolina was responsive to precipitation for more months (Figure 11b), having significant positive relationships with both previous and current June and July. Virginia ring width showed positive relationships with previous June and current March precipitation (Figure 11c), while West Virginia RWI responded to the precipitation of the previous May, June and July (Figure 11d). The northernmost sites, Pennsylvania and Massachusetts, were the only sites with significant negative relationships between growth and precipitation. Pennsylvania showed a negative relationship with the precipitation of the previous April and current February (Figure 11e), while Massachusetts showed a negative relationship with the previous April, current February, and current July (Figure 11f).

Table 8. Multiple linear regression models of crown variables and competition index on last 4-years of radial growth.

	Georgia	North Carolina	Virginia	West Virginia	Pennsylvania	Massachusetts
Intercept	-2.56	2.03	-0.33	0.11	1.33	3.14*
LCR	-0.03*	0.02	0.01*	0.01*	–	0.02
Crown Density	0.08*	–	–	–	–	–
Crown Transparency	0.08*	-0.02	–	–	-0.01	-0.05*
Percent Dieback	–	-0.03	–	–	-0.01	-0.07*
CI	0.44*	-0.87*	0.57*	–	–	–
N	21	20	21	20	20	21
R^2	0.53	0.64	0.65	0.23	0.54	0.60

* - Significant at $\alpha = 0.05$

– Indicates the variable was rejected from the model using stepwise variable selection

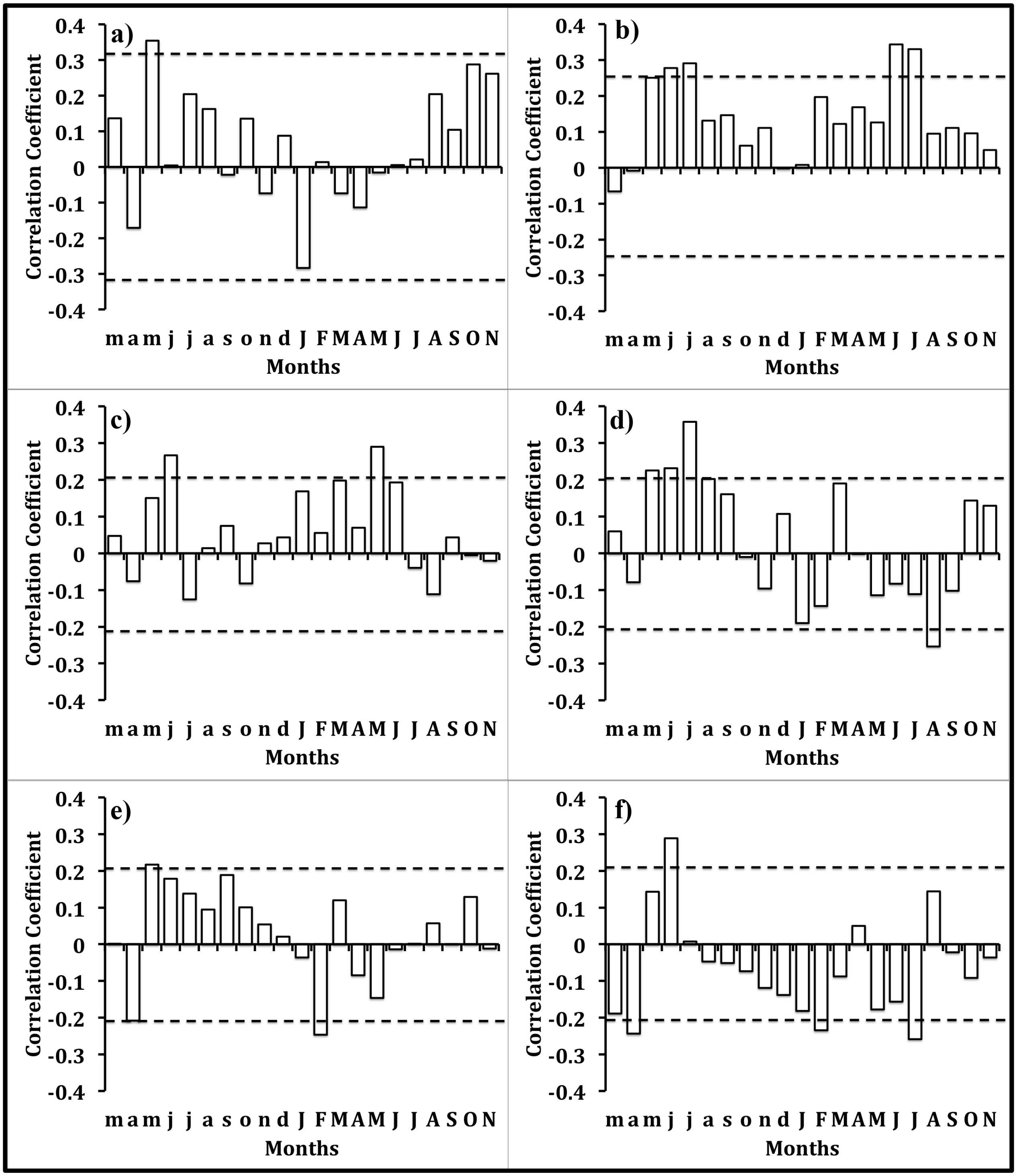

Figure 11. Correlation coefficients between the ring width indices (RWI) and precipitation for a) Georgia, b) North Carolina, c) Virginia, d) West Virginia, e) Pennsylvania, and f) Massachusetts. Lower-case letters indicate previous year. Dashed line indicates significant cutoffs (α = 0.05).

Georgia showed significant negative relationships between radial growth and previous July and September temperature, as well as current January (Figure 12a). North Carolina RWI had negative correlations with the previous and current July temperature, but was positively correlated with the current November temperature (Figure 12b). Radial growth at the Virginia site was negatively correlated to the previous June's temperature but was positively correlated with current January temperature (Figure 12c). West Virginia RWI showed negative correlations with the previous July, August and September temperature, and the current August's (Figure 12d). Pennsylvania RWI was negatively correlated with the previous September temperature and positively correlated with the current February and March temperature (Figure 12e). Radial growth at Massachusetts was negatively correlated with the previous August temperature and positively correlated with the previous November and current October temperature (Figure 12f).

At the Georgia site, RWI only had one significant correlation with the Palmer Drought Severity Index (PDSI) and that was in the current October (Figure 13a). North Carolina, however, had many significant relationships between RWI and PDSI. All months except for the previous April were significantly, positively correlated to RWI. The current June (r=0.54) and July PDSI (r=0.53) had the strongest correlation to radial growth of any monthly climate variable (Figure 13b). Virginia RWI was positively correlated with the previous May, June, and current January PDSI, but negatively correlated with the current April and August PDSI (Figure 13c). Both West Virginia (Figure 13d) and Pennsylvania (Figure 13e) showed significant correlations with the previous year's growing season PDSI and RWI. The Massachusetts site (Figure 13f) showed a negative correaltion between RWI and PDSI of the previous March and April, as well as the current year's spring and summer.

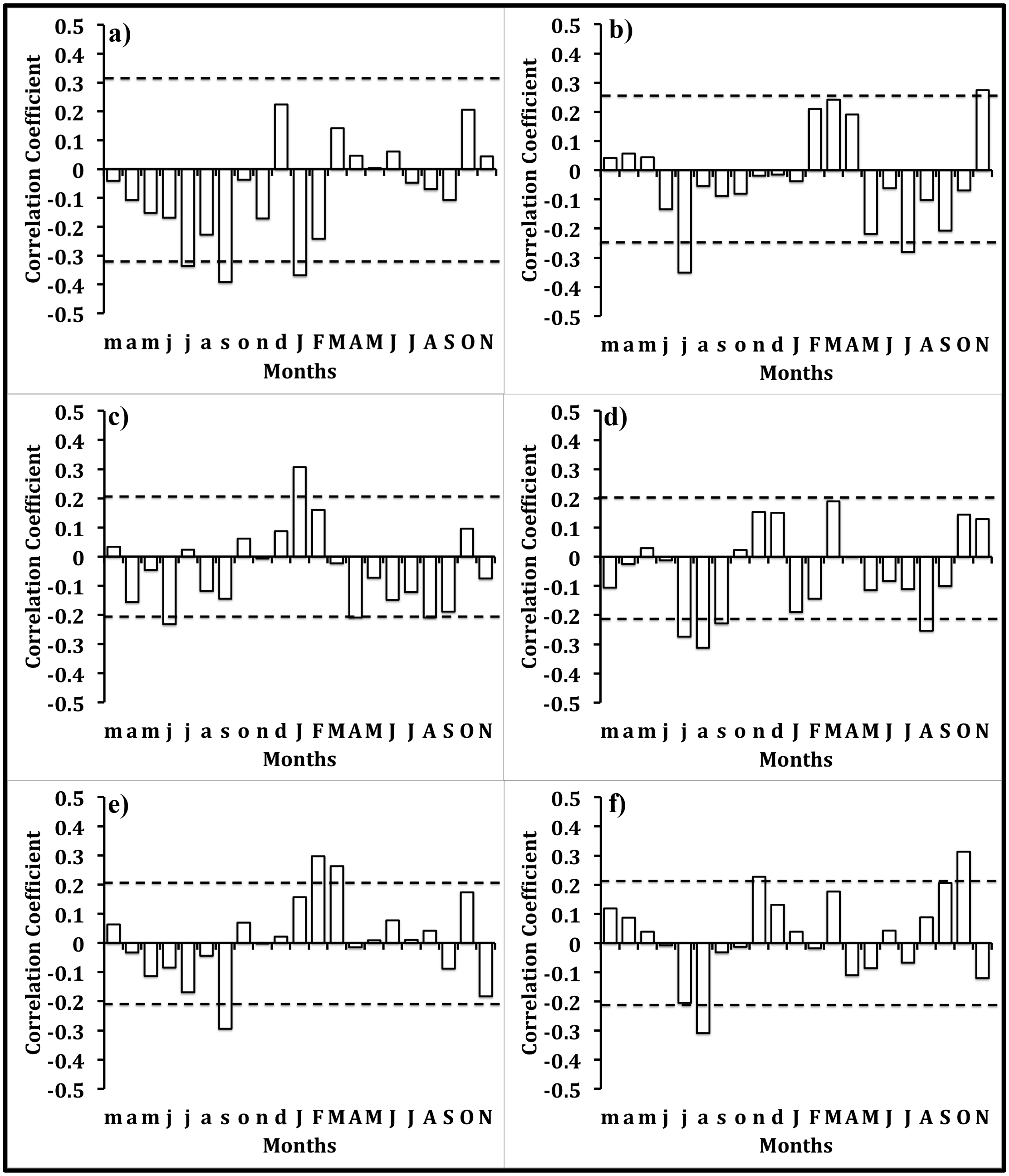

Figure 12. Correlation coefficients between the ring width indices (RWI) and temperature for a) Georgia, b) North Carolina, c) Virginia, d) West Virginia, e) Pennsylvania, and f) Massachusetts. Lower-case letters indicate previous year. Dashed line indicates significant cutoffs (α = 0.05).

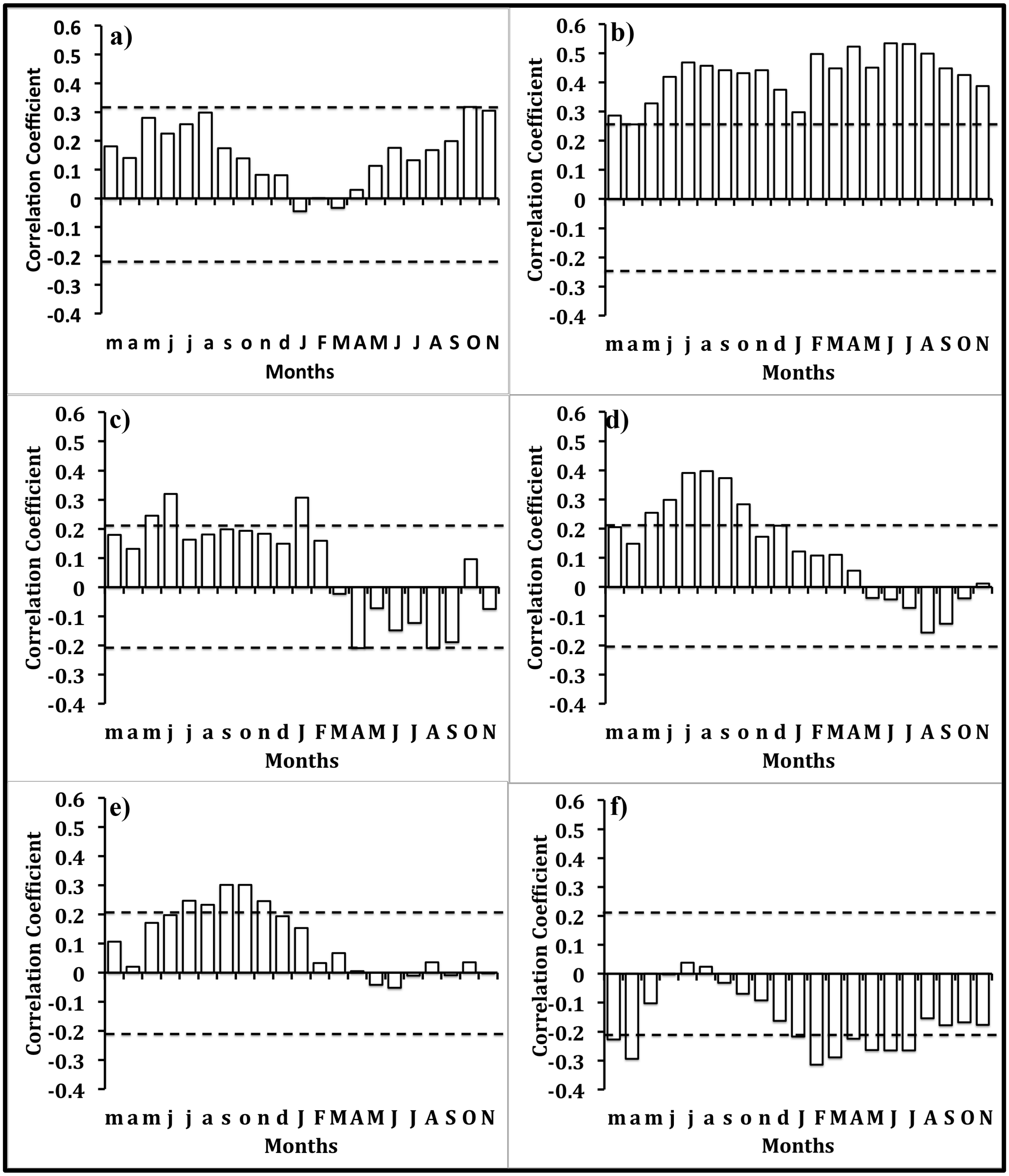

Figure 13. Correlation coefficients between the ring width indices (RWI) and the Palmer Drought Severity Index (PDSI) for a) Georgia, b) North Carolina, c) Virginia, d) West Virginia, e) Pennsylvania, and f) Massachusetts. Lower-case letters indicate previous year. Dashed line indicates significant cutoffs ($\alpha = 0.05$).

The average soil depth ranged from 20 cm at Pennsylvania to 110 cm at North Carolina (Table 8). Soil texture class was consistent within a site, with all samples falling in adjacent texture classes within the soil textural triangle (Table 8). Loamy sands have the smallest fraction of silt and clay particles, which are primarily responsible for a soil's water holding capacity, while sandy clay loam and clay loam have higher proportions of these particles.

Table 9. Mean soil depth and soil texture class by site

Site	Mean soil depth (cm)	Soil Texture Class
Georgia	36	Sandy Clay Loam/Clay Loam
North Carolina	110	Sandy Loam/Sandy Clay Loam
Virginia	20	Sandy Clay Loam*
West Virginia	99	Sandy clay loam/Clay loam
Pennsylvania	24	Loam/Organic
Massachusetts	49	Loamy sand/Sandy loam

* - Large fraction of stones and other large rocks

V. Discussion

In eastern hemlock, radial growth is reduced following infestation by hemlock woolly adelgid (Figure 3; Orwig 2002; Rentch et al. 2009). The reduction in growth can be attributed to the adelgid’s feeding habits. Hemlock woolly adelgid feeds by attaching to the base of hemlock needles and inserting its stylet bundle (Young et al. 1995). The stylet bundle then penetrates through the tree’s tissue until it reaches the xylem ray parenchyma in the twigs. Carbohydrates produced during photosynthesis and used for growth are stored in parenchyma cells (Pallardy 2008). As HWA feeds, it removes a substantial amount of the stored sugars, limiting the tree’s ability to grow. Winter feeding by HWA on stored carbohydrates is particularly harmful because eastern hemlock is not actively photosynthesizing (Figure 1). HWA’s salivary compounds may be toxic to eastern hemlocks and are thought to cause rapid cell death in response to adelgid feeding (Radville et al. 2011; Young et al. 1995). The removal of the stored carbohydrates coupled with a hypersensitive response that causes premature needle drop could explain the reduction in radial growth.

Hemlock woolly adelgid also causes significant needle drop and subsequent reduction in photosynthetic rate, with infested trees frequently losing over 50% of their foliage (Orwig et al. 2002). All sites in this study showed reduced crown volume and density with North Carolina, Virginia, and Pennsylvania having the highest percent crown dieback and significantly reduced radial growth post-HWA arrival (Table 6). This could indicate that the trees growing here are more sensitive to the effects of HWA feeding or that HWA had higher population densities at these sites. These 3 sites have the highest average winter temperature relative to the other study sites (Table 1) and because prolonged, cold temperatures cause significant mortality of HWA (Parker et al. 1998, 1999), it is possible that adelgid population density is higher. Additionally, adelgids found in warmer areas have been shown to be physiologically active earlier in the growing season compared to those found in colder climates (Joseph et al. 2011b), allowing them to feed and cause more damage to host trees. Although Georgia had the highest average temperature, HWA has been present for the fewest number of years and it is possible that cumulative effect of HWA feeding has not manifested yet. Matching this idea, the mean ring-width for 2011 (2.4 mm) was smaller than the overall average (2.97 mm) and will probably continue to decrease.

The Massachusetts site was unique in that it showed a significant increase in growth post-HWA arrival. Although this seems counter-intuitive, this site had substantial overstory mortality and many trees were removed in sanitation cuts (Steven Ward, Watershed Forester, Massachusetts Department of Conservation and Recreation, personal communication). The death or removal of a neighboring tree frequently results in a growth release that is shown by an increase in tree-ring width (Nowacki and Abrams 1997). The surviving hemlock trees were able to benefit from the death of their more susceptible neighbors. Similarly, Davis et al. (2007) noted that the radial growth of severely infested hemlocks rapidly increased post-HWA arrival before abruptly decreasing. They also attributed this to the death of competing hemlocks. Orwig (2002) found similar growth releases in oaks and maples growing in stands with high hemlock mortality. Growth releases due to mortality of competing trees have also been observed in stands heavily impacted by gypsy moth (*Lymantria dispar* L.) and in forests with spruce bark beetle outbreaks (Fajvan and Wood 1996; Veblen et al. 1991).

Older trees are more sensitive to HWA induced decline, with tree age being negatively correlated with the last 4 years of radial growth ($r=-0.32$, $p<0.001$). Rentch et al. (2009) also found that older trees were more susceptible to decline. In general, photosynthesis is reduced with tree age (Bond 2000). Although the exact mechanisms behind this can vary, the increased hydraulic resistance often found in older trees has been cited as a causal mechanism. This increased hydraulic resistance is due to gravity and an increased hydraulic path through the stem (Bond 2000). Given this reduced water use-efficiency, radial growth in older trees is more sensitive to drought stress (Copenheaver et al. 2011). Therefore, trees growing on drought-sensitive sites would be more susceptible to an additional stressor, such as insect attack. If this is the case then drought-sensitive sites should show a stronger correlation between tree age and reduced growth. North Carolina, which had the highest correlation between radial growth and growing season drought conditions (Figure 13b), also had the strongest correlation between tree age and the last 4-years of radial growth ($r=-0.76$, $p<0.001$).

In addition to affecting tree physiology, water stress can affect insect performance. When trees are stressed, piercing-sucking insects, such as HWA, tend to cause more damage than when feeding on non-stressed trees (Huberty and Denno 2004; Jactel et al. 2012). Davis et al. (2007) found that slower growing hemlocks became more severely infested than did faster growing ones. These slower growing trees were thought to be growing on drier micro-sites within the stand indicating that trees already stressed due to low water availability may be more susceptible to HWA infestation. Higher hemlock mortality rates have been observed on xeric sites compared to less dry stands (Orwig et al. 2002) and sites with a deeper depth to bedrock or finer-textured soils had a higher proportion of healthy hemlocks compared to shallow or coarse textured soils (Bonneau et al. 1999). The Virginia and Pennsylvania sites from our study had the shallowest soils (Table 8) as well as a significant decrease in radial growth, supporting the idea that water availability affects hemlock susceptibility to HWA.

In addition to affecting radial growth, HWA infestation may change wood anatomical structure. The secondary cell wall is formed from microfibrils, which are primarily composed of cellulose and hemicellulose, both of which are polymers of glucose and other sugars, which are the primary food source of HWA (Pallardy 2008; Panshin and de Zeeuw 1980). As latewood tracheid size and cell-wall thickness of wood produced post-HWA arrival were found to be significantly smaller compared to tracheids produced pre-HWA arrival (Table 5), it is possible that HWA feeding reduces the amount of cellulose available for wood formation. Similarly, a study investigating the effects of larch sawfly on eastern larch found that following defoliation, the mean latewood tracheid size was reduced and that a light ring with thinner than normal cell walls was formed (Filion and Cournoyer 1995).

Visual Crown Rating Methods were developed by the US Forest Service and are used to assess and monitor the health of trees (Mangold 1998). Crown conditions have been used to monitor tree growth (Renaud and Mauffette 1991) as well as health and mortality (Dobbertin 2005). The average live-crown ratio and crown density of the trees used in this study were similar to ratings obtained from healthy hemlocks (Montgomery et al. 2006), but the average crown transparency and percent crown dieback were higher (Table 6). Similarly, Montgomery et al. (2006) found little change in live crown ratio (4% lower), crown density (3% higher), and percent crown dieback (4% lower) after HWA arrival, but saw that crown transparency was 86% higher after the arrival of HWA. Although they are related, the large difference in the change in density and transparency his could be due to a ‘time-lag,’ where transparency changes more rapidly than density following HWA arrival. Crown transparency has been shown to be a good predictor of future tree mortality (Dobbertin and Brang 2001). This could indicate that a high crown transparency is the best indicator of HWA infestation because it is an estimation of the amount of foliage lost.

The use of crown variables to predict radial growth was dependent on site (Table 7). No two models used all the same variables and no variable was used in all models. This could be explained by differences in site characteristics, stand age, and climate. Site location and aspect have been shown to affect predictors of HWA induced decline, with signs of decline varying based on location (Rentch et al. 2009). The West Virginia model was the weakest predictor of radial growth, with only LCR being included, which explained 23% of the variation. This weak relationship could be explained as foliage tends to decline with age and older trees tend to have smaller and thinner crowns (Dobbertin 2005; Pederson 2010). Therefore, the thin crown found at West Virginia could be an artifact of tree age (241 years) and not indicative of HWA induced decline.

Live crown ratio appeared in 5 of the 6 models, more than any other variable. As eastern hemlock is the most shade-tolerant tree species in North America, it often maintains live branches much lower along its bole compared to other trees (Godman and Lancaster 1990). Therefore, a tree with a higher LCR would have a better chance of producing new shoots to offset the effects of HWA feeding. Crown density, was only included in the Georgia model. Eschtruth et al. (2006) found that crown density was a moderate indicator of HWA infestation, with a significant decrease in crown density after the arrival of HWA at half of their sites. Based on these findings, crown density may not be a good indicator of HWA infestation or radial growth.

Eastern hemlock is very shade tolerant, but it has been shown to be sensitive to competition (Woods 2000). Increased competitive stress was associated with a decrease in radial growth at North Carolina, but coincided with increases in growth at Georgia and Virginia (Table 7). This positive reaction to competition could be a reflection of the spatial distribution of HWA. Trees with high populations of HWA tend to have a greater proportion of adelgids in the lower crown compared to the upper crown (Evans and Gregoire 2007b). This was explained as a lack of insulation against high temperature, because during the summer adelgids in the upper crown were more prone to desiccation. Therefore, as trees with higher competitive stress tend to have fewer low branches and concentrate their foliage in the upper crown, HWA may be forced from the preferred feeding sites in the lower bole into the upper crown.

All sites had significant positive correlations between radial growth and the previous year's growing season precipitation (Figure 11). This agrees with other dendroclimatic studies of this species (Abrams et al. 2000; Tardif et al. 2001). Photosynthetic rates in eastern hemlock are associated with available moisture (Adams and Loucks 1971) and the previous year's climate is particularly important for hemlocks because they retain their needles for multiple years. The amount of foliage produced one year, therefore affects the growth of the next year. The current year's growing season precipitation was also significantly related to radial growth at the North Carolina and Virginia sites (Figure 11b,c). This is similar to the findings of Hart et al. (2010), who found that eastern hemlocks growing at the southern edge of its range responded to current May precipitation and is probably related to the amount of moisture available for photosynthesis.

Pennsylvania and Massachusetts showed negative correlations between RWI and current February precipitation (Figure 11e,f). This agrees with dendroclimatic studies conducted in Pennsylvania and southern Ontario (Black and Abrams 2005; Tardif et al. 2001). This negative correlation can be attributed to damaging snow or ice storms. Average February temperatures for both Pennsylvania and Massachusetts are below freezing and the majority of precipitation would be snow or ice. Since hemlock keeps its needles for multiple years, needle and branch loss due to ice and snow damage would reduce photosynthesis.

Radial growth at all sites showed negative correlations between the previous year's growing season temperature (Figure 12). Previous studies have also shown negative relationships between the previous year's growing season temperature and the radial growth of eastern hemlocks in the southern portion of its range (Cook and Cole 1991; Hart et al. 2010). This could be due to decreased available moisture levels, as well as the direct effect high temperature has on photosynthesis. The average temperatures for these months were between 20.2 and 25.8° C which are above the optimum temperature for photosynthesis (Adams and Loucks 1971). When temperatures exceed this level, hemlock tends to reduce photosynthesis in order to minimize losses due to evapotranspiration. North Carolina, Virginia, West Virginia, and Massachusetts all showed a negative correlation with the current year's growing season temperature (Figure 12b,c,d,f). This is again most likely related to exceeding the optimum photosynthesis temperature.

Pennsylvania showed a positive correlation between RWI and current March temperature (Figure 12e). This could be due to soil thawing, which would allow hemlock to begin growing. The initiation of growth in eastern hemlock has been shown to be controlled by late winter and early spring temperature, which causes the soil temperature to increase to a level where photosynthesis can begin (Fraser 1956). Similar to our study, Tardif et al. (2001) showed that hemlock growing at the northern edge of the range responded positively to March temperature. They attributed this to increased snowmelt, which would lead to more available moisture for growth. However, their study site was located approximately 600 km north of the Pennsylvania site and receives more snow (165 cm/year vs 85 cm/year, NOAA 2012).

North Carolina, Virginia, West Virginia, and Pennsylvania all had positive correlations between radial growth and previous growing season PDSI (Figure 13b,c,d,e). Eastern hemlock has been shown to be sensitive to growing-season drought stress, particularly trees located at the southern edge of its range (Hart et al. 2010; Kessel 1979). Although Pennsylvania is more centrally located in the range of hemlock compared to North Carolina, Virginia, and West Virginia, the shallow soil found at Pennsylvania (Table 8) could explain its sensitivity to drought. The current year's October PDSI was also correlated with radial growth at Georgia (Figure 13a). Although this is near the end of the growing season, eastern hemlock is still physiologically active during this time (Skene 1971).

Radial growth at North Carolina was significantly, positively correlated to monthly PDSI for every month used in this study (Figure 13b). This can partially be explained by the high degree of autocorrelation that is built into the index because values from previous months are used to calculate the current month's value (Alley 1984). Other studies conducted in the southeastern US have noted similar strong correlations between radial growth and PDSI for multiple successive months (Hart et al. 2010; Speer et al. 2009). However, because prior studies have shown that hemlocks growing in the southern part of their range belong to an ecotype that is sensitive to moisture stress (Kessel 1979), our results should not be discounted.

Massachusetts had significant negative relationships between radial growth and PDSI in the late winter and current growing season (Figure 13f). This could be attributed to soil saturation which negatively impacts tree growth, especially as eastern hemlock prefers well-drained soils (Godman and Lancaster 1990). The Massachusetts site was located in a low-lying area with creeks and signs of periodic flooding. Floods during the growing season can restrict gas-exchange between roots and soil macropores as air is replaced with water (Brady and Weil

2001). Flooding tends to stop photosynthesis and it does not immediately resume once the flooding subsides (Pallardy 2008). Therefore, prolonged soil saturation could reduce the radial growth of trees growing in riparian zones. Abrams et al. (2000) found a similar negative relationship between growth and PDSI for eastern hemlock growing in Massachusetts

The correlation between eastern hemlock radial growth and climate varies with latitude and site, with trees growing further south or on shallow soils being more sensitive to moisture levels. This sensitivity to drought can also partially explain the variation in hemlock response to adelgid feeding, as trees affected by moisture stress tend to be more sensitive to piercing-sucking insect attack (Jactel et al. 2012). The 3 sites with significantly reduced growth post-HWA arrival were all sensitive to drought conditions (Figure 13 b,c,e). Plant stress also affects insect performance, with piercing-sucking insects having higher growth rates, fecundity and survival on stressed plants compared to healthy ones (Koricheva et al. 1998). This also explains why HWA is more destructive and has spread faster in the southern part of hemlock's range (Evans and Gregoire 2007a).

VI. Summary and Conclusion

The radial growth response of eastern hemlocks to infestation by hemlock woolly adelgid was highly variable. Although every site had some trees that showed significant growth suppression after HWA arrival only three sites had a stand-level reduction. HWA-induced decline did not seem to be related to latitude, soil depth and texture, or duration of infestation but was associated with individual tree age, with older trees having greater reductions in growth. Visual crown rating variables were inconsistent predictors of decline, as was the competition index. No variable was significant at every site and variables were often positively associated with decline at one site and negatively associated at another. The three sites with significant reductions did have the highest percent crown dieback. Latewood tracheids produced post-HWA arrival had significantly reduced cell-wall thickness and radial cell diameter compared to tracheids produced before HWA arrival. There was no change in earlywood cell-wall thickness or radial cell diameter post-HWA arrival.

Radial growth at all sites had a positive correlation with precipitation during the previous year's growing season and a negative correlation with the previous year's growing season temperature. The two northernmost sites had a negative correlation between ring width and winter precipitation and a positive correlation with winter temperature. There were no overall patterns in correlation between radial growth and PDSI. However, the three sites with significantly reduced growth post-HWA arrival all had significant positive correlations between ring width and PDSI.

There are many factors that affect eastern hemlock's response to infestation by hemlock woolly adelgid and the large amount of variation between sites made isolating these factors difficult. The sites used in this study had different average temperatures, precipitation amounts, elevation, average tree age, stand history, overstory species composition, soil depth and texture, and duration of HWA infestation. Additionally, any differences in hemlock woolly adelgid population density between sites could not be quantified. Records of population densities were simply not available. This highlights one of the difficulties with observational studies: that a researcher cannot control or account for every factor that may influence his or her findings. The interactions between HWA, eastern hemlock and the environment are myriad. The results of this study serve to both better understand these interactions and to underline the difficulties that exist in studying hemlock woolly adelgid.

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Appendix A. Competition index

Table A1. Distance to nearest tree from selected eastern hemlock, tree species and diameter for Georgia.

Eastern hemlock number	Eastern hemlock Diameter (cm)	Closest Species	Distance (m)	DBH of tree (cm)
1	25.7	*Quercus rubra*	2.7	48.7
2	56.1	*Tsuga canadensis*	0.8	18.5
3	48.5	*Acer rubrum*	3.1	11
4	37.4	*Liriodendron tulipifera*	2.8	50.9
5	38.4	*Tsuga canadensis*	0.6	17
6	26.5	*Quercus prinus*	1.9	15.8
7	24.5	*Liriodendron tulipifera*	0.9	41
8	29	*Tsuga canadensis*	3.3	15.1
9	22	*Pinus strobus*	2.3	25.1
10	29.5	*Tsuga canadensis*	1.1	18.7
11	16.8	*Quercus rubra*	2.8	42.3
12	18.5	*Acer rubrum*	0.8	53.3
13	35.2	*Quercus prinus*	3.1	29.4
14	28.7	*Quercus prinus*	3.1	29.4
15	25	*Quercus rubra*	1.4	21.4
16	33.4	*Acer rubrum*	3	37.7
17	36.5	*Sassafras albidum*	2.8	14.7
18	29.8	*Nyssa sylvatica*	2.1	17.1
19	50	*Liriodendron tulipifera*	3.4	23.8
20	28	*Quercus rubra*	4.5	40
21	35	*Tsuga canadensis*	4.9	46.4
22	46.4	*Tsuga canadensis*	4.9	35
23	34.7	*Liriodendron tulipifera*	3.9	31.8

Table A2. Distance to nearest tree from selected eastern hemlock, tree species and diameter for North Carolina.

Eastern hemlock number	Eastern hemlock Diameter (cm)	Closest Species	Distance (m)	DBH of tree (cm)
1	22.7	*Tsuga canadensis*	3.1	20.9
2	16.8	*Tsuga canadensis*	1.8	25.2
3	42.4	*Fagus americana*	1.9	48.6
4	30.5	*Tsuga canadensis*	1.5	26.4
5	26.4	*Tsuga canadensis*	1.5	30.5
6	21.2	*Nyssa sylvatica*	1.3	31.1
7	31.8	*Tsuga canadensis*	1.7	11.1
8	14.7	*Acer rubrum*	2.0	14.0
9	24.8	*Liriodendron tulipifera*	2.8	49.2
10	8.4	*Liriodendron tulipifera*	1.9	34.5
11	20.1	*Acer rubrum*	2.9	43.3
12	24.0	*Carpinus caroliniana*	2.3	11.1
13	27.7	*Platanus occidentalis*	2.5	35.2
14	20.8	*Acer rubrum*	2.2	13.8
15	32.6	*Betula lenta*	2.6	12.6
16	16.8	*Rhododendron maximum*	1.8	11.5
17	30.1	*Tsuga canadensis*	1.2	31.1
18	31.1	*Tsuga canadensis*	1.2	30.1
19	17.0	*Fagus americana*	0.8	10.4
20	15.7	*Tsuga canadensis*	0.6	15.5
21	19.8	*Fagus americana*	2.7	22.0
22	35.9	*Tsuga canadensis*	1.2	41.2
23	13.2	*Quercus falcata*	1.6	40.0

Table A3. Distance to nearest tree from selected eastern hemlock, tree species and diameter for Virginia.

Eastern hemlock number	Eastern hemlock Diameter (cm)	Closest Species	Distance (m)	DBH of tree (cm)
1	48.6	*Tsuga canadensis*	0.8	20.3
2	49.6	*Tsuga canadensis*	4.45	20.6
3	64.9	*Tsuga canadensis*	3.6	31.8
4	37.0	*Fraxiuns americana*	2.7	15.7
5	28.9	*Betula lenta*	2.7	11.2
6	31.7	*Acer rubrum*	2.05	11.2
7	19.7	*Tsuga canadensis*	1.5	34.8
8	49.1	*Quercus prinus*	1.2	42.4
9	29.9	*Quercus prinus*	1.95	31.8
10	52.5	*Acer rubrum*	4.8	49.8
11	42.3	*Carpinus caroliniana*	2.1	14.7
12	33.0	*Tsuga canadensis*	1.25	24.3
13	24.3	*Tsuga canadensis*	1.25	33.0
14	25.0	*Tsuga canadensis*	2.55	21.5
15	27.7	*Acer rubrum*	1.55	10.9
16	21.5	*Tsuga canadensis*	1.7	20.3
17	16.5	*Tsuga canadensis*	2.8	23.7
18	23.7	*Tsuga canadensis*	2.8	16.5
19	39.0	*Quercus rubra*	4.2	36.3
20	29.5	*Tsuga canadensis*	1.3	17.0
21	56.3	*Tsuga canadensis*	1.25	29.7
22	16.9	*Pinus virginiana*	3.15	16.8
23	25.0	*Quercus prinus*	2	10.4

Table A4. Distance to nearest tree from selected eastern hemlock, tree species and diameter for West Virginia.

Eastern hemlock umber	Eastern hemlock Diameter (cm)	Closest Species	Distance (m)	DBH of tree (cm)
1	43.3	*Betula alleghaniensis*	1.7	15.1
2	74.1	*Betula alleghaniensis*	3.3	19.6
3	54.9	*Picea rubens*	1.3	42.2
4	50.8	*Prunus serotina*	2.9	24.1
5	53.3	*Tsuga canadensis*	1.2	22.3
6	46.2	*Tsuga canadensis*	1	43.2
7	60.8	*Betula alleghaniensis*	4	22.5
8	47.7	*Betula alleghaniensis*	2.4	14.9
9	56.5	*Tsuga canadensis*	0.5	26.9
10	79	*Picea rubens*	4.1	21.9
11	71.9	*Acer rubrum*	2.7	40.2
12	46	*Tsuga canadensis*	1.1	19.3
13	70.5	*Prunus serotina*	2.1	25.3
14	31.7	*Betula alleghaniensis*	1.2	26.8
15	65.7	*Tsuga canadensis*	3.7	22.5
16	58.3	*Picea rubens*	2.8	46
17	62.4	*Prunus serotina*	2.4	19
18	64.9	*Betula alleghaniensis*	3.6	20.8
19	47.1	*Picea rubens*	2.5	31.1
20	24.5	*Tsuga canadensis*	4.2	25.2
21	25.2	*Tsuga canadensis*	4.2	24.5
22	24.4	*Tsuga canadensis*	1.7	12.8
23	37	*Tsuga canadensis*	1.2	17.6

Table A5. Distance to nearest tree from selected eastern hemlock, tree species and diameter for Pennsylvania.

Eastern hemlock number	Eastern hemlock Diameter (cm)	Closest Species	Distance (m)	DBH of tree (cm)
1	31.6	*Betula alleghaniensis*	2.5	21.1
2	42.7	*Tsuga canadensis*	3.75	26.8
3	32.8	*Betula alleghaniensis*	1	11.1
4	31.9	*Tsuga canadensis*	1.05	9.5
5	49.7	*Liriodendron tulipifera*	2.5	46.3
6	42	*Liriodendron tulipifera*	2.6	46.3
7	38.5	*Tsuga canadensis*	2.35	27.5
8	57	*Tsuga canadensis*	2.4	56.5
9	50	*Betula alleghaniensis*	2.8	21.6
10	41.7	*Acer rubrum*	2.35	30.3
11	27.9	*Betula lenta*	2.65	28
12	40.4	*Tsuga canadensis*	1.6	19.9
13	23	*Tsuga canadensis*	2.4	19.8
14	26.9	*Tsuga canadensis*	2.7	19.4
15	35.4	*Tsuga canadensis*	1.05	33.4
16	27.1	*Tsuga canadensis*	1.1	12.6
17	34.2	*Betula alleghaniensis*	1.2	21.3
18	48.2	*Betula lenta*	2.6	22.2
19	38.2	*Acer rubrum*	2.1	21.1
20	27.4	*Tsuga canadensis*	3.2	29.8
21	40.9	*Acer rubrum*	1.7	29.8
22	37.2	*Tsuga canadensis*	0.85	24.7
23	31.2	*Tsuga canadensis*	0.75	9.9

Table A6. Distance to nearest tree from selected eastern hemlock, tree species and diameter for Massachusetts.

Eastern hemlock number	Eastern hemlock Diameter (cm)	Closest Species	Distance (m)	DBH of tree (cm)
1	56.6	*Betula lenta*	1.2	24.3
2	50.8	*Quercus rubra*	1.8	29.3
3	31.3	*Tsuga canadensis*	2.4	18.6
4	69.7	*Tsuga canadensis*	4.5	32.5
5	43.5	*Tsuga canadensis*	1.2	22.6
6	36.3	*Tsuga canadensis*	1.2	14.6
7	32.8	*Tsuga canadensis*	1.5	13.8
8	37.2	*Tsuga canadensis*	1.9	32.8
9	40.2	*Tsuga canadensis*	1.5	13.6
10	55.8	*Tsuga canadensis*	0.7	11.4
11	45.5	*Tsuga canadensis*	3.1	14.8
12	56.7	*Tsuga canadensis*	2	43.1
13	44.4	*Tsuga canadensis*	2	48.9
14	68.9	*Tsuga canadensis*	4.5	18.8
15	48.8	*Tsuga canadensis*	1.6	53.3
16	47.8	*Tsuga canadensis*	3.9	23.7
17	34.9	*Acer rubrum*	4.4	18.4
18	40.8	*Tsuga canadensis*	4.2	37.2
19	23.7	*Tsuga canadensis*	1.4	36.9
20	27.2	*Tsuga canadensis*	1.7	49
21	49	*Tsuga canadensis*	1.7	27.2
22	43.1	*Betula nigra*	2.7	14.9
23	31.4	*Betula lenta*	2.3	29.5

Appendix B. Visual crown rating measurements by site

Table B1. Visual crown rating measurements for Georgia

Georgia				
Tree Number	LCR	Crown Density	Crown Transparency	Percent Dieback
1	92	40	45	10
2	94	55	45	10
3	96	35	65	15
4	84	50	45	15
5	82	45	30	5
6	82	45	40	10
7	88	40	50	15
9	84	55	45	10
10	73	65	40	5
12	87	35	55	10
13	85	35	60	15
14	81	35	45	5
15	85	30	60	5
16	83	50	45	5
17	81	35	60	10
18	39	40	45	5
19	70	55	30	5
20	94	35	50	20
21	49	35	45	10
22	74	45	50	25
23	76	60	35	5
Mean	80	44	47	10
STDV	13.87	9.86	9.42	5.58

Table B2. Visual crown rating measurements for North Carolina

Tree Number	LCR	Crown Density	Crown Transparency	Percent Dieback
1	85	30	50	15
2	95	35	60	5
3	55	20	40	50
4	30	50	50	20
6	85	35	75	20
7	40	50	55	10
9	75	45	50	10
11	70	50	35	40
12	95	60	35	5
13	90	60	30	5
14	90	40	65	10
15	90	60	60	20
16	55	30	75	25
17	50	65	25	15
18	60	45	50	40
19	70	35	55	10
20	75	45	50	15
21	65	10	80	55
22	45	50	55	40
23	95	50	40	35
Mean	71	43	52	22
STDV	20.08	14.07	14.98	15.60

Table B3. Visual crown rating measurements for Virginia

Tree Number	LCR	Crown Density	Crown Transparency	Percent Dieback
1	90	80	20	5
2	50	40	55	10
3	55	40	30	5
4	40	45	55	5
5	60	45	50	10
6	80	35	65	30
8	50	55	45	10
9	55	30	55	25
10	50	50	50	10
11	90	75	20	5
12	60	35	50	25
13	80	30	45	30
14	95	55	35	10
16	95	55	30	10
17	75	55	35	10
18	80	45	45	20
19	90	50	35	30
20	60	45	35	25
21	55	55	30	30
22	90	50	35	10
23	75	60	40	10
Mean	70	49	41	15
STDV	17.71	12.81	12.00	9.61

Table B4. Visual crown rating measurements for West Virginia

Tree Number	LCR	Crown Density	Crown Transparency	Percent Dieback
1	90	40	45	30
2	82	40	45	10
3	78	55	35	10
5	79	35	60	5
6	61	45	50	5
7	83	45	40	10
8	52	35	65	10
10	74	45	35	5
11	92	55	30	15
12	73	50	45	15
13	74	50	35	10
15	79	55	35	15
16	74	45	35	20
17	74	40	40	15
18	80	40	35	10
19	38	35	55	20
21	49	45	45	15
22	40	35	55	20
23	53	45	40	10
Mean	70	44	43	13
STDV	16.08	6.79	9.73	6.28

Table B5. Visual crown rating measurements for Pennsylvania

Tree Number	LCR	Crown Density	Crown Transparency	Percent Dieback
1	39	45	45	10
2	46	50	45	5
3	46	70	25	5
4	56	40	45	20
5	81	75	15	5
6	42	40	60	35
7	39	35	50	15
8	71	45	40	15
9	83	60	35	15
12	43	55	35	10
14	47	55	35	5
15	51	55	40	30
16	71	30	65	10
17	56	60	30	25
18	56	65	40	15
19	63	50	55	20
20	50	65	30	10
21	55	65	25	10
22	73	50	40	30
23	70	35	50	15
Mean	57	52	40	15
STDV	13.78	12.51	12.30	8.96

Table B6. Visual crown rating measurements for Massachusetts

Tree Number	LCR	Crown Density	Crown Transparency	Percent Dieback
1	53	35	60	5
2	58	50	40	5
3	57	55	40	10
4	75	60	25	15
5	59	60	25	15
6	46	70	15	20
7	17	55	30	5
8	73	45	35	15
9	57	50	35	10
10	65	75	15	5
11	52	60	25	5
12	49	40	45	15
13	49	60	25	20
14	51	30	65	10
15	54	55	35	5
16	38	50	45	15
17	41	45	40	5
18	37	55	40	10
21	45	55	35	10
22	38	60	30	10
23	44	45	45	10
Mean	50	53	36	10
STDV	12.95	10.67	12.58	4.98

Appendix C. COFECHA output showing correlations of 50-year dated segments.

Table C1. COFECHA output showing correlations of 50-year dated segments, lagged 25 years for Georgia. A = correlation under .3281 but highest as dated; B = correlation higher at other than dated position.

Series	Time Span	1925-1974	1950-1999	1975-2024
GA01A	1967 2011		.30A	
GA01B	1966 2011		.57	
GA02B	1980 2011			.57
GA02D	1963 2011		.55	
GA03A	1948 2011	.48	.58	.38
GA04A	1949 2011	.35	.34	.20B
GA04D	1947 2011	.38	.42	.32A
GA05A	1960 2011		.45	.43
GA05B	1968 2011		.20B	
GA06A	1970 2011		.34	
GA06B	1965 2011		.46	
GA07A	1969 2011		.47	
GA07B	1971 2011		.55	
GA09A	1960 2011		.39	.39
GA09B	1960 2011		.46	.56
GA10A	1962 2011		.36	
GA10B	1958 2011		.59	.57
GA12A	1960 2011		.43	.46
GA12B	1960 2011		.47	.45
GA13A	1953 2011		.53	.39
GA13B	1957 2011		.72	.72
GA14A	1959 2011		.51	.50
GA14B	1960 2011		.51	.46
GA15A	1960 2011		.34	.33
GA15B	1960 2011		.60	.59
GA16A	1974 2011		.59	
GA16B	1960 2011		.65	.63
GA17A	1967 2011		.55	
GA17B	1962 2011		.30A	
GA18A	1967 2011		.42	
GA18B	1963 2011		.58	
GA19B	1963 2011		.47	
GA20A	1957 2011		.35	.35
GA20C	1969 2011		.40	
GA21A	1966 2011		.29B	
GA21B	1966 2011		.40	
GA22A	1967 2011		.46	
GA22B	1967 2011		.50	
GA23A	1961 2011		.44	.44
GA23B	1964 2011		.53	
Average segment correlation		.40	.46	.46

Table C2. COFECHA output showing correlations of 50-year dated segments, lagged 25 years for North Carolina. A = correlation under .3281 but highest as dated; B = correlation higher at other than dated position.

Series	Time Span	1900-1949	1924-1974	1950-1999	1975-2024
PNF01a	1973 2010				.52
PNF01b	1974 2010				.28A
PNF02a	1973 2010				.39
PNF02b	1981 2010				.54
PNF03a	1940 2010		.53	.58	.69
PNF04a	1923 2010	.28A	.29A	.49	.46
PNF06b	1957 2010			.43	.45
PNF07a	1964 2010				.57
PNF07b	1957 2010			.61	.63
PNF09a	1965 2010				.45
PNF09b	1973 2010				.40
PNF11a	1967 2010				.23A
PNF11b	1975 2010				.34B
PNF12a	1981 2010				.66
PNF12c	1970 2010				.29A
PNF13a	1971 2010				.55
PNF13b	1976 2010				.40
PNF14a	1955 2010			.55	.65
PNF14b	1950 2010			.56	.57
PNF15a	1951 2010			.46	.48
PNF15b	1949 2010		.68	.68	.69
PNF16a	1942 2010		.52	.53	.70
PNF16c	1934 2010		.46	.50	.62
PNF17a	1935 2010		.68	.51	.48
PNF17b	1927 2010		.57	.49	.60
PNF18a	1936 2010		.67	.63	.58
PNF18c	1949 2010		.46	.46	.47
PNF19a	1934 2010		.61	.65	.66
PNF19b	1947 2010		.47	.46	.51
PNF20b	1947 2010		.49	.45	.51
PNF20a	1948 2010		.25A	.25A	.24A
PNF21a	1929 2010		.59	.65	.68
PNF21c	1945 2010		.63	.62	.66
PNF22a	1916 2010	.57	.74	.73	.73
PNF22c	1910 2010	.51	.59	.52	.57
PNF23b	1982 2010				.38
PNF03b	1929 2002		.45	.46	.48
Average segment correlation		0.45	0.54	0.50	0.55

Table C3a. COFECHA output showing correlations of 50-year dated segments, lagged 25 years for Virginia. A = correlation under .3281 but highest as dated; B = correlation higher at other than dated position.

Series	Time Span	1850-1899	1875-1924	1900-1949	1925-1974	1950-1999	1975-2024
fhtc01a	1938 2010				.55	.66	.62
fhtc01b	1948 2010				.49	.49	.64
fhtc02a	1880 2010		.79	.78	.73	.74	.70
fhtc02b	1870 2010	.74	.78	.78	.62	.54	.61
fhtc03a	1909 2010			.74	.75	.68	.66
fhtc03b	1943 2010				.52	.55	.48
fhtc04a	1869 2010	.67	.72	.62	.30A	.25B	.41
fhtc04b	1902 2010			.73	.74	.59	.49
fhtc05a	1956 2010					.72	.68
fhtc05b	1959 2010					.46	.48
fhtc06a	1943 2010				.30B	.36	.44
fhtc06b	1957 2010					.42	.45
fhtc08b	1956 2010					.33B	.29A
fhtc09a	1957 2010					.61	.57
fhtc09b	1928 2010				.60	.62	.60
fhtc10a	1919 2010			.60	.63	.36	.32A
fhtc10b	1954 2010					.65	.61
fhtc11a	1945 2010				.57	.59	.65
fhtc11b	1910 2010			.70	.66	.72	.62
fhtc12a	1957 2010					.40	.46
fhtc12b	1956 2010					.55	.54
fhtc14a	1951 2010					.61	.69
fhtc13a	1954 2010					.47	.53
fhtc13b	1985 2010						.25A
Average segment correlation		0.70	0.76	0.71	0.55	0.52	0.52

Table continued on next page

Table C3b. COFECHA output showing correlations of 50-year dated segments, lagged 25 years for Virginia. A = correlation under .3281 but highest as dated; B = correlation higher at other than dated position.

Series	Time Span	1850-1899	1875-1924	1900-1949	1925-1974	1950-1999	1975-2024
fhtc14a	1951 2010					.61	.69
fhtc13a	1954 2010					.47	.53
fhtc13b	1985 2010						.25A
fhtc14b	1939 2010				-.02B	.47	.56
fhtc16b	1960 2010					.50	.49
fhtc17a	1954 2010					.55	.56
fhtc18a	1958 2010					.37	.42
fhtc19a	1978 2010						.38
fhtc19b	1941 2010				.35	.44	.56
fhtc20a	1932 2010				.62	.56	.51
fhtc20b	1934 2010				.68	.57	.51
fhtc21a	1928 2010				.68	.64	.68
fhtc21b	1925 2010				.71	.71	.74
fhtc22a	1986 2010						.46
fhtc22b	1985 2010						.23B
fhtc23a	1955 2010					.26B	.26B
fhtc23b	1954 2010					.25B	.41
fhtc16a	1939 2010				.40	.53	.62
Average segment correlation		0.70	0.76	0.71	0.55	0.52	0.52

Table C4a. COFECHA output showing correlations of 50-year dated segments, lagged 25 years for West Virginia. A = correlation under .3281 but highest as dated; B = correlation higher at other than dated position.

Series	Time Span	1775 1824	1800 1849	1825 1874	1850 1899	1875 1924	1900 1949	1925 1974	1950 1999	1975 2024
wvm01a	1895 2010					.50	.53	.50	.49	.47
wvm01b	1913 2010						.47	.47	.63	.60
wvm02a	1917 2010						.47	.52	.55	.61
wvm02b	1944 2010							.69	.70	.62
wvm03a	1913 2010						.59	.52	.52	.60
wvm05a	1770 2010	.07B	.03B	.11B	.25B	.48	.49	.63	.74	.74
wvm05b	1924 2010						.66	.68	.80	.84
wvm06a	1914 2010						.51	.63	.67	.71
wvm06b	1923 2010						.61	.64	.68	.54
wvm07a	1906 2010						.68	.72	.81	.70
wvm07b	1876 2010					.54	.42	.77	.80	.77
wvm08a	1907 2010						.50	.65	.75	.54
wvm08b	1908 2010						.39	.68	.73	.61
wvm09a	1887 2010					.40	.40	.61	.67	.67
wvm09b	1920 2010						.70	.69	.70	.60
wvm10a	1856 2010				.41B	.54	.52	.72	.78	.65
wvm10b	1893 2010					.36	.37	.72	.67	.56
wvm11a	1857 2010				.47	.51	.38	.63	.74	.70
wvm11b	1922 2010						.61	.64	.59	.65
wvm12a	1922 2010						.66	.64	.70	.59
wvm12b	1915 2010						.70	.69	.74	.64
wvm13a	1889 2010					.47	.37	.56	.79	.79

Table continued on next page

Table C4b. COFECHA output showing correlations of 50-year dated segments, lagged 25 years for West Virginia. A = correlation under .3281 but highest as dated; B = correlation higher at other than dated position.

Series	Time Span	1775 1824	1800 1849	1825 1874	1850 1899	1875 1924	1900 1949	1925 1974	1950 1999	1975 2024
wvm13b	1787 2010	.04B	.04B	.53	.60	.44	.51	.67	.86	.79
wvm15a	1844 2010			.52	.57	.48	.42	.58	.60	.59
wvm15b	1834 2010			.38	.57	.26B	.40	.70	.66	.58
wvm16a	1841 2010			.21B	.33B	.39	.30A	.60	.63	.57
wvm16b	1866 2010				.44	.44	.47	.62	.77	.73
wvm17a	1921 2010						.81	.82	.79	.67
wvm17b	1919 2010						.52	.59	.76	.73
wvm18a	1910 2010						.70	.68	.69	.68
wvm18b	1907 2010						.48	.59	.79	.83
wvm19a	1911 2010						.58	.66	.68	.53
wvm19b	1929 2010							.72	.67	.53
wvm21a	1916 2010						.53	.53	.60	.61
wvm21b	1916 2002						.46	.46	.67	.69
wvm22a	1919 2010						.40	.47	.62	.66
wvm22b	1919 2010						.58	.61	.69	.55
wvm23b	1920 2010						.58	.56	.63	.53
wvm23c	1918 2010						.48	.52	.51	.57
Average segment correlation		.05	.04	.35	.46	.45	.52	.63	.69	.64

Table C5a. COFECHA output showing correlations of 50-year dated segments, lagged 25 years for Pennsylvania. A = correlation under .3281 but highest as dated; B = correlation higher at other than dated position.

Series	Time Span	1900-1949	1925-1974	1950-1999	1975-2024
bsf14b	1927 2010		.47	.55	.64
bsf08b	1912 2010	.67	.64	.67	.60
bsf21a	1914 2010	.29B	.43	.42	.59
bsf01a	1931 2010		.33A	.54	.57
bsf23b	1917 2010	.62	.63	.49	.37
bsf07a	1929 2010		.29A	.45B	.61
bsf05b	1912 2010	.48	.46	.70	.66
bsf03a	1919 2010	.24B	.25B	.29A	.53
bsf14a	1938 2010		.56	.61	.61
bsf03b	1915 2010	.41	.43	.38	.42
bsf17a	1909 2010	.31A	.48	.67	.62
bsf01b	1930 2010		.28B	.44	.47
bsf17c	1931 2010		.71	.71	.65
bsf09a	1930 2010		.49	.55	.63
bsf02a	1941 2010		.35	.41	.57
bsf21b	1896 2010	.10B	.46	.43	.52
bsf15a	1913 2010	.62	.64	.67	.58
bsf19b	1904 2010	.42	.42	.50	.54
bsf17b	1911 2010	.41	.49	.62	.59
bsf20a	1908 2010	.43	.50	.67	.67
bsf19a	1901 2010	.35	.45	.37	.36
bsf15b	1906 2010	.30A	.65	.74	.74
bsf18a	1911 2010	.58	.59	.57	.46
bsf16a	1913 2010	.46	.58	.51	.39
bsf20b	1911 2010	.43	.43	.28A	.50

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Table C5b. COFECHA output showing correlations of 50-year dated segments, lagged 25 years for Pennsylvania. A = correlation under .3281 but highest as dated; B = correlation higher at other than dated position.

Series	Time Span	1900-1949	1925-1974	1950-1999	1975-2024
bsf08a	1943 2010		.62	.62	.51
bsf02b	1923 2010	.42	.42	.42	.58
bsf22a	1923 2010	.51	.52	.51	.64
bsf22b	1908 2010	.37	.52	.61	.63
bsf06a	1915 2010	.24B	.38	.52	.47
bsf05a	1926 2010		.23B	.52	.70
bsf04b	1922 2010	.57	.58	.60	.65
bsf16b	1914 2010	.67	.65	.51	.47
bsf23a	1917 2010	.65	.68	.44	.35
bsf06b	1922 2010	.54	.55	.57	.38B
bsf07b	1936 2010		.47	.47	.55
bsf09b	1930 2010		.25B	.49	.55
bsf12b	1914 2010	.36	.39	.69	.60
bsf04a	1939 2010		.56	.62	.46
bsf20c	1906 2010	.51	.66	.67	.67
bsf12a	1946 2010		.70	.72	.60
bsf18b	1902 2010	.45	.70	.73	.57
Average segment correlation		0.44	0.50	0.55	0.55

Table C6a. COFECHA output showing correlations of 50-year dated segments, lagged 25 years for Massachusetts. A = correlation under .3281 but highest as dated; B = correlation higher at other than dated position.

Series	Time Span	1875 1924	1900 1949	1925 1974	1950 1999	1975 2024
quab01a	1900 2010		.33B	.61	.70	.70
quab01b	1934 2010			.56	.65	.72
quab01c	1947 2010			.49	.51	.67
quab02a	1925 2010			.68	.70	.70
quab02b	1932 2010			.58	.69	.70
quab03a	1922 2010		.66	.61	.47	.27A
quab03b	1922 2010		.58	.58	.61	.55
quab04a	1923 2010		.58	.56	.71	.72
quab04b	1924 2010		.68	.68	.78	.77
quab05a	1940 2010			.57	.60	.51
quab05b	1940 2010			.49	.58	.50
quab06a	1906 2010		.47	.66	.69	.51
quab06b	1918 2010		.48	.42	.33B	.19B
quab07a	1930 2010			.55	.55	.49
quab07b	1934 2010			.36	.47	.52
quab08a	1933 2010			.62	.70	.55
quab09a	1947 2010			.63	.63	.64
quab09b	1936 2010			.44	.51	.54
quab10a	1887 2010	.13B	.29B	.70	.59	.49
quab10b	1937 2010			.57	.50	.29A
quab11a	1902 2010		.67	.72	.63	.51

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Table C6b. COFECHA output showing correlations of 50-year dated segments, lagged 25 years for Massachusetts. A = correlation under .3281 but highest as dated; B = correlation higher at other than dated position.

Series	Time Span	1875 1924	1900 1949	1925 1974	1950 1999	1975 2024
quab11b	1933 2010			.35	.37	.41
quab12a	1933 2010			.60	.66	.70
quab12b	1910 2010		.47	.61	.61	.61
quab13a	1923 2010		.60	.59	.74	.64
quab13b	1889 2010	.51	.72	.67	.64	.54
quab14a	1927 2010			.53	.73	.67
quab14b	1931 2010			.23B	.53	.55
quab15a	1924 2010		.78	.76	.74	.67
quab15b	1899 2010	.27B	.45	.69	.68	.62
quab16a	1924 2010		.63	.61	.70	.58
quab16b	1918 2010		.60	.51	.59	.45
quab17a	1924 2010		.56	.60	.53	.53
quab18a	1917 2010		.59	.55	.61	.43
quab18b	1931 2010			.60	.68	.53
quab21a	1940 2010			.55	.65	.55
quab21b	1903 2010		.51	.34B	.50	.47
quab22a	1930 2010			.39B	.55	.58
quab22b	1931 2010			.33	.53	.57
quab23a	1948 2010			.67	.73	.59
quab23b	1938 2010			.34	.42	.56
Average segment correlation		0.30	0.56	0.55	0.60	0.56